

This article was downloaded by: [University of Washington Libraries]

On: 12 November 2013, At: 21:48

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/utaf20>

Partial Migration and Diel Movement Patterns in Puget Sound Coho Salmon

Jessica Rohde ^a, Anna N. Kagley ^b, Kurt L. Fresh ^b, Fred A. Goetz ^{a c} & Thomas P. Quinn ^a

^a School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington, 98195, USA

^b National Oceanic and Atmospheric Administration-Fisheries, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington, 98122, USA

^c U.S. Army Corps of Engineers, Seattle District, 4735 East Marginal Way South, Seattle, Washington, 98134, USA

Published online: 25 Oct 2013.

To cite this article: Jessica Rohde, Anna N. Kagley, Kurt L. Fresh, Fred A. Goetz & Thomas P. Quinn (2013) Partial Migration and Diel Movement Patterns in Puget Sound Coho Salmon, Transactions of the American Fisheries Society, 142:6, 1615-1628

To link to this article: <http://dx.doi.org/10.1080/00028487.2013.822421>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

ARTICLE

Partial Migration and Diel Movement Patterns in Puget Sound Coho Salmon

Jessica Rohde*

School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195, USA

Anna N. Kagley and Kurt L. Fresh

National Oceanic and Atmospheric Administration–Fisheries, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington 98122, USA

Fred A. Goetz

School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195, USA; and U.S. Army Corps of Engineers, Seattle District, 4735 East Marginal Way South, Seattle, Washington 98134, USA

Thomas P. Quinn

School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, Washington 98195, USA

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 in offshore waters of the North Pacific Ocean; however, some Coho Salmon (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 with fixed receivers in the Salish Sea. Seven individuals were detected as departing Puget Sound through the Strait of Juan de Fuca, but these fish did not differ in body size, origin (wild or hatchery), or tagging date from fish that remained in Puget Sound. 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 during the night, whereas they were more often present and moved more at deep, offshore sites during the day. We suggest that rather than being a discrete behavior, residence in Puget Sound by Coho Salmon is part of a continuum of migratory behavior patterns.

Spatial distribution and movement patterns are fundamental aspects of the behavior of animals, with ramifications 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

*Corresponding author: rohdej@uw.edu

Received January 22, 2013; accepted June 25, 2013

a continuum of movement patterns from sessile or sedentary species to species occupying home ranges and 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., Japanese Eel *Anguilla japonica*) are typically catadromous, but some individuals remain in marine waters (Tsukamoto and Arai 2001). 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). Some populations of Common Bream *Abramis brama* 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. Striped Bass show spatiotemporal variation in movement patterns ranging from characteristic anadromous migration to 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 to 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); thus, an understanding of this variation is imperative for managing harvested or threatened species.

Salmonid fishes exemplify the great variety of migration patterns in fishes, including discrete anadromous and nonanadromous populations in allopatry and sympatry and nonanadromous individuals within populations that are predominantly anadromous (Hendry et al. 2004; Quinn and Myers 2005). In addition, nonanadromous populations vary greatly in the extent of movement within freshwater (Northcote 1992; Jonsson and Jonsson 1993), and the anadromous individuals vary in their patterns of marine migrations. Among the Pacific salmon *Oncorhynchus* spp., Chinook Salmon *O. tshawytscha* and Coho Salmon *O. kisutch* have more variable marine migration patterns than Sockeye Salmon *O. nerka*, Chum Salmon *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, a greater understanding of migration patterns and their 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 associated interconnected waters in British Columbia and Washington)

is the southernmost complex of inland marine waters used by salmonids as an alternative to the coastal or open waters of the eastern North Pacific Ocean. Puget Sound (defined here as the inland waters south of Admiralty Inlet, including Hood Canal) is a large, fjord-like estuarine complex characterized by deep water, extensive shoreline, multiple tributaries and subestuaries, and urbanized surrounding landscape in some areas (Figure 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 approximately 18 months in marine waters before returning to spawn in the fall of the next year, although a fraction of the males (i.e., 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 the absence of 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 Salmon and Coho Salmon in the nearby Canadian waters (Milne and Ball 1958). Recent research has focused on understanding the 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). Immature Coho Salmon (i.e., postsmolts that have not initiated their homing migration for spawning) also feed in the marine waters of the Salish Sea during all months of the year, but their movement patterns, the population fraction that they represent, and the 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 by immature Coho Salmon in Puget Sound at a series of spatial scales. We used ultrasonic telemetry to determine whether (1) individuals that were resident in Puget Sound remained there or subsequently moved to the coastal Pacific Ocean; (2) fish size or hatchery rearing influenced the tendency of individuals to remain resident in Puget Sound; (3) individuals that were resident in one basin of Puget Sound remained there or moved to other basins; (4) the sites most often visited by Coho Salmon had discernible physical attributes, including depth and distance to shore; and (5) there was a diel pattern in general activity and specifically in onshore–offshore movement (i.e., temporal patterns in movement).

We expected that (1) some fish captured in Puget Sound as residents would subsequently leave Puget Sound, (2) hatchery-reared fish would be more likely to remain resident than wild fish, (3) there would be little tendency to move from one basin to another, (4) sites that were more often visited by fish would have

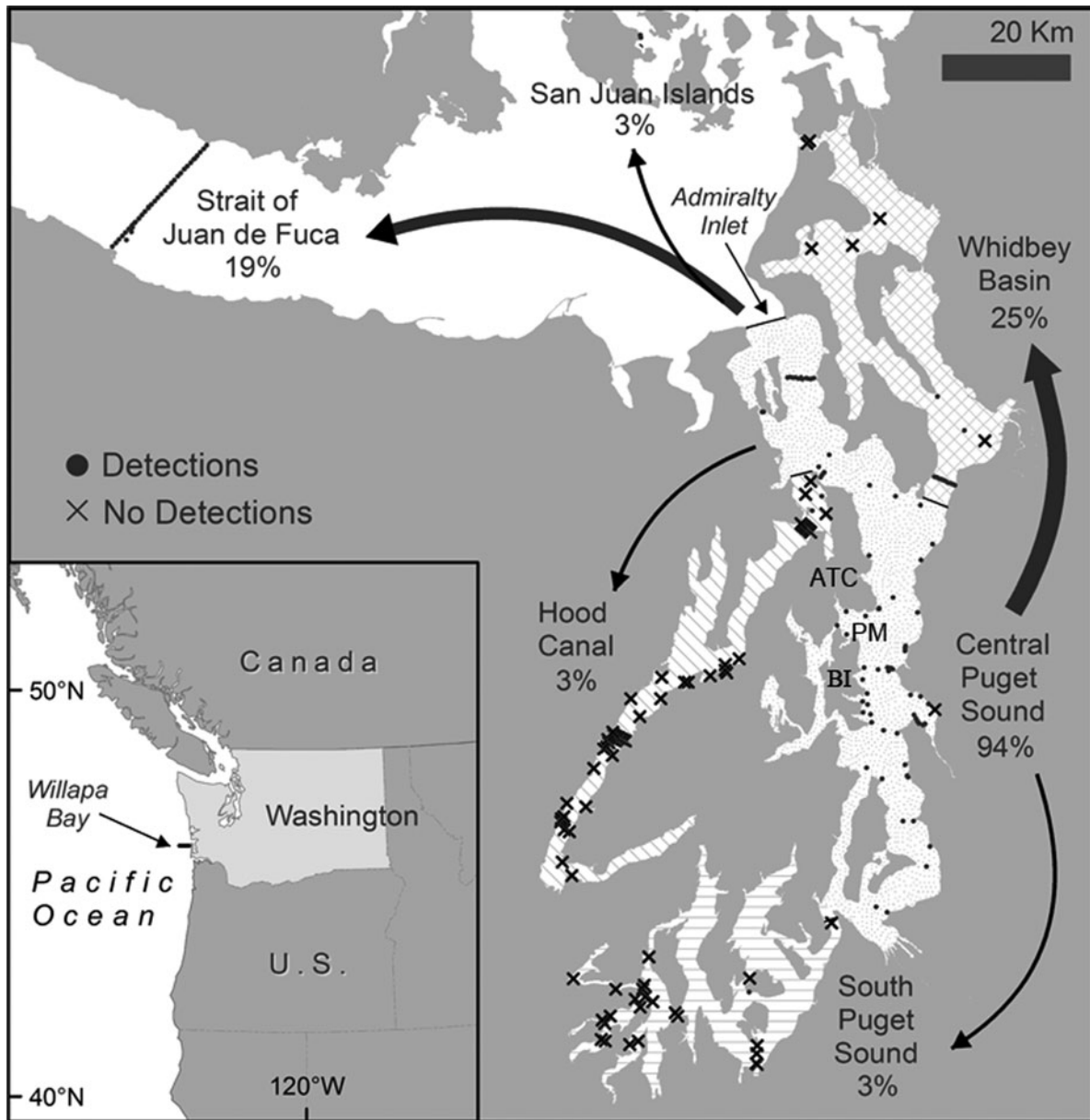


FIGURE 1. Map of the study area, including receivers within the four main basins of Puget Sound (distinguished by the different patterned backgrounds); receivers that detected fish and those that did not detect fish and were deployed for at least 90 d are shown. Most Coho Salmon were captured and tagged on the west side of central Puget Sound between Port Madison (PM) and Apple Tree Cove (ATC), except fish 23 and 24, which were tagged just south of Bainbridge Island (BI). The relative size of arrows represents the number of tagged fish that moved between basins. Percentages represent the number of fish detected in a given basin out of all fish detected at least once during the study period (Table 1). Note that although all fish were tagged in the central basin, only 94% of the fish were detected there.

similar physical attributes of depth and distance to shore, and (5) there would be diel patterns in movement from shallow/onshore sites at night to deep/offshore sites during the day.

STUDY AREA

Puget Sound is a partially mixed estuary–fjord complex encompassing an area of 2,330 km² in Washington State and consists of four interconnected basins (Burns 1985): central Puget

Sound, Hood Canal, 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 Whidbey Basin; Burns 1985). We adopted the boundaries of the Puget Sound basins as 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 1). Admiralty Inlet is a subbasin of the central basin with sills (bathymetric shallow points) at both ends and 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 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 1; Table 1). Most were captured on the west side of central Puget Sound between Port Madison and Apple Tree Cove, except fish 23 and 24, which were tagged just south of Bainbridge Island. All fish were tagged between November and June, 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); many Coho Salmon 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 tag 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 then 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 they were, by definition, residents.

Each fish was visually examined for a clipped adipose fin, and a magnetic wand was used to check for the presence of a coded wire tag to distinguish hatchery fish from wild fish (Table 1). The vast majority of Coho Salmon from hatcheries in Puget Sound are marked (Washington Department of Fish and Wildlife; wdfw.wa.gov/hatcheries/overview.html), although inevitably there are some unmarked fish of hatchery origin. Based on measurements of FL (range = 319–457 mm; Table 1) and the capture dates, we estimated brood year and age, concluding that all but one tagged individual had spent only one summer at sea (Table 1). Coded transmitters (VEMCO V13, V9, and V7; Amirix Systems, Inc.; Table 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). In addition, a small piece of ventral fin tissue was removed for genetic analysis because postsmolt Coho Salmon and Chinook Salmon can be difficult to distinguish. Genomic DNA was isolated from salmon fin clip tissues by using Wizard genomic DNA purifica-

tion kits (Promega Corp.) in accordance with 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 that were genetically confirmed to be Coho Salmon were included in the analysis.

Many VEMCO VR2 and VR3 receivers (Amirix Systems) have been deployed in Puget Sound by researchers from multiple organizations. Detection data were shared via an online database known as Hydra (Sound Data Management 2008). This network has been utilized to study the movement patterns of many species, including Bluntnose Sixgill Sharks *Hexanchus griseus* (Andrews et al. 2007), Broadnose Sevengill Sharks *Notorynchus cepedianus* (Williams et al. 2012), Spotted Ratfish *Hydrolagus colliciei* (Andrews and Quinn 2011), Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii*, steelhead *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; only a fraction of the receivers were explicitly deployed for this project. Consequently, we had to determine the receiver locations with times of operation 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 operating during our study period (between the first tagging event on 28 June 2006 and the last detection of any of our tagged fish on 27 September 2008), including sites in all basins of Puget Sound, in the Strait of Juan de Fuca, and the coast of Washington. Sites had continuous receiver coverage for durations of up to 889 d (mean = 324.7 d). Detections were queried from the Hydra database based on the tag identification numbers, and we found that 142 receiver sites detected our tagged fish. Additionally, we obtained the locations of 150 receiver sites that were deployed for at least 90 d during our study period, but those sites did not detect any of our tagged fish.

We used GIS to extract environmental characteristics at the receiver sites (Figure 1). Environmental variables included distance from the shoreline (Washington State Department of Ecology 2012) and mean depth (within a 540-m radius of the receiver, which is the maximum detection range of the VEMCO V9P-2L 30-90 transmitter, the most common type used in this study; VEMCO 2013) using a 30-m digital elevation model of Puget Sound bathymetry (Finlayson 2005).

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 analyses.—We categorized each fish as remaining resident in or departing from Puget Sound based on whether the fish was detected at the line of receivers across the Strait of Juan de Fuca (Figure 1).

TABLE 1. Attributes of Coho Salmon (W = wild; H = hatchery) that were tagged in the central basin of Puget Sound. Fish 1–16 were from brood year 2004, and fish 17–45 were 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 (fish 32) was detected inside Puget Sound after detection at SJdF. Month of departure refers to the month in which fish were confirmed to have left Puget Sound (detected at SJdF). Asterisks indicate fish that were never detected after tagging.

| Fish | FL (mm) | Rearing type | Tag type | Tagging latitude | Tagging longitude | Tagging date | Date at SJdF, days after tagging | Number of receivers in SJdF, days in SJdF | Other basins |
|------|---------|--------------|---------------|------------------|-------------------|--------------|----------------------------------|---|-------------------|
| 1 | 210 | W | V9-6L 30-90 | 47.738 | -122.4903 | 28 Jun 2006 | | | |
| 2 | 220 | H | V9-6L 30-90 | 47.738 | -122.4903 | 28 Jun 2006 | 4 Aug 2006, 37 | 7, 4 | |
| 3 | 215 | H | V9-6L 30-90 | 47.738 | -122.4903 | 28 Jun 2006 | 15 Nov 2006, 140 | 1, 1 | South Puget Sound |
| 4 | 255 | H | V9-1L 30-90 | 47.70917 | -122.5146 | 28 Jun 2006 | | | |
| 5* | 270 | H | V9-1L 30-90 | 47.70917 | -122.5146 | 28 Jun 2006 | | | |
| 6* | 380 | H | V13-1L 30-90 | 48.4085 | -122.5793 | 26 Sep 2006 | | | |
| 7* | 330 | H | V9-1L 30-90 | 48.2862 | -122.5097 | 27 Sep 2006 | | | |
| 8 | 200 | H | V9-6L 30-90 | 47.70917 | -122.5146 | 1 Nov 2006 | | | |
| 9 | 280 | W | V13-1L 30-90 | 47.70917 | -122.5146 | 1 Nov 2006 | 18 Nov 2006, 17 | 22, 11 | Coast |
| 10 | 273 | H | V13-1L 30-90 | 47.70917 | -122.5146 | 1 Nov 2006 | | | |
| 11 | 269 | W | V13-1L 30-90 | 47.70917 | -122.5146 | 1 Nov 2006 | 17 Nov 2006, 16 | 30, 11 | |
| 12 | 286 | H | V13-1L 30-90 | 47.70917 | -122.5146 | 1 Nov 2006 | 3 Mar 2007, 122 | 25, 13 | Coast |
| 13 | 289 | W | V13-1L 30-90 | 47.70917 | -122.5146 | 1 Nov 2006 | | | |
| 14* | 236 | H | V9P-2L 30-90 | 47.70917 | -122.5146 | 1 Nov 2006 | | | |
| 15 | 303 | W | V13P-1L 30-90 | 47.70917 | -122.5146 | 1 Nov 2006 | 26 Jan 2007, 86 | 2, 1 | |
| 16 | 362 | W | V13P-1H 20-60 | 47.8174 | -122.4831 | 7 Jun 2007 | | | San Juan Islands |
| 17 | 193 | H | V7-4L 30-90 | 47.7606 | -122.4489 | 7 Jun 2007 | | | |
| 18 | 193 | W | V7-4L 30-90 | 47.7606 | -122.4489 | 7 Jun 2007 | | | |
| 19* | 165 | H | V7-4L 30-90 | 47.8 | -122.49 | 7 Jun 2007 | | | |
| 20 | 176 | H | V7-4L 30-90 | 47.7606 | -122.4489 | 7 Jun 2007 | | | |
| 21* | 191 | H | V7-4L 30-90 | 47.765 | -122.438 | 8 Jun 2007 | | | |
| 22* | 182 | W | V7-4L 30-90 | 47.765 | -122.438 | 8 Jun 2007 | | | |
| 23 | 326 | H | V9-6L 30-90 | 47.5516 | -122.4746 | 13 Dec 2007 | | | |
| 24 | 268 | H | V9-6L 30-90 | 47.5516 | -122.4746 | 13 Dec 2007 | | | |
| 25 | 457 | H | V13-1L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | |
| 26 | 376 | H | V13-1L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | |
| 27* | 297 | H | V9-2L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | |
| 28 | 338 | H | V9-2L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | |
| 29 | 330 | H | V9-2L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | |
| 30 | 324 | W | V9-2L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | Whidbey |
| 31 | 288 | H | V7-4L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | |
| 32 | 319 | H | V9-2L 60-180 | 47.8167 | -122.4667 | 29 Feb 2008 | 21 Sep 2008, 205 | 2, 2 | Whidbey |
| 33 | 320 | H | V9-2L 60-180 | 47.8167 | -122.4667 | 29 Feb 2008 | | | |
| 34* | 298 | W | V9-2L 60-180 | 47.8167 | -122.4667 | 29 Feb 2008 | | | |
| 35 | 340 | H | V9-2L 60-180 | 47.8167 | -122.4667 | 29 Feb 2008 | | | Whidbey |
| 36* | 350 | H | V9-2L 60-180 | 47.8167 | -122.4667 | 29 Feb 2008 | | | |
| 37 | 334 | H | V9P-2L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | Whidbey |
| 38 | 320 | H | V9P-2L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | |
| 39 | 350 | H | V9P-2L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | Whidbey |
| 40 | 330 | H | V9P-2L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | |
| 41 | 344 | H | V9P-2L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | Whidbey |
| 42 | 324 | H | V9P-2L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | Hood, Whidbey |
| 43 | 323 | H | V9P-2L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | Whidbey |
| 44 | 341 | H | V9P-2L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | |
| 45 | 346 | H | V9P-2L 30-90 | 47.8167 | -122.4667 | 29 Feb 2008 | | | Whidbey |

This receiver line was one of several operating in the Salish Sea throughout the study period, as described by Chittenden et al. (2009). The Strait of Juan de Fuca line along with 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 the individual had left Puget Sound. Delineations of the Puget Sound basins (south Puget Sound, central Puget Sound, Hood Canal, and Whidbey Basin) were based on a GIS data set produced by the U.S. Department of Agriculture (USDA-NRCS et al. 2004). The movement of tagged fish through these areas was assessed by using GIS.

Within-basin analysis.—To assess the patterns of site use by Coho Salmon, we examined a subset of the data representing the most complete coverage in terms of the number of operating receivers and the number of fish with functioning transmitters. This included 21 receivers in the central basin (Figure 1; Table 2) that were deployed continuously from 1 March to 12 April 2008 (42 d) and 21 fish that were tagged on 29 February 2008. Of the 21 tagged fish, three were never detected (fish 27, 34, and 36; Table 1) and one fish (39) was not detected during the 42-d period after release (Table 1). Therefore, the within-basin 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 that were detected there; (2) the number of days on which there was one or more detections of any fish; (3) the total amount of time (h) the fish were detected, summed over all fish; and (4) the number of return visits, summed over all fish. For calculating the latter two measurements, we defined movement based on the work of 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 into 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 data set confirmed that as in the study by Chamberlin et al. (2011b), most of the detections were less than 1 h apart (data not shown). Therefore, apparent movements (i.e., gaps in detection) of less than 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 had left the receiver, and the period without detections was not included in the time spent

TABLE 2. Attributes of receiver sites examined in the within-basin analyses, including measurements of Coho Salmon site use that were incorporated into the principal coordinates analysis (PCoA; fish = number of individual fish that were detected at the site; days = number of days on which there was one or more detections of any fish at the site; returns = number of return visits to the site, summed over all fish; time = total amount of time the fish were detected at the site, summed over all fish), and the first axis scores from the PCoA. Receivers 19–23 had no detections during the study period and were not included in the PCoA.

| Site | Latitude | Longitude | Depth (m) | Distance (km) | Receiver 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 |

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 the receiver [h], and number of return visits) and were correlated (correlations between all variable combinations > 0.85), but they captured slightly different aspects of fish behavior, individually and collectively. Rather than analyzing these four variables in separate tests, we integrated the data by using principal coordinates 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 of a given variable 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 Gower's similarity coefficient was used. Eigenvalues of each principal coordinate were compared with the broken-stick model to assess significance. Principal coordinate loadings were calculated by correlating the original (log-transformed and standardized) variables with the 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 two groups: 13 were less than 1 km from shore and in water less than 100 m deep; and 7 were over 1.5 km from shore and in water greater than 100 m deep (Table 2). To test the null hypothesis that fish activity measurements would not differ between deep/offshore and shallow/onshore receivers, we used permutational multivariate ANOVA (Anderson 2001) and a test of multivariate homogeneity of group dispersions to assess differences in within-group variation in site use variables (Anderson 2006), with Gower's similarity coefficient used in both analyses. These analyses and the principal coordinates 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 by Coho Salmon varied according to diel period and receiver location, as this 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 as described above (for the within-basin analysis), we reduced the data to 738 discrete movements. We then represented the time of day of each movement as a circular variable with a phase of 24 h, and we 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 U^2 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 that were present at each receiver during each hour of the day over the 42-d 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 a_i and the average set of angles is 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 SD of angles and has a value between 0 and 1 ($r = 1$ indicates that all movements occur at the same time; $r = 0$ indicates that timing of movements is random). All diel period analyses were performed using Oriana (Kovach Computing Services 2012). During the 42-d subset, sunrise ranged from 0527 to 0649 hours and sunset ranged from 1755 to 1854 hours (NOAA-ESRL 2012).

RESULTS

Movement from Puget Sound

Of the 45 Coho Salmon that were tagged as residents, 35 were subsequently detected and 10 were not. Coho Salmon that were never detected were smaller in size than fish that were detected (269.9 mm versus 297.8 mm FL at tagging), but the difference was not significant ($t = 1.21$, $df = 43$, $P = 0.12$ [one-tailed test, as we assumed that smaller fish were more likely to go undetected because smaller fish are generally less likely to survive]). The proportions of wild and hatchery fish were similar between the fish that were detected (27 hatchery fish, 8 wild fish) and those that were not detected (8 hatchery fish, 2 wild fish). Fish that were not detected had a range of tag sizes (Table 1) and power outputs, so there was no indication that the failure to detect certain fish resulted from transmitters with a limited range. We did not conduct subsequent analyses on fish that were not detected; we examined only the 35 fish that were detected at least once.

Seven (20%) of the 35 tagged fish that were detected at least once were detected as leaving Puget Sound at the Strait of Juan de Fuca (Table 1), and none of these fish was detected at the array across the Strait of Georgia. The fish that remained in Puget Sound tended to be somewhat larger at tagging than those that left (304.6 mm versus 270.3 mm FL), but the difference was not significant ($t = 1.34$, $df = 33$, $P = 0.19$ [two-tailed test]) and power analysis revealed only a 25% chance of rejecting the

null hypothesis that there was no size difference between fish that remained in Puget Sound and fish that departed the sound ($\alpha = 0.05$). For fish that were detected as leaving Puget Sound, these departures occurred soon after release in some cases (16, 17, and 37 d later) 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 9, 11, and 12; Table 1), whereas others spent only a few days there and were detected at only a few receivers (fish 2, 3, 15, and 32).

The departure dates included five in late fall–winter (15 November–3 March) and two in mid- to late summer (4 August–21 September). Of the five fish departing Puget Sound in fall–winter, two were subsequently detected at the array of receivers off the coast of Washington near Willapa Bay (Figure 1 inset). Fish 9 was detected at the Strait of Juan de Fuca for several days in November 2006, February 2007, and April 2007 and reached the coast on 6 June 2007, 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. Fish 12 then returned to the Strait of Juan de Fuca several months later in late July 2007 and continued to be detected there until August. Of the two individuals that departed Puget Sound in the summer, one (fish 32; Table 1) was subsequently detected back in Puget Sound 4 d after its detection in the Strait of Juan de Fuca, whereas the other individual (fish 2) was not detected again in Puget Sound. There did not appear to be relationships between the departure season, the number of days between tagging and departure, or the number of Strait of Juan de Fuca receivers at which each fish was detected; however, the two fish that left during the summer (fish 2 and 32) were detected at only a few Strait of Juan de Fuca receivers.

Between-Basin Movements

Only 11 (31%) of the 35 fish were detected in Puget Sound basins other than the central basin, where they were tagged (Table 1). Whidbey Basin was visited by nine individuals, while the Hood Canal, south Puget Sound, and San Juan Islands areas each had only one individual detected. Fish 42 was detected in both Hood Canal and Whidbey Basin (Table 1). Receiver coverage was not uniform by any means, and the San Juan Islands had much lower coverage than the other basins. However, many receivers were 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 the 21 receivers in central Puget Sound that were operational over the 42-d period, three receivers (14%) did not detect any of the 17 fish, and three other receivers accounted for 65% of the total time the fish were detected (summed over all fish).

The data used for within-basin movement analysis amounted to 4,354 individual detections, corresponding to 219.2 h of site association and 738 discrete movements.

The principal coordinates 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 a comparison of eigenvalues with the broken-stick model. Principal coordinate loadings of the four site use variables (number of fish detected at a receiver, number of days of detections, return visits, and time spent near the receiver) were all significant, and all were correlated with each other and with the first axis, indicating a single dominant gradient of variation. Sites with high levels for all site use variables were represented by more negative scores along the first axis, and sites with low values of activity variables were represented by positive scores (Table 2). Thus, site use at each receiver was represented by the receiver's score on the first principal coordinate axis.

In general, sites with higher use were located to the south of the tagging site (all 17 fish were tagged at one site; Table 1; Figure 2). Some sites without any use during the 42-d period were located only a few kilometers away from receivers with higher use, so fine-scale rather than broad-scale features seem to have determined use patterns. The permutational multivariate ANOVA results indicated a tendency for greater use of deep/offshore sites compared with 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 that were most heavily used by the fish were all deep/offshore receiver sites (Table 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; Table 2). Deep/offshore sites with relatively low use were located at the northern and southern edges of the central basin (sites 10, 13, and 16). The three sites with no detections could not be included in the analysis because it did not accommodate zero values, but all three were shallow/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 at others. The activity patterns also differed from random when separated into movements at deep/offshore sites (Rao's test of uniformity: $U = 145.6$, $P < 0.001$) and shallow/onshore sites ($U = 163.1$, $P < 0.001$). Timing of movements differed significantly between nearshore and offshore sites (Watson's two-sample test: $U^2 = 1.841$, $P < 0.001$). At deep/offshore sites, the fish moved more often during the day ($\mu = 1412$ hours [213.209°], $r = 0.2$), whereas at shallow/onshore sites the fish were more active at night ($\mu = 0356$ hours [59.184°], $r = 0.357$; Figure 3). Analysis of fish presence (as opposed to activity)

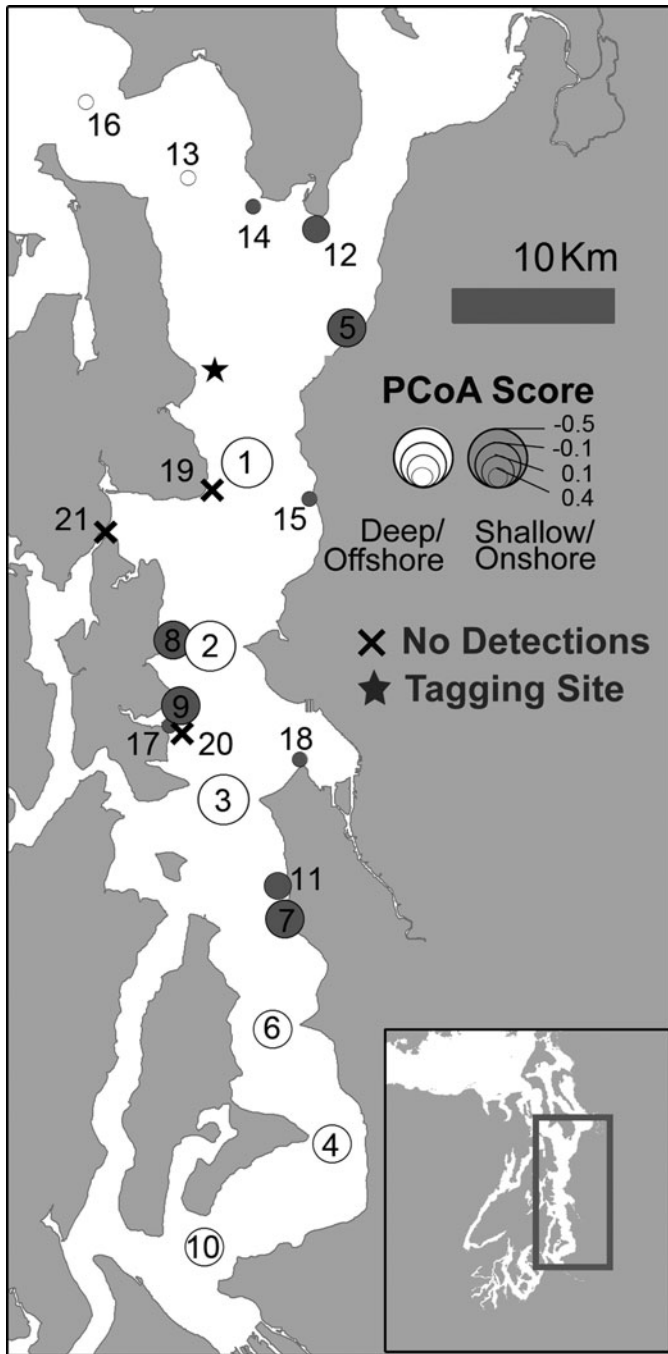


FIGURE 2. Locations of 21 receivers used for within-basin analysis of Coho Salmon site use, with circle size representing the score of that location on the first axis from principal coordinates analysis (PCoA). Receivers are numbered in order of decreasing site use (1 = most frequently used; see Table 2); white circles represent deep/offshore receivers, and gray circles represent shallow/onshore receivers.

showed a similar pattern: fish were more often at deep/offshore receivers during the day ($\mu = 1542$ hours [235.545°], $r = 0.102$) and at shallow/onshore sites during the 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 Coho Salmon for which we had sufficient data, 28 of 35 fish that were initially tagged as residents remained within Puget Sound and showed very limited movement there. We infer that those 28 fish displayed continued residency because most of them were detected inside Puget Sound on multiple occasions. On the other hand, seven fish that were tagged in Puget Sound during the period used to define residency subsequently left Puget Sound. Five of them left in winter or early spring, and several were detected along the coast of Washington. Coded wire tag data indicated that Coho Salmon caught in Puget Sound included fish originating from Vancouver Island, the British Columbia mainland, the Olympic Peninsula, and the coast of Washington (Weitkamp and Neely 2002). It is therefore unclear whether (1) 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 (2) the fish originated from areas outside Puget Sound, entered the sound, and then left. In either case, they were displaying behavior that did not fit the strict definition of “resident” or “migrant.”

There were also two Coho Salmon that left Puget Sound in late summer and early fall. One fish was detected at the Strait of Juan de Fuca, but it returned to Puget Sound 4 d later. This fish could be considered to have remained resident in a slightly broader sense, as the location of the Strait of Juan de Fuca receiver line was somewhat arbitrary as a “gateway” to the coastal ocean. The other fish was detected as leaving Puget Sound and was not detected again, and we cannot determine whether that individual survived to spawn or, if so, where it spawned. Departure in late summer would be consistent with the hypothesis that the fish originated from outside Puget Sound, entered and resided in the sound, and then left at the onset of maturity.

The uncertain natal origin of the tagged Coho Salmon used in our study complicates interpretation of results from 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 Coho Salmon that migrate to the coastal region, a feeding area for Puget Sound residents, and 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

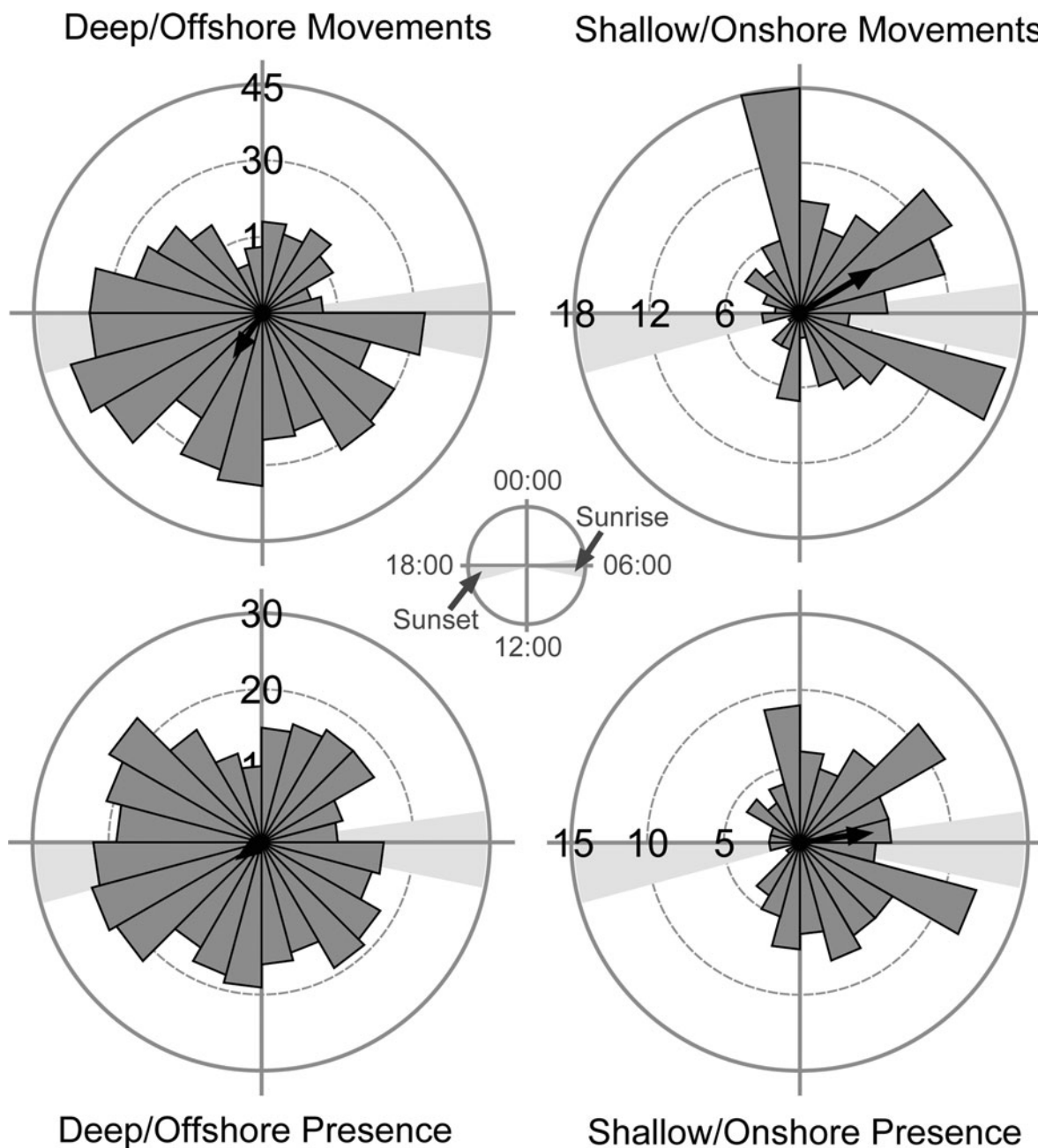


FIGURE 3. Circular histograms representing the discrete movements of Coho Salmon and their presence at deep/offshore and shallow/onshore receiver sites on a 24-h scale. The mean vector μ is shown as a black arrow, representing the mean time of movement and presence; the length of the arrow represents r , a measure of concentration of the data (movements at deep/offshore receivers: $\mu = 1412$ hours, $r = 0.2$; movements at shallow/onshore receivers: $\mu = 0356$ hours, $r = 0.357$; fish presence at deep/offshore receivers: $\mu = 1542$ hours, $r = 0.102$; fish presence at shallow/onshore receivers: $\mu = 0528$ 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.

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 body size is associated with shorter migration distances in some partially migratory populations of salmonids, including Atlantic Salmon *Salmo salar* entering the Baltic Sea (Kallio-Nyberg et al. 1999) and Chinook Salmon entering Puget Sound (Chamberlin et al. 2011a). However, analy-

sis of coded wire tag data indicates that Coho Salmon that were resident were smaller at capture (at age 2+) than those that migrated to the coast (J. Rohde and T. P. Quinn, unpublished data); this is consistent with earlier reports of reduced growth in Puget Sound (Allen 1956, 1959). Thus, while large body size can predispose a fish to residency, the effect of remaining resident may be slower growth such that after a time, residents appear to

be smaller. The relationships among initial size, residency, and growth rate have yet to be fully understood.

Several kinds of analysis common to telemetry studies of fish movement (e.g., mean distance traveled, amount of time the fish was stationary, estimated velocities, and pathways taken) could not be conducted rigorously in our study due to the nature of the 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 kilometers apart. Unlike (1) studies that employ closely spaced receiver arrays in smaller estuarine or freshwater environments and (2) active tracking studies, we cannot know the pathways of individual fish without many gaps in space and time. Thus, estimates of distance traveled, velocity, or pathway taken would rarely have reflected 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 (tens of kilometers) could be accomplished in a few days for fish of this size. Salmonids commonly swim about 1 body length/s in marine waters (Quinn 1988). At that speed, a 30-cm fish could travel 1.08 km/h and therefore 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 the canal throughout their initial summer at sea, indicating that the lack of movement between basins is not unique to species. Of the few fish that we detected outside of central Puget Sound (i.e., where they were tagged), most were detected in Whidbey Basin. This is consistent with the report that juvenile Chinook Salmon exchange was greatest between the central basin and Whidbey Basin, whereas lower mixing was observed 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 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 (e.g., currents or topography).

Within-Basin Activity and Diel Patterns

Values of the four activity variables were generally higher at deep/offshore receiver 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 shallow/onshore and deep/offshore sites. Fish were present more often and were more active at deep/offshore receivers during the day, whereas they were more often detected and more active at shallow/onshore receivers during the 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 3).

Diel patterns of movement have been found in the marine migrations of many salmonid species (e.g., Pearcy et al. 1984; Walker et al. 2000). It has been suggested that diel movement patterns are a response to changes in bioenergetic efficiency, feeding opportunities, or predation risk at different depths during different diel periods, as was 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, is limited. We do know that juvenile Coho Salmon consume primarily crustaceans during their first fall–winter in Puget Sound (Kirkness 1948). By their first spring (~March) in Puget Sound, Coho Salmon have begun to incorporate more fish (Pacific Herring *Clupea pallasii* and Pacific Sand Lance *Ammodytes hexapterus*) into their diets. Fish (especially Pacific Herring) may be a more prominent feature of the diets 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 the stomach contents of fish sampled 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 from visual predators during daylight hours by moving to deep/offshore sites, where they have access to deeper water. Diel patterns of movement are probably the result of a complex set of exogenous and endogenous factors, which could also include season, temperature, or fish size (Reebs 2002).

Partial migration in fishes is thought to be dependent on a trade-off 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). For Chinook Salmon and Coho Salmon, remaining as residents in Puget Sound has several costs, including increased exposure to polychlorinated biphenyls and other contaminants (O'Neill and West 2009) and a lower growth rate relative to salmon that feed in the coastal ocean (Pressey 1953; Buckley 1969). However, survival rates of Coho Salmon smolts entering Puget Sound

are consistently higher than those of smolts entering the Pacific Ocean along the coast of Washington (Beetz 2009), indicating that residency in Puget Sound may be driven by a trade-off between body size and the probability of survival. Similarly, it has been suggested that differences in oceanographic and food conditions on the east and west coasts of Vancouver Island, British Columbia, may account for the smaller size of apparently resident Coho Salmon on the east side (Prakash and Milne 1958). Over the past several decades, the Salish Sea has experienced important changes in phytoplankton (Allen and Wolfe 2013), zooplankton (Li et al. 2013), and Coho Salmon survival (Beetz 2009; Beamish et al. 2010), 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.

ACKNOWLEDGMENTS

We thank the many agencies responsible for deployment and retrieval of receivers and for sharing their data with us, including but not limited to the National Oceanic and Atmospheric Administration (NOAA) Northwest Fisheries Science Center, the University of Washington's School of Aquatic and Fishery Sciences, the Washington Department of Fish and Wildlife, the U.S. Army Corps of Engineers, the Seattle Aquarium, Seattle City Light, the Nisqually and Squaxin Island tribal fisheries departments, and the Pacific Ocean Shelf Tracking Project. We thank Joshua Chamberlin for help in the field and with data analysis and interpretation and Jennifer Scheuerell and Dawn Spillsbury Pucci for help with database management. Genetic analysis to verify the species identification was conducted by David Kuligowski and David Teel (NOAA Fisheries). Funding for this project was provided by the State of Washington's Salmon Recovery Funding Board through the Washington Recreation and Conservation Office, NOAA Fisheries, and the H. Mason Keeler Endowment at the School of Aquatic and Fishery Sciences, University of Washington.

REFERENCES

- Allen, G. H. 1956. Migration, distribution, and movement of Puget Sound Silver Salmon. Doctoral dissertation. University of Washington, Seattle.
- Allen, G. H. 1959. Growth of marked Silver Salmon (*Oncorhynchus kisutch*) of the 1950 brood in Puget Sound. *Transactions of the American Fisheries Society* 88:310–318.
- Allen, G. H. 1966. Ocean migration and distribution of fin-marked Coho Salmon. *Journal of the Fisheries Research Board of Canada* 23:1043–1061.
- Allen, S. E., and M. A. Wolfe. 2013. Hindcast of the timing of the spring phytoplankton bloom in the Strait of Georgia, 1968–2010. *Progress in Oceanography* 115:6–13.
- Anderson, M. J. 2001. Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences* 58:626–639.
- Anderson, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245–53.
- Andrews, K. S., P. S. Levin, S. L. Katz, D. Farrer, V. F. Gallucci, and G. Bargmann. 2007. Acoustic monitoring of Sixgill Shark movements in Puget Sound: evidence for localized movement. *Canadian Journal of Zoology* 85:1136–1143.
- Andrews, K. S., and T. P. Quinn. 2011. Combining fishing and acoustic monitoring data to evaluate the distribution and movements of Spotted Ratfish *Hydrolagus coliei*. *Marine Biology* 159:769–782.
- Baker, R. R. 1978. *The evolutionary ecology of animal migration*. Hodder and Stoughton, London.
- Batschelet, E. 1981. *Circular statistics in biology*. Academic Press, London.
- Beamish, R. J., R. M. Sweeting, K. L. Lange, D. J. Noakes, D. Preikshot, and C. M. Neville. 2010. Early marine survival of Coho Salmon in the Strait of Georgia declines to very low levels. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 2:424–439.
- Beauchamp, D. A., and E. J. Duffy. 2011. Stage-specific growth and survival during early marine life of Puget Sound Chinook Salmon in the context of temporal-spatial environmental conditions and trophic interactions. Washington Cooperative Fish and Wildlife Research Unit, WACFWRU-11-01, Seattle. Available: www.coopunits.org/Washington/Research/ (July 2012).
- Beetz, J. L. 2009. Marine survival of Coho Salmon (*Oncorhynchus kisutch*) in Washington State: characteristic patterns and their relationship to environmental and biological factors. Master's thesis. University of Washington, Seattle.
- Buckley, R. M. 1969. Analysis of the Puget Sound sport fishery for resident Coho Salmon, *Oncorhynchus kisutch* (Walbaum). Master's thesis. University of Washington, Seattle.
- Burns, R. E. 1985. *The shape and form of Puget Sound*. University of Washington Press, Seattle.
- Candy, J. R., and T. P. Quinn. 1999. Behavior of adult Chinook Salmon (*Oncorhynchus tshawytscha*) in British Columbia coastal waters determined from ultrasonic telemetry. *Canadian Journal of Zoology* 77:1161–1169.
- Chamberlin, J. W., T. E. Essington, J. W. Ferguson, and T. P. Quinn. 2011a. The influence of hatchery rearing practices on salmon migratory behavior: is the tendency of Chinook Salmon to remain within Puget Sound affected by size and date of release? *Transactions of the American Fisheries Society* 140:1398–1408.
- Chamberlin, J. W., A. N. Kagley, K. L. Fresh, and T. P. Quinn. 2011b. Movements of yearling Chinook Salmon during the first summer in marine waters of Hood Canal, Washington. *Transactions of the American Fisheries Society* 140:429–439.
- Chapman, B. B., C. Brönmark, J.-Å. Nilsson, and L.-A. Hansson. 2011. The ecology and evolution of partial migration. *Oikos* 120:1764–1775.
- Chapman, B. B., K. Hulthén, J. Brodersen, P. A. Nilsson, C. Skov, L. A. Hansson, and C. Brönmark. 2012. Partial migration in fishes: causes and consequences. *Journal of Fish Biology*.
- Chittenden, C. M., R. J. Beamish, C. M. Neville, R. M. Sweeting, and R. S. McKinley. 2009. The use of acoustic tags to determine the timing and location of the juvenile Coho Salmon migration out of the Strait of Georgia, Canada. *Transactions of the American Fisheries Society* 138:1220–1225.
- Clark, C. W., and D. A. Levy. 1988. Diel vertical migrations by juvenile Sockeye Salmon and the antipredation window. *American Naturalist* 131:271–290.
- Dean, C. A., T. W. Kassler, and G. Mendel. 2010. Genetic identification of Brook Trout or Brook/Bull trout hybrids in Pataha Creek, WA. Washington Department of Fish and Wildlife. Available: <http://wdfw.wa.gov/publications/01139/wdfw01139.pdf>. (November 2012).
- Dingle, H. 1996. *Migration: the biology of life on the move*. Oxford University Press, New York.
- Finlayson, D. P. 2005. Combined bathymetry and topography of the Puget lowland, Washington State. Available: www.ocean.washington.edu/data/pugetsound/ (December 2011).
- Fresh, K. L., R. D. Cardwell, and R. R. Koons. 1981. Food habits of Pacific salmon, baitfish, and their potential competitors and predators in the marine waters of Washington, August 1978 to September 1979. State of Washington Department of Fisheries, progress report 145, Olympia.

- Haw, F., H. O. Wendler, and G. Deschamps. 1967. Development of Washington State salmon sport fishery through 1964. Washington Department of Fisheries Research Bulletin 7.
- Healey, M. C. 1991. Life history of Chinook Salmon (*Oncorhynchus tshawytscha*). Pages 311–394 in C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.
- Hendry, A. P., T. Bohlin, B. Jonsson, and O. K. Berg. 2004. To sea or not to sea? Anadromy versus non-anadromy in salmonids. Pages 92–125 in A. P. Henry and S. Stearns, editors. Evolution illuminated. Oxford University Press, New York.
- Jonsson, B., and N. Jonsson. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3:348–365.
- Kallio-Nyberg, I., H. Peltonen, and H. Rita. 1999. Effects of stock-specific and environmental factors on the feeding migration of Atlantic Salmon (*Salmo salar*) in the Baltic Sea. Canadian Journal of Fisheries and Aquatic Sciences 861:853–861.
- Kerr, L. A., S. X. Cadrin, and D. H. Secor. 2010. The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. Ecological Applications 20:497–507.
- Kerr, L. A., D. H. Secor, and P. M. Piccoli. 2009. Partial migration of fishes as exemplified by the estuarine-dependent white perch. Fisheries 34:114–123.
- Kirkness, W. 1948. Food of the Chinook and Silver salmon of Puget Sound. Washington Department of Fisheries Annual Report 28-31.
- Kokko, H., and A. López-Sepulcre. 2006. From individual dispersal to species ranges: perspectives for a changing world. Science 313:789–91.
- Kovach Computing Services. 2012. Oriana. Anglesey, Wales, UK. Available: www.kovcomp.com. (June 2012).
- Koyama, A., K. Kavanagh, and A. Robinson. 2005. Marine nitrogen in central Idaho riparian forests: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 62:518–526.
- Li, L., D. Mackas, B. Hunt, J. Schweigert, E. Pakhomov, R. I. Perry, M. Galbraith, and T. J. Pitcher. 2013. Zooplankton communities in the Strait of Georgia, British Columbia, track large-scale climate forcing over the Pacific Ocean. Progress in Oceanography 115:90–102.
- Melnchuk, M. C., and C. J. Walters. 2010. Estimating detection probabilities of tagged fish migrating past fixed receiver stations using only local information. Canadian Journal of Fisheries and Aquatic Sciences 67:641–658.
- Milne, D. J., and E. A. R. Ball. 1958. The tagging of spring and Coho Salmon in the Strait of Georgia in 1956. Fisheries Research Board of Canada Progress Reports of the Pacific Coast Stations 111:14–18.
- Moore, M. E., F. A. Goetz, D. M. Van Doornik, E. P. Tezak, T. P. Quinn, J. J. Reyes-Tomassini, and B. A. Berejikian. 2010. Early marine migration patterns of wild Coastal Cutthroat Trout (*Oncorhynchus clarki clarki*), steelhead trout (*O. mykiss*), and their hybrids. PLoS ONE [online serial] 5:1–10.
- Morales, J. M., P. R. Moorcroft, J. Matthiopoulos, J. L. Frair, J. G. Kie, R. A. Powell, E. H. Merrill, and D. T. Haydon. 2010. Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society of London Series B (Biological Sciences) 365:2289–301.
- Moring, J. R. 1976. Contributions of delayed release, pen-cultured Chinook Salmon to the sport fishery in Puget Sound, Washington. Progressive Fish-Culturist 38:36–39.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences of the USA 105:19052–19059.
- NOAA-ESRL (National Oceanic and Atmospheric Administration-Earth System Research Laboratory). 2012. NOAA solar calculator. Available: http://www.esrl.noaa.gov/gmd/grad/solcalc./ (January 2012).
- Northcote, T. G. 1992. Migration and residency in stream salmonids—some ecological considerations and evolutionary consequences. Nordic Journal of Freshwater Research 67:5–17.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, H. H. Stevens, and H. Wagner. 2011. Vegan: community ecology package. Available: vegan.r-forge.r-project.org./ (May 2012).
- O'Neill, S., and J. West. 2009. Marine distribution, life history traits, and the accumulation of polychlorinated biphenyls in Chinook Salmon from Puget Sound, Washington. Transactions of the American Fisheries Society 138:616–632.
- Pearcy, W. G., T. Nishiyama, T. Fujii, and K. Masuda. 1984. Diel variations in the feeding habits of Pacific salmon caught in gill nets during a 24-hour period in the Gulf of Alaska. U.S. National Marine Fisheries Service Fishery Bulletin 82:391–399.
- Prakash, A., and D. J. Milne. 1958. Food as a factor affecting the growth of Coho Salmon off the east and west coasts of Vancouver Island, British Columbia. Fisheries Research Board of Canada Progress Report of the Pacific Coast Stations 112:7–9.
- Pressey, R. T. 1953. The sport fishery for salmon on Puget Sound. Washington Department of Fisheries Fisheries Research Papers 1:33–48.
- Purcell, M., G. Mackey, E. LaHood, H. Huber, and L. Park. 2004. Molecular methods for the genetic identification of salmonid prey from Pacific harbor seal (*Phoca vitulina richardsi*) scat. U.S. National Marine Fisheries Service Fishery Bulletin 220:213–220.
- Quinn, T., B. Dickerson, and L. A. Vøllestad. 2005. Marine survival and distribution patterns of two Puget Sound hatchery populations of Coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytscha*) Salmon. Fisheries Research 76:209–220.
- Quinn, T. P. 1988. Estimated swimming speeds of migrating adult Sockeye Salmon. Canadian Journal of Zoology 66:2160–2163.
- Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle.
- Quinn, T. P., and R. D. Brodeur. 1991. Intra-specific variations in the movement patterns of marine animals. Integrative and Comparative Biology 31:231–241.
- Quinn, T. P., and K. W. Myers. 2005. Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. Reviews in Fish Biology and Fisheries 14:421–442.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: www.cran.r-project.org./ (June 2012).
- Rees, S. G. 2002. Plasticity of diel and circadian activity rhythms in fishes. Reviews in Fish Biology and Fisheries 12:349–371.
- Rensel, J. E., R. P. Harris, and T. J. Tynan. 1988. Fishery contribution and spawning escapement of Coho Salmon reared in net-pens in southern Puget Sound, Washington. North American Journal of Fisheries Management 8:359–366.
- Rice, C. A., C. M. Greene, P. Moran, D. J. Teel, D. R. Kuligowski, R. R. Reisenbichler, E. M. Beamer, J. R. Karr, and K. L. Fresh. 2011. Abundance, stock origin, and length of marked and unmarked juvenile Chinook Salmon in the surface waters of greater Puget Sound. Transactions of the American Fisheries Society 140:170–189.
- Robinson, R. A., H. Q. P. Crick, J. A. Learmonth, I. M. D. Maclean, C. D. Thomas, F. Bairlein, M. C. Forchhammer, C. M. Francis, J. A. Gill, B. J. Godley, J. Harwood, G. C. Hays, B. Huntley, A. M. Hutson, G. J. Pierce, M. M. Rehfish, D. W. Sims, M. B. Santos, T. H. Sparks, D. A. Stroud, and M. E. Visser. 2009. Travelling through a warming world: climate change and migratory species. Endangered Species Research 7:87–99.
- Sandercock, F. K. 1991. Life history of Coho Salmon (*Oncorhynchus kisutch*). Pages 394–445 in C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.
- Scheuerell, M. D., and D. E. Schindler. 2003. Diel vertical migration by juvenile Sockeye Salmon: empirical evidence for the antipredation window. Ecology 84:1713–1720.
- Secor, D. 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. Fisheries Research 43:13–34.
- Secor, D. H., J. R. Rooper, E. Zlokovitz, and V. S. Zdanowicz. 2001. Identification of riverine, estuarine, and coastal contingents of Hudson River Striped Bass based upon otolith elemental fingerprints. Marine Ecology Progress Series 211:245–253.

- Simenstad, C. A., K. A. Fresh, and E. O. Salo. 1982. The role of Puget Sound and Washington coastal estuaries in the life history of Pacific salmon: an unappreciated function. Pages 343–364 *in* V. Kennedy, editor. Estuarine comparisons. Academic Press, New York.
- Skov, C., H. Baktoft, J. Brodersen, C. Brönmark, B. B. Chapman, L.-A. Hansson, and P. A. Nilsson. 2011. Sizing up your enemy: individual predation vulnerability predicts migratory probability. *Proceedings of the Royal Society B (Biological Sciences)* 278:1414–1418.
- Sound Data Management. 2008. Hydra—the hydrophone data repository. Available: <http://hydra.sounddatamanagement.com/> (July 2011).
- Tsukamoto, K., and T. Arai. 2001. Facultative catadromy of the eel *Anguilla japonica* between freshwater and seawater habitats. *Marine Ecology Progress Series* 220:265–276.
- USDA-NRCS (U.S. Department of Agriculture-Natural Resources Conservation Service), U.S. Geological Survey, and U.S. Environmental Protection Agency. 2004. Watershed boundary dataset for Washington State. Available: <http://datagateway.nrcs.usda.gov/>. (June 2012).
- Van Doornik, D., D. Teel, D. Kuligowski, C. Morgan, and E. Casillas. 2007. Genetic analyses provide insight into the early ocean stock distribution and survival of juvenile Coho Salmon off the coasts of Washington and Oregon. *North American Journal of Fisheries Management* 27:220–237.
- VEMCO. 2013. 69-kHz sea water range calculator. Available: <http://www.vemco.com/education/range.php>. (January 2013).
- Walker, R. V., K. W. Myers, N. D. Davis, K. Y. Aydin, K. D. Friedland, H. R. Carlson, G. W. Boehlert, S. Urawa, Y. Ueno, and G. Anma. 2000. Diurnal variation in thermal environment experienced by salmonids in the North Pacific as indicated by data storage tags. *Fisheries Oceanography* 9:171–186.
- Washington State Department of Ecology. 2012. Washington State base map. Available: <http://www.ecy.wa.gov/services/gis/data/data.htm>. (December 2011).
- Weitkamp, L. 2012. Marine distributions of Coho and Chinook salmon inferred from coded wire tag recoveries. Pages 191–214 *in* J. R. McKenzie, B. Parsons, A. C. Seitz, R. K. Kopf, M. G. Mesa, and Q. Phelps, editors. Advances in fish tagging and marking technology. American Fisheries Society, Symposium 76, Bethesda, Maryland.
- Weitkamp, L., and K. Neely. 2002. Coho Salmon (*Oncorhynchus kisutch*) ocean migration patterns: insight from marine coded-wire tag recoveries. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1100–1115.
- Welch, D. W., G. W. Boehlert, and B. R. Ward. 2003. POST—the Pacific Ocean salmon tracking project. *Oceanologica Acta* 25:243–253.
- Williams, G. D., K. S. Andrews, S. L. Katz, M. L. Moser, N. Tolimieri, D. A. Farrer, and P. S. Levin. 2012. Scale and pattern of Broadnose Sevengill Shark *Notorynchus cepedianus* movement in estuarine embayments. *Journal of Fish Biology* 80:1380–1400.
- Wingate, R. L., D. H. Secor, and R. T. Kraus. 2011. Seasonal patterns of movement and residency by Striped Bass within a subestuary of the Chesapeake Bay. *Transactions of the American Fisheries Society* 140:1441–1450.