Migration and Residence Patterns of Salmonids in Puget Sound, Washington

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Abstract

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Diadromy is an unusual but widely distributed form of migration in fishes, and thus understanding these fishes requires a full knowledge of their behavior in both marine and freshwater environments. Freshwater ecology is easier to study and so our understanding is more advanced compared to our understanding of their marine ecology. This dissertation was focused on anadromous salmonids that were hypothesized to express a range of marine migration patterns from estuarine resident to ocean-bound migrants, in a suite of species native to Puget Sound: steelhead trout (*Oncorhynchus mykiss*), coastal cutthroat trout (*O. clarkii clarkii*), bull trout (*Salvelinus confluentus*), and Chinook salmon (*O. tshawytscha*). The study results will help inform a general model of the marine migrations of these salmonids within the Puget Sound. The study is organized into chapters by species. Abstracts for each chapter are described below.

This dissertation describes the movements of individual anadromous salmonids of four species to determine the extent to which migration patterns vary among the species, populations and marine sub-basins within Puget Sound. The study took a comparative approach between

species and was part of a larger suite of studies that investigated 1) marine migrations of ocean-bound stream-type fish (steelhead); 2) marine distribution, residency, and movement of resident and semi-resident pelagic species (Chinook and coho salmon, conducted by other researchers and reported in other publications); 3) movement and habitat use of two different estuarine and nearshore resident species (cutthroat and bull trout); and 4) movement and habitat use in estuarine and freshwater areas by maturing pelagic species (Chinook and sockeye salmon).

Enhanced understanding of marine migrations and habitat use by anadromous salmonids is necessary for their conservation. The Puget Sound's estuaries and shorelines have been affected in many ways by human actions including industrial and agricultural development of estuaries, construction of docks and marinas, and armoring of beaches. The tendency for salmonids to use these estuarine and marine habitats may cause their populations to decline if preferred habitats are degraded or lost. Information on movements and habitat use patterns is an essential component of conservation plans for these species and provides important links to species that prey on salmon, notably killer whales and other marine mammals.

Three species considered in this study are listed as threatened under the Endangered Species Act; information on their life history and habitat use will provide essential information to sustain and recover Puget Sound populations. The study resulted in collaborative relationships between tribes, agencies and sporting groups acting as a nexus for organizations interested in research needed to manage Puget Sound salmonids. The results fostered research in other areas that will be useful for generating an understanding of marine life histories elsewhere.

Comparative migratory behavior and survival of wild and hatchery steelhead (*Oncorhynchus mykiss*) smolts in riverine, estuarine, and marine habitats of Puget Sound, Washington

Declines in the survival of steelhead (*Oncorhynchus mykiss*) populations in protected waters of Washington and British Columbia have drawn attention to the need for more information on migratory patterns and losses in river, estuary, and nearshore habitats. Accordingly, acoustic telemetry was used to quantify movements by wild and hatchery steelhead smolts released from 2006-2009 in the Green River, and tracked through Puget Sound, Washington. Survival varied by release group and migration segment but overall survival rates from release to the Strait of Juan de Fuca were 9.7% for wild and 3.6% for hatchery fish. These rates are low relative to similar studies on steelhead. Survival was higher for wild fish along all

migration segments than hatchery-origin fish; the greatest loss for both groups coincided with the slowest travel rates as fish first entered the estuary and as they exited Puget Sound. Wild fish travelled faster than hatchery fish in the river (15.1 vs. 4.4 km/d) with the fastest travel in the lower river (41 vs. 20.2 km/d) and slowest immediately after release (3.7 vs. 2.4 km/d). The travel rates of wild and hatchery fish became progressively more similar over time: 15.4 vs. 10.6 km/d in the estuary, and 10.3 vs. 9.3 km/d in nearshore areas. Movement was primarily nocturnal in the river, nearly equal between day and night in the upper estuary, and predominately diurnal in the lower estuary and nearshore waters, with no difference between wild and hatchery fish. The migration in marine water showed an early offshore movement and a strong northward and westward orientation, and all fish exited the Strait of Juan de Fuca rather than the Strait of Georgia. The findings support research suggesting that declines in wild and hatchery steelhead populations may be caused primarily by factors in the early marine period.

Diversity of movements by individual anadromous coastal cutthroat trout in Hood Canal, Washington

Wild, downstream-migrating cutthroat trout, *Oncorhynchus clarkii clarkii,* smolts and adults were captured at a weir in Big Beef Creek, Hood Canal, Washington, surgically implanted with acoustic tags and tracked to identify spring and summer movements using stationary receivers to test the assumption that the species moves little while in marine waters. Overall, 93-96% migrated from the stream into the east side of the long narrow fjord, where they dispersed north and south along the shoreline. Most *O. clarkii clarkii* were detected near shore within 10 km of the release site, with declining detection rates to 77 km. Over one third (36%) crossed ~ 2-4 km of deep water to the other side but only one *O. clarkii clarkii* left the Hood Canal basin. Movements and behaviour patterns did not differ between smolts and adults but cluster analysis revealed two modes of distribution, here categorized as residents and migrants. Within these categories of overall distribution, a range of finer-scale behaviour patterns was observed, including sedentary individuals, daily “commuting” between proximate sites, and more continuous long-distance travel. Diel movement patterns varied markedly among individuals but overall activity increased near dawn, peaked around mid-day, and declined but continued at night. These patterns contrast with sympatric and closely related steelhead trout, *O. mykiss*, providing new insights into the diversity of trout behaviour

Migrations of anadromous bull trout in estuarine and marine waters of Puget Sound, Washington: Thermal constraints on foraging opportunities

Anadromous fishes migrate to sea to take advantage of superior opportunities for foraging and growth compared to less productive freshwater habitats but the species vary greatly in the temporal duration and spatial extent of marine migrations. Char, *Salvelinus spp.*, characteristically display short migrations and it has been hypothesized that thermal constraints may affect migration timing. Our objective was to study the timing, period of marine residence, and major habitats occupied by anadromous bull trout, *S. confluentus*, during their migrations to and from Puget Sound, Washington. We predicted that bull trout would have a well-defined period of estuary and marine habitation and that fish would undertake "premature migrations" back to freshwater in early summer to avoid rising temperatures, prior to spawning in the fall. We used a combination of traps and beach seining to capture juveniles and adults, and acoustic telemetry to quantify movements in river, estuary, and marine waters in relation to thermal regimes. The overall period of marine residence was similar among fish from different river basins and life stages; larger bull trout entered marine waters in late winter-early spring, juveniles in late spring, and most fish migrated back into rivers by late spring-early summer as temperatures were increasing. However, the timing of return migration was similar among rivers despite differences in their thermal regimes. Some fish entered and exited the rivers in the fall but few overwintered in marine areas. Most fish occupied estuary and nearshore areas near natal rivers but some moved over 100 km from the river mouth. These timing patterns and use of marine habitats contrast strongly with those of other salmonids in Puget Sound, revealing the diversity in migratory behavior under the broad category of anadromy, and emphasizing the importance of estuarine and nearshore habitats for the conservation of bull trout, listed as Threatened under the U. S. Endangered Species Act.

Behavioral thermoregulation by adult Chinook salmon (*Oncorhynchus tshawytscha*) and comparison to sockeye salmon (*O. nerka*) in estuary and freshwater habitats prior to spawning

The movements and thermal experience of Pacific salmon during their homeward migration through marine waters and into freshwater systems pose challenges for their physiology, especially in river basins altered by human structures and activities, and under

regimes of increasingly high temperatures. This study determined the thermal regimes experienced by maturing Chinook salmon, *Oncorhynchus tshawytscha*, entering the Lake Washington basin via a navigational locks and canal, and migrating through the lake to spawning grounds or hatcheries. We then compared these patterns, determined from a combination of acoustic tracking and temperature loggers attached to the fish, with comparable data on sockeye salmon collected in an independent study in overlapping years. Chinook salmon exhibited complex patterns, occupying cool water refuges in stratified marine and freshwater areas: 1) in Puget Sound (28-30 ppt, 12-15 °C), 2) in deeper water in the salt wedge (upper estuary) above the locks (12-15 ppt, 18-21 °C), and 3) intermittently in deeper fresh water in Lake Washington (9-21 °C). Most Chinook salmon (> 75%) left the estuary after tagging and spent a short period (mean 4.6 d) in Puget Sound). Upon return to the upper estuary Chinook salmon either held in a small, cool area in the salt wedge (mean 11.1 d) or went back to Puget Sound twice to hold in tidally influenced saltwater. Sockeye salmon exhibited a fairly simple migration pattern, holding for a short period in warm water (median 18.4 °C) in the upper estuary and canal (mean 3.6 d), then migrating to the lake and residing in cold-water areas (mean 10.3 °C) at depths of 40 m (mean 88.3 d). Sockeye and Chinook salmon travelled through a 10.8 km canal to Lake Washington in relatively short periods, 2 d and 0.5 d (mean) respectively, but Chinook salmon experienced higher temperatures (20-22.5 °C) because they migrated later in summer. In Lake Washington Chinook salmon exhibited vertical migrations above and below the thermocline and used the lake as a thermal refuge to a lesser extent than did sockeye salmon, which remained below the thermocline almost exclusively until they ascended rivers to spawn. Individual fish utilized different migration paths and so had distinct thermal experiences but survived to reach breeding sites. The ability to exploit multiple refuges in this highly modified migratory corridor may be essential for the persistence of these species and especially the Chinook salmon. In the face of climate change, understanding how fish use available thermal refuges may help identify management alternatives to retain or increase these areas in the future.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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DEDICATION

To Debbie

for her patience, love

and valued assistance

as a

critical member of the research team.

General Introduction

Anadromy is one of the defining life history traits in salmonid fishes, allowing them to take advantage of foraging opportunities at sea, and facilitating gene flow among spawning populations (Quinn 2005). However, the spatial and temporal extent of marine migration varies greatly among salmonid species (Quinn and Myers 2004). Sockeye (*Oncorhynchus nerka*), chum (*O. keta*), and pink salmon (*O. gorbuscha*) from the west coast of North America leave their natal streams in spring, migrate north along the continental shelf during the summer, and move to the open Gulf of Alaska in their first fall or winter (Beamish et al. 2005). Coho (*O. kisutch*) and Chinook salmon (*O. tshawytscha*) from the southern end of their distribution (California, Oregon and Washington) tend to remain in coastal waters, over the continental shelf, during their years at sea whereas populations farther north more often migrate to the open ocean (Brodeur et al. 2004). Steelhead trout (*O. mykiss*) are believed to move offshore quickly rather than remain along the coast, and many migrate long distances (Melnychuk et al. 2007). Anadromous coastal cutthroat trout (*O. clarkii clarkii*) and bull trout (*Salvelinus confluentus*) are believed to remain in the vicinity of their natal streams during their marine residency periods (Jauquet 2002; Goetz et al. 2004; Brenkman and Corbett 2005).

These patterns of migration are undoubtedly affected, at least in part, by the physical and biological conditions encountered by populations entering marine waters at different locations. Off the California coast, the waters are sufficiently cold and productive to support salmonids and the warmer waters offshore are dominated by other fishes (Pearcy 1992; Brodeur et al. 2004), whereas waters off southeastern Alaska are colder and more nutrient-rich. In addition, the physical complexity of the coastline likely affects fish distribution (Orsi and Jaenicke 1996; Orsi et al. 2000; Beamish et al. 2005). The coastline south of the Strait of Juan de Fuca is relatively simple, indented by only a few large estuaries. However, the coast of British Columbia north through Prince William Sound, Alaska, is exceptionally complex, with a vast shoreline and maze of islands, bays, peninsulas, and long fjords. The southern most of these fjords is Puget Sound, a complex inland sea with 3700 km of irregular shorelines, draining over 10,000 streams. Marine waters of the Pacific Ocean flow directly into the Puget Sound through the Strait of Juan de Fuca from the north and west, indirectly through the protected waters in the Strait of Georgia to the north, and terminating in the southern regions in a series of long inlets. Several shallow sills functionally divide Puget Sound into oceanographic sub-basins (Moore et al. 2008).

Given the diverse physical features of Puget Sound, it is not surprising that salmonid fishes found there have different migration patterns compared to other geographic areas. Analysis of catches in recreational fisheries have documented coho and Chinook salmon; and, much more rarely, pink and chum salmon rearing in Puget Sound for all or a large portion of their lives at sea, (Pressey 1953; Weitkamp and Neely 2002; Ruggerone and Goetz 2004), rather than migrating to the coast and offshore waters. There is even some evidence of repeated migrations to and from Puget Sound on a seasonal basis by immature Chinook salmon, along with the return migration of maturing fish (Healey and Groot 1987; Brannon and Setter 1989). These resident Chinook salmon (locally termed “blackmouth”) and coho salmon seem to represent natural life history patterns but the tendency to remain within or near Puget Sound may be affected by rearing conditions (Buckley 1969; Rohde et al. 2014). Specifically, release of large smolts from hatcheries is thought to increase their tendency to become residents, and some hatchery programs in Puget Sound seek to accomplish this (Appleby and Doty 1995; Chamberlin et al. 2011). There may also be variation among populations in the tendency to remain resident in Puget Sound or there may be a north-south environmental gradient that structures variation.

In addition to the use of Puget Sound by the resident component of the Chinook and coho salmon populations, Puget Sound is thought to be the primary or even the exclusive habitat for anadromous cutthroat trout spawned in its tributaries. These trout enter marine waters at a younger age than populations from the open coast, and they also occupy intertidal and shallow subtidal habitats to a greater extent than coastal populations (Johnston 1982). They feed on small fishes and salmon eggs (Jauquet 2002) and may move among estuaries to take advantage of changing prey availability. There has been virtually no research on the marine movements of cutthroat trout in Puget Sound and much that is known comes from reports by experienced recreational anglers (Haw and Buckley 1971; Raymond 1996; Jauquet 2002; Johnson 2004). Steelhead (a related species with similar freshwater habitat needs), are believed to move to oceanic waters rather than reside in the Puget Sound year-round (Pearcy et al. 1990). However, this conclusion is inferred from the absence of catches in Puget Sound and there is little, if any, direct information on the movements of these fishes (Beamish et al. 2003 and 2005; Melnychuk et al. 2007). Neither of these trout species nor bull trout are subject to commercial fisheries and are managed for catch-and-release in Puget Sound (Washington Department of Fish and Wildlife regulations), as a result, information on their behavior is very limited (Johnson et al. 1999; Goetz et al. 2004).

Variation in movement and habitat use patterns of different salmonid species within Puget Sound, and the contrasts between movement patterns in the sound and elsewhere, are not only interesting aspects of their life history but they are closely linked to the conservation of these species. The Puget Sound shoreline has been affected in many ways by human activities including industrial development of estuaries, construction of docks and marinas, armoring of beaches and installation of net pens to farm salmon. Some of these activities have only affected the physical environment whereas others have affected the ecological attributes of the shoreline (e.g., loss of eelgrass beds) and introduced toxic contaminants or reduced levels of dissolved oxygen (Bortelson et al. 1980; PSNERP 2003). Therefore, the tendency of salmonids to utilize certain habitat features of Puget Sound may cause their populations to decline if the preferred habitats are degraded or lost, or it may bring them into contact with lower trophic levels with contaminants (O'Neill and West 2009; Ross et al. 2013). Information on movements and habitat-use patterns may be essential components of conservation plans for these species, and also provide important links to species that prey on salmon, notably killer whales (*Orcinus orca)* and other marine mammals (Ford et al. 1998; NOAA 2005).

Brodeur et al. (2000) recommended that NOAA marine research focus on 1) distribution and movement patterns of salmon in marine waters, 2) health and condition of hatchery and wild salmon, 3) trophic dynamics of salmon, and 4) large-scale effects of the atmosphere and ocean. These authors recognized that understanding the diversity of Pacific salmon species, geographic ranges, life history, and habitat-use patterns requires a broad-based approach to address these information needs. They also stated that comparisons between divergent river and coastal systems, species, and life history patterns will advance understanding of Pacific salmon.

Many insights can be drawn by comparing behaviors and life history patterns among salmonid species. Hansen and Quinn (1998) demonstrated the utility of comparing research on the more abundant and heavily studied Pacific salmon species to Atlantic salmon (*Salmo salar*). For example, migration patterns of Atlantic salmon seem to be most comparable to stream-type Chinook salmon or steelhead in their size at seawater entry, migratory patterns, trophic status, and overall abundance. Hansen and Quinn (1998) also encouraged further comparative analyses as a means to increase the state of knowledge of salmonids in both oceans.

Life history trajectories or pathways within a population include shared behaviors, such as ocean entry timing (e.g., age at ocean entry or seasonal timing) or migration pattern during freshwater residence (e.g., freshwater residence in natal streams or redistribution to non-natal streams for overwintering). For example, the potential variation in migration patterns of salmonids in Puget Sound, including freshwater and marine movements, can be visualized as shown in Figure 1. In the Puget Sound and the Columbia River, losses of tributary habitat, wetland and estuarine habitats have reduced the diversity of life history trajectories that can be supported (McClure et al. 2008, Waples et al. 2008).

This dissertation was organized around development of a general model of the marine life history stage of a series of anadromous salmonids found within the Puget Sound. Life history theory has been developed to explain the variation in timing of fertility, growth, developmental rates, and death of living organisms, as well as events directly tied to these parameters. Life history of salmon is described as consisting of a favorable spatial-temporal distribution of a chain of habitats to enable its continuity (Thompson 1959). The life history encompasses many more or less distinct developmental life stages, each having its own set of environmental requirements (Bjornn and Reiser 1991).

Life history pattern refers to a collection of similar pathways. Chinook salmon have been defined by their juvenile life history pattern as either ocean-type or stream-type with additional specificity within the type (Reimers 1973; Healey 1991). These traits may refer to other salmonids and marine systems (Table 1). In Puget Sound the various life history patterns are modified to fit the different landscape conditions of the region with ocean-type fry and fingerlings described in various stages of rearing in estuary and nearshore areas while stream-type fish are hypothesized to move rapidly through these areas, with the final destination for these types is uncertain. A successful life history pattern is one that is brought to *closure* - individuals following the pattern that survive through all life stages and return to their natal spawning ground (Sinclair 1988). A sustainable life history pattern is one that remains successful over the range of prevailing environmental and man-induced mortality conditions (Winemiller and Rose 1992). These models are designed for semelparous salmon and will require further expansion to incorporate iteroparous species with more complex migrations such as steelhead, bull trout and cutthroat trout.

This dissertation focused on the study of species that express a range of marine life history patterns. This range can be considered a continuum of life history patterns between the various anadromous species found in the Puget Sound (Winemiller et al. 1992). This continuum of patterns, and resultant behaviors (Cucherousset et al. 2005), can be expressed as a function of space and time distance from freshwater rearing areas to estuarine and marine locations (Figure 1). The hypothesized list of patterns includes resident, semi-resident, and ocean-bound Chinook and coho salmon; ocean-bound steelhead trout; estuarine semi-resident, estuarine resident, and marine resident coastal cutthroat trout and bull trout (Table 1). As a reference, anadromous bull trout provide an example of a series of these types by their occupation of various locations within Puget Sound. Dispersal patterns of acoustic-tagged bull trout emigrating from three northeast Puget Sound rivers include display of fluvial, estuarine semi-resident/transient, estuarine resident, and nearshore resident life history patterns (Goetz et al. 2004).

This dissertation describes the movements of individual anadromous salmonids of four species to determine the extent to which migration patterns vary among the species, populations and marine sub-basins within Puget Sound. The study took a comparative approach between species and was part of a larger suite of studies that investigated 1) marine migrations of ocean-bound stream-type fish (steelhead); 2) marine distribution, residency, and movement of resident and semi-resident pelagic species (Chinook and coho salmon, conducted by other researchers and reported in other publications); 3) movement and habitat use of two different estuarine and nearshore resident species (cutthroat and bull trout); and 4) movement and habitat use in estuarine and freshwater areas by maturing pelagic species (Chinook and sockeye salmon).

Table 1. Hypothesized marine life history patterns for selected Puget Sound salmonids.

Species	Migratory Type	Marine Residence
Cutthroat Trout	Freshwater Resident	
	Fluvial/Adfluvial	
	Anadromous	*Estuarine Semi-resident*
		Estuarine Resident
		Nearshore Resident
Bull Trout	Freshwater Resident	
	Fluvial/Adfluvial	
	Anadromous	*Estuarine Semi-resident*
		Estuarine Resident
		Nearshore Resident
Chinook	Anadromous	*Puget Sound Resident*
		Puget Sound Semi-resident
		Ocean-bound
Coho	Anadromous	*Puget Sound Resident*
		Puget Sound Semi-resident
		Ocean-bound
Steelhead/Rainbow	Fluvial (Rainbow)	
	Anadromous (Steelhead)	*Ocean-bound*

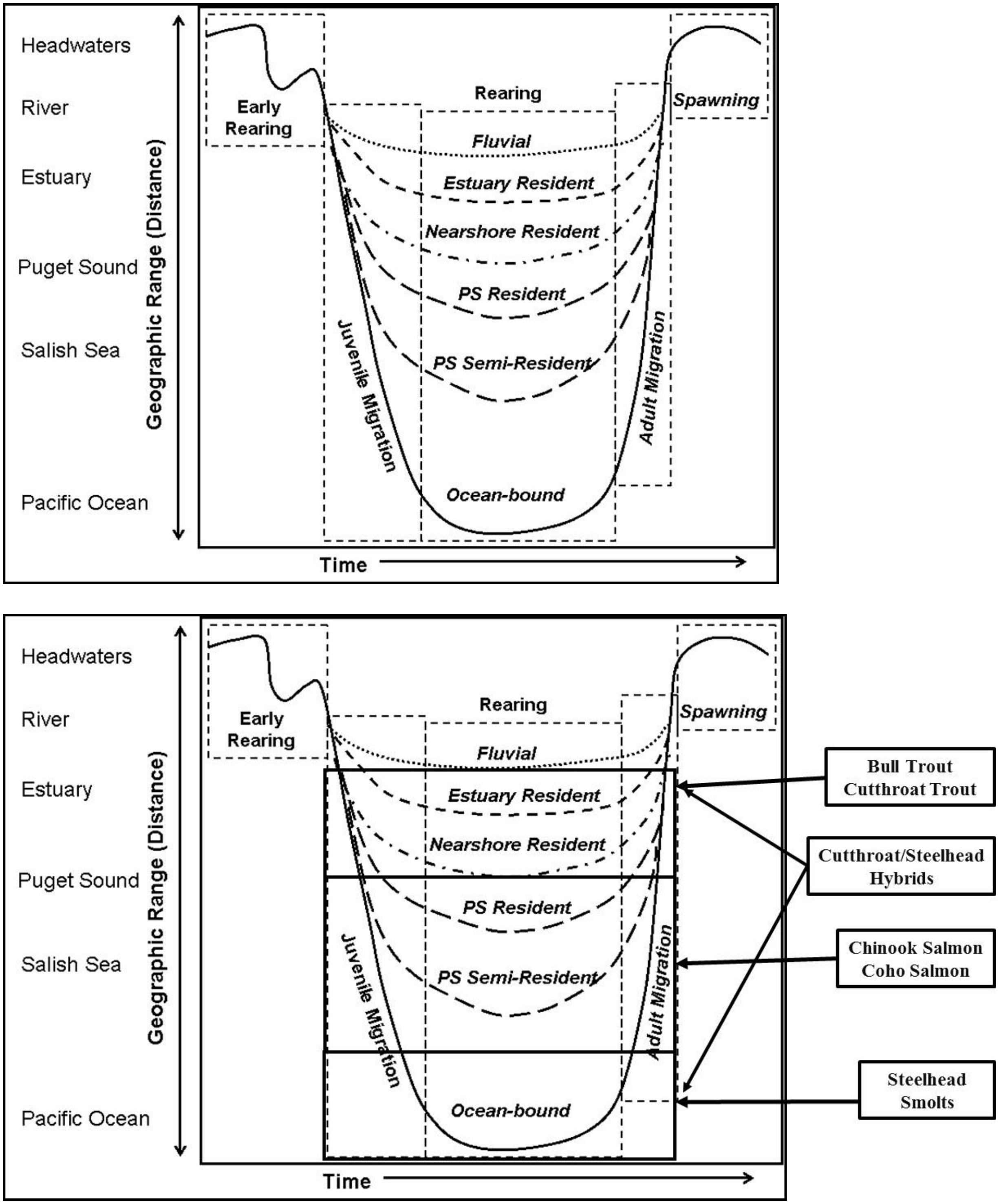

Figure 1. Conceptual model of Puget Sound resident salmonids showing juvenile and adult migration over geographic range from spawning groups to the Pacific Ocean and in time from juvenile rearing to return to spawning (top). The species of interest that were studied are assigned to particular life history types in the boxed squares with lines pointing to the appropriate life history type (bottom).

Chapter 1. Comparative migratory behavior and survival of wild and hatchery steelhead (Oncorhynchus mykiss) smolts in riverine, estuarine, and marine habitats of Puget Sound, Washington

1.1 Introduction

Anadromy is a defining life history trait in salmonid fishes, allowing them to take advantage of foraging opportunities at sea, and facilitating gene flow among spawning populations (Quinn 2005). Juveniles of most salmon species rear in freshwater and migrate downstream through a series of ecotypes, from rivers to brackish and tidally influenced estuaries, to protected, nearshore marine areas, and finally open marine waters along the continental shelf or offshore regions. This period is a critical life stage for juvenile salmon as they experience major physiological changes (Clarke and Hirano 1995) but little is known about behavioral changes during movement through changing physical and biological environments, and whether particular behaviors can influence survival. High mortality rates have been observed during this early migration period that can strongly affect adult returns (Holtby et al. 1990; Ward 2000; Pearcy 1992). Survival rates of wild salmonid smolts are often higher than those of hatchery-produced fish (Raymond 1988; Chittenden et al. 2008; Melnychuk 2009a; Moore et al. 2010a) but there are many possible explanations for this difference, including but not limited to behavior patterns. Behavior and movement rate differ between species, populations, rearing types, and fish of different body size in river, estuary and marine environments (Saloniemi et al. 2004; Melnychuk et al. 2010; Drenner et al. 2012; Chapman et al. 2012). Differences in migratory behavior could affect foraging success and survival through timing of movement (diel and tidal cycles), direction of movement (compass orientation and responses to tides), habitat (nearshore or offshore), migration route and timing within the season (Quinn 2005; Chittenden et al. 2008; Scheuerell et al. 2009; Melnychuk et al. 2010). Migration patterns may also explain differences in fitness between wild and hatchery fish, possibly due to differences in physiology, behavior, genetic background, and size (Holtby et al. 1990; Kostow 2004; Saloniemi et al. 2004; Chittenden et al. 2008; Melnychuk 2009a; Johnson et al. 2010).

Populations of steelhead (*Oncorhynchus mykiss)* in North America have declined in abundance in the past two decades (Ward 2000; Welch et al. 2000; Hard et al. 2007) but the causal factors are largely unknown. Puget Sound steelhead were listed as threatened under the U. S. Endangered Species Act (ESA) in 2007 (NOAA 2007) and steelhead abundance in this region is less than 4% of historical levels (Gayeski et al. 2011). Until recently little was known about their seaward migration, as most monitoring methods were not well suited to study this life-stage. High mortality rates of steelhead were documented during the first month in the Strait of Georgia, British Columbia by Melnychuk et al. (2007) and Moore et al. (2010a), and Welch et al. (2000) suggested that declines in wild and hatchery steelhead populations may be caused primarily by marine rather than freshwater factors. Studies from British Columbia have provided information on movement and survival of Pacific salmon exiting the Fraser River, and other, smaller rivers (Welch et al. 2004, Melnychuk et al. 2007) but there is a need for a comprehensive comparison of the behavior and survival of hatchery and wild fish released higher in the watershed during their entire migration in riverine, estuarine, and marine waters.

Our objective was to 1) quantitatively characterize steelhead behavior as they transition from riverine to estuarine to nearshore and open water habitats, and 2) compare the behavior of wild and hatchery origin fish in the river and, if different, determine at which point in the migration their behavior became similar. We predicted that wild smolts would survive at higher rates during their migration to the Pacific Ocean, begin their migration sooner after tagging as hatchery fish may need more acclimation time, travel faster than hatchery fish, and move more at night than hatchery fish, reducing predation risk. Upon entering the estuary wild fish were predicted to show a shorter period of delay, and migrate through Puget Sound more rapidly and by more direct routes than hatchery fish. We also predicted that both groups would alter their behavior to become progressively more day-active, as smolt migrations in rivers are typically nocturnal whereas adults tend to be more active in the daytime (Ruggerone et al. 1990).

1.2 Methods

1.2.1 Study Area

Puget Sound is a large (3700 km^2) interior marine system in western Washington, USA, bordered by British Columbia to the north (Figure 1). Its physical attributes have been extensively described (Strickland 1983; Moore et al. 2008; Sutherland et al. 2011). Puget Sound is oriented north to south, and Admiralty Inlet is considered the northern extent and outlet of Puget Sound, connecting it to the Pacific Ocean through the Strait of Juan de Fuca, and to the Strait of Georgia. The average depth of Puget Sound is 62.5 m at mean low tide with average surface water temperatures of 12.8^o C in summer. The tidal range varies from 2.4 m at the north to 4.6 m in the south, producing strong currents in constricted areas between basins. Flow is dominated by tidal currents of up to 1 m/s in Strait of Juan de Fuca and 1-2 m/s at Admiralty Inlet, decreasing to approximately 0.5 m/s in central Puget Sound. There are a series of inlets, islands, and passages on the west side and large bays on the east side, including Elliott Bay at the mouth of the Green-Duwamish River.

The Green-Duwamish River flows from elevations over 1500 m (Figure 1) through the city of Seattle into Elliott Bay (Table 1). The Duwamish River is the 16 km estuarine portion and the Green River is the entirely freshwater portion (126 km). The Duwamish River has been extensively modified, with over 98% of freshwater and intertidal habitats lost to development and maintenance of the river as a navigation channel. The estuary was defined as beginning at the upper extent of tidal influence (i.e., the Duwamish River) and ending at edge of the river delta. Areas external to the estuary were defined as marine waters, separated into shoreline (< 18 m deep) and offshore waters. The Duwamish estuary has three components. The lower estuary (RK 0-4) has two main waterways; the main channel and east channel (RK 1.2), and is most heavily influenced by tides and saltwater. The middle estuary (RK 4-10) terminates at the end of the navigation channel, and the upper estuary (RK 10-16) has decreasing influence of tides and is primarily fresh water. The lower Green River (Tukwila to Auburn, RK 16-51) has few tributaries and little or no connection to the floodplain as a consequence of human development of the riparian area. The middle Green River (RK 51-72) has the most complete connection to the floodplain with accumulation of large woody debris, a meandering channel, and numerous side channels. At RK 53, Soos Creek meets the Green River, and approximately 1.5 km upstream is the Washington Department of Fish and Wildlife (WDFW) Soos Creek Hatchery.

1.2.2 Steelhead Tagging and Release

Wild and hatchery-origin steelhead smolts were tagged in 2006 – 2009. A floating screw trap (Seiler et al. 2002) was used to capture downstream migrating wild steelhead smolts at RK 55. Wild fish were trapped as they migrated at night, tagged the next morning, held in the live trap at the capture site and released in the evening in May and June, around the peak of migration in this river. Wild smolts are predominately 2 years of age, are progeny of wild and hatchery parents, and average 150 to 175 mm in length. At the Soos Creek Hatchery, adult steelhead (non-native Chambers Creek stock) are spawned between the January and March and the progeny are transferred to ponds in April where they are reared for one year. There they are maintained on ambient photoperiod, raised in spring water, fed commercial diets and then moved to surface waters prior to release at an average size of 201 mm and 75 g. Smolts were tagged one week before release, and then released from the hatchery during the day on April 30 or May 1, as is typical practice at this facility.

Steelhead smolts (n = 187 wild and 150 hatchery) were tagged by surgical implant (e.g., Moore et al. 2010a) using Vemco V7-2L (1.6 g, 7 mm diameter, and 18.5 mm length) and V7-4L (1.8 g, 7 mm diameter, 20.5 mm length) acoustic tags. The tagged fish were well within the normal size range but above average for the populations so that the tags were < 3% of body weight, corresponding to fish at least 165 mm and 60-85 g, depending on tag size (see also Moore et al. 2012). This was conservative, relative to the standards used by other investigators (e.g., Winter 1996; Welch et al. 2004). The hatchery fish tended to be larger than wild fish (hatchery mean length = 191.3 mm (± 1.0 SE) and weight = 66.2 g (± 1.0 SE) vs. wild mean length = 184.4 (± 1.2) and 62.4 (± 2.3) and there was variation in size among years as well (ANOVA P < 0.001).

1.2.3 Receiver Deployment and Retrieval

The objective of the receiver placement was to achieve a high probability of detecting smolts migrating from release through freshwater and from Puget Sound to the Pacific Ocean. In all years 2 or 3 receivers were deployed in the middle Green River near Auburn, 1 or 2 in the lower river, and 6 – 11 along the length of the Duwamish River from Tukwila to the mouth (Table 1). A combination of receivers (VR2, VR2W, and VR3) were deployed at shoreline and off-shore sites in Elliot Bay and in all major bays and river deltas in Puget Sound (Figure 1; Table 1). A line of receivers was deployed at Admiralty Inlet in 2006 (VR2), 2008 (VR2) and 2009 (VR3) at the outlet of Puget Sound, as was a line of receivers at Possession Sound, the outlet to Whidbey Basin, in 2006 (VR2) and 2008 (VR2), and at the outlet to Hood Canal from 2006-2009. The distance of receivers from the Duwamish River to Admiralty Inlet ranged from 48 km (2006-2007) to 62 km (2008-2009). The Pacific Ocean Tracking Project (POST; Welch et al. 2002) maintained receiver lines at the Strait of Juan de Fuca, the northern Strait of Georgia, northern Vancouver Island, and Queen Charlotte Strait (Figure 1). The receiver spacing of these lines were based on potential detection range of a V9 (400-m) or V7 (200-250 m) tags. All Puget Sound lines in 2006 and POST lines outside of Puget Sound were designed for V9 tags (800-m spacing between receivers) while Puget Sound lines were designed for V7 tags (400-m) in all other years. Data from other researchers were collected either through direct contact or from on-line databases (hydra.sounddatamanagement.com/; www.postcoml.org/). In 2006, boat surveys were conducted three times over two months in the river from 10-km above the release site to 20 km below to identify potential mortalities or fish that did not migrate.

Analyses were designed to describe steelhead behavior and to estimate survival through five segments of the migration route corresponding to distinct habitats: 1) middle Green River, from the release site to Auburn (RK 55-48); 2) lower Green River (Auburn to Tukwila, RK 48-16); 3) Duwamish estuary (Tukwila to river mouth, RK 16- 0); 4) Puget Sound (Duwamish River mouth to Admiralty Inlet, ~ 60 km); and 5) Strait of Juan de Fuca, from Admiralty Inlet to the line of receivers across the Strait of Juan de Fuca, ~ 110-124 km from the river mouth. For some analyses the two segments in the Green River were combined and categorized as in-river, with the other segments referred to as estuary, Puget Sound, and Strait of Juan de Fuca.

1.2.4 Survival Analysis

Cormack-Jolly-Seber (CJS) mark-recapture methods (Lebreton et al. 1992), adapted for spatial analysis (see Melnychuk and Walters 2010), were used to estimate apparent survival probabilities (φ), and detection probabilities (*p*) for steelhead smolts at five points: lower Green River (LR), Duwamish River estuary (EST), nearshore (NS), Admiralty Inlet (AI), and the Strait of Juan de Fuca (JDF; Figure 1, Table 1). The CJS model uses maximum likelihood techniques to simultaneously estimate the probability of survival and detection at the end of each migration segment. Migration segments were defined based on the deployed receivers, and are referred to as point of release (PR) to LR (7 km), LR to EST (32 km), EST to NS (16 km), NS to AI (42-58 km, mean 50 km), and AI to JDF (110 km). Overall freshwater survival was estimated as the product of the PR-LR and LR-EST survival probabilities, and early marine survival was estimated as the product of the EST-NS, NS-AI, and AI-JDF survival probabilities. The standard errors for these products were calculated using the delta method (Cooch and White 2010). The R package RMark (Laake and Rexstad 2007) was used to construct φ and *p* models for the program MARK (White and Burnham 1999). Detection data from all 337 tagged individuals were incorporated into the MARK models.

Several candidate models were constructed using different variables to estimate steelhead smolt survival to and detection at each receiver line. Akaike's Information Criteria (AIC) were used to identify the set of variables that most parsimoniously explained the variation in survival and detection (Burnham and Anderson 1998). Goodness-of-fit to the CJS model, as measured by the variance inflation factor ĉ, was tested using the median ĉ method (Cooch and White 2010). The variance inflation factor was high (ĉ = 3.18), but modeling results were adjusted accordingly to compute AIC values that compensate for extra-binomial variation and small sample sizes ($QAIC_c$). The detection probability portion of each model was parameterized to represent varying *p* at each receiver line. Year was tested as a source of variation in *p* at all receiver lines, and average yearly Green River flow during the tagging period (May 1-June 15, covariate), measured at RK 51.5 (USGS 12113000), was tested as a source of variation at the LR line (Table 2). Two covariates, length (L) and rearing type (rear) were included in some φ sub-models as linear or multiplicative terms in relation to the migration segment variable either with or without a "year" factor. A separate term was also included in each model to estimate a separate detection probability at Admiralty Inlet in 2008 and 2009, when 10-12 more receivers were deployed than in 2006 and 2007. All *p* models were first tested in combination with a general φ model (Table 2). The *p* model with the lowest QAICc was then used to test all φ models to determine the most likely model structure.

The CJS model uses subsequent detection occasions to estimate *p* for each previous occasion; therefore, φ and *p* are confounded for the last receiver line. To address this problem, empirically derived estimates from a similarly sited and configured receiver line were used to fix *p* at the JDF line (Melnychuk 2009b, Welch et al. 2011). Melnychuk (2009b) calculated mean and 95% confidence limit estimates of *p* for V7 VEMCO tags passing a receiver line spanning the Strait of Georgia, British Columbia, in 2004, 2005, 2006, and 2007, so an average of the 2005-2007 values (2004 was an anomalous year) was used for all years to fix the value of *p* for the JDF line in our models ($p_{JDF,\text{ fixed}} = 0.685$). All other estimates of φ and *p* and associated standard errors were derived from the model with the lowest $QAIC_c$ (Table 2).

1.2.5 Travel Rate and Migration Timing

Travel rate (km/d) was calculated for each fish in each segment as the time from last detection at one site to the first detection at the next site over the segment's migration distance. The shortest distances were calculated between in-river arrays using river length and between marine lines or individual receivers in nearshore areas using the program AquaTracker (Reyes-Tomassini et al. 2011). Freshwater (LR-EST) and estuarine (EST-NS) travel rates (km/d) were calculated by subtracting the time of last detection at an upstream receiver line from the time of first detection at the downstream receiver line, then dividing that value by the distance between the two lines. Too few fish were detected on the NS, AI and JDF receiver arrays to analyze travel rates for the entire NS-AI or AI-JDF segments so detections from single receivers located throughout these two segments were utilized. Travel rate in the NS was calculated using the time between detections at two or more receivers at least 2-km apart divided by the distance between those two receivers. Factors affecting freshwater, estuarine, and marine travel rate were explored by constructing and comparing several general linear models. Candidate models used travel rate (km/d) as the response variable, and included all linear and multiplicative combinations of rearing type (i.e., hatchery or wild; "rear"), year ("year"), and length ("L"). Marine travel rate models included a factor variable ("area") to designate whether the rate was calculated in nearshore areas (6 to 40 km from the estuary), Admiralty Inlet, or the Strait of Juan de Fuca. Candidate models for each migration segment were compared using AIC_c (Burnham and Anderson 2002) (Tables 4, 5 and 6).

Several aspects of travel and residency were measured to evaluate migration behavior. Migration timing was examined by comparing the initial date of downstream migration after exit from the middle Green River for each individual detected at that receiver line. The migration period was bracketed for the middle Green and lower estuary using the minimum, 1st quartile, median, 3rd quartile, and maximum dates of detection. A one-way ANOVA was used to test whether mean travel rates to the estuary for wild fish by differed release week (i.e., first week of tagging was week 1). We defined the estuary residence period from the first detection at the upper estuary to the last detection in the estuary. A linear regression of mean river flow and the proportion of fish using the east channel assessed the tendency of fish to use this secondary exit from the estuary. The residence period in Puget Sound was defined from the last lower estuary detection to the last detection at Admiralty Inlet, and the ocean-entry migration window was the number of days from first to last detection at the JDF line.

1.2.6 Fish Behavior on Diel and Tidal Time Scales

The diel and tidal patterns of movement were determined using the detections at fixed receivers. Following the method described by Chamberlin et al. (2011), the initial detection at a receiver after a period without detections and the last detection at that receiver if more than 1 h elapsed between these detections were discrete movement events. These “first” and “last” detections were clearly a small subset of all movements but, given the number of fixed receivers, they provided many movement events for analysis with respect to time of day and stage of tide. Movement events were binned by hour of the day for analysis. The detections were considered to have occurred in the day if they were between sunrise (dawn) and sunset (dusk), and night if they occurred after dusk and before dawn as determined by U.S. Naval Observatory data for Bangor, Washington. Tidal currents (hourly) for a nearby nearshore station (Nobeltec Tides and Currents Pro, v. 3.3) were used to evaluate movements relative to tidal cycles. Tides were categorized tides by current direction and speed for ebb (outgoing, predicted current velocity > 0.25 m/s), flood (incoming, velocity > 0.25 m/s), and slack (velocity < 0.25 m/s). The first and last detections at estuary and nearshore receivers or arrays were used to evaluate the influence of diel period and tidal stage on movements.

The Watson Test (Watson 1962, Zar 1999) indicated that there were no significant difference between the timing of detections for hatchery and wild fish in freshwater or nearshore habitats ($U^2 = 0.11$, $P > 0.2$); therefore, the data were pooled to assess changes in diel activity. Rayleigh's Uniformity Test (Zar 1999) was used to test the null hypothesis that fish movements were distributed uniformly over a 24-h period. The Watson-Williams F-test (Fisher 1993, Zar 1999) was used to compare paired hourly movement patterns between hatchery and wild fish (by migration segment) to determine if their timing differed significantly as they transitioned through these shorter migration areas both at reach (river, estuary, and nearshore) and sub-reach scales (middle Green, lower Green, upper estuary, lower estuary, and nearshore). The chi-square test for goodness-of-fit was used to test the hypothesis that fish movement was independent of the tidal phase and whether it varied by day or night periods.

1.3 Results

1.3.1 Receiver Detection Effectiveness

The probability of detecting transmitters using pooled receivers varied along migration segments from river to nearshore areas. The model with the lowest $QAIC_c$ for *p* included the segment variable and an additive "flow" term to constrain the LR detection probability with average yearly flow rates (*p* (segment + flow), Table 2). The difference in QAICc between models with and without yearly variation was small ($\triangle$QAICc = 1.07), so separate yearly detection rate estimates were not used. The lower river detection rate was estimated at 70.5 ± 4.1% but the detection rates at the estuary (94.8 ± 1.8%) and nearshore (98.0 ± 2.0%) lines were much higher. As expected, the Admiralty Inlet line had a lower estimated detection rate in 2006 and 2007 (33.9 ± 11.4%) than in 2008 and 2009 (54.3 ± 20.5%) when more receivers were present. The Strait of Juan de Fuca line detection rate was fixed at 68.5%. A total of 184 smolts were detected at lower river receivers, 244 in the estuary, 154 at nearshore receivers, 41 at Admiralty Inlet, and 16 at the Strait of Juan de Fuca. Due to the lower probability and higher variability in detections in the river, estuary detections were used to estimate in-river survival rates for 2008 and 2009. Estuary detections were also used for analysis of travel time in freshwater and two years with high detection probability (2006, 2007) to assess travel times in the lower river.

1.3.2 Survival

The survival portion of the model with the lowest $QAIC_c$ included just the segment and rearing type variables (φ, segment + rear) (Table 2), indicating different survival rates for each migration segment and higher survival rates for wild fish (Table 3). The reduced model not including the rearing factor had a similar $QAIC_c$ ($\triangle$ $QAIC_c = 1.369$), though the model estimating different survival rates for hatchery and wild smolts was twice as likely when considering the model weights (Table 2). Yearly variation in φ was not evident ($\triangle QAIC_c = 3.93$). Length was included in the model with the second lowest $QAIC_c$ ((φ (segment + rear + length), $\triangle$ $QAIC_c = 1.117$, Table 2), and therefore may have an additive effect on survival probability of steelhead smolts. The coefficient for length in that model was positive (0.009), meaning that larger smolts experienced a slightly higher probability of survival than smaller smolts. Survival probabilities of both hatchery and wild smolts tended to be lower in the estuary and marine environment than in freshwater segments of the migration route (Table 3; Figure 2). The distance based instantaneous mortality rates (% mortality per km) were highest from release to the lower river (average 2.0% wild, 3.3% hatchery) and from the estuary to the nearshore (2.5% wild; 3.8% hatchery). The instantaneous mortality over time (mortality/d) was highest in the estuary (wild 2.5%, hatchery 3.8%), lowest in freshwater (wild 0.6%, hatchery 1.0%), and intermediate in nearshore (wild 0.9%, hatchery 1.3%). The composite freshwater survival probability estimate from release to the estuary was more than 13 times higher than the marine survival estimate (estuary to Strait of Juan de Fuca) for hatchery smolts, and nearly seven times higher the one for wild smolts (Table 3). The cumulative survival rate from release to the Strait of Juan de Fuca was 9.7% for wild and 3.6% for hatchery smolts (Table 3).

1.3.3 Travel Rate and Time

Wild fish travelled faster than hatchery fish through all migration segments except marine waters, where they were similar (Figure 2), and this was the most important factor describing freshwater travel rate. Hatchery smolts travelled much more slowly downriver than wild fish (mean = 4.4 km/d ± SE 0.4 vs. 15.1 km/d ± SE 1.1). The model including rearing type and length (FW rate ~ rear + length) was also supported by the data ($\triangle AIC_c = 1.67$), so length may have had a small effect on freshwater travel rate, with larger fish migrating faster. Travel rates from release to the estuary varied by tagging week for wild fish, with faster travel rates later in the tagging period. There was a significant decrease in the average travel time from week 1 (7.2 km/d, travel time 6.3 d ± SE 0.6) to week 4 (19.1 km/d, 2.8 d ± SE 0.4; ANOVA; $P < 0.01$).

Smolts moved more rapidly through some of the river segments than others. In 2006 and 2007 hatchery and wild fish were tracker over shorter migration segments from point of release to middle Green River, through the lower Green River to the estuary, and through the estuary.

Fish from both groups resided for the longest period and traveled slowest in the reach immediately below the release site, with hatchery fish traveling slower (mean = 2.4 km/d, SE ± 0.4) than wild fish (mean = 3.7 km/d, SE ± 0.8). Then, wild fish migrated rapidly between the middle and lower sections (mean = 41.4 km/d, SE ± 3.3); hatchery fish migrated more slowly (mean = 20.2 km/d, SE ± 2.4) between the sections. Average travel rates in the estuary for 2006-2007 were similar for hatchery and wild fish ($\text{mean}_{\text{hatchery}}$ = 10.8 km/d, SE ± 1.5, $\text{mean}_{\text{wild}}$ = 13.8, SE ± 1.8).

Estuarine travel rate was best explained by an interaction between rearing type and year (Estuary rate ~ rear x year). Hatchery and wild smolts traveled at similar rates through the estuary in 2006 ($\text{mean}_{\text{hatchery}}$ = 9.4 km/d ± SE 2.9; $\text{mean}_{\text{wild}}$ = 10.3 km/d ± SE 2.2) but hatchery smolts travelled more slowly than did wild smolts in 2007 ($\text{mean}_{\text{hatchery}}$ = 11.5 km/d ± SE 1.8; $\text{mean}_{\text{wild}}$ = 17.5 km/d ± SE 2.6) and in 2008 ($\text{mean}_{\text{hatchery}}$ = 10.3 km/d ± SE 2.7; $\text{mean}_{\text{wild}}$ = 22.4 km/d ± SE 2.2). No hatchery smolts were tagged in 2009 but wild smolts traveled at a similar rate to 2006 and 2008 ($\text{mean}_{\text{wild}}$ = 10.4 km/d ± SE 1.3). Length did not influence estuarine travel rate ($\triangle$ AIC_c = 2.863). Wild smolts tended to spend less time in the estuary than hatchery smolts but the difference was not significant ($P > 0.15$, $\text{mean}_{\text{wild}}$ = 1.1 d ± SE 0.2; $\text{mean}_{\text{hatchery}}$ = 1.9 d ± SE 0.3). Some smolts moved back upstream on flood tides in the upper estuary, and hatchery fish did so more often (average 16%) than wild fish (7.8%); these fish had longer residence (average 4.7 d) compared to smolts that did not migrate upstream (1.2 d).

The best model for marine travel rate included only the area through which the fish were travelling. Mean travel rates in nearshore areas (9.5 km/d) and Admiralty Inlet (10.6 km/d) were similar, and much slower than the mean rate calculated for the Strait of Juan de Fuca (20.6 km/d). Fish length was included along with area in the next best model (Marine rate ~ area +

length, $\triangle AIC_c = 1.672$), so may have had a small effect on travel rate within each marine area with larger fish migrating faster, though the model including just "length" performed poorly (Marine rate ~ length, $\triangle AIC_c = 12.011$). Wild fish spent only 5.1 days (SE ± 0.7) and hatchery fish 7.5 days (SE ± 0.9) in Puget Sound, from the time they left the estuary.

After entering marine waters, 99% of the smolts migrated north through Puget Sound (only 1% initially moved south) and then all fish moved west through the Strait of Juan de Fuca rather than continuing north through the Strait of Georgia. The timing of movement varied by release group and year as they migrated down the river and through the estuary but in general the hatchery fish migrated earlier than the wild fish, as a function of the dates of tagging and release (Figure 3). The pooled timing for all tags at the JDF shows a migration window from first to last detection of 22 days in 2006, 36 days 2007, 49 days 2008, and 23 days 2009.

1.3.4 Migration routes

At the exit from the Green River to the Duwamish River, the number of fish using the east channel or main channel varied by year but was similar in wild and hatchery fish. Pooled averages ranged from 6% in 2007 to 31% in 2009 and 53% in 2008, and higher flows were associated with more fish using this secondary channel ($F_{1,2} = 275$, $P < 0.01$). Use of these channels affects the subsequent route in Puget Sound either along the shoreline or as movement offshore. In the years with highest flow (2008), fish using the east channel tended to use shoreline areas in Elliott Bay: 67% of the fish detected in the east bay and 88% in the west bay were first detected in east channel. In total 93% of the wild fish detected along Elliott Bay shoreline areas in 2008 were detected in the east channel. In contrast, in 2009 only 33% of wild fish detected in Elliott Bay were first detected in the east channel.

Irregularities in the shoreline may influence smolt migration paths. For example, at a major point (Duwamish Head) 2.5 km west of the river in 2006, 17 fish were detected only on the river side of the point but none were detected only on the marine side of the point (0.5 km west). Thus most fish were already moving off-shore and northward rather than following the shoreline west-ward around the point. Similarly, in 2008 13 fish were detected on the river side of the point but only two fish were detected west of the point.

In central Puget Sound the fish moved northward and westward (e.g., Figure 4 illustrates the distribution of detections by receiver location for 2008). A few fish were detected south of Elliott Bay (1.5% of wild and 0.6% of hatchery fish were detected 7 km, and 1% of wild fish up to 28 km south). Migration in central Puget Sound in 2008 and 2009 was predominately along the west shore (ca. 2/3 vs. 1/3 of detections on the east shore). The initial shoreline orientation in Elliott Bay (i.e., east or west shore) had no effect on whether the fish were eventually detected at Admiralty Inlet, so northward migration was accomplished without any bias from initial shoreline choice.

All fish detected exiting Puget Sound migrated through the Admiralty Inlet (i.e., none was detected using another route) and all fish detected migrated west through the Strait of Juan de Fuca rather than north through the Strait of Georgia. At Admiralty Inlet most smolts were off-shore or in the center of the channel; 81% of detections in 2008 and 88% in 2009 were at receivers at least 1.6 km offshore (i.e., the middle 50% of the channel). At the Strait of Juan de Fuca, 31 receivers were deployed at the same locations each year across 21 km from Vancouver Island to the Olympic Peninsula. The distribution of smolt detections was equally divided between the shorelines and center of channel.

The most complete individual migration paths in Puget Sound were for two wild fish from 2008 and one hatchery fish from 2006. The wild fish both moved west and north and one was detected at Admiralty Inlet (120 km at 10.3 km/d, detected on 10 receivers) whereas the other used a more tortuous path (72 km, 6.2 km/d, detected on 7 receivers). These fish showed much slower net travel rates than other wild fish that exited Puget Sound and reached the Strait of Juan de Fuca line in 2008 at 20.1-34.2 km/d. The hatchery fish moved much slower (66 km, 2.3 km/d, detected on 10 receivers) than the wild fish but ultimately reached Admiralty Inlet. Each of these three fish was detected crossing the basin three times. Even with these multi-receiver tracks there were gaps from days to a week with no detections, implying even more complex movements or holding in some areas. Most fish tracked in Puget Sound areas were detected on only 1-4 receivers, providing less complete histories.

1.3.5 Diel Behavior

There were approximately 15.5 h of light and 8.5 h of dark (65% day, 35% night) during the spring months when the fish were migrating. Overall activity patterns inferred from the discrete movement events varied by migration segment ($P < 0.001$), beginning as primarily nocturnal in the riverine segments (70% night), progressing to nearly equal day (48%) and night (52%) in the upper estuary. Once smolts reached the lower estuary and Puget Sound their movements approximated those expected for daylight in May and June (68% day, 32% night). There were significant differences in diel timing between the lower Green River (90% night movement) and upper estuary (52% day, 48% night, $P < 0.001$) and the upper to lower estuary (68% day, 32% night) ($P < 0.05$) but no difference from the middle to lower Green ($P = 0.355$) and from the lower estuary to Puget Sound ($P = 0.24$). There were peaks in activity within the diel period, shifting from near midnight in the middle Green River, to near 01:00 -02:00 h in the lower Green River, near dawn in the upper estuary, late morning in the lower estuary, and throughout the day in Puget Sound (Figure 5). Movements were non-uniformly distributed in all freshwater, estuary and Puget Sound migration segments for all fish except hatchery fish in the lower estuary (Raleigh's $_{Z= 0.05}$, $P < 0.05$). There were differences in the primary period of movement (mean angle) using paired and multiple hourly samples for release group by migration segment at the upper estuary and Puget Sound (Raleigh's $_{Z= 0.05}$, $P < 0.001$, Watson-Williams F Test, Fisher 1993, Zar 1999).

Wild and hatchery smolts moved in the estuary more frequently on the ebb tide and less frequently on the flood tide than expected as a function of the time of day in those tidal stages ($P = 0.01$ wild, $P < 0.0001$ hatchery) whereas in Puget Sound both groups moved in proportion to tidal periods ($P > 0.4$). In migrating from the upper to lower estuary, the movements of wild fish transitioned from more frequent than expected movements at ebb tide in the upper estuary ($P < 0.01$) to proportional in the lower estuary ($P = 0.8$) whereas hatchery fish moved more often than expected on ebb tides in both estuary segments ($P < 0.01$). In relation to diel and tidal period, wild smolts tended to move through the estuary and Puget Sound in proportion to the expected periods of current direction during the day ($P > 0.1$ estuary and Puget Sound) and night ($P = 0.2$ Puget Sound), except in the estuary at night ($P < 0.05$) where they moved more during ebb tides (Table 4). Hatchery fish in the estuary moved more often on ebb tides and less on floods than expected during both the day ($P < 0.0001$) and night($P < 0.05$) but in the Puget Sound did not differ in the frequency of expected tides ($P = 0.44$ day, $P = 0.9$ night).

1.4 Discussion

1.4.1 Survival

Wild Green River steelhead smolts survived at higher rates than hatchery smolts through all migration segments (Figure 2) but rates were generally low during the 215 km migration from release to the Strait of Juan de Fuca (wild smolts = 9.7% survival, 1.1%/km mortality rate; hatchery smolts = 3.6% survival, 1.5%/km mortality rate) compared to other studies of steelhead in the region. Moore et al. (2010a, 2012) and Melnychuk (2007) used similar mark-recapture models to estimate steelhead survival rates from release to Salish Sea exit and found survival rates ranging from 28% (wild) to 10% (hatchery) for Hood Canal smolts from river release to Strait of Juan de Fuca (163-210 km) and 27% for Cheakamus River, British Columbia wild smolts through the Strait of Georgia (155-230 km). In Hood Canal, the distance-based instantaneous mortality rate during the 13 km freshwater migration for the Skokomish River wild smolts was low (0.3%/km) but was much higher for hatchery smolts (4.8%/km). Mortality rates within Hood Canal (3.25-3.5%/km) and between the Admiralty Inlet and Strait of Juan de Fuca lines (1-1.2%/km) were similar for both groups (Moore et al. 2012). The high mortality rates for steelhead smolts migrating through the Salish Sea could limit overall productivity because they are on the order of the total marine mortality estimated from steelhead populations in general from earlier periods (Quinn 2005). These rates varied little between years, unlike the higher variability found in Oregon coastal rivers and estuaries (Romer et al. 2012), but without a longer period of record and larger samples it is difficult to interpret this difference. In comparison to the Puget Sound results, steelhead from the Napa River, California had lower mortality rates during the entire migration from release, through San Francisco Bay, to the ocean (0.67%/km: Sandstrom et al. 2013).

In the present study, hatchery smolts survived at a consistently lower rate through all migration segments relative to wild smolts; there was a slight increase in survival relative to fish size and larger hatchery smolts migrated to the estuary at a faster rate. Higher probability of survival was reported for larger compared to smaller smolts in British Columbia's Keogh River steelhead (Ward et al. 1989) and other Pacific salmon species (Henderson and Cass 1991; Holtby et al. 1990), and for smaller smolts that reached a large size by feeding in a California coastal estuary (Bond et al. 2008).

While early marine survival may be important, and high mortality has been documented for Puget Sound smolts, further mortality takes place during the 2 or 3 subsequent years at sea prior to return as adults. The general perspective is that the additional mortality in the ocean likely declines as fish size increases over time (Ricker 1976, Quinn 2005). In contrast, smolt survival estimates from the POST array (16%) in the first month out of the Salish Sea compared to the entire mortality from juvenile to adult returns (1-4%) suggests that the cumulative mortality is 4-17 times greater in the ocean than in the Salish Sea (Welch et al. 2011). Survival rates for hatchery steelhead released in the Puget Sound region (e.g., Green River) were the lowest of any region in Washington State (Scott and Gill 2008), declining from 7.0% for smolts entering the ocean in 1983 to 0.2% in 1996, and remaining near that level since (Scott and Gill 2008). The low survival of Green River steelhead appears to be a combination of lower estuarine and early marine survival relative to other Salish Sea populations (Moore et al. 2012; Welch et al. 2004; Welch et al. 2011) and continuing low survival during ocean rearing for all populations.

1.4.2 Travel Rates

The marine travel rates observed for Green River steelhead were consistent with previously published values. Welch et al. (2011) found that juvenile sockeye salmon (*O. nerka*) and steelhead migrated in the Salish Sea at rates corresponding to ca. 0.95 and 0.86 body lengths per second (BL/sec, respectively), consistent with the optimal migration speeds of 0.8-2.0 BL/sec calculated for small sockeye salmon (Brett 1995). Swimming speed estimates for Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) smolts also averaged about 1 BL/sec (Finstad et al. 2005). Similar marine travel speeds were also observed for steelhead in a number of Washington and BC populations (Melnychuk et al. 2007, Moore et al 2010a, Payne et al. 2010). The Green River smolt migration speeds varied by migration segment with wild fish migrating faster than hatchery fish in the river (0.93 vs. 0.27 BL/sec), more similar in the estuary (0.95 vs. 0.64 BL/sec), even more similar in Puget Sound (0.64 vs. 0.56 BL/sec) and accelerating as they exited the Strait of Juan de Fuca (0.99 (wild) and 1.11 (hatchery) BL/sec).

The mean travel rates of wild smolts were faster than those of hatchery fish from release to the estuary and from the upper to lower estuary. These differences may be related to the hatchery's release strategy, as all smolts were released at a single time each year (early May), irrespective of environmental conditions or any assessment of the physiological state of the fish. The release of hatchery fish into the river provided no period for learning and acclimation, and perhaps they were not physiologically ready to migrate (Gale et al. 2009; Lorenzen et al. 2012). Hatchery fish had the most variable and slowest travel rates near the release site; some fish immediately migrated downstream to the estuary but others remained near the release site for several days before leaving. Hatchery fish also had the slowest and most variable travel rate in the upper estuary, similar to behavior shown elsewhere (Kennedy et al. 2007). The hatchery smolts were released earlier than the wild fish, and wild migrants tagged earlier moved slower than later migrants but without controlled experiments involving both groups it is not possible to distinguish rearing effects from those related to time of year.

Estuaries are important rearing areas for a variety of juvenile salmonids during initial entry into marine waters (Thorpe 1994) but the importance of residency in nearshore waters is largely unknown for steelhead. The use of estuaries by steelhead is considered to be short relative to other smaller-bodied salmonids (Quinn 2005). The shorter estuary residence time of smolts considered physiologically prepared for ocean entry has been considered proportional to the probability of survival to the ocean (Schreck et al. 2006; Kennedy et al. 2007). In our study estuary residence time (wild 1.1 d SE 0.3, hatchery 1.9 d SE 0.4) was significantly less than river residence (wild 5.9 d, hatchery 16.4), thus consistent with the idea that steelhead do not spend long in estuaries. Telemetry studies in Hood Canal tributaries (Moore et al. 2010, 2012), and the Alsea and Nehalem rivers in Oregon (Clements et al. 2012, and Johnson et al 2010) also indicated short (1 – 2 d) estuary rearing period for wild and hatchery steelhead. Although migrants in Hood Canal spent little time in the estuaries, the average residence time for smolts in nearshore areas before exit from the canal was 14.7- 17.2 days (travel rates 8.0-10.1 km/d) with 1/3 of these smolts backtracking substantial distances, suggesting that conditions within Hood Canal promoted retention of steelhead smolts (Moore et al. 2010). Green River smolts in this study resided in Puget Sound for a mean of 5.1 days (wild travel rate 15.3 km/d) or 7.5 days (hatchery travel rate 5.3 km/d). Unlike Hood Canal in this study there were few fish found south of the initial entry point into Puget Sound (1%) with the large majority of fish moving westward and northward.

1.4.3 Migration Route and Direction

Our study provides new data on marine migratory behavior of steelhead during their migration from river to ocean. In British Columbia there may be species-specific migration routes through the Strait of Georgia, with some typically exiting northwards through Queen Charlotte Strait (Groot et al. 1989, Tucker et al. 2009), and others migrating westward through the Strait of Juan de Fuca (Trudel et al. 2009). Upon entry to Puget Sound a portion of wild and hatchery steelhead used local shoreline areas in Elliott Bay before moving offshore, after which almost all migrated west and north through Puget Sound and west to the ocean. The direction of travel after arrival in coastal waters may be important as shorter routes may reduce time and hence exposure to predators in coastal waters. Recent studies suggest that most steelhead from northern Vancouver Island and the lower mainland migrate north via Queen Charlotte Strait whereas southern populations may use both the northern and southern (Strait of Juan de Fuca) routes (Melnychuk et al. 2010, Welch et al. 2011). The current study and other telemetry research during the same years indicated that Puget Sound and Hood Canal steelhead migrated exclusively through the Strait of Juan de Fuca (Moore et al. 2010, 2012).

1.4.4 Timing and Diel Behavior

Drenner et al. (2012) noted there have been few studies of the diel behavior of smolts along their entire migration path through ecotypes from river and marine waters. Smolt migrations down rivers typically occur predominately at night, and particularly during periods with low water temperatures, with a transition to day-time activity as fish reach estuary waters (Godin 1982; Moser et al. 1991; Crittenden 1994; Ibbotson et al. 2006). Steelhead smolts generally follow this pattern in coastal rivers, moving primarily after dusk (Melnychuk et al.

2007; Johnson et al. 2010) but becoming diurnal once they reach the estuary (Ledgerwood et al. 1991), and these patterns were evident in the present study. In contrast, the movements of steelhead smolts in the Sacramento River did not show a strong diel pattern and they often moved during the day along the entire migration path (Chapman et al. 2012). In our study the movement period from river to the estuary was transitional from nocturnal to daytime, with approximately half the movements during day and night in the upper estuary, while movement through the lower estuary and marine water was mostly during the day, but in proportion to the amount of day. The transition at the upper estuary towards diurnal movement may be a response to the first exposure to tidal currents which alternate between up and downstream movements twice during the day vs. the downstream flows of rivers, and wild fish may make this transition more rapidly than hatchery fish. Johnson et al. (2010) found that hatchery steelhead tended to move downstream during daytime ebb and upstream during night-time flood tides whereas wild fish moved downstream regardless of diel or tidal period. Martin et al. (2009) suggested that as Atlantic salmon experience higher salinity moving through the leading edge of saltwater this induces a transition from passive, fluvial migration to a more active and seaward migration. In marine waters, adult steelhead are day-active and remain near-surface (Ruggerone et al. 1990; Nielsen et al. 2011).

Most of these previous studies relied on one to two years of study and reported on two segments of the migration path but our work spanned three (hatchery) and four (wild) years, and included movements along the entire course of movement from in-river release to the ocean. This study advances the understanding of how the migratory behaviour of wild and hatchery smolts may explain differences in survival during their river and early marine migration through Puget Sound. This understanding will be valuable in informing where data gaps exist to guide further examination of factors influencing early marine survival and longer-term smolt to adult survival. Although hatchery fish survived at lower rates through all migration segments, both rearing types experienced high initial mortality in the river, and in transitions from river to estuary and marine environments. Some of the reasons for the high mortality may be specific to the Green River and local marine areas (i.e., habitat modification, pollution and predators); however, the breadth of salmon populations experiencing low marine survival indicates a more general problem affects other steelhead populations and other salmonid species. It will be important to incorporate this loss into models of ocean survival to ensure that recovery planning options target the areas and factors most likely to yield benefits.

Table 1.1: Number of receivers by river and marine segment or major geographic area and year.

Segment	**2006**	**2007**	**2008**	**2009**
Middle Green River (RK 48-55)	2	3	2	2
Lower Green River (RK 17-48)	1	1	2	2
Duwamish River Estuary (Upper RK 4-16 , Lower RK 0-4)	6	11	11	9
Elliott Bay (single receivers)	3	6	12	10
South Central Puget Sound (Elliott Bay south to Tacoma)	9	8	12	18
North Central Puget Sound (Elliott Bay north to President Point)	16	17	32	15
Admiralty Line (06-07 Kitsap Peninsula to Whidbey I.) (08-09 Marrowstone to Whidbey I.)	5	3	15	15
Strait of Juan de Fuca Line	31	31	31	31

Table 1.2: MARK Model results showing all models tested to determine which factors likely affected detection (top panel) and survival (bottom panel) probability. Factors tested in detection probability (p) models included migration segment (segment), annual average river flow (flow), and annual variation (year). Factor variables year and rearing history (i.e., hatchery or wild; rear), and a continuous fork length variable (length) were tested in survival (φ) models.

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Model (φ constant)	**Number of parameters**	**QAICc**	**ΔQAICc**	**weight**
φ(~segment)p(~segment x flow)	11	442.982	0	0.618
φ(~segment)p(~segment x flow + year)	14	444.049	1.07	0.362
φ(~segment)p(~segment x year)	22	450.357	7.375	0.015
φ(~segment)p(~segment + year)	13	452.787	9.805	0.005
φ(~segment)p(~segment x flow x year)	26	458.787	15.805	0.000
φ(~segment)p(~segment)	10	490.091	47.109	0.000
Model (*p* constant)				
φ(~segment + rear)p(~segment x flow)	12	441.613	0.000	0.375
φ(~segment + rear +length)p(~segment x flow)	13	442.730	1.117	0.215
φ(~segment)p(~segment x flow)	11	442.982	1.369	0.189
φ(~segment + length)p(~segment x flow)	12	444.784	3.171	0.077
φ(~segment + year + rear)p(~segment x flow)	15	445.542	3.929	0.053
φ(~segment + year)p(~segment x flow)	14	445.939	4.326	0.043
φ(~segment + year + rear + length)p(~segment x flow)	16	447.386	5.774	0.021
φ(~segment +year + length)p(~segment x flow)	15	447.995	6.382	0.015
φ(~segment x rear + length)p(~segment x flow)	17	449.728	8.116	0.006
φ(~segment x rear + year)p(~segment x flow)	19	452.640	11.027	0.002
φ(~segment + rear + year + length)p(~segment x flow)	20	454.513	12.900	0.001
φ(~segment * year + length)p(~segment x flow)	27	462.676	21.063	0.000

Table 1.3: Survival probability (percent) estimates of steelhead trout smolts ± SE based on the model with the lowest $QAIC_c$ value (φ (segment + rear), *p* (segment + flow). Instantaneous mortality rates (mortality/km) are shown in parentheses.

Migration Segment	**Hatchery Smolts**	**Wild Smolts**
PR (Point-of-Release)-Lower River (LR)	79.6 ± 3.0 (-3.3)	86.9 ± 2.2 (-2.0)
LR-Estuary (EST)	86.4 ± 3.2 (-0.5)	91.5 ± 2.1 (-0.3)
EST-Nearshore (NS)	54.3 ± 4.2 (-3.8)	66.9 ± 3.5 (-2.5)
NS-Admiralty Inlet (AI)	51.7 ± 19.5 (-1.3)	64.6 ± 18.2 (-0.9)
AI-Juan de Fuca (JDF)	18.6 ± 8.1 (-1.5)	28.1 ± 10.2 (-1.2)
Freshwater (PR-LR x LR-EST)	68.7 ± 3.5 (-1.0)	79.5 ± 2.1 (-0.6)
Early Marine (EST-NS x NS-AI x AI-JDF)	5.2 ± 1.7 (-1.8)	12.1 ± 4.4 (-1.3)

Table 1.4: Proportion of observed movements by hatchery and wild fish by day (top) and night (bottom) and tidal current period compared to the expected proportion with significance value.

Day

	Hatchery Observed	Hatchery Expected	P-Value	Wild Observed	Wild Expected	P-Value
			Estuary			
Ebb	0.66	0.50	<0.0001	0.55	0.49	0.12
Flood	0.20	0.34		0.32	0.34	
Slack	0.14	0.16		0.14	0.17	
			Nearshore			
Ebb	0.44	0.50	0.44	0.53	0.49	0.12
Flood	0.36	0.34		0.35	0.34	
Slack	0.20	0.16		0.12	0.17	

Night

	Hatchery Observed	Hatchery Expected	P-Value	Wild Observed	Wild Expected	P-Value
			Estuary			
Ebb	0.58	0.47	0.04	0.56	0.48	0.02
Flood	0.26	0.34		0.24	0.32	
Slack	0.16	0.18		0.20	0.20	
			Nearshore			
Ebb	0.46	0.47	0.9	0.52	0.48	0.2
Flood	0.33	0.34		0.24	0.32	
Slack	0.21	0.18		0.25	0.20	

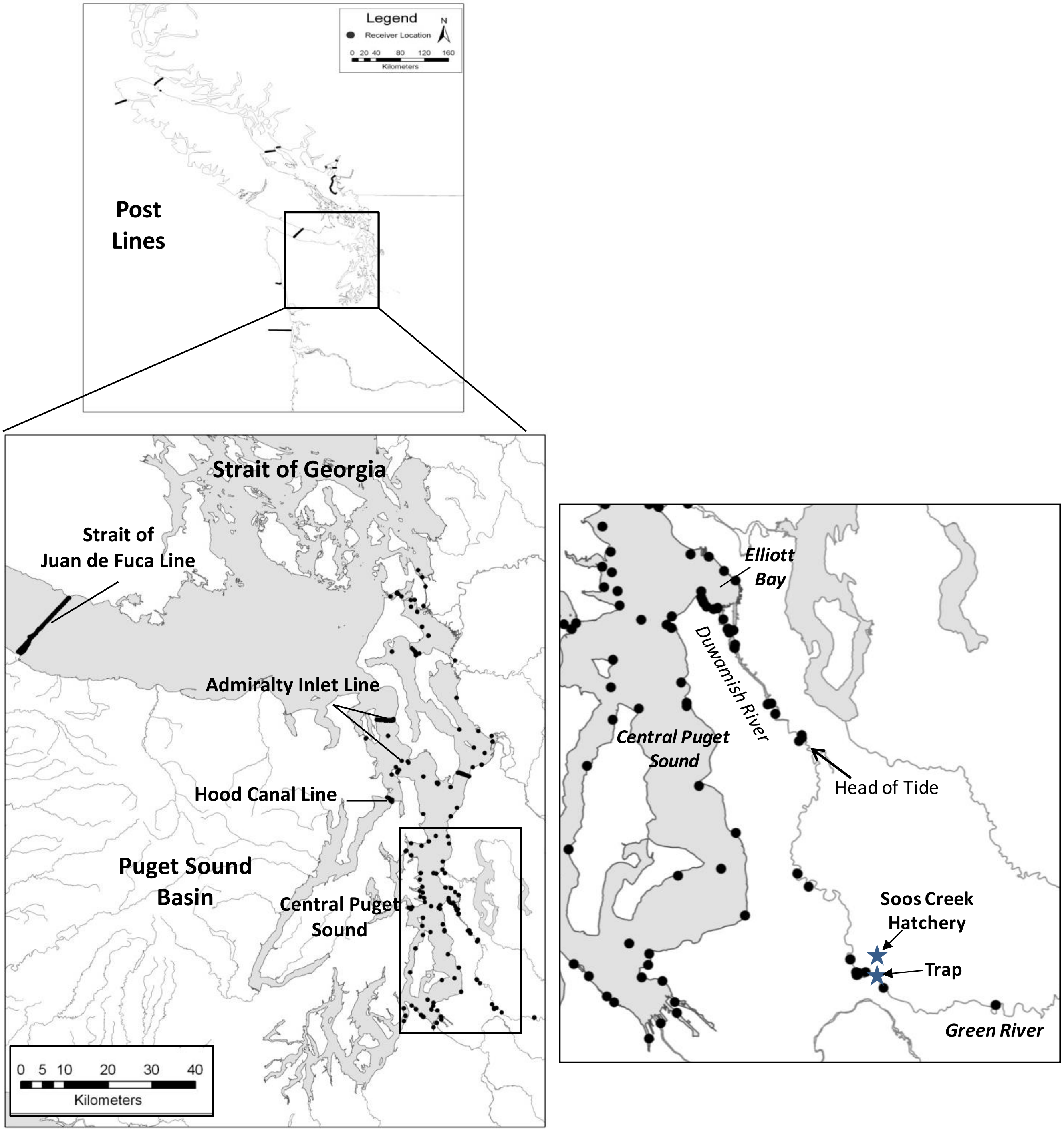


Figure 1.1: Receiver lines in the Salish Sea and coastal waters near Puget Sound deployed and maintained by the POST Project (top) and receiver lines and single receivers in Puget Sound and Strait of Juan de Fuca (bottom). Receivers and tagging and release locations (stars) in the Green and Duwamish Rivers inset shown side inset.

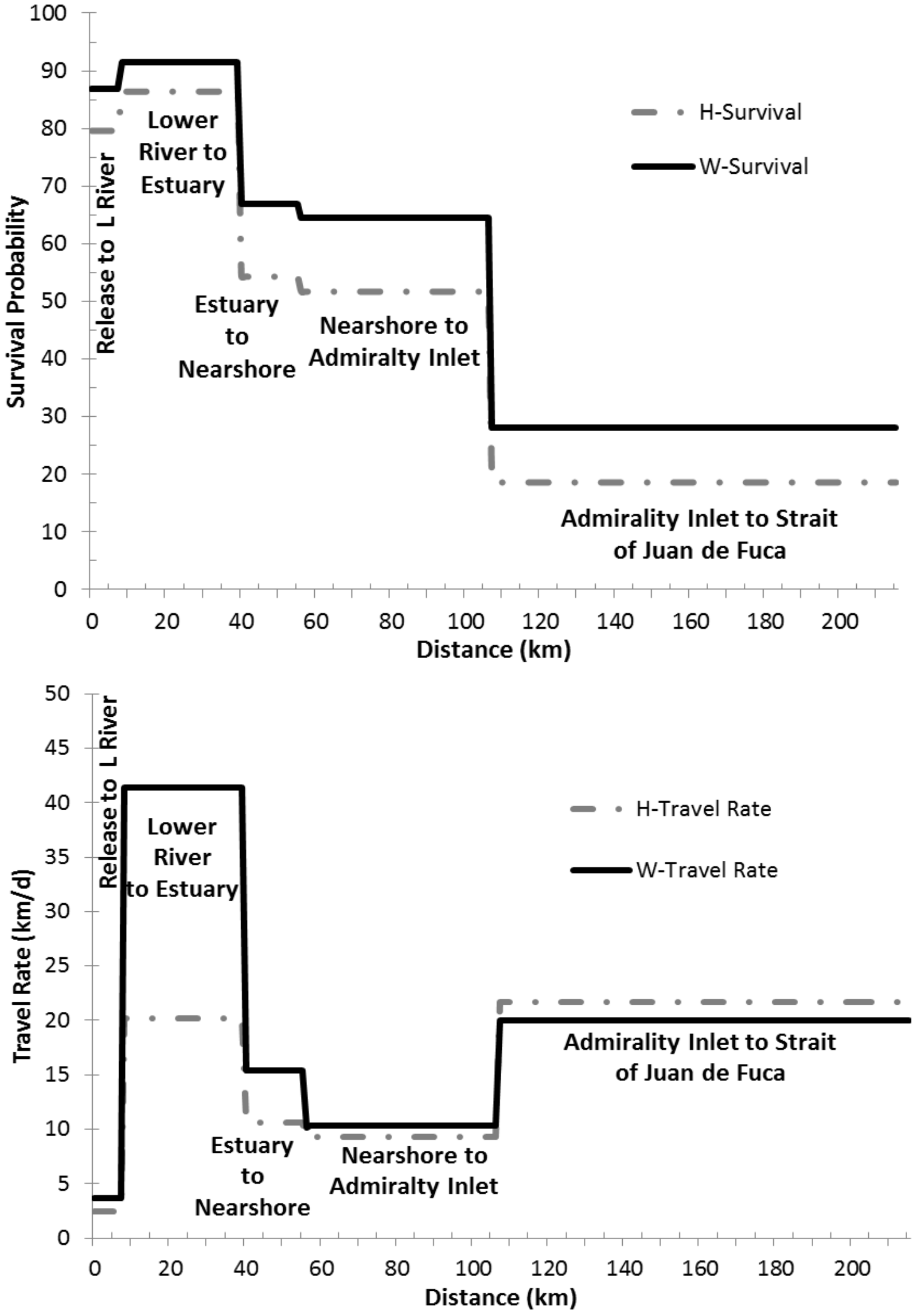
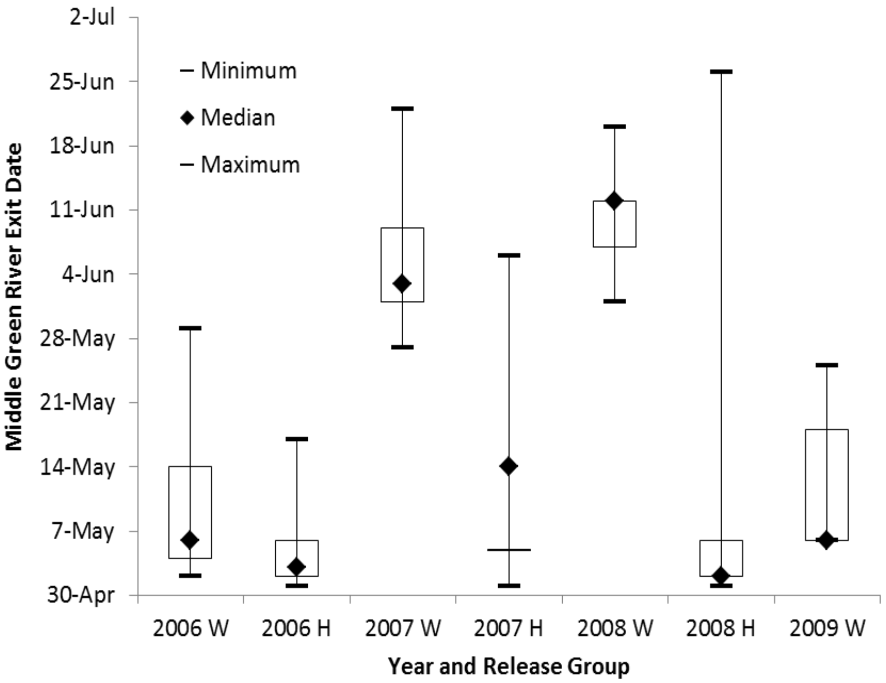


Figure 1.2: Survival probability (mean, top panel) and travel rate (mean, bottom panel) by distance for wild (W) and hatchery (H) smolts from release to Strait of Juan de Fuca. Travel rates for freshwater segments use 2006-2007 data to differentiate release to the lower river and lower river to estuary.



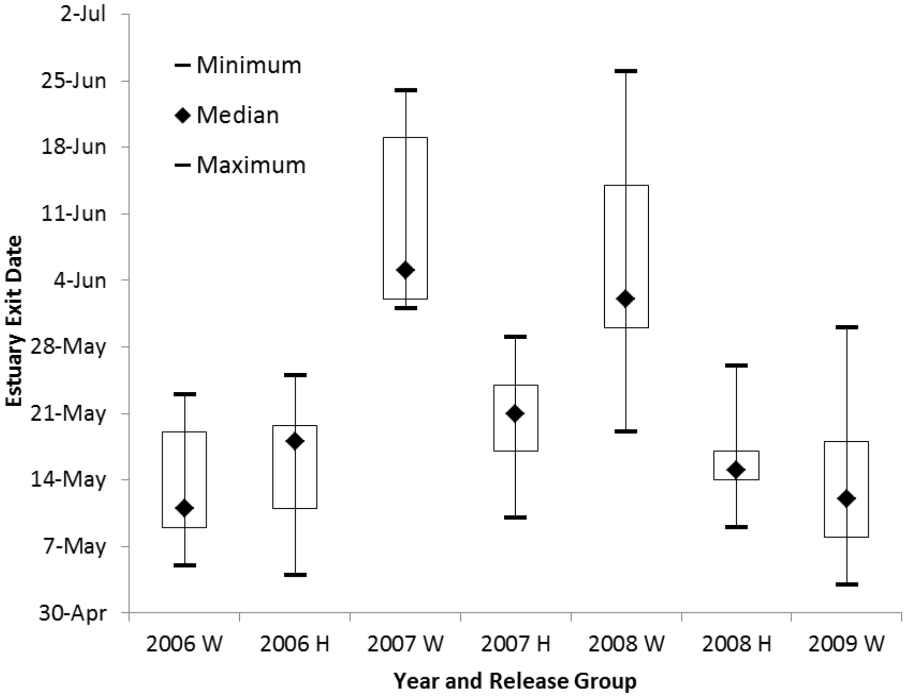


Figure 1.3: Migration timing (number of tags detected per day) of wild (W) and hatchery smolts (H) by year exiting the middle river (top) and the lower estuary (bottom). Box includes 1st and 3rd quartile.

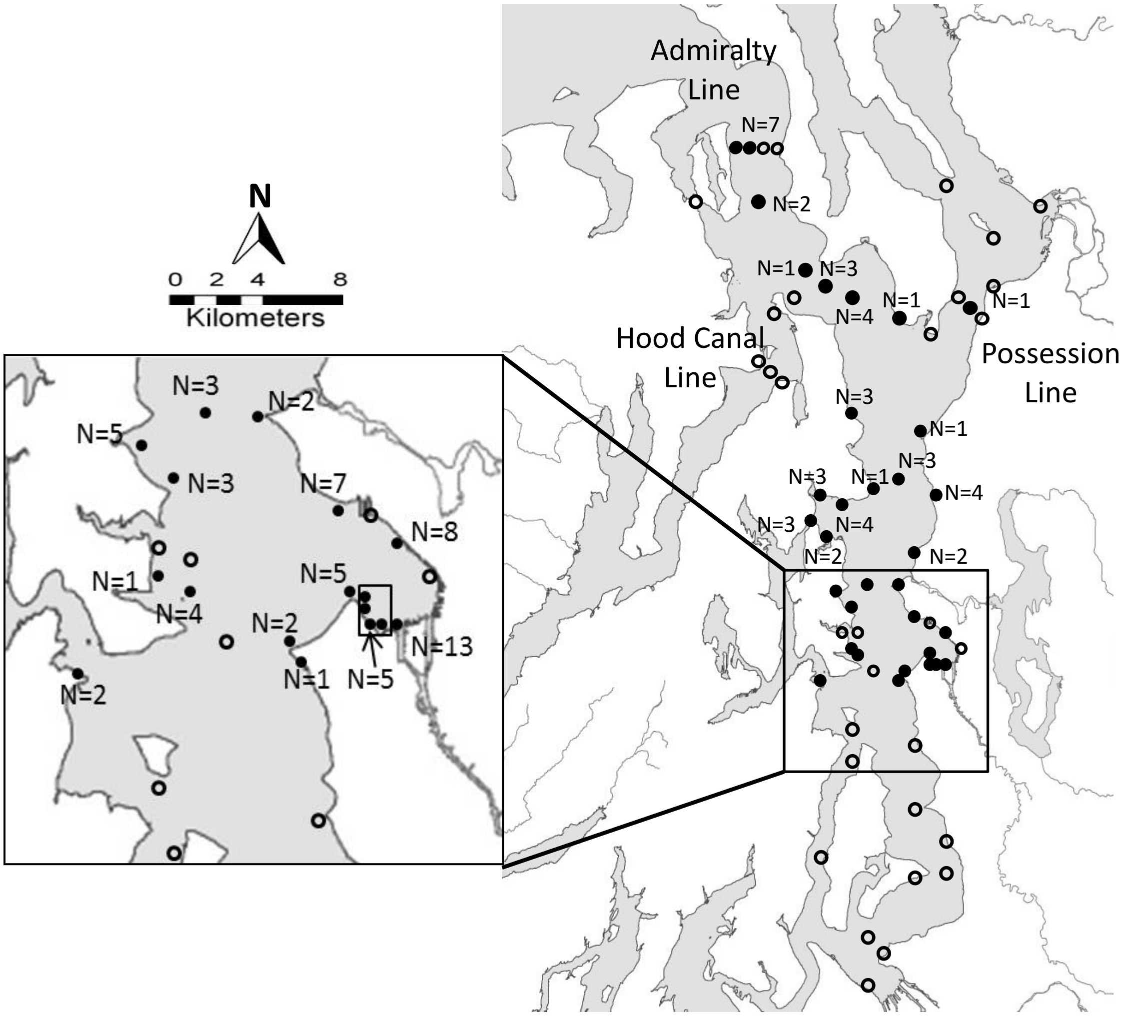


Figure 1.4: Number of individual tags detected by receiver location (black circle with number of tags detected, e.g. N=x; open circle receiver with no detections) in Puget Sound in 2008, lines of receivers do not show all receivers (legend and scale are for inset).

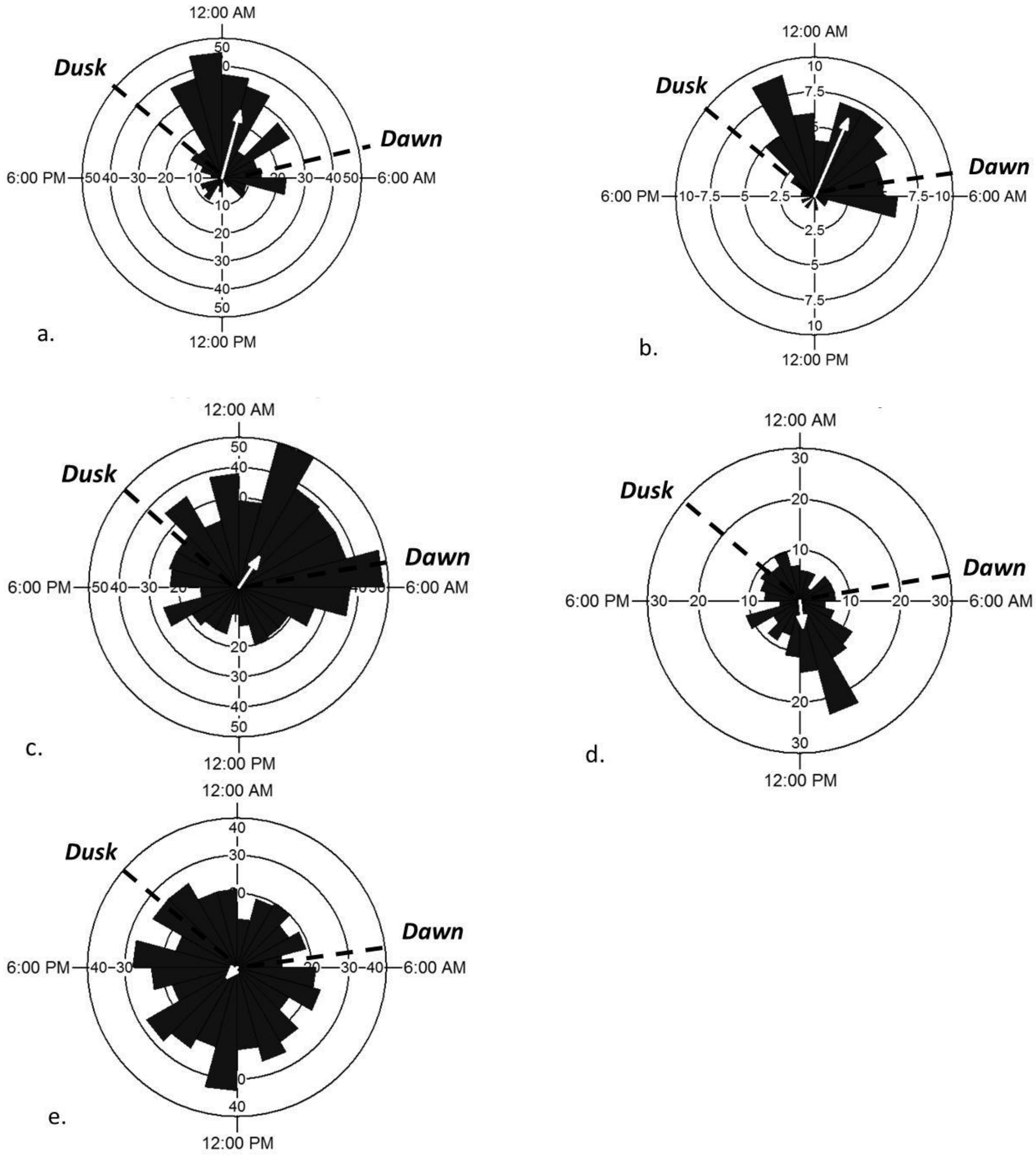


Figure 1.5: Rose diagrams of hourly detections of all fish through migration segments a) middle river (337 detections); b) lower river (69); c) upper estuary (638); d) lower estuary (207); and e) nearshore (470). The axis scale varies by segment and the white arrow shows mean vector.

Chapter 2. Diversity of movements by individual anadromous coastal cutthroat trout in Hood Canal, Washington

2.1 Introduction

Salmonid fishes vary greatly in the degree of anadromy from obligate (*i.e.*, no naturally-existing non-anadromous populations or individuals) to fully non-anadromous (Rounsefell, 1958; Quinn and Myers, 2004). The marine period typically provides better growth opportunity but higher mortality risk from larger predators than are found in freshwater, especially shortly after entry into marine waters (Quinn, 2005). The ways in which species and populations use the marine environment affect their population dynamics and opportunities for exchange with conspecific populations. The migration patterns of salmonids in marine waters have been studied by tagging or marking juveniles in fresh water and recovering them at sea (*e.g.*, Kallio-Nyberg *et al.*, 1999; Weitkamp and Neely, 2002) or population-specific DNA analyses (*e.g.*, Seeb *et al*., 2011) but such techniques typically yield information only at the point of recapture and so provide only limited insights into the movements of individuals. Sampling in fisheries can be further limited if the species is scarce or protected by regulation.

Of the Pacific salmon and trout of the genus *Oncorhynchus* (Walbaum), the vast majority of information on migration and distribution has been reported on the semelparous salmon, and information is much more limited on the iteroparous trout species: steelhead *O. mykiss* (Walbaum 1792), and especially anadromous coastal cutthroat trout *O. clarkii clarkii* (Richardson 1836). *O. mykiss* migrate long distances on the high seas (Burgner *et al.*, 1992) and are native to both Asian and North American coasts of the Pacific Rim. In contrast, *O. clarkii clarkii* are native only in North America, from northern California to south-central Alaska

(Behnke, 1992), and are generally thought to have limited marine migrations in distance and duration (Trotter, 1989; Wenburg and Bentzen, 2001). Juvenile *O. clarkii clarkii* may spend several years in fresh water before migrating to sea (Trotter, 1989), and many populations stay in freshwater throughout their lives, with stream-resident, fluvial or adfluvial migratory patterns. In addition, populations vary in the duration of marine residence. In the northern part of their range (southeastern Alaska), they spend only a few summer months in marine waters (Armstrong, 1971; Saiget *et al.*, 2007) whereas in coastal Oregon they may spend 4 to 6 months at sea (Sumner, 1962), and nearly a full year in some Puget Sound populations (Wenburg, 1998). Thus in many respects *O. clarkii clarkii* contrast with *O. mykiss* as brown trout *Salmo trutta* L. 1758, contrast with Atlantic salmon *S. salar* L. 1758, as *S. trutta* are native to only the eastern side of the Atlantic Ocean, more readily remain in freshwater (in streams and lakes) and seem to migrate less far from their natal streams than do *S. salar* (Jonsson and Jonsson, 2011).

O. clarkii clarkii display a wide variety of migration behaviour. In the Salmon River, Oregon, Krentz (2007) identified two main anadromous life history types: “ocean migrants” that migrated rapidly through the estuary and out to sea, and “estuarine residents” that remained in the estuary for the spring and summer. Krentz (2007) also reported other migration patterns, including variation in site fidelity and movement within the estuary and between the estuary and the ocean. Other than studies within estuaries, the movements of anadromous *O. clarkii clarkii* are poorly known once they leave their natal streams. In coastal waters of Oregon and Alaska they appear to remain close to shore (Trotter, 1989; Jones and Siefert, 1997) but some were caught 20 km or more offshore in low salinity waters of the Columbia River plume (Loch and Miller, 1988; Pearcy *et al.*, 1990). Otherwise, *O. clarkii clarkii* are believed to rarely migrate across bodies of open water more than 3–8 km wide (Johnston, 1982; Trotter, 1989). In Puget

Sound, *O. clarkii clarkii* are routinely captured in shallow nearshore habitats by anglers and with beach seines or gill nets (Raymond, 1996; Trotter, 1997; Johnson, 2004; Haque, 2008; Duffy and Beauchamp, 2008), but are very rarely captured offshore. Washington Department of Fish and Wildlife regulations do not permit anglers to retain *O. clarkii clarkii* caught in the state's marine waters so there are no catch records for this species, as there are for Pacific salmon and *O. mykiss*. Increased information on their movement patterns (*i.e.*, site fidelity, limited movement, or extensive movement) is important for conservation purposes as well as understanding their life history as part of the continuum of salmonid migration patterns.

In addition to the uncertainty about movement patterns in space, the diel activity period of *O. clarkii clarkii* in marine waters is entirely unknown. Salmonids show complex and diverse patterns of diel activity, including variation among species, populations, life history stages, habitats and seasons (Groot and Margolis, 1991; Quinn, 2005; Railsback *et al.*, 2005; Walker *et al.*, 2007). For example, telemetry studies of migrating adult salmonids in marine waters revealed faster or more prolonged movements during the day but substantial variation among species (Quinn *et al.*, 1989; Ruggerone *et al.*, 1990; Candy and Quinn, 1999). *O. clarkii clarkii* exhibit diurnal activity in streams during the summer with increased night-time activity during fall and winter, and during migrations to and from natal streams (*e.g.*, Armstrong, 1971; Henderson and Northcote, 1985; Jakober *et al.*, 2000). On the other hand, *O. clarkii clarkii* foraging in a large lake showed little variation in movement from day to night (Nowak and Quinn, 2002). There is limited published information on timing of their movements in estuaries and none in marine waters (Saiget *et al.*, 2007; Zydlewski *et al.*, 2009).

The goal of the present study was to use acoustic telemetry to characterise the migratory behaviour of *O. clarkii clarkii* in Puget Sound to better understand their life history. The specific objectives were to 1) describe the spatial distribution of *O. clarkii clarkii* leaving a stream and entering estuarine and nearshore marine waters, 2) identify movement patterns in marine waters over a range of temporal and spatial scales, 3) determine if smolts and adults differed in movements, and if there were discrete modes in movement behaviour or a single overall pattern, and 4) determine whether individuals showed fidelity to specific sites or moved widely during their period in marine waters. It was predicted that, 1) upon entry into marine waters, movements would be along the shore but random in direction (*i.e.* north or south), 2) movements across open water would be rare, 3) larger *O. clarkii clarkii* would travel farther than smaller *O. clarkii clarkii*, and 4) *O. clarkii clarkii* would not depart from Hood Canal, their natal basin. Movements were predicted to be primarily during the day or twilight because their foraging is guided by vision (Henderson and Northcote, 1985: Mazur and Beauchamp, 2003). Contrasting predictions were tested relating movement to tides. *O. clarkii clarkii* might move more often during periods with current than during slack periods because of passive displacement from drift or they might move less during tidal current periods because they might hold station and feed on drift, as *O. clarkii clarkii* do in streams.

2.2 Methods

2.2.1 Study Site

The study was conducted in Big Beef Creek (BBC) estuary and the nearshore waters of Hood Canal, a narrow (2-4 km wide), deep (up to 175 m) fjord-like tributary to Admiralty Inlet and the Strait of Juan de Fuca in Washington, U.S.A (Figure 1). Hood Canal is 110 km long with 575 km of shoreline and 386 km^2 surface area, and is part of a greater complex of seven sub-basins within Puget Sound. Hood Canal is generally oriented north to south with eastern and western shorelines with a floating bridge 10 km from the outlet at the northern end. Hood Canal can be highly stratified, with a tidal range of ~ 4 m and mean salinity in late spring and summer of 26 to near the surface and 30 below 15 m. Water temperatures in late spring and summer average 14° C near the surface and 10-12° C below 6 m (Moore *et al.*, 2008; Sutherland *et al.*, 2011).

BBC is one of many streams on the east side of Hood Canal draining small, low-elevation watersheds with small, protected estuaries and gravel/cobble stream deltas that extend into marine waters. BBC is an 18 km tributary (Figure 1 inset) that flows through a 0.5 km long, 1.5 ha, tidally influenced inner embayment and adjacent 0.7 km-long stream delta that extended into the canal. At high tide, the upstream portion of estuary reaches salinity levels of 10–15, whereas the salinity near the estuary mouth is 20–25 (Polivka, 2005). At low tide the embayment and most of the delta are dry, exposing a series of tidal channels upstream and downstream of a road causeway. In this paper areas upstream and downstream of the causeway are referred to as the inner and outer estuary, respectively. Hood Canal has a complex of nearshore habitats including long stretches of beach shoreline punctuated by small tidal deltas on east canal streams, larger deltas on west side rivers, and small embayments and spits throughout the canal. A narrow shelf-like terrace, 0-20 m deep and 200-300 m wide and up to 500-m in selected areas, extends along shorelines with sand, gravel and cobble substrate and narrow bands of eelgrass from low-tidal flats to 10 m depth.

2.2.1 Fish Capture and Tagging

O. clarkii clarkii were captured as they migrated downstream from BBC at a weir between mid-April and late-May, near the end of the adult migration and near the peak of smolt migration based on weir counts. A total of 62 *O. clarkii clarkii* were tagged with acoustic transmitters: 24 in 2006, 21 in 2007 and 17 in 2008, including smolts (165-240 mm) and larger *O. clarkii clarkii* (240-425 mm) termed adults here, based on length frequency distributions (Wenburg, 1998; F. Goetz, unpublished data). *O. clarkii clarkii* were transferred to a container with freshwater and buffered tricaine methanesulfonate (MS-222) at a concentration of 70 mg l^{-1}, measured for fork length (L_f), and weighed. A tissue sample was collected from the anal fin for later DNA analysis and only *O. clarkii clarkii* confirmed to be *O. clarkii clarkii* (as opposed to *O. mykiss* or *O. clarkii clarkii*-*O. mykiss* hybrids: Moore et al., 2010*b*) were included in the analysis. *O. clarkii clarkii* were surgically implanted with different sizes of acoustic transmitters (Vemco, Inc., Shad Bay, Nova Scotia, http://vemco.com) so that the average tag weight was < 5% of *O. clarkii clarkii* mass: V7-4L (1 fish), V9-6L (43), V9-1L (6), V9-2L (5), V9-2LP (4), and V13-1L (3) coded transmitters. The transmitters were programmed at pulse rates between 30 to 90 sec to accommodate a battery life of 85 (V7 tag) to 450 days (V13). Tagged *O. clarkii clarkii* were held in recovery tanks at the tagging site for 1-2 days and then released into the stream below the weir (see Moore *et al.*, 2010*b* for more details).

2.2.2 Acoustic Monitoring

Fixed, continuous data loggers (VR-2 and VR2-W, Vemco Ltd.) were deployed in BBC estuary, Hood Canal, and in lines at Admiralty Inlet and the Strait of Juan de Fuca (Figure 1). Data from *O. clarkii clarkii* passing within range of the receivers were recorded in the receiver and later downloaded. Receivers in Hood Canal were deployed in major river deltas and in nearshore areas in March - April each year and retrieved in August - September (Figure 1). Each year two receivers were deployed in the inner BBC estuary and another on the delta near the drop-off into deeper waters of Hood Canal (Figure 1 inset). In 2008, additional receivers were deployed in the BBC delta area and all receivers near BBC functioned until spring 2009. The

BBC estuary dewaters at low tides so the ability to detect *O. clarkii clarkii* there was limited to periods when tidal stage was greater than 1 to 1.5 m. Four to seven receivers were suspended in a line from the Hood Canal Bridge and a second line was deployed at the mid-point of Hood Canal in 2007. There were 26 nearshore receivers in 2006, 36 in 2007, and in 2008 there were 57, with the most complete coverage of the entire canal at 5-10 km intervals on both shores. Outside Hood Canal there were over 200 receivers in nearshore marine waters of Puget Sound in all the major river deltas, and in lines at Admiralty Inlet (the outlet to Puget Sound), west in the Strait of Juan de Fuca, and north in the Strait of Georgia, British Columbia (Melnychuk *et al.*, 2007; Moore *et al.*, 2010*a*).

To complement the fixed station receivers, boat surveys to determine *O. clarkii clarkii* position in and around BBC were conducted on transects along the shoreline during daylight hours on 6 days in 2006, 16 days in 2007, and 5 days in 2008. Transects began in BBC estuary and followed the outer edge of the terrace within range of transmitters, followed by more precise positioning with GPS when *O. clarkii clarkii* were detected. Range-testing indicated that, depending on environmental conditions, *O. clarkii clarkii* with V-13 tags could be detected from the terrace to 200-300 m inshore and 400-600 m or more offshore from the terrace, V9 tags could be detected from 50-300 m inshore and 300-500 m offshore, and V7 tags at 50-200 m inshore and 300-400 m offshore.

2.2.3 Analyses of Spatial Distribution

Analysis of the movements of *O. clarkii clarkii* was conducted at a series of spatial scales. The first analysis concerned whether individuals crossed Hood Canal or not. Subsequent analysis concerned the distance *O. clarkii clarkii* travelled along each shoreline, followed by classification analysis to determine whether or not the *O. clarkii clarkii* clustered into groups differing in patterns or were all behaving similarly (see Supporting Information for individual *O. clarkii clarkii* metrics and detection data).

Three way contingency tables were used to test for effects of year and life stage, treating whether or not *O. clarkii clarkii* crossed the Hood Canal as a categorical response variable (Feinberg, 1978). The model set was hierarchical, including main effects (*i.e.,* canal crossing independent of year and life stage), main effects with two-way associations (*i.e.* canal crossing dependent on year or life stage only), and the fully saturated model with main effects and three-way association (*i.e.*, canal crossing dependent on year and life stage). Maximum likelihood estimates were obtained for contingency tables using log-linear models that assumed that the counts had a Poisson distribution, and model selection used likelihood ratio tests (Feinberg, 1978). A logit-link generalized linear mixed model (GLM) assuming a binomial distribution was used to test for a relationship between the number of different days on which the *O. clarkii clarkii* was detected at any receiver ("detection days") and whether or not an *O. clarkii clarkii* was detected crossing Hood Canal.

GLMs were used assuming a quasi-Poisson distribution with a log-link for exploratory analysis, testing for relationships between the total number of canal crossings made by an individual and their life stage, year of tagging, and total detection days. A forward stepwise regression approach was used in which univariate models were considered and significant variables were then included in multiple variable models and models including interaction terms. This exploratory modelling approach identified and ranked a series of plausible models explaining cross-canal movements.

Having first considered whether or not *O. clarkii clarkii* crossed Hood Canal, a series of models was then created to explain the spatial distribution of *O. clarkii clarkii* detections. The independent variables included year, whether the receiver was located on the east or west shore of Hood Canal, if it was north or south of BBC, and distance from BBC. A GLM was used assuming a binomial distribution to correlate the proportion of *O. clarkii clarkii* observed at each receiver, weighted by the number of *O. clarkii clarkii* available to be detected, with the set of independent variables. An all subsets regression was used including interactions to create candidate models, including additive models, interaction models with slope adjustments, intercept adjustments, slope and intercept adjustments, and all combinations thereof. Because these models were not nested, Akaike's Information Criterion corrected for small sample sizes (AICc) and was used to compare and rank the various models, and to select the model with the best support from the data (Hilborn and Mangel, 1997). AICc was also preferable to significance testing because proportions of *O. clarkii clarkii* detected were calculated based on the same set of individuals for each receiver, violating the assumption of independent observations, and possibly resulting in overestimating significance values. The lowest AICc value denoted the best model and models with ΔAICc < 2 were considered very plausible as well (Table 1) (Burnham and Anderson, 2002). Statistical analyses were performed in R (R Development Core Team, 2011).

To further examine movement patterns, the data set was reduced to 36 *O. clarkii clarkii* that were detected on eight or more days over a time period of 15 days or more. For these *O. clarkii clarkii*, eight variables were defined, three pertaining to temporal patterns: 1) *detection days* (number of different dates on which the *O. clarkii clarkii* was detected on any receiver), 2) *residence time* (number of days from the first to the last detection), and 3) *estuary residence* (proportion of the detection days in the BBC estuary). In addition, five spatial variables were defined for each *O. clarkii clarkii*: 4) *total distance* [in km, integrating all detected movements from release to final detection, though this measure underestimates true total distance (Rowcliffe *et al.*, 2012)], 5) *final location* (in km, from BBC to the final location where a *O. clarkii clarkii* was detected), 6) *farthest location* (in km, from BBC to the most distant location where the *O. clarkii clarkii* was detected), 7) *range* (in km, distance from the northernmost to southernmost locations), and 8) *canal crossings* (number of times the *O. clarkii clarkii* crossed Hood Canal). A correlation matrix was used to examine relationships between the five spatial and three temporal movement metrics to identify variables with significant relationships for use in a cluster analysis. Two different forms of cluster analyses were conducted: a hierarchical analysis and a K-means cluster analysis, to identify groups of *O. clarkii clarkii* with similar patterns of movement. Variables were log transformed to normalize the distributions and standardize variables of different scales. Statistical analyses were performed in R (R Development Core Team, 2011). Comparison between the results of the two analyses was used to indicate the robustness of the conclusions.

To further describe the tendency for an *O. clarkii clarkii* to remain at a site, using only data for *O. clarkii clarkii* tagged in 2008 (when the receiver network was most complete), calculations were made of the proportion of all detection days at the site most frequently used and all other sites increasingly distant from that site. Travel distance, time, and rates (km d^{-1}) for each segment (*i.e.*, sequential detections at different receivers) were calculated as the distance and time from last detection at one site to the first detection at the next site using a tracking program (Moore *et al.*, 2010*a*). Travel rates were also converted to body lengths per second (BL s^{-1}) for each *O. clarkii clarkii*. Travel rates of smolts and kelts were compared using an independent *t*-test for equality of means. Residence time at a given site was the difference between the first and last detections at that site (*i.e.*, how long the *O. clarkii clarkii* was within the detection range of the receiver). Mean travel rate was the total travel distance divided by the total time. Using data from 2008, the frequency of longer distance movements was evaluated by considering *O. clarkii clarkii* that made > 10 movements between sites > 2 km apart. The seasonal rate of movement was assessed using data from 2008 by calculating the mean rates of movement between detections for each month during the study period, by summing the cumulative distance moved each month, and by dividing by the time between first and last detection of that month. Seasonal (spring, early-summer, late-summer) movement rate data was analysed using a one-way ANOVA.

2.2.4 Analyses of Individual Fish Behavior

The timing of movement by individual *O. clarkii clarkii* was determined using data from 2008 (when receiver coverage was most extensive) following the method described by Chamberlin *et al.* (2011). In brief, the initial detection at a receiver after a period without detections was tallied as a movement (because the *O. clarkii clarkii* must have moved to enter the range of the receiver) and the last detection at the receiver was also tallied as a movement (because it must have moved to no longer be within detection range of the fixed receiver). Periods < 1 h without detection were not counted as movements because a *O. clarkii clarkii* could be at the periphery of the receiver and slight changes in conditions might cause it to be undetected for a few minutes without substantial movement. These discrete movement events were then used for analysis of movement timing on diel and tidal periods.

The day and night periods were defined by sunrise and sunset using U.S. Naval Observatory data for Bangor, Washington. To evaluate movements relative to tidal cycles the hourly predicted currents for a location 3-km west of BBC (Hazel Point) (Nobeltec Tides and Currents Pro, v. 3.3) were used. Tides were categorized by current direction and speed for ebb (outgoing, predicted current velocity > 0.25 m s^{-1}), flood (incoming, velocity > 0.25 m s^{-1}), and slack (velocity < 0.25 m s^{-1}). A GLM model was used with movement as a function of diel period (day or night), tidal state (ebb, slack or flood), and life stage (adult or smolt). In addition, detections within the first 48 h after release were separated from the subsequent ones because the downstream movement of salmonids tends to be at night and because handling might affect the behaviour of the *O. clarkii clarkii*. This model and its assumptions are similar to those used by Beaudreau (2009); the response was binary, so logistic regression was used. Rayleigh's Test was used to test the hypothesis that hourly *O. clarkii clarkii* movements were uniformly distributed over the 24-h period, and the Watson-Williams F-test was used to compare hourly movement patterns by month to determine if their means differed significantly (Zar, 1999).

2.3 Results

2.3.1 General Distribution and Detection Patterns

Fifty-nine tagged *O. clarkii clarkii* provided data from > 300,000 detections in marine waters for up to about 6 months in spring and summer of 2006, 2007 and 2008. About half of the *O. clarkii clarkii* (51%) were detected > 50 days after release and 65% were detected > 30 days after release but 25% were not detected > 5 days after release. Three smolts, never detected during the study, were excluded from the analysis. The data set was reduced to 6956 unique combinations of *O. clarkii clarkii*, receivers, and periods of detection. Upon entry into marine waters 60% of the 59 detected *O. clarkii clarkii* moved north of BBC (60%, 63%, and 50% by year, 2006-2008, respectively) and 40% moved south (37% and 50%, 2007-2008). Over the course of the study 43% moved both north and south (48% and 35%, 2007-2008).

A total of 36% of the *O. clarkii clarkii* (smolts 37%, $n = 17$; adults 33%, $n = 5$) crossed the canal from the east side to the west. *O. clarkii clarkii* that were detected on more days were more likely to be detected crossing Hood Canal (logit-link binomial GLM, $z_{58} = 3.7$, $P < 0.001$), and crossed more often (log-link quasi-Poisson GLM, $F_{1,58} = 14.74$, $P < 0.001$), but tagging year (log-link quasi-Poisson GLM, $F_{2,56} = 0.73$, $P = 0.49$) and life stage (log-link quasi-Poisson GLM, $F_{2,55} = 0.1.48$, $P = 0.23$) were not correlated with the number of crossings. *O. clarkii clarkii* that crossed the canal made an average of 7.1 (10.4 S.D.) crossings, ranging from 13 *O. clarkii clarkii* that crossed from 1-5 times, four that crossed 6-9 times, three that crossed 10-20 times, and two that crossed 22 and 47 times. Thus many *O. clarkii clarkii* crossed open water and some did so repeatedly but there were no identified factors associated with whether individuals did so or not, other than the duration over which the *O. clarkii clarkii* were tracked.

The average canal width at several identified crossing areas was 2.4 km (S.D. = 0.4). There were limited instances when crossings were directly monitored, however two *O. clarkii clarkii* were detected crossing along the Hood Canal Bridge and two at the Hamma Hamma River receiver line. In one case, an *O. clarkii clarkii* was detected on six consecutive receivers along the bridge, crossing 1.65 km from east to west in 43 minutes. In total, 11 *O. clarkii clarkii* were detected at offshore receivers, most (seven *O. clarkii clarkii*) on one to two days but one *O. clarkii clarkii* was detected offshore on 18 different days. This individual crossed Hood Canal more often (47 times) than any other tagged *O. clarkii clarkii*. During 27 days of mobile tracking along shoreline areas, no *O. clarkii clarkii* was observed > 500 m offshore and most detections were < 200 m from shore.

The proportion of *O. clarkii clarkii* detected decreased with distance from BBC to the north and south along both shores of Hood Canal, and fewer *O. clarkii clarkii* were detected on the west shore than the east shore (Table 1, Figure 2). No *O. clarkii clarkii* was detected outside Puget Sound but one *O. clarkii clarkii* left Hood Canal, reached central Puget Sound near Seattle (77 km from BBC), remained there for two months, and then returned to BBC. In Hood Canal, three *O. clarkii clarkii* were detected beyond the Hood Canal Bridge, within 4-7 km of the outlet to the canal. Eight *O. clarkii clarkii* were only detected in the BBC estuary, six of which were detected < 5 days and could have either migrated beyond the estuary and not been detected, returned to fresh water where no receivers were deployed, or died.

2.3.2 Migratory Behavior

A variety of migratory behaviours were observed based on daily and cumulative movements. Analysis revealed significant correlations between distance metrics for range, final location, farthest location, total distance, and canal crossings (0.49-0.80, $F_{1,34}$ = 11.15–59.12, $P < 0.05$). The highest correlation was between farthest location and range. Estuary residence time was negatively correlated with total distance, range, detection days, and residence time (0.40-0.52, $F_{1, 34}$ = 6.36-12.84, $P < 0.05$), and detection days had a positive correlation with residence time and total distance travelled (0.59, 0.65, $F_{1, 34}$ = 18.21-24.21, $P < 0.01$). The 36 *O. clarkii clarkii* used in the cluster analyses formed two groups, with 14 *O. clarkii clarkii* (11 smolts (79%), 3 adults (21%)) in Cluster 1 and 22 *O. clarkii clarkii* (17 smolts (77%), 5 adults (23%)) in Cluster 2 (Table 2). Both clustering methods produced two clusters and *O. clarkii clarkii* were placed in the same cluster with both methods. The clusters were well explained by the range, farthest location, canal crossings, and estuary residence metrics. The *O. clarkii clarkii* in Cluster 1, hereafter termed residents, covered the least total distance, used a small range, did not cross the canal, and spent more time in the estuary. *O. clarkii clarkii* in Cluster 2, termed migrants, had greater total distance (up to 428 km) and range (up to 49 km), crossed the canal more often (up to

47 times), and spent less time in the estuary (Figure 3). There was no difference in the proportion of smolts and adults by cluster (Fisher's Test, *P* = 1.0).

The average daily travel distance (total distance/detection days) was 1.1 km d^{-1} for residents and 3.5 km d^{-1} for migrants. Migrants showed both long-distance movements and periods of residency at one or more sites whereas residents showed short-distance movements and longer periods of residency throughout the monitoring period (Figure 4). Using data from 2008, most residents (75%) established a long-term site within 4 days after release whereas most migrants (71%) reached a residency site in less than 7 days. Half of the residents and migrants reached their farthest location within 9 days and the others did so at 26-50 days. Notwithstanding the fact that two clusters were defined by objective criteria, separating *O. clarkii clarkii* that moved widely from those with more limited movements, there was also variation among individuals within the clusters in patterns of movement. For example, one resident and one migrant each travelled > 400 km but had very different travel patterns and routes (Figure 4, dashed lines). The resident remained within 4 km of the BBC estuary, was detected on 121 days, had a north-south range of only 7.7 km, a mean daily travel distance of 3.6 km, and did not cross the canal but accumulated a total distance of 432 km by making many short movements within a small area. The other *O. clarkii clarkii* made longer movements; it was detected on 60 days, had a range of 39.2 km, a mean daily travel distance of 7.1 km, and crossed the canal 47 times for a total of 428 km. The first of these two *O. clarkii clarkii* moved about 3 km north or south of BBC every one or two days whereas the more wide-ranging of the two *O. clarkii clarkii* had an exploratory path, repeatedly crossing the canal.

The tendency for a *O. clarkii clarkii* to remain at a site was evaluated using detection data from 2008 (14 *O. clarkii clarkii*). Residents (three smolts and one adult) consistently showed high fidelity, remaining within 1 km of a single site an average of 94% of the time. Migrants (7 smolts and 3 adults) averaged 73% of detections within 1 km of a site but ranged from 40-97%. All migrants undertook multiple daily movements of 2 km or more, the proportion of total movements ranging from 3-70%, whereas residents seldom moved > 2 km.

Mean rates of total movement among *O. clarkii clarkii* were generally < 3 km d^{-1}, but mean individual rates of movement (2008 data) for travel between sites > 2 km apart ranged from 12-35 km d^{-1}. Adults moved faster than smolts in absolute rate (average: 32.3 vs. 22.8 km d^{-1}, $t = -4.44$, d.f. = 527, $P < 0.01$) but not after adjustment for body size (BL s^{-1}: adults = 1.2 vs. 1.4 for smolts, $t = 1.24$, d.f. = 527, $P > 0.2$). Mean movement rate for all *O. clarkii clarkii* did not differ between day (1.3 BL s^{-1}) and night (1.1 BL s^{-1}, $t = 1.45$, d.f. = 527, $P > 0.15$). The mean rate of movement by season was 2.9 km d^{-1} (S.D. = 3.0) in spring, 1.4 km d^{-1} (S.D. = 1.9) in mid-summer, and 2.6 km d^{-1} (S.D. = 3.9) in late-summer, with no significant difference between seasons ($F_{2, 55} = 1.48$, $P > 0.2$).

2.3.4 Diel and Tidal Patterns of Movement

Data from 2008 were used to determine whether movement varied with diel period, tide, and life stage. The influences of diel period and tides were highly significant (logit - link binomial GLM, $F_{2, 4430} = 9.33$, $P < 0.0001$) but there was no effect of life stage ($F_{2, 4430} = 1.05$, $P > 0.3$) so for subsequent analyses the smolts and adults were combined. Most movements occurred during daylight hours (76%), exceeding the proportion of daylight hours during this time of the year (64%). The proportion of movements increased with increasing day length from April to July (April movements 8% < expected day length (ex), May 6% > ex, Jun 11% > ex, Jul 13% > ex) and then decreased in August and September (Aug 11% > ex, Sep 1% > ex) when the days became shorter (Figure 5). The only exception to the pattern of diurnal activity was during the first 48 h in marine waters, when the *O. clarkii clarkii* moved more often at night. The significant effect of tidal current on probability of movement reflected the fact that flooding, ebbing and slack currents are not equally distributed during the 24 h period. *O. clarkii clarkii* movements were in proportion to the fractions of the day and night in the three categories of tidal currents (Figure 6). Of the 1313 movements showing a change in location (a subset of all detected movements, from one receiver to another as distinguished from return to the same receiver), 609 (46%) were moving south (inward) and 704 (54%) were moving north (outward) of the study area. Thus the overall tendency was for diurnal movement without regard to tidal currents, and a slight northerly tendency.

The hourly distribution of movements deviated significantly from uniformity for all years (Rayleigh's $z_{0.05}$, $P < 0.001$) and all months (Rayleigh's $z_{0.05}$, $P < 0.01$) except September 2008 (Rayleigh's $z_{0.05}$, $P > 0.45$). There were significant differences between hourly movements in spring (April and May) compared to summer (June to August, F-test, $P < 0.01$) but not among most months within the summer period (F-test, $P > 0.10$) nor between April and May compared to September (F-test, $P > 0.20$). The period of peak movement was between late morning and early afternoon except in April when the peak was near midnight, but this was influenced by the nocturnal movements immediately after release. Many *O. clarkii clarkii* showed a sharp increase in activity just before or at dawn and a cessation near dusk (Figure 7). For one individual detected at a single site on 31 days, the increased movements at dawn and decrease at dusk corresponded with arrivals and departures at the site, respectively. This type of behaviour has been described as "commuting" (Dingle, 1996) with regular movements to and from one or more sites (Figure 7).

2.4 Discussion

Large variation in *O. clarkii clarkii* migratory behaviour was observed; some individuals moved directly north or south of the estuary at distances up to 26 km, whereas others made multiple movements with changes in direction, and some remained near the stream mouth. In most cases *O. clarkii clarkii* ceased long distance movements within 4-7 days of release and established moderate to long-term residency at nearshore sites outside and to a lesser extent within the estuary. The movements within marine waters were similar between adults and smolts. Indeed, only absolute travel rate (km d^{-1}) differed between life stages and in all other respects, including relative travel rate (BL s^{-1}), they were similar. This similarity is noteworthy because the smolts would be experiencing marine waters for the first time and adults would have had the opportunity to explore on previous trips, and trade-offs between foraging needs and predation risk would likely vary with body size.

Notwithstanding the variation, cluster analysis identified two groups displaying different types of behaviour: residents remained in the estuary or near their natal stream and migrants moved greater distances and crossed open water. The "migrants" showed what Dingle (1996) described as dispersal or ranging behaviour. Dingle (1996) also described "commuters" as animals making regular, local movements. Such commuting behaviour was shown by some migrants and residents as described here. Some residents commuted between sites proximate to each other and the natal stream whereas some migrants moved long distances but then commuted between nearby sites at some distance from the natal stream. The main characteristic of ranging is long-distance movement that ceases when patches with suitable resources are encountered (Dingle, 1996). Likewise, *O. clarkii clarkii* classified as migrants and as residents showed site fidelity as defined here. That is, residents remained in a limited area near the natal stream and some migrants moved long distances but then limited their subsequent movements for some period of time. These modes of behaviour did not correspond to the age/size modes of the *O. clarkii clarkii*, so they apparently do not depend on prior migration experience. Presumably, there is a balance between the likelihood of locating superior foraging areas and predation risk associated with the migrant behaviour (Jonsson and Jonsson, 1993). The Big Beef Creek estuary largely de-waters at the extremes of the tidal cycle, which can reach 4 m, forcing the *O. clarkii clarkii* to move from the estuary and into the nearshore marine area or be restricted to the narrow tidal channel, where they might be vulnerable to predators. In contrast, along the shoreline of Hood Canal the *O. clarkii clarkii* only have to move short distances offshore and onshore as the tides rise and fall.

The scale of movement observed depends, in part, on the geography of the study site and the monitoring methods (Rowcliffe *et al.*, 2012). Krentz (2007) reported site fidelity on the order of 100s of meters, and identified more specific habitat features important to the *O. clarkii clarkii* than were possible in a body of water the size of Hood Canal, with receivers spaced ~ 1 – 10 km apart. In Hood Canal, *O. clarkii clarkii* moved north and south along the shorelines after leaving BBC but many crossed open water to reach the far shore where they resumed shoreline-oriented movement. *O. clarkii clarkii* generally remain in close proximity to their natal stream, with distances ranging from 50 km in Puget Sound to 70 km in Alaska (Johnston, 1982; Trotter, 1989). In contrast, *O. mykiss* move directly to the ocean and migrate thousands of km (Burgner *et al.*, 1992). All but one *O. clarkii clarkii* remained within the Hood Canal basin, that individual moved 77 km. In contrast to the limited distance *O. clarkii clarkii* travelled, most naturally produced *O. clarkii clarkii*-*O. mykiss* hybrids from BBC left Hood Canal and many left the Salish Sea (157 km distant). Hybrids also had more complex movements, resulting in long, directed movements within Hood Canal whereas the *O. mykiss* smolts migrated to the ocean (Moore *et al.*, 2010*a*). The array of receivers within and outside Hood Canal allowed the broad-scale patterns of *O. clarkii clarkii* movements to be defined, including distribution throughout the fjord, tendency to cross open water, and the range and distances *O. clarkii clarkii* travelled but finer scale resolution of movement and site fidelity would require more extensive mobile tracking (*e.g.*, Hayes *et al.* 2011) or a denser array of receivers or tracking system that triangulated the positions of *O. clarkii clarkii* precisely (*e.g.*, Espinoza *et al.*, 2011).

The reported reluctance of anadromous *O. clarkii clarkii* to cross open waters (Johnston, 1982; Trotter, 1989) was not evident in the present study, as over a third of the tagged *O. clarkii clarkii* crossed 2-4 km of open water. Wenburg and Bentzen (2001) also found evidence of genetic exchange between east and west shore populations of *O. clarkii clarkii* in Hood Canal. When they cross open water, *O. clarkii clarkii* seem to do so rapidly, based on the data from this study and the infrequency of captures in open water (Duffy and Beauchamp, 2008). In contrast to these protected waters, in the open ocean off the coast of Oregon and Washington, *O. clarkii clarkii* were caught offshore up to 45 km, no closer to shore than 3-10 km, and never inside the 30 m depth contour (Loch and Miller, 1988; Pearcy *et al.*, 1990). The offshore distribution of these *O. clarkii clarkii* has either been attributed to their remaining in the Columbia River plume (Loch and Miller, 1988) or avoiding high wave energy along shoreline areas (Johnston, 1982; Pearcy *et al.*, 1990). Populations from coastal rivers may have fundamentally different marine movement patterns than those from inland waters such as Puget Sound, though it is also possible that *O. clarkii clarkii* sampled offshore were *O. clarkii clarkii*-*O. mykiss* hybrids, which can be indistinguishable without genetic analyses (Moore *et al.*, 2010*a*).

Similar to *O. clarkii clarkii*, *S. trutta* exhibit diverse life-history patterns in freshwater and coastal habitats (Knutsen *et al*., 2001; Middlemas *et al*., 2009). Tracking studies show that some *S. trutta* individuals move large distances while others remain close to natal rivers, similar to results in this study (Finstad *et al*., 2005; Thorstad *et al*., 2007; Middlemas *et al*., 2009). Although most *S. trutta* are found within 100 km of the mouth of the home river, longer migrations between major geographic areas may occur (Jonsson, 1985; Klemetsen *et al*., 2003). In contrast, all *O. clarkii clarkii* in this study remained within 80 km of their natal stream. Individual *S. trutta* in marine waters show different patterns of habitat use, consistent with their plasticity in habitat use throughout their range (Cucherousset *et al*., 2005), suggesting flexibility in their behaviour at sea (Middlemas *et al*., 2009). *O. clarkii clarkii* in Hood Canal display a range of behaviours, with individuals undertaking long-distance movements but then returning to smaller areas and others remain near their natal stream with near daily excursions to and from sites. The movements of anadromous *O. clarkii clarkii* are perhaps most similar to those of bull trout, *Salvelinus confluentus* (Suckley 1859), which move from basin to basin through marine waters along the Pacific coast of Washington (Brenkman and Corbett, 2005) yet also show extended use of limited (~ 2-3 km) shorelines areas within Puget Sound (Hayes *et al*., 2011).

The mean rate of all movements of *O. clarkii clarkii* in 2008 (0.19 BL s^{-1}, 2008 data) and seasonal rates (0.06-0.22 BL s^{-1}) were lower than rates in other studies of *O. clarkii clarkii*, while movement rates of *O. clarkii clarkii* traveling > 2 km (1.3 BL s^{-1}) were similar to other studies (Nowak and Quinn, 2002; Baldwin *et al*., 2002). Similar to rates of migrating *O. clarkii clarkii*, the mean speeds of *S. salar* and *S. trutta* smolts migrating through a Norwegian fjord were 0.49 to 1.82 BL s^{-1} for *S. salar* and 0.11–2.60 BL s^{-1} for *S. trutta* (Finstad *et al*., 2005). Differences in travel rates may reflect the behaviour of the fishes but are also strongly affected by the temporal and spatial scale of sampling. In Hood Canal the movement rates by *O. clarkii clarkii* did not vary between day and night, unlike Baldwin *et al.* (2002) who found the highest speeds during the day, intermediate at dusk/dawn, and lowest at night. The fixed receivers -could not detect finer scale movements of *O. clarkii clarkii* which could include faster movements. In marine waters of Hood Canal the mean travel rate of resident Chinook salmon *O. tshawytscha* (Walbaum 1792) (0.86 BL s^{-1}; Chamberlin *et al.*, 2011) was lower than the rate of migratory *O. clarkii clarkii* but much higher than overall movements of *O. clarkii clarkii* tracked in this study, including the resident component of the population.

Salmonids vary in visual sensitivity and this may, in part affect activity patterns (Mazur and Beauchamp, 2003; Rader *et al.*, 2007). *O. clarkii clarkii* in fresh water are generally day-active but may move at twilight and night depending on conditions, and in this study they showed a peak in activity at mid-day with a noticeable increase in activity near dawn and decline near dusk. In streams, *S. trutta* are active at nocturnal and crepuscular periods, *O. clarkii clarkii* may be crepuscular or day-active and *O. mykiss* are day-active (Bunnell *et al*., 1998, Rader *et al*., 2007). Piscivorous fishes such as *S. trutta* and *O. clarkii clarkii* are often active during crepuscular periods, feeding during the change-over from light and dark (Beauchamp *et al.*, 1992; Young *et al*., 1997). The *O. clarkii clarkii* in the present study showed more nocturnal movements during the first two days in marine waters than subsequently, similar to the nocturnal downstream migration of *O. clarkii clarkii* and other salmonids (Melnychuk *et al.*, 2007; Zydlewski *et al*., 2009). After residing in the nearshore the *O. clarkii clarkii* became increasingly day-active, and as the season advanced movements in the day continued to exceed the daytime proportion of the 24-h period.

Few studies have considered the movements of *O. clarkii clarkii* relative to tidal cycles but tides are widely perceived by anglers to influence foraging behaviour (*e.g.*, Raymond, 1996; Johnson, 2004). The findings suggest that *O. clarkii clarkii* tended to move with the currents in proportion to the frequency of those currents during the 24-h period, thus providing no evidence that tides affected the *O. clarkii clarkii*. *O. clarkii clarkii* in the Salmon River estuary were found most often at high tide at the mouth of marsh channels and a small stream, then returning to deeper channels at low tide (Krentz, 2007). *O. clarkii clarkii* leaving the Columbia River estuary moved quickly on outgoing tides but tended to remain in small areas during flood and slack tides (Zydlewski *et al.*, 2008). Fine-scale movements in these smaller areas (10s-100s of meters) probably reflect the local features of tidal currents that facilitate foraging, just as locations where *O. clarkii clarkii* forage in streams can be quite specific at small scales but the scale of detection was too coarse to detect these movements.

In conclusion, *O. clarkii clarkii* exhibit a wide array of life history and migration patterns, with a distinction commonly made between freshwater resident and anadromous individuals. The migrations in marine waters have seldom been studied but it is becoming clear that there is great variation in movements even among *O. clarkii clarkii* of the same life history stage from a single population. Generalizations about the shoreline-orientation of the species are not entirely true, as movements across open, deep water were common. The data revealed two discrete types of behaviour, though no single variable distinguished the two groups. These different movement behaviours in estuarine and marine waters could allow *O. clarkii clarkii* to take advantage of spatially separated and temporally dynamic resources, as Northcote (1992) suggested for migratory and non-migratory forms in a single watershed. Studies of other populations may reveal additional movement patterns, and finer-scale positioning might be especially informative (*e.g.*, Hayes *et al.*, 2011). Data of this type may prove very useful in deciding how the species may benefit from shoreline protection, fishery management, and other policies pertaining to human use of the nearshore marine environment.

Table 2.1: Model selection results for variables affecting the proportion of O. clarkii clarkii detected at 63 sites throughout Hood Canal in 2007 and 2008. Additive linear models are denoted by a +, multiplicative models (interactions) with a :, and combined additive and multiplicative by * (interaction + additive effect). Models are listed from most plausible ($\Delta AICc = 0$) to least plausible. The Akaike weight *wi* indicates the relative likelihood of the best fitting model compared to other models. The best five approximating models are shown.

Model Structure (Predictor Variables)	**K**	**AICc**	**Δ AICc**	***wi***	**Log Likelihood**
log (Distance) + Shore	3	222.46	0	0.2	-108.22
log (Distance) * Shore	4	222.92	0.46	0.16	-107.44
log (Distance) * Shore : Year	6	224.22	1.77	0.08	-106.08
log (Distance) + Shore : Year	4	224.42	1.96	0.08	-108.19
log (Distance) + Shore + Year	4	224.42	1.96	0.08	-108.19

Table 2.2: Summary statistics for O. clarkii clarkii classified by hierarchical and k-means cluster analysis as resident (n = 14, 11 smolts and 3 adults) and migrant (n = 22, 17 smolts, 5 adults) individuals. An additional metric not included in the cluster analysis (travel rate) is included for comparison and indicated with an asterisk.

	Resident		**Migrant**	
	Mean	**SD**	**Mean**	**SD**
Detection Days	34.4	34.6	42.3	33.7
Estuary Residence	51%	36%	13%	14%
Residence Time	64.9	37.5	93.9	37.5
Range (km)	5.2	2.8	24.6	13.6
Total Distance (km)	55.0	111.8	115.4	103.4
Furthest Location (km)	5.4	2.8	23.4	16.2
Final Location (km)	3.2	3.2	9.0	10.2
Canal Crossings (no.)	0.0	0.0	7.2	10.3
Travel Rate (km day^{-1})*	1.1	0.9	3.5	2.5

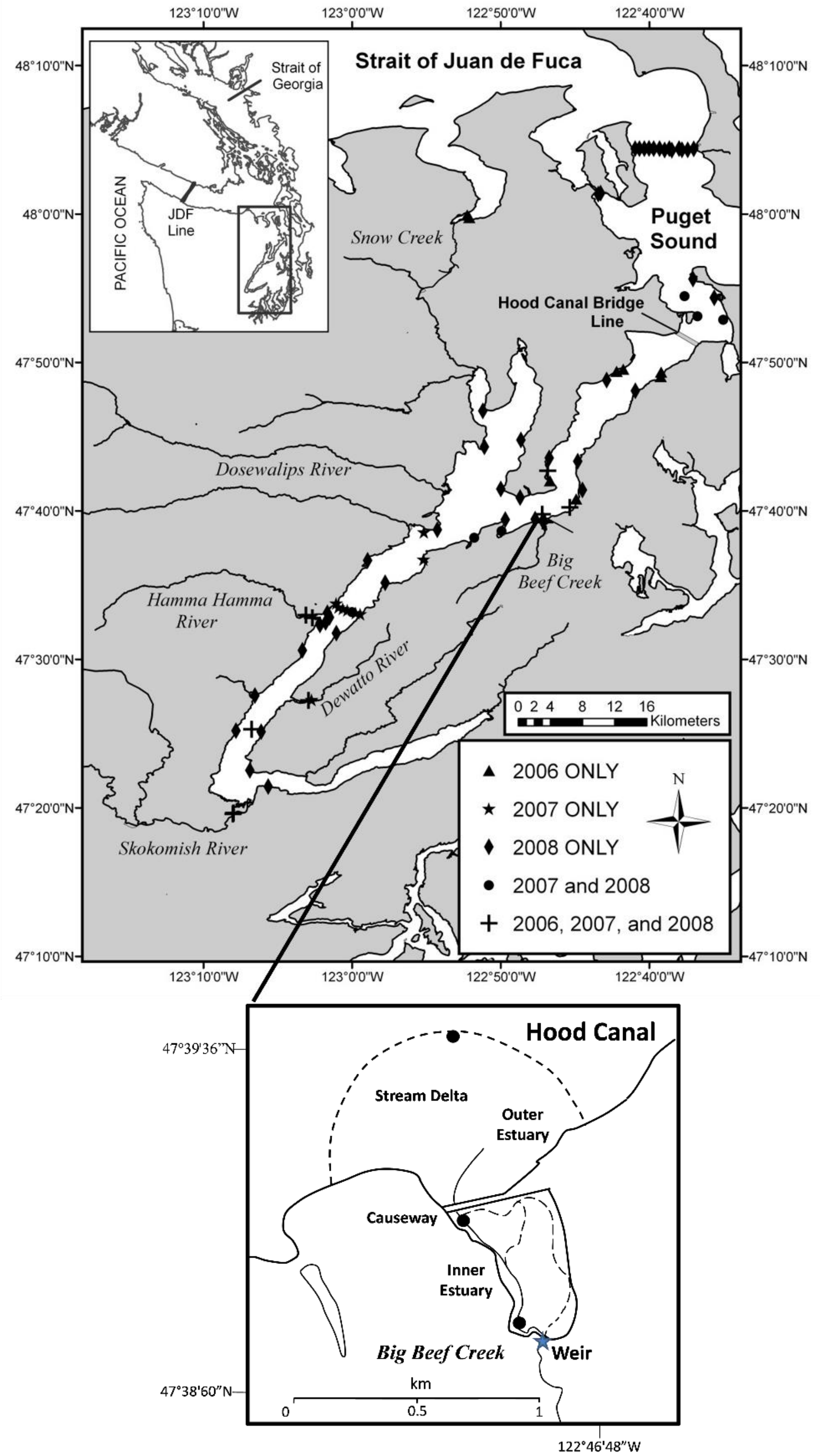


Figure 2.1: Hood Canal study area with acoustic receiver locations from 2006-2008 (top), the *O. clarkii clarkii* capture and tagging location (star) and nearby receivers (circles) in Big Beef Creek (bottom).

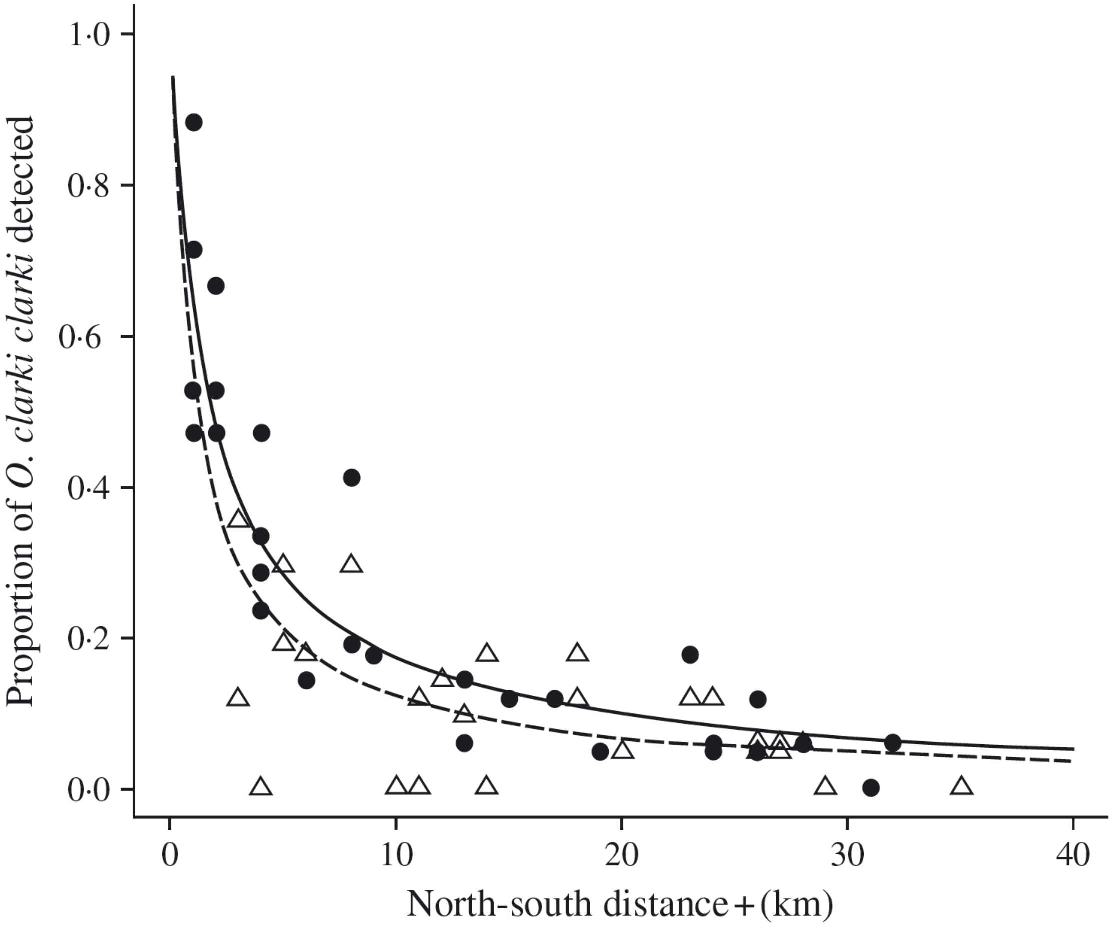


Figure 2.2: The proportion, the ratio of the number of *O. clarkii clarkii* detected to the number tagged, of *O. clarkii clarkii* detected at increasing distances from Big Beef Creek along the east (circles), and west (squares) shores of Hood Canal. Lines are fitted model results from the best candidate GLM model which included significant differences in detection probability by shoreline (east; solid line, west; dashed line) and as a function of distance, but with no significant interaction.

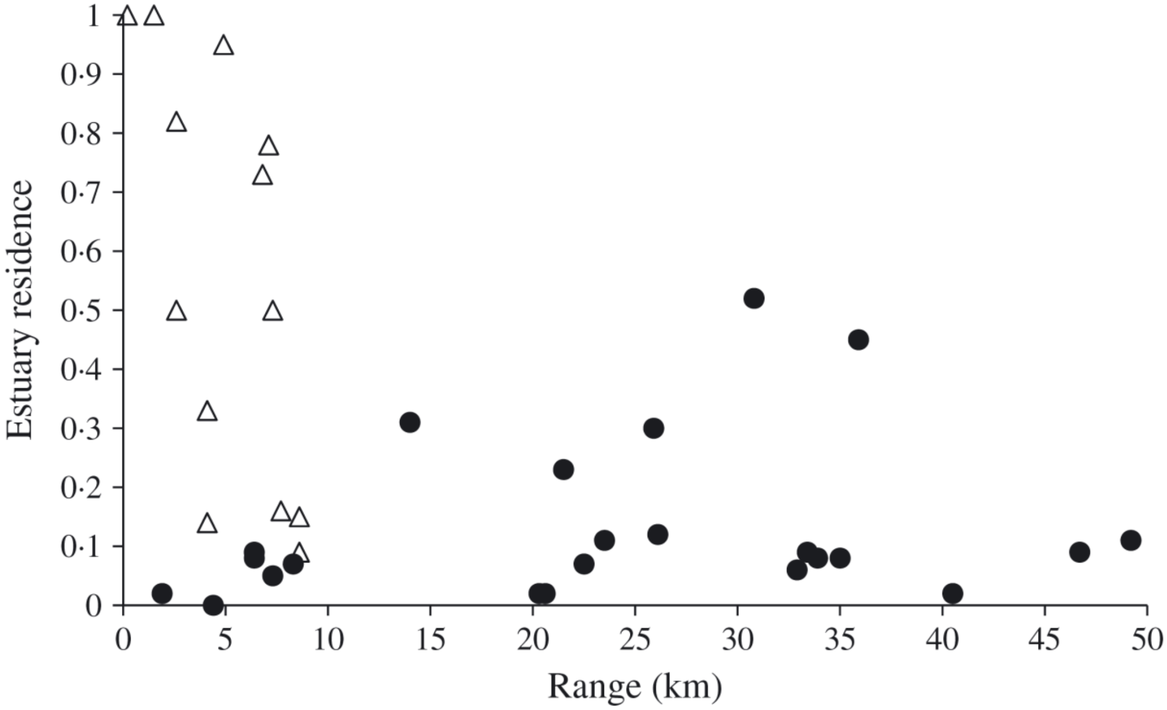


Figure 2.3: Range of *O. clarkii clarkii* (maximum distance north and south) compared to residence time in the Big Beef Creek estuary (estuary detection days/total detection days) for *O. clarkii clarkii* classified as migrants (circle) and residents (triangle): range and residence time represent two factors used in the cluster analysis to identify movement patterns.

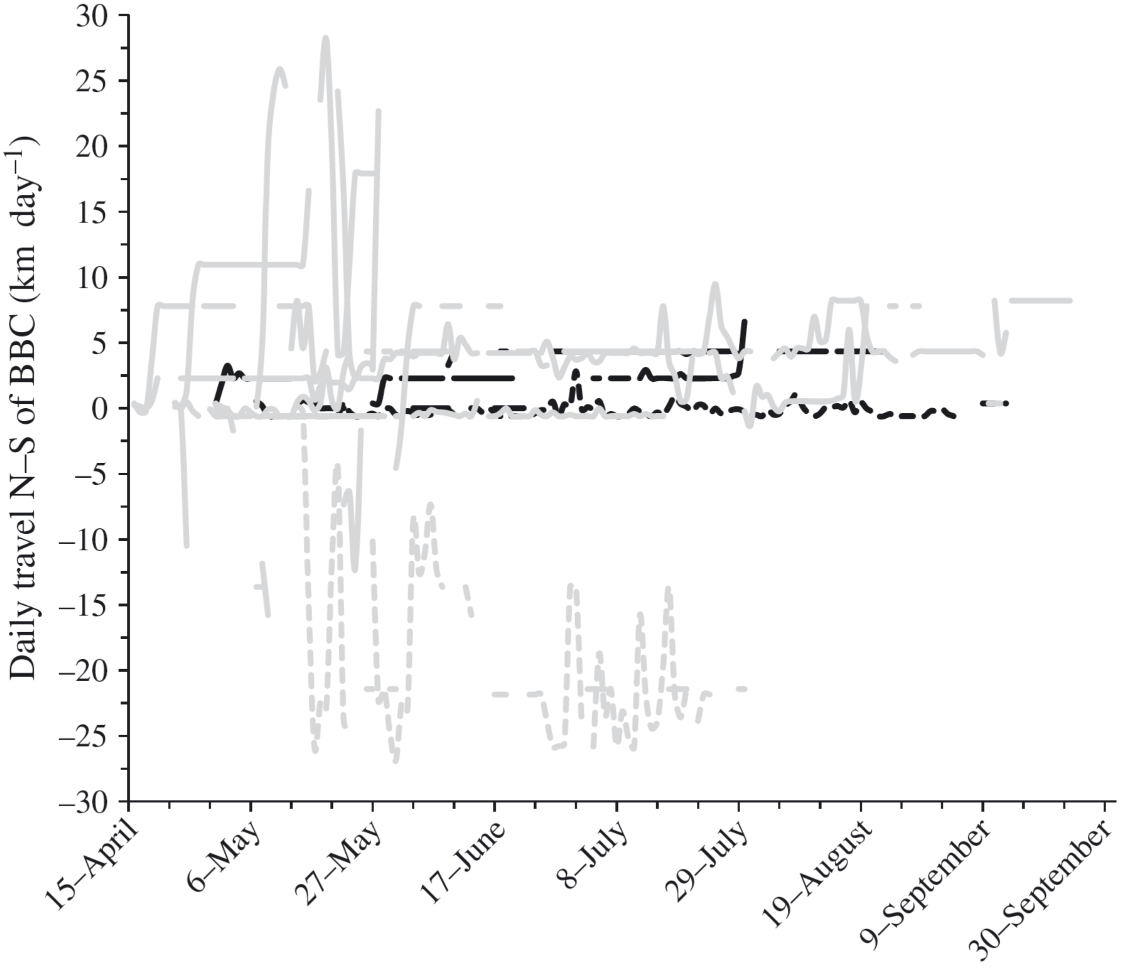


Figure 2.4: Comparison of daily travel distance (km) north and south from BBC for 14 *O. clarkii clarkii* tagged in 2008 and categorized as resident (solid black line) and migrant (solid grey line) with individual *O. clarkii clarkii* examples (dashed lines).

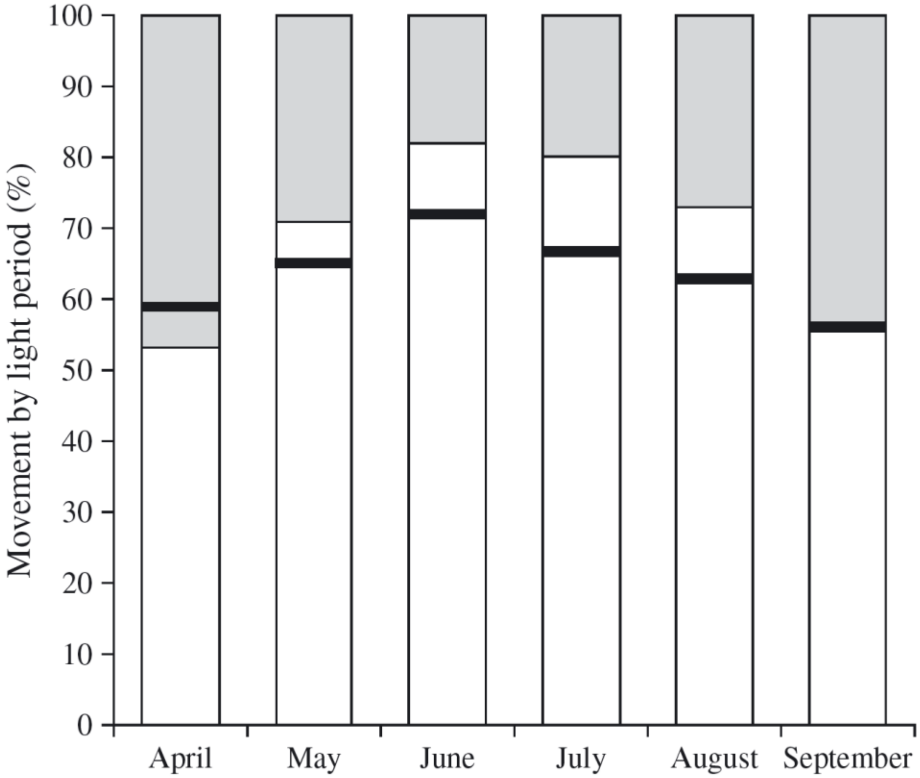


Figure 2.5: Percentages of daytime (white) and night-time (grey) movements of *O. clarkii clarkii* during spring and summer months compared to the observed periods of daylight, indicated by the black bar on each column.

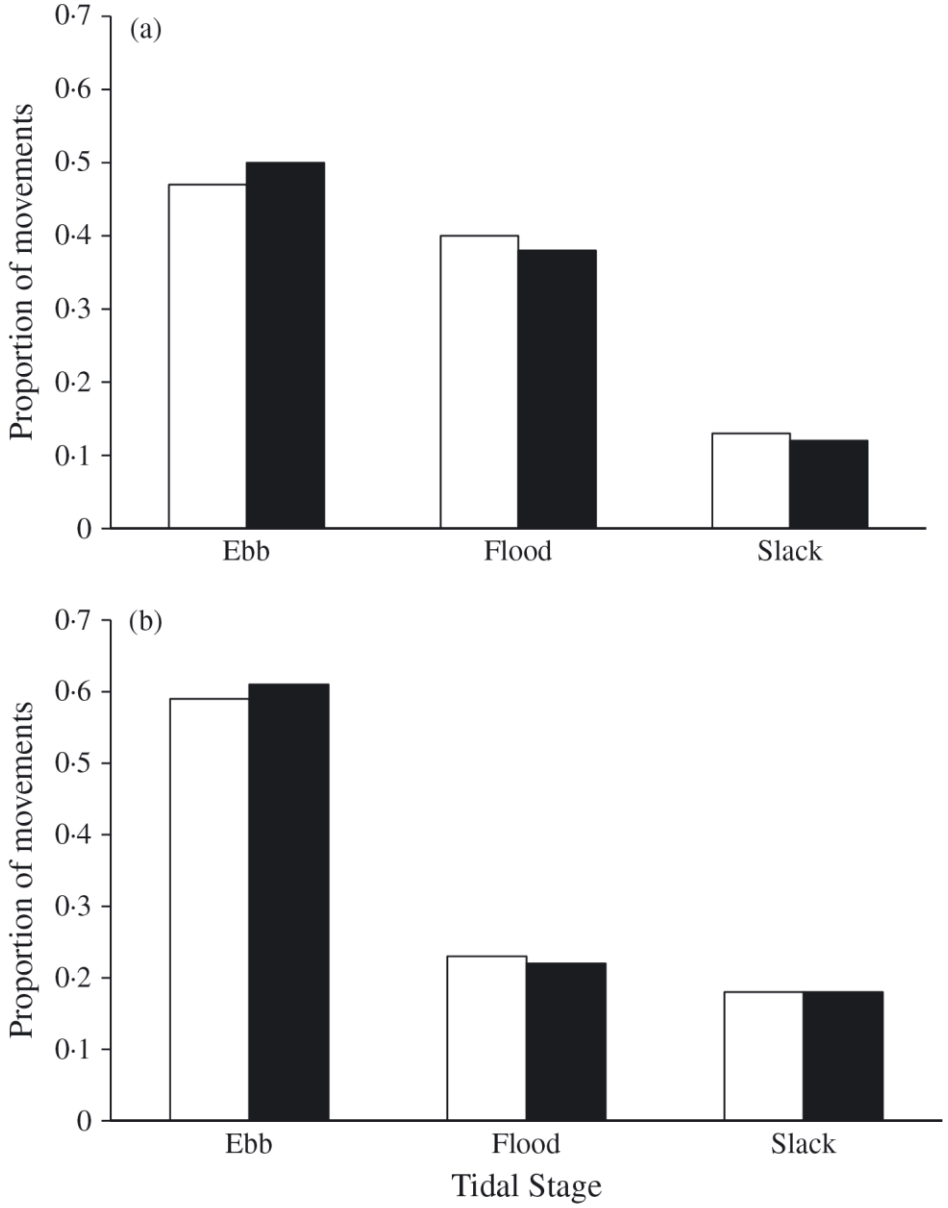


Figure 2.6: Proportion of observed (white) movements by day (top panel) and night (bottom panel) and tidal current period compared to the expected (black) proportion.

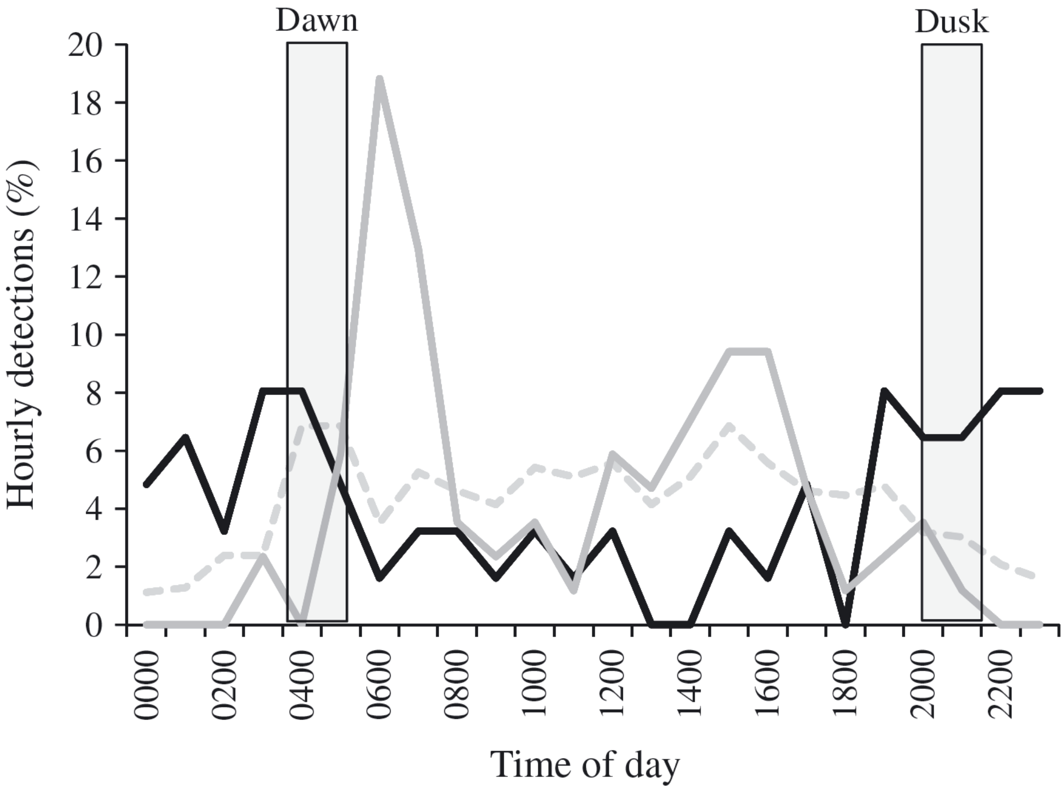


Figure 2.7: Daily activity patterns for two day active (diurnal; dashed grey line, and commuter; solid grey line) and one night active (nocturnal; black line) *O. clarkii clarkii*. Periods of dawn and dusk with nautical twilight are indicated with light grey bars.

Chapter 3. Migrations of anadromous bull trout in estuarine and marine waters of Puget Sound, Washington: Thermal constraints on foraging opportunities

3.1 Introduction

Anadromous species vary greatly in the duration and spatial extent of migration at sea, and the extent to which the population migrates. This variety indicates complex tradeoffs between the benefits and costs of marine residence (Quinn and Myers 2004; Kerr et al. 2009; Gahagan et al. 2015). Anadromy provides fish with the opportunity for more rapid growth (Morita 2001), larger size and higher fecundity (Wood and Foote 1996) through the exploitation of rich food resources and favorable growing temperatures in the sea (Baker 1978). However, anadromy exposes fish to larger predators than are found in freshwater habitats (e.g., marine mammals: Ford and Ellis 2006; Lance et al. 2012; and sharks: Nagasawa 1998). Movement between freshwater and marine habitats also poses challenges for osmoregulation (Staurnes et al. 1992; Clarke and Hirano 1995). Consequently, many species vary in the expression of anadromy (Jonsson and Jonsson 1993). This variation can play an important role in the dynamics of the populations (Kerr et al. 2010), exposure to fisheries, chemical contaminants (O’Neill and West 2009; Ross et al. 2013), and other human-related stressors.

A full understanding of the phenomenon of anadromy depends on documenting the variation among and within species. Salmonids are the best-known group of anadromous fishes but the archetypal long distance migrants such as Atlantic (*Salmo salar*) and Pacific salmon (*Oncorhynchus* spp.) do not fully represent the family’s diversity of patterns in duration and spatial extent of migration, and few studies have evaluated the potential drivers of that migration (Drenner et al. 2012). Of the Pacific salmon, the vast majority of information on migration has been reported on ocean-bound semelparous species and steelhead (*O. mykiss*), with much less information on the more limited migrations of cutthroat trout (e.g., *O. clarkii*, Sumner 1962; Armstrong 1971; Goetz et al. 2013). Migrations of char (*Salvelinus spp.*) have been studied in arctic regions but species or populations in lower latitudes are less well known (Quinn 2005). Rounsefell (1958, see also Quinn and Myers 2004) used six characteristics to assess the degree of anadromy in the life cycles of different salmonids species: distance of migration at sea, length of time spent at sea, maturity state achieved at sea, spawning habitats, mortality after spawning, and occurrence of freshwater forms. The comparison showed that anadromy in salmonids is least developed in char, more developed in the genus *Salmo*, and most developed in Pacific salmon. Dolly Varden (*S. malma*), brook trout (*S. fontinalis*), and Arctic char (*S. alpinus*) were all classified as “optionally anadromous.” Bull trout (*S. confluentus*) were not classified by Rounsefell (1958) because this species was not distinguished from Dolly Varden at the time (Cavender 1978). Dolly Varden are native to both Asian and North American drainages of the Pacific Rim, consistent with a high degree of anadromy, and the northern form migrates to offshore waters (Morita et al. 2009), and occasionally moves between continents (DeCicco 1992). In contrast, brook trout and bull trout are native only to the Atlantic and Pacific drainages of North America, respectively, and white-spotted char (*S. leucomaenis*) are found only in Asia (Dunham et al. 2008). These facultatively anadromous species spend brief periods in marine waters but may do so repeatedly during their lives (e.g., brook trout: Curry et al. 2010; white-spotted char: Morita et al. 2013). Of the North American char species, bull trout are the least studied, and almost all research has investigated their ecology in stream and lake habitats (Dunham et al. 2008).

Anadromy provides fish with the opportunity for more rapid growth (Morita 2001), larger size and higher fecundity (Wood and Foote 1996) through the exploitation of rich food resources and favorable growing temperatures in the sea (Baker 1978). However, some populations of anadromous salmonids migrate from the marine or estuary environment to freshwater months prior to spawning. This premature migration reduces feeding opportunities because freshwater habitats are less productive than marine habitats, and also exposes them to disease, predation and stress from high temperatures (Quinn et al. 2015). Therefore, anadromous bull trout may experience a conflict between the benefits of foraging in productive marine areas in the summer prior to fall spawning, and the drawbacks of experiencing warm water in estuaries and lower rivers as they ascend to spawn or overwinter in freshwater.

Bull trout display non-migratory, fluvial, adfluvial, and anadromous life histories (Fraley and Shepard 1989; Hayes et al. 2011; Barnett and Paige 2013). In coastal British Columbia and Washington, anadromous bull trout are found in lower reaches of larger rivers or in the marine environment, whereas upper reaches contain fluvial or non-migratory fish (Haas and McPhail 2001). The optimum temperature for bull trout growth is as low as 10-13 °C (Selong and McMahon 2001) to 12-17 °C with sufficient food resources (Mesa et al. 2013). Adfluvial and fluvial adults typically migrate to natal streams in the summer as temperatures increase and flows decrease (Goetz 1989; Brenkman et al. 2001; Swanberg 1997), spawn in fall at temperatures < 10 °C, and then migrate into rivers and lakes for the winter after spawning (Fraley and Shepard 1989; Bahr and Shrimpton 2004). Juveniles and sub-adults may move downstream throughout the year (Downs et al. 2006) but peak movements are often in spring and summer months (Fraley and Shepard 1989; Homel and Budy 2008).

Bull trout are listed as threatened under the U.S. Endangered Species Act (ESA) throughout the state of Washington and their retention by anglers is prohibited in Puget Sound marine waters by the Washington Department of Fish and Wildlife (WDFW). Retention in some rivers is allowed but no catch record is required (in contrast to Pacific salmon and steelhead), hence there are no catch data from marine waters or rivers on which to infer seasonal movement patterns and test hypotheses regarding timing.

The goal of this study was to describe migratory characteristics of bull trout in the lower reaches of major rivers, their estuaries, and in Puget Sound to better understand the life history of this facultatively anadromous salmonid as part of the diversity of salmonid migration patterns. The specific objectives were to describe the migration timing and spatial distributions of juvenile, sub-adult and adult bull trout with emphasis on the Skagit River and Snohomish River populations, and compare habitat use patterns between river basins and marine areas. We predicted that juvenile bull trout would migrate downstream synchronously with sub-adult and adult bull trout and other salmonid smolts to access shared marine prey resources. We predicted that bull trout would return to freshwater before rising temperatures peaked in marine waters and lower river areas (Poole et al. 2001; Hodgson and Quinn 2002; Quinn et al. 2015). Alternatively, the bull trout might return just prior to spawning, as water temperatures cool in the fall, which would maximize access to marine prey all summer. The Skagit, Snohomish and Stillaguamish rivers differ in thermal regimes and therefore allow a contrast of two alternative hypotheses regarding temperature and timing. If the timing patterns reflect the thermal regimes in fresh water habitats, then migration timing might differ between rivers (the Skagit being cooler than the others). On the other hand, if conditions in the marine environment are most important, the timing would be similar because Puget Sound presents a thermally stable environment that does not differ substantially between areas proximate to the different rivers.

3.2 Methods

3.2.1 Study Area

Puget Sound is a large coastal fjord estuarine system located in western Washington, USA and bordered by British Columbia to the north (Figure 3.1), connected to the coastal ocean via the Strait of Juan de Fuca and the Strait of Georgia. The region as a whole is known as the Salish Sea, with well-described physical attributes (Strickland 1983; Moore et al. 2008; Sutherland et al. 2011). The average off-shore surface water temperature in Puget Sound is 12.8 °C in summer and 7.2 °C in winter. The tidal range within Puget Sound (ca. 4 m) produces strong currents in constricted areas between basins.

The Skagit and Snohomish rivers are the two largest rivers in Puget Sound with mean annual discharge of 470 m^3 s-1 and 261.4 m^3 s-1, respectively. Both rivers exceed marine temperatures (13-14 °C) by late spring but the Skagit River is cooler (maximum 16-17 °C) than the Snohomish River (19-21 °C) (Figure 3.2). The Skagit River delta and estuary (13-km total length) includes north and south forks, a large complex of distributary channels, sloughs and marshes, and merges into the open waters of Skagit Bay and its nearshore. The Snohomish River delta and estuary has a 14 km upper estuary and a 7 km lower estuary, connecting to Possession Sound through a large intertidal river delta. Two adjacent rivers to the Skagit include the Nooksack River to the north (mean flow 107.6 m^3s-1) and Stillaguamish River to the south (84 m^3s-1). Both rivers have a much smaller estuarine and inter-tidal zones than the Skagit and Snohomish rivers. The most southerly Puget Sound river with bull trout is the Puyallup River, with a 5 km estuary and a small river delta extending into Commencement Bay.

3.2.2 Juvenile Fish Traps

Juvenile bull trout were caught annually in the Skagit River over 12 years (2001-2012) with two types of traps: a floating inclined-plane screen trap and a screw trap. The traps, hereafter referred to as the “Skagit downstream trap,” were operated in parallel from January through August in the lower Skagit River at river kilometer (rkm) 39.1. During each trapping season, the trap was fished every night and every third day. Each day, the trap was checked for fish at dawn and dusk. Total catch was summarized by statistical week, biweekly and monthly periods and FL was measured from a subsample of bull trout (2001-2012). The purpose of this sampling was to determine the size distribution and timing of migratory juvenile bull trout rather than the total abundance. The trap is not efficient for larger fish, which were sampled by beach seines and fyke traps (below).

3.2.3 Beach Seining in the Skagit and Snohomish River Deltas and Shorelines

The Skagit River delta, bay and nearby marine areas were sampled biweekly in 2001-2003 with fyke nets and large and small beach seines (Figure 3.1) to assess the presence, relative abundance, and size of salmonids (Beamer and Henderson 2004). A fyke net was used on ebb tides to sample seven blind tidal channels on the river delta as the fish were caught when the water receded. A small beach seine was used in shallow habitats (~ 0.75 m depth) in six delta distributary channels and 12 intertidal shoreline areas, and a large beach seine was used to sample 13 deeper (~ 2.5 m depth) intertidal and subtidal sites. Three beach seine sets were completed per site on each sampling day. Sampling on the delta was conducted from February through August and from February through October in the bay and nearby marine areas. In 2003 sampling occurred throughout the year. Sampling areas generally fall into three major habitat zones: nearshore shorelines, river delta (vegetated delta and delta flats) and lagoons regions

(Beamer and Henderson 2004). Water temperature, depth, salinity, and habitat type were collected during each sampling event (described below).

Bull trout were caught in the Snohomish River delta and nearshore from 2002-2012 with fyke nets and large beach seines (Figure 3.1) as part of biweekly sampling of salmonids (Rice et al. 2013). A fyke net was used on ebb tides to sample two blind tidal channels on the river delta and a large beach seine was used at 10 sites along the margin of the main channel and four distributary sloughs, from the channel mouth to head, in the intertidal lower river and estuary. Sampling occurred twice per month between February and August, one to two times in September, and once per month October through January in selected years. The sites were stratified into three zones longitudinally, generally corresponding with salinities of 0 -1 ppt in the upper river, 0 to 5 ppt in the middle to the lower river, and 5 - 18 ppt in the estuary delta, depending on season and river flows. Surface temperature and salinity were recorded at each sampling event.

3.2.4 Fish Capture for Telemetry

A total of 286 bull trout were tagged with acoustic transmitters from 2002-2010, including smaller bull trout (85 fish, 223-395 mm FL) termed sub-adults, and larger bull trout (201 fish, 400-650 mm) termed adults (Appendix Tables 3.1 and 3.2). Bull trout were captured by hook and line in rivers and marine waters, by beach seining in Skagit and Shilshole bays, and at a fish trap on the White River, from late winter to early summer. The capture areas from north to south included the Nooksack, Skagit, and Snohomish rivers and nearshore waters from Swinomish Channel to Shilshole Bay (see details on fish capture and tagging in Supplementary Materials). Once captured, bull trout were transferred to a container with freshwater and buffered tricaine methanesulfonate (MS-222) at a concentration of 70 mg l^{-1}, measured for fork length

(FL), and weighed. Different sizes of acoustic transmitters (Vemco, Inc., Shad Bay, Nova Scotia, http://vemco.com) were surgically implanted so that the average tag weight was 1% of body mass: V7 (4 fish), V8-V9 (132), V13 (33), and V-16 (89) coded transmitters. The surgical procedures to insert the transmitters followed those described previously (e.g., Hayes et al. 2011; Goetz et al. 2013). Tagged bull trout were held in recovery tanks for 2-4 h and then released along shore near the capture site. The transmitters were programmed at pulse rates that varied from 20-60 or 30 to 90 seconds to accommodate a battery life of 85-150 d (V7), 180-465 d (V8-9), 350-450 d (V13), and 450-900 d (V16); most V8-9 transmitters had a 30-90 sec pulse rate with a life of 410-465 d. Hence, over 90% of fish tagged in one year could be detected the next year, and over 20% could be detected in the third year.

3.2.5 Receiver Deployments

Transmitters were detected by fixed acoustic receivers (Vemco Ltd., VR-20, VR-2, VR2-W, and VR3). The number of receivers deployed in Puget Sound increased from 28 in 2002 to over 240 in 2008 (Table 3.1, Figure 3.1). Receiver locations were categorized as river or freshwater (above high tide), river delta or estuary, and nearshore or marine. Detection data were collected from a shared receiver network deployed in Puget Sound (Goetz et al. 2013, 2014; Smith et al. 2015). The receivers were deployed and retrieved at locations and on schedules that served the purposes of each set of investigators. Before 2005, 90% of the receivers in Puget Sound were explicitly deployed for this project and thereafter approximately 50-60% were deployed by the researchers for this and companion studies. To identify sites where bull trout could have been detected, we determined the locations and dates when receivers were operational that overlapped with the dates when our tagged fish could have been detected, given the anticipated battery life of the transmitters.

Individual fish positions were also determined using mobile receivers (VR-60 and VR-100) deployed from a boat in the lower Snohomish River, Port Susan and Swinomish Channel (2002-2004), and in Skagit Bay and the lower Skagit River (2006-2007) (Hayes et al. 2011). Surveys in tidally influenced areas occurred at 1-2 week intervals during the highest abundance period(s) of tagged bull trout from May – July. Surveys of river segments above tideline in the Skagit, Snohomish and Skykomish rivers (2002) occurred in late summer and fall after fish left tidally influenced areas.

3.2.6 Flow and Water Temperature Data

Temperature data were collected daily at fixed sites next to receivers in the Snohomish River and its delta in 2002-2005 (rkm 1, 21). Temperatures were also collected during biweekly beach seining events in lower river and estuary (Figure 3.1) and in mobile acoustic surveys in Port Susan marine and Snohomish Basin estuary and freshwater locations where bull trout were detected. Daily temperature data were collected in Skagit Bay, the lower Skagit River next to receivers in 2004-2005 (rkm 7, 27) and the upper Skagit (rkm 127, U.S. Geological Survey (USGS) gage 12181000), in biweekly beach seining surveys in lower river and Skagit Bay 2001-2003 (Figure 3.1), in biweekly sampling in lower river 2004-2012 (Skagit County unpublished data), and in mobile acoustic surveys in Skagit Bay in 2006 (Hayes et al. 2011). Daily temperature data during spring and early summer were also collected in the upper Skagit River (rkm 127) from 2002-2012. Daily temperature data during summer were collected in the Nooksack River from USGS gage (12209000, rkm 23.3 South Fork Nooksack) in 2007 and in the Stillaguamish River (Washington Department of Ecology station 05A070, rkm 18) in 2002-2005 along with monthly sampling at the same site. Daily flow data were collected from USGS gages on the lower Skagit (12200500, rkm 25.3) and Snohomish (12150800, rkm 30.5) rivers.

The common frequency for monitoring temperature in most areas was a biweekly sample during seining events or by other agency for water quality trends (i.e., Skagit County). If temperature was measured by data logger (Snohomish delta and river 2002-2004, Skagit delta and nearshore 2004, Stillaguamish 2002-2005 (July September only), these data were averaged into a daily mean temperature for detailed analysis with telemetry data, and averaged into biweekly periods for comparison with other years or areas with biweekly sampling. When water temperature was not measured daily, the daily temperatures were estimated by interpolation of the available data. Where data were available for several locations along a migration route, the warmest place for which data were available was used for analysis.

3.2.7 Description and Quantification of Movement Patterns

Migration timing at the Skagit River downstream trap for each year was described based on the cumulative catch over each trapping season, and for each year the percent of that year's total (proportion) was calculated to provide an overall timing. The onset and end of migration were established as the first and last dates when the proportion of fish captured exceeded or fell below 1.5% of the year's total. Unlike the capture of juvenile bull trout during their downstream migration, biweekly seining in the river delta and nearshore sampled fish that had been in the estuary for an unknown period, so there was some lag between the fish's arrival and its capture. Nevertheless, the proportion of fish captured per month and biweekly period indicated the overall patterns of occupancy and, by extension, the general timing of arrival and departure from these habitats.

For the telemetry data, the following characteristics were quantified during the monitoring period in marine waters for each fish: 1) river of return (which river the fish returned to after a period of marine or estuary residence; 2) the farthest location (in km) following shorelines from the upstream extent of tidal influence in a river to the most distant location where the fish was detected in estuary or marine waters 3) the farthest offshore distance (km) from Skagit Bay as measured by mobile tracking (2006-2007, data previously reported in Hayes et al 2011); 4) whether individuals crossed open water bodies from major islands in Whidbey Basin or across the main basin of Puget Sound; 5) timing of river *exit* (last detection in freshwater or first detection in estuary or marine water) and river *entry* (last detection in estuary or marine water prior to freshwater); 6) residence time (number of days from the first to the last detection), and location (river delta or nearshore) in estuary and marine waters in spring and summer, and fall and winter. Fish tagged in the White River were captured on their upstream migration and were included in the analysis of the farthest location but were excluded from marine migration timing.

Fish were tagged in river locations to identify when they first entered and then exited estuary or marine waters, and fish were tagged in estuary and marine waters to see when they exited the marine environment. Give the longevity of the transmitters, fish in either location could be monitored into the following year providing the location for overwintering and the timing of river exit and river return in the second year. Sub-adults received smaller tags so there were fewer opportunities to track them through more than an entire year.

The timing of downward migration to lower river areas (juvenile trap), residence in the estuary and marine environment (seining, telemetry), and freshwater / marine exit/entry (telemetry) was evaluated relative to water temperature in areas near the estuary or marine residence location or in lower river areas. Pre-mature upstream migration was evaluated as departure to freshwater prior to when tidally-influenced or lower river areas water temperatures exceeded 16 °C, the upper temperature considered tolerable for bull trout (Poole et al. 2001) although somewhat higher thermal tolerances have been observed based on experimental temperature-dependent respiration and feeding trials (Mesa et al. 2013).

3.2.8 Statistical Analysis

We used a paired t-test to evaluate whether Skagit River daily water temperatures differed from the lower river (rkm 27) to river delta (rkm 7). A General Linear Model (GLM) was used to evaluate the influence of year (2002-2005), river of return (Skagit, Snohomish, Stillaguamish) and water temperature on the date of river entry during the late spring to summer time period (May to August) for 159 telemetered fish. We used a best sub-sets model (normal distribution) and selected the highest-ranked models based on Akaike's information criterion (AIC; Burnham and Anderson 2002). A separate GLM was used to evaluate the influence of year (2002-2006) and temperature on date of river entry for the Skagit River for 139 telemetered fish: the only river with detections in 2006. A GLM was used for exploratory analysis of residence time of telemetered fish as a response variable, testing for relationships between the total number of days an individual was detected in marine areas by life stage, sex, major habitat type (nearshore or river delta), and river of return for the Skagit, Stillaguamish, Snohomish, and Nooksack: the rivers where individuals with both a river exit and river entry were detected. The two-way ANOVA test was used to examine whether the distance telemetered fish migrated was related to life-stage (sub-adult, adult) and river of return for the Skagit, Stillaguamish and Snohomish; the rivers with the greatest number of returning fish.

3.3 Results

3.3.1 Environmental Conditions

From March through August, temperatures in the major river deltas and lower rivers varied from 4.3 to 17.2 °C in the Skagit River, 3.4 to 21.5 °C in the Snohomish River, and in the nearshore area from 5.1-20.3 °C in Skagit Bay. Skagit River mean temperatures during spring and summer varied by up to 3 °C between years, with lowest (8.3-9.5°C) in 2010-2012 and highest (12.3-12.9 °C) in 2003-2005. Skagit River temperatures at rkm 7 (delta) were similar to those at rkm 27 (lower river: + 0.3 °C, $P > 0.23$). During the same period in the upper Skagit River (rkm 127), near bull trout spawning areas, temperatures were 1.0-4.9 °C cooler than the lower river and delta. Temperatures in March-June were similar in both river deltas (+/- 0.5 °C) while in July-August temperatures in the Snohomish delta and river exceeded the Skagit by 1.1-3.4 °C (Figure 3.2). Temperatures in outer Skagit Bay were similar to the river delta in spring and fall, but cooler in the summer, and warmer during late fall and winter. The salinity levels during the same periods ranged from 0-33 ppt in the Skagit and Snohomish River delta and nearshore areas. Mean salinity values by sampling period ranged from 0-6.1 ppt in delta and 1-14.4 ppt in nearshore areas of the Snohomish River and 3.4-19.3 in delta (vegetated and delta flats) and 16-23.5 ppt in nearshore areas of the Skagit River. Salinity values consistently increased as river flows declined as summer progressed into fall.

River flows peaked during the spring snow melt in May and June with the lower Skagit River mean of 588.9 cms (SD 203.46) for that period and the lower Snohomish River's mean flow was 382.5 cms (SD 162.3). By year, Skagit River mean flows during spring and summer were lowest (364-364 cms) in 2001, 2005 and highest (721-811 cms) in 2002, 2012. The lowest river flows occurred in August and September with the lower Skagit mean 261.7 cms (SD 97.3) and lower Snohomish mean 83.1 cms (SD 67.6).

3.3.2 Seasonal Timing

Trapping and Seining

Juvenile bull trout were captured in the Skagit River downstream trap between early April and late July (Figure 3.3), ranging from 90-290 mm FL, with few longer than 200 mm. Only 1.0% were caught before April and 1.3% after mid-July. The onset of migration (first date greater than 1.5%) was between April 3 and May 23. Median catches occurred between May 16 and June 15. The peak catch by month was May and June. The mean final capture date (last date greater than 1%) was July 12 and varied from June 17 (2005) to July 23 (2001, 2003, 2009).

Fish were caught in the Skagit River marine areas from February to December (Figure 3.3) but few were caught after August in the delta and nearshore. Slightly higher catch rates occurred in February and March in the delta and nearshore. An average of 28.5 juvenile, 31.5 sub-adult, and 45.5 adult bull trout were caught annually in the Skagit River delta and nearshore. In the Snohomish marine areas there were fewer fish caught compared to the Skagit River (means: 1 juvenile, 3 sub-adult, and 2 adult bull trout annually; Figure 3.3). Based on these limited data, there was a distinct period of nearshore residence between April and July.

Telemetry

The monthly proportion of telemetered fish detected in river delta and nearshore areas followed the pattern observed in seining data: an increasing proportion of detections from March to June, a decline in July, and very few detections in other months (Figure 3.3 bottom). Tag detections were rare in the river delta and nearshore between August and February, never exceeding 2% of the annual total in any month for either habitat. Most of the detected fish in fall and winter (90%) were only detected in a single month (two fish were detected over 2 months, and one fish was detected for 4 months). A total of 247 tagged bull trout (173 adult, 74 sub-adult) were detected over the course of the study. Fish that were not detected (N = 39) and those determined to be mortalities or could not be assigned to a river of return (N = 12) were removed from the dataset. Of the remaining fish, 72% were detected for one year, 24% for two years, and 4% for 3 years. A total of 797,944 detections were recorded with 40.6% (323,847) from 142 fish in nearshore areas, 58.5% (466,818) from 201 fish in river deltas, and 0.9% (7,279) from 134 fish in rivers.

River of Return

The river that fish returned to depended on tagging location; fish tagged in marine areas returned to one of three rivers in different proportions, whereas fish tagged in fresh water tended to return to the river they were tagged in (Table 3.2). In northern marine areas 98% of fish tagged in Skagit Bay and Swinomish Channel returned to the Skagit River while fish tagged in areas south of the bay returned in different proportions to the Skagit, Stillaguamish or Snohomish River. Fish tagged in the Nooksack, lower Skagit and White Rivers all returned to the same river but some fish tagged in the Snohomish River returned to Skagit and Stillaguamish rivers.

Detections by river of return followed the overall pattern of monthly detections (primarily in March through July: Figure 3.3, bottom) with minor differences. In nearshore areas, fish that returned to the Skagit were detected in every month, fish returning to the Snohomish were not detected in August-October and February-March, while fish returning to the Stillaguamish were not detected from August to November and in February. In river deltas, fish returning to the

Skagit and Snohomish rivers were detected in every month while fish returning to the Stillaguamish were not detected from August to February (Figure 3.4).

3.3.3 Environment and Timing

Trapping and Seining

As predicted, the peak occurrence of juvenile downstream migration and sub-adult and adult marine residence in Skagit River and Bay was in late spring as water temperatures and flows increased, though a few fish were in marine areas in late fall and winter (Figure 3.5). The last date of summer capture at the trap and by seining occurred at temperatures below 15 °C before river flows declined to summer low.

The onset of bull trout catches at the juvenile trap began when temperatures at the fish trap exceeded 7 °C (mean 9.0 °C, SD 1.3) in all but one year (6.1 °C 2011) and every year when temperatures at the upper Skagit River exceeded 4.5 ºC (mean 6.2 °C, SD 1.1 °C). The initial fish capture by seining in Skagit Bay occurred in mid-February at a mean temperature of 7.2 °C (SD 0.4). The peak period (central 50% of catch) took place at the trap as temperatures were rising from an average 10.4 °C (SD 1.1, May 1) to 11.4 °C (SD 1.2, June 1), and peak seining catch took place at temperatures 11.2 °C (SD 1.0, May 15) to 13.6 °C (SD 0.9, July 1). The mean temperature for the last biweekly capture period at the juvenile trap and seining was 14.2 °C (trap SD 1.2, seine SD 1.0) with a range from 12.5-16.0 °C (trap) and 13.7-15.4 °C (seine). The mean temperature from the last capture by seining in summer (August 1) to October 1 was 14.5 °C (SD 0.4 °C).

Telemetry

As predicted, the peak occurrence of telemetered sub-adult and adult marine residence in all nearshore and estuary areas was in late spring as water temperatures and flows increased, though a few fish re-entered marine areas in late fall and winter (Figure 3.6). Most fish left the marine environment before temperatures exceeded 16 °C and all but a few fish exited before temperatures reached 18 °C.

The onset of marine residency for tagged bull trout (more than 1.5% present) occurred in early-mid March at similar river exit temperatures for Skagit River fish (mean 7.7 °C March 16) and Snohomish River fish (mean 7.6 °C March 1). The peak abundance (highest two biweekly periods) in marine areas occurred later and at a higher temperature for fish returning to the Skagit River (mean 12.3 °C June 1, 12.9 °C June 16) than those returning to the Snohomish River (mean 10.9 °C May 1, 11.6 °C May 16). The peak abundance coincided with the peak discharge for spring and summer in the Skagit (633 cms June 1, 589 cms June 16) and Snohomish (356 cms May 16). The end of marine residency (< 1.5% present) occurred at lower temperatures for Skagit River fish (15.1 ^{o}C August 1) than Snohomish River fish (18.3 °C July 16) (Figure 3.6 and 3.7).

The late spring to summer river entry timing varied among years and rivers, and was influenced by temperature. The two highest ranked models (variables: year, river, year*temperature, and river*temperature: AIC 1220.28, and year, river and river*temperature delta: ΔAIC 3.05) did not differ significantly. The latest mean river entry date occurred in the coldest year in 2002 (July 4, mean 12.5 °C with earlier dates in 2003-2005 (June 20-22, mean 13.6-13.9 °C) ($F_{3,147} = 5.5$, P < 0.01). The Skagit River had the latest mean entry date (June 28, mean 13.5 °C), while the Snohomish (mean 13.6 °C) and Stillaguamish (mean 14 °C) rivers did not differ in mean entry date (June 18) ($F_{2,147} = 5.7$, $P < 0.01$). There was no significant influence of year (2002-2006) on river entry in the Skagit River ($F_{4,134} = 2.25$, $P = 0.06$) although the latest dates were in the two coldest years of the study in 2002 (July 14, 12.5 mean °C) and 2006 (June 29, mean 13.5 °C). The latest entry dates for individual fish occurred in mid to late August with three returning to the Skagit (mean 16.1 °C) and one to the Snohomish (16.7 °C), in comparison August temperatures in Skagit Bay were 13-14 °C. A total of 27 fish (13%) experienced temperatures greater than 16 °C with four fish entering rivers (3 Stillaguamish, 1 Snohomish) at temperatures over 18 °C in July 2003 (Figure 3.7). Fish returning to upper river reaches in June-August experienced mainstem river temperatures of 11-12 °C in the Skagit, 12-13 °C in the Skykomish River (where bull trout spawn in the Snohomish River basin), and 14-15 °C in the North Fork Stillaguamish River.

3.3.4 Characteristics of Marine Residence

<u>River Tagged Fish and Alternate Year Freshwater Residence</u>

Fish tagged in the Snohomish River (N = 29) resided in multiple locations; 24% remained in freshwater, 29% exited to other rivers, 41% resided in the river delta and 7% in the nearshore. In the Skagit River all 20 fish exited the river (and returned to the same river); 60% resided in the river delta and 40% in the nearshore. After rearing in marine waters the previous year, a small proportion (3.2%) of all tagged fish (N = 247, all rivers) switched to freshwater residency the next year.

<u>Marine Residence Time</u>

Two groups of fish provided data sufficient to determine the duration of marine residence: those tagged in freshwater that exited and re-entered the river in the same year, and those tagged in one year and then detected at exit and entry the following year (Table 3.3). Residence time did not differ between fish returning to the Nooksack, Skagit, Snohomish and Stillaguamish ($F_{3,82} = 1.0$, $P = 0.39$) for an overall average of 62.8 d (SD = 37.6) days. Residence time was significantly shorter in river delta compared to nearshore areas (mean 55 d versus 72.8 d, $F_{1,82} = 8.7$, $P < 0.01$). There was no difference in residence time between sub-adult and adult fish (mean 60.1 d versus 64.4 d, $F_{1,82} = 1.144$, $P = 0.29$) or female and male fish (mean 59.6 versus 65.3 d, $F_{1,82} = 1.1$, $P = 0.30$).

Distance from river and marine shorelines

There was a significant difference among rivers in the distance fish traveled to or from the farthest marine location to a particular river (ANOVA: $F_{2,204} = 4.64$, $P = 0.01$) but no difference in farthest distance traveled between sub-adult and adult fish (mean 26.1 versus 28.4 km; ANOVA: $F_{1,202} = 0.16$, $P = 0.69$). The longest migrations were performed by fish returning to the Skagit (mean = 37, SD = 34.6 km) and Stillaguamish (mean = 27.2, SD = 18.6 km) rivers. Fish returning to the Skagit River from tagging sites south of Camano Island had the greatest potential range of distances depending on the path of return, fish could either return directly north through a short tidal channel between Camano Island and the mainland to the South Fork Skagit (route 1) or migrate the entire distance around Camano Island to the South Fork (route 2). Fish taking route 2 could migrate an additional 71 km. Moderate distances were observed in fish returning to the Snohomish 19.4 ± 13.4 km and Nooksack 15.3 ± 28.3. The shortest migration distance was observed in fish tagged in the White River 4.5 ± 5.0 (Figure 3.8). The migration distance for Nooksack River fish is likely underestimated as there was more limited receiver coverage, especially to the north, limiting the detection probability of fish moving long distances.

Bull trout in Skagit Bay were usually detected less than 0.4 km from the shoreline (83% of measurements) and 28% of detections were less than 100 m from shore. In Skagit Bay, bull trout can access all shoreline areas except Whidbey Island by traveling from the Skagit River along the shoreline and remaining in intertidal or shallow subtidal waters. To get to Whidbey Island they must cross the open and deeper waters of Skagit Bay (7 – 84 m deep). Three bull trout were detected by fixed receivers as they crossed from the east shore of Skagit Bay to west shore on Whidbey Island. Two fish were tracked during open water crossings of 0.5 to 1.0 km (9.8 and 13.4 m mean depth), and one fish at 3.2 km (48.2 m mean depth). Two fish were tracked crossing greater distances in deeper waters (up to 250 m) of Puget Sound, one in Possession Sound (near Everett) which crossed over 3.6 km (94.5 m mean depth) and the other in Central Puget Sound (near Seattle) that crossed 6.9 km (105.7 m mean depth).

3.4 Discussion

The patterns of bull trout migration timing and marine residence in Puget Sound observed in this study were only partially consistent with the predicted pattern of well-defined periods of movement and marine habitation and a premature migration back to freshwater before temperatures reached annual peaks. All evidence, from traps, seining, and telemetry indicated that most bull trout migrated downstream in early spring and returned to rivers only a few months later, prior to annual maximum temperatures. The residence time in marine waters for sub-adult and adult fish averaged two months and ranged from a few days to a maximum of four months. However, some individuals were caught or detected on receivers over a much wider range of dates, contrary to predictions. The fish in Puget Sound in winter remained for short periods; most moved to other rivers to overwinter rather than remaining in Puget Sound.

The migration timing was similar between fish from different river basins despite differences in thermal regimes, and between life stages; larger bull trout entered marine waters in late winter-spring, juveniles arrived shortly thereafter, and almost all fish, including all life stages, migrated back into rivers by early summer as flows declined and river temperatures exceeded 15-16 °C, at a time when marine temperatures were 13 °C or less. The temperatures when sub-adult and adult fish returned varied by river, with the Skagit River fish experiencing the lowest temperatures and latest return time compared to higher temperatures and earlier return to the Snohomish and Stillaguamish Rivers.

Puget Sound Ecosystem and Salmonids

The entry timing, movements, habitat associations, and return timing of migratory salmonids in Puget Sound vary widely, making this an informative system in which to make comparisons among species and life history types. Bull trout seem to be at the end of the salmonid continuum for the limited distance they travel from their natal stream and the short duration of time at sea. Being interoparous as are the cutthroat trout, migrants include juvenile "first-time migrants" as well as larger sub-adult and adult fish. Like cutthroat trout, they are shoreline oriented and do not range far from their natal rivers but the bull trout spend a short period in the marine environment than the other species (Quinn 2005; Goetz et al. 2013. The Pacific salmon found in Puget Sound include large runs of pink, chum, and sockeye salmon and steelhead trout. The juveniles of these species include many millions of fish entering Puget Sound early in the spring that all migrate to the ocean. They range in size, timing, and rapidity with which they move through estuaries (Simenstad 1982; Healey 1982). Coho and Chinook salmon differ in that some of the fish remain in Puget Sound for all or a significant fraction of their marine residence period rather than going directly to the ocean. The proportion of these "residents" is greater in Chinook salmon (O'Neill and West 2009; Chamberlin et al. 2011) than coho salmon (Rohde et al. 2013).

Downstream Migration Timing

The migration of juvenile salmonids from fresh to salt water marks a critical phase in the life history of anadromous salmonids and has been hypothesized to be timed to favorable ocean conditions for foraging success and growth. As predicted, the downstream migration of juvenile bull trout through the lower Skagit River coincided with the timing of semelparous Pacific salmon smolts caught at the trap including coho and Chinook salmon and residency period of other juvenile salmonids in Puget Sound (Duffy et al. 2005; Zimmerman and Kinsel 2010). A similar overlap in migration timing occurs with anadromous Arctic char, brown trout, and Atlantic salmon smolts in Europe, with differences in the duration of migration; Arctic char have the shortest window of migration (Jensen et al. 2012). This downstream migration occurred with increasing temperatures (and flows) and the bull trout migration ended as temperatures peaked. In most years, the annual median migration dates of juvenile bull trout in spring were comparable to Chinook but were later than coho, while the duration of bull trout migration was shorter than Chinook and longer than coho (Zimmerman and Kinsel 2010). The juvenile bull trout migration also coincides with the timing of juvenile Puget Sound coastal cutthroat trout (e.g., median late April, Big Beef Creek, WDFW unpublished data) and steelhead trout (e.g., median mid-May, Moore et al. 2015). The migration of juvenile bull trout in the Dungeness River on the Olympic Peninsula is similar to the Skagit River, the migration begins one month later (median mid-June) but still ends in late July before peak temperatures are reached (WDFW unpublished catch data, WDOE unpublished temperature data).

Although juvenile salmonid trapping in Puget Sound tributaries typically ends in midsummer, the seining and trapping in the Skagit delta and nearshore continued into fall, where no fish were caught from early August through October. This apparent departure is consistent with the end of marine residence of larger acoustic tagged fish, in advance of the peak temperatures. Unlike the regularity in timing of downstream migration in Puget Sound tributaries, the timing of juvenile and sub-adult bull trout in interior drainages of the Columbia River occurs over a broader continuum, with some basins having spring and fall migration peaks, while others have peak periods in summer (Downs et al. 2006; Homel and Budy 2008; Howell et al. 2016). These movements have been related to snowmelt runoff and increasing water temperature in spring and declining temperature and increasing flow in late summer and fall (Muhlfeld and Marotz 2005; Downs et al. 2006).

The downstream movement of acoustic tagged sub-adult and adult bull trout overlapped with migration of post-spawning adult cutthroat trout and steelhead trout into Puget Sound (WDFW, Big Beef Creek, unpublished catch data). The outmigration of anadromous Dolly Varden and Arctic char also occurs in the spring as temperatures warm and after ice-break up in northern latitudes (Bernard et al. 1995; Berg and Berg 1993). The spring marine arrival of acoustic tagged fish matched the beach seine captures of larger bull trout in the Skagit and Snohomish river deltas at a time of increasing temperatures but before the snowmelt peak. After entering Puget Sound, most acoustic tagged bull trout moved about 20-40 km from the river mouth but some fish moved up to 150 km, similar downstream movement in spring has not been observed in non-anadromous adults in interior populations or in sub-adult or adult Pacific coast bull trout (Howell et al. 2016). Non-anadromous bull trout typically reach their farthest downstream location in fall and winter with no additional downstream movement in the late winter and spring (Bahr and Shrimpton 2004; Monnot et al. 2008) and anadromous bull trout on the Pacific coast left their natal river in the fall and migrated to other tributaries, returning to spawn in spring and early summer (Brenkman and Corbett 2005).

Upstream Migration Timing

River entry timing and upstream migration timing by anadromous bull trout appears similar in both Pacific Coast (Olympic Peninsula) and Puget Sound groups. Entry at the Hoh River and upstream migration timing in the White River (May-July), matched the timing of acoustic tagged fish (Brenkman and Corbett 2005, F. Goetz, US Army Corps unpublished data). The migration in both rivers was largely complete before river water temperatures exceeded 16 °C (Washington Department of Ecology Hoh River, unpublished data, USGS White River, unpublished data). This upstream migration timing is well in advance of peak spawning in the studied Puget Sound rivers of October-November, this compares to the late September to early December migration timing for adfluvial bull trout (Brenkman et al. 2001, Barnett and Paige 2013). Spawn timing for both anadromous and adfluvial populations peak when temperatures fall below 10 °C. The migration timing could be related to migration distance, the anadromous fish undertake long migrations from marine to upper river areas (Puget Sound range 10-150 km marine, 85-110 km freshwater, Pacific coast range 20 km marine, 75 km freshwater) while the adfluvial fish have a short migration distance from lake to tributary spawning areas (6 km).

Also, similar to Dolly Varden, bull trout may enter rivers earlier to make use of salmon subsidies in summer and early fall, the timing of such re-entry could parallel that of salmon that are the predominant prey sources of char in fresh water (Bond and Quinn 2013; Sargeant et al. 2015; Lowery and Beauchamp 2015). The Skagit River supports the largest run of native Chinook salmon (spring, summer, and fall runs) in the Puget Sound and the largest runs of pink and chum salmon in the coterminous United States. Salmon spawn timing begins with Chinook from August-October, pink salmon from September-October, and chum salmon November-December (Connor and Pflug 2004). Fluvial and anadromous bull trout eat a limited amount of salmon eggs in that system in late summer while 90% or more of diet is eggs and carcasses in fall (Lowery and Beauchamp 2015). Anadromous bull trout leave the marine environment by June or July and do not spawn until October, so the migration is considered premature (Quinn et al. 2015).

The upstream migration of adfluvial and fluvial bull trout in interior basins (Swanberg 1997; Hogen and Scarnecchia 2006; Starcevich et al. 2012) has typically been linked to the need to reach spawning sites or to reach areas with cooler temperatures. The initiation and duration of this migration varies, including a protracted migration by adfluvial bull trout in the Flathead River from April-October and Metolius River May-October (Fraley and Shepard 1989; Ratliff 1992), and compressed migrations by fluvial bull trout in the Blackfoot River (June-July: Swanberg 1997) and Lostine River (May-July: (Howell et al. 2010). In these latter systems the migrations took place as temperatures increased, and were completed by September. Unlike the warmer temperatures experienced in short migrations, adfluvial bull trout in the spring-fed Metolius River migrate short distance at temperatures below 12 °C (USGS Metolius River, unpublished data), while in the Flathead River, the migration occurs at temperatures less than 16 °C (Fraley and Shepard 1989; Muhlfeld and Marotz 2005).

Puget Sound Resident Salmonids

The movements of anadromous bull trout are perhaps most similar to those of anadromous cutthroat trout, which stay within marine basins of Puget Sound but migrate similar distances along shorelines, and show extended use of limited shorelines areas (2-3 km) within Puget

Sound. Unlike bull trout, cutthroat may undertake multiple crossings of deep, open-water bodies (Goetz et al. 2013). Cutthroat enter the marine environment in spring but exit later than bull trout, in late summer or fall in large rivers like the Skagit and Snohomish, and in winter (just prior to spawning) in small streams (Quinn and Myers 2004). The migratory behaviors of immature and mature life stages of cutthroat and bull trout are similar within each species in distance traveled and habitat used in river deltas and nearshore shorelines. Further, cutthroat prey upon similar sizes and species of fish compared to bull trout in North Puget Sound (e.g., Pacific sand lance, Pacific herring, and salmon) (Goetz et al. 2004; Duffy 2003; Duffy and Beauchamp 2008). Another important difference is that the cutthroat trout spawn in spring, prior to entering marine waters, whereas the bull trout spawn in fall, several months after returning to their natal rivers.

Marine Residence and Prey Resources

The duration of spring and summer marine residence of acoustic tagged bull trout is shorter than cutthroat trout but longer than Dolly Varden and Arctic char (Sumner 1962; Gulseth and Nilssen 2000; Armstrong 1971). Overwintering is relatively uncommon in interoparous species and the short period observed for the few acoustic tagged bull trout parallels this (Berg and Berg 1993; Quinn and Myers 2004; Gulseth and Nilssen 2000). In Puget Sound Hayes et al. (2011) suggested that bull trout marine residency is probably affected by temperature, and could be linked to other factors such as fish age or life stage, the seasonal availability of food resources, and predation risk. River temperatures may influence iteroparous species residence time in different manners, Arctic char marine residence may be extended in periods with lower river temperatures while brown trout may have reduced marine residence under the same conditions (Berg and Berg 1993). The emigration of Dolly Varden is related to sea surface temperatures in June, although the median timing of that migration across the range can vary by 2 months, with some migrants returning in late summer or fall (Bond and Quinn 2013). Iteroparous salmonids often show an early return characteristic of larger and older salmonids that would benefit less from additional time in marine waters (Quinn et al. 2015). Unlike this pattern, Puget Sound bull trout did not show an earlier return of older fish.

The development of anadromy in char is hypothesized as a response to greater food availability in the marine environment. In marine waters Dolly Varden and Arctic char prey items includes zooplankton and pelagic fish, such as Pacific herring for Dolly Varden, but also epibenthos (Sturdevant et al. 2012; Berg and Berg 1993). Coincident with the Puget Sound telemetry study, 92 sub-adult and adult bull trout were captured and evaluated for prey items in late spring and early summer in the nearshore and river delta of Skagit Bay and 31 were captured in Port Susan and Snohomish River delta (Goetz et al. 2004; Duffy 2003). The diets of these fish were predominately composed of fish (>96%), mostly surf smelt, Pacific sand lance and Pacific herring, with a smaller percentage of juvenile salmon. The abundance of these forage fish is highest in May-July, overlapping with peak abundance of bull trout (Pentila 2007). Similar to bull trout, cutthroat trout feed upon a greater proportion of forage fish in north Puget Sound and a wider variety of fish in south Puget Sound (Duffy and Beauchamp 2008). Since the bulk of the anadromous bull trout migration occurs months prior to salmon spawning in rivers there is little opportunity to forage on a salmon subsidy in summer (Lowery and Beauchamp 2015).

Predator Avoidance

Anadromy exposes fish to larger predators than are found in freshwater habitats and avoidance of such predators could be a factor in early returns to freshwater. In the Salish Sea marine predators of salmon, trout and other large fish include otters (Buzzell et al. 2014), harbor seals (Lance et al. 2012), sea lions (Kinsey 2007), killer whales (Ford and Ellis 2006), spiny dogfish (Sturdevant et al. 2012), and otters, bald eagles, and black bears prey on bull trout in streams (Barnett and Paige 2013). Overall, it is not clear where the greater danger lies but in all likelihood bull trout are safer in large rivers like the Skagit than they are in Puget Sound, but have less to eat (Quinn et al. 2015).

Overwintering in Marine Waters

Many iteroparous salmonids such as Arctic char, brown trout and cutthroat trout do not routinely over-winter in marine waters, though there seem to be some exceptions (Bernard et al. 1995; Quinn and Myers 2004; Jensen and Rikardsend 2012). On the Pacific Ocean coast, radio tagged bull trout moved between river systems in winter (Brenkman and Corbett 2005). Acoustic tagged bull trout were detected in Puget Sound during every month of the year although very few were detected in the winter. Some fish detected in Puget Sound during fall and winter appeared to be moving between rivers rather than residing there, similar to behaviors seen in Pacific Ocean bull trout (Brenkman and Corbett 2005), Dolly Varden, (Bernard et al. 1995) and Arctic char and brown trout (Jensen and Rikardsen 2012). Sub-adult and adult bull trout were also captured in the Skagit River delta and bay in late fall and winter in 2003; the only year sampling started in early February and continued into December. The low numbers of bull trout in winter could be explained by reduced activity levels at low temperatures in relation to the long distance fish must migrate to reach Puget Sound, or due to sufficient availability of freshwater prey items compared to marine sources (Staurnes et al. 1992; Muhlfeld et al. 2003; Bond and Quinn 2013).

Conclusion

In this study, we used a variety of techniques to evaluate the movements of juvenile, sub-adult, and adult anadromous bull trout. As predicted, all life stages of bull trout moved downstream in late winter and spring as water temperatures increased similar to other Puget Sound salmonids, and salmonids in general. The late spring - early summer return to fresh water occurred as river temperatures increased but was synchronous in several rivers despite differences in thermal regimes. This return time also occurred prior to when the anadromous fish could utilize the salmon subsidy from later spawning Pacific salmon. Overall, the anadromous bull trout migration timing is well defined and the early return migration to freshwater is typical of partial migration patterns of other iteroparous species.

Table 3.1: Receiver deployments by Sub-region in Puget Sound including freshwater rivers (FW), estuaries (EST) and marine (M) areas.

Receiver Area	Water Body	2002	2003	2004	2005	2006	2007	2008
Fraser River	FW, EST	0	0	6	4	12	14	14
North Puget Sound	FW, EST, M	0	0	4	9	11	20	31
Skagit Bay to Deception Pass	M	1	12	11	14	20	8	8
Skagit River	FW, EST	6	12	12	14	31	26	25
Saratoga Passage to Possession Sound	F, EST, FW	21	31	23	31	24	23	18
North Central Puget Sound	FW, EST, M			2	22	30	39	59
South Central Puget Sound[1, 2]	FW, EST, M				24	22	20	24

1. Includes northern boundary of South Puget Sound.
2. 20 receivers were deployed in 2010.

Table 3.2: Proportion of fish returning to or remaining in major Puget Sound Rivers (north to south from left to right in columns) by tagging site (north to south from top to bottom in rows) with the number of fish in parentheses.

	River of Return				
Capture Location	**Nooksack**	**Skagit**	**Stillaguamish**	**Snohomish**	**Puyallup**
Nooksack River (8)	100%	0%	0%	0%	0%
Swinomish Channel (61)	0%	100%	0%	0%	0%
Lower Skagit River (22)	0%	100%	0%	0%	0%
Skagit Bay (49)	0%	98%	2%	0%	0%
Port Susan (33)	0%	45%	48%	6%	0%
Snohomish Delta (73)	0%	53%	22%	25%	0%
Lower Snohomish River (37)	0%	22%	11%	68%	0%
Shilshole Bay (3)	0%	33%	67%	0%	0%
White River (10)	0%	0%	0%	0%	100%

Table 3.3: Marine timing during spring and summer (river exit and river entry date), and residence time of bull trout tagged in freshwater in major rivers of Puget Sound (Nooksack – NO, Skagit – SK, Snohomish, SN) and habitat locations fish resided in (Stillaguamish - ST, Nearshore - NS, River Delta - RD).

Tagging Site	River of Return	Habitat	N	Mean Distance (km)	Mean Entry	Mean Exit	Residence Time (days)			
							Mean	Min	Max	SD
NO	NO	NS	6	28.4	6-Apr	10-Jun	65.3	58.0	76.0	7.6
SK	SK	NS	13	15.0	30-Mar	9-Jul	100.0	67	133	21.8
SN	SN	NS	1	30.1	26-Mar	26-Jul	122.0			
		RD	17	14.9	26-Mar	27-May	63.1	2	128	37.2
	SK	NS	1	80.6	21-Jun	22-Jul	31.0			
		RD	4	71.0	4-Apr	12-Apr	8.0	1	25	11.4
	ST	NS	2	29.5	17-Apr	14-Jun	57.5	24	91	47.4
		ST	1	48.2	12-Apr	13-Apr	1.0			

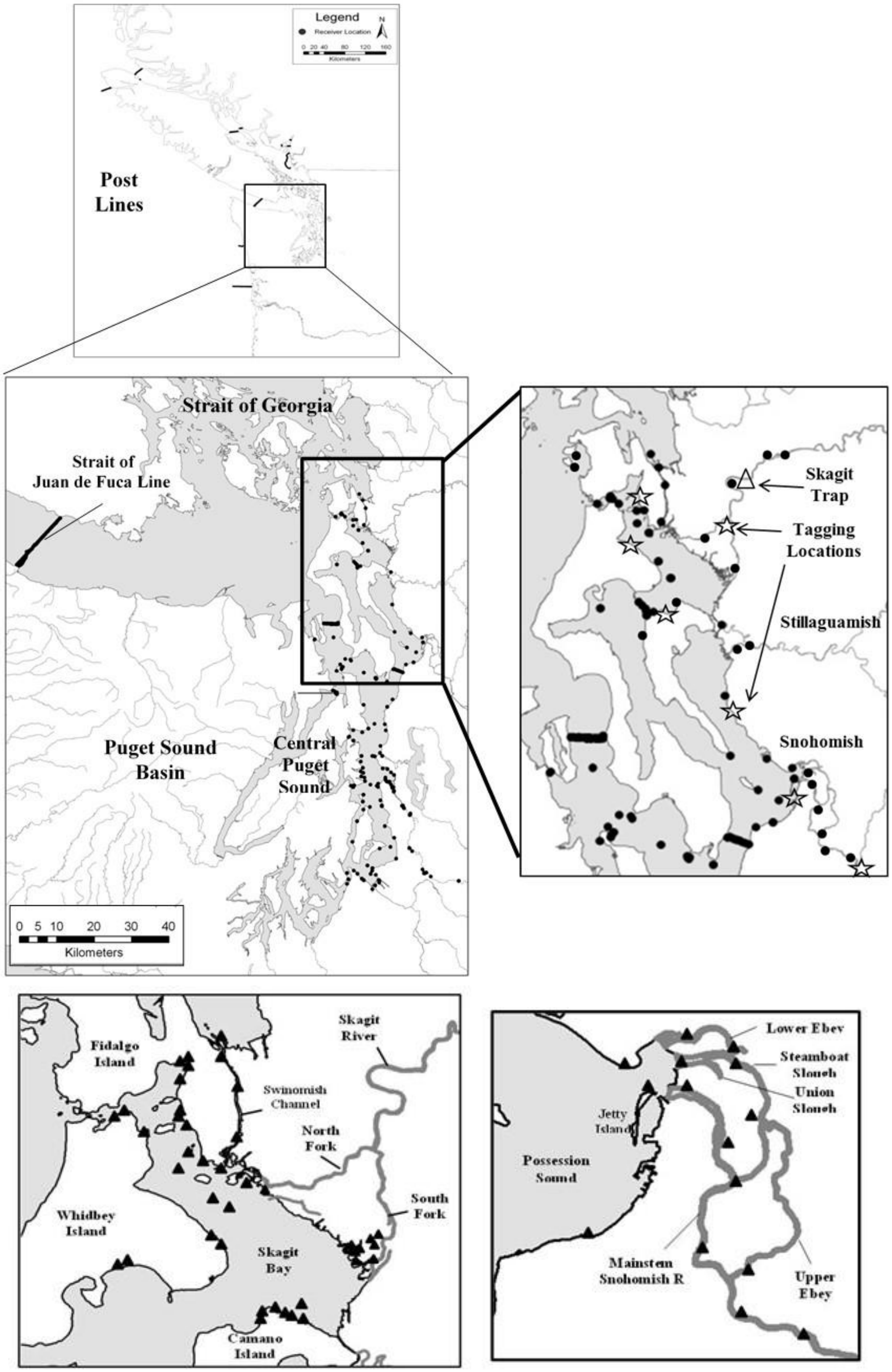


Figure 3.1: Puget Sound study area with acoustic receiver (black circle) and tagging (open star) locations from rivers and coastal waters with Skagit River juvenile trap location (open triangle) and seining areas (solid triangle) in the Snohomish and Skagit river deltas and nearby marine waters.

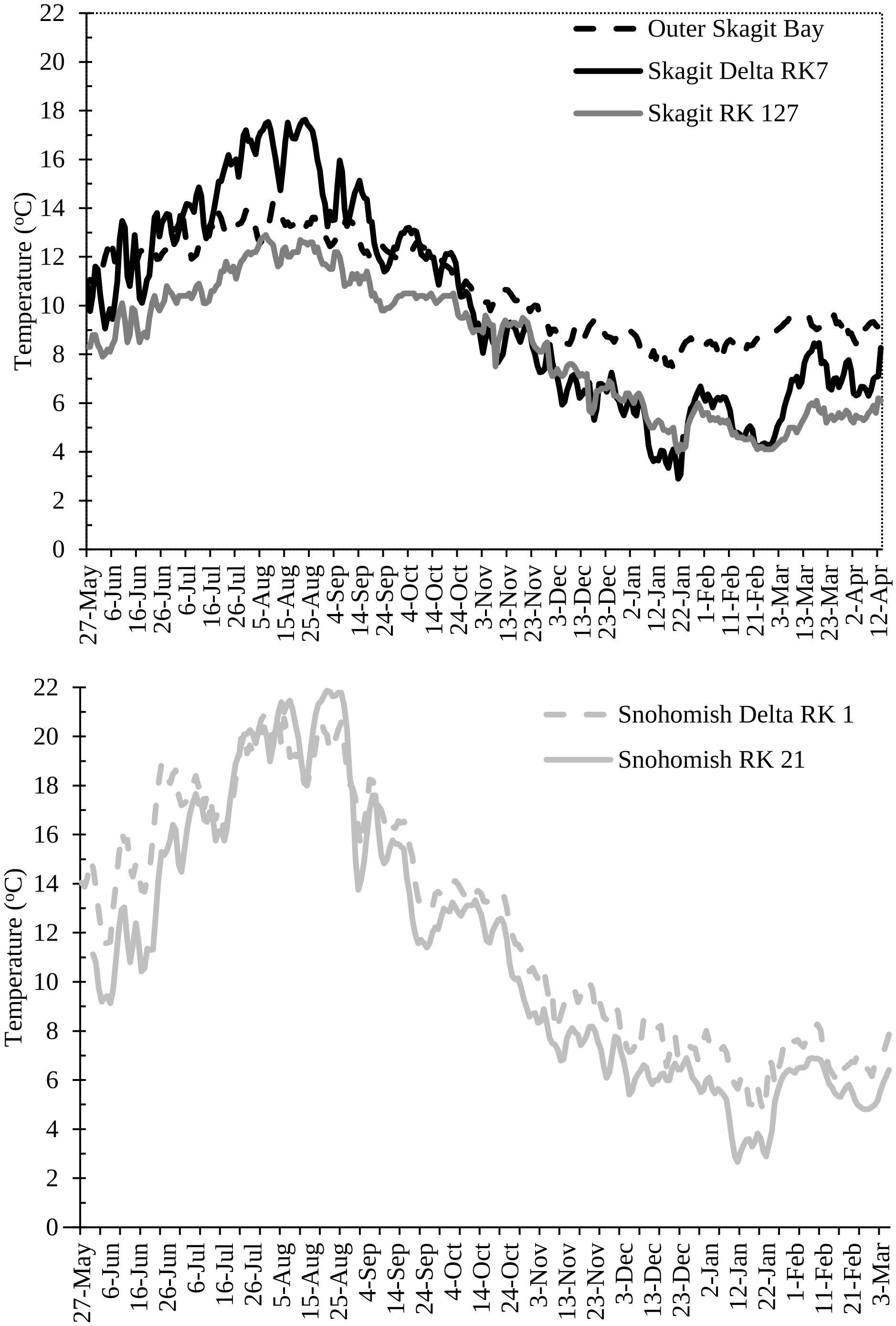


Figure 3.2: Daily temperatures from loggers for one year (2004-2005) for freshwater sites in Skagit (rkm 127) and Snohomish (rkm 21) River, estuarine river delta sites in Skagit (rkm 7) and Snohomish (rkm 1), and nearshore marine site in Skagit Bay.

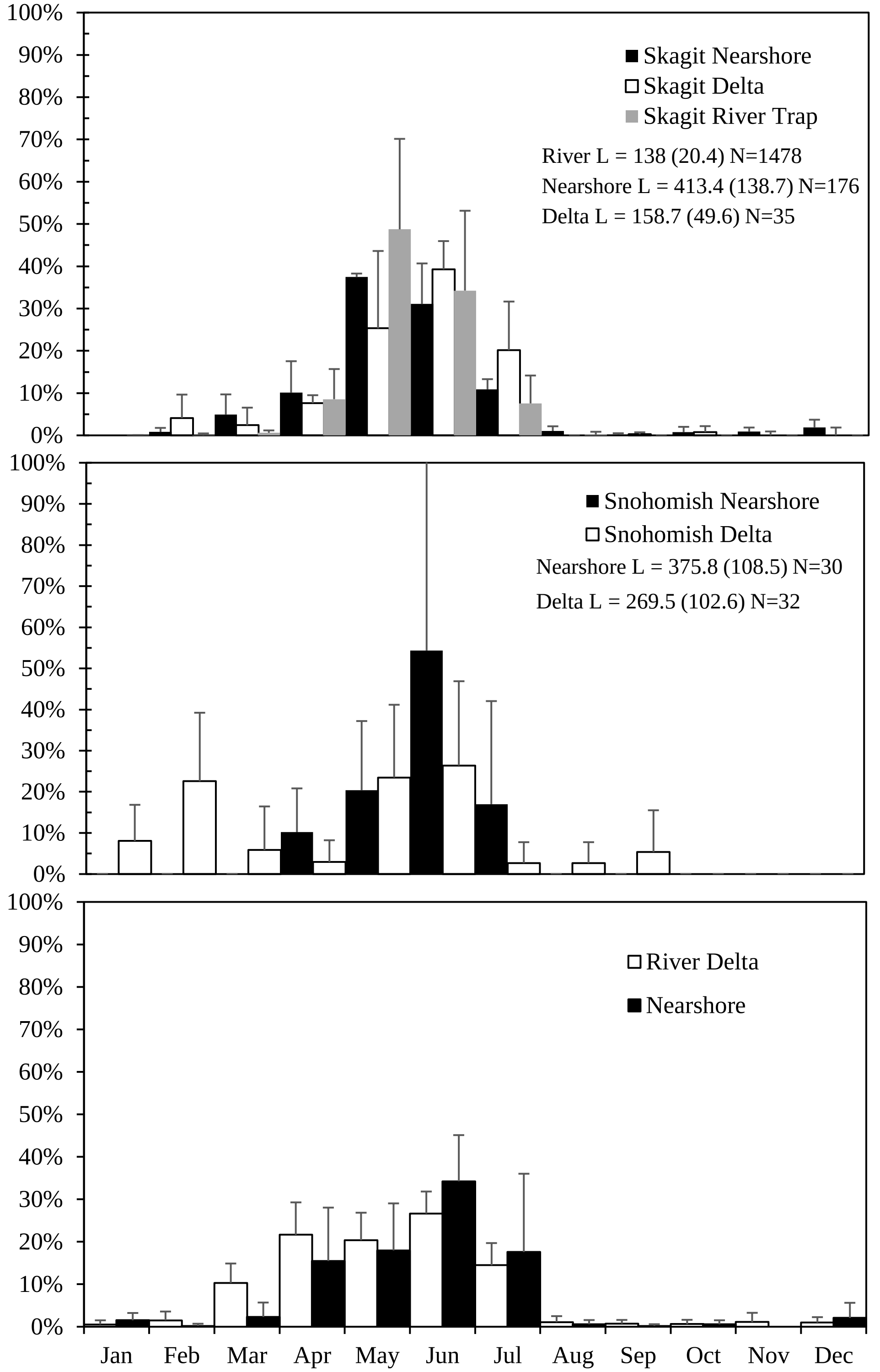


Figure 3.3: Temporal pattern (monthly with SD) of juvenile bull trout migration from the Skagit River to marine waters (trapping, 2001-2012, top) and occupancy of river delta and marine areas by juvenile, subadult and adult bull trout in Skagit (seining, 2001-2003, top), Snohomish River (seining, 2001-2012, middle), and subadult and adult bull trout in river delta and nearshore areas of Skagit, Stillaguamish and Snohomish Rivers (telemetry, 2002-2007, bottom). Fish lengths in text box as mean and SD in parentheses.

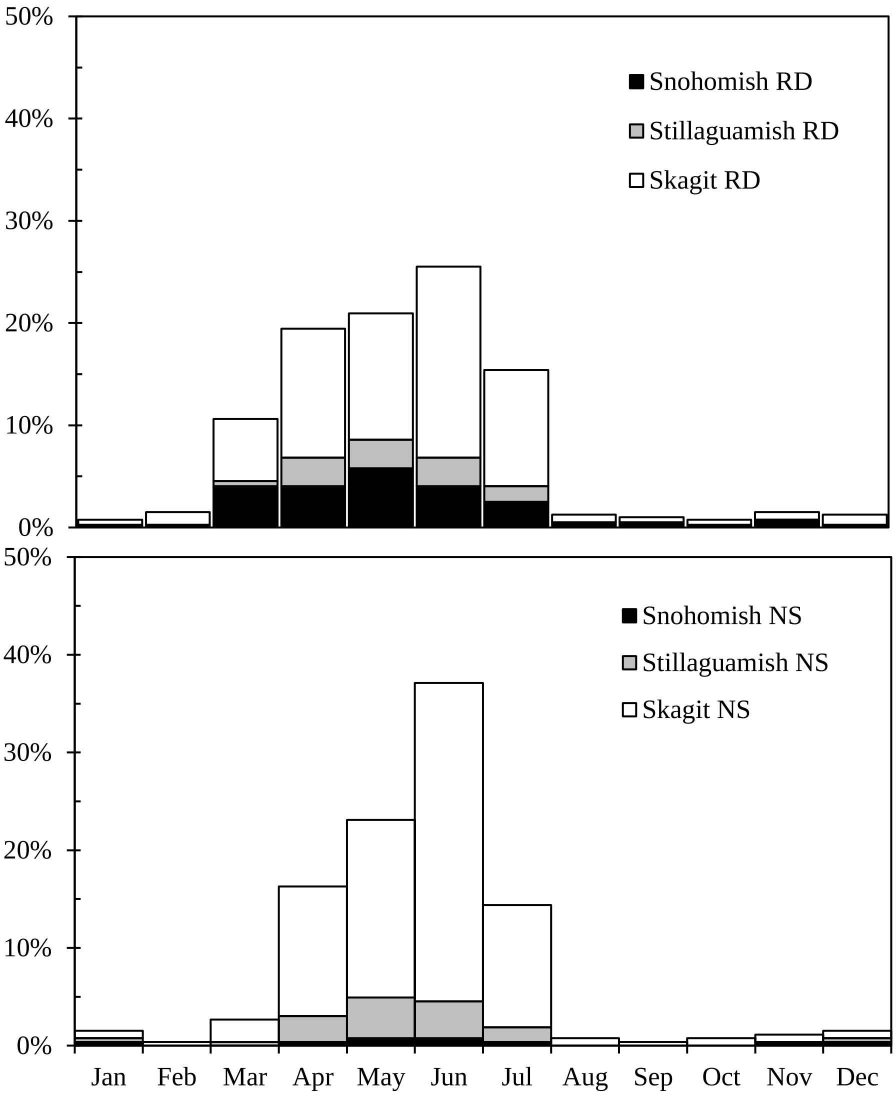


Figure 3.4: Proportion of fish by river of return (Skagit, Stillaguamish, and Snohomish) residing in river delta ("RD" top) and nearshore ("NS" bottom) areas throughout the year (telemetry, 2002-2007): Skagit N = 165, Snohomish N = 39, Stillaguamish N = 33.

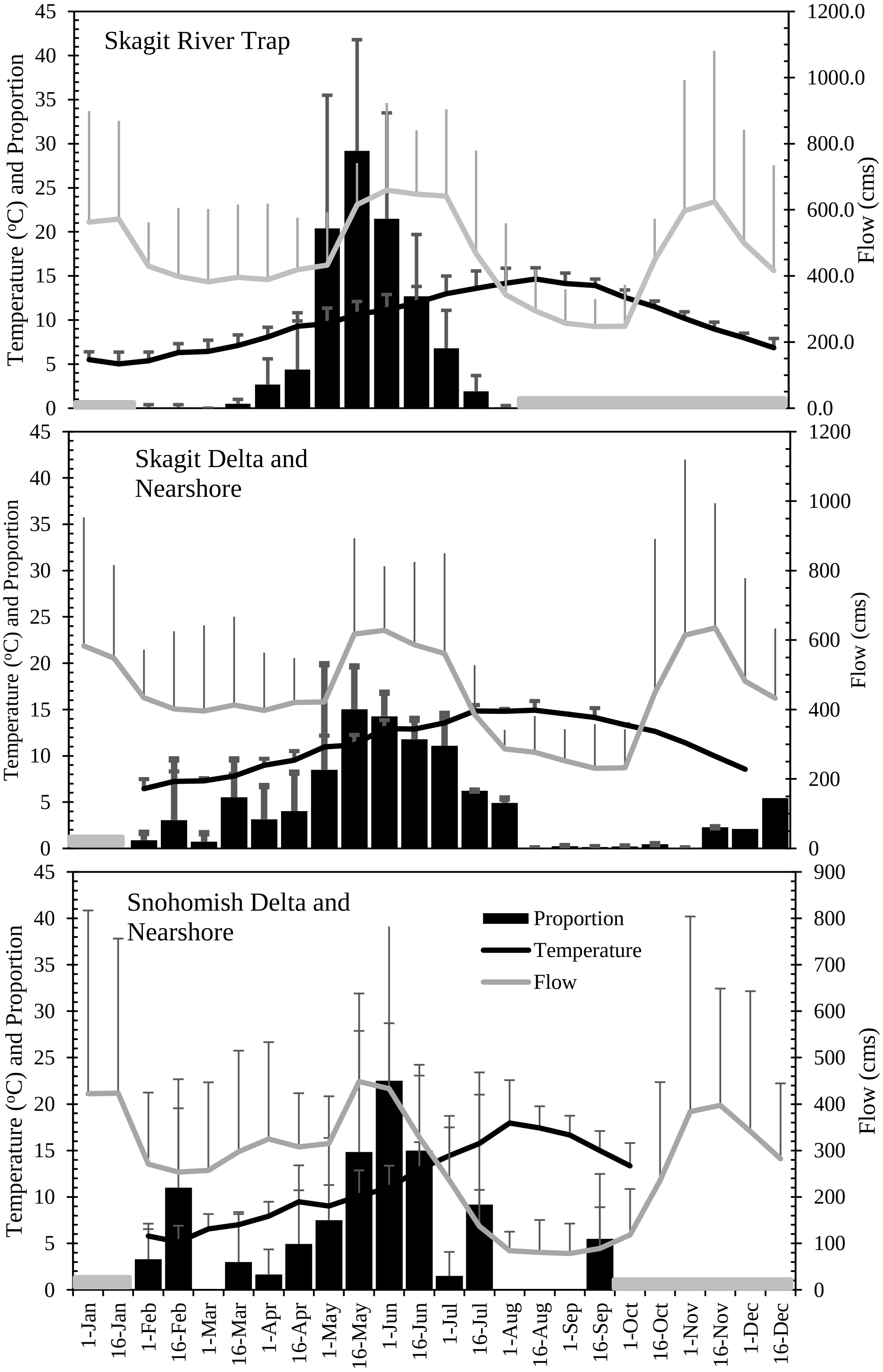


Figure 3.5: Mean (and SD) bi-weekly temperature (black line), flow (gray line) and proportion of bull trout captured (black column) by trapping in Skagit River (2001-2012, top, no data after Sep 1), seining in delta and nearshore (2001-2003, middle) and seining in Snohomish delta and nearshore (2002-2012, bottom). No data for areas with gray bar on x-axis.

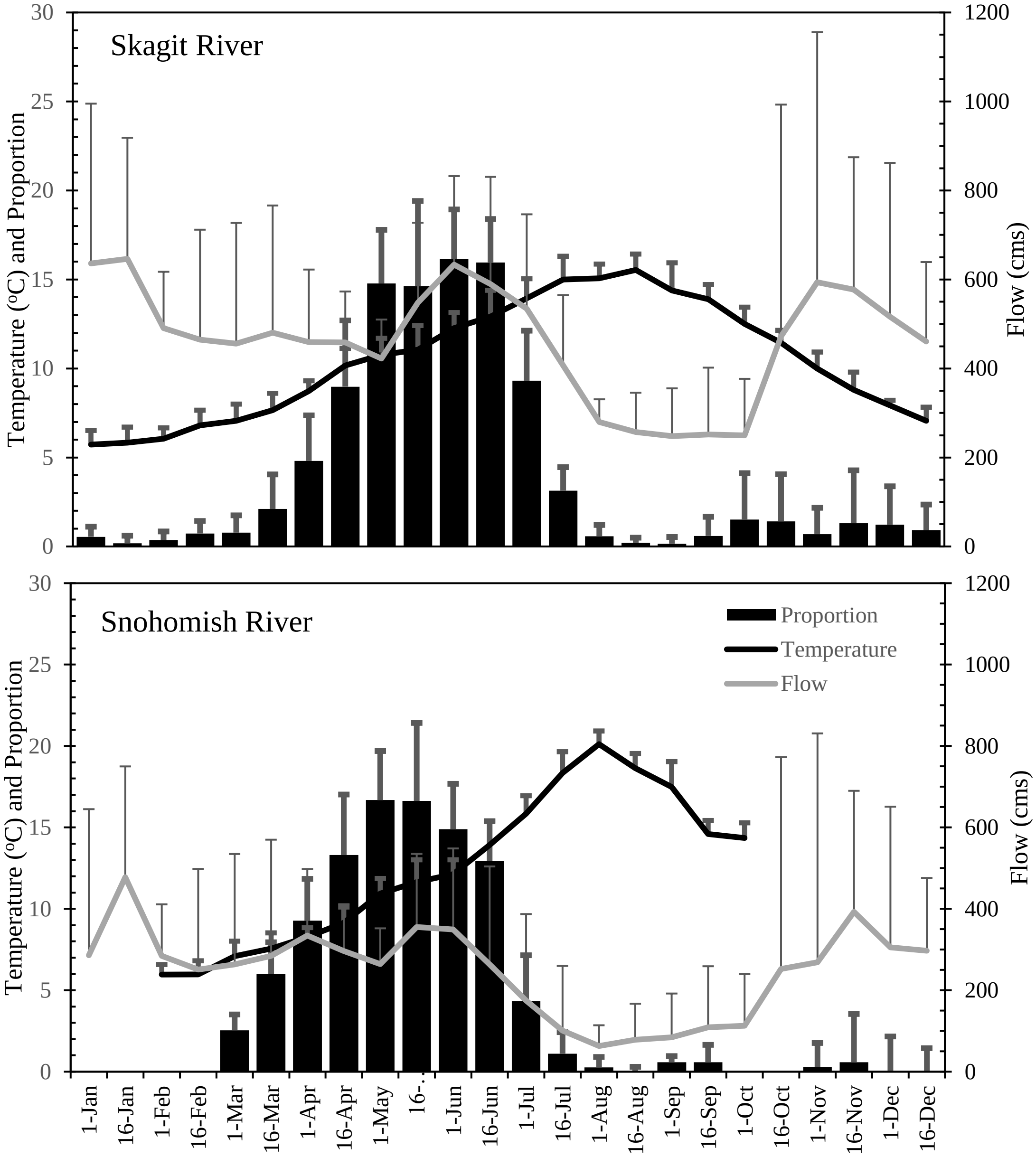


Figure 3.6: Mean (and SD) bi-weekly temperature (black line), flow (gray line) and proportion of all acoustic tagged bull trout detected (black column) in nearshore and river delta areas of the Skagit (top) and Snohomish River (bottom). The Stillagamish River is not included due to insufficient flow and temperature data.

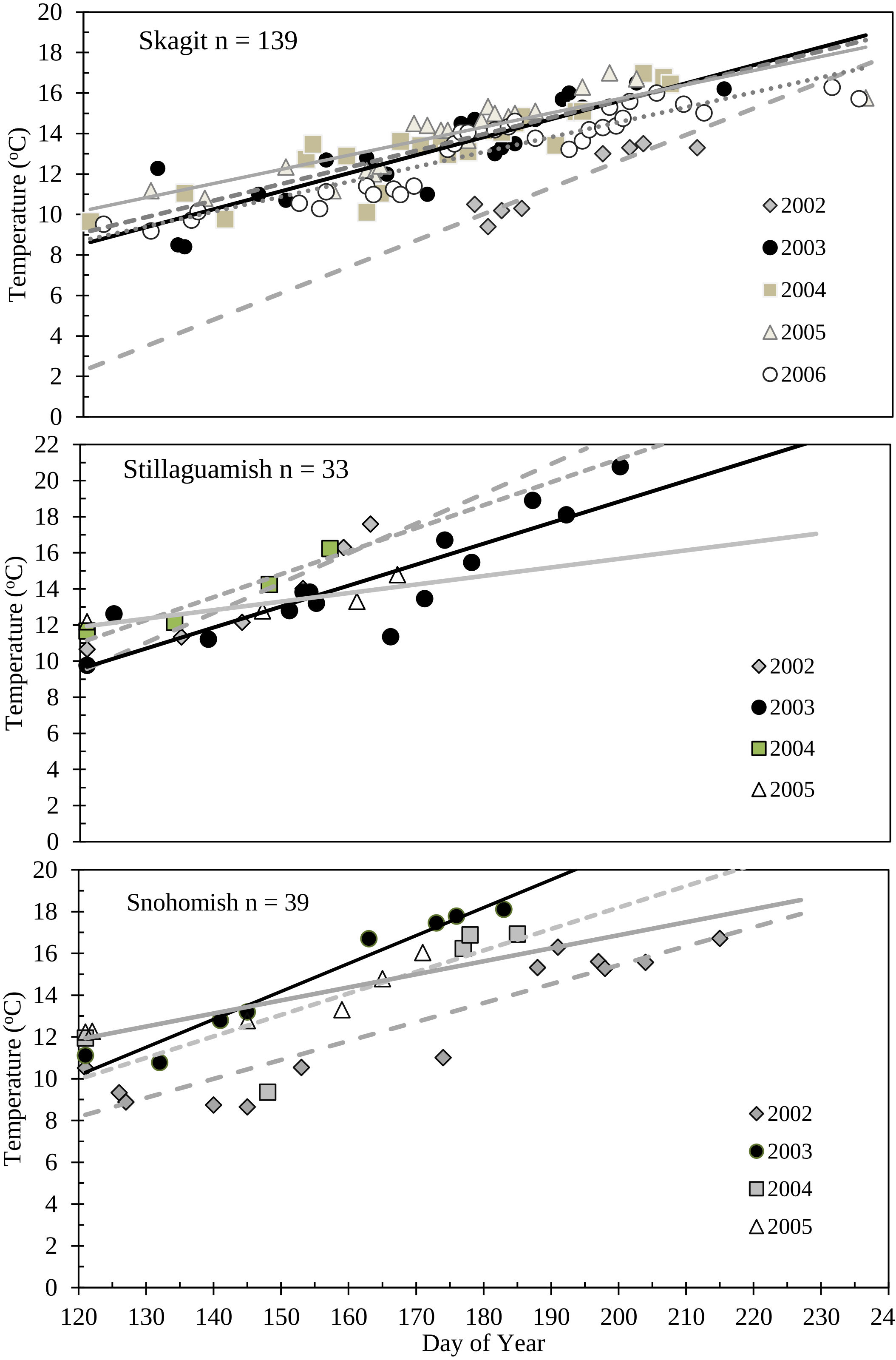


Figure 3.7: Temperature and day of the year (120 = May 2) at river entry for individual fish from nearshore and river delta areas by return river (panels) and by year. Linear regression lines are shown by year.

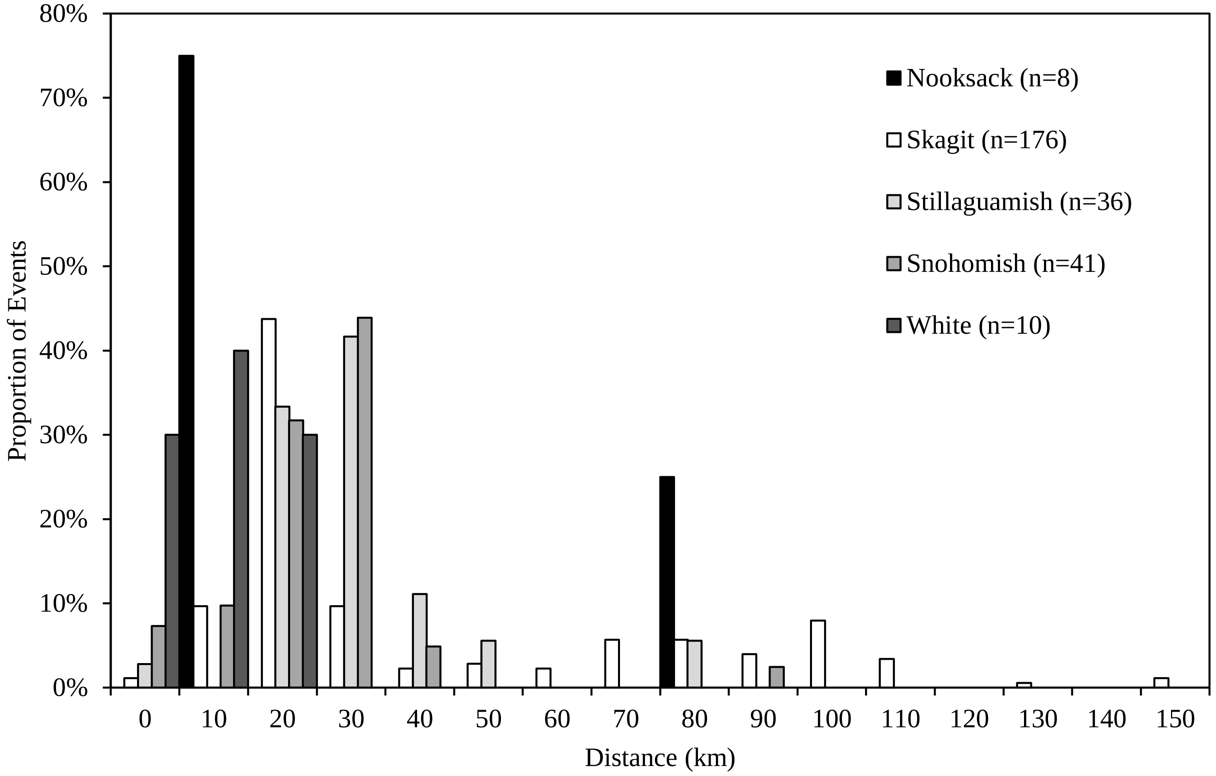


Figure 3.8: Comparison of the range (frequency) of migration distances for fish returning to rivers. The number of return events is shown in parentheses.

Chapter 4. Behavioral thermoregulation by adult Chinook salmon (*Oncorhynchus tshawytscha*) and comparison to sockeye salmon (*O. nerka*) in estuary and freshwater habitats prior to spawning

4.1 Introduction

Coastal ecosystems throughout the world have been impacted by human development, some over many centuries, and today many systems are being degraded at a rapid pace. Estuaries and their connecting waterways between rivers and marine systems are some of the most degraded because they are focal points for human development (Emmett et al. 2000). Interest in conserving and managing coastal waters is strong and widespread but resources are limited and require prioritization, particularly in systems that cannot be restored to a more natural self-sustained situation (Lotze et. 2006, Halpern et al. 2008, Vörösmarty et al. 2010). Cumulative impacts to habitat that occur in highly developed coastal areas include those from engineering for flood control, water supply, navigation and ports, tidal energy, and development in adjacent lands for industry, cities and agriculture purposes. Engineering structures include dams, locks, tidal barriers and barrages, development actions including dredging, draining wetlands, channelization and filling, rerouting waterways, and other hydrologic connections. In these highly developed areas aquatic resources such as pathways for migratory fish, fish diversity, and water quality decline, and restoration efforts often fail (Brown and Moyle 2005, Vörösmarty et al. 2010, Kadiri et al. 2012). In addition to the impacts from habitat development, climatic change is increasingly recognized as influencing terrestrial and aquatic ecosystems (Halpern et al. 2008, McClure et al. 2013).

Water temperature strongly affects a variety of processes in fishes, including metabolism, locomotion, growth, maturation, susceptibility to disease, behavior and distribution (e.g., Magnuson et al. 1980). Temperature has often been considered the abiotic "master" factor of fishes because it has such extensive effects on them (Brett 1971; Dingle 1996). For example, adult anadromous salmonids such as Pacific salmon, *Oncorhynchus* spp. and Atlantic salmon, *Salmo salar,* show a number of behavioral responses to temperature including changes in vertical distribution while migrating through marine waters (Quinn et al. 1989; Ruggerone et al. 1990; Tanaka et al. 2000; Walker et al. 2000), holding in river plumes outside estuaries (Cooke et al. 2008; Strange 2013) changing vertical distribution in turbidity maximum zones and the salt wedge in estuaries (Fujioka 1970; Brawn 1982; Olson and Quinn 1993), avoidance of warm water during upstream migration by selection of coolwater inputs from tributaries or holding in deep pools (Goniea et al. 2006), residing below the thermocline in lakes (Newell and Quinn 2005; Mathes et al. 2010), and holding in rivers until favorable conditions emerge in spawning tributaries (Berman and Quinn 1991; Strange 2010).

The transition from marine to freshwater is especially complex, as the process of thermoregulation interacts with the variation in salinity associated with different water masses, and the optimization of temperature and salinity is further complicated by the rapid onset of sexual maturation and cessation of feeding. Research has indicated that temperatures salmon experience in coastal marine waters and during upriver migration can affect survival in complex ways (Gilhousen 1990, Crozier et al. 2008; Hinch et al. 2012).

The response of adult salmon to rising water temperatures, related to climate change and altered environmental conditions, may result in a suite of proximate and ultimate outcomes in behavior, survival and population persistence (Dingle 1996; Quinn 2005; Crozier et al. 2008). Many salmon stocks located in the southern margins of their range or in other areas with higher water temperature (e.g., Sacramento, Klamath, and Fraser rivers) are at low population levels and salmon have experienced *en route* or pre-spawning mortality (Richter and Kolmes 2005; Mathes et al. 2010; Strange 2010; Eliason et al. 2011). Model predictions suggest that these declines and events are likely to continue into the foreseeable future (Yates et al. 2008; Mantua et al. 2010). The changing thermal regimes may be especially stressful for populations migrating through estuaries and river corridors that have been modified through channelization (dredging, levees) and barrier development (locks and dams), have lower water quality (e.g., increased temperature, modified salinity, reduced dissolved oxygen), altered tidal regimes and hydrology, and loss of suitable holding habitat (Hallock et al. 1970; Potter 1988; Russell et al. 1998; Schaller and Petrosky 2007; Holbrook et al. 2009).

These complex physical processes are exemplified by Lake Washington (Figure 4.1), in Washington state, USA (Williamson et al. 2009). The peak migration period for adult Chinook salmon entering the Lake Washington system is late July to early September - the warmest period of the year (Figure 4.2, top). Temperatures in the lake have been increasing, especially in summer, and are predicted to increase at greater rates than other coastal watersheds (Winder and Schindler 2004; Mantua et al 2010, Figure 4.2, bottom). Lakes have been described as sentinels for climate change because they are sensitive to climate, respond rapidly to change, and integrate information about changes in the watershed (Williamson et al. 2009). This trend in increasing temperature may dramatically affect Chinook salmon and other salmon species in this system but the nature and extent of the effects may depend in part on the behavioral thermoregulation and other tactics used by the salmon when migrating through these warming urbanized waterways.

In this study we used acoustic transmitters and archival temperature loggers to determine how adult Chinook salmon negotiate the complex marine, estuarine, and freshwater habitats from Puget Sound to their spawning grounds in tributaries of Lake Washington. They migrate through a small marine-influenced lower estuary and tidal barrier at a set of locks into a short, stratified upper estuary immediately above the tidal barrier, then move through a relatively shallow (10 m) and warm navigation canal and Lake Union (maximum depth 15 m) where temperatures in the summer are in the range of 18–25 °C and DO levels of < 5 mg/l, into Lake Washington, and from there to spawning tributaries. Our overall goal was to characterize Chinook salmon behavior during migration from salt to fresh water as they minimize exposure to high temperature, acclimate to fresh water, and avoid low DO levels. Specifically, we posed the following questions (1) how long do Chinook salmon remain in marine waters downstream of the upper estuary and its thermo-halocline; (2) do water temperatures and DO levels affect transit time in the navigation canal; and (3) upon reaching Lake Washington, do they hold below the thermocline? Assuming that the Chinook salmon tended to avoid the warmest surface waters, our second goal was to determine whether they (1) occupied temperatures that minimized metabolic expenses during the period of fasting prior to spawning, (2) occupied temperatures that reflected a balance between thermal efficiency, osmoregulation and DO levels, or (3) displayed a gradual decrease in thermal preference consistent with thermal effects on maturation (Newell and Quinn 2005). Finally, we compared the data collected in this study with comparable data on sockeye salmon (Newell and Quinn 2005) to contrast the patterns of migration and behavioral thermoregulation by these two species whose timing of arrival and spawning overlap broadly in this system. Chinook salmon are more tolerant of warm water than are sockeye salmon, so we predicted that the former would occupy warmer water during their migration in this system.

4.2 Methods

4.2.1 Study Area

Puget Sound is a large (3700 km^2) Northeast Pacific coastal system located in western Washington, USA and bordered by British Columbia to the north (Figure 4.1). The Lake Washington watershed covers 1274 km^2 and flows from tributaries of lakes Sammamish and Washington through a navigation channel (henceforth, the ship canal) through the north end of Lake Union, to the Hiram Chittenden Locks ("the locks"), and into Shilshole Bay. The area immediately upstream of the locks (Salmon Bay) has a saltwater wedge and we refer to this as the upper estuary, and refer to the area from the locks (large lock) down to Shilshole Bay the lower estuary. The marine-influenced lower estuary has summer mean temperatures of 12-13 ^{o}C and salinity from 15-30 ppt. The salt wedge intrudes into the ship canal above the locks for up to 6 km (nearly to Lake Washington) but the highest salinities (1-20 ppt) and most mixing occurs within 1 km of the locks (Figure 4.1 inset). The ship canal is 12.5 km long from Shilshole Bay to Lake Washington (10.8 km from locks to lake) with a mean depth of 9 m and includes Lake Union which is similarly shallow (mean depth: 10.5 m, 16 m maximum). Lake Washington has a surface area of 87.6 km^2, a mean depth of 32.9 m (maximum depth: 65.2 m), and a summer epilimnion depth at about 10 m. Lake Washington's two largest tributaries are the Cedar River (at the south end) and Sammamish River (at the north end); the latter drains Lake Sammamish (21 km^2 surface area, mean depth 18 m; King County 2011).

The locks include a tidally influenced fish ladder, small lock chamber (8 m deep), large lock chamber (16 m deep), spillway bay (5 m deep), and a large drain above the large lock (16 m deep) to return salt water to Puget Sound. The large lock itself is used by migrating salmon and is included in the area defined as the lower estuary. The locks physically separate the freshwater and saltwater systems, eliminating tidal influence above the locks, though there is some intrusion of salt water. In contrast, the tidal range below the locks varies up to 3.7 m over one cycle. The exchange of freshwater and salt water occurs predominantly in localized pulses during lockings, resulting in unusual circulation patterns within the estuarine portion of the ship canal. Salt water enters when the locks lift vessels from Puget Sound up and into the ship canal, so temperatures in the large lock chamber can change over a range of 9 ^{o}C in less than an hour. Saltwater intrusion in spring and early summer is usually restricted to the lower 1.5 km of the ship canal but by late summer it reaches Lake Union (4-6 km upstream) although at lower concentrations (0-2 ppt) than near the locks (0-15 ppt).

Vertical stratification in temperature and salinity occurs in Puget Sound, below the locks, within the large lock, in the salt wedge in Salmon Bay, in the ship channel (salinity only) and Lake Union, and temperature stratification occurs in Lake Washington and Lake Sammamish. Low dissolved oxygen (DO) levels (< 5 mg/l) occur near the bottom from the upper estuary several km upstream starting in August. The tidal barrier and hydrologic management of the lake system eliminates the influence of flow fluctuations on the timing of freshwater entry by adults in contrast to a natural river system.

The primary migration period for adult Chinook salmon is from late July to early September, when temperatures are highest (Figure 4.2); sockeye salmon enter earlier, from early June to August with a peak in early July. The Chinook salmon spawn in the Cedar River and in tributaries to the Sammamish River, and are also produced at a hatchery on Issaquah Creek upstream of Lake Sammamish, and at the University of Washington (UW) at the head of the ship canal, just below Lake Washington.

4.2.2 Fish Capture and Tagging

Our goal was to capture and mark approximately 185 Chinook salmon or 1.5% of the average Lake Washington adult return in 2005 and again in 2006. The Washington Department of Fish and Wildlife and R2 Resource Consultants conducted weekly purse seining and tagging in the lower half of the large lock from early August through early September. The fish were released immediately below the locks in the lower estuary (see Goetz et al. 2001 for details on the capture methods).

We tagged a total of 368 maturing adult Chinook salmon with a combination of acoustic tags (approximately 25% of tagged fish), PIT-tags (all fish), and archival temperature data loggers (all fish), using tagging techniques similar to Newell and Quinn (2005; Table 4.1). A PIT tag was injected into the body cavity of each fish. The fish ladder had PIT tag detectors in a pool immediately upstream of the exit, indicating the proportion of fish using the ladder. We used archival loggers attached externally just behind the dorsal fin to record the water temperatures of individual adult Chinook salmon. We attached model iBCod (Alpha Mach) type Z (high resolution +/- 0.125 °C, precision +/- 1 °C, temperature range of -5 to 26 °C), a size appropriate for tagging 50-100 cm fish, to the salmon using nickel pins and vinyl disks. The temperature loggers were recorded once every hour for 95 d. A total of 95 Chinook salmon were also tagged by gastric implant using Vemco V13-1L (22), V13P-1L pressure sensors (63) and V9-6L (11) acoustic tags with 20-60 and 30-90 second minimum and maximum pulse rates. The detection range of the tags in marine and deep areas in freshwater was about 100-400 m for the V9 and 200-600 m for the V13 tags; detection ranges for all tags declined to about 10-100 m in shallow areas.

The archival tag data were compared to data from a similar study on sockeye salmon during 2003 (Newell and Quinn 2005). In total, 257 sockeye salmon were captured in a trap in the fish ladder at the locks and tagged with iBCod tags (2-h record rate) over 9 d from 16 - 28 July 2003, near the typical peak of the migration period. Thermal histories were determined from the tags recovered from 37 individuals, mostly in the Cedar River.

4.2.3 Tag Data Retrieval

Acoustic receivers (Vemco VR2) were installed in marine, estuary, and freshwater areas (Figure 4.1, Appendix Table 4.1) before the Chinook salmon were tagged and released in summer and were then retrieved after the normal spawning season in fall. In the Lake Washington system, 16 receivers were deployed in 2005 and 21 in 2006. In both years, receivers were deployed in Shilshole Bay, the locks, the ship canal, Lake Washington, the Cedar River and Sammamish River deltas, and in 2006 in Lake Sammamish. A receiver was deployed in the large lock chamber in both years but only limited data were collected in 2006 due to damage to the receiver during lock operation. Transmitter codes in 2005 included 32 tags with regular acoustic receiver programming, whereas 10 tags used a custom-code program. Marine receivers deployed earlier that year were not programmed to detect the custom-code so no marine detections were logged for those tags. All retrieved data were checked and erroneous records, inconsistencies, and data anomalies were removed. Data from other researchers were obtained either through direct contact or from on-line databases (hydra.sounddatamanagement.com/; www.postcoml.org/). Four sets of antennae and PIT tag readers were installed in the fish ladder just downstream of the viewing chamber pool; multiple detections indicated the direction of movement and likelihood of successful passage.

All but one acoustic-tagged fish were detected at least once in the basin (42 of 42 in 2005 and 52 of 53 in 2006), and 63 PIT-tagged fish were detected in the fish ladder (40 in 2005 and 23 in 2006). Archival tags were recovered each year in various locations (2005: 59 tags; 2006: 54 tags), including spawning streams and the Issaquah Creek and UW fish hatcheries. Data were also collected from 28 fish tagged with both archival and acoustic tags (11 in 2005 and 17 in 2006; Table 4.1). Data from sockeye salmon were collected from 36 tags recovered in the Cedar River between 3 October and 18 December 2003 and 2 tags from fish caught in nets.

4.2.4 Environmental Data

To identify the thermal regime experienced by each fish and the vertical strata they used, we obtained data from fixed stations and mobile water quality profiles collected by various agencies (Table 4.2) indicating salinity in marine and estuarine waters, and temperature and DO in all waters. In 2013, we collected hourly measurements of DO above the lock and detailed data in the large lock during one day each year of the study by measuring temperature and salinity changes over a series of lock filling events. We monitored temperature hourly in the large lock during the course of the study using a thermistor at 10 m depth (2005) and near surface (2006). In general, the temperatures fish encountered during migration to Lake Washington tributaries were coldest in Puget Sound (range 10-18 ^{o}C), much warmer in Salmon Bay (15.4-22.6 ^{o}C) and the ship canal (17.3-22.5 ^{o}C), and variable with depth in Lake Washington (8.5-22.5 ^{o}C; Table 4.3).

4.2.5 Data Analysis

We used telemetry data to identify horizontal and vertical distributions of Chinook salmon and their movements and behavior in Puget Sound marine, estuary, and freshwater of

Lake Washington We combined data from telemetry and archival temperature loggers to determine the thermal experience of individual adults during their migration. Fish were excluded from analysis if they apparently died, were not detected at a receiver upriver of the locks, or if the archival tag recovery date and location could not be verified. Some fish were collected at the UW hatchery or the last acoustic detection was near the hatchery entrance. This hatchery is located along the ship canal and so movements within the canal could not be compared to fish migrating into and through Lake Washington. Preliminary analysis indicated that the UW-origin fish remained in the ship canal longer than would otherwise be the case because a gate prevented them from entering the hatchery until early-mid-October. For this reason, we excluded data from the 44 fish returning to the UW hatchery.

Analyses were designed to describe the behavior and environmental experience of fish by recovery location and by segments of the migration route. We also analyzed differences by weekly tagging group and between years. The study reaches were 1) marine waters outside Shilshole Bay to the locks (Puget Sound), 2) upper estuary above the locks in Salmon Bay (Locks), 3) ship canal and Lake Union (Ship Canal), 4) Lake Washington including north tributary delta (Sammamish River) and south tributary delta (Cedar River), 5) Sammamish River, 6) Lake Sammamish outlet area in the Sammamish River, and 7) tributaries including the Cedar and Sammamish rivers, and Issaquah, Cottage, and Kelsey creeks. We combined study reaches into larger areas for comparison of thermal regimes for temperatures fish experienced: marine-lower estuary (Puget Sound to include large lock below tidal barrier), upper estuary (above the tidal barrier), entire estuary (Puget-Sound to upper estuary), ship canal, lake (Lake Washington and Lake Sammamish), and tributary (spawning streams).

Telemetry data were used to determine the residence time and thermal experience of fish in different parts of the migration route. Residence time was defined by the date and time of first and last detections in each migration segments. For fish with only archival temperature data, we inferred the transitions between segments by comparing that fish's temperature record with those of fish carrying both archival and acoustic tags (n = 5 in 2005 and n = 12 in 2006; Table 4.1; Figures 4.3 and 4.4, top). Residence time by migration segment (measured by acoustic or archival tags) was evaluated by ANOVA with year and tagging week as factors, using the duration of residence and also the proportion of the total time spent in a migration segment (segment time/total travel time).

Distinct thermal regimes included marine, lower estuary, upper estuary, ship canal, lakes, and tributaries (examples, Figure 4.3 and 4.4, top), distinguished by the thermal signatures of fish with known locations and temperatures recorded. Similar to residence time, for fish with acoustic tags the depth recorded on the receiver was compared with ambient temperatures at that depth strata and location, and archival tag data were compared to distinct thermal signature of dual-tagged fish or to ambient conditions (locations in Table 4.2). In regimes with vertical stratification, data on the fish's depth or temperatures were linked to the thermo-halocline (in marine and estuary areas) and the thermocline in the lakes to calculate the thermal experience of individual adults. Thermal refuges were defined as locations where fish resided at least 12 h (e.g., Goniea et al. 2006, Strange 2012). Use of thermal regime areas and thermal refuges was determined to the nearest hour by comparison of ambient marine or freshwater temperature with archival temperature loggers and fish with dual tags.

Mean daily temperatures experienced by migrants were calculated from archival tag records of temperatures experienced by fish at depth (*n* = 68 fish for non-UW origin). The accumulated degree days (DD, mean daily temperature exposure above 0 °C) for each fish were calculated by summing the mean daily temperatures experienced by a given migrant during the entire migration or for specific migratory reaches. To assess cumulative stress, each mean daily temperature that exceeded thresholds of 18.0 °C and 20.0 °C was also summed for each migrant. The two thresholds are associated with stress response in Pacific salmon (McCullough et al. 2009, Eliason et al. 2011), and potential changes in behavior for thermoregulation (e.g., Berman and Quinn 1991, Goniea et al. 2006). We compared the total number of days exceeding 18 °C and total migration time to tributary entry.

4.3 Results

4.3.1 Chinook salmon movements and residence time

Transmitters in 94 Chinook salmon provided over 450,000 detections for up to 61 days in 2005 and 2006; transmitter failure precluded data from one other fish. Most (60%) of the fish were detected at least two weeks after tagging. Forty percent of the fish entered marine waters, leaving the lower estuary for some period, and the final detection locations included 10.5% in marine waters, 16.8% in the lower estuary, 5.3% in the upper estuary, 17.9% in Lake Washington and 49.5% in tributaries. The telemetry data set was reduced from 94 to 62 fish after removing fish that had transmitter failure or malfunction limiting the number of detections (9.5%), died or had a regurgitated tag which limited the data (7.4%), left the watershed (13.7%), or remained in the lower estuary (7.4%).

Many Chinook salmon moved directly upstream along the migration corridor but others moved back and forth at various places along the route. After entering the lower estuary following tagging, 51% of acoustic tagged fish moved continuously upstream, 21% returned once to Puget Sound, 16% returned twice, and 13% returned three or more times. To reach the upper estuary, 17% of the fish used the fish ladder and were detected by the PIT tag reader and 83% used the large locks. After reaching the upper estuary, 62% of the fish continued upstream, 21% returned once to the lower estuary, 9% returned twice, and 8% returned three or more times.

Individual Chinook salmon displayed distinct patterns of thermal experience, resulting from their duration in different areas along the migration route. From warmest-to-coolest, these patterns were: 1) short duration in the lower estuary, followed by long duration in the upper estuary and lake; 2) short duration in the lower estuary, long duration in the upper estuary, and short duration in the lake; 3) long duration lower and upper estuary and short duration in the lake, and 4) long duration lower estuary and lake and short in upper estuary. In the upper estuary, Chinook remained below the thermo-halocline and occupied cooler temperatures in the late afternoon and evening and rose in the water column to shallower depths during the rest of the day, while a number of fish returned to the lower estuary. In the lake, Chinook salmon performed repeated excursions above and below the thermocline.

The total time to reach spawning grounds was longer in 2005 than 2006 and was longer for fish tagged earlier in August than later in both years (Table 4.3). The salmon took longer to move through the lower estuary (from Puget Sound to Salmon Bay) in 2005 than 2006 but moved through the upper estuary faster in 2005 than 2006. Once they exited the upper estuary, Chinook salmon moved quickly (mean 0.6 d) through the 10.8 km from the ship canal to Lake Washington. The fish spent on average 7.9 d in Lake Washington, migrated through the Sammamish River in 7.5 d and spent 4.8 d in Lake Sammamish.

To determine if residence time in Lake Washington was influenced by time spent in the entire estuary we evaluated the proportion of time a fish spent in each of the segments using linear regression. The proportion of total residence time in the estuary (lower + upper) did not vary by year or tagging group (mean 47.1%, SD 17.9%, Table 4.3). The proportion of time spent between the two estuary segments ranged from a longer lower estuary period with short time in the upper estuary to a short lower estuary period to long upper estuary. The proportion of total residence time in the estuary resulted in trade-offs with residence in Lake Washington, with a longer estuary period generally resulting in a shorter time in the lake, and a short estuary period corresponding to a longer time in Lake Washington ($R^2 = 0.4$, $P < 0.001$).

4.3.2 Thermal Experience in relation to water stratification

The depths occupied by Chinook salmon varied by reach and were influenced by bottom depth and the presence or absence of thermal stratification (Figure 4.5, Table 4.5). Chinook salmon used a wide range of depths in the open waters of Puget Sound from near surface to > 150 m (mean 15 m in 2005, 20 m in 2006). In the cooler highly-mixed lower estuary, most detections were at depths < 5 m and ship canal, between 5-15 m in open waters of Lake Washington, and less than 3 m near tributary deltas. In the large lock and upper estuary, they remained near the bottom at depths of 10-14 m (Figure 4.6, top). These latter locations contain a bisected salt wedge, a zone of dynamic short-term mixing of warm fresh water (20-23 °C) and cold salt water (12-15 °C) environments with filling of the large lock. The large lock and a small area of the upper estuary have a halocline at depths below 10-m, with the upper estuary halocline (19.5 °C) averaging 4 °C warmer (e.g., August) than the large lock (15.5 °C). Dissolved oxygen (DO) levels at lower depths in the upper estuary ranged from 5.7-7.1 mg/l (13-10 m) while in Lake Washington DO was 6.4-7.4 (13-10 m).

Overall the upper estuary was slightly warmer (20.8 °C) than Lake Washington (20.2 °C) at depths from 2 to 10-m, while Lake Washington was significantly colder than the upper estuary at 12-m (17.9 °C vs 19.6 °C) and at all greater depths (Table 4.4). By year, 2005 was

1.3 °C warmer than 2006 at all depths above 12 m in the upper estuary and 0.4 °C warmer in Lake Washington at depths above 10-m. By month, temperatures in the upper estuary were similar at each depth between August and September in 2005, while in 2006 temperatures were more than 2.0 °C cooler in August than September at each depth. In Lake Washington temperatures in August at depths less than 10-m were slightly warmer in 2005 than 2006 while temperatures were similar each year in September; in both years August was 1-2 °C warmer than September.

In total, 60,406 temperature records from archival data loggers were collected for Chinook salmon prior to entering spawning tributaries (mean: 875 records per fish, range: 477 - 1477 records). About 15% of the records were assigned to the lower estuary, 31.3% to the upper estuary, 1.4% to the ship canal, 21% to Lake Washington, 19.7% to the Sammamish River, and 11.6% to Lake Sammamish. In both years, most individuals experienced a wide range of water temperatures with typical minima of 9–12 °C and maxima of 20-22 °C (examples in Figure 4.3-4.4, top). Diel fish temperature fluctuations were evident in all reaches, but daily ranges were largest (up to 4-6 °C) in Lake Washington and Lake Sammamish, moderate in the estuary and river (2-3 °C), and smallest in ship canal (1-2 °C). The highest temperatures and greatest change in temperatures fish experienced was from the time of entry (lower estuary, mean 15.1 °C) in the fish ladder to exit (surface of upper estuary, mean 21.6 °C) with an average 2-hr change of 6.4 °C.

As was expected, Chinook salmon utilized all migration segments as thermal refuges from the lower estuary to the lake (remaining longer than 12-24 h), except in the ship canal, where almost all traveled the 10.8 km in less than 1 day. The typical acoustic tagged Chinook salmon behavior in the estuary showed multiple days holding below the thermo-halocline in the lower estuary in the large lock (mean depth 10-m; salinity range 12-27 ppt) and upper estuary (mean depth 13-m; range 1-18 ppt) (Figure 4.6, top). Temperatures at the most often used depths varied markedly between the large lock (14-17 °C) and the upper estuary above the locks (19-21 °C). In the upper estuary, fish experienced warmer temperatures in the morning (mean 19.9 °C) as their depth shallowed after dawn (~ 11-m), through late morning and then increased depth (~ 13-m) into the evening with lower temperatures (18.6 °C) (Figure 4.6). Chinook salmon in Lake Washington utilized depths from near-surface to greater than 20 m, above and below the thermocline (Figure 4.3-4.4). Most (73%) of temperatures were 15-20 °C, corresponding to depths near the thermocline (10-15 m) (Figure 4.7). By year, 2006 had the highest proportion of temperatures at shallow depths (21%) compared to 2005 (4%). Chinook salmon occupied shallow depths primarily near the river deltas.

The maximum temperatures experienced by individual Chinook salmon were 22.6 °C (2005) and 22.5 °C (2006). The average temperature maxima among fish were equal for both years (21. 4 °C), with the warmest temperatures in the upper estuary (22.6 °C), Lake Washington (22.6 °C), ship canal (22.5 °C) and Lake Sammamish (21.5 °C) (Figure 4.8). All salmon experienced one or more 12-24 h periods of temperatures > 18 °C, and 85% (74% in 2005, 94% in 2006) had one or more periods > 20 °C. Overall, 40.1% of all the records were > 18 °C and 2.1% were > 20 °C but the extent of exposure to warm water was greater in 2006. In 2005 31.5% of the records were > 18 °C and 1.7% > 20 °C compared to 49.2% and 2.6%, respectively, in 2006. Chinook salmon were not exposed to water > 18 °C in Puget Sound, but had extended exposure in the upper estuary (98% of daily mean temperatures in August) and in Lake Washington (45% of daily means in September > 18 °C).

Total degree days (DD) experienced varied between years and depended on the number of days at large ($R^2 = 0.99$, $n = 35$ in 2005, $R^2 = 0.67$, $n = 34$ in 2006; Figure 4.9). The average daily thermal experience for individual salmon ranged between 9-22^{o}C but most were between 15-19 ^{o}C and the average was 17.1 ^{o}C for an average accumulated 632 DD (16% of fish had 300-500 DD, 52% had 500-700; and 32% had 700-1050).

<u>Sockeye salmon</u>

All except four of the 37 tagged sockeye salmon spent several days (mean 3.6 d, SD 2.8 d) after release at continuously high temperatures (mean 18.4, range 14.6-22.5) in the upper estuary and ship canal prior to entering Lake Washington and then experienced an abrupt reduction in temperature (10–11 °C, example Figure 4.3, bottom) in cooler water that could only have been found below the lake's thermocline. Four sockeye spent distinctly longer periods in warm water areas (mean 47.7 d, SD 16.7; example Figure 4.4, bottom). No intermediate periods of occupancy in warm water were observed. The 33 sockeye salmon that did not spend extended periods in the ship canal spent from two to four months in Lake Washington (mean 88.3 d, SD 15.7 d) were restricted to these fish. During their period in the lake, the temperatures available to them ranged from 8.4 to 25.8 °C but 92% of temperature records in August and 95% of in September were between 9.0 and 11.0 °C.

There were distinct differences between Chinook salmon and sockeye salmon in their use of thermal refugia as shown by the mean temperatures experienced and duration of time spent in migration segments (archival estimates). Overall, Chinook used a variety of refugia but still experienced significantly warmer total mean temperatures than sockeye, which utilized a single refuge at depths below the thermocline in Lake Washington (17.7 vs 10.6 °C, *t*-test: $P < 0.001$).

In the upper estuary and ship canal Chinook tagged in August experienced slightly warmer mean temperatures than sockeye tagged in July (19.0 vs 18.4 °C, *t*-test: $P < 0.05$), while in the lake Chinook moved above and below the thermocline and experienced much warmer mean temperatures than sockeye that held below the thermocline (17.4 vs 10.2 °C, *t*-test: $P < 0.001$). Residence time in the upper estuary and the ship canal was longer for Chinook salmon than sockeye (11.1 vs 3.6 d, *t*-test: $P < 0.001$) while in the lake Chinook spent significantly less time than sockeye (7.7 vs 88.3 d, *t*-test: $P < 0.001$).

4.4 Discussion

In the modified Lake Washington estuary, Chinook salmon encountered discrete habitats within 0.5 km that graded from cool marine waters of the lower estuary to warm stratified brackish waters of the upper estuary, with a temperature change of 5-9 °C. Faced with this very unnatural, abrupt transition of physical habitats and thermal regimes, Chinook salmon occupied thermal refuges in stratified marine and freshwater areas. Most Chinook salmon left the estuary after tagging and spent a few days in Puget Sound, often below the thermo-halocline. Upon return to the upper estuary they either held in the salt wedge for a week or more or went back to Puget Sound again. To reach the upper estuary most Chinook migrated through the locks rather than the fish ladder, and often resided below the thermo-halocline in the lock, where temperatures were intermediate between those in Puget Sound and the upper estuary. The warmest and likely most stressful conditions were encountered in the upper estuary, which received little marine input and was dominated by the warmest surface waters from Lake Washington and Lake Union. Fish in that location occupied the deepest waters below the thermo-halocline for extended periods prior to migration to Lake Washington while balancing temperature and DO constraints. Chinook salmon tagged during the highest temperature periods in early August remained for the longest period of time in the estuary (lower and upper) before migrating rapidly upstream through the warmer ship canal. Once in Lake Washington most fish resided for some period at depths near the thermocline with vertical migrations to use cooler water, and eventually moved towards shallower river deltas where they experienced high temperatures before entering rivers with cooler water.

Despite avoiding the warmest surface waters, all Chinook salmon and almost all sockeye salmon experienced temperatures > 18 °C and 85% of the Chinook salmon experienced temperatures > 20 °C, a threshold associated with adult migration delay, stress and potential mortality (Goniea et al. 2006; Keefer et al. 2009). Chinook salmon in the upper estuary and Lake Washington occupied vertical positions that minimized their exposure to the warmest temperatures, as do Pacific salmon in other man-made and natural impoundments (Keefer et al. 2009; Strange 2012; Keefer et al. 2015). Diel patterns in the upper estuary followed those seen in some other salmonids: deeper during the day than at night (Newell and Quinn 2005; Mathes et al. 2010; Roscoe et al. 2010. However, the Chinook salmon did not display this diel pattern in Lake Washington. Even with behavioral adaptation, fish residing in the upper estuary were continuously exposed to stressful temperatures (18-21 °C) while experiencing pulses of brackish water (1-18 ppt) and variable periods of low DO. The available alternatives to this refuge were to move back down to marine waters or up 10.8 km through even warmer waters (21-22 °C) to Lake Washington. Lake Union provided access to cooler water (14-15 °C at 11 m) between the upper estuary and Lake Washington but the salmon did not occupy this habitat. In that lake, DO levels below the thermocline fall below 5 mg/l in August and early September (USACE, unpublished data), a level that Pacific salmon avoid or will delay migration to avoid (Fujioka

1970; Hallock et al. 1970; Alabaster 1989). In Lake Washington Chinook salmon had access to cooler water below the thermocline without restriction by low DO.

Most Chinook salmon tagged in the Klamath River estuarine lagoon returned to the ocean to hold for about 10 days near the river plume before moving upriver (Strange 2013), as did salmon in the present study although for a shorter period. Similarly, some sockeye salmon populations hold in the Fraser River plume prior to upriver migration (Cooke et al. 2008). The migratory behavior of Pacific salmon returning to estuaries and rivers includes several species (e.g., Chinook, sockeye, steelhead) that exhibit diel vertical movement patterns in stratified and unstratified waters (Drenner et al. 2012). Limited available data indicates that while residing in estuaries salmon are often associated with thermo-haloclines (Brawn 1982; Westerberg 1982; Døving et al. 1985; Potter 1988; Olson and Quinn 1993; Strange 2013), although greater variation in vertical position has been observed in coastal waters and the marine portion of estuaries (Quinn et al. 1989; Ruggerone et al.1990; Walker et al. 2000; Ishida et al. 2001). In the Columbia River estuary, individual Chinook salmon show complex vertical movements relative to varying thermal and salinity gradients (Olson and Quinn 1993). Vertical placement near clines presumably provides advantages for behavioral thermo-osmoregulation and detection of olfactory homing cues at shear zones as predicted by Westerberg (1982). Tagging studies conducted during the adult migratory stage have revealed rapid transitions from saline to fresh waters and tolerance for substantial, brief changes in salinity among salmonids (Potter 1988; Olson and Quinn 1993).

Some Chinook salmon populations migrate upriver during the highest temperatures (e.g., Sacramento, Columbia, and Fraser river systems) while coastal sockeye populations in systems subject to high temperatures (mean 19 °C) often migrate prior to peak temperatures (Alabaster

1989, Hodgson and Quinn 2002, Keefer et al. 2015). At more southerly latitudes Chinook may be better adapted to higher temperatures than sockeye salmon (Quinn 2005; Richter and Kolmes 2005, Strange 2010). Selective pressures on life history traits (temperature tolerance, migration timing) and adaptive behaviors have resulted in salmon migrations that largely avoid stressful or lethal effects of warm temperatures along migration routes (Crozier et al. 2008).

Individual Chinook salmon appear to use a variety of behavioral techniques to adapt to high temperatures in rivers, such as delaying migration until temperatures decline, migrating at greater depths and utilizing cool water refuges (Berman and Quinn 1991; Strange 2013; Keefer and Caudill 2015). In this study Chinook salmon delayed in the estuary, utilized multiple refuges (estuary and lake) and conducted diel vertical migrations in those refuges. As most Chinook migrate at near sexual maturity, a long delay in migration at high temperatures may result in lost reproductive opportunity, in contrast, the timing of steelhead and some early arriving sockeye populations provides more flexible timing before spawning, where they may delay, seeking cool water refuge sites when temperatures are stressful (Keefer et al. 2009; Mathes et al. 2010). Individual sockeye salmon may be less adaptable in their response to temperatures, instead relying on life history traits developed over longer time periods with earlier migration timing and use of vertical stratification in lakes (Hodgson and Quinn 2002; Hinch et al. 2012). In this study sockeye salmon displayed both responses, migrating earlier and residing for extended periods below the thermocline in Lake Washington. Earlier migration timing can be counterproductive for selective sockeye stocks, in the Fraser River early entry for otherwise late migrants in estuary and lower river, or holding in warm shallow water lakes, has led to greater mortality (Eliason et al. 2011).

Dams have contributed to Chinook salmon population declines in coastal tributaries including the Willamette, Columbia, and Sacramento Rivers, with impacts from passage barriers and modified temperatures and flows (Myers et al. 1998, Quinn 2005; Angilletta et al. 2008). Similarly, the Lake Washington watershed has seen impacts from the passage barrier and stratified temperature regime at the estuary, along with water withdrawals from the basin and impacts from the highly urbanized watershed area. In the Columbia River and Snake River the highest temperatures are experienced when fish migrate through fish ways and reservoirs, albeit for short periods (less than 24 hr). Additional time to pass the dams and reservoirs can increase susceptibility to disease, impaired ovulation, increased stress, and decreased migration success (Caudill et al. 2013). During periods of physiological stress, the additional time at high temperatures from passage delays combined with swimming at metabolic thresholds further stresses fish and increase potential *en route* or prespawning mortality (Goniea et al. 2006; Angilletta et al. 2008). Because Pacific salmon cease feeding during their upstream migration, the speed and efficiency of the migration can significantly affect their energy reserves and consequently their spawning fitness (Brett 1995). The least delay and most efficient swimming for Chinook occurs at temperatures between 16-17 °C whereas the greatest delay may occur at temperatures exceeding 18-20 °C (Goniea et al. 2006; Salinger and Anderson 2006). In this study Chinook salmon experienced short-term exposure to the highest temperatures at the fish ladder exit (hours) but with long duration in the upper estuary above the fish ladder and locks. Unlike the Columbia River where Chinook must migrate long distances in high temperatures, Lake Washington Chinook salmon have a short migration from the estuary to the thermal refuge of the lake where temperatures are within the optimum range.

Exposure to warm water temperatures and the accumulation of degree-days (DD) have been correlated with prespawning mortality (Crossin et al. 2008; Keefer et al. 2009; Eliason et al. 2011), which can reach 90% in the upper reaches of the Willamette River (Keefer et al. 2015). Temperatures outside the acceptable range of 14 – 20 °C for Chinook salmon can deplete energy that could have been used for migration, reproduction, and immune responses (Richter and Kolmes 2005, McCullough et al. 2001; McCullough et al. 2009). In this study Chinook salmon accumulated DD ranging from 350-1050 DD, with an average 500-750 DD, compared with 700-900 average in Willamette River (maximum of 1500 DD) (Keefer et al. 2015). Most of the Chinook salmon in this study were estimated to have had sufficient energy for spawning, a small increase in residence period or elevated temperature exposure for earlier arriving fish could increase the proportion with depleted energy reserves with reduced spawning potential (Goetz, unpublished data).

Lake Washington has continued to get warmer in the summer and fall over the past five decades (Figure 4.2), and in the future the watershed is expected to see greater increases in temperature than any watershed in Puget Sound (Mantua et al. 2010). How salmon will respond to this marked change in water temperatures is of concern. Responses to avoid warm water can include adaptive or facultative changes in run timing to avoid the peak temperatures, or in thermoregulatory behavior by seeking cool water refuges at depth, or migrating faster to reach cooler areas (Hodgson et al. 2006; Hinch et al. 2012; Strange 2012; Keefer et al. 2015). Of ultimate concern is how warming will impact the survival of salmon runs. The temperatures at the upper estuary in most summer months already approaches or exceeds levels associated with disease and energy depletion in migrating salmon, so en route or prespawning mortality may result (McCullough et al. 2001; Crossin et al. 2008). Cool water will remain in Lake

Washington if Chinook salmon and sockeye can continue to migrate successfully from the Locks through the Ship Canal, however future temperatures could delay their migration where they may remain at the estuary in conditions that already are at stressful levels. Chinook salmon response to water temperatures as to where (e.g., estuary or lake) and how long they delay is uncertain, given the wide range of behaviors observed in this study. The longer residence at higher temperature will require a longer fasting period with accelerated energy demand from higher temperatures before spawning (Brett 1995, Beauchamp 2009). If water temperatures in Lake Washington continue to rise to levels greater than what is optimum or useable for final maturation, the spawning success of Chinook and sockeye salmon will likely be compromised.

Table 4.1: Adult Chinook capture, tagging, and recovery data for 2005 and 2006.

Tag and Release Date	**Mean Fork Length (mm)**	**St Dev (mm)**	**Archival/PIT Tags**	**Acoustic Tags**	**PIT Detections**	**Archival Recoveries**	**Archival & Acoustic Recoveries**
11-Aug-05	780.7	84.7	19	15	5	4	3
17-Aug-05	738.1	117.5	57	7	11	9	1
24-Aug-05	735.1	82.0	72	10	17	27	3
31-Aug-05	750.1	105.7	50	10	7	19	4
2005 Mean & Total	**744.1**	**99.8**	**198**	**42**	**40**	**59**	**11**
9-Aug-06	795.7	63.9	50	19	12	13	7
16-Aug-06	768.4	96.0	32	11	3	8	4
23-Aug-06	820.3	72.3	29	9	2	11	2
30-Aug-06	789.7	64.5	32	7	4	13	3
6-Sep-06	796.7	64.8	21	5		6	1
13-Sep-06	842.0	117.3	10	2	2	3	
2006 Mean & Total	**794.2**	**82.6**	**174**	**53**	**23**	**54**	**17**

Table 4.2: Water quality stations in the Ship Canal USACE (hourly) and Muckleshoot Tribe CTD (weekly), marine and lake monitoring data from King County DNR buoys (hourly), CTD profiles (bi-weekly) Lake Washington, Lake Sammamish, and monthly Central Puget Sound (marine).[1]

Ship Canal Location	Year	Frequency	Depth (m)	Parameters	Latitude	Longitude
Shilshole Bay (below Locks)	2005-06	Hourly	0.5, 1, 4	Temp, Sal	47.666	-122.400
Large Locks	2005-06	Hourly	1, 10	Temp	47.665	-122.396
Salmon Bay1 (above Locks)	2005-06	Hourly	5.3, 8.3, 11, 13	Temp, Sal	47.665	-122.395
Salmon Bay2 (upstream)	2005-06	Hourly	2, 5, 7, 9-13	Temp	47.665	-122.392
Salmon Bay (above Locks)	2006	Weekly	1-15	Temp, DO, Sal	47.665	-122.394
Ship Canal West	2005	Weekly	1-9	Temp, DO, Sal	47.656	-122.367
L Union North	2005-06	Weekly	1-12	Temp, DO, Sal	47.643	-122.336
Ship Canal East	2005-06	Weekly	1-8	Temp, DO	47.648	-122.312
L Washington at 520 NW	2005-06	Hourly	2,6,8,10, 20*	Temp	47.643	-122.271
Cedar River	2005-06	Hourly	1	Temp, Flow	47.482	-122.203
Sammamish River 1	2005-06	Hourly	1	Temp, Flow	47.703	-122.143
Sammamish River 2	2005-06	Hourly	1	Temp, Flow	47.662	--122.124
Cottage Creek	2005-06	Hourly	1	Temp, Flow	47.717	-122.088
Issaquah Creek	2005-06	Hourly	1	Temp	47.552	-122.048
Marine, Jefferson Head	2000-09	Monthly	1-25+	Sal, Temp, DO	47.749	-122.428
Marine, West Point	2000-09	Monthly	1-25+	Sal, Temp, DO	47.663	-122.448

*Missing 14, 16 m depth data in 2005 from 8/9-9/19

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[1] Hourly data used for estuary and ship channel from fixed station USACE/KCDNR for temperature and salinity and biweekly estuary to lake bi-weekly profiles by KCDNR and Muckleshoot Tribe. Tributary hourly temperature and discharge from Cedar River (USGS gage 12119000), Sammamish River (KCDNR gage 51m), and Issaquah Creek (USGS 12121600 flow, KCDNR 46a temperature).

Table 4.3: Residence time (days and proportion of time) as measured by acoustic (AC, N =26) and archival (Ibutton -IB, N = 67) tags or by archival tags only by migration segment and year. Total number of tags used by segment is shown in (). ANOVA values for residence time in days per migration segment shown for year and tagging group.

	2005		**2006**		**Total**						
Migration Segment (Days)	**Mean**	**Stdv**	**Mean**	**Stdv**	**Mean**	**Stdv**	**Tags**	**Year F (df)**	***P***	**Group F (df)**	***P***
Lower Estuary (86)	7.8	5.2	3.2	3.6	5.4	5.0	AC+IB	$36.4_{1,85}$	0.001	$2.3_{3,85}$	0.08
Upper Estuary (93)	8.6	5.6	13.4	7.3	11.1	7.0	AC+IB	$6.4_{1,85}$	0.01	$1.4_{3,85}$	0.25
Estuary (Lower+Upper) (93)	15.8	7.3	17.2	7.7	16.5	7.5	AC+IB	$0.2_{1,85}$	0.66	$3.3_{3,85}$	0.02
Ship Canal (92)	0.6	0.3	0.4	0.3	0.5	0.3	AC+IB	$7.4_{1,84}$	0.01	$0.4_{3,84}$	0.75
Lake Washington (93)	6.8	6.5	8.9	7.9	7.9	7.3	AC+IB	$0.1_{1,85}$	0.75	$2.4_{1,85}$	0.07
Sammamish River (N = 66)	8.8	6.2	6.3	6	7.5	6.2	IB	$0.67_{1,56}$	0.41	$0.84_{3,56}$	0.07
Lake Sammamish (N = 62)	4.6	3.9	4.8	4.1	4.7	3.9	IB	$0.34_{1,54}$	0.56	$1.63_{3,54}$	0.19
Total (N = 93)	34.1	9.7	36.0	8.9	35.1	9.3	AC+IB	$6.5_{1,85}$	0.01	$6.1_{3,85}$	0.01
Migration Segment (Proportion of Time)											
Lower Estuary (N = 86)	22%	16%	9%	9%	15%	14%	AC+IB				
Upper Estuary (N = 93)	27%	16%	28%	21%	27%	19%	AC+IB				
Estuary (N = 93)	47%	19%	47%	17%	47%	18%	AC+IB				
Ship Canal (N = 92)	2%	1%	1%	1%	2%	1%	AC+IB				
Lake Washington (N = 93)	15%	12%	20%	21%	18%	17%	AC+IB				
Sammamish River (N = 66)	24%	16%	17%	13%	20%	15%	IB				
Lake Sammamish (N = 62)	13%	13%	13%	10%	13%	11%	IB				

Table 4.4: Temperatures experienced (range, minimum to maximum, and time-weighted means) by Chinook salmon by location during their upriver migration in relation to tagging date (week and year).

	Lower Estuary		Upper Estuary		Ship Canal		L Washington		L Sammamish		Sammamish R		Tributary Entry
Group	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Mean**
2005	**11.9-18.3**	**14.6**	**15.9-22.6**	**19.0**	**17.9-22.3**	**20.2**	**8.5-21.5**	**16.8**	**11.9-20.5**	**17.0**	**10-19.5**	**15.2**	**12.2**
Week 1	11.9-17.9	14.0	16.3-21.9	19.1	18.9-21.4	20.4	9.6-21.4	16.4	13.3-20.4	17.4	13-19.5	16.6	11.0
Week 2	12.1-17.8	14.6	16-22.3	19.1	17.9-22	20.2	9.6-21.5	17.1	13-20.4	17.2	12.5-18.9	15.2	12.5
Week 3	12.4-17.9	14.7	16-22.6	19.1	18.3-22.3	20.4	9.3-21.5	16.9	12.8-20.5	16.9	12.5-19.3	15.3	12.4
Week 4	12.5-18.3	14.9	15.9-21.3	18.5	18-20.6	19.7	8.5-20.5	16.8	11.9-19.4	16.5	10-17.1	14.5	12.2
2006	**10.1-18.3**	**14.1**	**15.4-22.5**	**19.0**	**17.3-22.5**	**20.4**	**9.1-22.5**	**17.8**	**12.5-21.5**	**17.2**	**11.6-21.4**	**16.1**	**12.5**
Week 1	10.1-18.3	13.8	15.4-22.5	19.5	17.3-22.5	20.9	9.5-22.5	18.1	12.5-21.5	17.1	13.1-21	16.5	12.8
Week 2	11.9-17.4	13.3	15.6-21.8	18.9	18.1-22.1	20.4	9.1-21.6	17.5	13-20.3	17.1	13.5-21.4	16.7	12.7
Week 3	11.9-17.8	14.4	15.9-20.9	18.4	18.1-21	19.8	10.6-21.1	17.2	13-20	17.2	13.1-19.3	15.4	12.0
Week 4	13.3-18	15.2	16.3-21.1	18.7	17.4-21.1	20.2	9.1-21.4	17.4	13-20.5	17.2	11.6-18	15.3	12.3
Grand Total	**10.1-18.3**	**14.4**	**15.4-22.6**	**19.0**	**17.3-22.5**	**20.3**	**8.5-22.5**	**17.3**	**11.9-21.5**	**17.1**	**10-21.4**	**15.6**	**12.4**

Table 4.5: Ambient temperatures in upper estuary (UE) and Lake Washington (LW, 520 NW station) at common depths by month and year with temperatures difference between 2005 and 2006. The maximum depth for temperature records in the upper estuary is 13-m (see Figure 4.7).

Depth and Location	Aug-05	Aug-06	Sep-05	Sep-06	2005	2006	Total
2-m UE	21.6	21.4	19.6	21.6	21.6	20.4	21.0
7-m UE	21.2	21.2	19.5	21.8	21.6	20.3	20.9
10-m UE	21.0	20.8	19.0	21.8	21.4	19.8	20.6
12-m UE	19.8	20.0	18.3	20.6	20.3	19.0	19.7
13-m UE	19.6	19.8	17.9	20.6	18.6	20.3	19.5
2-m LW	22.7	21.7	19.9	19.9	21.0	20.7	20.9
8-m LW	22.1	21.1	19.7	19.5	20.7	20.2	20.5
10-m LW	20.7	20.5	19.6	19.3	20.0	19.8	19.9
12-m LW	17.0	17.6	18.3	18.4	17.7	18.1	17.9
14-m LW	NA	13.7	NA	15.3		14.6	14.6
20-m LW	10.5	10.1	10.7	10.2	10.6	10.2	10.4

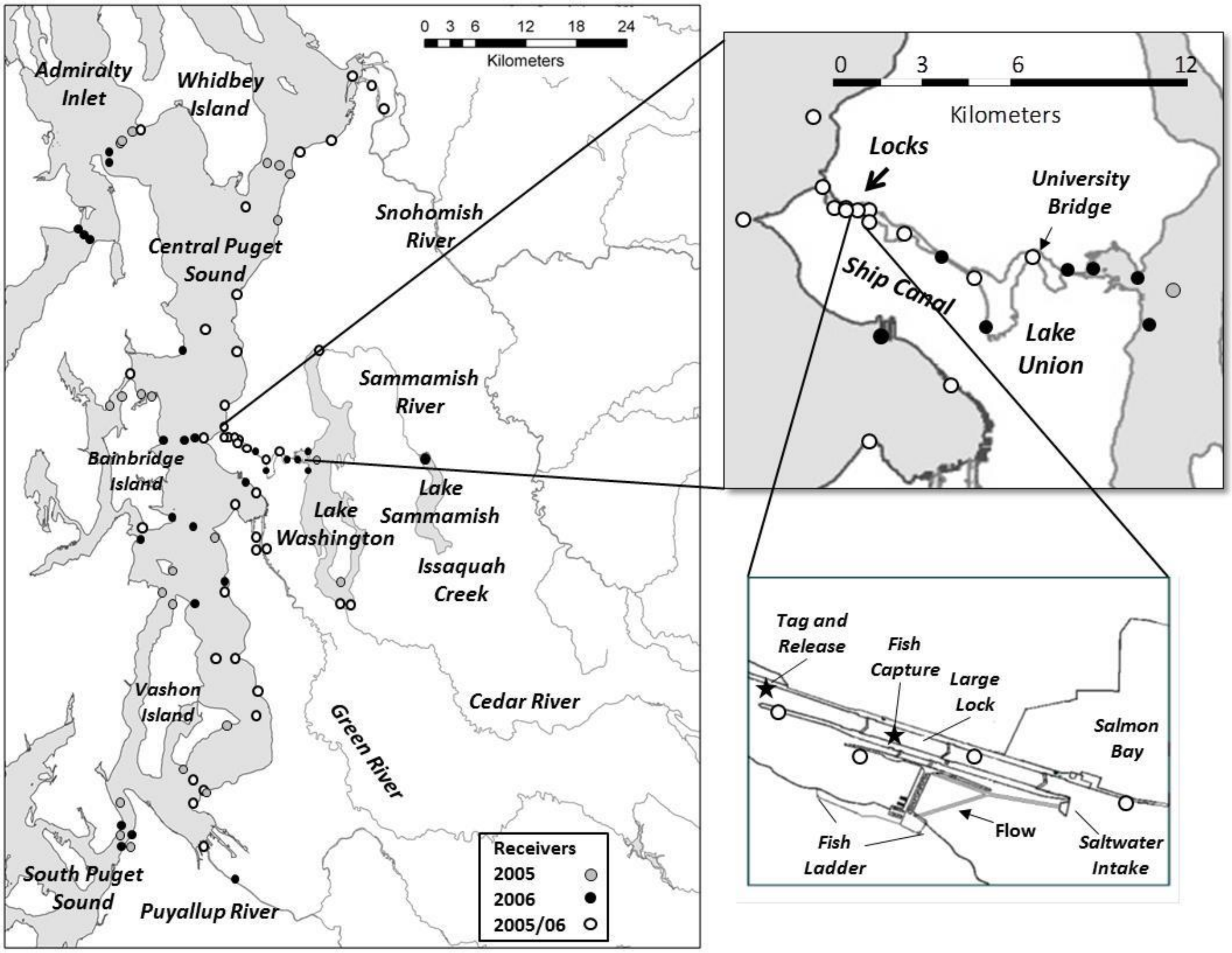


Figure 4.1: Acoustic monitoring network in coastal waters near Puget Sound with receivers shaded by years of deployment. Receivers (circles) and tagging and release locations (stars) in the Lake Washington Ship Canal and Locks shown in side inset.

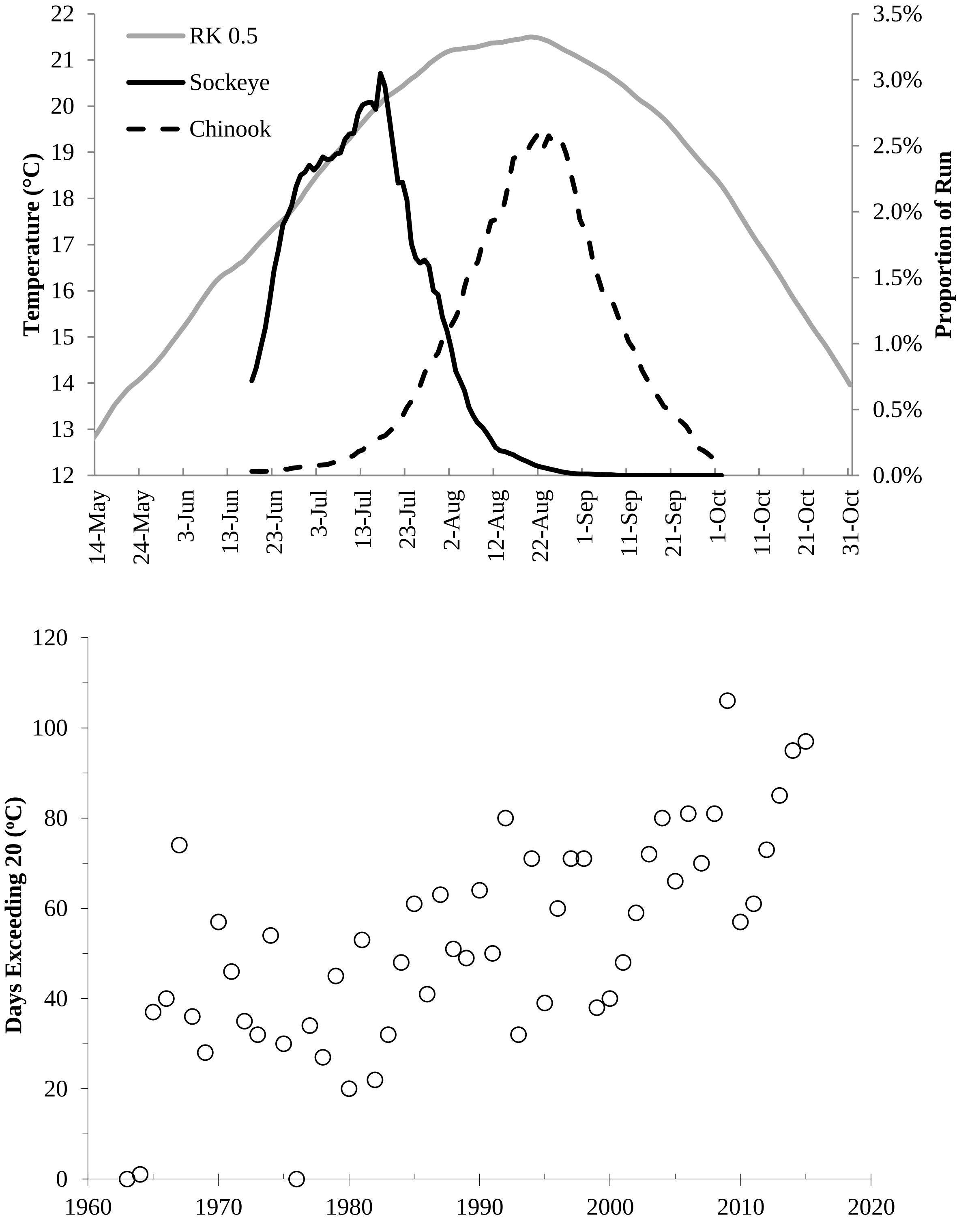


Figure 4.2: Migration timing of sockeye and Chinook salmon at the Locks and mean temperature (top) and number of days epilimnetic temperatures exceeded 20 oC in Lake Washington (bottom) (King County DNR unpublished data).

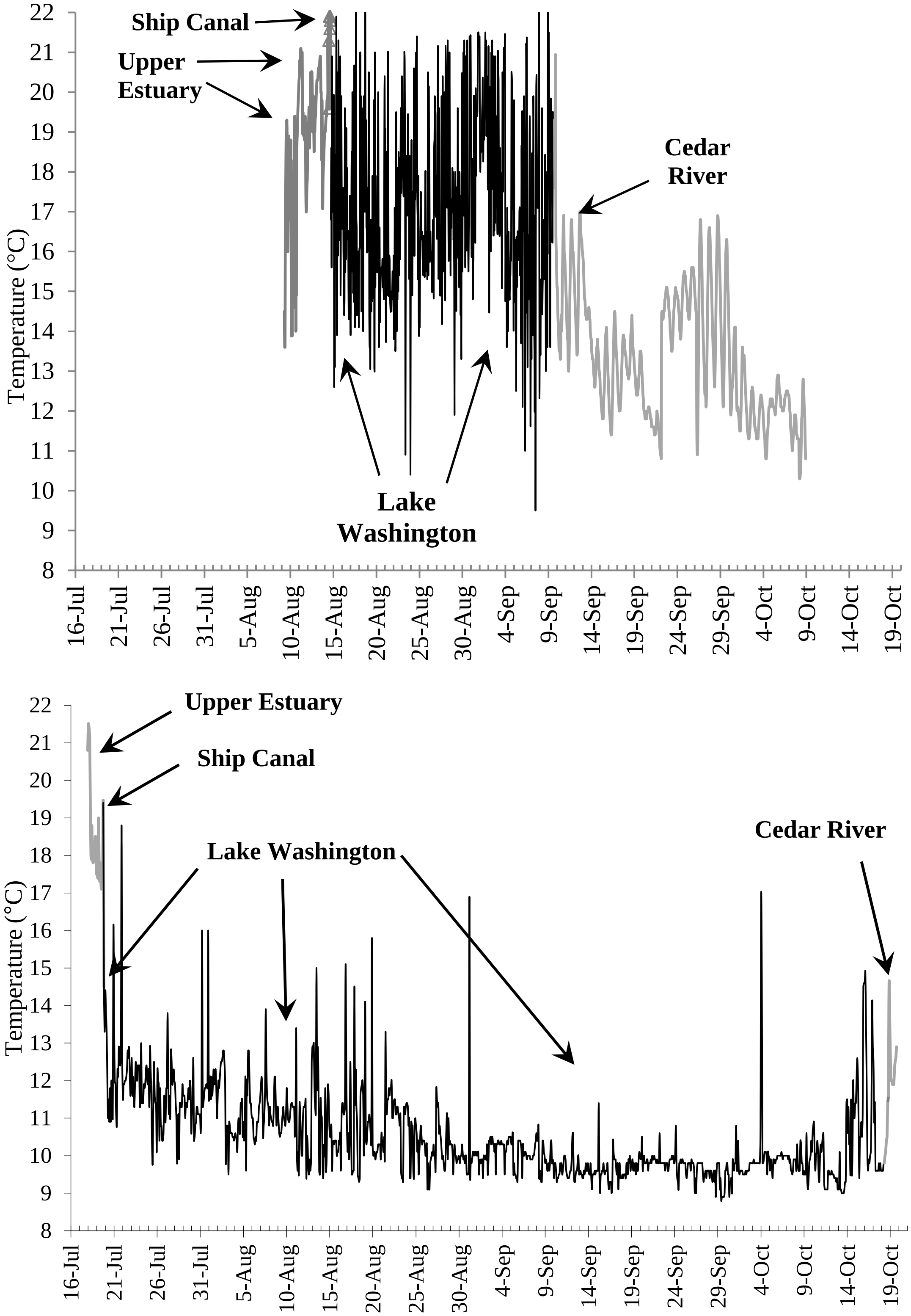


Figure 4.3: Thermal signature (hourly temperature by location) for typical patterns of Chinook salmon (2005, top panel) and sockeye salmon (2003, bottom panel) migrating from the upper estuary to final capture location in Cedar River (both): Gray line at left – Upper Estuary and Ship Canal: Black line - Lake Washington; Gray line at right – Cedar River.

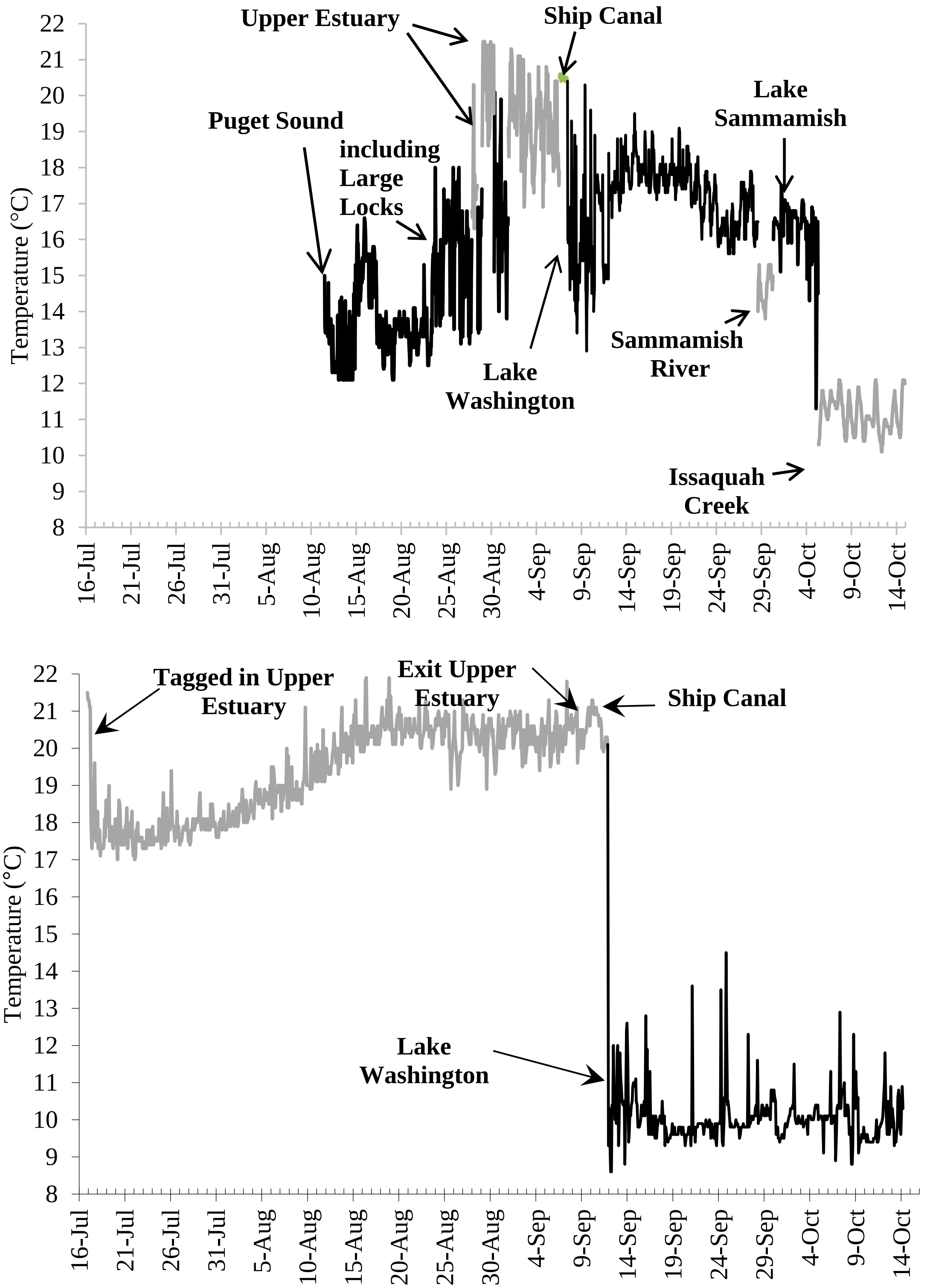
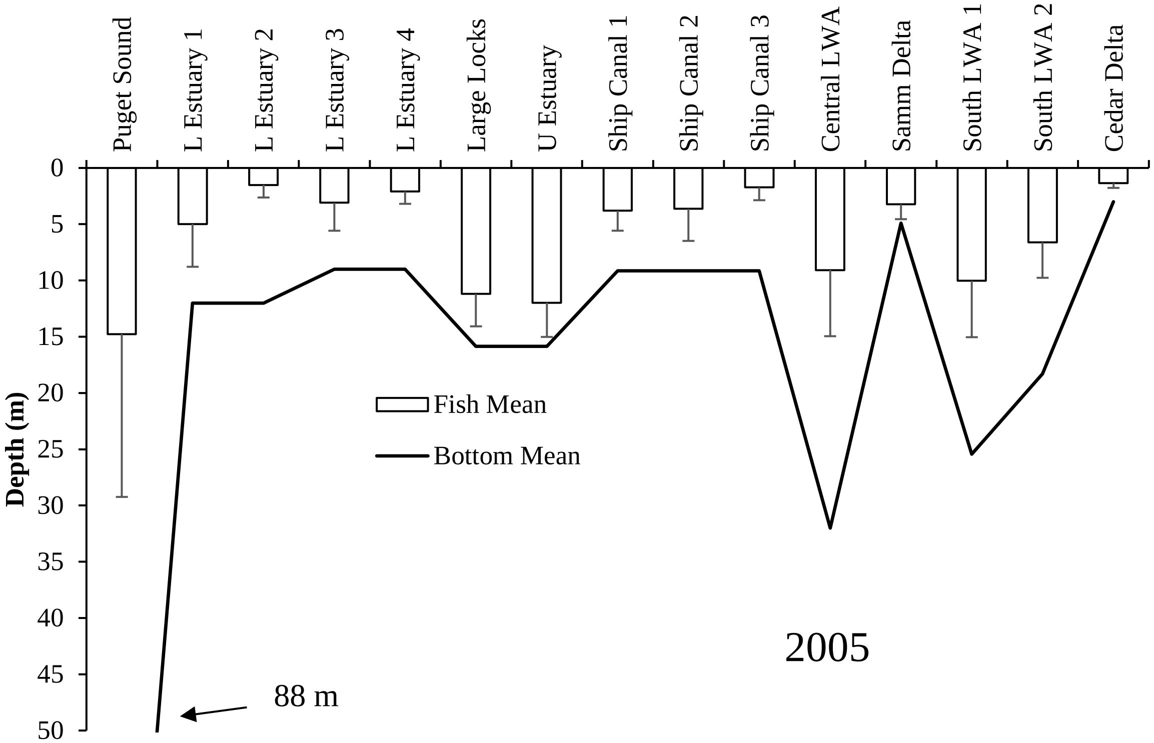


Figure 4.4: Thermal signature (hourly temperature by location) for typical patterns of Chinook salmon (2005, top panel) and sockeye salmon (2003, bottom panel) migrating from upper estuary to final capture locations at Issaquah Creek (Chinook) and North Lake Washington (sockeye). Gray line at left – Upper Estuary and Ship Canal: Black line - Lake Washington; Gray lines at right – tributaries.



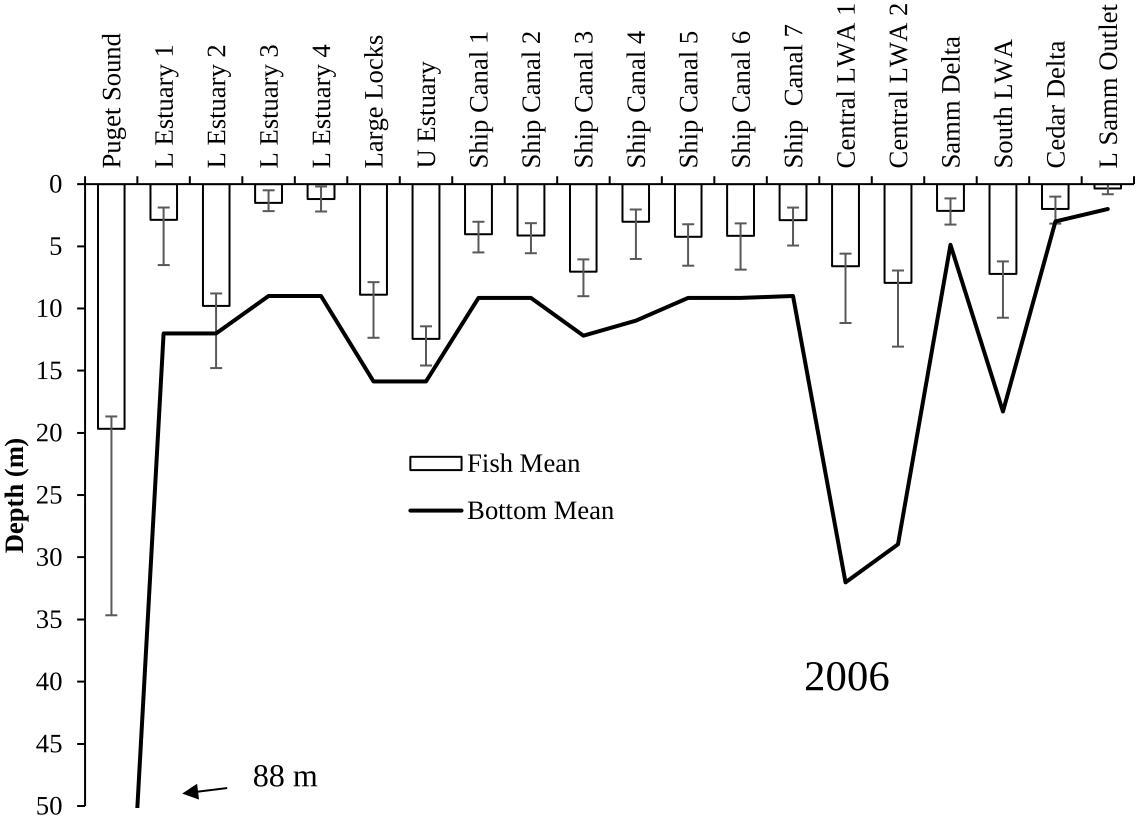


Figure 4.5: Mean fish depth (with St Dev) and mean bottom depth near receivers by receiver location: 2006 Large Lock depth data was limited after Aug 31. Additional receivers were deployed in 2006 in the Ship Canal, Central Lake Washington and Lake Sammamish.

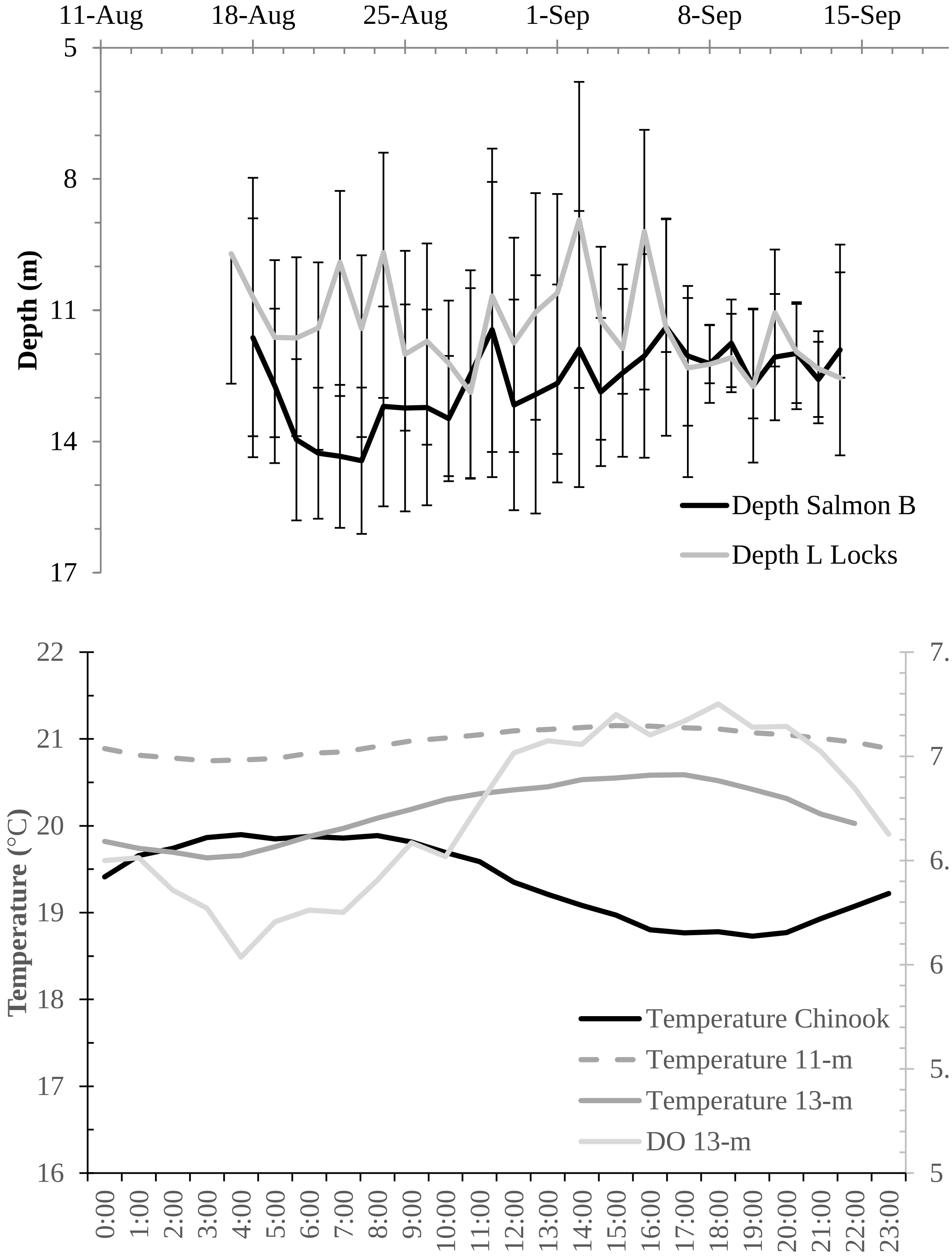


Figure 4.6: Mean daily fish depth (with St Dev) for acoustic tagged fish occupying the Large Lock or Salmon Bay in 2005 (top panel) and August mean hourly values in Salmon Bay for archival tagged Chinook salmon and ambient temperature (11 and 13-m), and DO (13-m) (bottom panel): DO levels from 2013, values that are typical for August.

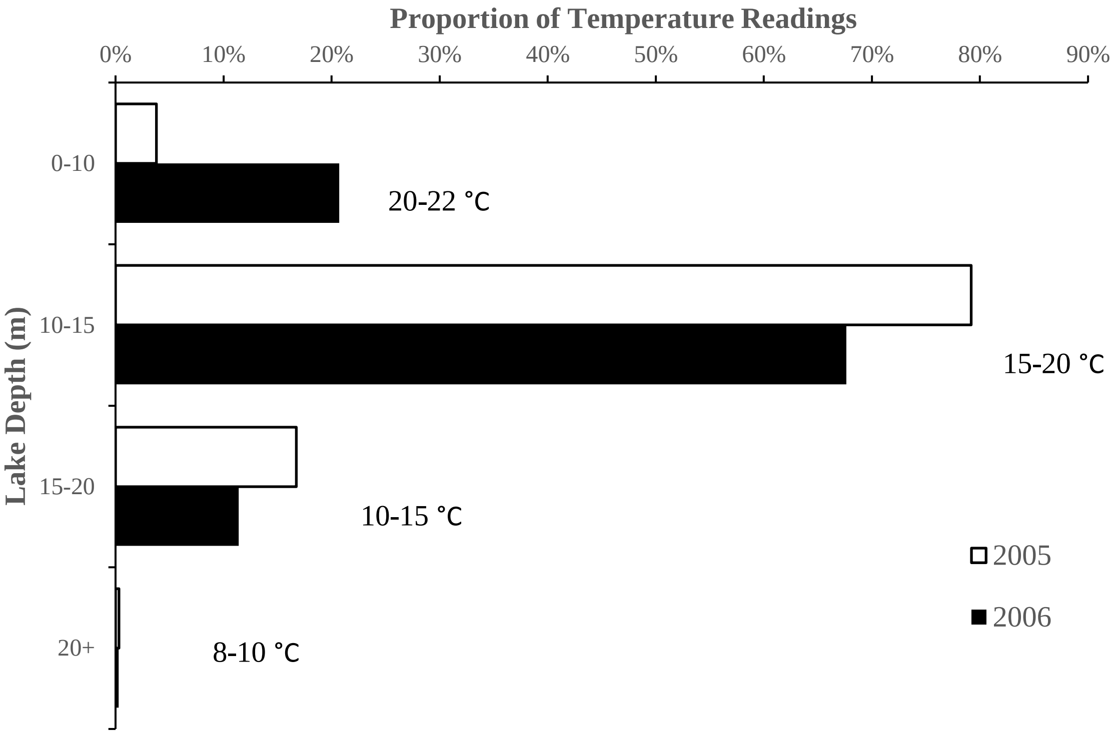


Figure 4.7: Proportion of Chinook temperature records at increasing depths in Lake Washington in 2005 and 2006.

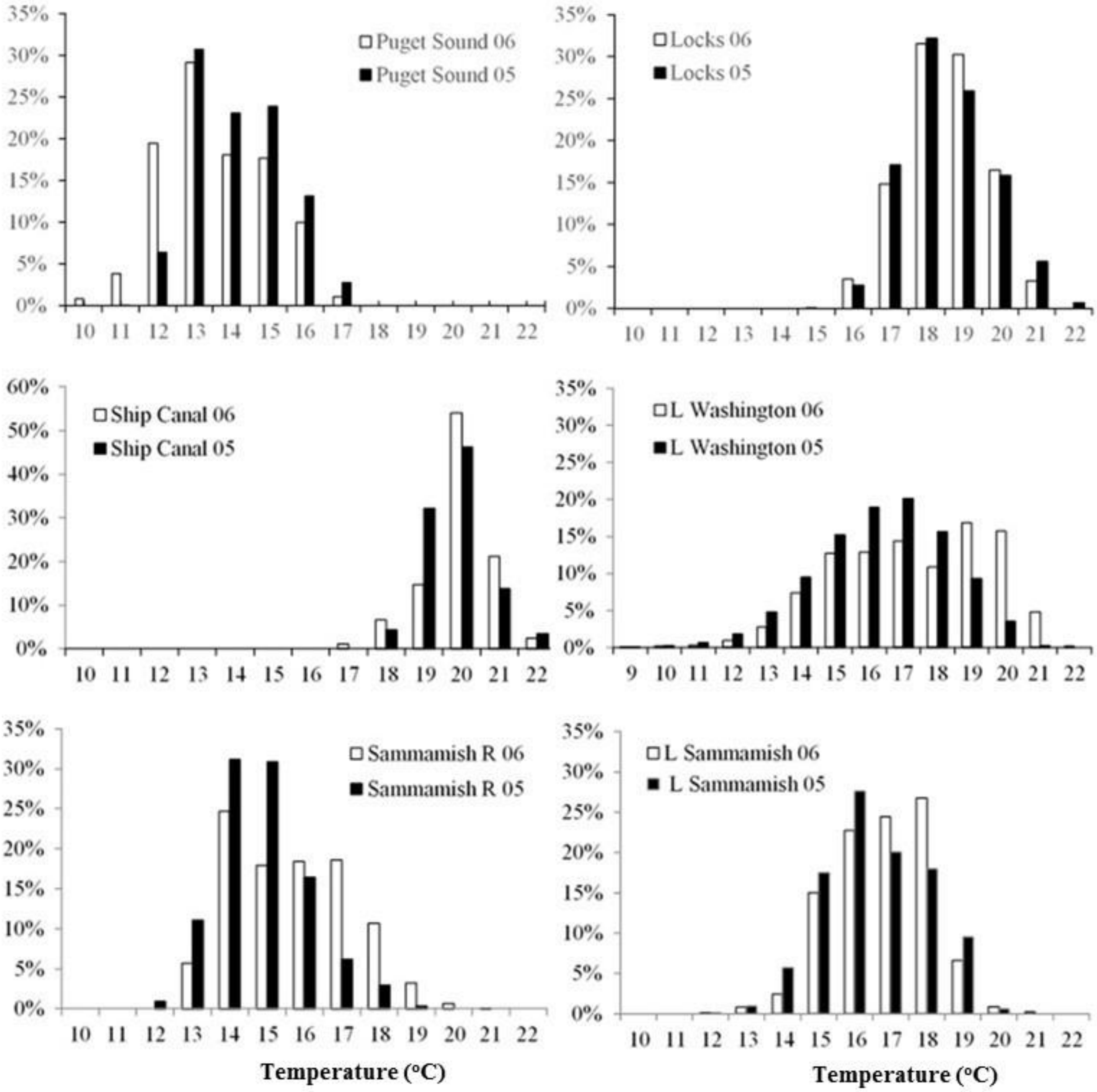


Figure 4.8: Temperature frequency distribution (hourly proportion) of Chinook salmon (2005 (05), 2006 (06)) by migration segment from Puget Sound to final location before entry into a spawning tributary.

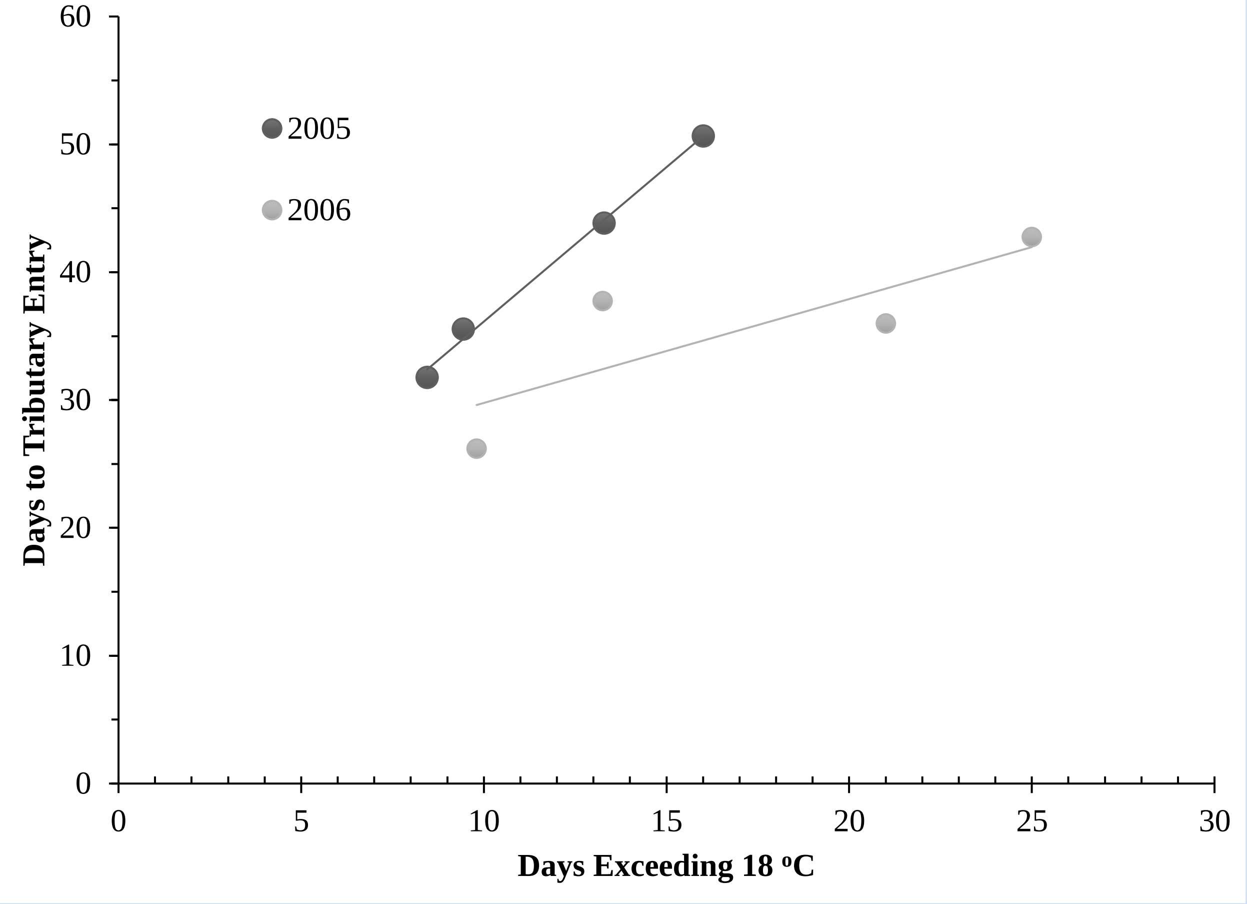


Figure 4.9: Number of days Chinook salmon experienced temperatures exceeding 18 °C by year and tagging week (each circle) prior to tributary entry.

General Conclusions

This research along with the work of other collaborators provides the first investigation of the geographic variation in estuarine and marine migrations of resident and ocean-bound Puget Sound salmon, trout, and char (bull trout). The chapters in this dissertation describe important characteristics of these anadromous salmonids during their marine phase such as distribution in time and space, movement patterns, and length of time spent in Puget Sound sub-basins. The research compared marine life histories to find common patterns within populations and between species using acoustic telemetry as a common monitoring method. The short-term goal of this research was to describe the movements of individual anadromous fish within four species: steelhead, bull trout, coastal cutthroat trout, and Chinook salmon, to determine the extent to which migration patterns vary among the species, populations, and oceanographic sub-basins within Puget Sound.

Among the findings in the first chapter was identification of the differences in survival and behaviors between wild and hatchery steelhead in the migration from the Green River to the Strait of Juan de Fuca. Based on 4 years of study, the wild fish outperformed the hatchery fish, surviving at higher rates in almost every migration segment. The greatest loss for both groups coincided with the slowest travel rates as fish first entered the estuary and as they exited Puget Sound. This research was part of a planned multi-agency effort to conduct a comparative analysis of migratory behavior and survival of wild and hatchery steelhead from all major sub-basins in Puget Sound (Moore et al. 2015). The findings from this research and the collaborative research suggest that declines in wild and hatchery steelhead populations may be caused primarily by factors in the early marine period.

The results of the second chapter indicate that cutthroat trout have a range of behaviors but move relatively short distances along the shorelines of Puget Sound. The observed movement patterns of cutthroat trout were markedly different than ocean-bound steelhead trout. The majority of cutthroat remained close to shore within 10 km of Big Beef Creek with no cutthroat leaving the Hood Canal basin. A cluster analysis of several migratory characteristics suggested a continuum of behavioral patterns but with two general modes of resident and migratory fish. The resident group included fish that utilized the estuary for a majority of time and fish that occupied shoreline areas just outside the estuary, while others migrated longer distances and spent little time in the estuary. At a finer scale, other behaviors included activity levels ranging from sedentary fish, commuters with repeated movements, and individuals with more continuous long-distance travel. A companion study showed that hybrid cutthroat/steelhead trout displayed unusual behaviors but ultimately had intermediate migratory characteristics between steelhead and cutthroat trout (Moore et al. 2010b).

The results of the third chapter defined the period of marine migration of Puget Sound bull trout and considered factors that could explain the period of residency and the return to freshwater. Residence periods were similar for sub-adult and adults from several major rivers, with most fish found in marine areas between March and July and with few overwintering in the Puget Sound. The timing of the return migration to freshwater was similar for fish returning to each river despite differences in their thermal regimes. Individual bull trout showed characteristics of different migratory patterns including occupancy of a single estuary, movement between estuaries, and residence in open shoreline areas. The migratory behaviors of cutthroat and bull trout were found to be similar within each species in distance traveled and habitat used in river deltas and nearshore shorelines. Bull trout differ from cutthroat trout in that they remain in marine areas for shorter periods and do not cross deeper water areas as frequently.

The results of the fourth chapter compared the thermoregulatory behavior of maturing adult Chinook and sockeye salmon during their migration from a heavily modified estuary and navigation channel through Lake Washington. The Chinook salmon exhibited complex patterns, delaying in the estuary, occupying cool water refuges in the stratified estuary and freshwater areas over periods of days to weeks. Sockeye salmon exhibited a simpler pattern, holding for a short period in warm water in the estuary, then migrating to the lake and residing in deep cold-water areas for up to 3 months. In Lake Washington Chinook took vertical migrations above and below the thermocline and used the lake as a thermal refuge to a lesser extent than did sockeye salmon. Even though Chinook used a variety of refugia, they still experienced significantly warmer total mean temperatures than sockeye. Lake Washington has continued to get warmer in the summer and fall and will likely to continue increasing in the future, while Chinook salmon response to water temperatures as to where (e.g., estuary or lake) and how long they delay is uncertain, given the wide range of behaviors observed in this study. Understanding how Chinook and sockeye may use available thermal refuges under current and future climate conditions may help identify management alternatives to retain or increase these areas in the future.

This research was part of a larger suite of studies that investigated the habitat use, movements and survival of additional populations and species within Puget Sound. In the dissertation there were hypothesized patterns of movements for a number of salmonids, including resident, semi-resident, and ocean-bound fish (Table 1 and Figure 1). The results from the research support the patterns of estuary and nearshore resident cutthroat trout and bull trout

(Chapter 2 and 3, Hayes et al. 2011), intermediate behaviors for hybrids of cutthroat and steelhead (Moore et al. 2010b), and an ocean-bound pattern for steelhead smolts (Chapter 1, Moore et al. 2015). Further, research by others has demonstrated that sub-adult Chinook and coho salmon include individuals that displayed resident and semi-resident behavioral patterns (Chamberlin et al. 2011; Rohde et al. 2013, 2014; Smith et al. 2015).

The long-term goal of this research and the collaborative efforts with others, is to integrate information about these Puget Sound salmonid alternative life history patterns with information on oceanographic processes and human habitat modifications, and assess what affect these stressors play in organizing the productivity and diversity of these species.

References

Alabaster, J.S. 1989. The dissolved oxygen and temperature requirements of King Salmon, *Oncorhynchus tshawytscha,* in the San Joaquin Delta, California. J. Fish Biol. **34**: 331–332.

Angilletta, M.J., Steel, E.A., Bartz, K.K., Kingsolver, J.G., Scheuerell, M.D., Beckman, B.R., and Crozier, L.G. 2008. Big dams and salmon evolution: changes in thermal regimes and their potential evolutionary consequences. Evolutionary Applications **1**: 286–299.

Appleby, A.E., and Doty, D.C. 1995. Status and trends in the survival and distribution of resident coho and Chinook salmon in Puget Sound, Washington. Pages 882-890 in Proceedings of the Puget Sound Research Conference, Bellevue, WA. Puget Sound Water Quality Authority.

Armstrong, R.H. 1971. Age, food, and migration of sea-run cutthroat trout, *Salmo clarki,* at Eva Lake, Southeastern Alaska. Transactions of the American Fisheries Society **100**: 302-306.

Bahr, M.A., and Shrimpton, J.M. 2004. Spatial and quantitative patterns of movement in large bull trout (*Salvelinus confluentus*) from a watershed in northwestern British Columbia, Canada, are due to habitat selection and not differences in life history. Ecology of Freshwater Fish **13:** 294–304.

Baker, R.R. 1978. The Evolutionary Ecology of Animal Migration. Holmes and Meier, New York.

Baldwin, C.M., Beauchamp, D.A. and Gubala, C.P. 2002. Seasonal and diel distribution and movement of cutthroat trout from ultrasonic telemetry. Transactions of the American Fisheries Society **131**: 143-158.

Barnett, H.K., and Paige, D.K. 2013. Movements by adfluvial Bull Trout during the spawning season between lake and river habitats. Transaction of the American Fisheries Society **142**: 876-883.

Beamer, E., and Henderson, R. 2004. Distribution, abundance, timing, and size of anadromous bull trout in the Skagit River Delta and Skagit Bay. Manuscript submitted to Puget Sound Bull Trout Technical Recovery Team.

Beamish, D., Folkes, M., Sweeting, R., and Mahnken, C. 2003. Intra-Annual changes in the abundance of coho, Chinook, and chum salmon in Puget Sound in 1997. Pages 531-541 in Proceedings of the Puget Sound Research Conference.

Beamish, R.J., McFarlane, G.A., and King, J.R. 2005. Migratory patterns of pelagic fishes and possible linkages between open ocean and coastal ecosystems off the Pacific coast of North America. Deep-Sea Research II **52**: 739–755.

Beauchamp, D.A., Vecht, S.A. and Thomas, G.L. 1992. Temporal, spatial, and size-related foraging of wild cutthroat trout in Lake Washington. Northwest Science **66**: 149–159.

Beauchamp, D.A., and Van Tassell, J. 2001. Modeling seasonal trophic interactions of adfluvial bull trout in Lake Billy Chinook, Oregon. Transactions of the American Fisheries Society **130:** 204-216.

Beauchamp, D. 2009. Bioenergetic ontogeny: linking climate and mass-specific feeding to life-cycle growth and survival of salmon. *Pages* 1-19 *in* Knudsen, E.E. and J.H. Michael, Jr., *eds*. American Fisheries Society Symposium 70.

Beaudreau, A.H. 2009. The predatory role of Lingcod (*Ophiodon elongatus*) in the San Juan Archipelago, Washington. PhD Thesis, University of Washington, Seattle, Washington.

Behnke, R.J. 1992. Native Trout of Western North America. Bethesda, MD: American Fisheries Society.

Berg, O.K., and Berg, M. 1993. Duration of sea and freshwater residence of Arctic char (*Salvelinus alpinus*), from the Vardnes River in northern Norway. Aquaculture **110**: 129-140.

Berman, C.H., and Quinn, T.P. 1991. Behavioural thermoregulation and homing by spring Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. Journal of Fish Biology **39**: 301–312.

Bernard, D.R., Hepler, K.R., Jones, J.D., Whalen, M.E., and McBride, D.N. 1995. Some tests of the “migration hypothesis” for anadromous Dolly Varden (southern form). Transactions of the American Fisheries Society **124**: 297–307.

Bjornn, T.C., and Reiser, D.W. 1991. Habitat requirements of salmonids in streams. Pages 83-138 in W.R. Meehan (ed.), Influences of forest and rangeland management on salmonid fishes and their habitats. Am. Fish. Soc. Spec. Pub. 19, Bethesda, MD.

Bond M.H., Hayes, S.A., Hanson, C.V., and MacFarlane R.B. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Canadian Journal of Fisheries and Aquatic Sciences **65:** 2242–2252.

Bond, M.H., and Quinn, T.P. 2013. Patterns and influences on Dolly Varden migratory timing in Chignik Lakes, Alaska, and comparison to populations throughout the Northeastern Pacific and Arctic oceans. Canadian Journal of Fisheries and Aquatic Sciences. **70**: 655-665.

Bortelson, G.C., Chrzastowski, M.J., and Helgerson, A.K. 1980. Historical changes of shoreline and wetland at eleven major deltas in the Puget Sound region, Washington. U.S. Geological Survey Hydrologic Investigations Atlas HA-617, 11 sheets.

Brannon, E., and Setter, A. 1989. Marine distribution of a hatchery fall Chinook salmon population. Pages 63-69 *in* E. Brannon, and B. Jonsson (eds.) Proceedings of the salmonid migration and distribution symposium, School of Fisheries, University of Washington, Seattle.

Brawn, V.M. 1982. Behavior of Atlantic salmon (*Salmo salar*) during suspended migration in an estuary, Sheet Harbor, Nova Scotia, observed visually and by ultrasonic tracking. Canadian Journal of Fisheries and Aquatic Sciences **39**: 248-256.

Brenkman, S.J., Larson, G.L., and Gresswell, R.E. 2001. Spawning migration of lacustrine-adfluvial bull trout in a natural area. Transactions of the American Fisheries Society **130:** 981-987.

Brenkman, S.J., and Corbett, S.C. 2005. Extent of anadromy in bull trout and implications for conservation of a threatened species. North American Journal of Fisheries Management **25:** 1073–1081.

Brett, J.R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). American Zoologist **11:** 99-113.

Brett, J.R. 1995. Energetics. Pages 3–68 in C. Groot, L. Margolis, and W.C. Clarke, editors. Physiological ecology of Pacific salmon. University of British Columbia Press, Vancouver.

Brodeur, R.D., Boehlert, G.W., Casillas, E., Eldridge, M.B., Helle, J.H., Peterson, W.T., Heard, W.R., Lindley, S., and Schiewe, M.H. 2000. A coordinated research plan for estuarine and ocean research on Pacific salmon. Fisheries **25**:7-16.

Brodeur, R.D., Emmett, R.L., Fisher, J.P., Casillas, E., Teel, D.J., and Miller, T.W. 2004. Juvenile salmonid distribution, growth, condition, origin, and environmental and species associations in the Northern California Current. Fishery Bulletin **102**: 25-46.

Brown, L.R., and Moyle, P.B. 2005. Native fish communities of the Sacramento–San Joaquin watershed, California: a history of decline. *Pages* 75–98 *in* Rinne, F., Hughes, R. and R. Calamusso, *eds.* Fish Communities of Large Rivers of the United States. American Fisheries Society.

Buckley, R.M. 1969. Analysis of the Puget Sound sport fishery for resident coho salmon, *Oncorhynchus kisutch*, (Walbaum). M.S. thesis, University of Washington, Seattle, WA. 73. pp.

Bunnell, D.B. Jr., Isely, J.J., Burrell, K.B., and Van Lear, D.H. 1998. Diel movement of brown trout in a southern Appalachian river. Transactions of the American Fisheries Society **127:** 630–636.

Burgner, R.L., Light, J.T., Margolis, L., Okazaki, T., Tautz, A. and Ito, S. 1992. Distribution and origins of steelhead trout (*Oncorhynchus mykiss*) in offshore waters of the North Pacific Ocean. International North Pacific Fisheries Commission Bulletin **51**: 1-92.

Burnham K.P, and Anderson D.R. 1998. Model selection and inference: practical information theoretic approach. Springer-Verlag, London.

Burnham, K.P., and Anderson, D.R. 2002. Model Selection and Inference: Practical Information Theoretical Approach. New York: Springer-Verlag.

Buzzell, B., Lance, M.M., and Acevedo-Gutiérrez, A. 2014. Spatial and temporal variation in river otter (*Lontra canadensis*) diet and predation on rockfish (Genus *Sebastes*) in the San Juan Islands, Washington. Aquatic Mammals **40:** 150-161.

Candy, J.R., and Quinn, T.P. 1999. Behaviour of adult Chinook salmon (*Oncorhynchus tshawytscha*) in British Columbia coastal waters determined from ultrasonic telemetry. Canadian Journal of Fishery and Aquatic Sciences **77**: 1161–1169.

Caudill, C.C., Keefer, M.L., Clabough, T.S., Naughton, G.P., Burke, B.J., and Peery, C.A. 2013. Indirect effects of impoundment on migrating fish: temperature gradients in fish ladders slow dam passage by adult Chinook salmon and steelhead. PLoS One **8**: e85586.

Cavender, T.M. 1978. Taxonomy and distribution of the bull trout, (*Salvelinus confluentus*) (Suckley), from the American Northwest. California Fish and Game **64**: 139-174.

Chamberlin, J.W., Kagley, A.N., Fresh, K.L. and Quinn, T.P. 2011. Movements of yearling Chinook salmon during the first summer in marine waters of Hood Canal, Washington. Transactions of the American Fisheries Society **140**: 429-439.

Chapman E.D., Hearn, A.R., Michel, C.J., Ammann, A.J., Lindley, S.T., Thomas, M.J., Sandstrom, P.T., Singer, G.P., Peterson, M.L., MacFarlane, R.B., and Klimley, A.P. 2012. Diel movements of out-migrating Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) smolts in the Sacramento/San Joaquin watershed. Environmental Biology of Fish doi:10.1007/s10641-012-0001-x.

Chittenden, C.M., Sura, S., Butterworth, K.G., Cubitt, K.F., Manel-La, N.P. et al. 2008. Riverine, estuarine and marine migratory behaviour and physiology of wild and hatchery-reared coho salmon *Oncorhynchus kisutch* (Walbaum) smolts descending the Campbell River, BC, Canada. Journal of Fish Biology **72**: 614–628.

Clarke, W.C, and Hirano, T. 1995. Osmoregulation. *In* Physiological Ecology of Pacific Salmon. *Edited* by C. Groot, L. Margolis and W.C. Clarke. University of British Columbia Press, Vancouver. pp. 317-377.

Clements, S., Stahl, T., and Schreck, C.B. 2012. A comparison of the behavior and survival of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) in a small estuary system. Aquaculture doi:10.1016/j.aquaculture.2011.11.029.

Connor, E.J., and Pflug, D.E. 2004. Changes in the distribution and density of pink, chum, and Chinook salmon spawning in the upper Skagit River in response to flow management measures. North American Journal of Fisheries Management **24:** 835-852.

Cooch, E., and White, G**.** 2010. Program MARK: a gentle introduction. http://www.phidot.org/software/mark/docs/book/.

Cooke, S.J., Hinch, C.G., Crossin, G.T et al. 2008. Physiological correlates of coastal arrival and river entry timing in later summer Fraser River sockeye salmon (*Oncorhynchus nerka*). Behavioral Ecology **19:** 747-758.

Crittenden, R.N. 1994. A diffusion-model for the downstream migration of sockeye-salmon smolts. Ecological Modelling **71**: 69–84.

Crossin, G.T., Hinch, S.G., Cooke, S.J., Welch, D.W., Lotto, A.G., Patterson, D.A., Jones, S.R.M., Leggeatt, R.A., Mathes, M.T., Shrimpton, J.M., Van Der Kraak, G., and Farrell, A.P. 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. Canadian Journal of Zoology **86:** 127–140.

Crozier, L.G., Hendry, A.P., Lawson, P.W., Quinn, T.P., Mantua, N.J., Battin, J., Shaw, R.G., and Huey, R.B. 2008. Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. Evolutionary Applications **1**: 252-270.

Cucherousset, J., Ombredane, D., Charles, K., Marchand, F., and Baglinière, J. 2005. A continuum of life history tactics in a brown trout (*Salmo trutta*) population. Canadian Journal of Fisheries and Aquatic Sciences **62**: 1600–1610.

Curry, R.A., Bernatchez, L., Whoriskey, F., and Audet, C. 2010. The origins and persistence of anadromy in brook charr. Reviews in Fish Biology and Fisheries **20**: 557-570.

DeCicco, A.L. 1992. Long-distance movements of anadromous Dolly Varden between Alaska and the U.S.S.R. Arctic **45**: 120-123.

Dingle, H. 1996. Migration: The Biology of Life on the Move. New York: Oxford University Press.

Dingle, H., and Drake, V.A. 2007. What is migration? Bioscience **57**: 113–121.

Døving, K.B., Westerberg, H, and Johnsen, P.B. 1985. Role of olfaction in the behavioral and neuronal responses of Atlantic salmon, Salmo salar, to hydrographic stratification. Canadian Journal of Fisheries and Aquatic Sciences **42**: 1658-1667.

Downs, C.C., Horan, D., Morgan-Harris, E., and Jakubowski, R. 2006. Spawning demographics and juvenile dispersal of an adfluvial bull trout population in Trestle Creek, Idaho. North American Journal of Fisheries Management **26:** 190-200.

Drenner, S.M., Clark, T.D., Whitney, C.K., Martins, E.G., Cooke, S.J., et al. 2012. A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. PLoS ONE **7**: e31311 doi:10.1371/journal.pone.0031311.

Duffy, E.J. 2003. Early marine distribution and trophic interactions of juvenile salmon in Puget Sound. University of Washington, Thesis, Seattle, WA.

Duffy, E.J., Beauchamp, D.A., and Buckley, R.M. 2005. Early marine life history of juvenile Pacific salmon in two regions of Puget Sound. Estuarine, Coastal and Shelf Science **64:** 94-107.

Duffy, E.J., and Beauchamp, D.A. 2008. Seasonal patterns of predation on juvenile Pacific salmon by anadromous cutthroat trout in Puget Sound. Transactions of the American Fisheries Society **137**: 165–181.

Dunham, J., Baxter, C., Fausch, K., Fredenberg, W., Kitano, S., Koizumi, I., Morita, K., Nakamura, T., Rieman, B., Savvaitova, K., Stanford, J., Taylor, E., and Yamamoto, S. 2008. Evolution, ecology and conservation of Dolly Varden, white-spotted char, and bull trout. Fisheries **33**: 537-550.

Eliason, E.J., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., Gale, M.K., Patterson, D.A., Hinch, S.G., and Farrell, A.P. 2011. Differences in thermal tolerance among sockeye salmon populations. Science **332**: 109-112.

Emmett, E., Llansó, R., Newton, J., Thom, R., Hornberger, M., Morgan, C., Levings, C., Copping, A. and P. Fishman. 2000. Geographic signatures of North American west coast estuaries. Estuaries **23**: 765-792.

Espinoza, M., Farrugia, T.J., Webber, D.M., Smith, F. and Lowe, C.G. 2011. Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fisheries Research **108:** 364–371.

Feinberg, S.E. 1978. The Analysis of Cross-classified Categorical Data. Cambridge, MA: MIT Press.

Finstad, B., Økland, F., Thorstad, E.B., Bjørn, P.A. and McKinley, R.S. 2005. Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. Journal of Fish Biology **66:** 86–96.

Fisher, N.L. 1993. Statistical analysis of circular data. Division of Applied Physics, CSIRO, Canberra, Australia.

Ford, J.K.B., and Ellis, G.M. 2006. Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. Marine Ecology Progress Series **316**: 185-199.

Fraley, J.J., and Shepard, B.B. 1989. Life history, ecology and population status of migratory bull trout (Salvelinus confluentus) in the Flathead Lake and River system, Montana. Northwest Science **63**: 133–143.

Fujioka, J.T. 1970. Possible effects of low dissolved oxygen content in the Duwamish River estuary on migrating chinook salmon. Master's Thesis, University of Washington, Seattle.

Furey, N.B., Hinch, S.G., Lotto, A.G., and Beauchamp, D.A. 2015. Extensive feeding on sockeye salmon *Oncorhynchus nerka* smolts by bull trout *Salvelinus confluentus* during initial outmigration into a small, unregulated, and inland British Columbia river. Journal of Fish Biology **86**: 392-401.

Gahagan, B.I., Fox, D.A., and Secor, D.H. 2015. Partial migration of striped bass: revisiting the contingent hypothesis. Marine Ecology Progress Series **525**: 185-197.

Gale, W.A., Pasley, C.R., Kennedy, B.M., and Ostrand, K.G. 2009. Juvenile steelhead release strategies: A comparison of volitional- and forced-release practices. North American Journal of Aquaculture **71**: 97-106.

Gayeski, N., McMillan, B., and Trotter, P. 2011. Historical abundance of Puget Sound steelhead, *Oncorhynchus mykiss*, estimated from catch record data. Canadian Journal of Fisheries and Aquatic Sciences **68**: 498-510.

Gilhousen, P. 1990. Prespawning mortalities of sockeye salmon in the Fraser River system and possible causal factors. International Pacific Salmon Fisheries Commission Bulletin **26**: 58 p.

Godin, J.J. 1982. Migrations of salmonid fishes during early life history phases: daily and annual timing. In: Brannon EL, Salo EO (ed) Salmon and trout migratory behavior symposium. University of Washington, pp 22-50.

Goetz, F.A., Dawson, J.J., Shaw, T., and Dillon, J. 2001. Evaluation of low-frequency sound transducers for guiding salmon smolts away from a navigation lock. American Fisheries Society, Symposium **26**: 91-104.

Goetz, F.A., Jeanes, E., Moore, M.E., and Quinn, T.P. 2014. Comparative migratory behavior and survival of wild and hatchery steelhead (*Oncorhynchus mykiss*) smolts in riverine, estuarine, and marine habitats of Puget Sound, Washington. Environmental Biology of Fish DOI 10.1007/s10641-014-0266-3.

Goetz, F.A., Baker, B., Buehrens, T., and Quinn, T.P. 2013. Diversity of movements by individual anadromous coastal cutthroat trout *Oncorhynchus clarkii clarkii*. Journal of Fish Biology **83**: 1161–1182.

Goetz, F. 1989. Biology of the bull trout, *Salvelinus confluentus*, a literature review. Eugene, OR U.S. Department of Agriculture, Forest Service, Willamette National Forest. 53 p.

Goetz, F.A., Jeanes, E., and Beamer, E. 2004. Bull trout in the nearshore. Technical Report for the U.S. Army Corps of Engineers, Seattle District. Available at: http://www.nws.usace.army.mil/publicmenu/DOCUMENTS/Prelim_Bull_Trout_Report.pdf.

Goniea, T. M., Keefer, M.L., Bjornn, T.D., Peery, C.A., Bennett, D.H., and Stuehrenberg, L.C. 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. Transactions of the American Fisheries Society **135**: 408–419.

Groot, C., Bailey, R.E., Margolis, L., and Cooke, K. 1989. Migratory patterns of sockeye salmon (*Oncorhynchus nerka*) smolts in the Strait of Georgia, British Columbia, as determined by analysis of parasite assemblages. Canadian Journal of Zoology **67:** 1670-1678.

Groot, C., and Margolis, L. 1991. Pacific Salmon Life Histories. Vancouver, BC: University of British Columbia Press.

Gulseth, O.A., and Nilssen, K.J. 2000. The brief period of spring migration, short marine residence, and high return rate of a northern Svalbard population of Arctic char. Transactions of the American Fisheries Society **129**: 782–769.

Gutowsky, L.F.G., and coauthors. 2013. Diel vertical migration hypotheses explain size-dependent behaviour in a freshwater piscivore. Animal Behaviour **86**: 365-373.

Haas, G.R., and McPhail, J.D. 2001. The post-Wisconsinan glacial biogeography of bull trout (*Salvelinus confluentus*): a multivariate morphometric approach for conservation biology and management. Canadian Journal of Fisheries and Aquatic Sciences **58**: 2189-2203.

Hallock, R.J., Elwell, R.F., and Fry Jr., D.H. 1970. Migrations of adult king salmon *Oncorhynchus tshawytscha* in the San Joaquin Delta as demonstrated by the use of sonic tags. California Department of Fish and Game, Fisheries Bulletin 151.

Hansen, L.P., and Quinn, T.P. 1998. The marine phase of Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences **55** (Suppl. 1): 104–118.

Halpern, B.S., et al. 2008. A global map of human impact on marine ecosystems. Science **319**: 948-952.

Haque, S.R. 2008. Movement patterns of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in south Puget Sound, Washington 2006-2007. MS Thesis, Evergreen State College, Olympia, Washington.

Hard, J.J., Myers, J.M., Ford, M.J., Cope, R.G., Pess, G.R., Waples, R.S., Winans, G.A., Berejikian, B.A., Waknitz, F.W., Adams, P.B., Bisson, P.A., Campton, D.E., and Reisenbichler, R.R. 2007. Status review of Puget Sound steelhead *(Oncorhynchus mykiss)*. U.S. Dept. Commerce, NOAA Technical Memorandum NMFS-NWFSC-81, Seattle, WA.

Hayes, M.C., Rubin, S.P., Reisenbichler, R.R., Goetz, F.A., Jeanes, E. and McBride, A. 2011. Marine habitat use by anadromous bull trout (*Salvelinus confluentus*) from the Skagit River, Washington. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science **3**: 394-410.

Healey, M.C. 1982. Juvenile Pacific salmon in estuaries: the life support system. In Estuarine Comparisons. Edited by V.S. Kennedy. Academic Press, New York, NY. pp. 315–342.

Healey, M.C. 1991. Life history of Chinook Salmon (*Oncorhynchus tshawytscha*). Pages 311-394 in C. Groot and L. Margolis (eds.), Pacific salmon life histories. University of British Columbia Press, Vancouver.

Healey, M.C., and Groot, C. 1987. Marine migration and orientation of ocean-type Chinook and sockeye salmon. American Fisheries Society Symposium **1**: 298-312

Henderson, M.A., and Northcote, T.G. 1985. Visual prey detection and foraging in sympatric cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*). Canadian Journal of Fisheries and Aquatic Sciences **42**: 785-790.

Henderson, M.A., and Cass, A.J. 1991. Effect of smolt size on smolt-to-adult survival for Chilko Lake sockeye salmon *(Oncorhynchus nerka)*. Canadian Journal of Fisheries and Aquatic Sciences **48**: 988-994.

Hilborn, R., and Mangel, M. 1997. The Ecological Detective: Confronting Models with Data. Princeton, NJ: Princeton University Press.

Hinch, S.G., Cooke, S.J., Farrell, A.P., Miller, K.M., Lapointe, M., and Patterson, D.A. 2012. Dead fish swimming: a review of research on the early migration and high premature mortality in adult Fraser River sockeye salmon *Oncorhynchus nerka*. Journal of Fish Biology **81**: 576–599.

Hodgson, S., and Quinn, T.P. 2002. The timing of adult sockeye salmon migration into fresh water: adaptations by populations to prevailing thermal regimes. Canadian Journal of Zoology **80**: 542-555.

Hodgson, S., Quinn, T.P, Hilborn, R., Francis, R.C., and Rogers, D.E. 2006. Marine and freshwater climatic factors affecting interannual variation in the timing of return migration to fresh water of sockeye salmon. Fisheries Oceanography **15**: 1–24.

Hogen, D.M., and Scarnecchia, D.L. 2006. Distinct fluvial and adfluvial migration patterns of a relict charr, Salvelinus confluentus, stock in a mountainous watershed, Idaho, USA. Ecology of Freshwater Fish **15:** 376–387.

Holbrook, C.M., Zydlewski, J., Gorsky, D., Shepard, S.L., and Kinnison, M.T. 2009. Movements of prespawn adult Atlantic salmon near hydroelectric dams in the lower Penobscot River, Maine. North American Journal of Fisheries Management **29**: 495-505.

Holtby, L.B., Andersen, B.C., and Kadowaki, R.K. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences **47**: 2181-2194.

Homel, K., and Budy, P. 2008. Temporal and spatial variability in the migration patterns of juvenile and subadult bull trout in Northeastern Oregon. Transactions of the American Fisheries Society **137**: 869–880.

Howell, P.J., Dunham, J.B., and Sankovich, P. 2010. Relationships between water temperatures and upstream migration, cold water refuge use, and spawning of adult bull trout from the Lostine River, Oregon, USA. Ecology of Freshwater Fish **19:** 96-106.

Howell, P.J., M. Colvin, M.E., Sankovich, P.M., Buchanan, D.V., and Hemmingsen, A.R. 2016. Life histories, demography, and distribution of a fluvial bull trout population, Transactions of the American Fisheries Society **145:** 173-194.

Ibbotson, A.T., Beaumont, W.R.C., Pinder, A., Welton, S., and Ladle, M. 2006. Diel migration patterns of Atlantic salmon smolts with particular reference to the absence of crepuscular migration. Ecology of Freshwater Fish **15**: 544–551.

Ishida, Y., Yano, A., Ban, M. and Ogura, M. 2001. Vertical movement of a chum salmon *Oncorhynchus keta* in the western North Pacific Ocean as determined by a depth-recording archival tag. Fisheries Science **67**: 1030–1035.

Jakober, M.J., McMahon, T.E., and Thurow, R.F. 2000. Diel habitat partitioning by bull charr and cutthroat trout during fall and winter in Rocky Mountain streams. Environmental Biology of Fishes **59**: 79–89.

Jauquet, J.M. 2002. Coastal cutthroat trout (*Oncorhynchus clarki clarki*) diet in South Puget Sound, Washington 1999 – 2002. Evergreen State College, Olympia. 79 pp.

Jensen, A.J., Finstad, F.B., Fiske, P., Hvidsten, N.A., Rikardsen, A.H., and Saksgård, L. 2012. Timing of smolt migration in sympatric populations of Atlantic salmon (Salmo salar), brown trout (*Salmo trutta*), and Arctic char (*Salvelinus alpinus*). Canadian Journal of Fisheries and Aquatic Sciences **69:** 711–723.

Jensen, J.L.A., and Rikardsen, A.H. 2012. Archival tags reveal that Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* can use estuarine and marine waters during winter. Journal of Fish Biology **81:** 735–749.

Johnson, L. 2004. Fly-fishing Coastal Cutthroat Trout. Portland, OR: Frank Amato Publishers.

Johnson, O.M., Ruckelshaus, M.H., Grant, W.S., Waknitz, F.W., Garrett, A.M., Bryant, G.J., Neely, K., and Hard, J.J. 1999. Status review of coastal cutthroat trout from Washington, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-37.

Johnson, S.L., Power, J.H., Wilson, D.R., and Ray, J. 2010. A comparison of the survival and migratory behavior of hatchery-reared and naturally reared steelhead smolts in the Alsea River and estuary, Oregon, using acoustic telemetry. North American Journal of Fisheries Management **30**: 55-71.

Johnston, J.M. 1982. Life history of anadromous cutthroat trout with emphasis on migratory behavior. In Proceedings of the Salmon and Trout Migratory Behavior Symposium (Brannon, E. L. and Salo, E. O., eds.), pp. 123-127. Seattle, WA: School of Fisheries, University of Washington.

Jones, J.D., and Siefert, C.L. 1997. Distribution of mature sea-run cutthroat trout overwintering in Auke Lake and Lake Eva in southeastern Alaska. In Sea-run Cutthroat Trout: Biology, Management, and Future Conservation *(*Hall, J. D., Bisson, P. A. and Gresswell, R. E., eds.), pp. 27-28. Corvallis, OR: Oregon Chapter, American Fisheries Society.

Jonsson, B. 1985. Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. Transactions of the American Fisheries Society **114**: 182–194.

Jonsson, B., and Jonsson, N. 2011. Ecology of Atlantic Salmon and Brown Trout: Habitat as a Template for Life Histories. New York: Springer.

Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries **3:** 348-365.

Kadiri, M., Ahmadian, R., Bockelmann-Evans, B., Rauen, W., and Falconer, R. 2012. A review of the potential water quality impacts of tidal renewable energy systems. Renewable and Sustainable Energy Reviews **16**: 329–341.

Kallio-Nyberg, I., Peltonen, H., and Rita, H. 1999. Effects of stock-specific and environmental factors on the feeding migration of Atlantic salmon (*Salmo salar*) in the Baltic Sea. Canadian Journal of Fisheries and Aquatic Sciences **56:** 853-861.

Keefer, M.L., Peery C.A., and High, B. 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): variability among sympatric populations. Canadian Journal of Fisheries and Aquatic Sciences **66**: 1734-1747.

Keefer, M.L and Caudill, C.C. 2015. Estimating thermal exposure of adult summer steelhead and fall Chinook salmon migrating in a warm impounded river. Ecology of Freshwater Fish doi: 10.1111/eff.12238.

Keefer, M.L., Clabough, T.S., Jepson, M.A., Naughton, J.P., Blubaugh, T.J., Joosten, D.C., and Caudill, C.C. 2015. Thermal exposure of adult Chinook salmon in the Willamette River basin. Journal of Thermal Biology **48**: 11–20.

Kennedy, B.M., Gale, W.L., and Ostrand, K.G. 2007. Relationship between smolt gill Na+, K+ ATPase activity and migration timing to avian predation risk of steelhead trout (*Oncorhynchus mykiss*) in a large estuary. Canadian Journal of Fisheries and Aquatic Sciences **64**: 1506–1516.

Kerr, L.A., Secor, D.H., and Piccoli, P.M. 2009. Partial migration of fishes as exemplified by the estuarine-dependent white perch. Fisheries **34**: 114-123.

Kerr, L.A., Cadrin, S.X., and Secor, D.H. 2010. The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. Ecological Applications **20**: 497-507.

King County. 2011. Major lakes and offshore marine monitoring data. King County Department of Land and Water Resources webpages http://green.kingcounty.gov/lakes/lakeunion.aspx and http://green.kingcounty.gov/marine/CTD.aspx accessed January 2011.

Kinsey, W.W. 2007. "*Zalophus*" (Sea Lion) and "*Oncorhynchus*" (Salmon/Steelhead): Protected predator versus protected prey. Natural Resources and Environment **22:** 36-40.

Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F. and Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish **12**: 1–59.

Knutsen, J.A., Knutsen, H., Gjosaeter, J., and Jonsson, B. 2001. Food of anadromous brown trout at sea. Journal of Fish Biology **59:** 533–543.

Kostow, K.E. 2004. Differences in juvenile phenotypes and survival between hatchery stocks and a natural selection provide evidence for modified selection due to captive breeding. Canadian Journal of Fisheries and Aquatic Sciences **61**:577-589.

Krentz, L.K. 2007. Habitat use, movement, and life history variation of coastal cutthroat trout *Oncorhynchus clarkii clarkii* in the Salmon River Estuary, Oregon. MS Thesis, Oregon State University, Corvallis, Oregon.

Laake J., and Rexstad, E. 2007. RMark – an alternative approach to building linear models in MARK, RMark ver. 2.1.3.1. *In* Cooch E, White G (ed) Program MARK: a gentle introduction, Appendix C, pp C1-113. Available from http://www.phidot.org/software/mark/docs/book/. Accessed 12 September 2012.

Lance, L.L., Chang, W., Jeffries, S.J., Pearson, S.F., and Acevedo-Gutiérrez, A. 2012. Harbor seal diet in northern Puget Sound: implications for the recovery of depressed fish stocks. Marine Ecology Progress Series **464:** 257–271.

Lebreton, J.D., Burnham, K.P., Clobert, J., and Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monograph **62**: 67-118.

Ledgerwood, R.D., Thrower, F.P., and Dawley, E.M. 1991. Diel sampling of migratory juvenile salmonids in the Columbia River Estuary. Fishery Bulletin US **89**: 69–78.

Loch, J.J., and Miller, D.R. 1988. Distribution and diet of sea-run cutthroat trout captured in and adjacent to the Columbia River plume, May–July 1980. Northwest Science **62**: 41–48.

Lorenzen, K., Beveridge, M.C.M., and Mangel, M. 2012. Cultured fish: integrative biology and management of domestication and interactions with wild fish. Biological Review doi:10.1111/j.1469-185X.2011.00215.x.

Lotze, H.K, et al. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas science. Science **312**: 1806-1809. DOI: 10.1126/science.1128035.

Lowery, E.D., and Beauchamp, D.A. 2015. Trophic ontogeny of fluvial Bull Trout and seasonal predation on Pacific salmon in a riverine food web. Transaction of the American Fisheries Society **144**: 724-741.

Magnuson, J.J., Brandt, S.B., and Stewart, D.J. 1980. Habitat preferences and fishery oceanography. In Fish Behavior and Its Use in the Capture and Culture of Fishes (Bardach, J. E., Magnuson, J. J., May, R. C. & Reinhart, J. M., eds), pp. 371–382. ICLARM Conference Proceedings 5.

Mantua, N., Tohver, I., and Hamlet, A. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Climatic Change **102**: 187–223.

Martin F., Hedger, R.D., Dodson, J.J., Fernandes, L., Hatin, D., Caron, F., and Whoriskey, F.G. 2009. Behavioural transition during the estuarine migration of wild Atlantic salmon (*Salmo salar* L.) smolt. Ecology of Freshwater Fish **18**: 406–417.

Mathes, M.T., Hinch, S.G., Cooke, S.J., Crossin, C.T., Patterson, D.A, Lotto, A.G., and Farrell, A.P. 2010. Effect of water temperature, timing, physiological condition and lake thermal refugia on migrating adult Weaver Creek sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences **67**: 70–84.

Mazur, M.M., and Beauchamp, D.A. 2003. A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities. Environmental Biology of Fishes **67**: 397-405.

McClure, M., Carlson, S., Beechie, T., Pess, G., Jorgensen, J., Sogard, S., Sanderson, B., et al. 2008. Evolutionary consequences of habitat loss for Pacific anadromous salmonids. Evolutionary Applications **1**:300–318.

McClure, M.M., et al. 2013. Incorporating climate science in applications of the U.S. Endangered Species Act for aquatic species. Conservation Biology **27**: 1222–1233.

McCullough, D., Spalding, S., Sturdevant, D., and Hicks, M. 2001. Issue Paper 5. Summary of technical literature examining the physiological effects of temperature on salmonids. Prepared as part of U.S. EPA Region 10 Temperature Water Quality Criteria Guidance Development Project. EPA-910-D-01-005.

McCullough, D.A., and coauthors. 2009. Research in thermal biology: burning questions for coldwater stream fishes. Reviews in Fisheries Science **17**: 90-115.

Melnychuk, M.C. 2009a. Estimation of survival and detection probabilities for multiple tagged salmon stocks with nested migration routes, using a large-scale telemetry array. Marine and Freshwater Research **60**: 1231-1243.

Melnychuk, M.C. 2009b. Mortality of migrating Pacific salmon smolts in Southern British Columbia. Dissertation, University of British Columbia.

Melnychuk, M.C., Welch, D.W., Walters, C.J., and Christensen, V. 2007. Riverine and early ocean migration and mortality patterns of juvenile steelhead trout (*Oncorhynchus mykiss*) from the Cheakamus River, British Columbia. Hydrobiologia **582**: 55–65.

Melnychuk, M.C., and Walters, C.J. 2010. Estimating detection probabilities of tagged fish migrating past fixed receiver stations using only local information. Canadian Journal of Fisheries and Aquatic Sciences **67**: 641-658.

Melnychuk, M.C., Welch, D.W., and Walters, C.J. 2010. Spatio-temporal migration patterns of Pacific salmon smolts in rivers and coastal marine waters. PLoS ONE **59**: e12916 doi:10.1371/journal.pone.0012916.

Mesa, M.G., Weiland, L.K., Christiansen, H.E., Sauter, S.T., and Beauchamp, D.A. 2013. Development and evaluation of a bioenergetics model for bull trout. Transactions of the American Fisheries Society **142:** 41-49.

Middlemas, S.J., Stewart, D.C., Mackay, S. and Armstrong, J.D. 2009. Habitat use and dispersal of post-smolt sea trout *Salmo trutta* in a Scottish sea loch system. Journal of Fish Biology **74**: 639–651.

Monnot, L., Dunham, J.B., Hoem, T., and Koetsier, P. 2008. Influences of body size and environmental factors on autumn downstream migration of bull trout in the Boise River, Idaho. North American Journal of Fisheries Management **28:** 231-240.

Moore, M.E., Berejikian, B.A. and Tezak, E.P. 2010a. Early marine survival and behavior of steelhead smolts through Hood Canal and the Strait of Juan de Fuca. Transactions of the American Fisheries Society **139:** 49-61.

Moore, M.E., Goetz, F.A., Van Doornik, D.M., Tezak, E.P., Quinn, T.P., Reyes-Tomassini, J. and Berejikian, B. 2010b. Early marine migration patterns of wild coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. PLoS ONE **5**: e12881. doi:10.1371/journal.pone.0012881.

Moore, M.E., Berejikian, B.A., and Tezak, E.P. 2012. Variation in the early marine survival and behavior of natural and hatchery-reared Hood Canal steelhead. PLoS ONE **7**: e49645 doi:10.1371/journal.pone.0049645.

Moore, M.E., Berejikian, B.A., Goetz, F.A., Berger, A.G., Hodgson, S.S., Connor, E.J., and Quinn, T.P. 2015. Multi-population analysis of Puget Sound steelhead survival and migration behavior. Marine Ecology Progress Series **537**: 217–232, 2015 doi: 10.3354/meps11460.

Moore, S.K., Mantua, N.J., Newton, J.A., Kawase, M., Warner, M.J., and Kellogg, J.P. 2008. A descriptive analysis of temporal and spatial patterns of variability in Puget Sound oceanographic properties. Estuarine, Coastal and Shelf Science **80**: 545-554.

Morita, K. 2001. The growth history of anadromous white-spotted charr in northern Japan: a comparison between river and sea life. Journal of Fish Biology **59:** 1556–1565.

Morita, K., Morita, S.H., Fukuwaka, M.A., and Nagasawa, T. 2009. Offshore Dolly Varden charr (*Salvelinus malma*) in the North Pacific. Environmental Biology of Fishes **86:** 451–456.

Morita, K., Morita, S.H., Nagasawa, T., and Kuroki, M. 2013. Migratory patterns of anadromous white-spotted charr Salvelinus leucomaenis in eastern Hokkaido, Japan: the solution to a mystery. Journal of Ichthyology **53:** 809-819.

Moser, M.L., Olson, A.F., and Quinn, T.P. 1991. Riverine and estuarine migratory behavior of coho salmon (*Oncorhynchus kisutch*) smolts. Canadian Journal of Fisheries and Aquatic Sciences **48**: 1670–1678.

Muhlfeld, C.C., and Marotz, B. 2005. Seasonal movement and habitat use by subadult bull trout in the Upper Flathead River System, Montana. North American Journal of Fisheries Management **25**: 797–810.

Muhlfeld, C.C., Glutting, S., Hunt, R., Daniels, D., and Marotz, B. 2003. Winter diel habitat use and movement by subadult bull trout in the upper Flathead River, Montana. North American Journal of Fisheries Management **23:** 163–171.

Myers, J.M., Kope, R.G., Bryant, G.J., Teel, D., Leirheimer, L.J., Wainwright, T.C., and Grant W.S, et al. 1998. Status Review of Chinook Salmon from Washington, Idaho, Oregon, and California. Washington, DC: U.S. Department of Commerce. NOAA Technical Memorandum NMFS-NWFSC-35.

National Oceanic and Atmospheric Administration (NOAA). 2005. Proposed conservation plan for southern resident killer whales (*Orcinus orca*). NOAA, Northwest Regional Office, Seattle, WA. 183 pp.

NOAA Fisheries. 2007. Endangered and threatened species: notice of public hearing on proposed listing determination for Puget Sound Steelhead. Federal Register/Vol. 72, No. 91/Friday, May 11, 2007/Rules and Regulations 26722-26735.

Nagasawa, K. 1998. Predation by salmon sharks (*Lamna ditropis*) on Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean. North Pacific Anadromous Fish Commission Bulletin **1**: 419-433.

Newell, J.C., and Quinn, T.P. 2005. Behavioral thermoregulation by maturing sockeye salmon (*Oncorhynchus nerka*) in a stratified lake prior to spawning. Canadian Journal of Zoology **83**: 1232-1239.

Nielsen, J.L., Turner, S.M., and Zimmerman, C.E. 2011. Electronic tags and genetics explore variation in migrating steelhead kelts (*Oncorhynchus mykiss*), Ninilchik River, Alaska. Canadian Journal of Fisheries and Aquatic Sciences **68**: 1–16.

Northcote, T.G. 1992. Migration and residency in stream salmonids – some ecological considerations and evolutionary consequences. Nordic Journal of Freshwater Research **65**: 5-17.

Northcote, T.G. 1997. Potamodromy in Salmonidae: living and moving in the fast lane. North American Journal of Fishery Management **17**: 1029–1045.

Nowak, G.M., and Quinn, T.P. 2002. Diel and seasonal patterns of horizontal and vertical movements of telemetered cutthroat trout in Lake Washington, Washington. Transactions of the American Fisheries Society **131**: 452–462.

Olson, A.F., and Quinn, T.P. 1993. Vertical and horizontal movements of adult chinook salmon, *Oncorhynchus tshawytscha,* in the Columbia River estuary. Fishery Bulletin **91**: 171-178.

O'Neill, S.M., and West, J.E. 2009. Marine distribution, life history traits, and the accumulation of polychlorinated biphenyls in Chinook salmon from Puget Sound, Washington. Transactions of the American Fisheries Society **138**: 616-632.

Orsi, J.A., and Jaenicke, H.W. 1996. Marine distribution and origin of prerecruit Chinook salmon, *Oncorhynchus tshawytscha*, in southeastern Alaska. Fishery Bulletin **94**: 482-497.

Orsi, J.A., M.V. Sturdevant, J.M. Murphy, D.G. Mortensen, and B.L. Wing. 2000. Seasonal habitat use and early marine ecology of juvenile Pacific salmon in Southeastern Alaska. North Pacific Anadromous Fish Commission Bulletin **2**: 111-122.

Payne, J., Andrews, K., Chittenden, C., Crossin, G., Goetz F., et al. 2010. Studying movements and survival of marine animals with large-scale acoustic arrays. In: McIntyre AD (ed) Life in the World’s Oceans: Diversity, Distribution, and Abundance. Blackwell Publishing Ltd, Oxford, pp 269-290.

Pearcy, W.G. 1992. Ocean ecology of North Pacific salmonids. University of Washington Press, Seattle.

Pearcy, W.G., Brodeur, R.D. and Fisher, J.P. 1990. Distribution and biology of juvenile cutthroat trout *Oncorhynchus clarki* and steelhead *O. mykiss* in coastal waters off Washington and Oregon. Fishery Bulletin **99**: 697–711.

Penttila, D. 2007. Marine forage fishes in Puget Sound. Puget Sound Nearshore Partnership Report No. 2007-03. Published by Seattle District, U.S. Army Corps of Engineers, Seattle, Washington.

Polivka, K.M. 2005. Resource matching across habitats is limited by competition at patch scales in an estuarine-opportunist fish. Canadian Journal of Fisheries and Aquatic Sciences **62**: 913–924.

Poole, G., Dunham, J., Hicks, M. et al. 2001. Scientific issues relating to temperature criteria for salmon, trout, and char native to the Pacific Northwest. A summary report submitted to the policy workgroup of the U.S. EPA Region 10 Water Temperature Criteria Guidance Project. EPA 910-R-01-007.

Potter, E.C.E. 1988. Movements of Atlantic salmon, *Salmo salar* L., in an estuary in South-west England. Journal of Fish Biology **33(Suppl. A)**: 153-159.

Pressey, R.T. 1953. The sport fishery for salmon on Puget Sound. Fisheries Research Papers. Washington Department of Fisheries **1**: 33-48.

Puget Sound Nearshore Ecosystem Restoration Program (PSNERP). 2003. Guidance for protection and restoration of the nearshore ecosystems of Puget Sound. Prepared by the Nearshore Science Team. Fresh, K., Brennan, J., Dethier, M., Gelfenbaum, G., Goetz, F., Logsdon, M., Meyers, D., Mumford, T., Newton, J., Shipman, H., Simenstad, C., and Tanner, C.

Quinn, T.P. 2005. The Behavior and Ecology of Pacific Salmon and Trout. Seattle, WA: University of Washington Press.

Quinn, T.P., and Myers, K.W. 2004. Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. Reviews in Fish Biology and Fisheries **14**: 421–442.

Quinn, T.P., terHart, B.A., and Groot, C. 1989. Migratory orientation and vertical movements of homing adult sockeye salmon, *Oncorhynchus nerka*, in coastal waters. Animal Behaviour **37**: 587-599.

Quinn, T.P., McGinnity, P., and Reed, T.E. 2015. The paradox of "premature migration" by adult anadromous salmonid fishes: patterns and hypotheses. Canadian Journal of Fisheries and Aquatic Sciences 10.1139/cjfas-2015-0345.

R Development Core Team. 2011. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Rader, R.B., Belish, T., Young, M.K. and Rothlisberger, J. 2007. The scotopic visual sensitivity of four species of trout: a comparative study. Western North American Naturalist **67:** 524–537.

Railsback, S.F., Harvey, B.C., Hayse, J.W., and LaGory, K.E. 2005. Tests of theory for diel variation in salmonid feeding activity and habitat use. Ecology **86**: 947-959.

Ratliff, D.E., and Howell, P.J. 1992. The status of bull trout populations in Oregon. Pages 10–17 in P. J. Howell and D.V. Buchanan, editors. Proceedings of the Gearhart Mountain Bull Trout Workshop. Oregon Chapter of the American Fisheries Society, Corvallis.

Raymond, H.L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River basin. North American Journal of Fisheries Management **8**: 1-24.

Raymond, S. 1996. The Estuary Flyfisher. Portland, OR: Frank Amato Publishers.

Reimers, P.E. 1973. The length of residence of juvenile fall Chinook salmon in Sixes River, Oregon. Research Reports of the Fish Commission of Oregon **4**: 1-42.

Reyes-Tomassini, J., Moore, M., Berejikian, B., Lee, J., and Goetz, F. 2011. AquaTracker telemetry track analysis software program Version 1.00A. NOAA, Manchester Research Station, WA.

Rice, C., Chamberlin, J., Hall, J., Zackey, T., Schilling, J., Kubo, J., Rustay, M., Leonetti, F., and Guntenspergen, G. 2013. Monitoring ecosystem response to restoration and climate change in the Snohomish River estuary: field operations and data summary. Report to Tulalip Tribes.

Richter, A., and Kolmes, S.A. 2005. Maximum temperature limits for Chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. Reviews in Fisheries Science **13**: 23–49.

Ricker, W.E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. Journal of the Fisheries Research Board of Canada **33**: 1483-1525.

Rohde, J., Kagley, A.N, Fresh, K.L., Goetz, F.A., and Quinn, T.P. 2013. Partial migration and diel movement patterns in Puget Sound coho salmon (*Oncorhynchus kisutch*). Transactions of the American Fisheries Society **142**: 1615-1628.

Rohde, J., Fresh, K.L., and Quinn, T.P. 2014. Factors affecting partial migration in Puget Sound coho salmon. North American Journal of Fisheries Management 34:3 559-570.

Romer, J.D., Leblanc, C.A., Clements, S., Ferguson, J.A., Kent, M.L., Noakes, D., and Schreck, C.B. 2012. Survival and behavior of juvenile steelhead trout (*Oncorhynchus mykiss*) in two estuaries in Oregon, USA. Environmental Biology of Fish DOI 10.1007/s10641-012-0080-8.

Roscoe, D.W., Hinch S.G., Cooke, S.J., and Patterson, D.A. 2010. Behaviour and thermal experience of adult sockeye salmon migrating through stratified lakes near spawning grounds: the roles of reproductive and energetic states. Ecology of Freshwater Fish **19**: 51–62.

Ross, P.S., Kennedy, C.S., Shelley, L.K., Tierney, K.B., Patterson, D.A., Fairchild, W.L., Macdonald, R.W., and Kidd, K. 2013. The trouble with salmon: relating pollutant exposure to toxic effect in species with transformational life histories and lengthy migrations. Canadian Journal of Fisheries and Aquatic Sciences **70**: 1252-1264.

Rounsefell, G.A. 1958. Anadromy in North American Salmonidae. Fishery Bulletin **131**: 171–185.

Rowcliffe, J.M, Carbone, C., Kays, R., Kranstaube, B. and Jansen, P.A. 2012. Bias in estimating animal travel distance: the effect of sampling frequency. Methods in Ecology and Evolution DOI: 10.1111/j.2041-210X.2012.00197.x

Ruggerone, G.T, Quinn, T.P., McGregor, I., and Wilkinson, T.D. 1990. Horizontal and vertical movements of maturing steelhead trout, *Oncorhynchus mykiss*, in Dean and Fisher channels, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences **47**: 1963-1969.

Ruggerone, G., and Goetz, F. 2004. Survival of Puget Sound Chinook salmon (*Oncorhynchus tshawytscha*) in response to climate-induced competition with pink salmon (*Oncorhynchus gorbuscha*). Canadian Journal of Fisheries and Aquatic Sciences **61**: 1756–1770.

Russell, C., Moore, A., Ives, S., Kell, L.T., Ives, M.J., and Stonehewer, R.O. 1998. The migratory behaviour of juvenile and adult salmonids in relation to an estuarine barrage. Hydrobiologia **371/372**: 321–333.

Saiget, D.A., Sloat, M.R. and Reeves, G.H. 2007. Spawning and movement behavior of migratory coastal cutthroat trout on the western Copper River Delta, Alaska. North American Journal of Fisheries Management **27**: 1029-104.

Salinger, D.H., and Anderson, J.J. 2006. Effects of water temperature and flow on adult salmon migration swim speed and delay. Transactions of the American Fisheries Society **135**: 188–199.

Saloniemi, I., Jokikokko, E., Kallio-Nyberg, I., Jutila, E., and Pasanen, P. 2004. Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. ICES Journal of Marine Science **61**: 782-787.

Sandstrom, P.T., Keegan, T., and Singer, G. 2013. Survival and movement patterns of central California coast native steelhead trout (*Oncorhynchus mykiss*) in the Napa River. Environmental Biology of Fish doi:10.1007/s10641-012-0092-4.

Sargeant, C.J., Armstrong, J.B., and Ward, E.J. 2015. Predator-prey migration phenologies remain synchronized in a warming catchment. Freshwater Biology **60**: 724–732.

Schaller, H.A., and Petrosky, C.E. 2007. Assessing hydrosystem influence on delayed mortality of Snake River stream-type Chinook salmon. North American Journal of Fisheries Management **27**: 810-824.

Scheuerell, M.D., Zabel, R.W., and Sandford, B.P. 2009. Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus spp*.). Journal of Applied Ecology **46**: 983–990.

Schreck, C.B., Stahl, T.P., Davis, L.E., Roby, D.D., and Clemens, B.J. 2006. Mortality estimates of juvenile spring-summer Chinook salmon in the lower Columbia River and estuary, 1992–1998: evidence for delayed mortality? Transactions of the American Fisheries Society **135**: 457–475.

Scott, J.B., and Gill, W.T. 2008. *Oncorhynchus mykiss*: assessment of Washington State's steelhead populations and programs. Washington Department of Fish and Wildlife, Olympia.

Seeb, L.W., Seeb, J.E., Habicht, C., Farley Jr., E.V. and Utter, F.M. 2011. Single-nucleotide polymorphic genotypes reveal patterns of early juvenile migration of sockeye salmon in the eastern Bering Sea. Transactions of the American Fisheries Society **140:** 734-748.

Seiler, D., Volkhardt, G., Kishimoto, L., and Topping, P. 2002. 2000 Green River juvenile salmonid production evaluation. Report # FPT 02-03 Washington Department of Fish and Wildlife Fish Program, WA.

Selong, J.H., and McMahon, T.E. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerances in fishes. Transactions of the American Fisheries Society **130**: 1026–1037.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. Washington Sea Grant Program, University of Washington Press, Seattle.

Simenstad, C.A., Fresh, K.L., and Salo, E.O. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. In: Kennedy, V.S. (Ed.), Estuarine Comparisons. Academic Press, New York, NY, pp. 343–364.

Smith, J.M., Fresh, K.L., Kagley, A.N., and Quinn, T.P. 2015. Ultrasonic telemetry reveals seasonal variation in depth distribution and diel vertical migrations of sub-adult Chinook and coho salmon in Puget Sound. Marine Ecology Progress Series **532:** 227–242.

Sound Data Management LLC. 2008. Hydra - the hydrophone data repository. Available: 725 http://hydra.sounddatamanagement.com/ (July 2011).

Starcevich, S.J., Howell, P.J., Jacobs, S.E., and Sankovich, M. 2012. Seasonal movement and distribution of fluvial adult bull trout in selected watersheds in the Mid-Columbia River and Snake River Basins. PLoS ONE 7: e37257. doi:10.1371/journal.pone.0037257.

Staurnes, M., Sigholt, T., Lysfjord, G., and Gulseth, O.A. 1992. Difference in the seawater tolerance of anadromous and landlocked populations of arctic char *(Salvelinus alpinus)*. Canadian Journal of Fisheries and Aquatic Sciences **49**: 443-447.

Strange, J.S. 2013. Factors influencing the behavior and duration of residence of adult Chinook salmon in a stratified estuary. Environmental Biology of Fish **96**: 225–243.

Strange, J.S. 2012. Migration strategies of adult Chinook salmon runs in response to diverse environmental conditions in the Klamath River Basin, Transactions of the American Fisheries Society **141**: 1622-1636.

Strange, J.S. 2010. Upper thermal limits to migration in adult Chinook salmon: evidence from the Klamath River Basin. Transactions of the American Fisheries Society **139**: 1091–1108.

Strickland, R.M. 1983. The Fertile Fjord. University of Washington Press, Seattle.

Sturdevant, M.V., Orsi, J.A., and Fergusson, E.A. 2012. Diets and trophic linkages of epipelagic fish predators in coastal Southeast Alaska during a period of warm and cold climate years, 1997–2011. Marine and Coastal Fisheries **4:** 526-545.

Sumner, F.H. 1962. Migration and growth of the coastal cutthroat trout in Tillamook County, Oregon. Transactions of the American Fisheries Society **91:** 77–83.

Sutherland, D.A., MacCready, P., Banas, N.S. and Smedstad, L.F. 2011. A model study of the Salish Sea estuarine circulation. Journal of Physical Oceanography **41**: 1125–1143.

Swanberg, T.R. 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. Transactions of the American Fisheries Society **126**: 735–746.

Tanaka, H., Takagi, Y., and Naito, Y. 2000. Behavioral thermoregulation of chum salmon during homing migration in coastal waters. Journal of Experimental Biology **203**: 1825-1833.

Thompson, W.F. 1959. An approach to population dynamics of the Pacific red salmon. Transactions of the American Fisheries Society **88**: 206-209.

Thorpe, J.E. 1994. Salmonid fishes and the estuary environment. Estuaries **17**(1A): 76-93.

Thorstad, E.B., Økland, F., Finstad, B., Sivertsgård, R., Plantalech, N., Bjørn, P.A. and Mckinley, R.S. 2007. Fjord migration and survival of wild and hatchery-reared Atlantic salmon and wild brown trout post-smolts. Hydrobiologia **582**: 99–107.

Trotter, P.C. 1989. Coastal cutthroat trout: a life history compendium. Transactions of the American Fisheries Society **118:** 463–473.

Trotter, P.C. 1997. Sea-run cutthroat trout: life history profile. In Sea-run Cutthroat Trout: Biology, Management, and Future Conservation *(*Hall, J. D., Bisson, P. A. and Gresswell, R. E., eds.), pp. 7-15. Corvallis, OR: Oregon Chapter, American Fisheries Society.

Trudel, M., Fisher J., Orsi, J.A., Morris, J.F.T., Thiess, M.E., Sweeting, R.M., Hinton, I.S., Fergusson, E.A., and Welch, D.W. 2009. Distribution and migration of juvenile Chinook salmon derived from coded wire tag recoveries along the continental shelf of western North America. Transactions of the American Fisheries Society **138**: 1369–1391.

Tucker. S., Trudel, M., Welch, D.W., Candy, J.R., Morris, J.F.T, Thiess, M.E., Wallace C., Teel, D.J., Crawford, W., Farley, E.V. Jr., and Beacham, T.D. 2009. Seasonal stock-specific migrations of juvenile sockeye salmon along the west coast of North America: Implications for growth. Transactions of the American Fisheries Society **138**: 1458–1480.

U.S. Fish and Wildlife Service (USFWS). 2004. Recovery Plan for the Coastal-Puget Sound Distinct Population Segment of Bull Trout (*Salvelinus confluentus*). Volume I (of II): Puget Sound Management Unit. Portland, Oregon.

Volkhardt, G.C., Johnson, S.L., Miller, B.A., Nickelson, T.E., and Seiler, D.E. 2007. Rotary screw traps and inclined plane screen traps. Pages 235-266 *in* D. H. Johnson, B. M. Shrier, J. S. O'Neal, J. A. Knutzen, X. Augerot, T. A. O-Neil, and T. N. Pearsons, editors. Salmonid field protocols handbook: techniques for assessing status and trends in salmon and trout populations. American Fisheries Society, Bethesda, Maryland.

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., et al. 2010. Global threats to human water security and river biodiversity. Nature **467**: 555–61, doi:10.1038/nature09440.

Walker, R.V., Myers, K.W., Davis, N.D., Aydin, K.W., Friedland, K.D., Carlson, H.R., Boehlert, G.W., Urawa, S., Ueno, Y., and Anma, G. 2000. Diurnal variation in thermal environment experienced by salmonids in the North Pacific as indicated by data storage tags. Fisheries Oceanography **9**: 171-186.

Walker, R. J., Sviridov, V. V., Urawa, S. and Azumaya, T. 2007. Spatio-temporal variation in vertical distributions of Pacific salmon in the ocean. North Pacific Anadromous Fish Commission Bulletin **4**: 193–201.

Waples, R.S., Pess, G.R., and Beechie, T. 2008. Evolutionary history of Pacific salmon in dynamic environments. Evolutionary Applications **1**: 189–206.

Ward, BR. 2000. Declivity in steelhead (*Oncorhynchus mykiss*) recruitment at the Keogh River over the past decade. Canadian Journal of Fisheries and Aquatic Sciences **57**: 298-306.

Ward, B.R., Slaney, P.A., Facchin, A.R., and Land, R.W. 1989. Size-biased survival in steelhead trout: backcalculated lengths from adults' scales compared to migrating smolts at the Keogh River, B.C. Canadian Journal of Fisheries and Aquatic Sciences **46**: 1853-1858.

Watry, C.B., and Scarnecchia, D.L. 2008. Adfluvial and fluvial life history variations and migratory patterns of a relict charr, *Salvelinus confluentus*, stock in west-central Idaho, USA. Ecology of Freshwater Fish **17**: 231–243.

Watson, G.S. 1962. Goodness of fit tests on a circle: II. Biometrika **49**(1-2): 57-63.

Welch, D.W., Ward, B.R., Smith, B.D., and Eveson, J.P. 2000. Temporal and spatial responses of British Columbia steelhead (*Oncorhynchus mykiss*) populations to ocean climate shifts. Fisheries Oceanography **9**: 17–32.

Welch, D.W., Boehlert, G.W., and Ward, B.R. 2002. POST–the Pacific Ocean salmon tracking project. Oceanologica Acta **25**: 243–253.

Welch, D.W., Ward, B.R., and Batten, S.D. 2004. Early ocean survival and marine movements of hatchery and wild steelhead trout (*Oncorhynchus mykiss*) determined by an acoustic array: Queen Charlotte Strait, British Columbia. Deep-Sea Research II **51**: 897–909.

Welch, D.W., Melnychuk, M.C., Payne, J.C., Rechisky, E.L., Porter, A.D., Jackson, G.D., Ward, B.R., Vincent, S.P., Wood, C.C., and Semmens, J. 2011. In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. Proceedings of the National Academy of Sciences USA **108**: 8708-8713.

Weitkamp, L., and Neely, K. 2002. Coho salmon (*Oncorhynchus kisutch*) ocean migration patterns: insight from marine coded-wire tag recoveries. Canadian Journal of Fisheries and Aquatic Sciences **59**: 1100-1115.

Wenburg, J.K. 1998. Coastal cutthroat trout (*Oncorhynchus clarki clarki*): genetic population structure, migration patterns, and life history traits. PhD Thesis, University of Washington, Seattle, Washington.

Wenburg, J.K., and Bentzen, P. 2001. Genetic and behavioral evidence for restricted gene flow among coastal cutthroat trout populations. Transactions of the American Fisheries Society **130**: 1049–1069.

Westerberg, H. 1982. Ultrasonic tracking of Atlantic salmon *(Salmo salar* L.) - II. Swimming depth and temperature stratification. Institute of Freshwater Research Drottningholm **60**: 102-120.

White, G.C., and Burnham, K.P. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Studies **46**(1, suppl): 120–138.

Williamson, C.E., Saros, J.E., Vincent, W. F., and Smol, J.P. 2009. Lakes and reservoirs as sentinels, integrators, and regulators of climate change. Limnological Oceanography **54**: 3273–2282.

Winder, W., and Schindler, D.E. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. Ecology **85**: 2100–2106.

Winemiller, K.O., and Rose, K.A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences **49**: 2196-2218.

Winter, J. 1996. Advances in underwater telemetry. In: Murphy BR, Willis DW (ed) Fisheries techniques, 2nd edn. American Fisheries Society, Maryland, pp 555-590.

Wood, C.C., and Foote, C.J. 1996. Evidence for sympatric genetic divergence of anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). Evolution **50**: 1265-1279.

Yates, D., Galbraith, H., Purkey, D., Huber-Lee, A., Sieber, J., West, J., Herrod-Julius, S., and Joyce, B. 2008. Climate warming, water storage, and Chinook salmon in California's Sacramento Valley. Climatic Change DOI 10.1007/s10584-008-9427-8.

Young, M.K., Wilkison, R.A., Phelps, M., and Griffith, J.S. 1997. Contrasting movement and activity of large brown trout and rainbow trout in Silver Creek, Idaho. Great Basin Naturalist **57**: 238-244.

Zar, J. H. 1999. Biostatistical Analysis, 4th edn. Upper Saddle River, NJ: Prentice Hall.

Zimmerman, M.S., and Kinsel, C. 2010. Migration of anadromous juvenile bull trout in the Skagit River, 1990–2009. Washington Department of Fish and Wildlife, Olympia.

Zydlewski, J., Johnson, J., Brunzell, J., Hogle, J., Clements, S., Karnowski, M. and Schreck, C. 2008. Seaward migration of coastal cutthroat trout *Oncorhynchus clarkii* from four tributaries of the Columbia River. In The 2005 Coastal Cutthroat Trout Symposium: Status, Management, Biology, and Conservation (Connolly, P. J., Williams, T. H. and Gresswell, R. E., eds.), pp. 65-74. Portland, OR: Oregon Chapter, American Fisheries Society.

Zydlewski, G.B., Zydlewski, J. and Johnson, J. 2009. Patterns of migration and residency in coastal cutthroat trout *Oncorhynchus clarkii* from two tributaries of the lower Columbia River. Journal of Fish Biology **75**: 203–222.

APPENDIX A

SUPPLEMENTAL TABLES

Chapter 3

Appendix Table 3.1: Bull trout capture and acoustic tagging by location (north to south), year and months of tagging, in nearshore areas and rivers (River, R; river kilometer, rkm) from North Puget Sound (Nooksack River), Skagit Bay to Deception Pass (Swinomish Channel, Skagit Bay), Saratoga Passage to Possession Sound (Port Susan, Snohomish River), and Central Puget Sound (Shilshole Bay).

Tagging Area	Months	2002	2003	2004	2005	2006	2007	2010	Total
Nooksack R (rkm 68)	Feb 2-28						11		11
Swinomish Channel	May 4-Jun 25[1]		13	1	21	16			51
North Skagit Bay	Apr 29-Jun 11		9	6					15
East Skagit Bay	9-May		2						2
West Skagit Bay	Apr 13-Jun 15		4	11	10				25
South Skagit Bay	Apr 13-May 25			8					8
Skagit R Delta (rkm 13, 8.9)	Feb 17-Apr 3					20			20
Port Susan	Apr 2-Jun 10	11	17	2					30
Snohomish R Delta (rkm 0)	Apr 13-Jun 10	24	11	16	10				61
Snohomish R (rkm 20.8, 26.1)	Mar 4-Apr 1	25			8				33
Shilshole Bay	Jun 2-Jul 1		1	1					2
White River	Jun 1-Jul 14				10	10		8	28
Total		**60**	**57**	**45**	**59**	**46**	**11**	**8**	**286**

1. One fish tagged July 23.

Appendix Table 3.2: Length of tagged female and male bull trout (SD in parentheses).

	Count		**Female Fork Length**		**Male Fork Length**	
Year	**Female (N)**	**Male (N)**	**Mean (mm)**	**Range (Min-Max)**	**Mean (mm)**	**Range (Min-Max)**
2002	35	25	425 (94)	282-590	409 (84)	318-625
2003	32	25	459 (78)	332-650	461 (71)	373-615
2004	22	23	467 (58)	358-605	465 (88)	310-638
2005	24	35	442 (80)	280-604	490 (67)	355-603
2006	17	29	403 (57)	313-487	426 (95)	223-563
2007	5	6	479 (20)	460-509	496 (55)	433-560
2010	2	6	500 (49)	465-535	478 (56)	415-565
Total	**137**	**149**	**442 (79)**	**280-650**	**454 (84)**	**223-638**

Chapter 4

Appendix Table 4.1. Chinook salmon size at release, date of tributary entry, total days from release to tributary entry, mean temperature and standard deviation, and number of days where mean temperature exceeded 18 ºC and 20 ºC.

Release Date	Length	Weight	Entry to Spawning Tributary	Total Days	Mean Temperature	Stdev	Days Exceeding 18 ºC	Days Exceeding 20 ºC
8/11/05	845	4.5	10/6/05	56	16.4	2.2	11	1
8/11/05	715	4.6	10/3/05	53	16.9	2.5	22	1
8/11/05	728	4.9	9/23/05	43	17.0	2.2	15	0
8/17/05	730	4.7	10/8/05	52	16.1	2.2	11	0
8/17/05	560	2.7	9/21/05	35	17.8	2.0	13	2
8/17/05	688	3.7	9/30/05	44	17.6	2.0	22	1
8/17/05	645	5.9	10/3/05	47	16.0	2.3	13	1
8/17/05	892	9.2	9/20/05	34	16.8	2.2	10	2
8/17/05	718	7.0	10/7/05	51	16.0	1.8	5	0
8/17/05	611	2.4	10/1/05	45	16.6	2.5	19	1
8/24/05	896	5.0	10/2/05	39	16.9	2.0	13	1
8/24/05	675	2.2	9/30/05	37	16.9	2.2	10	2
8/24/05	769	4.0	9/29/05	36	16.8	2.0	11	1
8/24/05	905	2.9	10/1/05	38	17.9	2.3	15	5
8/24/05	815	8.9	9/23/05	30	16.8	2.0	6	1
8/24/05	582	9.0	9/14/05	21	17.8	2.1	10	0
8/24/05	748	5.4	10/7/05	44	16.7	2.1	11	4
8/24/05	905	9.2	10/2/05	39	17.1	2.3	15	7
8/24/05	761	5.7	9/23/05	30	17.8	2.0	14	2
8/24/05	681	3.8	10/5/05	42	16.2	2.3	11	0
8/24/05	544	2.0	9/21/05	28	16.9	2.1	7	0
8/24/05	758	5.7	9/24/05	31	17.0	2.0	6	1
8/24/05	720	4.7	10/2/05	39	15.7	2.0	4	0
8/24/05	739	5.2	10/1/05	38	16.8	2.2	12	2
8/24/05	705	4.4	10/2/05	39	15.3	1.8	1	0
8/24/05	761	4.6	10/1/05	38	15.8	1.7	5	0
8/31/05	757	5.6	10/1/05	31	16.8	2.1	14	0
8/31/05	763	5.8	10/7/05	37	16.6	1.8	10	0
8/31/05	557	2.2	9/23/05	23	17.7	1.4	8	0
8/31/05	902	9.2	10/2/05	32	15.9	1.7	5	0
8/31/05	802	6.7	9/30/05	30	16.2	1.9	6	0
8/31/05	741	5.3	10/2/05	32	15.6	1.8	3	0
8/31/05	611	2.7	10/6/05	36	16.6	2.5	17	0
8/31/05	654	3.2	10/3/05	33	16.1	1.9	5	0
8/31/05	688	4.0	10/2/05	32	16.5	1.9	8	0
8/9/06	940	10.1	9/6/06	28	18.9	1.5	22	7

8/9/06	850	7.8	9/20/06	42	18.6	1.3	26	7
8/9/06	750	5.5	9/22/06	44	17.7	2.7	24	9
8/9/06	860	8.1	9/23/06	45	17.6	2.3	25	3
8/9/06	870	7.6	9/14/06	36	17.0	2.5	23	6
8/9/06	650	6.2	9/10/06	32	17.4	1.2	23	0
8/9/06	900	8.4	9/20/06	42	18.0	1.8	23	8
8/9/06	840	3.0	9/16/06	38	17.6	2.0	23	1
8/9/06	840	9.1	9/20/06	42	18.4	1.7	23	8
8/9/06	710	7.6	9/20/06	42	18.4	1.5	27	3
8/9/06	840	4.5	10/8/06	60	16.2	2.6	27	2
8/9/06	810	7.6	10/10/06	62	17.9	2.0	34	5
8/16/06	740	2.8	9/21/06	36	17.5	1.9	19	0
8/16/06	850	6.2	9/19/06	34	18.6	0.9	27	4
8/16/06	780	9.6	9/22/06	37	16.1	2.5	15	0
8/16/06	860	6.9	9/22/06	37	17.6	1.8	16	4
8/16/06	860	4.7	9/22/06	37	17.9	1.6	21	3
8/16/06	760	4.3	9/20/06	35	18.2	1.3	26	1
8/16/06	530	4.0	9/20/06	35	18.0	1.0	22	0
8/16/06	820	7.4	9/22/06	37	17.7	1.6	22	2
8/23/06	910	8.1	9/22/06	30	17.6	1.7	17	0
8/23/06	880	5.7	10/4/06	42	17.7	1.1	19	0
8/23/06	740	7.2	10/6/06	44	16.9	1.4	9	0
8/23/06	760	9.3	9/20/06	28	17.0	1.4	8	0
8/23/06	780	8.6	9/20/06	28	18.2	1.2	18	1
8/23/06	920	5.2	10/8/06	46	15.8	1.5	6	0
8/23/06	810	5.7	10/4/06	42	16.4	2.0	11	0
8/23/06	720	7.4	10/4/06	42	17.6	1.0	18	0
8/30/06	700	5.2	9/22/06	23	18.1	1.5	13	0
8/30/06	690	7.9	9/22/06	23	17.7	1.2	11	0
8/30/06	830	6.2	9/22/06	23	16.8	1.6	7	0
8/30/06	760	8.1	9/20/06	21	17.5	1.3	8	1
8/30/06	830	5.7	10/10/06	41	16.6	1.7	10	0

Appendix Table 4.2. Dissolved oxygen levels (mg/l) at depths from 4-14 m from the upper estuary to central Lake Washington.

Location	Date	4-m	8-m	9-m	10-m	12-m	14-m
Upper Estuary	8/30/2006	7.11	6.83		6.3	5.85	5.61
	9/6/2006	7.62	7.06		6.9	6.89	6.94
	9/20/2006	7.54	7.26		6.82	6.42	5.55
Lower Ship Canal	8/4/2005	6.73	6.17	5.19			
	8/18/2005	7.26	6.9	5.68			
	9/13/2005	6.86					
	9/22/2005	7.02	6.94	5.72			
North Lake Union	8/4/2005	7.41	5.79	3.75	2.42		
	8/18/2005	7.73	6.72	3.71	2.03		
	9/2/2005	7.65	7.43	7.22	2.58		
	9/22/2005	7.53	7.41	7.41	7.31		
	8/3/2006	7.73	5.82	4.52	1.7		
	8/16/2006	7.85	7.84	5.57	1.15		
	9/6/2006	7.63	7.15	6.41	3.74		
	9/20/2006	7.47	7.31	7.31	7.18		
Upper Ship Canal	8/4/2005	7.24	6.4	5.68			
	8/18/2005	7.59	7.24	6.73			
	9/13/2005	7.62	7.49	7.12			
	9/22/2005	8.06	8.01	7.87			
	8/3/2006	7.79	5.84	4.22			
	8/16/2006	8.04	7.33	6.84			
	9/6/2006	7.87	6.47	5.37			
	9/20/2006	7.95	7.72	7.91			
Central Lake Washington	8/1/2005	8.4	8.4		7.9	7.2	6.6
	8/15/2005	8.3	8.1		7.0	6.4	6.3
	9/6/2005	8.8			8.7	6.3	5.8
	9/19/2005	8.8			8.8	6.3	5.5
	8/7/2006	7.9	8.1		7.9	7.8	7.7
	8/21/2006	7.5	7.8		7.5	7.1	7.0
	9/6/2006	8.1	8.2		8.1	7.0	6.6
	9/18/2006	8.3	8.4		8.4	8.4	6.7

VITA

Fred Goetz is originally from Williamston, Michigan. He always enjoyed the outdoors starting at an early age, from fishing with his grandfather, growing up on the Red Cedar River where he collected various frogs, turtles and insects, or on vacations along the Lake Michigan shoreline. He obtained his B.Sc. in Environmental Science and Geography from Michigan State University. He obtained his M.Sc. in Fisheries Science and Physical Geography from Oregon State University supervised by Doug Markel, where he studied the biogeography of bull trout and developed survey methods for finding juvenile bull trout and assessing their habitat needs. He began his professional career working for the U.S. Forest Service at the Mt. Baker/Snoqualmie National Forest, and then moved to the U.S. Army Corps of Engineers in Seattle, Washington. While working at the USACE, Fred returned to school at the University of Washington School (UW) of Aquatic and Fisheries Science to obtain his Doctorate, supervised by Tom Quinn. At the UW Fred conducted a multi-species study of marine resident and ocean-bound salmonids in the Puget Sound and facilitated a multi-organizational marine monitoring network for studying anadromous and marine fishes. After completing his dissertation Fred continues his work at the USACE.