

Partial Migration of Puget Sound Coho Salmon (*Oncorhynchus kisutch*)
Individual and Population Level Patterns

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Abstract

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Partial migration, the behavior pattern in which a portion of a population migrates while others do not, is a widespread phenomenon with ecological and evolutionary consequences. Most Coho Salmon from streams in the Puget Sound, Washington basin rear over the continental shelf or offshore waters of the North Pacific Ocean after leaving fresh water, but some rear in the semi-estuarine waters of Puget Sound and are termed residents. The movements of residents are poorly documented and it is unclear whether they ever leave Puget Sound and move to the coast of Washington, and what factors might influence fish to adopt a resident migration pattern. To understand this migration pattern at the population level, we used coded-wire tag data to evaluate the effect of several factors on the tendency of Coho Salmon to remain resident in Puget Sound rather than migrating outside. We found that location of origin, day of release, and year of

release most strongly affected residency, with fish released later and from south Puget Sound the most likely to remain resident. These factors together indicate that environmental variation plays a strong role in resident migration pattern. Additionally, fish remaining resident were more likely to be recovered in the basin they were released from than in neighboring basins. To understand this migration pattern at the individual level, we investigated the patterns of movement by resident Coho Salmon in Puget Sound at a series of spatial scales using acoustic telemetry. Some residents were detected departing Puget Sound, though they rarely moved between the different basins of Puget Sound. Additionally there was strong evidence of movement to deep, offshore environments during day, and shallow, close to shore environments at night. Rather than a discrete behavior, we suggest that residence in Puget Sound by Coho Salmon is part of a continuum of migratory behavior patterns.

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General Introduction

“Now we must consider in general the common reason for moving with any movement whatever.”

Aristotle, De Motu Animalium, 4th century B.C.

Movement is one of the most fundamental processes of life on earth. It not only determines the distribution of organisms, but also influences some of the greatest issues of our time, including invasions of foreign species, the spread of disease, the fragmentation of habitats, and the change of global climate (Nathan 2008). Humans have considered the nature of movement for centuries, but perhaps no form of movement has fascinated us more than migration. One of the great phenomena of biology, migration can be considered an adaptive form of movement. The concept often evokes a stereotype: that of the epic, transcontinental journey. For example, Arctic terns (*Sterna paradisaea*) migrate the longest distance recorded of any animal (Alerstam 1990). Each year terns journey from their breeding grounds in the arctic to their winter feeding grounds in Antarctica. Similarly, we often think of migration as the “seasonably synchronized relocation of populations between the ‘two worlds’ of breeding grounds and wintering area” (Dingle 1996).

Despite this stereotype, migration is actually an incredibly diverse phenomenon. Spatially, migrations range from a few meters to transcontinental journeys; temporally, individuals may migrate once in their lifetime, every day, or at irregular intervals (Dingle and Drake 2007). Additionally, within a single species or population, individuals may exhibit different migratory patterns. Partial migration is the term for a population in which some

individuals migrate, while others remain resident. The phenomenon is widespread across taxa and particularly well studied in birds (Sekercioglu 2010) and fishes (Chapman et al. 2012).

The research presented herein examines the partial migration of Coho Salmon (*Oncorhynchus kisutch*,) from Puget Sound, a large, fjord-type estuarine complex in Washington State. Like most Pacific Salmon, these fish are anadromous: born in freshwater, they migrate to the marine environment to rear, then return to freshwater to spawn. However, while most Coho Salmon spend the marine phase of their lifecycle over the continental shelf or offshore waters of the North Pacific Ocean, some fraction of the individuals spend all or part of their marine phase within the semi-enclosed, urbanized waters of Puget Sound (Haw et al. 1967, Chamberlin et al. 2011b, 2011a). As the species is both ecologically and economically important to the region, this alternative migration pattern has many consequences. The resident Coho Salmon in Puget Sound may affect food web structure and trophic dynamics (Beauchamp and Duffy 2011), contaminant exposure and bioaccumulation in the food web (O'Neill and West 2009), fishery interceptions, and hatchery management (Moring 1976, Rensel et al. 1988, Chamberlin et al. 2011a). Therefore, greater understanding of this alternative migration pattern is very important for a range of conservation applications.

We have strategically designed this thesis to examine the migration system of Puget Sound Coho Salmon from two complementary levels: the population level and the individual level, and these levels are reflected in the two-chapter structure. As the study of migration has evolved, researchers have come to view both population and individual level understanding of migratory populations at two necessary halves of the holistic understanding of the migration system (Dingle and Drake 2007). The process by which they came to this conclusion is well

illustrated by the history of research on a well-known terrestrial migrant: the New World monarch butterfly (*Danaus plexippus*).

The monarch population in eastern North America is known for their extraordinary annual autumn migration of over 3000 km to specific sites in Mexico (Brower and Malcolm 1991). There, aggregations of millions of butterflies overwinter, and begin returning north in the spring. Until the 1980's it was assumed that the individuals arriving at the north end of the range in the summer had come all the way from their overwinter sites in Mexico. However, closer inspection revealed that this was not the case. As caterpillars, monarchs feed on the milkweed plant. There are different species of milkweed present at different latitudes along the monarch's migratory path, and monarchs can be physiologically "fingerprinted" to identify which species of milkweed they fed on as caterpillars. When researchers examined the physiology of individual monarchs at different points along this path, they found that monarchs in Mexico had been feeding on northern milkweeds, as expected. However, monarchs reentering the northern end of the range had fed on Gulf Coast milkweeds. Contrary to the original population-level description of their migration as a straightforward to-and-fro north to south single-generation movement, examination at the individual level revealed that the northward leg of the monarch migration takes place over at least two generations, possibly more. Thus, while the ecological outcomes of migration are often relevant at the level of populations, to view a migratory system completely, one also needs to examine individual level behaviors (Taylor 1986, Dingle and Drake 2007).

Standing on the shoulders of these giants, the first chapter of this thesis examines partial migration of Puget Sound Coho Salmon at the population level using mark-recapture techniques, and the second tracks individual level behaviors using acoustic telemetry. Mark-recapture is as it sounds: fish are captured at one point in their migration, marked so that they can be later

identified, then recovered at later point in their migration. The benefit of this method is the potential to study large numbers of fish. In fact, the coded-wire tag of the greater Pacific region of North America program has tagged and released millions of salmonids annually since the 1960s (Nandor et al. 2004). However, this method is limited by the amount of information that can be learned from any tagged individual. While information is available at the point of release and recapture, where the fish moved between these two points is unknown, leading to a coarse-scale picture of the migration system. To examine the migration of Coho Salmon at a finer scale, the second chapter of this thesis employs acoustic telemetry. In this method, stationary receivers are deployed throughout Puget Sound, and detect sounds emitted from tags surgically implanted in individual fish. This method provides us with multiple locations of fish during their migration, allowing us to better understand their movements at the individual level. The expense and effort involved in catching and tagging fish with acoustic tags limits the number of individuals that it is feasible to collect data for, making the mark-recapture chapter especially important.

While we have known about (and fished) Puget Sound resident Coho Salmon for decades, until now we have known remarkably little about their migration system. For years, it has been widely assumed that when juvenile Coho Salmon are released from the hatchery later and at a larger size, they are more likely to alter their migration pattern and remain resident. Thus, the first chapter of this work evaluates the relative influence of several internal and external factors on the tendency of Coho Salmon to remain resident. Additionally, while it has long been thought that residents spend their entire marine phase within Puget Sound, in actuality we do not know where and when residents move, or if they ever leave Puget Sound. The second chapter examines the movement of individuals in order to determine if residents and migrant coho have two distinct migration patterns, or if their migration behavior lies on a continuum.

Together, these analyses provide a fundamental and holistic understanding of the partial migration system of Puget Sound Coho Salmon.

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Chapter I: The relative influences of geographic region, date of release, body size, and hatchery or wild origin on partial migration in Puget Sound Coho Salmon (*Oncorhynchus kisutch*)

Abstract

Partial migration, the behavior pattern in which a portion of a population migrates while others do not, is a widespread phenomenon with ecological and evolutionary consequences. Most Coho Salmon from streams in the Puget Sound, Washington basin rear over the continental shelf or offshore waters of the North Pacific Ocean after leaving fresh water, but some rear in the semi-estuarine waters of Puget Sound and are termed residents. The objective of this study was to determine which of several factors influenced residency in Puget Sound Coho Salmon, and the general distribution of residents within the marine basins of Puget Sound. We first used coded wire tag recovery data to show that resident Coho Salmon were smaller than their migratory counterparts caught outside Puget Sound, and we used this size difference and the relative catch patterns along the coast and in Puget Sound to infer that Coho Salmon caught in Puget Sound between November and August were residents. We then analyzed the effect of location of origin, day of release, weight at release, hatchery or wild rearing, and year on the proportion of fish remaining resident in Puget Sound rather than migrating outside, and catch location within Puget Sound. Based on 258 releases between 1975 and 1992 we classified 3.4% of fish recovered as residents, 61.3% as outside Puget Sound, and 35.3% as ambiguous because they were recovered in Puget Sound in September and October, when residents and migrants were mixed. Later releases tended to produce more residents but the best model also included release basin and year, but not rearing type (wild or hatchery origin) or release weight on the proportion

of resident recoveries. Fish originating in south Puget Sound had the highest proportion of residents, and resident fish tended to be recovered in the basin they were released from. While other factors may influence residency in Coho Salmon and salmonids in general, the effects of day of release and location of origin may be useful for the management of these populations.

Introduction

The migration patterns of animals drive many aspects of their population dynamics, ecology, and evolution (Baker 1978, Nathan et al. 2008, Morales et al. 2010). There is great variation within and among species in the propensity to migrate, as well as migratory patterns. The great variation in temporal and spatial scales of migration has complicated evaluation of the causes and consequences of migratory behavior. Spatially, migrations range from a few meters to transcontinental journeys; temporally, individuals may migrate once in their lifetime, every day, or at irregular intervals (Dingle and Drake 2007). Intra-specific variation in migration patterns is also observed in many taxa (Quinn and Brodeur 1991), and may drive complex spatial structures with consequences for population dynamics, as well as productivity and resilience (Kerr et al. 2010). Therefore, knowledge of the factors influencing intra-specific variation is needed for the sustainable management and conservation of migratory species (Kokko and López-Sepulcre 2006, Robinson et al. 2009, Kerr et al. 2010).

Partial migration is the term commonly applied to populations containing both migratory and resident individuals, and such variation had been documented in many fishes and especially salmonids (Jonsson and Jonsson 1993, Chapman et al. 2012). Typically, the term resident has been applied in salmonids to individuals or subsets of the population that complete their entire life cycle in fresh water, in contrast to anadromous individuals. Three types of factors combine to

influence the “decision” to express anadromous and resident life history and migration patterns (reviewed by Quinn and Myers 2005, Pavlov and Savvaitova 2008, Dodson et al. 2013). Size, growth rate, body fat content or other aspects of internal condition are important but the relationship between size or growth is population-specific, so there is genetic influence as well. In addition, the condition of the environment also plays a role in determining whether individuals migrate or not, presumably through some feedback to growth, optimization of physiological conditions, or other process.

Partial migration in salmonids is more complex than a simple distinction between anadromy and non-anadromy, as there is a great range of migratory behavior patterns within the freshwater and marine environments (Quinn 2005, Quinn and Myers 2005, Jonsson and Jonsson 2011). For example, some Chinook Salmon, *Oncorhynchus tshawytscha*, migrate to the open North Pacific Ocean whereas others remain in the coastal zone (Healey 1991, Sharma and Quinn 2012). In addition to these migration patterns, some Chinook Salmon spend their time in marine waters within the protected inland seas proximate to their natal rivers such as Puget Sound and the Strait of Georgia, a large, fjord-type estuarine complex (Haw et al. 1967, Chamberlin et al. 2011b, 2011a). Salmon that migrate to sea (i.e., are anadromous) yet remain within these protected inland waters are commonly known as residents. Recent research on resident Chinook Salmon has examined their spatial distribution, biotic and abiotic factors influencing their partial migration, and relationship between migration and uptake of contaminants (O’Neill and West 2009, Beauchamp and Duffy 2011, Chamberlin et al. 2011b, 2011a). However, immature Coho Salmon, *O. kisutch*, are also found in Puget Sound during all months of the year (Allen 1956, Buckley 1969) though their movements, and the causes and consequences of this distribution pattern are not well known. Decades ago researchers reported that Puget Sound resident Coho

Salmon were smaller than their migratory counterparts, and speculated that differences in food availability inside and outside of Puget Sound or differences in individual body size affected the likelihood of remaining resident (Jensen 1948). The partial migration of the salmon is important, as it affects Puget Sound's food web structure and trophic dynamics (Beauchamp and Duffy 2011), contaminant exposure (O'Neill and West 2009), fishery interceptions, and hatchery management (Moring 1976, Rensel et al. 1988, Chamberlin et al. 2011a).

Previous investigations have revealed intrinsic and external factors influencing movement patterns and residency in some species and life-stages of salmonids, providing hypotheses for factors affecting resident behavior of Coho Salmon in Puget Sound. Non-migratory fish are typically smaller than migrants but it can be difficult to determine whether the size difference is a cause or a consequence of residency (e.g. Jonsson and Jonsson (1993), Chapman et al. (2012)). Groups of Chinook Salmon smolts that were larger when released from hatcheries produced a higher proportion of residents in Puget Sound than did groups with smaller smolts but the effect was slight (Chamberlin et al. 2011a). The feeding distribution of adult salmon also depends on where they entered marine waters (Weitkamp 2010), and area of origin was the most important factor affecting residency in juvenile Puget Sound Chinook Salmon (Chamberlin et al. 2011a). Hatchery rearing practices typically influence body size relative to wild conspecifics, and so might also affect the tendency to remain resident, as might inter-annual environmental variation in features such as prey availability and temperature. Finally, there is a genetic influence on marine distribution, as revealed by the catch distribution of different populations and their hybrids after release from a common location (Quinn et al. 2011).

The overall purpose of this study was to examine the relative influences of selected factors on the tendency of Puget Sound Coho Salmon to spend their marine period within Puget

Sound (i.e., remain resident). To do so, we first used spatio-temporal patterns in catch and size distribution to determine if fish rearing in the coastal Pacific Ocean were larger than residents, as has long been assumed (Milne 1950, Buckley 1969). We then used this information to test the assertion by Buckley (1969) that the resident contingent of Coho Salmon, which had been feeding inside Puget Sound, is joined by the migrant contingent of their year class in September. Based on this information, we could then determine the months in which the vast majority of individuals recovered inside of Puget Sound could be considered resident, and the months when recoveries consisted of both resident and migratory individuals that would mature and spawn that fall. We used the data on fish during months when resident (in Puget Sound) and migrant (outside Puget Sound) salmon could be distinguished to determine which factors most strongly affected the tendency of being resident: 1) region where they entered Puget Sound, 2) wild or hatchery rearing history, 3) body size as smolts, 4) year of release, or 5) day of release. Then, for the salmon that were residents, we determined whether there were common locations to which fish from all regions of origin converged, or whether each region produced fish that adopted distribution patterns differing from those of fish from other regions.

Methods

Study site and species.—Puget Sound is a partially mixed estuary-fjord complex in Washington State, encompassing an area of 2330 km² (Burns 1985). It is composed of four interconnected basins that influence its circulation and other oceanographic properties: central Puget Sound, Hood Canal, the Whidbey basin, and south Puget Sound (Moore et al. 2008a). The central basin is the primary outlet to the Strait of Juan de Fuca (SJdF), the San Juan Islands, the Strait of Georgia, and associated water bodies of the Salish Sea (Figure 1.1), and has a sub-basin

known as Admiralty Inlet at its northernmost outlet. For the purposes of this study, we delineated boundaries of Puget Sound and its basins using the statistical areas of the Washington Department of Fish and Wildlife (formerly, the Department of Fisheries). Puget Sound included areas numbered from 7 - 13 (map): Hood Canal (Area 12), south Puget Sound (Area 13), central Puget Sound (areas 9, 10 and 11), and the Whidbey Basin (Area 8). The San Juan Islands (Area 7) were included in Puget Sound for the purposes of recovery analysis, as they encompass habitats of similar protected nature and are proximate to some sources of salmon, though no salmon were released into this area. We did not include the Canadian Gulf Islands or other parts of the Strait of Georgia in Puget Sound for analysis purposes, though salmon originating from Canadian rivers might be considered to be resident if they were in these areas.

Coho Salmon smolts migrate downstream and arrive in the marine waters of Puget Sound between April and June, with a peak in early May (Simenstad et al. 1982). Most Coho Salmon spend that summer and another full year in marine waters before returning to spawn in the fall of the following year (i.e., after ca. 18 months in marine waters), though a fraction of the males, known as jacks, mature in the fall of the year in which they entered marine waters (Sandercock 1991, Quinn 2005). When they enter Puget Sound as smolts the Coho Salmon are ca. 120 mm long and they do not become large enough to be routinely retained by fishermen until their first fall or winter, when they are ca. 300 mm or longer. At this time the previous cohort has left the marine waters and entered freshwater to spawn, or can be readily distinguished from the younger fish by size and tag code (see below).

Coded-wire tag (CWT) data.—Data were acquired from the Regional Mark Processing Center CWT Database, which houses all release, recovery, and effort data for CWT programs along the west coast of the U.S. and British Columbia (Nandor et al. 2010). Releases refer to

groups of fish reared and released together with the same “tag code” on their CWT. In most cases this refers to fish released from a hatchery in a given year, but some wild fish were captured and tagged and their “release” data were recorded. For every release group the data indicated the species, brood year (i.e., year when their parents were spawned), location of the hatchery or stream, rearing type (hatchery or wild), release location, mean weight per fish of the release group (g) and release date. Release day of year was calculated as number of days since January 1 of the release year, but for 27 groups of wild fish, only release month was listed in the database, so the 15th of the month was used. Additionally, for 105 of the 258 release groups, a range of release dates was given, and we used the median of this range (mean range = 27.1 days, SE = 4.4 days). When caught by commercial or sport fishermen in the waters from Alaska to California, data were recorded for a sample of each recovery, including date and location, weight and fork length of the recovered fish.

We limited our analyses to data on Coho Salmon released from the four Puget Sound basins between 1975 and 1992 (Table 1.1) because significant changes in fishing regulations precluded comparable analysis after this period and too few fish were tagged and released in earlier years. Release and recovery data used met specific requirements (as in Weitkamp (2010) and Chamberlin et al. (2011)): release groups were excluded if they contained only experimental fish (type “e” in the database), if the fish originated from other river basins (i.e., transfers between rivers), or if the fish were released in a different location than the hatchery or stream where they had been reared. Exceptions to this rule included the use of two experimental release groups from central Puget Sound hatcheries in 1978 because non-experimental release groups from this year and release region were not available. Recovery data were then obtained for the tag codes defined by the above criteria and categorized spatially as being in Puget Sound or

elsewhere, and the statistical area of recovery. We restricted our analyses to Coho Salmon for which 1) the marine recovery location was known, and 2) the average size of the sample had been recorded.

The goal of the study was to determine the relative importance of body size, geographical area of origin, and wild or hatchery rearing history on the tendency to be recovered as a resident or migrant. Variation in the sizes of the different recovery areas, survival rates of the salmon in different areas, and unknown variation in fishing effort and anglers' tendency to retain or release fish prevented us from determining the absolute numbers of resident and migrant salmon produced by each tagging group. We assumed, however, that Coho Salmon of different body sizes as smolts, rearing types, and locations of origin were equally catchable and likely to be retained, given that they were in a particular location. For example, fish originating from Hood Canal were assumed to be equally likely to be caught in the Whidbey Basin as were fish from central Puget Sound, in proportion to their abundance in the Whidbey Basin. In practice, larger fish may be more likely to be retained by anglers than smaller fish, but this would tend to homogenize the size distributions in different areas rather than to create a difference where none existed. Therefore, if we detected a difference in size between fish rearing outside and inside Puget Sound, then the true difference is likely larger than what was actually observed.

Definition of residents.— The Coho Salmon are too small to be caught or retained in significant numbers until they have spent at least a summer in saltwater; moreover, those caught in Puget Sound in their first summer might have been en route to the coast. Therefore, we only considered a Coho Salmon caught within Puget Sound from November 1 of its first year at sea onward to be a resident. We excluded any fish caught before that first November at sea, regardless of location, but there were very few such fish. We also knew a priori that maturing

Coho Salmon that rear in the coastal ocean return to Puget Sound streams to spawn in the fall, and so are passing through the marine waters en route to these streams in late summer. Until that time the fishery in Puget Sound catches residents, by definition. Buckley (1969) and Pressey (1953) reported that length-frequency distributions of Coho Salmon in the Puget Sound sport fishery transitioned from unimodal in August to bimodal in September. This shift in size distribution was inferred to reflect the influx of larger Coho Salmon migrating from the coast and joining the smaller resident fish already in Puget Sound. To test the validity of our definition of residents as those found in Puget Sound through August, we first compiled the size distributions in each month, and they indeed showed that the fish in Puget Sound were smaller than those caught elsewhere. We then performed a two-way ANOVA on the average length of release groups based on two factors: location (inside or outside of Puget Sound) and month (August or September). The linear model was weighted by the number of fish measured to produce the average in each recovery stratum. We were particularly interested in whether there was a significant interaction between these terms, as that would indicate that the mean lengths were different in the two regions, but the size of the difference depended on the month.

Index of Residency.— We calculated the relative contribution of each release group to the resident population, which was used as the response variable for our analyses. We calculated an index of residency (R_i) for each release group i following Weitkamp and Neely (2002), Weitkamp (2010), and Chamberlin et al. (2011a), using the following equation:

$$R_i = r_{ps, i} / r_{tot, i} \quad (1)$$

where $r_{ps, i}$ is the number of resident recoveries for each release group within Puget Sound in all years and $r_{tot, i}$ is the total number of recoveries of the release group from all areas (coast-wide) in all years.

We applied generalized linear models to the coded-wire tag data to evaluate the effects of several categorical and continuous predictor variables on the proportion of that group subsequently recovered as residents in Puget Sound. The response variable was modeled using a binomial variance structure (logit link). Predictor variables included average weight of fish at release (g), release day of year (days after January 1 of the release year), release year, location of origin, and rearing type. The variables were not transformed prior to analysis. While weight at release and day of release are related, as fish released later are typically larger, the correlation between these two predictor variables was low (Spearman's $\rho = 0.04$) so both were included in the model. Initial results revealed high deviance estimates, and transformations of the continuous predictor variables did not improve model output. We concluded the data were over-dispersed, and used a quasi-binomial distribution model to estimate a dispersion parameter for the data. We used forward and backward model selection procedures to select the most parsimonious model. We then used a Pearson's Chi-square test on the fish that were residents to test the null hypothesis that the relative proportion recovered in each basin was independent of the basin where they originated (i.e., all residents were similarly distributed in Puget Sound, regardless of their origin). The alternative hypothesis was that one or more basins produced fish whose distributions within Puget Sound differed from those from fish from one or more other basins.

Results

We considered a total of 258 release groups from 24 locations in the four basins of Puget Sound for analysis (Table 1.1), including 84 groups of wild fish. Releases occurred from February through July, but most (82%) were between days 100 and 160 (10 April to 9 June). The average weight of fish varied from approximately 6 to 45 g, but 82% were between 15 and 30 g.

Definition of residents.—A total of 466145 fish were recovered in all months of the year inside and outside Puget Sound, but only the months of June through October had more than 2000 fish recovered (Figure 1.2), and the numbers of recovered fish varied greatly with month and location of recovery (inside or outside of Puget Sound). Coho Salmon recovered outside Puget Sound were significantly larger than those recovered inside Puget Sound in all months but we were most interested in the summer months so we could ascertain when the larger fish from the ocean entered Puget Sound in sufficient numbers that the fish caught could not be considered to be residents. The mean length of recovered Coho Salmon depended on recovery location (inside or outside Puget Sound: $F = 4.6479$, $P = 0.03$, $DF=10603$), whether they were recovered in August or September ($F = 938$, $P < 0.001$, $DF=10603$), and an interaction between these two factors ($F = 56.5208$, $P < 0.001$, $DF=10603$). Fish caught outside Puget Sound were larger in August (outside = 555.9 mm, SE = 0.66 vs. inside = 543.2 mm, SE = 3.5) but smaller in September (outside = 579.8 mm, SE = 0.88 vs. inside = 584.9 mm, SE = 0.59; Figure 2.3). Combined with the rapid increase in catches in Puget Sound in September (Figure 2.2), the length data indicated that the difference in size between outside and inside Puget Sound changed in September because the migrating contingent of Coho Salmon outside Puget Sound had joined the resident contingent in Puget Sound. While there are residents present in Puget Sound in late summer as well, these results showed they could be largely distinguished from migrant fish based on their presence in Puget Sound between the months of November and August

(inclusive), and we used data from these months to calculate the resident index of each release group.

Relative contributions.— Overall, 3.4% of the fish from the selected release groups were recovered as residents (inside Puget Sound between November and August), 61.3% were recovered as migrants outside Puget Sound, and 35.3% were recovered inside Puget Sound during September and October, and were of ambiguous migration history. The proportion of resident recoveries per release group (resident index) varied with year and release basin. In general, the proportion of resident recoveries was higher in 1976-1978 and 1991-1992 across all regions (Figure 1.4). The proportion of resident recoveries also varied with release basin; south Puget Sound had the highest contribution (weighted mean = 7.6%) followed by central Puget Sound (3.0%), Whidbey Basin (2.7%), and Hood Canal (2.7%). The hatchery reared fish produced a slightly lower proportion of residents compared to wild fish (mean = 3.2% vs. 4.3%).

The best model to explain residency included effects of day of release ($F = 27.1$, $P < 0.001$), release region ($F = 40.2$, $P < 0.001$), and year ($F = 9.9$, $P < 0.001$), but not rearing type or release weight (Table 1.2). Later releases tended to produce more residents but the strength varied among regions and years (Figure 1.5). In all years, fish originating in south Puget Sound had the highest resident index followed by fish from central Puget Sound, Hood Canal and the Whidbey Basin, though resident indices from the latter three basins were more similar to each other than to that of south Puget Sound. The resident index of south Puget Sound showed the strongest increase with day of release in 1977, 1991 and 1992 reaching a resident index of approximately 30% at a release day of 200.

The null hypothesis that recovery basin was independent from release basin was rejected; that is, that fish from the different release basins were not similarly distributed within Puget

Sound ($\chi^2 = 4786.687$, $P < 0.001$). Fish from all release basins were more often recovered in the basin where they were released than was expected under the null hypothesis (Table 1.3).

Additionally, fish released in central Puget Sound, Hood Canal, and the Whidbey Basin were recovered in the San Juan Islands more than was expected, but fewer fish from South Puget Sound were recovered there than expected. For all other release-recovery basin combinations, fish were recovered less often than would be expected.

Discussion

Date, location, and year of release were the factors most influencing the tendency of Puget Sound Coho Salmon to reside there rather than migrate to the coastal waters, whereas hatchery or wild rearing type and size at release did not have significant effects. These results indicated the importance of environmental conditions, rather than the intrinsic factor of fish size, in determining this migratory behavior. We also confirmed that the hatchery practice of delaying the release of smolts had the intended effect of increasing residency of Coho Salmon in Puget Sound, especially in populations from south Puget Sound. Interestingly, the influence of delayed release does not appear to be related to weight of the fish at release. Finally, resident Coho Salmon tended to be recovered in the basin where they originated, indicating limited between basin movement of residents in Puget Sound.

The effect of origin location on migration patterns, residency, and marine distribution is not unique to Coho Salmon, and location affects marine residency in other partially migratory fish species, including Chinook Salmon from Puget Sound. Location of origin was the most important predictor of residency in Puget Sound Chinook salmon at a range of sizes and entry dates, and Hood Canal produced the highest proportions of residents (Chamberlin et al. 2011a).

The present results indicated that origin was important but not the primary factor, and that fish from South Puget Sound were the most likely to be resident. Similarly, Coho Salmon (Weitkamp and Neely 2002) and Chinook Salmon (Weitkamp 2010) from common release regions generally shared common marine distributions, and origin also affected residency of Atlantic Salmon (*Salmo salar*) in Canada (Lacroix 2013).

There are several possible explanations for the effect of origin on residency in salmon, one of which is the geographic distance between the origin location and the continental shelf or the open ocean. Fish from rivers in the inner Bay of Fundy (farther from the open ocean) were more likely to remain resident than fish from the outer Bay of Fundy (Lacroix 2013), which parallels our finding that fish from south Puget Sound were most likely to be resident. However, Puget Sound Chinook Salmon originating in Hood Canal were most likely to be resident, indicating that some other factor mediated the effect of origin on residency (Chamberlin et al. 2011a). However, distance itself is not a barrier as the fish can easily swim to the outlet of Puget Sound and indeed most salmon smolts do so. Rather, some environmental conditions that the fish encounter upon entering marine waters seem to affect their behavior. These conditions could be related to the unique oceanographic properties of the basins of Puget Sound, including bathymetry, connectivity, freshwater input, tidal regime (Burns 1985) and also circulation and water residence times (Moore et al. 2008a). These physical features may influence the biotic composition of each basin (Strickland 1983) in ways that affect salmon. Fish may adjust their migration patterns with changes in tides or current strength (e.g. Lacroix et al. (2005)) but this would not explain the differences between Coho Salmon and Chinook Salmon.

The effect of origin on residency in Coho Salmon might also be explained by the spatial distribution of prey species in Puget Sound. Low food availability is associated with migration in

partially migratory populations of brown trout (Wysujack et al. 2009), and Atlantic salmon in the Baltic Sea migrated shorter distances when food was more available near their river of origin (Kallio-Nyberg et al. 1999). The diet of juvenile Coho Salmon consists primarily of crab larvae, copepods, amphipods, and at larger sizes, Sand Lance and Pacific Herring (Fresh et al. 1981, Brennan et al. 2004). However, there is little information available spatial distribution of zooplankton and forage fish distribution in Puget Sound. Rice et al. (2012) showed that the pelagic biomass in the Whidbey Basin and Rosario (a region encompassing Bellingham Bay and Padilla Bay, just east of the San Juan Islands) was dominated by fish, including species eaten by Coho Salmon such as Sand Lance and Pacific Herring, whereas jellyfish dominated the biomass of central and south Puget Sound, and that mean fish species diversity in Puget Sound increased with latitude. Additionally, Duffy et al. (2010) showed that Puget Sound Chinook Salmon diet was of higher quality at sites in north Puget Sound (including Whidbey Basin) than south Puget Sound. Thus, paradoxically, the south Puget Sound basin produced the highest proportion of resident Coho Salmon yet seems to present them with poorer foraging opportunities than the more northerly basins. The relationship between the abundance of prey species within the basins of Puget Sound and the resident behavior of salmonids is a fruitful area for investigation but without better data on the interannual variation in community composition it is difficult to determine how residency and foraging opportunities are related (Fresh et al. 1981).

The most important factor influencing residency in our analysis was the day of release; fish released later in the year were more likely to be resident. Lacoix (2013) found, similarly, that residency by Atlantic Salmon smolts in the Bay of Fundy increased as the date of river exit was delayed, and hypothesized that increase of sea surface temperature (SST) may have trapped or terminated the migration of post-smolts that were released later. Alternatively, the effect of

day of release on residency may be related to the seasonal changes of prey distribution in the marine environment. However, there is little information available on the abundance and distribution of zooplankton and forage fish in Puget Sound, though there is seasonal variation in abundance of some Coho Salmon prey species (Fresh et al. 1981). Finally, physiological processes associated with the parr-smolt transition are linked to seasonal changes in photo-period and temperature (Clarke and Hirano. 1995), and delayed entry into marine waters may affect the behavior of the fish through physiology.

Finally, patterns in resident behavior varied inter-annually, as has been shown in other partially migratory fish species (Kallio-Nyberg et al. 1999, Jutila et al. 2003, Lacroix 2013) including Chinook Salmon from Puget Sound (Chamberlin et al. 2011a). Re-analysis of data from Chamberlin et al. (2011a) showed that the weighted mean annual resident index of Chinook Salmon tended to correlate positively with that of Coho Salmon ($\rho = 0.43$, $P = 0.041$, 1-tailed), suggesting that yearly environmental variation in Puget Sound influenced residency in both species. Puget Sound experiences inter-annual variation in temperature and salinity linked to solar heating and inflow of water from rivers (Moore et al. 2008b, 2008a). This variation might affect the salmon directly, or via correlations with the abundance of Sand Lance and Pacific Herring (Reum et al. 2011), the dominant prey species for Coho Salmon > 150 mm (Fresh et al. 1981, Brennan et al. 2004) or other elements of the ecosystem. Annual variation in the prey species of partially migratory populations is thought to influence resident behavior, for example, in Baltic salmon (Kallio-Nyberg et al. 1999). However, our current knowledge of biotic and abiotic environmental factors in Puget Sound is too limited to support firm conclusions on the causal nature of the inter-annual variation in residency.

Interestingly, neither rearing type nor weight at release affected the probability that Coho Salmon would be recovered as residents. Artificial rearing typically accelerates the growth of juvenile salmon, resulting in larger sizes at seawater entry compared to wild salmon, as well as other effects on behavior. In fact, the practices of delaying the release day of Chinook and Coho Salmon in some Puget Sound hatcheries was intended to encourage residency by increasing the size at release (Moring 1976, Mahnken et al. 1982, Rensel et al. 1988). Body size had a negative effect on migration distance for juvenile Atlantic salmon entering the Baltic Sea (Salminen et al. 1994, Kallio-Nyberg et al. 1999), and larger Chinook salmon smolts had higher probability of remaining resident in Puget Sound, but the effect was slight (Chamberlin et al. 2011a). Thus, we expected higher resident indices from release groups of larger fish. In the present analysis, hatchery reared Coho Salmon were larger than wild fish (mean hatchery weight = 25.9 g SE = 0.37, mean wild weight = 15.35 g SE = 0.50). Previous investigations have not found a clear effect of hatchery rearing on movement. Hatchery-reared and wild Atlantic salmon differed in early marine migration patterns (Juttila et al. 2003), but there was no difference in the distributions of wild and hatchery-produced Coho Salmon (Labelle et al. 1997).

The tendency for residents to be recovered in the basin where they originated is consistent with evidence that acoustically tagged resident Coho Salmon seldom moved between the basins of Puget Sound (Rohde et al. *In press*), and with the limited movements of Chinook Salmon residents in Hood Canal (Chamberlin et al. 2011b). However, resident Coho Salmon from central Puget Sound, Hood Canal, and the Whidbey Basin were more likely to be recovered in the San Juan Islands than expected under a null hypothesis of no relationship between release basin and recovery basin, indicating that this area may be important rearing habitat for resident Coho Salmon. Finally, fish from south Puget Sound were less likely to be recovered in the San

Juan Islands, which is consistent with recent research showing little exchange of juvenile Chinook Salmon populations from south Puget Sound and Rosario (Rice et al. 2011).

Our findings should inform current management strategies for Puget Sound Coho Salmon. For decades, some hatcheries in Puget Sound have implemented delayed release programs in order to increase the size at release of fish, with the goals of enhancing survival and encouraging residency (Moring 1976, Rensel et al. 1988). Our results show that while delaying release may promote residency in Puget Sound, the effect does not appear to be very strong, and is not necessarily related to size but to some other factors, perhaps seasonal changes in environmental conditions. Given the increased expense of delayed release programs and the interest of the Washington State Auditor's office in the effectiveness of the Chinook Salmon delayed release program (Washington State Auditor's Office 2010), our results should be of interest to hatchery management programs. Specifically, managers may increase the effectiveness of their delayed release programs by emphasizing south Puget Sound facilities. However, in general the resident component is apparently smaller for Coho Salmon than Chinook Salmon. Precise comparisons cannot be made because the methodologies differed somewhat and the fisheries also differ, but the mean indices of residency (weighted by number of fish recovered in each release group) were 30% for Chinook Salmon (Chamberlin et al. 2011a) vs. 5.4% for Coho Salmon in the present study.

Finally, this study is important to the health of salmon and their predators as resident behavior is linked to contaminant accumulation. O'Neill and West (2009) hypothesized that residency of Chinook Salmon in Puget Sound contributed to the higher concentrations of polychlorinated biphenyls (PCB) relative to other West Coast populations. PCB concentrations of Coho Salmon recovered in south Puget Sound were also significantly greater than those

caught in central Puget sound (O'Neill et al. 1996). Future efforts could investigate the relationship between residency in Puget Sound and the exposure to PCBs and other contaminants.

In conclusion, the hatchery practice of delayed release tended to increase resident behavior of Puget Sound Coho Salmon, though the great majority of fish were caught in coastal waters rather than in Puget Sound as residents, or during the late summer when the two groups were mixed as they prepared to enter streams for spawning. Moreover, wild fish were at least as likely to become residents as were hatchery-produced fish. Residency is apparently related to environmental factors that vary with year, season, or the local conditions at the location of marine entry. Moreover, the environmental variation in Puget Sound seems to influence resident behavior in Chinook Salmon as well. By revealing the importance of environmental conditions our results have raised fundamental questions about the biotic and abiotic variation of Puget Sound. Which environmental factors most strongly influence resident behavior in salmon: the distribution and dynamics of prey and predators, or oceanographic conditions? While these results provide some insights, the future of research on the migration of Puget Sound salmon will benefit greatly from increased monitoring of biotic and abiotic environmental conditions.

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Table 1.1. List of hatcheries, years of data and number of releases. Sources of data on coded wire tagged Coho Salmon released into different basins of Puget Sound including the number of tag codes (representing unique release groups), and recoveries of tagged fish by region, hatchery or stream, and rearing type.

Basin	Release Location	Rearing Type	Years	Tag Codes	Fish Released	Fish Recovered
Central Puget Sound	Issaquah Creek	Hatchery	5	5	208819	19407
	Portage Bay	Hatchery	2	5	67498	4341
	Soos Creek	Hatchery	14	42	893100	66439
	Voights Creek	Hatchery	13	42	882889	76128
	Little Bear Creek	Wild	3	3	26248	678
	North Creek	Wild	3	3	14650	487
Hood Canal	George Adams	Hatchery	11	18	528511	21342
	Quilcene	Hatchery	2	3	40915	3084
	Big Beef Creek	Wild	13	17	296199	36982
South Puget Sound	Kalama Creek	Hatchery	6	6	297635	5669
	Minter Creek	Hatchery	7	17	286410	18473
	Deschutes River	Wild	12	15	118037	12978
Whidbey Basin	Bernie Gobin	Hatchery	9	11	641409	65266
	Marblemount	Hatchery	6	16	296873	11440
	Wallace River	Hatchery	9	12	380925	39891
	Baker River	Wild	2	3	45864	1834
	Skagit River	Wild	2	14	78079	2732
	Skykomish River	Wild	9	11	154042	11292

Table 1.2. Coefficients and standard errors for the best model. Coefficients and standard errors for the best fitting model of proportion of resident recoveries per release group. The estimate of each parameter is based on the estimated proportion of resident recoveries in Central Puget Sound for all years. All estimates reported on the logit-link scale, and standard errors are corrected for overdispersion.

Main Effect	Estimate	SE	T	P
Central Puget Sound	-4.9769	0.3601	-13.82	< 0.001
Hood Canal	-0.116	0.1494	-0.78	0.44
South Puget Sound	0.7515	0.1232	6.1	<0.001
Whidbey Basin	-0.1848	0.148	-1.25	0.21
1976	-0.2287	0.2261	-1.01	0.31
1977	0.884	0.264	3.35	<0.001
1978	-0.0153	0.2653	-0.06	0.95
1979	-0.9415	0.2597	-3.63	<0.001
1980	-0.0921	0.2275	-0.41	0.69
1981	-0.3626	0.2401	-1.51	0.13
1982	0.0839	0.2468	0.34	0.73
1983	-0.7412	0.3358	-2.21	0.03
1984	-1.027	0.3	-3.42	<0.001
1985	-1.2104	0.2931	-4.13	<0.001
1986	-1.1138	0.2641	-4.22	<0.001
1987	-1.2996	0.3408	-3.81	<0.001
1988	-0.6822	0.2943	-2.32	0.02
1989	-1.4373	0.3582	-4.01	<0.001
1990	-1.8537	0.5615	-3.3	<0.01
1991	0.3187	0.2502	1.27	0.2
1992	0.3568	0.324	1.1	0.27
Day of Release	0.0155	0.0024	6.5	<0.001

Table 1.3. Expected and observed recoveries of Coho Salmon by release and recovery

basin. Counts of coho salmon recovered as residents within Puget Sound as a function of the basin of Puget Sound into which they had entered or been released. Numbers indicate recoveries of residents from each basin in each recovery area, and the percentages represent the proportion of fish from a release basin that were recovered that basin out of all fish that were recovered in Puget Sound from that basin (number recovered over column total). Expected percentages for each recovery basin were calculated as the proportion of the total number of fish recovered in that basin to the total number of fish recovered in all basins. Numbers in bold indicate when the observed percentage of recoveries was higher than expected percentage.

Recovery Basin	Expected Percentage	Release Basin								Total
		Central Puget Sound		Hood Canal		South Puget Sound		Whidbey Basin		
Central Puget Sound	70%	4739	79%	832	59%	2157	66%	1946	61%	9674
Hood Canal	3%	13	0%	320	23%	28	1%	15	0%	376
San Juan Islands	12%	762	13%	208	15%	191	6%	549	17%	1710
South Puget Sound	9%	345	6%	28	2%	793	24%	75	2%	1241
Whidbey Basin	6%	160	3%	14	1%	114	3%	591	19%	879
Total		6019		1402		3283		3176		13880

Figure 1.1. Map of Puget Sound and release sites. Map of the study area showing the origin locations of both hatchery and wild Coho Salmon and the boundaries of the marine basins of Puget Sound in different patterned backgrounds.

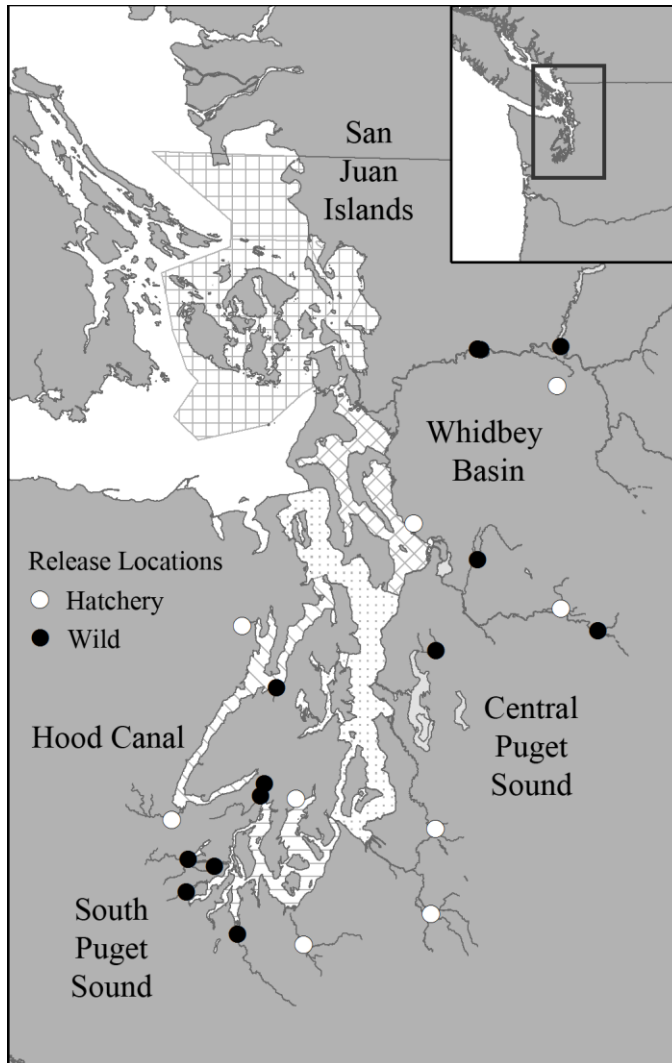


Figure 1.2. Monthly catch of Coho Salmon inside and outside of Puget Sound. Monthly estimated catch of Puget Sound Coho Salmon by location recovered: inside (pale gray bars) and outside Puget Sound (WA waters only – dark gray bars). Only months with total estimated catch of >2000 are included.

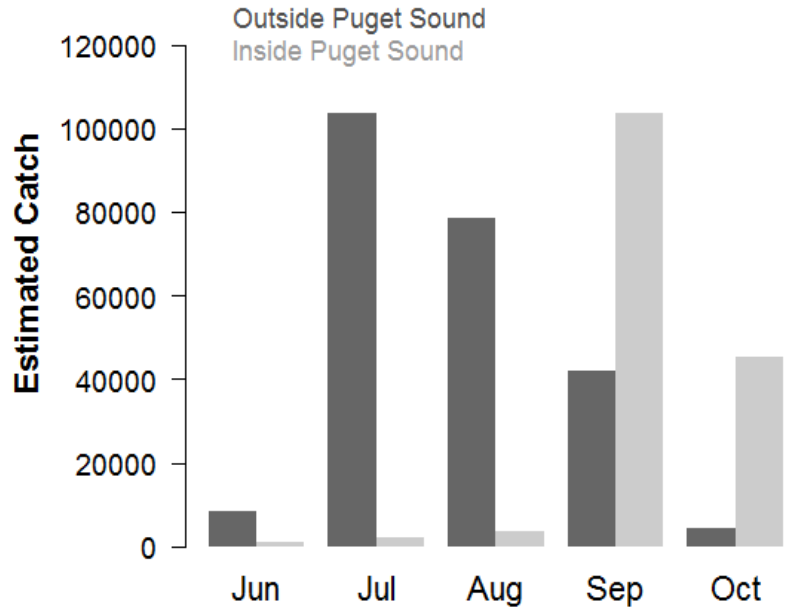


Figure 1.3. Monthly mean length of Coho Salmon at recovery inside and outside of Puget

Sound. Monthly size of recovered Puget Sound Coho Salmon by location recovered: inside (pale gray boxes) and outside Puget Sound (WA waters only – dark gray boxes). Only months with total estimated catch of >2000 are included.

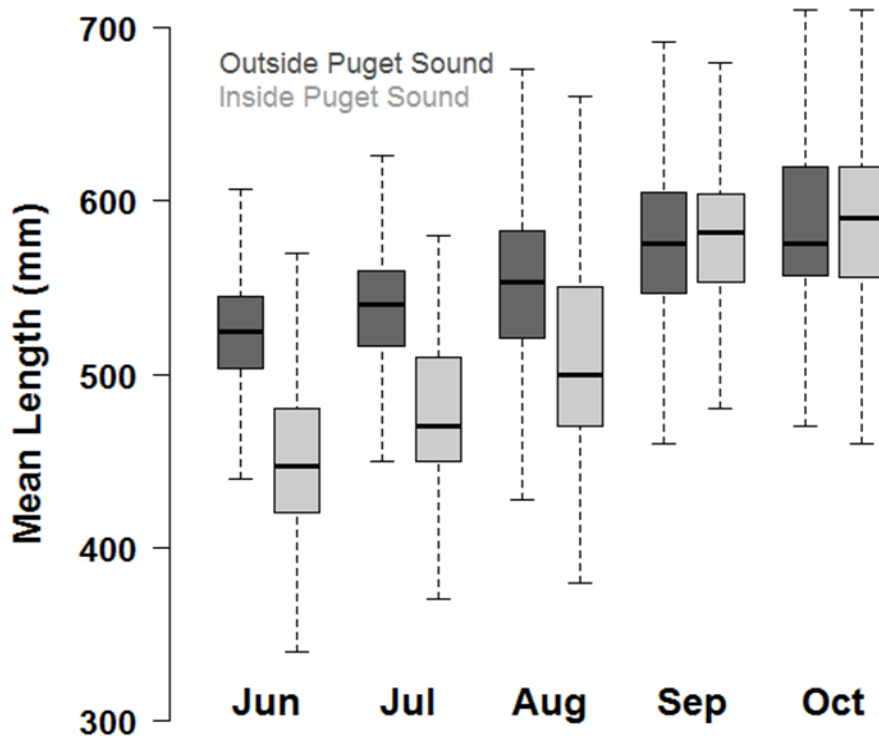


Figure 1.4. Observed mean annual proportions of residents, and predicted mean annual proportions based on the best fitting model.

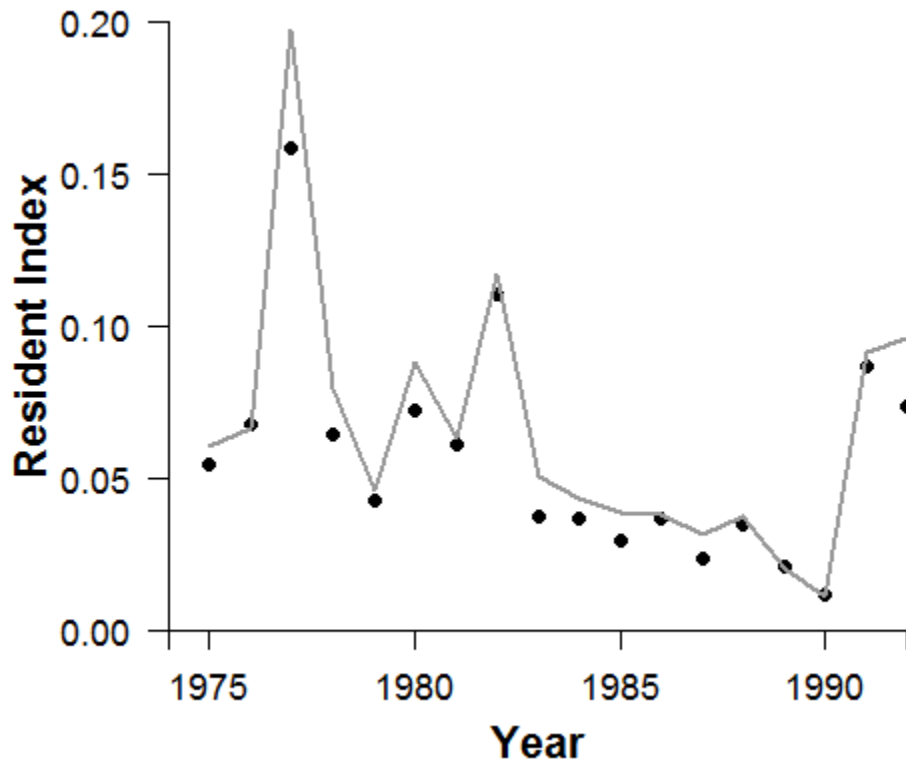
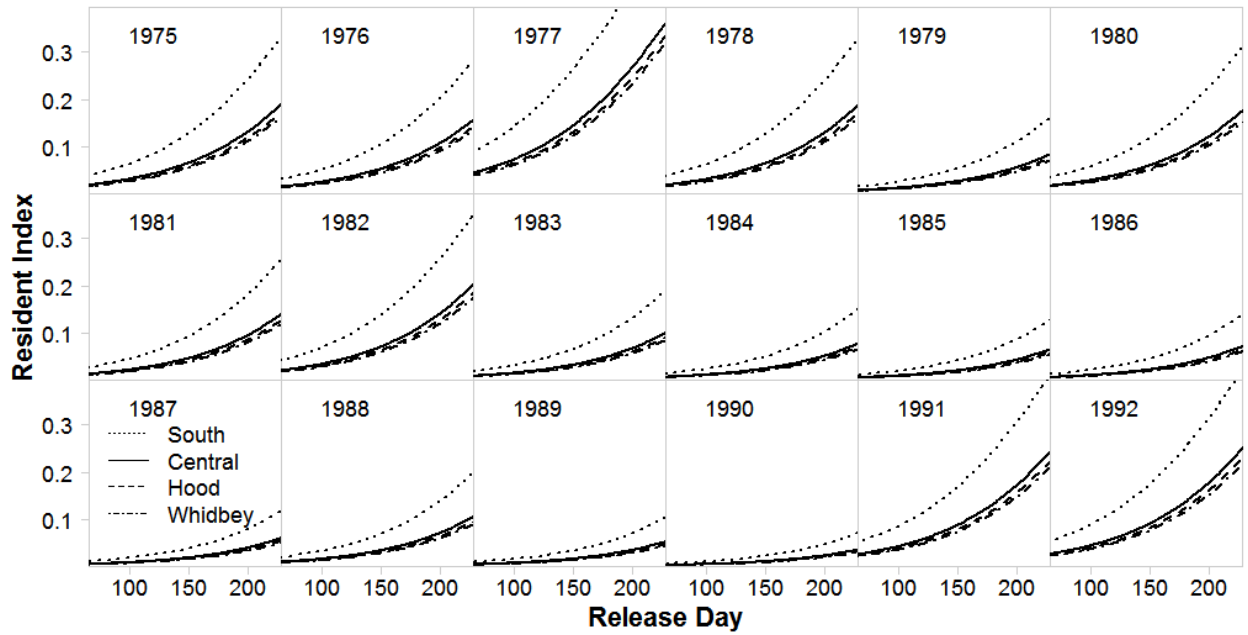


Figure 1.5. Resident index as a function of release day, region, and year as predicted by the best fitting model.



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Chapter II: Partial migration and diel movement patterns in Puget Sound Coho Salmon (*Oncorhynchus kisutch*)

Abstract

Partial migration, a term referring to populations in which only a fraction of the individuals migrate, is a widespread phenomenon among fishes. However, it is not always clear whether there are only two alternatives (migration or residency) or a continuum of movement patterns. For example, Coho Salmon, *Oncorhynchus kisutch*, are anadromous and most individuals rear over the continental shelf or offshore waters of the North Pacific Ocean but some, known as residents, spend all or part of their marine lives within Puget Sound. The movements of residents are poorly documented and it is unclear whether they ever leave Puget Sound and move to the coast of Washington, and to what extent they move within Puget Sound. Accordingly, the goal of this study was to investigate the patterns of movement by immature Coho Salmon in Puget Sound at a series of spatial scales. We tagged 45 resident Coho Salmon in the central basin of Puget Sound with acoustic transmitters and detected their movements within the Salish Sea with fixed receivers. Seven individuals were detected departing Puget Sound through the Strait of Juan de Fuca but these fish were not distinguished from those remaining in Puget Sound by body size, wild or hatchery origin, or tagging date. The fish remaining as residents seldom moved between the marine basins of Puget Sound. Within the central basin, deeper/offshore sites had higher frequencies of detection and other indices of site use. Fish were more often present and moved more often at shallow sites close to shore at night, and more at deep, offshore sites during day. Rather than a discrete behavior, we suggest that residence in Puget Sound by Coho Salmon is part of a continuum of migratory behavior patterns.

Introduction

Spatial distribution and movement patterns are fundamental aspects of the behavior of animals, with ramification for their ecology, population dynamics, and evolution (Baker 1978, Nathan et al. 2008, Morales et al. 2010), and for their sustainable management and conservation (Kokko and López-Sepulcre 2006, Robinson et al. 2009, Kerr et al. 2010). Animals display a continuum of movement patterns from sessile or sedentary species, to those occupying home ranges, to species making regular long distance migrations (Dingle 1996).

Although many species are characterized by one form of movement or another, there is also considerable within-species variation (Quinn and Brodeur 1991). For example, anguillid eels (e.g., *Anguilla japonica*) are typically catadromous but some individuals remain in marine waters (Tsukamoto and Arai 2001), and anadromous fishes such as Striped Bass (*Morone saxatilis*) also show a range of migratory behavior, including residence in estuaries and migration along the continental shelf (Secor 1999). Within-population variation in movement has been documented in many fishes, and the term partial migration has been applied to populations containing both migratory and resident individuals (Jonsson and Jonsson 1993, Chapman et al. 2011). For example, some Common Bream populations (*Abramis brama* L.) overwinter in lakes while others migrate to surrounding streams (Skov et al. 2011). However, migration and residency are not always discrete, clearly differentiated behavior patterns; there may be a continuum from highly migratory individuals to residents that show only very limited movement. For example, Striped Bass show spatio-temporal variation in movement patterns, ranging from characteristic anadromous migration, estuarine residence, and riverine residence (Secor et al. 2001, Wingate et al. 2011, and references therein). The factors affecting the tendency to remain resident or migrate are not well understood but such variation in movement patterns may benefit

the resilience, productivity, and stability of some species (Kerr et al. 2010), making our understanding of this variation imperative for managing harvested or threatened species.

Salmonid fishes exemplify the great variety of migration patterns in fishes, including discrete anadromous and non-anadromous populations in allopatry and sympatry, and non-anadromous individuals within populations that are predominantly anadromous (Hendry et al. 2004, Quinn and Myers 2005). In addition, non-anadromous populations vary greatly in the extent of movement within freshwater (Jonsson & Jonsson, 1993; Northcote, 1992), and the anadromous individuals vary in their patterns of marine migrations. Among the Pacific salmon, genus *Oncorhynchus*, Chinook, *O. tshawytscha*, and Coho, *O. kisutch*, salmon have more variable marine migration patterns than Sockeye, *O. nerka*, Chum, *O. keta*, and Pink salmon, *O. gorbuscha* (Healey 1991, Sandercock 1991, Quinn 2005, Quinn and Myers 2005). Variation in migration has implications for food web structure and trophic dynamics (Beauchamp and Duffy 2011), nutrient transport (Koyama et al. 2005), contaminant exposure (O'Neill and West 2009), fishery interceptions, and hatchery management (Moring 1976, Rensel et al. 1988, Chamberlin et al. 2011a). Therefore, greater understanding of the patterns of migration and the causal factors is very important for a range of conservation applications.

The Salish Sea (inland waters including Puget Sound, the Strait of Georgia, the Strait of Juan de Fuca and the associated inter-connected waters in British Columbia and Washington) is the southern-most complex of inland marine waters used by salmonids as an alternative to the coastal or open waters of the eastern North Pacific Ocean. A large, fjord-like estuarine complex, Puget Sound (here defined as the inland waters south of Admiralty Inlet including Hood Canal) is characterized by deep water, extensive shoreline, multiple tributaries and sub-estuaries, and urbanized surrounding landscape in some areas (Figure 2.1). Coho Salmon smolts from Puget

Sound migrate downstream and arrive in marine waters between April and June, with a peak in early May (Simenstad et al. 1982). Most Coho Salmon then migrate through the Strait of Juan de Fuca to rear over the continental shelf along Vancouver Island or the Washington coast (Weitkamp and Neely 2002; Quinn et al. 2005). They then spend ca. 18 months in marine waters before returning to spawn in the fall of the following year, though a fraction of the males, known as jacks, mature in the fall of the year in which they entered marine waters (Sandercock 1991; Quinn 2005). Additionally, some Coho Salmon reside within Puget Sound for all or part of their marine phase, and are known as residents (Allen 1966, Haw et al. 1967, Buckley 1969). In this context the term resident does not imply non-anadromy but rather a distribution that is restricted to the inland marine waters. Resident behavior is also found in Chinook Salmon from Puget Sound (Haw et al. 1967, O'Neill and West 2009, Chamberlin et al. 2011a, 2011b), and in Chinook and Coho salmon in the nearby Canadian waters as well (Milne and Ball 1958). Recent research has focused on understanding patterns of movement and spatial distribution of Chinook salmon from Puget Sound, as well as the biotic and abiotic factors that influence these patterns (Beauchamp and Duffy 2011, Chamberlin et al. 2011a, 2011b). However, immature (i.e., post-smolts that have not initiated their homing migration for spawning) Coho Salmon also feed in the marine waters of the Salish Sea during all months of the year, though their movement patterns, the fraction of the population that they represent, and reasons for and consequences of this distribution pattern are not well known.

Accordingly, the overall goal of this study was to investigate the patterns of movement at a series of spatial scales by immature Coho Salmon in Puget Sound. We used ultrasonic telemetry to determine **a)** whether individuals that were resident in Puget Sound remained there or subsequently moved to the coastal Pacific Ocean, **b)** whether fish size or hatchery rearing

influenced the tendency of individuals to remain resident in Puget Sound, **c**) whether individuals resident in one basin of Puget Sound remained there or moved to other basins, **d**) whether the sites most often visited by salmon had discernible physical attributes including depth and distance to shore. With respect to temporal patterns in movement, we **e**) determined whether there was a diel pattern in general activity and specifically in onshore - offshore movement.

We expected that, a) some fish captured in Puget Sound as residents would subsequently leave Puget Sound, b) hatchery reared fish would be more likely to remain resident than wild fish, c) there would be little tendency to move from one basin to another d) sites more often visited by fish would have similar physical attributes of depth and distance to shore, e) there would be diel patterns in movement from shallow/onshore sites and night to deep/offshore sites during day.

Study site.—Puget Sound is a partially mixed estuary-fjord complex, encompassing an area of 2330 km² in Washington State with four interconnected basins (Burns 1985): central Puget Sound, Hood Canal, the Whidbey basin, and south Puget Sound. These divisions are based on geographic position and the presence of bathymetric depressions in the seafloor, where deeper water in the middle is separated by shallower depths from deeper water beyond (except in the case of the Whidbey Basin (Burns, 1985). We adopted the boundaries of the Puget Sound basins described by Burns (1985): Whidbey Basin includes the waters north of a line between Possession Point and Meadowdale, Hood Canal runs southwest from a line between Tala Point and Foulweather Bluff, central Puget Sound includes the waters south of Admiralty Inlet and north of the shallowest part of the Tacoma Narrows, and south Puget Sound includes the waters south of the Tacoma Narrows (Figure 2.1). Admiralty Inlet, a sub-basin of the central basin with sills (bathymetric shallow points) at both ends, is the primary outlet to the Strait of Juan de Fuca,

the San Juan Islands, the Strait of Georgia, and associated water bodies of the Salish Sea (Figure 2.1).

Methods

Fish tagging and data collection.—Immature Coho Salmon ($n = 45$) were captured in Central Puget Sound via purse seine during seven tagging events between June 2006 and February 2008 (Figure 2.1, Table 2.1). Most were captured on the west side of Central Puget Sound between Port Madison and Apple Tree Cove, except fish #23 & #24 which were tagged just south of Bainbridge Island. All fish were tagged between the months of November and June, and this is outside the period when maturing salmon are migrating through Puget Sound from the Pacific Ocean (Haw et al. 1967). The typical pattern of migration to the coastal region would bring Puget Sound Coho Salmon to the coast by the end of their first summer at sea, as indicated by genetic analyses (Van Doornik et al. 2007), and many are found along the southwest coast of Vancouver Island and, to a lesser extent, the northern coast of Washington and the northwest coast of Vancouver Island, as indicated by analysis of coded wire tagging data (Weitkamp and Neely 2002, Quinn et al. 2005, Weitkamp 2012). These fish return through the Strait of Juan de Fuca and into Puget Sound primarily in September and early October, and spawn later that fall. The fish that we tagged were inside Puget Sound during their first winter at sea rather than along the coastal waters of the North Pacific Ocean and so were, by definition, residents.

Fish were visually examined for a clipped adipose fin and checked with a magnetic wand for presence of a coded-wire tag to distinguish hatchery from wild fish (Table 2.1). The vast majority of Coho Salmon from hatcheries in Puget Sound are marked (Washington Department of Fish and Wildlife: <http://wdfw.wa.gov/hatcheries/overview.html>), though inevitably there are

some unmarked fish of hatchery origin. Based on measurements of fork length (range: 319-457 mm; Table 2.1) and the capture dates, we estimated brood year and age, concluding that all but one had spent only one summer at sea (Table 2.1). VEMCO coded transmitters (V13, V9, and V7; AMIRIX Inc., Table 2.1) were surgically implanted into the peritoneal cavity of each fish according to procedures described by Chamberlin et al. (2011b). Battery life was estimated to sustain transmitter activity through each fish's projected spawning date (mean 489 d, SE=29 d). In addition, a small piece of ventral fin tissue was removed for genetic analysis because post-smolt Coho and Chinook salmon can be difficult to distinguish. Genomic DNA was isolated from salmon fin clip tissues using Wizard genomic DNA purification kits (Promega Corp.) following the manufacturer's protocols. Species identifications were carried out using the mitochondrial DNA fragment COIII/ND3 as outlined by Purcell et al. (2004) and Dean et al. (2010). Only fish confirmed to be Coho Salmon were included in the analysis.

Many VEMCO VR2 and VR3 receivers (AMIRIX Inc.) have been deployed in Puget Sound by researchers from multiple organizations. Detection data were shared via an on-line database known as Hydra (Sound Data Management LLC 2008). This network has been utilized to study movement patterns of many species, including Sixgill Sharks (*Hexanchus griseus*) (Andrews et al. 2007), Sevengill Sharks (*Notorynchus cepedianus*) (Williams et al. 2012), White-spotted Ratfish (*Hydrolagus coliei*) (Andrews and Quinn 2011), Cutthroat Trout (*Oncorhynchus clarki clarki*), Steelhead Trout (*O. mykiss*) (Moore et al. 2010), and Chinook Salmon (Chamberlin et al. 2011b). The receivers were deployed and retrieved at locations and on schedules that served the purposes of each set of investigators, and only a fraction of the receivers were explicitly deployed for this project. Consequently, we had to determine the locations and times 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. There were 292 unique receiver sites during our study period (between the first tagging event and the last detection of any of our tagged fish on 27 September 2008) including all basins of Puget Sound, in the Strait of Juan de Fuca, and the coast of Washington. Sites had continuous receiver coverage for durations up to 889 d (mean = 324.7 d). Detections were queried from the Hydra database based on the tag identification numbers and 142 receiver sites detected our tagged fish. Additionally, we obtained the location of 150 receiver sites that were deployed for at least 90 days during our study period but did not detect any of our tagged fish.

We used Geographic Information Systems (GIS) to extract environmental characteristics at the receiver sites (Table 2.2). These included mean depth (within a 540 m radius of the receiver, which is the maximum detection range of the V9P-2L 30-90 transmitter, the most common type used in this study: VEMCO, no date) using a 30 m digital elevation model of Puget Sound bathymetry (Finlayson 2005), as well as distance from the shoreline (Washington State Department of Ecology 2012).

Prior to data analysis, we eliminated data that may have resulted from equipment error, only analyzing detections if the fish was detected at least twice at a receiver within 1 h. This excluded 79 of the 23,631 detections. We also eliminated 319 detections that were so distant in space and proximate in time that they could not represent actual movement, based on plausible swimming speeds (Quinn 1988).

Puget Sound-level and between basin-level analysis.—We categorized each fish as ‘remaining resident’ or ‘departing’ based on whether it was detected at the line of receivers across the Strait of Juan de Fuca (Figure 2.1). This receiver line was one of several operating in the Salish Sea throughout the study period, as described in Chittenden et al (2009). This line

across the Strait of Juan de Fuca and the Strait of Georgia line at the northernmost exit of the Salish Sea, were designed to provide sufficient overlap so that most fish would be detected when crossing the array (Welch et al. 2003, Melnychuk and Walters 2010). Thus, if a fish was detected at either of these lines we inferred that it had left Puget Sound. Delineations of the Puget Sound basins (south, central, Hood Canal, and Whidbey) were based on a GIS dataset produced by the U.S. Department of Agriculture-Natural Resources Conservation Service (2004). The movement of tagged fish through these areas was assessed using GIS.

Within Basin Analysis.—To assess the site use patterns of Coho Salmon, we examined a subset of the data representing the most complete coverage in terms of number of operating receivers and fish with transmitters functioning. This included 18 receivers in the central basin (Figure 2.2) that were deployed continuously from March 1, 2008 until April 12, 2008 (42 days), and 21 fish that were tagged on February 29, 2008 (Table 2.2). Of the 21 tagged fish, three were never detected (fish # 27, 34, 36, Table 2.1) and fish #39 was not detected during the 42 day period after release (Table 2.1). Therefore, this analysis was carried out with detections from 17 fish. We began the analysis 1 d after tagging to minimize any bias from the behavioral effects of tagging (Candy and Quinn 1999). From these data, four different measurements of “site use” were calculated for each receiver: 1) the number of individual fish detected there (“fish”), 2) the number of days when there was one or more detections by any fish (“days”), 3) the total amount of time fish were detected, summed over all fish (“time”, in hours), and 4) the number of return visits, summed over all fish (“returns”). For calculating the latter two measurements, we defined movement following Chamberlin et al. (2011b), and Andrews and Quinn (2011). A fish’s first and last detections on a given visit to a receiver were unequivocal indications of movement in or out of the receiver’s range, and were used to calculate the time spent at the receiver. However, a

fish at the periphery of a receiver might have brief periods without detection even though the fish did not move substantially. A frequency histogram of elapsed time between detections for the entire dataset confirmed that, as in Chamberlin et al. (2011b), most detections were less than an hour apart (not shown). Therefore, apparent movements (i.e., gaps in detection) of < 1 h were not considered to be discrete movements and the short gaps were added to the total time at the receiver. However, if the gap exceeded 1 h we assumed that the fish left, and the period without detections was not included in the time at the receiver. The subsequent detection was considered to be a separate movement event if the fish returned to the vicinity of the receiver. This definition of discrete movement was also used in the analysis of diel activity (described below).

The variables associated with the four measures of site use were in different units (number of fish, number of days, time spent in vicinity of receiver (min), and number of return visits) and were correlated (correlations between all variable combinations > 0.85), but captured slightly different aspects of fish behavior, individually and collectively. Rather than analyzing these four variables in separate tests, we integrated the data using principal coordinate analysis. Using this multivariate ordination technique, we generated new composite variables from the measurements of the four original variables at each receiver, summarizing the dominant gradients of variation in fish use of the habitat near at each receiver. Original measurements were log-transformed and standardized by column total (measurement at each receiver divided by the sum of measurements of that variable at all receivers) to adjust for the different units of measurement for each variable, and the Gower's similarity coefficient was used. Eigenvalues of each principal coordinate were compared to the broken stick model to assess significance. Principal coordinate loadings were calculated by correlating original (log-transformed and standardized) variables to principal coordinate scores, and a permutation procedure was used to

test for significance. This analysis allowed us to determine the relative use of each of the 18 receivers in the core area of central Puget Sound by the group of 17 Coho Salmon.

We hypothesized that the depth and distance to shore at which a receiver was located would affect its short term use. We classified receivers as shallow/onshore (mean depth = 42 m, range = 9 – 90 m, mean distance from shore = 0.415 km, range = 0.180 – 0.848 km) or deep/offshore (mean depth = 110 m, range = 105 – 240 m, mean distance from shore = 2.134 km, range = 1.543 – 2.768 km) because receivers were naturally clustered into 2 groups: 13 were < 1 km from shore and in water < 100 m deep, and 7 were > 1.5 km from shore and in water >100 m deep (Table 2.2). To test the null hypothesis that activity measurements would not differ between deep offshore and shallow onshore receivers, we used permutational multivariate analysis of variance (Anderson 2001) and a test of multivariate homogeneity of group dispersions to assess differences in within group variation in site use variables (Anderson 2006), using the Gower's similarity coefficient in both analyses. These analyses, as well as the Principal coordinate analysis were performed using the “vegan” package (Oksanen et al. 2011) in the R statistical environment (R Development Core Team 2012).

Diel Pattern Analysis.—We were interested in whether site use varied according to diel period and the receiver's location, as that might indicate onshore-offshore movement patterns. Using the same 42-d subset of data, categorization of deep/offshore and shallow/onshore receivers, and definition of movement described above “within basin analysis”, we reduced the data to 738 discrete movements. We then represented time of day of each movement as a circular variable with a phase of 24 hours and used Rao's test of uniformity (Batschelet 1981) to determine whether the temporal distribution of movements at deep/offshore and shallow/onshore sites were different from random. To compare the timing of movements between deep/offshore

and shallow/onshore sites, we used Watson's two-sample U2 test (Batschelet 1981). We were also interested in whether fish were simply present more often at certain times of day, but not necessarily active, as might be shown by the movement variable. We evaluated this by summing the number of individuals present at each receiver during each hour of the day during the 42 day period. Finally, we calculated the average timing of movement and presence of fish at both deep/offshore and shallow/onshore sites. Using this approach, a time of day is at angle α_i and the average set of angles defined as a vector of angle μ . The vector's length, r , is a measure of the concentration of angles, which varies inversely with the standard deviation of angles and has values between 0 and 1 ($r = 1$ indicates all movements at the same time, $r = 0$ indicates random timing of movements). All diel period analyses were performed using Oriana (Kovach Computing Services 2012). Sunrise ranged from 05:27-6:49 h and sunset from 17:55-18:54 h during the 42 day subset of data (U.S. National Oceanic and Atmospheric Administration, Earth System Research laboratory 2012).

Results

Movement from Puget Sound.—Of the 45 Coho Salmon tagged as residents, 35 were subsequently detected and 10 were not. Those never detected were smaller than those detected (269.9 vs. 297.8 mm at tagging) but the difference was not significant ($t = 1.21$, P (1-tailed test, we assumed smaller fish were more likely to go undetected because in general smaller fish are less likely to survive) = 0.12, $df = 43$). The proportions of wild and hatchery fish were similar between the fish that were detected ($H = 27$, $W = 8$) and not detected ($H = 8$, $W = 2$). Fish that were not detected had a range of tag sizes (Table 2.1) and power outputs, so there was no indication that the failure to detect certain fish resulted from transmitters with limited range. We

did not conduct subsequent analyses on the fish that were not detected but examined only the 35 fish detected at least once.

Seven of the 35 tagged fish detected at least once (20%) were detected leaving Puget Sound at the Strait of Juan de Fuca (Table 2.1), and none was detected at the array across the Strait of Georgia. The fish that remained tended to be somewhat larger at tagging than those that left (304.6 vs. 270.3 mm) but the difference was not significant ($t = 1.34$, P (2-tailed) = 0.19, $df = 33$), and power analysis revealed only a 25% chance to reject the null hypothesis of no size difference between those that remained and those that departed ($\alpha = 0.05$). For fish that were detected leaving Puget Sound, these departures were soon after release in some cases (16, 17, 37 d) but long after release in others (86, 122, 140 and 205 d later). Additionally, some fish spent many days in the Strait of Juan de Fuca and were detected at many receivers (Fish #s 9, 11, 12, Table 2.1) whereas others spent only a few days and were detected at only a few receivers (Fish #s 2, 3, 15, 32).

The departure dates included five in late fall – winter (15 Nov to 3 Mar) and two in mid-late summer (4 Aug and 21 Sept). Of the five departing in fall-winter, two were subsequently detected at the array of receivers off the coast of Washington, near Willapa Bay (Figure 2.1). Fish #9 was detected at the Strait of Juan de Fuca for several days in November 2006, February, and April 2007, and reached the coast on 6/6/07, where it was detected for a single day. Fish #12 was detected at the Strait of Juan de Fuca for several days in March and April 2007, reached the coast on 31 May, and was detected there on several days in June. It then returned to the Strait of Juan de Fuca several months later in late July, and continued to be detected there until August. Of the two individuals that departed Puget Sound in the summer, one (#32, Table 2.1) was subsequently detected back in Puget Sound, four days after detection at the Strait of Juan de Fuca

but the other was not detected back in Puget Sound. There did not appear to be relationships between the departure season, the days between tagging and departure, or the number of Strait of Juan de Fuca receivers each fish was detected at, however, the two fish that left in the summer (#2 and #32, Table 2.1) were detected at only a few Strait of Juan de Fuca receivers.

Between Basin Movements.—Only 11 of the 35 fish (31%) were detected in Puget Sound basins other than the central basin where they were tagged (Table 2.1). Whidbey basin was visited by nine individuals, while Hood Canal, south Puget Sound, and the San Juan Islands had only one individual detected there each. One fish (#42) was detected in both Hood Canal and Whidbey basins, Table 2.1). Receiver coverage was not uniform by any means, and the San Juan Islands were much less well-covered than the other basins. However, there were many receivers operating in Hood Canal and south Puget Sound during the period when the fish were at large so the scarcity of detections in those areas cannot be simply attributed to limited receiver coverage.

Within Basin Movements.—Of 21 receivers in central Puget Sound that were operational over the 42 day period, three receivers (14%) did not detect any of these fish, and three others accounted for 65% of the total time fish were detected (summed over all fish). The data used for within basin movement analysis amounted to 4354 individual detections, totaling 219.2 h of site association and 738 discrete movements.

The principal coordinate analysis performed on the four activity variables for the 18 receivers that detected fish explained 84% of total activity variation in the first axis, which was the only significant axis based on comparison of the eigenvalues to the broken stick model. Principal coordinate loadings of fish, days, returns, and time were all significant, and all correlated with each other and this axis, indicating a single dominant gradient of variation. Sites with high levels of all site use variables were represented by more negative scores along the first

axis, and sites with low values of activity variables represented by positive scores (Table 2.2). Thus, we represented the “site use” at receivers with their score on the first principal coordinate axis.

In general, sites with higher use were located to the south of the tagging site, (all 18 fish were tagged at one site, Table 2.1, Figure 2.2). Some sites without any use during the 42 day period were located only a few km away from receivers with higher use so fine-scale rather than broad-scale features seem to have determined use patterns. The permutational multivariate analysis of variance results indicated a tendency for greater use of deep/offshore compared to shallow/onshore sites ($F_{1,16} = 3.93$, $p = 0.055$), and within-group site use dispersion was not significantly different between deep/offshore and shallow/onshore receivers ($F_{1,16} = 0.494$, $p = 0.492$). Specifically, the four sites most heavily used were all deep/offshore sites (Table 2.2). The three sites with the highest use, which accounted for 65% of the total detection time, were located near President Point, West Point, and Alki Point (sites #1, #2, and #3 respectively). Deep/offshore sites with relatively low use were located at the northern and southern edges of the central basin (#10, 13, 16, Table 2.2). The three sites with no detections could not be included in the analysis as it did not accommodate zero values but all three were onshore sites.

Diel Activity Patterns.—The distribution of all movements on a 24-h scale differed from random (Rao’s test of uniformity $U = 145.4$, $P < 0.001$), indicating that fish moved more often at certain times of day than others. The activity patterns also differed from random when separated into movements at deep/offshore ($U = 145.6$, $P < 0.001$) and shallow/onshore sites ($U = 163.1$, $P < 0.001$). Timing of movements differed significantly between nearshore and offshore sites (Watson’s $U_2 = 1.841$, $P < 0.001$). At deep/offshore sites the fish moved more often during the day ($\mu = 1412$ hours (213.209°), $r = 0.2$) whereas they were more active at night at

shallow/onshore sites ($\mu = 0356$ hours (59.184°), $r = 0.357$; Figure 2.3). Analysis of fish presence (as opposed to activity) showed a similar pattern: fish were more often at deep/offshore receivers during the day ($\mu = 1542$ hours (235.545°), $r = 0.102$) and shallow/onshore sites at night ($\mu = 0528$ hours (81.955°), $r = 0.289$).

Discussion

Movements from Puget Sound.—One of the fundamental questions addressed by this study was, “Are resident and migrant discrete categories of movement or points along a continuum of movement patterns?” Of the fish for which we had sufficient data, 28 of 35 initially tagged as residents remained within Puget Sound and showed very limited movement there. We infer that they displayed continued residency because most of them were detected inside Puget Sound on multiple occasions. On the other hand, seven Coho Salmon, tagged in Puget Sound during the period used to define residency, subsequently left. Five of them left in winter or early spring and several were detected along the coast of Washington. Coded wire tagging data indicated that Coho Salmon caught in Puget Sound include fish that originated from locations including Vancouver Island, the British Columbia mainland, the Olympic Peninsula, and the coast of Washington (Weitkamp and Neely 2002). It is therefore not clear whether the tagged fish that left Puget Sound originated there, resided in Puget Sound for some months, and then moved to the coast to feed, or whether they originated outside Puget Sound, entered, and then left. In either case they were displaying behavior not fitting the strict definitions of resident and migrant.

There were also two fish that left in late summer and early fall. One was detected at the Strait of Juan de Fuca but returned to Puget Sound 4 d later. This fish might be considered to

have remained resident in a slightly broader sense, as the location of the line of receivers in the Strait of Juan de Fuca was somewhat arbitrary as a “gateway” to the coastal ocean. The other fish was detected leaving Puget Sound and not detected again, and we cannot determine whether it survived to spawn and if so where. Departure in late summer would be consistent with the hypothesis that the fish originated outside Puget Sound, entered and resided there, and then left at the onset of maturity.

The uncertain natal origin of the fish we tagged complicates interpretation of the fish that left but overall we interpret the data to indicate that the terms resident and migrant represent modes of behavior along a continuum rather than discrete categories. Puget Sound is thus a source of salmon that migrate to the coastal region, a feeding area for Puget Sound residents, and also a feeding area for Coho Salmon from other areas. Kerr et al. (2009) suggested that partial migration in fishes could be more common than has been recognized. Likewise, we suggest that the study of many partially migratory individuals at finer spatial and temporal scales may reveal more instances of migration as a behavioral gradient.

We did not find differences in body size between fish that departed Puget Sound and those that remained resident. This may have been due to our limited sample size: power analysis revealed only a 25% chance of correctly rejecting the null hypothesis ($\alpha=0.05$). Larger size is associated shorter migration distances in some partially migratory populations of salmonids, including Atlantic salmon entering the Baltic Sea (Kallio-Nyberg et al. 1999), and Chinook salmon entering Puget Sound (Chamberlin et al. 2011a). However, analysis of coded wire tagging data indicates that Coho Salmon that were resident were smaller at capture (at 2+ years old) than those that migrated to the coast (Rohde and Quinn, unpublished data), consistent with earlier reports of reduced growth in Puget Sound (Allen 1956, 1959). Thus, while large size

can predispose residency, the effect of remaining resident may be slower growth, so after time residents appear smaller. The relationship between initial size, residency, and growth rate has yet to be fully understood.

Several kinds of analysis common to studies of fish movement employing telemetry could not be conducted rigorously in this study (e.g., mean distance traveled, amount of time stationary, estimated velocities, pathways taken) because of the nature of our study area and the limitations of our receiver network. Despite the large number of receivers that we and others in the Puget Sound-Strait of Georgia research community have deployed, these are very large bodies of water and most receivers were spaced km apart. Unlike closely spaced receiver arrays in smaller estuarine or freshwater environments or active tracking studies, we cannot know the pathway of individual fish without many gaps in space and time. Thus, estimates of distance traveled, velocity, or pathway taken would rarely reflect the true nature of a fish's movement. However, to characterize the movements of resident Coho Salmon, we have focused on showing presence and absence at a range of spatial scales: whether they moved between basins, which receivers were most popular within basins, and diel patterns of movement.

Between basin movement.—Coho Salmon seldom moved between basins, a surprising finding considering that movements on that order (10s of km) could be accomplished in a few days for fish of this size. Salmonids commonly swim about 1 body length per second in marine waters (Quinn 1988). At that speed a 30 cm fish could travel 1.08 km/h and so at least 10 km/d, even accounting for deviations from a straight line and reduction in activity at night. Similarly, Chamberlin et al (2011b) found that Chinook salmon smolts from Hood Canal tended to stay in Hood Canal throughout their initial summer at sea, indicating that the lack of movement between basins is not unique to species. Of the few fish detected outside the central Puget Sound, where

they were tagged, most were detected in the Whidbey basin. This is consistent with the report that juvenile Chinook salmon exchange was greatest between the central and Whidbey basins, and lower mixing between areas farther apart (Rice et al. 2011). Fish must swim past the entrances to both Whidbey basin and Hood Canal in order to exit Puget Sound through Admiralty Inlet, which may make them more likely to enter these basins than south Puget Sound when en route to the continental shelf or offshore waters of the North Pacific. However, the entrances to Hood Canal and south Puget Sound are partially isolated by shallow, narrow bathymetric sills whereas the entrance to the Whidbey basin is wider and deeper (Burns 1985), and so might afford the fish more opportunity to enter. The lack of fish movement between the basins of Puget Sound most likely results from a combination of factors, which may include the presence of favorable conditions in the basin where the fish was tagged and physical factors hindering movement between basins such as currents or topography.

Within-basin activity and diel patterns.—Values of the four activity variables were generally higher at receivers in deep/offshore sites than at shallow/onshore sites. Moreover, clear diel patterns emerged when fish movement and presence were analyzed on a 24-h scale that differed between onshore and offshore sites. Fish were present more often, as well as more active at deep/offshore receivers during the day, and more often detected and more active at shallow/onshore receivers at night. Peaks in each variable occurred near crepuscular periods: shallow/onshore sites had peaks of activity and presence within 1 – 2 h of dawn, while deep/offshore sites had peaks near dusk (Figure 2.3).

Diel patterns of movement have been found in the marine migrations of many species of salmonids (e.g. Pearcy et al. 1984, Walker et al. 2000). It has been suggested that it may be a response to changes in bioenergetic efficiency, feeding opportunities, or predation risk at

different depths during different diel periods, as proposed for diel vertical migrations of sockeye salmon in lakes (Clark and Levy 1988, Scheuerell and Schindler 2003). However, our knowledge of these factors in Puget Sound, especially the distributions of predators and prey of Coho Salmon, are limited. We do know that juvenile Coho Salmon consume primarily crustaceans in their first fall-winter in Puget Sound (Kirkness, 1948). By their first spring (ca. March) in Puget Sound they have begun to incorporate more fish (Pacific Herring and Sand Lance) into their diet. Fish (especially Pacific Herring) may be a more prominent feature of the diet of Coho Salmon found in the offshore pelagic habitats of Puget Sound (Fresh et al. 1981), but this may be related to the reported move from nearshore to offshore waters that many salmon make after reaching some size threshold (Simenstad et al. 1982). However, Pearcy (1984) found diel variation in the feeding habits of Coho Salmon caught in the Gulf of Alaska, with euphausiids dominating stomach contents at night. Thus, we might expect diel movements of Coho Salmon to track the movement or presence of different prey items. Coho Salmon might also be responding to the risk of predation by visual predators during daylight hours by moving to deep/offshore sites where they have access to deeper water. The reason for diel patterns of movement are probably the result of a complex set of exogenous and endogenous factors, which could also include season, temperature, or size of the fish (Reebs 2002).

Partial migration in fishes is thought to be dependent on a trade-offs between the costs and benefits of migration and residency, often involving multiple factors including physiological tolerance, predation risk, resource availability and growth potential (Jonsson and Jonsson 1993, Chapman et al. 2012). In Chinook and Coho Salmon, remaining resident in Puget Sound has several costs, including increased exposure to poly-chlorinated biphenyls and other contaminants (O'Neill and West 2009), and lower growth rate relative to salmon feeding in the coastal ocean

(Pressey 1953, Buckley 1969). However, survival rates of Coho Salmon smolts entering Puget Sound are consistently higher than those entering the Pacific Ocean coast of Washington (Beetz 2009), indicating that residency in Puget Sound may be driven by a trade-off between body size and probability of survival. Similarly, it has been suggested that differences in oceanographic and food conditions on the east and west coasts Vancouver Island, British Columbia may account for the smaller size of apparently resident Coho Salmon on the east side (Prakash and Milne 1958). The Salish Sea has experienced important changes over the past several decades in phytoplankton (Allen and Wolfe 2013), zooplankton (Li et al. 2013) and coho salmon survival (Beamish et al. 2010; Beetz 2009), so the tendency to reside in or migrate from these waters may reflect broader processes. Future investigations on the oceanographic features and productivity dynamics of Puget Sound may provide more information on the causes and consequences of resident behavior there.

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Conservation Office, NOAA-Fisheries, and the H. Mason Keeler Endowment at the School of Aquatic and Fishery Sciences, University of Washington.

Table 2.1. Summary of attributes of tagged Coho Salmon. Fish # 1-16 were from brood year 2004, 17-45 from brood year 2005. One fish (#12) was detected at the Strait of Juan de Fuca (SJdF) after detection at Willapa Bay, and another individual (#32) was detected inside Puget Sound after detection at the Strait of Juan de Fuca. Month of departure refers to the month when fish were confirmed leaving Puget Sound (detected at the Strait of Juan de Fuca). Gray background indicates the fish was never detected after tagging.

Fish #	Length (mm)	Rearing Type	Tag Type	Tagging Latitude, Longitude	Tagging Date	Date at SJdF, d after tagging	# Receivers in SJdF, # Days in SJdF	Other Basins
1	210	W	V9-6L 30-90	47.738, -122.4903	6/28/2006			
2	220	H	V9-6L 30-90	47.738, -122.4903	6/28/2006	8/4/06, 37	7,4	
3	215	H	V9-6L 30-90	47.738, -122.4903	6/28/2006	11/15/06, 140	1,1	South PS
4	255	H	V9-1L 30-90	47.70917, -122.5146	6/28/2006			
5	270	H	V9-1L 30-90	47.70917, -122.5146	6/28/2006			
6	380	H	V13-1L 30-90	48.4085, -122.5793	9/26/2006			
7	330	H	V9-1L 30-90	48.2862, -122.5097	9/27/2006			
8	200	H	V9-6L 30-90	47.70917, -122.5146	11/1/2006			
9	280	W	V13-1L 30-90	47.70917, -122.5146	11/1/2006	11/18/06, 17	22,11	Coast
10	273	H	V13-1L 30-90	47.70917, -122.5146	11/1/2006			

11	269	W	V13-1L 30-90	47.70917, -122.5146	11/1/2006	11/17/06, 16	30,11	
12	286	H	V13-1L 30-90	47.70917, -122.5146	11/1/2006	3/3/07, 122	25,13	Coast
13	289	W	V13-1L 30-90	47.70917, -122.5146	11/1/2006			
14	236	H	V9P-2L 30-90	47.70917, -122.5146	11/1/2006			
15	303	W	V13P-1L 30-90	47.70917, -122.5146	11/1/2006	1/26/07, 86	2,1	
16	362	W	V13P-1H 20-60	47.8174, -122.4831	6/7/2007			San Juan Islands
17	193	H	V7-4L 30-90	47.7606, -122.4489	6/7/2007			
18	193	W	V7-4L 30-90	47.7606, -122.4489	6/7/2007			
19	165	H	V7-4L 30-90	47.8, -122.49	6/7/2007			
20	176	H	V7-4L 30-90	47.7606, -122.4489	6/7/2007			
21	191	H	V7-4L 30-90	47.765, -122.438	6/8/2007			
22	182	W	V7-4L 30-90	47.765, -122.438	6/8/2007			
23	326	H	V9-6L 30-90	47.5516, -122.4746	12/13/2007			
24	268	H	V9-6L 30-90	47.5516, -122.4746	12/13/2007			
25	457	H	V13-1L 30-90	47.8167, -122.4667	2/29/2008			
26	376	H	V13-1L 30-90	47.8167, -122.4667	2/29/2008			

27	297	H	V9-2L 30-90	47.8167, -122.4667	2/29/2008			
28	338	H	V9-2L 30-90	47.8167, -122.4667	2/29/2008			
29	330	H	V9-2L 30-90	47.8167, -122.4667	2/29/2008			
30	324	W	V9-2L 30-90	47.8167, -122.4667	2/29/2008			Whidbey
31	288	H	V7-4L 30-90	47.8167, -122.4667	2/29/2008			
32	319	H	V9-2L 60-180	47.8167, -122.4667	2/29/2008	9/21/08, 205	2,2	Whidbey
33	320	H	V9-2L 60-180	47.8167, -122.4667	2/29/2008			
34	298	W	V9-2L 60-180	47.8167, -122.4667	2/29/2008			
35	340	H	V9-2L 60-180	47.8167, -122.4667	2/29/2008			Whidbey
36	350	H	V9-2L 60-180	47.8167, -122.4667	2/29/2008			
37	334	H	V9P-2L 30-90	47.8167, -122.4667	2/29/2008			Whidbey
38	320	H	V9P-2L 30-90	47.8167, -122.4667	2/29/2008			
39	350	H	V9P-2L 30-90	47.8167, -122.4667	2/29/2008			Whidbey
40	330	H	V9P-2L 30-90	47.8167, -122.4667	2/29/2008			
41	344	H	V9P-2L 30-90	47.8167, -122.4667	2/29/2008			Whidbey
42	324	H	V9P-2L 30-90	47.8167, -122.4667	2/29/2008			Hood, Whidbey

43	323	H	V9P-2L 30-90	47.8167, -122.4667	2/29/2008	Whidbey
44	341	H	V9P-2L 30-90	47.8167, -122.4667	2/29/2008	
45	346	H	V9P-2L 30-90	47.8167, -122.4667	2/29/2008	Whidbey

Table 2.2. Attributes of sites used for within basin analyses. Attributes of sites used for within basin analyses. including measurements of receiver site use that were used in principal coordinate analysis (Fish, Days, Returns, Time) and the first axis scores from principal coordinate analysis. Receivers 19-23 had 0 detections during the study period, and were not included in the principal coordinate analysis.

Site	Latitude	Longitude	Depth (m)	Distance (km)	Group	Fish	Days	Returns	Time (h)	PCoA axis 1 score
1	47.7652	-122.4380	222	2.46	Deep/Offshore	14	30	96	59.6	0.556
2	47.6619	-122.4650	233	2.09	Deep/Offshore	13	20	51	43.2	0.465
3	47.5759	-122.4510	240	2.27	Deep/Offshore	11	16	59	39.4	0.430
4	47.3843	-122.3540	204	1.54	Deep/Offshore	7	14	29	11.9	0.262
5	47.8418	-122.3576	51	0.34	Shallow/Onshore	9	7	9	15.8	0.174
6	47.4479	-122.4050	221	1.70	Deep/Offshore	6	15	15	4.2	0.154
7	47.5098	-122.3970	72	0.25	Shallow/Onshore	8	11	9	5.0	0.144
8	47.6647	-122.4953	25	0.36	Shallow/Onshore	8	8	6	13.6	0.144
9	47.6279	-122.4875	52	0.39	Shallow/Onshore	7	8	5	6.5	0.081
10	47.3248	-122.4570	177	2.00	Deep/Offshore	5	6	7	9.4	0.050
11	47.5280	-122.4038	90	0.27	Shallow/Onshore	5	7	4	1.7	-0.054
12	47.8968	-122.3850	20	0.85	Shallow/Onshore	3	3	1	2.6	-0.222
13	47.9234	-122.4926	166	2.77	Deep/Offshore	3	3	1	1.9	-0.239
14	47.9082	-122.4380	15	0.80	Shallow/Onshore	2	3	1	1.7	-0.282
15	47.7452	-122.3857	49	0.31	Shallow/Onshore	3	3	2	0.3	-0.288
16	47.9645	-122.5796	105	2.24	Deep/Offshore	2	1	0	0.6	-0.437

17	47.6162	-122.4966	9	0.18	Shallow/Onshore	1	1	0	1.3	-0.451
18	47.5990	-122.3880	37	0.39	Shallow/Onshore	1	1	0	0.6	-0.488
19	47.7488	-122.4662	21	0.43	Shallow/Onshore	0	0	0	0.0	NA
20	47.6122	-122.4857	10	0.87	Shallow/Onshore	0	0	0	0.0	NA
21	47.7237	-122.5537	7	0.17	Shallow/Onshore	0	0	0	0.0	NA

Figure 2.1. Map of receiver locations and summary of Coho Salmon movements. Map of the study area including receivers within the four main basins of Puget Sound (delineated with different patterned backgrounds) including those that detected fish, and those that did not detect fish and were deployed for at least 90 days. Most were captured and tagged on the west side of Central Puget Sound between Port Madison (PM) and Apple Tree Cove (ATC), except fish #23 & #24 which were tagged just south of Bainbridge Island (BI). The relative size of arrows represents the number of fish that moved between basins. Percentages represent the number of fish detected in at basin out of all fish detected at least once during the study period (Table 2.1). Note that although all fish were tagged in the central basin, only 94% of fish were detected there.

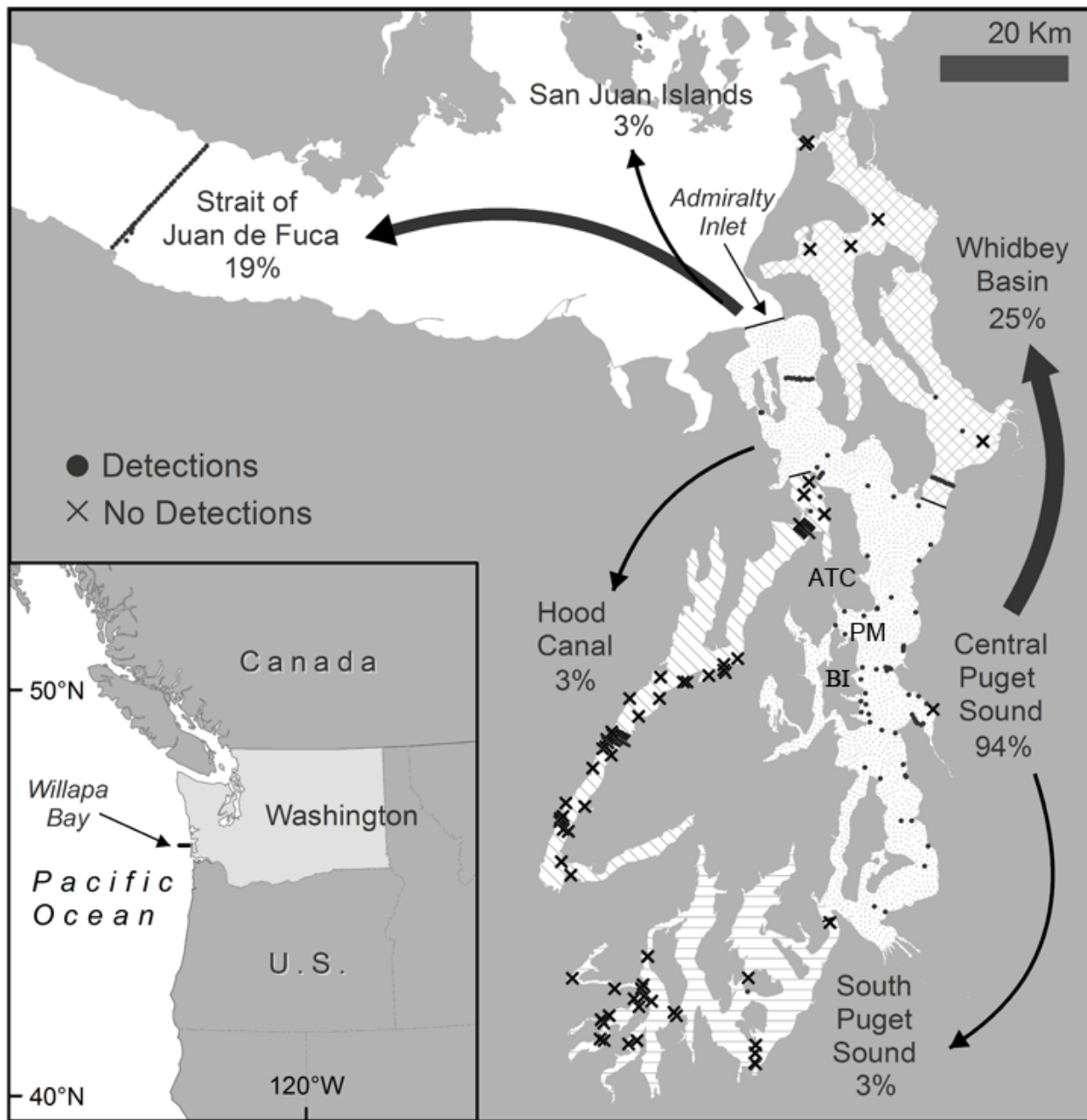


Figure 2.2. Locations of receivers used for within-basin analysis and principal coordinate scores. Locations of 21 receivers used for within-basin analysis with size of the circle representing the score of that location on the first principal coordinate. Receivers are numbered in order of decreasing site use (1 = most frequently used, see Table 2.2), with receivers categorized as deep/offshore in white and shallow/onshore in gray.

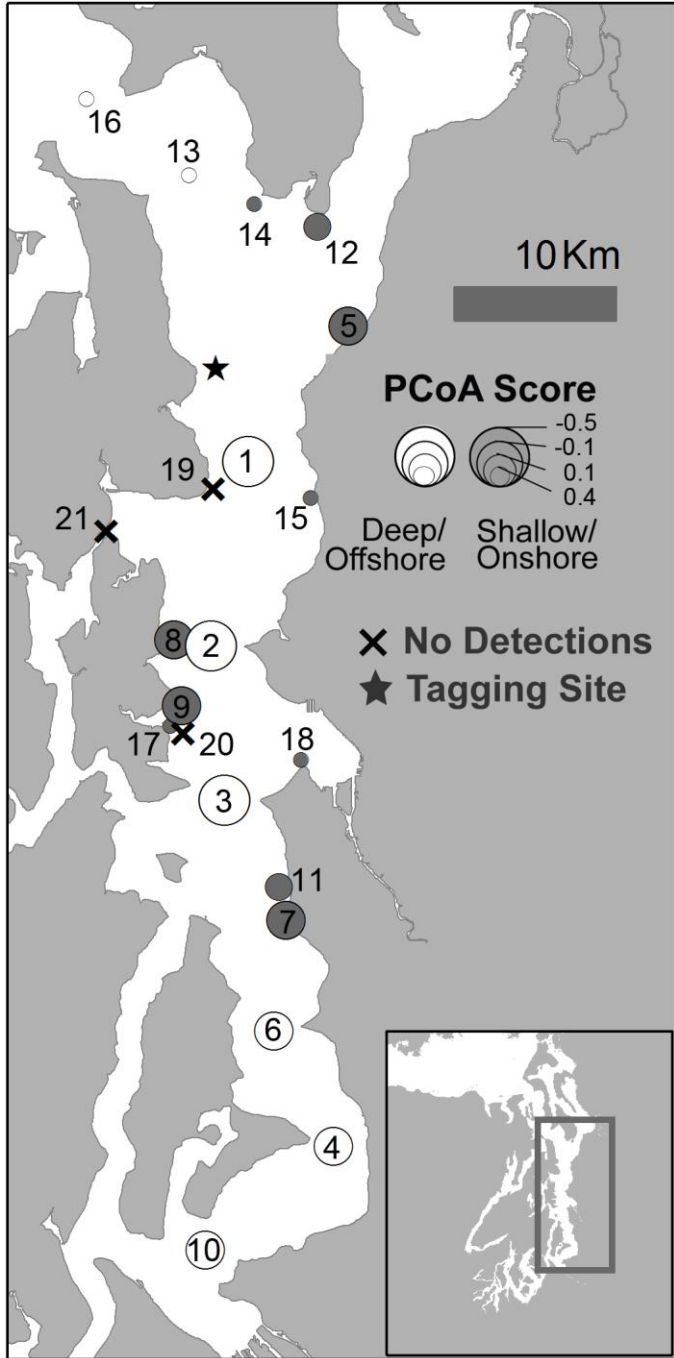
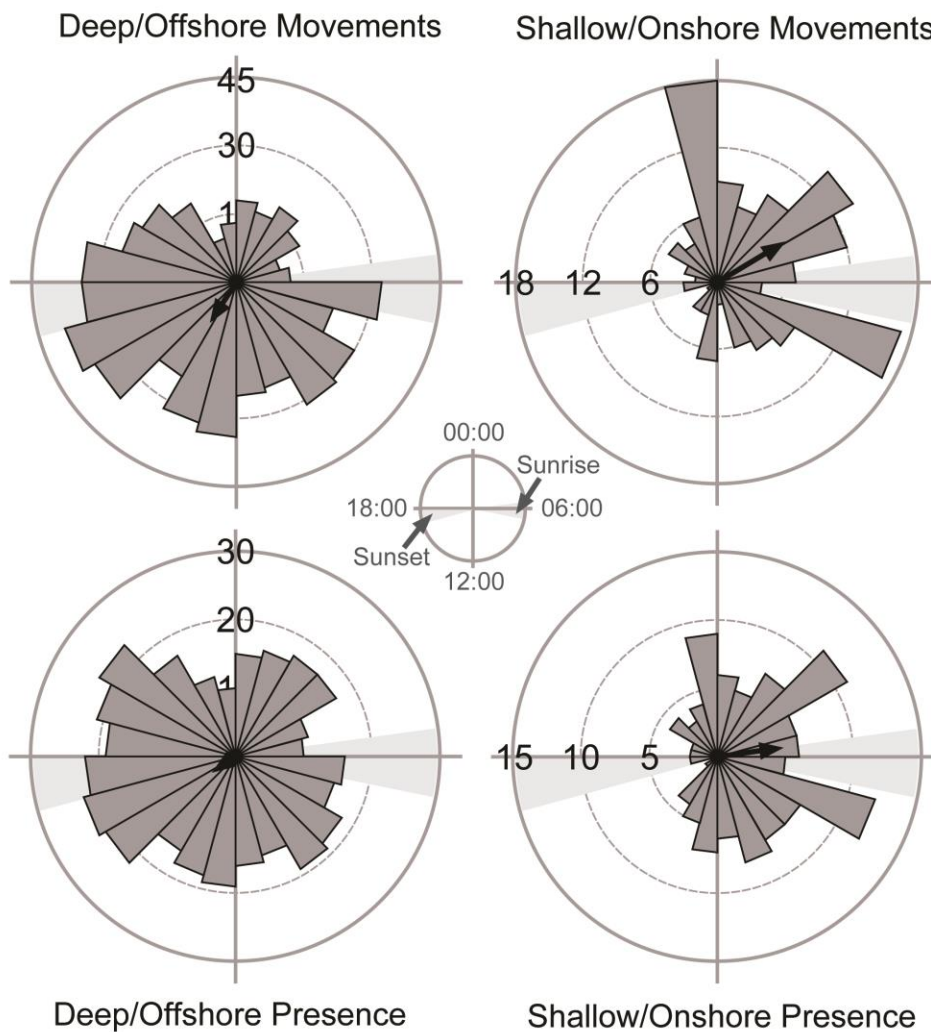


Figure 2.3. Histograms of Coho Salmon movements and presence at deep/offshore and shallow/onshore sites on 24-hour scale. Circular histograms showing discrete movements of Coho Salmon and their presence at deep/offshore and shallow/onshore sites on a 24 hour scale. The mean vector is shown as a black arrow, representing the mean time of movement and presence, and its length represents r , a measure of concentration of the data (movements deep/offshore: $\mu = 1412$ hours, $r = 0.2$; movements shallow/onshore: $\mu = 0356$ hours, $r = 0.357$; fish presence deep/offshore: $\mu = 1542$ hours, $r = 0.102$; fish presence shallow/onshore: $\mu = 0528$ hours, $r = 0.289$). The y-axis units are number of fish, but the scale varies between histograms. Sunrise and sunset periods during the tracking period are indicated by the light gray shading.



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