



U.S. Fish and Wildlife Service

Movement and Habitat Use of Chinook Salmon Smolts and Two Predatory Fishes in Lake Washington and the Lake Washington Ship Canal

2004-2005 Acoustic Tracking Studies

December 2008 *By Mark T. Celedonia, Roger A. Tabor, Scott Sanders, Daniel W. Lantz, and Ian Grettenberger*

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**MOVEMENT AND HABITAT USE OF CHINOOK SALMON SMOLTS AND
TWO PREDATORY FISHES IN LAKE WASHINGTON AND THE LAKE
WASHINGTON SHIP CANAL**

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FINAL REPORT TO SEATTLE PUBLIC UTILITIES

by

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EXECUTIVE SUMMARY

In Lake Washington and the Lake Washington Ship Canal (LWSC), basic data and information is needed regarding movement patterns and habitat use of federally-threatened Chinook salmon *Oncorhynchus tshawytscha* smolts and their predators in order to inform and guide management and restoration activities. Habitat use and movement patterns of juvenile ocean-type Chinook salmon in lake environments are poorly understood. In addition, Lake Washington and the LWSC are highly urbanized, altered, and managed, the consequences of which to Chinook salmon are not well known. The result is that resource managers are challenged to recommend and implement Chinook salmon conservation strategies in Lake Washington with few references to unaltered lacustrine habitats, and an incomplete understanding of how alterations to the Lake Washington ecosystem affect juvenile Chinook salmon. The main objectives of this study were to: 1) evaluate habitat use and movement patterns of Chinook salmon smolts during their outmigration in late-May, June, and July; and, 2) determine diel movement and habitat use of predators, including smallmouth bass and prickly sculpin, and evaluate spatial and temporal habitat overlap with Chinook salmon smolts.

We used an HTI fine-scale acoustic tracking system to evaluate the behavior of Chinook salmon smolts (> 105 mm FL) and two predators, smallmouth bass *Micropterus dolomieu* and prickly sculpin *Cottus asper*, in Lake Washington and the LWSC during May-June, 2004-05. This system allowed us to continuously track fine-scale horizontal fish movements at specific study sites. Under ideal conditions, the precise location (up to ± 1 m) of a tagged fish can be known every second it is in a tracking area. We tracked fish at four sites: Gene Coulon Park in south Lake Washington, the Seattle Tennis Club on the western shore of Lake Washington, and Portage Bay and north Lake Union (Gas Works Park) in the LWSC. The Portage Bay site was studied both years and the other sites were studied for one year only. In general, the HTI system was an effective tool for evaluating juvenile Chinook salmon and predator movement patterns and habitat use. Release location of tagged Chinook salmon smolts (on-site release versus off-site) appeared to influence on-site movement patterns and habitat use. Tagged hatchery Chinook salmon showed similar patterns in movement timing and habitat use as wild fish, albeit with some minor variations.

Chinook salmon movement patterns varied within each site, from site to site, and from year to year. Chinook salmon showed two predominant migratory behaviors: active migration, where they moved as quickly as possible from one destination to the next; and holding, where they appeared paused in their migration. Each site was used differently by migrating Chinook salmon, although considerable individual variability was observed. The Seattle Tennis Club area functioned primarily as a migrational corridor; Portage Bay served as a migrational corridor and as a short-term (< 24 hours) holding area; and Lake Union appeared to be a longer-term (1-7 days) holding area. Differences in site use may have been related to temperature, turbidity, predation risk, salinity, and timing of migrational cues, among other factors. The one site that was studied in both years - Portage Bay - showed differences in site use each year. In 2004, most fish spent several hours to several days at the site, whereas in 2005 most fish actively migrated through

spending less than one hour. Differences in timing of moon apogee relative to tagged fish release appeared to be the primary contributing factor to these differences. Environmental cues and habitat conditions may thus be more important than physical site characteristics in determining Chinook salmon smolt movement patterns.

Distinct diel patterns in habitat use were observed, and diel behavior varied by habitat. Spatial distribution and shoreline orientation of Chinook salmon was markedly different in the LWSC (Portage Bay and Gas Works Park) than in Lake Washington (Seattle Tennis Club). In Lake Washington, Chinook salmon were close to shore in shallow water (1-5 m) during the day, and far offshore in limnetic areas at night. In the LWSC, fish were broadly distributed across deep-water areas (>8-10 m) during all time periods, not just the day. Reasons for such drastic difference may be related to differences in turbidity, predator assemblage, and perceived predation risk between the LWSC and Lake Washington.

Overwater structures and macrophyte beds appeared to influence movement patterns and depth selection of Chinook salmon smolts. All Chinook salmon smolts generally avoided areas directly beneath overwater structures. However, some holding fish used areas along the edges of structures (within 2 m of the edge) for prolonged periods, up to 2 hours in one case. Actively migrating fish appeared to change course as they approached and moved around structures. Structure width and water depth appeared to influence degree of avoidance. Fish appeared less hesitant to pass beneath narrow structures. Fish also appeared to move into deeper water to travel beneath or around structures. When macrophytes were present, fish appeared to use deeper water column depths than they would if macrophytes were not present, moving above the macrophyte canopy rather than avoiding macrophytes altogether. Macrophytes thus appear to function as a false bottom. We hypothesize that water column depth selection as measured from the top of the macrophyte canopy to the water surface would be equivalent to water column depth selection (substrate to water surface) in the absence of macrophytes.

We tagged 24 smallmouth bass, of which we were able to get useful information on 19. The HTI acoustic tracking system was effective in determining smallmouth bass habitat use (depth selection, use of overwater structures, and shoreline type selection); however, information on home range size was often problematic because of the limited size of the arrays. Smallmouth bass were generally close to shore in water that was less than 4 m deep. Those associated with an overwater structure were generally in shallower water than those that were not associated with an overwater structure. Smallmouth bass were usually closely associated with at least one of three habitat types, either an overwater structure, steep sloping shoreline (riprap or bulkhead), or the offshore edge of aquatic macrophytes. Overlap in habitat between smallmouth bass and juvenile Chinook salmon appears to occur at each of these three main habitat types occupied by smallmouth bass. In Lake Washington, outmigrating Chinook salmon are in close proximity to smallmouth bass as they move along the shoreline and encounter piers. In the LWSC, overlap is reduced because Chinook salmon are usually farther offshore.

We also tagged 20 prickly sculpin. The HTI acoustic tracking system was effective in determining prickly sculpin habitat use at Gene Coulon Park site but at Portage Bay and Seattle Tennis Club sites we were unable to track them consistently. Prickly sculpin were primarily active at night, especially in shallow water. At Gene Coulon Park, some prickly sculpin had a well-defined home range which was consistent between nights. Prickly sculpin in offshore areas at the Seattle Tennis Club site moved in a variety of directions without any discernable pattern. Our results indicate prickly sculpin are far more mobile than has been documented for other freshwater cottid species. Nighttime movement patterns of prickly sculpin may help explain the distribution of juvenile Chinook salmon during the time period studied (May-June), as well as the broader time period of juvenile Chinook salmon residence in Lake Washington beginning in February.

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INTRODUCTION

Naturally-reared Chinook salmon *Oncorhynchus tshawytscha* in the Lake Washington basin belong to the Puget Sound Chinook salmon evolutionarily significant unit and are considered threatened under the federal Endangered Species Act. As a result, Lake Washington Chinook salmon have received considerable attention from regulators, resource managers and conservation-minded individuals. However, recovery of this species has been hindered by a general lack of knowledge pertaining to Chinook salmon habitat use in and movement through lakes. This is compounded by the highly urbanized and altered condition of Lake Washington and the Lake Washington ecosystem. The shoreline of Lake Washington has been extensively modified and is dominated by bank armoring, boat docks, and other overwater structures. The riparian zone consists largely of lawns, houses, and other buildings. Large trees in the riparian zone and large woody debris in the littoral zone are generally absent. The lake hydrograph is managed by dams on the Cedar River - the major tributary to Lake Washington - and by the Hiram M. Chittenden Locks and dam located at the outlet to Puget Sound. Self-sustaining populations of non-native fish species, including smallmouth bass *Micropterus dolomieu* and largemouth bass *M. salmoides*, have become prominent components of the ecosystem. Non-native aquatic macrophytes are also spread throughout the lake. The result is that resource managers are challenged to recommend and implement Chinook salmon conservation strategies in Lake Washington with few references to unaltered lacustrine habitats, and an incomplete understanding of how alterations to the Lake Washington ecosystem affect juvenile Chinook salmon.

Most naturally-produced Chinook salmon juveniles in Lake Washington originate in the Cedar River, and a smaller but notable number of juveniles originate in Bear Creek, a tributary to the Sammamish River (Figure 1). In addition, small numbers of Chinook salmon spawn in several tributaries to Lake Washington and Lake Sammamish, but juvenile production from these streams is unknown. Hatchery production in the basin occurs at the Issaquah Creek State Hatchery and the University of Washington (UW) Hatchery (Figure 1). Production goals are 2 million for Issaquah Creek State Hatchery and 180,000 for UW Hatchery. Chinook salmon also spawn below the hatchery in Issaquah Creek and other adults are allowed to migrate upstream of the hatchery if the hatchery production goal of returning adults is met.

Lake Washington Chinook salmon juveniles migrate to the ocean in their first year, and thus are considered “ocean-type” fish. Movement into the marine environment through the Chittenden Locks has been documented from May to August with peak passage occurring during late-May and early-June (DeVries et al. 2005; DeVries et al. 2007). Throughout their natural range, juvenile ocean-type Chinook salmon primarily occur in large rivers and coastal streams (Meehan and Bjornn 1991) and are not known to commonly inhabit lentic environments. Consequently, little research has been conducted on their habitat use in lakes (Graynoth 1999). Research efforts by the U.S. Fish and Wildlife Service (USFWS), the City of Seattle and others have attempted to understand how juvenile Chinook salmon use Lake Washington, and how various alterations to the ecosystem influence their behavior and survival. Within the Lake Washington basin,

juvenile Chinook salmon inhabit lentic environments, either as a migratory corridor (late-May, June, and July) from their natal stream to the marine environment, or as an extended rearing location (January-June). Initial research in 1998-2000 indicated that juvenile Chinook salmon in Lake Washington are primarily restricted to the littoral zone until mid-May when they are large enough to move offshore (Fresh 2000). Subsequent research in 2001-2004 by USFWS focused on littoral zone habitat use during January to mid-May (Tabor and Piaskowski 2002; Tabor et al. 2006). From 2000 to 2006, a large-scale PIT tagging study was conducted to characterize the migration of juvenile Chinook salmon through Lake Washington and the Lake Washington Ship Canal (LWSC) (DeVries et al. 2005; DeVries et al. 2007).

Naturally-produced fry in the basin emerge from redds during January, February, and March. These juveniles appear to have two rearing strategies: 1) rear in lotic habitat until May and then emigrate into lacustrine habitat during May or June as pre-smolts; or, 2) emigrate shortly after emergence and rear in lacustrine habitat as fry for three to five months. Hatchery reared Chinook salmon are released from the Issaquah State Hatchery in May or early June and large numbers enter Lake Sammamish a few hours after release (B. Footen, Muckleshoot Indian Tribe, personal communication). Juvenile Chinook salmon from the Cedar River enter Lake Washington and rear in the south end of the lake primarily from January to May (Tabor and Piaskowski 2002; Tabor et al. 2006). During this time, they inhabit shallow areas 0.1 to 1.3 m deep with a sandy substrate and gentle sloping gradient. Overwater structures can provide cover for small juvenile Chinook salmon in February and March but as they grow larger and predators such as smallmouth bass move inshore Chinook salmon tend to avoid these structures. In May through July, naturally- and hatchery-produced Chinook salmon are located throughout the lake and outmigrate to the marine environment through the LWSC.

Juvenile Chinook salmon emigrating from south Lake Washington have been observed moving northward along the western shoreline of the lake prior to encountering Union Bay and the entrance to the LWSC (Tabor and Piaskowski 2002; Tabor et al. 2006; R. Tabor, unpublished data). Migration has been observed during the early day (approximately 0800-1400 hours) and close to shore in shallow water 1.0 - 2.5 m deep. The extent of movement in deeper water and during other time periods is unknown due to methodological limitations. Migrating smolts do not appear to avoid non-native aquatic macrophytes (Tabor and Piaskowski 2002; Tabor et al. 2006; Celedonia et al. 2008). Instead, macrophytes appear to serve as a false-bottom that smolts simply move above. Migrating smolts have been observed in deeper water - up to 5 m deep - when macrophytes are present in dense stands along the shoreline. Migrating Chinook salmon smolts appear to avoid overwater structures such as boat docks (Tabor and Piaskowski 2002; Tabor et al. 2006; Celedonia et al. 2008; R. Tabor, unpublished data). Fish usually move farther from shore into deeper water to pass beneath the structure, or, rather than passing beneath the structure, fish move around the structure along its perimeter. Behavior at each structure appears to depend on a variety of factors, such as structure size, proximity to other structures, light conditions under the structure, and the occurrence of aquatic macrophytes, although these are based primarily on anecdotal observation.

Various studies have shed light on stage-specific habitat selection (Tabor and Piaskowski 2002; Sergeant and Beauchamp 2006; Tabor et al. 2006), diet and bioenergetics (Koehler et al. 2006), predation risks (Brocksmitth 1999; Nowak et al. 2004; Tabor et al. 2004; Tabor et al. 2007a; Tabor et al. 2007c), and broad-scale migratory patterns (DeVries et al. 2004; DeVries et al. 2005; DeVries et al. 2007) of juvenile Chinook salmon. However, little research has been conducted to understand habitat use or finer-scale movement patterns of juvenile Chinook salmon during their migratory phase in late-May, June, and July. Various methods such as snorkeling and hydroacoustic surveys have been tried to study the habitat use patterns of juvenile Chinook salmon after mid-May but these efforts were met with limited success.

Recently, fixed-array acoustic tracking systems have been developed that allow researchers to precisely track individual fish as they move through a specific area. One such system is produced by Hydroacoustic Technology, Incorporated (HTI), Seattle, Washington. In 2003, HTI tracking systems were used in two different pilot studies in the Lake Washington system. We used a small hydrophone array in the south end of Lake Washington to track two juvenile Chinook salmon for 18 hours. Also, the U.S. Army Corps of Engineers used an array at the Chittenden Locks to examine smolt passage routes; however, few fish were tagged due to high water temperatures. Celedonia et al. (2008) used this system to evaluate movement of tagged Chinook salmon smolts near the SR 520 bridge in Lake Washington. These studies successfully demonstrated the effectiveness of the HTI system in studying juvenile Chinook salmon movement and habitat use patterns. The primary purpose of this study was to expand on these efforts to develop a more comprehensive understanding of Chinook salmon smolt movement patterns and habitat use after mid-May.

Behavior and movement patterns of juvenile salmonids are influenced in large part by the habitat conditions and prey resources available to them, as well as by the presence and activity of predators. Fish predators of juvenile Chinook salmon in Lake Washington and the LWSC include cutthroat trout *O. clarkii*, northern pikeminnow *Ptychocheilus oregonensis*, smallmouth bass, largemouth bass, and prickly sculpin *Cottus asper* (Tabor et al. 2004). Cutthroat trout, northern pikeminnow, and prickly sculpin are native species; however, the two bass species are introduced. Of particular importance to resource managers is the interrelationship between artificial structures, predator habitat use, and predation of juvenile salmonids. To help shed light on these interrelationships, we tagged and tracked several predators in addition to juvenile Chinook salmon. Cutthroat trout make extensive movements throughout the lake, are often in deep limnetic areas, and do not have a noticeable home range (Nowak and Quinn 2002). Therefore, it is doubtful they can be effectively monitored with the HTI tracking system. For this study, we concentrated our efforts on smallmouth bass and prickly sculpin because they are abundant, usually do not have extensive diel horizontal movements, and often have a restricted home range. Prickly sculpin are probably only able to prey on Chinook salmon in February through April because prickly sculpin do not obtain a large size. Predation rates of juvenile Chinook salmon by prickly sculpin are generally quite low but prickly sculpin can be an important predator because they are abundant and inhabit a wide

variety of benthic habitats (Tabor et al. 2007b). We tracked prickly sculpin to provide some insight into their behavior and develop some preliminary models on how they may interact with small juvenile Chinook salmon. We also attempted to capture and tag largemouth bass and northern pikeminnow to collect preliminary information and determine the feasibility of using the HTI tracking system to monitor their movements. Largemouth bass are not common in many areas, and northern pikeminnow are known to be highly mobile (Martinelli and Shively 1997; Brocksmith 1999; Petersen et al. 2000).

The main objectives of this study were to: 1) evaluate habitat use and movement patterns of juvenile Chinook salmon during their migratory phase in late-May, June, and July; and, 2) determine diel movement and habitat use of predators, including smallmouth bass and prickly sculpin, and evaluate spatial and temporal habitat overlap with Chinook salmon smolts. We used the HTI fine-scale acoustic tracking system at four sites in Lake Washington and the LWSC for these purposes. Several factors were considered in selecting study sites, including: 1) location along known migrational corridors; 2) presence of certain features such as overwater structures that may impact migrating Chinook salmon; 3) importance to management and restoration activities; and, 4) logistical constraints of deploying and operating the acoustic tracking gear. Goals of the study were to: 1) document Chinook salmon smolt movement patterns and habitat use at and between the study sites; 2) determine the relationship in space and time between outmigrating juvenile Chinook salmon and piscivorous fishes; and, 3) evaluate the influence of certain features such as overwater structures and aquatic macrophytes on Chinook salmon and predators. We predicted that Chinook salmon movement and habitat use would be similar at and between the different sites. For both Chinook salmon and predators we predicted that habitat selection would be uniform throughout each study site, and that specific areas of each site would neither be selected for or against. Finally, we predicted that aquatic macrophytes and overwater structures would not influence movement or habitat use of Chinook salmon or predators.

We tagged and tracked fish from mid-May until the end of June. This corresponds with peak Chinook salmon outmigration into Puget Sound and the marine environment (DeVries et al. 2005; DeVries et al. 2007). Therefore, we assumed based on this timing, and size and appearance of the juvenile Chinook salmon we tagged, that our study fish were undergoing smoltification during the study period. Thus, we refer to juvenile Chinook salmon during this time as smolts, although we did not perform any formal physiological sampling (e.g., gill ATPase) to verify smolt status.

STUDY AREA

Lake Washington is a large monomictic lake located in the Puget Sound region of western Washington and lies within the greater Seattle metropolitan area (Figure 1). The lake has a total surface area of 9,495 hectares and a mean depth of 33 m. Thermal stratification typically occurs from June through October. Surface water temperatures range from 4-6°C in winter to over 20°C in summer. Lake level is artificially managed

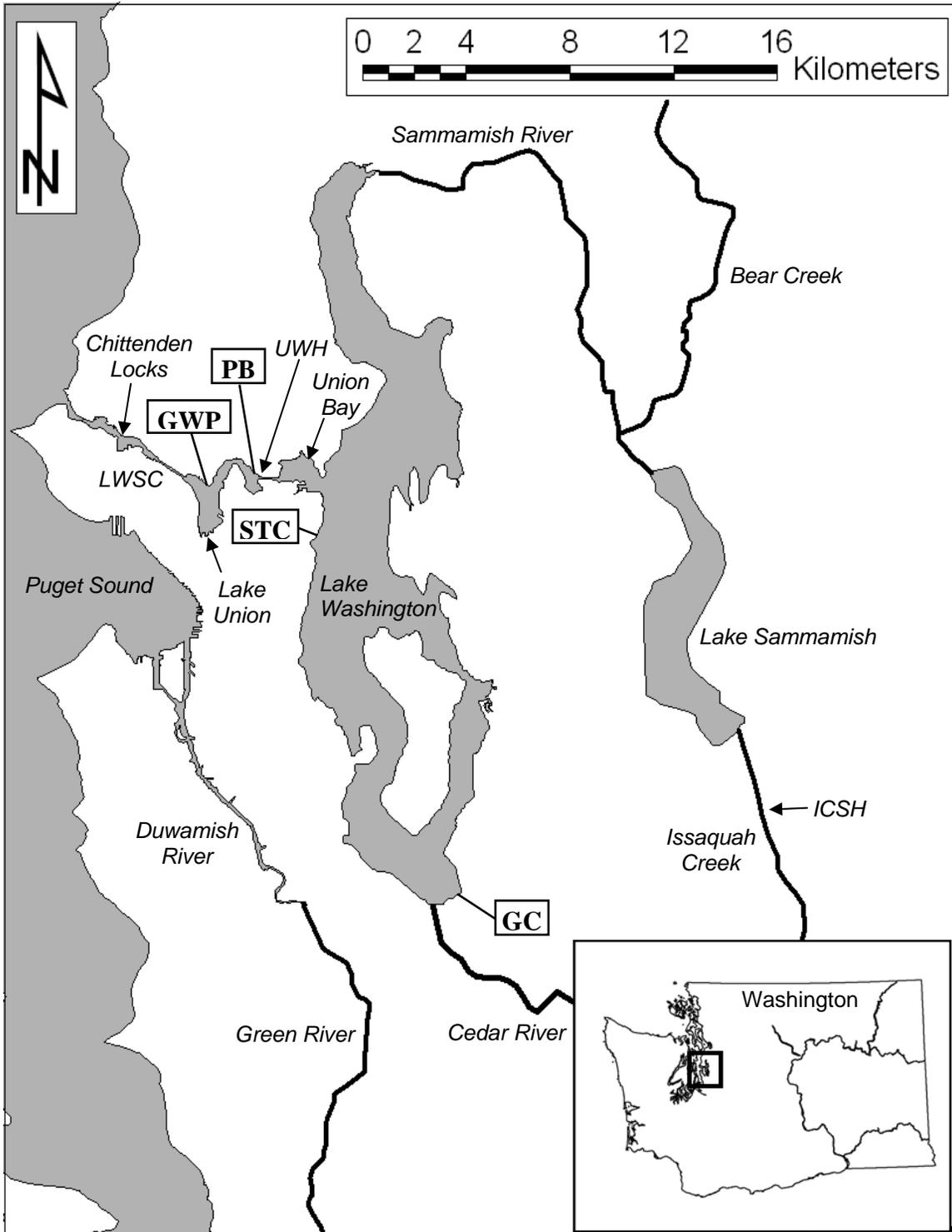


FIGURE 1. Map of lower Lake Washington basin and study site locations. Study sites: GC = Gene Coulon Park; STC = Seattle Tennis Club; PB = Portage Bay; GWP = Gas Works Park. Hatcheries in the basin: ICSH = Issaquah Creek State Hatchery; UWH = University of Washington Hatchery. The Lake Washington Ship Canal (LWSC) extends from Union Bay to Puget Sound.

via the Hiram M. Chittenden (or Ballard) Locks at the outlet to Puget Sound on the west end the LWSC. During winter (December to February) lake level is kept low at an elevation of 6.1 m. Starting in late February the lake level is slowly raised from 6.1 m in January to 6.6 m by May 1, and 6.7 m by June 1. The lake shoreline is comprised primarily of residential properties (Parametrix and Natural Resource Consultants 2000), and over 78% of upland cover consists of lawn and garden (Toft 2001). Over 70% of the shoreline is retained with bulkhead or riprap, and there are about 22 docks per kilometer of shoreline (Toft 2001). Natural shoreline structures, such as woody debris and emergent vegetation, are rare (Toft 2001).

The LWSC is a 13.8-km-long artificial waterway that allows navigation between Lake Washington and Puget Sound. The LWSC consists of five sections: Montlake Cut, Portage Bay, Lake Union, Fremont Cut, and Salmon Bay. The largest part of the LWSC is Lake Union which is 235 hectares in size and has a mean depth of 9.8 m. The shorelines of Portage Bay, Lake Union, and Salmon Bay are highly developed with numerous marinas, commercial shipyards, house boat communities, and drydocks (Parametrix and Natural Resource Consultants 2000). The shoreline is heavily armored with riprap and concrete bulkhead. The Fremont Cut and Montlake Cut are narrow channels with steep banks. The Chittenden Locks, located at the downstream end of the LWSC, control the water level of the LWSC and Lake Washington.

The major tributary to Lake Washington is the Cedar River, which enters the lake at its southern end (Figure 1). The river originates at an approximate 1,220-m elevation, and over its 80-km course falls 1,180 m. The lower 55 km are accessible to anadromous salmonids. Prior to 2003, only the lower 35 km were accessible to anadromous salmonids. Landsburg Dam, a water diversion structure, prevented Chinook salmon from migrating further upstream. A fish ladder was completed in 2003, which allows access past Landsburg Dam to an additional 20 km of the Cedar River. The escapement goal for adult Cedar River Chinook salmon is 1,250; however, this goal has not been met in recent years except in 2007.

Beginning in 1912, drainage patterns of the Cedar River and Lake Washington were extensively altered (Weitkamp and Ruggerone 2000). Historically, Lake Washington and its tributaries were part of the Duwamish River watershed, and the Cedar River did not flow into Lake Washington but rather flowed into the Black River and eventually into Puget Sound via the Duwamish River. One of the most significant changes made in 1912 was diversion of the Cedar River into Lake Washington, and rerouting of the lake outlet through the LWSC (Figure 1). These activities changed fish migration routes and environmental conditions encountered by migrants. Prior to 1912, Cedar River Chinook salmon were able to migrate between the lotic and marine habitats without having to move through Lake Washington, although the existence of a Chinook salmon population in the Lake Washington drainage prior to 1912 is not well documented. Once alterations were complete, 29 km of lacustrine habitat lay between the new mouth of the Cedar River in Lake Washington and the marine environment of Puget Sound.

In addition to Chinook salmon, other anadromous salmonids in the Lake Washington basin include sockeye salmon *O. nerka*, coho salmon *O. kisutch*, and steelhead *O. mykiss*. Sockeye salmon are by far the most abundant anadromous salmonid in the basin. Adult returns in excess of 350,000 fish have occurred in some years. In comparison to other similar-sized basins in the Pacific Northwest, the Lake Washington basin is inhabited by a relatively large number of fish species. Besides anadromous salmonids, there are 22 extant native species of fishes in the Lake Washington basin. An additional 27-28 species have been introduced, 20 of which are extant.

METHODS

Acoustic tracking system

Tracking was performed using an acoustic system developed by HTI of Seattle, Washington. This system uses acoustic tag transmitters implanted within the study fish, and a fixed array of underwater listening devices - termed hydrophones - to track fish movements in a specific area. Tags are programmed to periodically emit a signal, or ping. The length of time between each ping is called the ping rate. When a tagged fish moves through or near a hydrophone array, each ping is detected by the hydrophones at slightly different times depending on how far the fish is from each hydrophone. The system then uses these time differences to triangulate a 3-dimensional position or location for the origin of each ping. Calculated positions are relatively accurate, estimated to be ± 0.5 m in the horizontal plane when the fish is within the perimeter of the hydrophone array. Accuracy declines outside the array perimeter, but has been estimated to be approximately ± 3 m in the horizontal plane at a distance of 1 array width from the array perimeter. In general, we accepted calculated fish positions from both within and outside the array perimeters for these studies. We excluded positions that were apparently beyond the area that the equipment could effectively track within. Accurate results in the vertical dimension require that hydrophone positioning meet specific geometric parameters, which were not obtainable due to various constraints at each study site.

All hydrophones in a given array are cabled into a shared receiver which processes tag pings and other acoustic signals detected by the hydrophones. HTI Model 290 and 291 Acoustic Tag System receivers were used for these studies. Each receiver is connected to a standard personal computer that logs the acoustic data. An individual raw data file is created for each hour that the equipment is operating. Each raw data file contains all acoustic signals detected during that hour, including signals from tagged fish as well as noise from such sources as passing motor boats and falling rain. Each raw data file must be processed through HTI MarkTags software to identify fish signals and isolate them from any noise that might be present. This can be accomplished in two ways: manually, or through an "autotrack" feature built in to MarkTags. The manual method is more precise and certain, and was the method used for these studies. This method requires the researcher to open each raw data file, look for each fish that could possibly be present, and highlight any observed tag signals. Isolated tag signals are then processed through HTI AcousticTag software. AcousticTag performs the triangulation calculations

and provides a database of point locations for each fish. For the remainder of this report, we refer to these calculated point locations simply as “data points.” The “track” for an individual fish is the temporally sequenced collection of all its data points.

Hydrophone array configuration and operation

We used a fine-scale acoustic tracking system to track movements and habitat use of juvenile Chinook salmon, smallmouth bass, and prickly sculpin during May and June at four study sites in Lake Washington and the LWSC: Gene Coulon Park, the Seattle Tennis Club, Portage Bay, and Gas Works Park (Figure 1). This acoustic tracking system uses a fixed array of hydrophones to precisely track tagged fish movements at a given site. We conducted a pilot study in 2003 to assess the utility and feasibility of using this system to answer research and management questions important to juvenile Chinook salmon in Lake Washington and the LWSC. A small array of 4 hydrophones was operated for a short period of time (18 hours) to track two juvenile Chinook salmon at the Gene Coulon Park site. Results were encouraging, so the acoustic tracking program was expanded in 2004, and again in 2005. In 2004, tracking arrays were installed at the Gene Coulon Park and Portage Bay sites, and in 2005 arrays were installed at the Seattle Tennis Club, Portage Bay, and Gas Works Park sites.

The Gene Coulon Park study site was located on the south end of Lake Washington within the Gene Coulon municipal park and swim beach complex owned by the City of Renton. The swim beach area was enclosed by an overwater walkway with an apron that extended approximately 1.5 m below the water surface (Figure 2). Our study focused mainly on the area enclosed by this walkway. This area had a sandy substrate, lacked large debris, and had a gently sloping gradient to a distance 30 m from shore and 2 m depth. Beyond this point the gradient steepened, reaching depths of 7 m at a distance 65 m from shore. There were no aquatic macrophytes observed at this site. Total shoreline length of the study area was 135 m. The shoreline on either side of the study area consisted of rip rap. The 2003 pilot study was conducted from May 22-23 using 4 hydrophones. In 2004, we operated a similar 4-hydrophone array from May 25 to June 1, added a fifth hydrophone on June 1, and continued operation until June 4. In both years, the tracking area measured approximately 140 m long by 80 m wide, totaling 0.011 km². No tracking was performed here in 2005.

The Seattle Tennis Club site was located on the western shore of Lake Washington, approximately 2 km south of Union Bay. The majority of the shoreline here was riprap, which extended unbroken through the central portion of the site (Figure 3). Different shoreline types were found beyond the northern and southern extents of the riprap. A small swim beach and concrete bulkhead were located in the southern portion of the site, and a small gravel-beach boat launch and concrete bulkhead were located in the northern portion of the site. Much of the site had a gentle gradient from 0 to 2 m depth, and a steeper gradient from 2 to 4 m depth. The gradient was moderate at depths > 4 m. Substrate throughout most of the site was sand and silt, with an occasional large boulder. Large debris was absent. A dense swath of Eurasian milfoil *Myriophyllum spicatum* developed during June which extended for the length of the site at depths of 2-7 m.

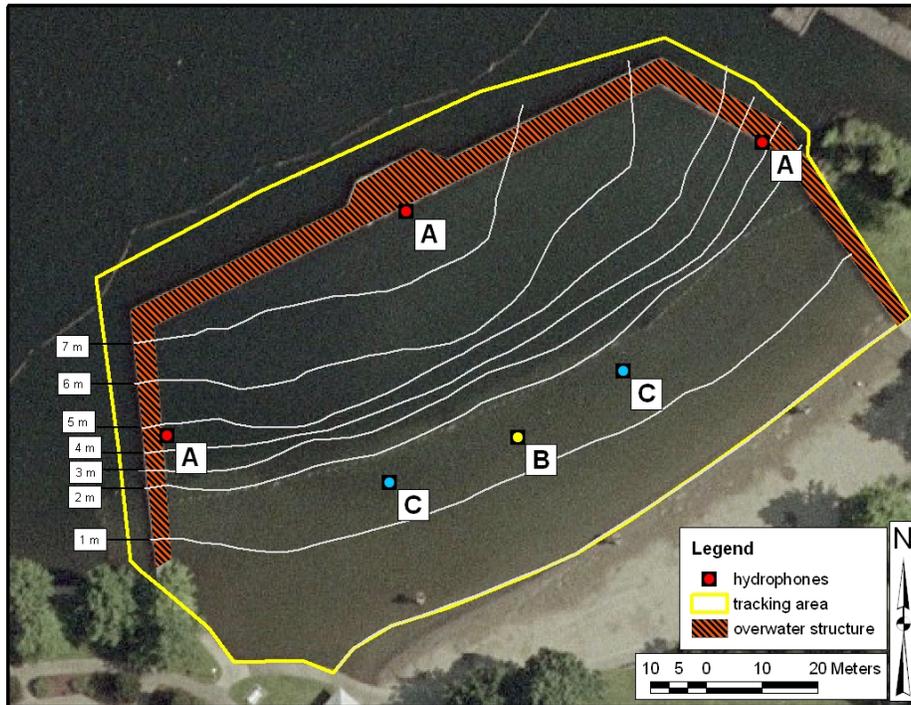


FIGURE 2. Map of the Gene Coulon Park site showing hydrophone locations, tracking area, overwater structures, and macrophytes. Hydrophones A and B were operated from May 22 to May 23, 2003, and from May 25 to June 1, 2004. Hydrophones A and C were operated from June 1 to June 4, 2004.

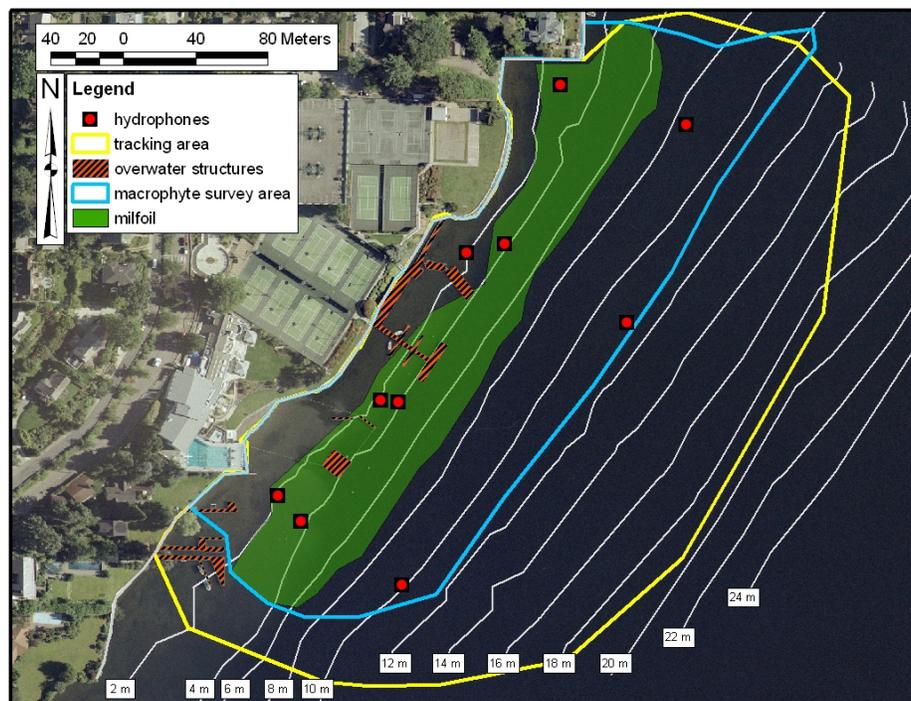


FIGURE 3. Map of the Seattle Tennis Club site showing hydrophone locations, tracking area, overwater structures, and macrophytes. The hydrophone array was operated from May 26 to July 11, 2005.

There were also several overwater structures (boat docks, boat house, diving platform) present within the site. In 2005, we operated a 10-hydrophone array at this site from May 26 to July 11. The tracking area measured approximately 500 m long by 230 m wide, totaling 0.116 km². No tracking was performed here in 2003 or 2004.

The Portage Bay study site included the western end of the Montlake Cut, and the northern portion of Portage Bay adjacent to the University of Washington campus (Figure 4). This site had a diversity of shoreline types and gradients. The eastern end of the site included the western end of the Montlake Cut, which had concrete bulkhead shorelines and steeply sloping gradients to depths of about 8-10 m on both the north and south sides. West of here, the site opened out into Portage Bay. Maximum depths here were the same as in the Montlake Cut, but gradients were much less severe. The shoreline along the northern portion of the study area included varying lengths of bulkhead, riprap, overwater structures, and a small restoration area. The southern and western ends of the study area were open water, except for the southeastern corner which was a riprap shoreline. Substrate throughout this site was predominantly sand and silt. There was a small area of more boulder-like substrate in the northwest corner of the site near the restoration area. Large debris was generally absent throughout the site. Dense stands of milfoil formed during June in the north part of the site from about 1-6 m depth (Figure 4). Also, a large, dense patch of Brazilian elodea *Egeria densa* was present during May and June in the

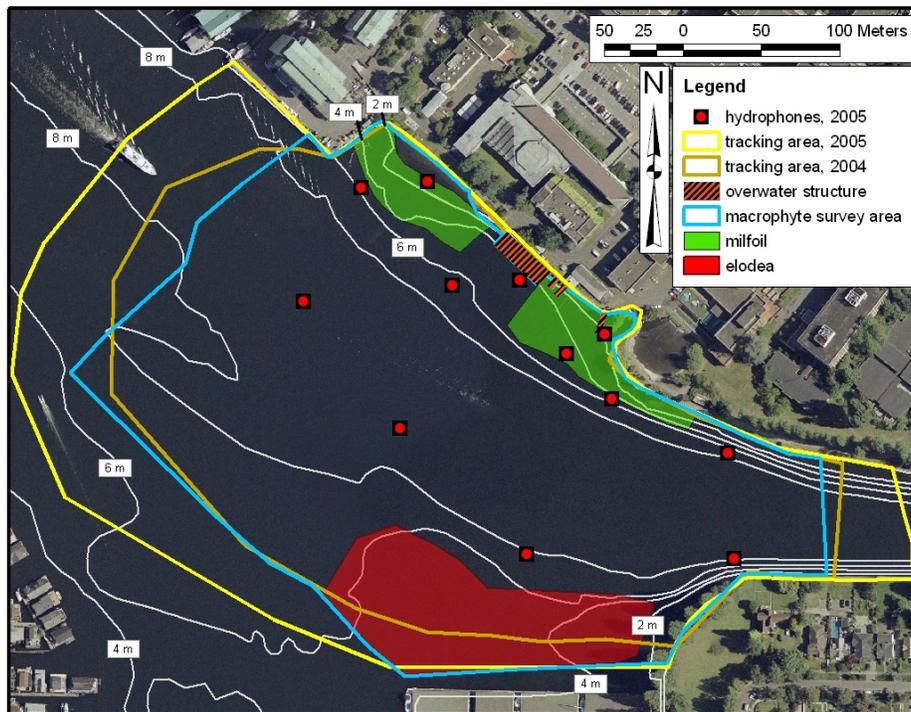


FIGURE 4. Map of the Portage Bay site showing hydrophone locations, tracking areas, overwater structures, and macrophytes. The hydrophone array in 2004 was similar to that shown for 2005, except that some of the deepwater hydrophones were closer to the northeastern shore in 2004 which created a slightly smaller tracking area. The hydrophone array was operated from May 13 to July 4, 2004, and from May 11 to July 11, 2005.

southeastern part of the site from 2-6 m depth. There were several overwater structures in the north-central part of the site. These consisted of a boathouse and 3 standard wood-plank boat docks.

In 2004, we operated a 12-hydrophone array from May 13 to July 4 at this site. The tracking area measured approximately 470 m long and 250 m wide, totaling 0.092 km². In 2005, we operated a similar yet slightly modified 12-hydrophone array from May 11 to July 11. The main difference was that we moved some hydrophones farther from shore in the western part of the site to increase array coverage in this area. The width of the tracking area remained the same, the length increased to 580 m, and the total area increased to 0.126 km². In 2005, we verified the extent and thoroughness of the coverage area by moving activated tags at different depths throughout the area. We used GPS to track our location during this procedure.

The Gas Works Park site was located on the northern end of Lake Union (Figure 5). The shoreline along this site was segregated into three main areas: the eastern part was concrete bulkhead, the central part was riprap, and the western part was largely obscured by numerous piers and docks. Gradient in the western part of the site was extremely steep, reaching depths of around 11 m within 40 m of shore. Gradient in the eastern part of the site was less severe, reaching similar depths within 100 m of shore. The lake bottom was largely flat at depths of about 11 m. Substrate throughout much of the site was sand and silt. Two small patches of milfoil were present along the north edge of the site in water 2-6 m deep (Figure 5). Large debris appeared present but sparse. In 2005, we operated a 10-hydrophone array at Gas Works Park from May 13 to July 11. The tracking area measured approximately 650 m long and 340 m wide, totaling 0.215 km². In 2005, we verified the extent and thoroughness of the coverage area in a similar manner as that described for the Portage Bay site. No tracking was performed here in 2003 or 2004.

Hydrophones at all sites were mounted on anchors consisting of 30-kg blocks of concrete. Posts of 2.54-cm diameter conduit protruded approximately 0.5-1.5 m above the top surface of the concrete. Hydrophones were mounted at or near the top of these posts using metal hose clamps. Metal rods of 0.64-cm or 0.95-cm diameter rebar extended approximately 0.5 m in four directions from the base of each anchor to stabilize them on the substrate. Eyebolts were embedded at the top of each anchor so that they could be deployed and retrieved with ropes from a boat. Deployed anchors were inspected to ensure that they were in an appropriate upright position. Shallow water locations were inspected visually from a boat, and deep water locations were inspected using an Aqua-Vu underwater camera. The water depth at each hydrophone location was measured, and a Global Positioning System (GPS) unit was used to record the location of each hydrophone. In 2005, StowAway TidbiT temperature loggers were mounted on each anchor near the hydrophone. Temperature loggers were programmed to record water temperature at 30-minute intervals.

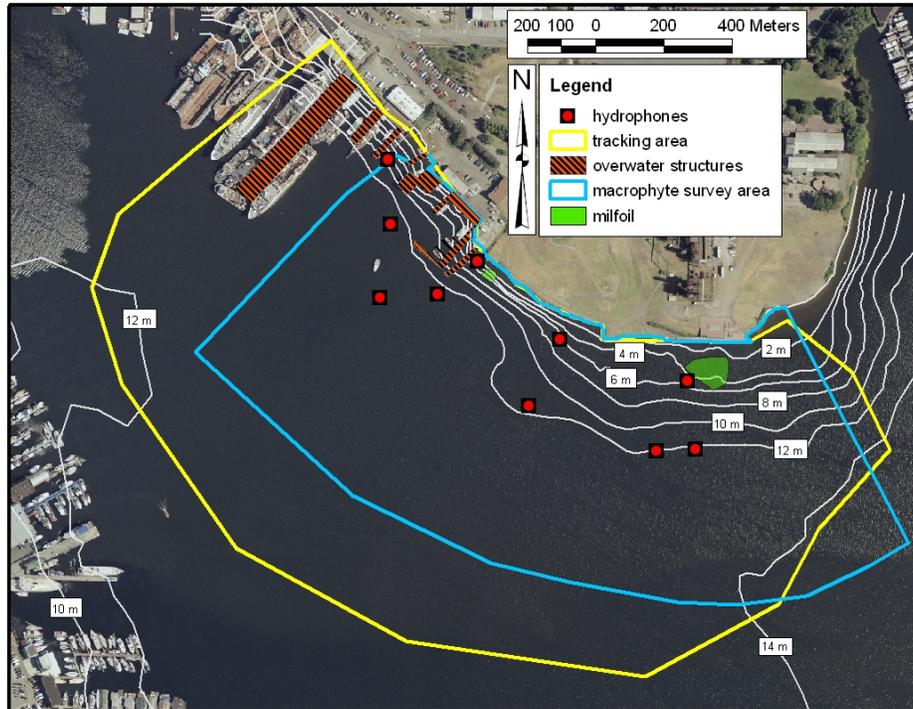


FIGURE 5. Map of the Gas Works Park site showing hydrophone locations, tracking areas, overwater structures, and macrophytes. The hydrophone array was operated from May 13 to July 4, 2004, and from May 13 to July 11, 2005.

Fish capture, tagging, and release

Chinook salmon

Our preference was to tag naturally reared fish taken from within or near study sites while not violating either fish size (12.5 g) or water temperature (17°C) thresholds. Tagging can affect fish behavior, especially when the tag is large relative to the size of the fish. Studies on the effects of tagging suggest that fish behavior is minimally affected when the ratio of tag weight to fish body weight is < 6% (Adams et al. 1998a; Brown et al. 1999; Anglea et al. 2004). This ratio corresponds with a 12.5 g fish weight for the 0.75-g tags used in these studies. Water temperature at time of tagging may also affect fish behavior. Our experience suggests that salmonids are less capable of enduring the stresses of handling and tagging when they are taken from water > 17°C. The added stress of tagging at higher water temperatures may cause fish to behave abnormally after release and increase post-tagging mortality.

Limitations of fish size and water temperature can critically impact acoustic tracking studies: study cannot begin until fish are big enough to tag, and the study cannot continue after water temperatures exceed a reasonable threshold. The timing of critical events in Lake Washington make preferred fish size and water temperature parameters difficult to

reliably and consistently achieve. Naturally reared juvenile Chinook salmon in Lake Washington do not attain 12.5 g - equivalent to a fork length (FL) of 105.6 mm - until late May or early June. This is about the same time that surface water temperatures in Lake Washington reach 17°C, thereby becoming unacceptably high at approximately the same time that fish become large enough to tag. The concurrence in the timing of these two critical events creates uncertainty into how much time and how many fish will be available to tag in a given year. To compensate for this, we implemented several measures to ensure a reasonably sufficient sample size of tagged fish and adequate time for study. First, we utilized hatchery-origin juvenile Chinook salmon from the University of Washington hatchery. These fish attain larger sizes earlier than naturally reared fish, thereby allowing tagging to start in early- to mid-May. In addition, we obtained naturally-reared fish directly from the Cedar River. The Cedar River is generally several degrees cooler than the lake, which allowed us to continue tagging fish after lake temperatures exceeded 17°C. Finally, we tagged some fish that were slightly smaller than the 12.5 g threshold when larger fish were unavailable. The implications of each of these measures on study results are evaluated in the discussion.

A total of 142 juvenile Chinook salmon were tagged and released during May and June of 2003, 2004, and 2005 (Table 1). Both hatchery and naturally-reared fish were used. We attempted to collect naturally-reared fish near or within study sites using a beach seine. Few fish were captured using this method. Most naturally-reared fish used in these studies were obtained from the Cedar River via the Washington Department of Fish and Wildlife (WDFW) smolt trap located 10.3 km upriver from Lake Washington. Hatchery fish tagged early in 2004 and 2005 were obtained directly from the University of Washington hatchery. In 2005, hatchery fish were also tagged later in the tracking period to supplement low numbers of naturally-reared fish. These fish were obtained incidentally as we collected naturally reared fish from the WDFW Cedar River smolt trap and during beach seining. These fish were believed to originate from Washington State's Issaquah hatchery, although this could not be confirmed.

All juvenile salmonids were implanted with HTI Model 795m MicroAcoustic Tags. These tags weighed 0.75 g in air, and measured 6.8 mm in diameter and 16.5 mm in length. Each tag was programmed to emit a signal unique from other tags, which allowed us to track movements of specific fish. Juvenile salmonid tags were programmed with ping rates of 1-2 s, providing nearly continuous tracks of fish movements. Tag life varies with water temperature, pulse width and ping rate. For these studies, the 795m tags were expected to last 10-14 d.

We considered two methods for implanting tags in the study fish: a surgical procedure and a gastric procedure. The surgical procedure was used to implant tags in the peritoneal cavity through an incision. The gastric procedure was used to implant tags in the stomach by pushing it through the esophagus with a thin rigid rod. We preferred the surgical procedure to minimize influence of normal feeding behaviors. Most fish were implanted surgically. We used the gastric procedure to minimize handling and implant time when fish were taken from water at or near 17°C or when tagging had to be completed quickly.

TABLE 1. Releases of tagged Chinook salmon smolts and number tracked at each site, May-June, 2003-2005. GC = Gene Coulon Park; STC = Seattle Tennis Club; PB = Portage Bay; GWP = Gas Works Park.

Release group	Release month/day	Release location ^a	Type ^b	Origin/Capture location ^c	Implant type ^d	Mean FL (mm)	No. Released	No. tracked			
								GC	STC	PB	GWP
2003											
1	5/22	GC	n	unk	s	95	2	2	-	-	-
2004											
2	5/26-6/3	GC	n	CRst, GCbs	s,g	103.8	10	9	-	0	-
3	5/13	UWH	h-UW	UWH	g	108.2	9	-	-	9	-
4	5/13	MC	h-UW	UWH	g	111.5	15	-	-	12	-
5	6/10	MC	n	CRst	s,g	105.5	26	-	-	16	-
6	6/16	CR	n	CRst	s	109.5	4	-	-	1	-
2005											
7	5/13	UWH	h-UW	UWH	s	111.8	10	-	-	9	2
8	5/13	MC	h-UW	UWH	s	115.4	10	-	-	10	2
9	6/10-6/17	MC	n	CRst, GCbs	s	105.4	14	-	0	10	8
10	6/7-6/24	STC	n	CRst, GCbs	s	107.7	14	-	8	6	6
11	6/7-6/24	STC	h-unk	CRst	s	118.2	17	-	9	5	5
12	6/17-6/24	MC	h-unk	CRst	g,s	120.5	11	-	1	8	3

^a GC = Gene Coulon Park; UWH = University of Washington hatchery mouth; MC = Montlake Cut; CR = Cedar River mouth; STC = Seattle Tennis Club

^b n = naturally reared (wild); h-UW = hatchery reared at University of Washington hatchery; h-unk = hatchery reared, unknown origin (ad clipped, most likely from WDFW Issaquah hatchery)

^c CRst = WDFW Cedar River smolt trap; GCbs = beach seined at Gene Coulon Park; UWH = University of Washington hatchery; unk = CRst or GCbs

^d s = surgical; g = gastric

For surgical implants, all surgical instruments and tags were sterilized in a solution of distilled water and 2-5% Nolvasan® disinfectant. Instruments and tags were allowed to soak for ≥ 5 min, then rinsed in a 5-10% saline bath. Each fish was anesthetized in a solution of tricaine methane sulphonate (MS-222) buffered with sodium bicarbonate. Most fish were adequately anesthetized within 3 min. The anesthetized fish was removed from the MS-222 solution and washed with cool fresh water. It was then placed on a customized surgical platform consisting of a piece of foam with a depression scored in the center. This was soaked in cold water prior to tagging. The foam surgical platform held the fish in a suitable and stable position, and helped keep it cool during the surgery. Fish were placed in the platform's depression with the ventral side exposed. During the surgery, a pipette was used to irrigate the gills with MS-222 solution at 30 s intervals. An incision approximately 8-12 mm long was made between the pectoral and pelvic fins. The tag was then inserted into the peritoneal cavity through the incision. Two or three sutures of 6-0 coated Vicryl® braided suture material were used to close the incision. Fish were then placed in a recovery tank of cool fresh water. The entire operation was usually completed in 5-8 min.

After implant, most salmonids were allowed to recover for approximately 18-48 hours prior to release. These fish were slowly acclimated to lake temperature after tags were implanted. Most 2004 and all 2005 fish obtained from the Cedar River were acclimated in temperature-controlled tanks at the King County Environmental Laboratory over a period of approximately 36-48 h. Cedar River fish released at the Gene Coulon Park site in 2004 were acclimated on-site. Implanted fish were placed in an insulated recovery container with river-temperature water. Lake water was then slowly added over a period of 0.5 h until the water in the container was the same temperature as the lake. Fish behaving abnormally after the recovery period were removed from the sample. A small number of fish were released after a shorter recovery period when circumstances required.

Tagged Chinook salmon were released in four primary areas: Gene Coulon Park (GC), Seattle Tennis Club (STC), Montlake Cut (MC), and University of Washington hatchery mouth (UWH). The GC release area was located in the center of the Gene Coulon Park study site 20 m from shore in 1.5 m of water. The STC release area was located approximately 500 m south of the Seattle Tennis Club study site. Most fish released here were placed in shallow water immediately adjacent to the shore. One group was released in deeper water approximately 10 m from shore. The MC release area was located 300-550 m east of the Portage Bay study site, in the Montlake Cut between the Montlake bridge and Union Bay. In 2004, study fish were released on the western edge of this area. Fish released on June 10 were released in the middle of the channel, and fish released on May 13 were released closer to the north shore. Most 2005 study fish were released near the eastern edge of the release area in the center of the channel. Some 2005 fish were released on the western edge of the release area adjacent to the north shore. The UWH release area was located at the mouth of the UW hatchery. In 2004, four tagged fish were released in the Cedar River at the WDFW smolt trap to test the feasibility of releasing fish here and tracking them in the LWSC.

Predators

A variety of techniques were used to collect predatory fishes. Most prickly sculpin and some bass were collected by snorkelers who slowly swam along the shoreline at night and captured fish with small hand-held dip nets. Small headlamps were used for illumination. Northern pikeminnow, most bass, and one prickly sculpin were collected by angling. A few additional prickly sculpin were collected with a beach seine. After capture, fish were held in a net pen until we were able to surgically implant an acoustic tag. The same Model 795m MicroAcoustic tags used for Chinook salmon were also used with prickly sculpin and small-sized bass (< 200 mm FL). Larger bass and northern pikeminnow were implanted with HTI Model 795E Acoustic Tags, which weighed 1.5 g in air and measured 6.8 mm in diameter and 21.0 mm in length. Tags were programmed with ping rates of 1-5 s and were given unique codes to identify individual fish. The 795m tags were expected to last 10-14 d, and the 795E tags were expected to last 20-28 d. All predator tags were surgically implanted following similar procedures described for Chinook salmon. Large predators were placed on a standard fish measuring board for the surgery. Smaller predators (i.e., sculpin) were placed on a foam platform. After tagging, most predators were released immediately after they recovered from the anesthetic. Some predators were allowed to recover for up to 18 hours. Most fish were released in the same location where they were captured. Some fish that were captured in different locations were mixed together in a net pen for post-tagging recovery. These fish were released together in a central location a short distance from the capture location.

Data points for the first 24 h after release of smallmouth bass, largemouth bass, and northern pikeminnow were not used to allow time for the fish to fully recover from capture, handling, and surgery, and to behave naturally. Prickly sculpin appear to be little affected by handling and appear to feed and behave naturally shortly after release; therefore, we used all prickly sculpin data points.

Data analysis

Chinook salmon

Each raw data file was evaluated for the presence of all fish released within 14 days prior to the time period included in the file. Fish from all release locations were considered. For example, Seattle Tennis Club data files were evaluated for the presence of all fish released at the STC, MC and UWH release areas. The sole exception was in 2004 when Gene Coulon Park data files were not evaluated for the presence of fish released in the LWSC (i.e., MC and UWH release areas).

Point data output from the AcousticTag software was imported into Geographic Information System (GIS) software ArcView 3.2. Fish tracks were overlaid on orthophotos and bathymetry contours of each site. Existing orthophotos and bathymetry for the Seattle Tennis Club, Portage Bay and Gas Works Park sites were obtained from Seattle Public Utilities (SPU). Bathymetry for each site was checked against depth measurements that we collected while surveying for aquatic macrophytes in 2005. SPU

bathymetry was largely accurate, however some minor adjustments were necessary. An existing orthophoto of the Gene Coulon Park site was obtained from a federal government database. Bathymetry of the Gene Coulon Park site was generated in ArcView based on depth measurements taken in 2004. Depth was measured every 5 m along three transects established perpendicular to shore, and along the inside perimeter of the boardwalk.

Each fish track had to meet three parameters to be considered for analysis: 1) it had to contain ≥ 40 points; 2) it had to span ≥ 5 minutes; and 3) it had to exhibit no evidence of mortality. Evidence of mortality included one or more of the following: 1) no sign of fish movement in the fish track; 2) no sign of fish movement in the raw hydrophone data; and, 3) extraordinarily unusual characteristics in the fish track. Mortality may occur after some period of apparently normal behavior. In these cases, the fish was removed from the data set, and no part of the fish track was used for analysis. For analyses involving diel periods, the part of the track contained within the given diel period was required to have ≥ 40 points and had to span ≥ 5 minutes.

Tracked fish at each site were combined into analytical units in order to account for factors that may influence behavior and habitat use. Factors considered in analytical unit grouping included fish origin (hatchery versus wild), release time (early season versus late season), implant type, release location, and fish size. Groupings were performed *a posteriori* due to the unpredictability of several variables, including availability of fish from different sources at different times, fish sizes, and ratio of fish tracked to fish released from different release sites. After all tagged fish were released and numbers of tagged fish detected at each study site became available, we segregated fish into analytical units based on two factors: 1) origin (hatchery or wild); and, 2) release location relative to study site (i.e., released on-site within the hydrophone array or released off-site outside the array perimeter). This yielded four possible analytical units at each study site: wild released on-site; wild released off-site; hatchery released on-site; and, hatchery released off-site. These two factors were chosen over others (e.g., size, release time) based on their perceived influence on fish movement and habitat use, and on interpretation of results. Volitional site entrance (i.e., off-site releases) was important for ensuring that our findings would best represent movement of untagged, naturally migrating smolts through the specific sites studied. Thus, on-site releases were excluded from many analyses. On-site releases were used only for evaluating macro-scale movement patterns and behavior around overwater structures, and were combined with off-site releases for these purposes. The analysis of behavior around structures was intended to have broad general applicability and was not intended to be site-specific. On-site releases were thus appropriate for these purposes.

We calculated site area residence time, water column depth selection (i.e., total water column depth, not position in the water column), and mean diel swim velocity for each tracked fish at each site. Site area residence time was calculated as the difference between the very first and very last time that the fish was tracked at the site regardless of any gaps in between (i.e., fish was tracked, then left the area for some amount of time, then returned and was tracked again). Fish showing such discontinuous tracks were

assumed to be in close proximity to the study site. For swim velocity, horizontal distances between sequential positions were summed and divided by the time difference between the first and last positions. This provided an average swim speed for each fish while it was in the tracking area. Time gaps ≥ 5 min between sequential points were excluded. This left independent track segments before and after any temporal gap. Track segments < 5 min were excluded. Track segments were weighted by time and combined to provide one average swim velocity per fish.

For depth selection calculations, each study site was segregated into water column depths at 2 m intervals (i.e., 0-2 m, 2-4 m, etc.). The 2-m depth intervals were selected for pragmatic reasons and were not based on any observed characteristics of the fish tracking data. The total horizontal area of each depth category contained within the tracking area was considered that category's availability. For each fish we calculated a basic, standard selection ratio for each depth category as (proportional habitat use)/(proportional habitat availability) (Manly et al. 2002). These values were then scaled from 0.0 to 1.0 by dividing each depth category's selection ratio by the maximum selection ratio of all depth categories (e.g., Mäki-Petäys et al. 2002; Al-Chokhachy and Budy 2007). Low values represent minimal selection, higher values represent greater selection, and 1.0 represents the most selected habitat. Population-level selection for each depth category was represented by the median selection ratio of all fish in a given analytical unit. Variability was represented by first and third quartiles. Each fish was weighted equally in the analytical unit summary calculations. For each fish, the proportion of points lying within each depth category was used as a surrogate for the amount of time spent in that water column depth. This assumes that the probability of obtaining a data point is equal throughout the array coverage area, and that array coverage is not biased for or against any depth categories. The point data for each fish were separated into appropriate depth categories using the XTools clipping function in ArcView. Each fish track had to contain ≥ 40 points and had to span ≥ 5 minutes to be included in the analysis. These parameters were set to exclude only incidental site use; for example, if a fish appeared only ephemerally on the outer margin of the site. These parameters were not so restrictive to exclude fish that migrated rapidly and directly through the site.

The methods used to evaluate depth selection avoid the problem of pseudoreplication by taking each animal as the experimental unit (Aebischer et al. 1993; Garton et al. 2001; Manly et al. 2002; Rogers and White 2007). Also, by evaluating each animal's proportional depth use, serial correlation between an individual's data points does not present a problem (Aebischer et al. 1993; Rogers and White 2007). In fact, the high frequency of location sampling achieved with the HTI system provides a concomitantly high level of detail with regard to habitat use. Such detail, according to Aebischer et al. (1993), provides more precise estimates of habitat use, and the associated high degree of serial correlation is rendered a non-issue as long as proportional habitat use of individuals is the basis for analysis.

The arrangement of sites and of hydrophones at each site facilitated analysis at three levels: micro-, meso-, and macro-scales. Micro-scale behaviors were defined as those

occurring on the order of a few meters. Meso-scale behaviors were defined as those occurring on the site-level, such as average swim velocity through a site and overarching behavior at the site. Macro-scale behaviors were defined as those observed between sites, such as characteristics of movement through the entire system of arrays (i.e., from site to site to site).

General meso-scale behaviors of tracked fish were identified based on characteristics of plotted fish tracks, on-site swim velocities, and site area residence times. Data from fish that volitionally entered the Seattle Tennis Club, Portage Bay (2004 and 2005), and Gas Works Park sites were collectively evaluated to identify common meso-scale behaviors. Each fish at each site served as an independent sample of fish behavior. In 2005, some fish were observed at two or more sites. In these cases, behavior at each site was treated as an independent sample. A total of 73 fish were tracked during 2004 and 2005: 43 fish were tracked at only one site, 21 fish were tracked at two sites, and 9 fish were tracked at three sites. This yielded 112 independent observations of fish behavior.

Data were represented by descriptive statistics most appropriate for the type of distribution observed. Minimally-skewed data were represented with means and standard deviations, and medians and percentile ranges were used for more strongly skewed data. Statistical comparisons were performed using standard procedures (Zar 1999; Sheskin 2000), and usually consisted of pooled-variance t-tests or single-factor between-subjects analysis of variance (ANOVA). Data sets were evaluated for normality using the procedures described by Zar (1999). Non-normal data sets ($\alpha = 0.05$) were log-transformed (Zar 1999) prior to statistical testing. Statistical significance was established at $\alpha = 0.05$. When results of ANOVA were significant, multiple and/or complex comparisons were performed using the Scheffé method (Sheskin 2000).

Spatial distribution and localized habitat use were evaluated using Tecplot 10 data visualization software and ArcView GIS. The relative intensity with which fish used different parts of each site was evaluated with Tecplot. All fish within each analytical unit were weighted equally regardless of residence time. Each site was partitioned into a grid of 5 m by 5 m cells. Smaller 1 m by 1 m cells were used for the Gene Coulon Park site. The relative amount of time spent by all fish within each cell was determined. These values were imported into Tecplot, as were site orthophotos and bathymetry contours. Tecplot images were expected to show areas of moderate to high relative use under the following scenarios:

- 1) intensive habitat use – two or more fish residing in a common localized area for extended periods of time;
- 2) common migrational pathway – two or more fish travelling along similar pathways;
- 3) pathway crossover – movement pathways of two or more fish crossing, or the pathway from one fish crosses over on itself;
- 4) individual resting – one fish residing in a localized area for a large proportion of its time in the tracking area; and,

- 5) few data points – the track from a fish is comprised of a relatively small number of points ($n < 40$).

Areas of moderate to high relative use that appeared on the Tecplot images were further evaluated using GIS plotted fish tracks to determine which of the above scenarios were present.

For analyses involving diel periods, day was defined as the period from one hour after sunrise to one hour before sunset. Night was defined as the period from one hour after sunset to one hour before sunrise. Dawn and dusk were defined as the periods between day and night.

Predators

Predator tracking data were separated into dawn, day, dusk, and night time periods to examine diel behavior. For smallmouth bass, we calculated selection of water column depth, shoreline type, and overwater structures. Selections were not calculated for prickly sculpin because selection could be biased by the location where prickly sculpin were captured (i.e., they were only captured in shallow water) because their home range is often quite small. Smallmouth bass are larger and more mobile than prickly sculpin, and thus are able to select habitat features over a larger area. Selections were not estimated for largemouth bass and northern pikeminnow because of small sample sizes. We calculated water column depth selection (2-m depth intervals) for each smallmouth bass using the same methods described for juvenile Chinook salmon.

To estimate shoreline type selection, we divided each shoreline into one of five shoreline types: beach, riprap, bulkhead, riprap with overwater structures (i.e., piers), and bulkhead with overwater structures. We only included detection points that were in water less than 4 m deep. Bass in deeper water were considered as being offshore and not in close contact with the shoreline. For each fish, the proportion of points lying within each shoreline type category was used as a surrogate for the amount of time spent in that shoreline type. The point data for each fish were separated into appropriate shoreline type categories using the XTools clipping function in ArcView. Availability of each shoreline type was based on shoreline length. Shoreline type selection for each smallmouth bass was calculated using the same methods (Manly et al. 2002) as water depth. Selection for overwater structures was determined by comparing the number of data points within 2 m of a structure (Fresh et al. 2001) to the number not associated with overwater structures. We only included points that were in water less than 6 m deep in order to include all overwater structures. Similar to other selection analyses, we used XTools clipping function in ArcView to categorize each data point. For each fish, a chi-square analysis was used to compare the observed number of data points associated with an overwater structure to the expected number. The expected number was based on the percentage of the total area (< 6 m deep) that was within 2 m of an overwater structure.

To estimate home ranges of predatory fish, we used kernel home ranges, a nonparametric estimation of an animal's utilization distribution (Worton 1989). Kernel

home ranges were calculated using the Animal Movement extension for ArcView 3.2 developed by the U.S. Geological Survey's Biological Resource Discipline, Alaska Science Center. We calculated 50% and 95% home ranges, which estimates the area (m²) where a fish spent 50% and 95% of its time. We used the number of detections as a surrogate for time. Separate home ranges were calculated for day and night (dawn and dusk were not included).

RESULTS

Chinook salmon

General results

Valid fish tracks were obtained at at least one tracking site for 103 of the 142 (73%) tagged juvenile Chinook salmon released (Table 1). Tracked fish at each site were organized into analytical units based on year, origin (wild or hatchery) and release location (on- or off-site; Table 2). For the Gene Coulon Park site, data from 2003 and 2004 were combined due to the small number of fish tracked in 2003 (n = 2). These groupings provided us with 8-23 fish per analytical unit. For most analytical units, substantially more observations occurred during the day than during other diel periods (Figure 6). This limited our ability to evaluate diel behavior.

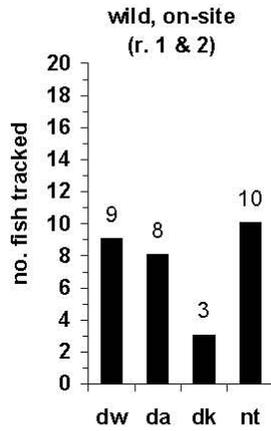
Hatchery fish tended to be larger than wild fish. For fish released off-site, analytical units of hatchery fish had mean fork lengths that were 5.7-11.0 mm longer than those of wild fish. These differences were significant at all sites (pooled variance t-test, Seattle Tennis Club: $P = 0.001$; Portage Bay 2004: $P = 0.005$; Portage Bay 2005: $P < 0.001$; Gas Works Park: $P < 0.001$). Hatchery fish released on-site at Portage Bay were smaller than those released off-site. Differences were small (3.1-5.6 mm) and were significant only in 2005 (pooled variance t-test, 2004: $P = 0.247$; 2005: $P = 0.024$).

The substantial majority of fish entered each site during the daytime. This was observed in 48 of 57 (85%) hatchery fish and 47 of 55 (84%) wild fish. Fish were usually released early in the day and this likely influenced when they were first observed: Most fish (71%) were first observed on the day that they were released, and the rest (29%) were not observed until a day or more after release. Of the 32 fish that were not observed until a day or more after release, 20 fish (63%) entered the study site during day and 6 fish (19%) entered at dawn. Few fish first entered a study site during either dusk (5 of 112 fish; 4%) or night (5 of 112 fish; 4%).

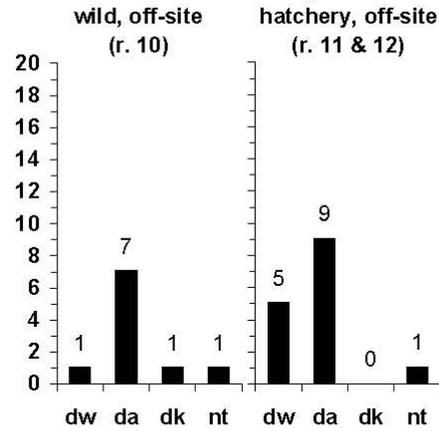
TABLE 2. Analytical units of tagged juvenile Chinook salmon used to evaluate tracking data at each site. Includes release groups (Table 1) assigned to each unit, total number of tracked fish, and mean fork length.

Analytical unit	Origin, release location	Release groups	No. valid tracks	Mean fork length (mm)
Gene Coulon Park, 2003-2004				
A	wild, on-site	1, 2	11	102.7
Seattle Tennis Club, 2005				
B	wild, off-site	10	8	107.0
C	hatchery, off-site	11, 12	10	117.5
Portage Bay, 2004				
D	wild, off-site	5, 6	17	105.6
E	hatchery, off-site	4	12	111.3
F	hatchery, on-site	3	9	108.2
Portage Bay, 2005				
G	wild, off-site	9, 10	16	106.9
H	hatchery, off-site	8, 11, 12	23	117.4
I	hatchery, on-site	7	9	111.8
Gas Works Park, 2005				
J	wild, off-site	9, 10	14	107.5
K	hatchery, off-site	7, 8, 11, 12	12	118.5

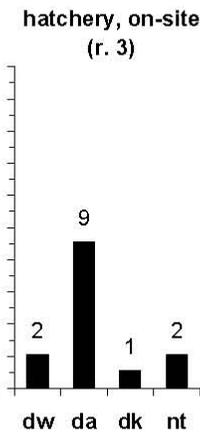
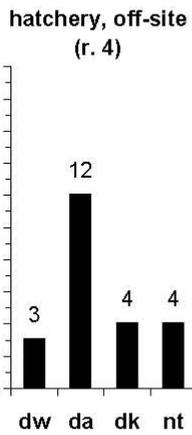
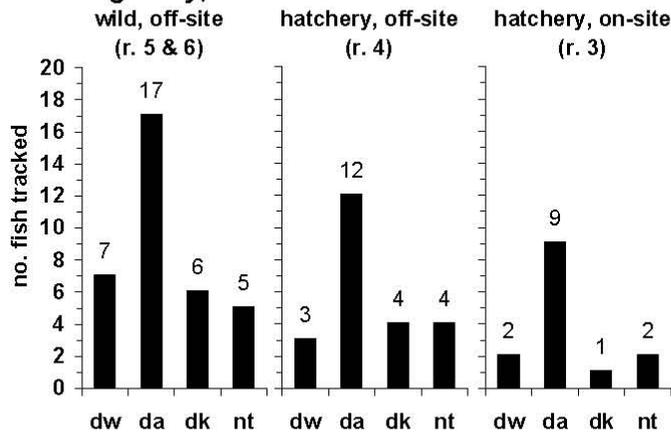
A. Gene Coulon Park, 2003-2004



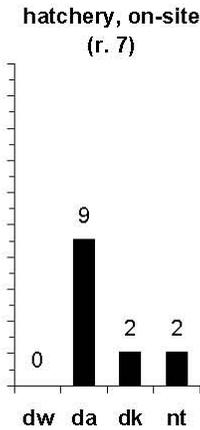
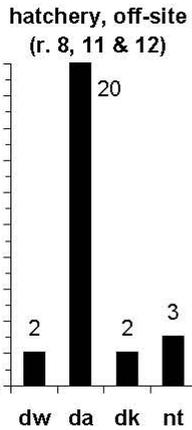
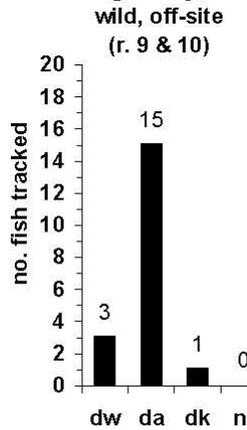
B. Seattle Tennis Club, 2005



C. Portage Bay, 2004



D. Portage Bay, 2005



E. Gasworks Park, 2005

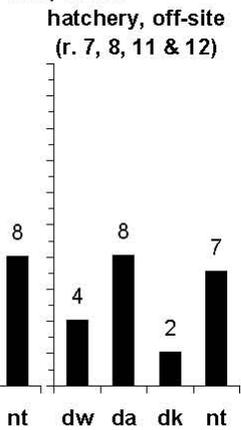
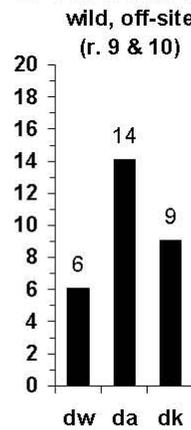


FIGURE 6. Number of valid fish tracks obtained at each site by diel period and analytical unit. Corresponding release numbers are shown (r.). Diel period is represented on the horizontal axis as follows: dw = dawn; da = day; dk = dusk; and, nt = night.

Meso-scale movement patterns

We identified five distinct meso-scale behaviors: active migration, holding, roaming, casual migration, and cycling. The active migration behavior was characterized by high swim velocities (mean, 4.5 BL/s), short area residence times (generally 0.1-0.5 h), and generally direct movement through the site toward Puget Sound (Table 3). These fish entered the site, quickly swam to the opposite end, and exited. Little or no milling about and no major changes in direction were observed as they moved from one end of the site to the other in an obvious general direction of travel (Figure 7). Actively migrating fish were tracked moving through the site only once (i.e., no repeated entrances and exits), suggesting that they were using the site as a migrational corridor to get from one destination to the next on their general migration toward the marine environment. Active migration was one of the most common behaviors observed. This behavior was observed in 40 of 112 (36%) fish: 19 of 55 (35%) wild fish and 21 of 57 (37%) hatchery fish. Active migration was observed at all sites, although only two actively migrating fish were observed at Gas Works Park (Table 4). Of the 40 observations of active migration, 37 (93%) occurred exclusively during daytime. The remaining 3 fish were observed during crepuscular periods: one fish entered and exited at dawn, one fish entered at dawn and exited during day shortly after dawn ended, and one fish entered and exited at dusk. Active migration was not observed at night.

The holding behavior was characterized by slow swim velocities, long area residence times, and no apparent general direction of travel (Table 3). These fish milled about in localized areas of the site and/or crisscrossed through or within the site for extended periods of time (Figure 8). Holding fish often entered and exited the tracking area repeatedly, presumably because the tracking area was part of a larger general area where they were temporarily residing. The slow swim velocities, long residence times and convoluted movement paths lacking clear directionality toward Puget Sound suggested that these fish were temporarily paused in their migration. The holding behavior was observed during all diel periods. Activity level of holding fish, as indicated by swim velocity, was comparable during dawn, day, and dusk, but was reduced at night. Mean swim velocities were 2.1 BL/s, 2.0 BL/s, and 2.1 BL/s during dawn, day, and dusk, respectively. During night, mean swim velocity was much lower at 1.5 BL/s. A single-factor between-subjects analysis of variance confirmed that swim velocity was not equivalent during all diel periods ($P = 0.013$), and that night was different from the other three periods (complex comparison Scheffé test: $P = 0.044$; Sheskin 2000). Daytime swim velocity of holding fish was significantly different from actively migrating fish (pooled variance t-test: $P < 0.001$). Holding was observed at all sites, although only three holding fish were observed at the Seattle Tennis Club site (Table 4). Duration of holding varied between sites and between years. Median site area residence time was 30, 4, and 77 h for the Portage Bay 2004, Portage Bay 2005, and Gas Works Park sites, respectively. A single-factor between-subjects analysis of variance using log-transformed values of residence time (Zar 1999) confirmed that site area residence time was not equivalent at all sites and years ($P < 0.001$). The Seattle Tennis Club site was excluded from this analysis due to the small number of holding fish observed ($n=3$). A

TABLE 3. Characteristics of meso-scale behaviors observed in tagged juvenile Chinook salmon that volitionally entered the Portage Bay site, May-June, 2004, and the Seattle Tennis Club, Portage Bay, and Gas Works Park sites, May-June, 2005. GC = Gene Coulon Park; STC = Seattle Tennis Club; PB04 = Portage Bay 2004; PB05 = Portage Bay 2005; GWP = Gas Works Park.

Behavior	No. obs.	Description	Primary diel period(s)	Mean swim velocity [SD] (BL/s)	Median site area residence time [10 th -90 th percentiles] (h)
Active migration	40	Fish moved through site quickly with direct movement pathway and little or no milling. Obvious general direction of travel toward estuary. Fish entered the site, quickly moved to other end, and were not observed again at that site. Observed almost exclusively during the day. Fish appeared to be actively engaged in migration.	day	4.5 [0.7]	0.3 [0.1-0.5]
Holding	54	Fish milled in localized areas of the site and/or crisscrossed through the site in various directions. Substantially reduced swim velocities and longer area residence times than actively migrating fish. No obvious general direction of travel toward estuary. Observed during all diel periods. Fish appeared to be temporarily paused in migration toward estuary. Duration of holding varied by site and year.	dawn day dusk night	dawn: 2.1 [0.9] day: 2.0 [0.6] dusk: 2.1 [0.6] night: 1.5 [0.7]	STC: 91 [3-155] PB04: 30 [7-74] PB05: 4 [1-24] GWP: 77 [25-153]
Roaming	5	Fish moved quickly with swim velocities comparable to active migration, but exhibited movement pathways similar to holding (i.e., milling in localized areas and/or crisscrossing through site). Roaming was not commonly observed. Loss of navigational ability or predation may explain this seemingly aberrant behavior. Four of the 5 observations of roaming were hatchery fish.	day	4.0 [0.5]	1.7 [0.4-8.2]
Casual migration	3	Movement pathways were similar to active migration (i.e., direct movement through site, obvious general direction of travel toward estuary), but swim velocities were much slower - more on the order of holding fish. Casual migration was rare and was only observed in hatchery fish.	dawn day	2.4 [0.5]	0.5 [0.4-0.7]
Cycling	6	Cycling was unique to Lake Washington (i.e., the Seattle Tennis Club site). Cycling fish appeared to travel in a big loop, generally moving north close to shore during the day, and moving south offshore during dusk, night and/or dawn. One or two complete loops were observed. Northward movement generally resembled active migration. Characteristics of southward movement are uncertain. Cycling was observed in 33% of tracked fish, and was observed in both wild and hatchery fish.	^a	dawn: 3.7 [1.0] ^b day: 4.6 [0.6] ^c dusk: ^d night: ^e	70 [28-138]

^a By definition, cycling required all diel periods, unlike the other behaviors which could be observed within a single period.

^b n = 3.

^c Track characteristics and swim velocities of northward movement during the day generally resembled active migration. The mean swim velocity presented is based on one or two northward passes of 5 fish. It excludes the second northward pass of two fish which exhibited different on-site behaviors.

^d There were no direct observations (i.e., tracks) at dusk.

^e Two cycling fish were tracked at night. Swim velocities of these two fish were 1.3 and 3.6 BL/s.

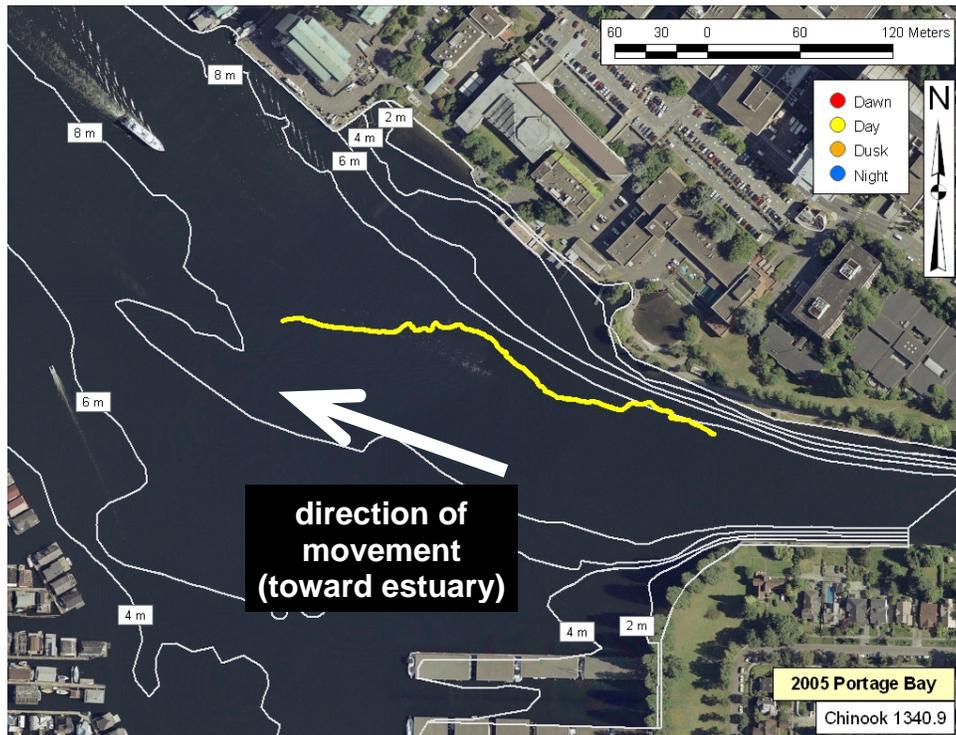
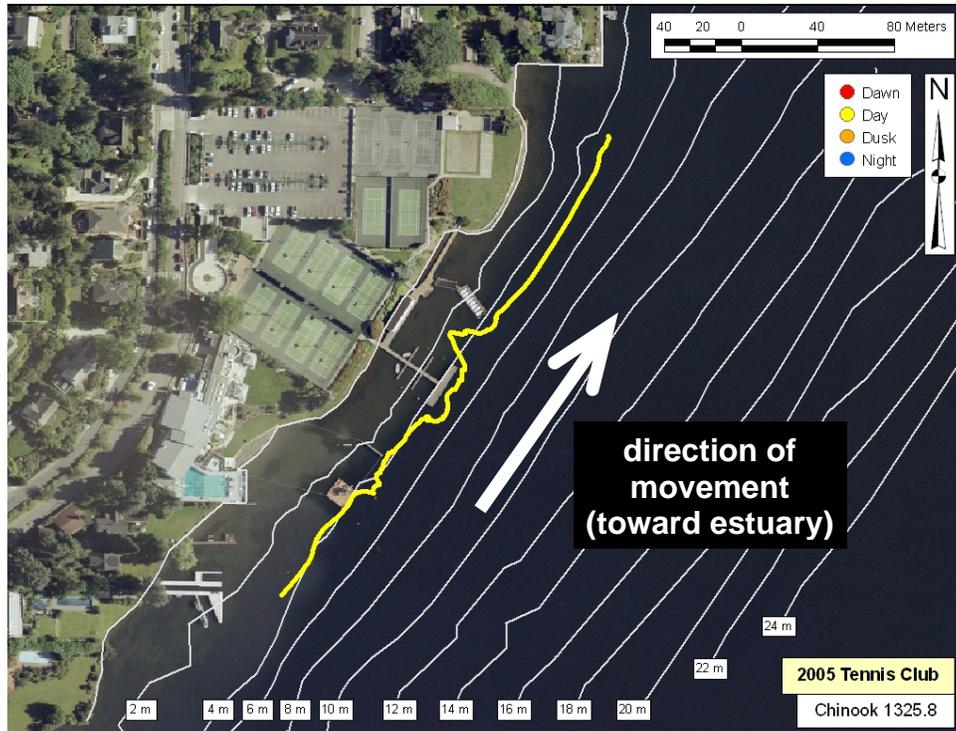


FIGURE 7. Examples of active migration behavior observed in Chinook salmon smolts at three study sites, May-June, 2005. These fish had high swim velocities (mean, 4.5 BL/s) and short site area residence times (median, 0.3 h), and traveled from one end of the site to the other with little or no milling about and no major changes in direction.

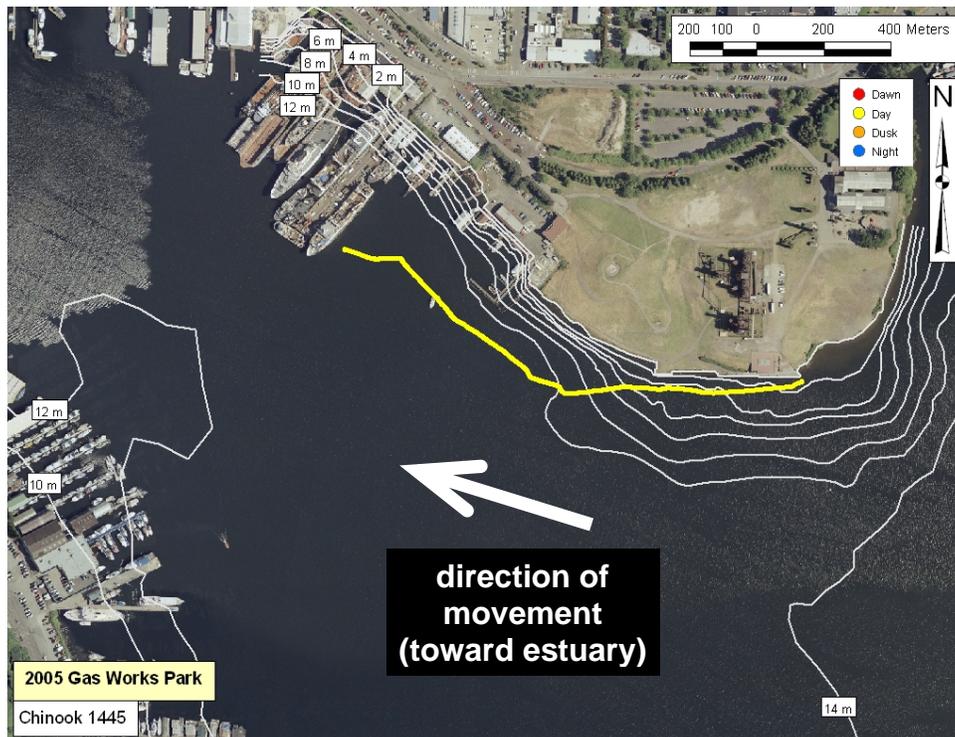


FIGURE 7. Continued.

TABLE 4. Number of tagged Chinook salmon smolts observed exhibiting different meso-scale behaviors at the Portage Bay site, May-June, 2004, and the Seattle Tennis Club, Portage Bay, and Gas Works Park sites, May-June, 2005. The percentage of fish exhibiting each behavior relative to all fish observed at the site is shown in parentheses. Behaviors are represented as follows: AM = active migration; HD = holding; RO = roaming; CM = casual migration; CY = cycling; and, ID = unable to identify due to insufficient data. Each fish at each site was classified into only one meso-scale behavior.

Site, year	AM	HD	RO	CM	CY	ID	No. obs.
Seattle Tennis Club, 2005	6 (33)	3 (17)	1 (6)	1 (6)	6 (33)	1 (6)	18
Portage Bay, 2004	8 (28)	19 (66)	1 (3)	1 (3)	0 (0)	0 (0)	29
Portage Bay, 2005	24 (62)	10 (26)	3 (8)	1 (3)	0 (0)	1 (3)	39
Gas Works Park, 2005	2 (8)	22 (85)	0 (0)	0 (0)	0 (0)	2 (8)	26

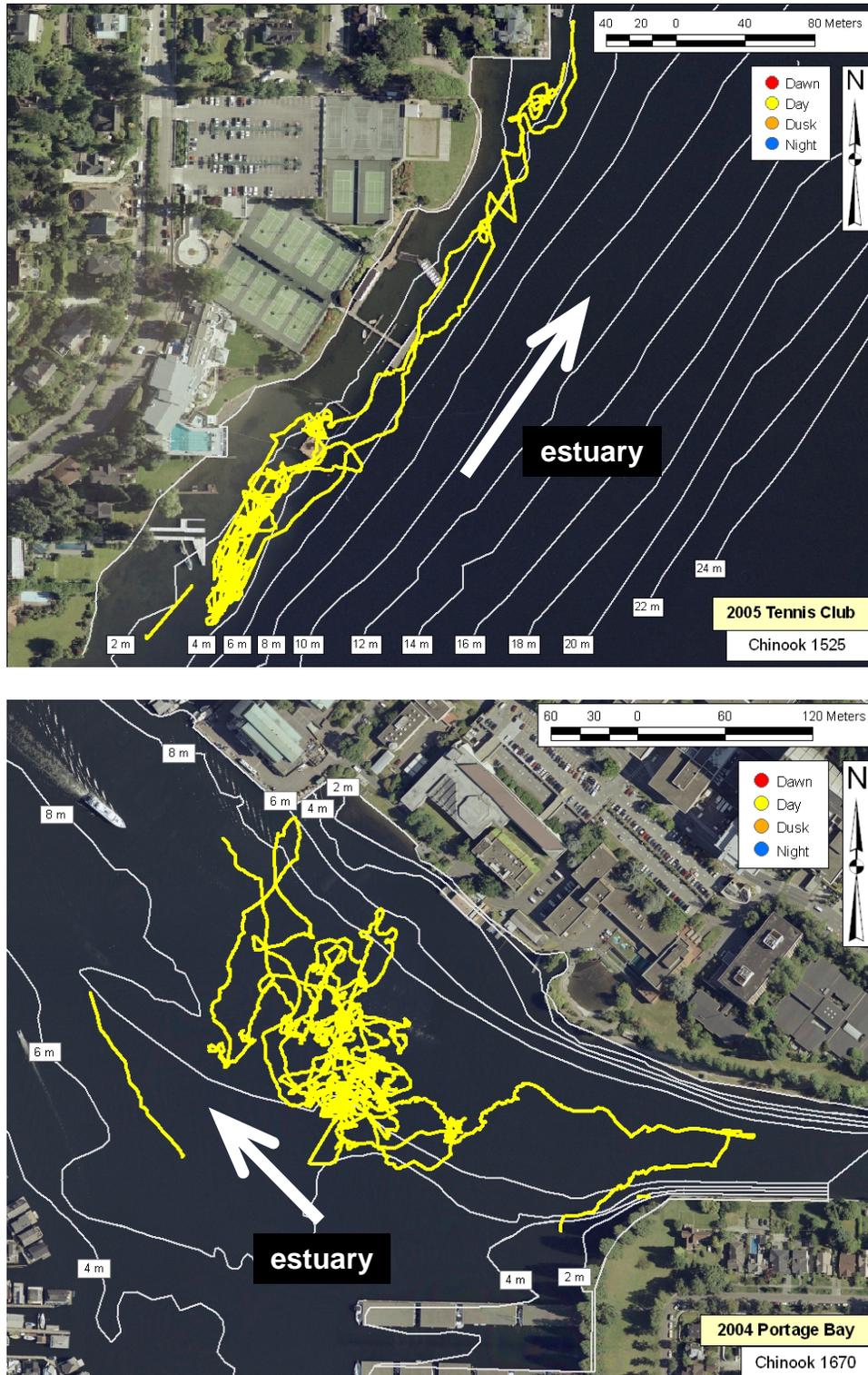


FIGURE 8. Examples of holding behavior observed in Chinook salmon smolts at three study sites, May-June, 2004-2005. These fish had slow swim velocities (mean, 1.5-2.1 BL/s depending on diel period) and long site area residence times (median, 4-91 h depending on site), and milled about often crisscrossing through large parts of the site.

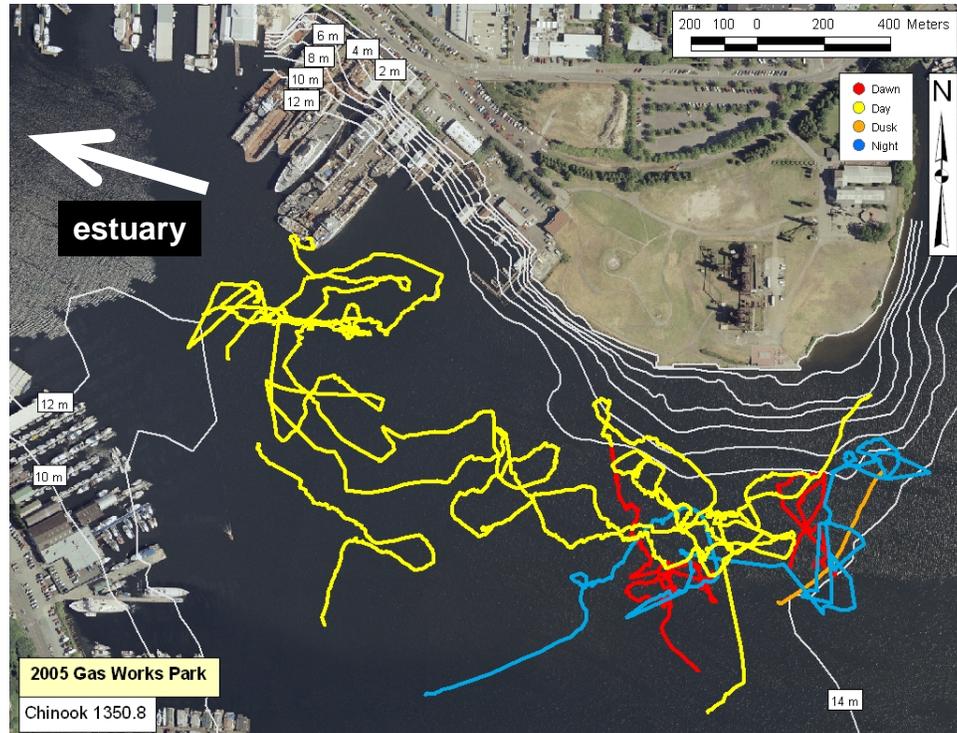


FIGURE 8. Continued.

multiple comparison Scheffé test (Sheskin 2000) found that area residence time was statistically different between all site and year pairings (Portage Bay 2004-2005: $P = 0.001$; Portage Bay 2004-Gas Works Park: $P = 0.036$; Portage Bay 2005-Gas Works Park: $P < 0.001$).

Holding was the most common behavior observed. It was observed in 54 of 112 fish (48%): 32 of 55 (58%) wild fish and 22 of 57 (39%) hatchery fish exhibited holding behaviors. Forty-eight fish (89%) entered the site during daytime, and 2 fish each entered during dawn, dusk, and night. Many fish were observed during two or more diel periods: 17, 14, 13, and 10 fish were observed during one, two, three, and four diel periods, respectively. Diel periods were equally represented except for day: 23, 54, 23, and 24 fish were observed holding during dawn, day, dusk, and night, respectively. The greater abundance of daytime observations appeared largely due to two factors. First, many fish ($n=13$) exhibited a short-term holding behavior whereby they entered a site during the day, held for a few hours, then moved off-site later in the day presumably continuing their migration. This occurred primarily at the Portage Bay site in both 2004 and 2005. The second factor appeared related to tagged fish use of Lake Union and array location and configuration at the Gas Works Park site in north Lake Union. Twenty holding fish tracked at Gas Works Park had area residence times > 24 h, and 14 of these fish had area residence times > 48 h. All 20 of these fish were tracked during the day, but only three fish were also observed during each of the other three diel periods despite the long area

residence times. Nine fish were observed during two other diel periods in addition to day. Many fish were observed moving on- and off-site to the south. These observations suggest: 1) that the tracking area at the Gas Works Park site encompassed only a small part of a larger area that holding fish were using, which included a larger part of Lake Union; and, 2) that fish holding in this area were more likely to use north Lake Union during the day, and less likely to use north Lake Union during other diel periods.

The roaming behavior was characterized by faster swim velocities - comparable to active migration - but movement pathways and site area residence times more similar to holding (Table 3). Plotted tracks of roaming fish generally resembled those of holding fish (Figure 9). Roaming fish were observed milling in localized areas of the site and/or crisscrossing through the site in different directions. Roaming fish did not show an obvious general direction of travel toward the marine environment. Rather, these fish were observed making substantial movements in directions that were 90-180° off the line of travel toward the estuary (Figure 9). Such behavior - i.e., prolonged fast swimming in directions not toward the estuary - appears to be a waste of energy. Loss of navigational ability may contribute to this behavior. Alternatively, predation may explain the behavior. That is, if a predator consumed a tagged Chinook salmon the acoustic tag would remain active and the resultant track would represent movement of the predator. Roaming was not commonly observed and was observed in only 5 fish. Four of the 5 roaming observations occurred at the Portage Bay site, three in 2005 and one in 2004 (Table 4). One roaming observation occurred at the Seattle Tennis Club site. Four of the 5 observations of roaming were hatchery fish. Roaming was observed primarily during the day. One roaming fish was also observed at dawn, and one was observed exclusively at dusk.

The casual migration behavior was characterized by residence times and movement pathways similar to active migration, but lacking the faster swim velocity (Table 3). Swim velocities were more similar to holding, albeit slightly higher. Casual migration was rare and was only observed in three fish, all of hatchery origin. All observations of casual migration occurred during dawn and/or day.

The cycling behavior was unique to Lake Washington and the Seattle Tennis Club site. This behavior was observed in 6 fish: 3 of hatchery origin and 3 naturally reared fish. This represented 33% of all tagged Chinook salmon tracked at the Seattle Tennis Club site (Table 4). Cycling fish appeared to travel in a big loop, generally moving north close to shore during the day, and moving south offshore during dusk, night and/or dawn. Cycling fish made 2-3 northward passes through the site, representing 1-2 complete loops, or cycles. The initial northward pass was usually observed close to shore during the day, with fish exiting the site to the north. These fish appeared at the site again 1-7 days later, usually entering the site from the south. One fish made 3 such passes through the site. Southward movement (i.e., moving south of the site after last being tracked exiting the site to the north) was usually not directly observed. During the day, all tracked Chinook salmon at the Seattle Tennis Club site were exclusively in the near shore (< 6 m depth) and were well within the detection limits of the hydrophone array (Figure 3). Crepuscular and nighttime observations were more distributed throughout the site

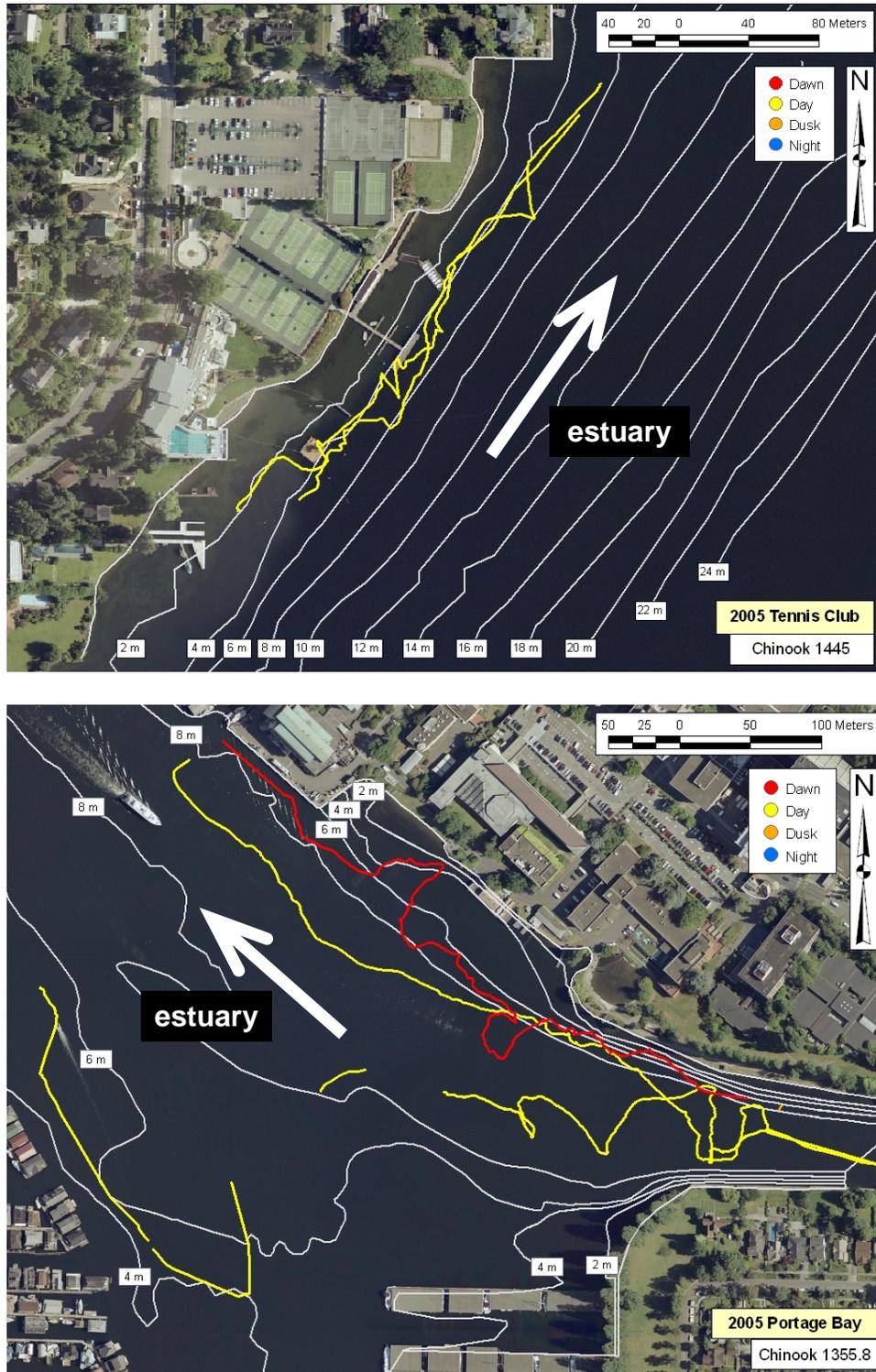


FIGURE 9. Examples of roaming behavior observed in Chinook salmon smolts at two study sites, May-June, 2005. These fish had fast swim velocities (mean, 4.0 BL/s) similar to actively migrating fish. However, unlike actively migrating fish, roaming fish had long site residence times (median, 1.7 h) and made substantial movements in directions that were not toward the estuary.

and extended out to the offshore edge of the tracking area. Chinook salmon use during these time periods almost certainly extended beyond the offshore edge of the tracking site. Thus, in order for fish to return south of the site without being tracked, it appears likely that they would have done so offshore (beyond the detection limits of the hydrophone array) during dusk, night, and/or dawn. Some southward movement was directly observed in the nearshore during the day, but this was minimal. Northward movement of cycling fish exhibited tracks and swim velocities resembling active migration (Table 3), although two fish exhibited different traits on the second of their two northward passes. One appeared to engage in a roaming behavior, moving south and north through the site at a high velocity (4.6 BL/s). The other fish appeared to hold at the site during its second pass, milling around at a slow velocity (2.2 BL/s) for over 5 h.

Site-specific migrational function

Chinook salmon smolts appeared to use the study sites in different ways, suggesting that different areas served different migrational functions. Distinct site migrational functions were apparent in dominant meso-scale fish behaviors and in site residence times. Based on these data, we identified three general site migrational functions: 1) migrational corridors, where fish spent little time and moved through quickly; 2) short-term holding areas, where fish spent a moderate amount of time milling about at slower velocities; and, 3) long-term holding areas, where fish spent long periods of time milling about at slower velocities. Migrational functions were not absolute: although many fish used a given site in a certain way, there was often a notable minority of fish that used it differently.

The Seattle Tennis Club site functioned primarily as a migrational corridor. Behaviors associated with minimal site use (active migration, cycling, roaming, and casual migration) were prevalent: 8 of 8 wild fish, and 6 of 10 hatchery fish were in these categories (Figure 10). Two additional hatchery fish – one holding and one with insufficient data to classify – also spent little time at the site. Differences in meso-scale behaviors were observed between hatchery and wild fish, although the small sample sizes limit interpretation of these results. Active migration was observed in 63% of wild fish, but only 10% of hatchery fish. Conversely, holding was observed in no wild fish but 30% of hatchery fish. Despite these differences, most hatchery (80%) and wild (63%) fish had residence times < 1 d (Figure 11). Of these, all wild fish and half of the hatchery fish had residence times < 1 h. Comparatively long residence times (≥ 1 d) were observed in three wild and three hatchery fish; however, these fish used the site much less than indicated by their residence times. All five exhibited the cycling behavior whereby they quickly moved through the site, exited, and returned 1-7 d later. Each fish went undetected for the 1-7 d between on-site appearances, which greatly inflated the calculated area residence times. Each on-site occurrence was actually quite short. Most (75%) on-site occurrences were < 1 h.

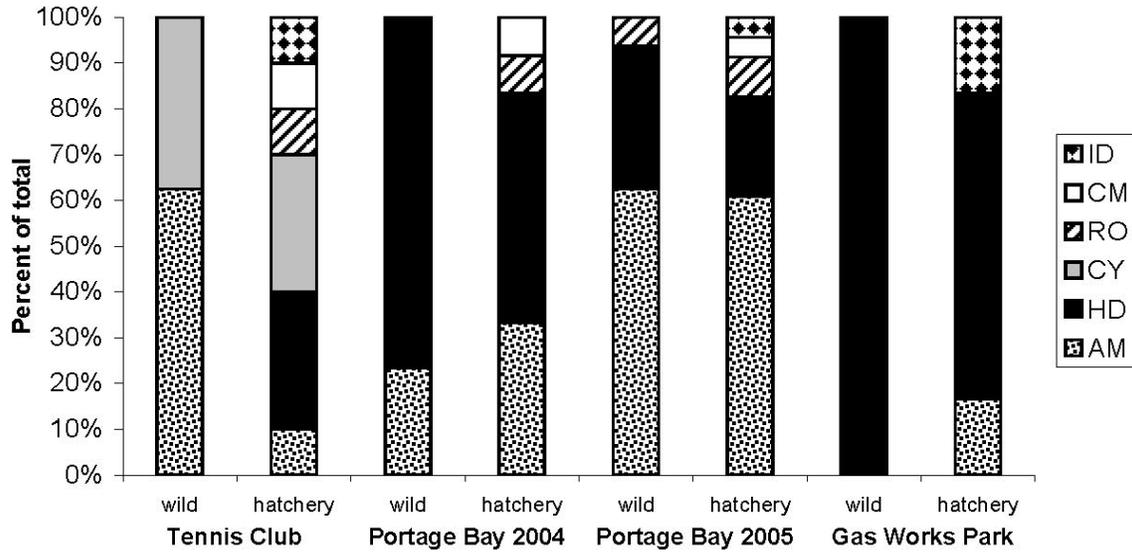


FIGURE 10. Relative proportion of different meso-scale migrational behaviors observed in Chinook salmon smolts at each site. Behaviors are represented as follows: AM = active migration; HD = holding; CY = cycling; RO = roaming; CM = casual migration; and ID = insufficient data.

The Portage Bay site in 2004 functioned as a short-term holding area for most fish, and as a migrational corridor for a notable minority of fish. Holding was observed in 76% of wild fish and 50% of hatchery fish (Figure 10). Median residence times were 30 h and 48 h for holding wild and hatchery fish, respectively. This difference was not significant (pooled variance t-test: $P = 0.713$). All hatchery fish and nearly all wild fish had residence times < 4 d. Only one wild fish was still at the site after 4 d (Figure 11). Despite the prevalence of holding, a notable proportion of fish used the site as a migrational corridor. Active migration was observed in 24% and 22% of wild and hatchery fish, respectively. An additional 17% of hatchery fish made minimal use of the site, exhibiting either casual migration or roaming behaviors. Unlike observations at the Seattle Tennis Club site, wild and hatchery fish at Portage Bay in 2004 showed largely similar patterns in meso-scale behavior (Figure 10).

In 2005, behavior patterns at the Portage Bay site were different from those observed in 2004. In 2005, the site functioned largely as a migrational corridor, and much less as a holding area. Behaviors associated with minimal site use were prevalent. Active migration was the dominant behavior and was observed in 63% and 61% of wild and hatchery fish, respectively (Figure 10). Other behaviors associated with minimal site use were observed in 6% and 13% of wild and hatchery fish, respectively. All hatchery fish and all but one wild fish had residence times < 1 d (Figure 11). Holding was observed in a notable minority of both wild (31%) and hatchery (22%) fish. Median area residence time of holding fish was 1.1 and 5.2 h for wild and hatchery fish, respectively. This difference was not significant (pooled variance t-test: $P = 0.647$). Area residence times

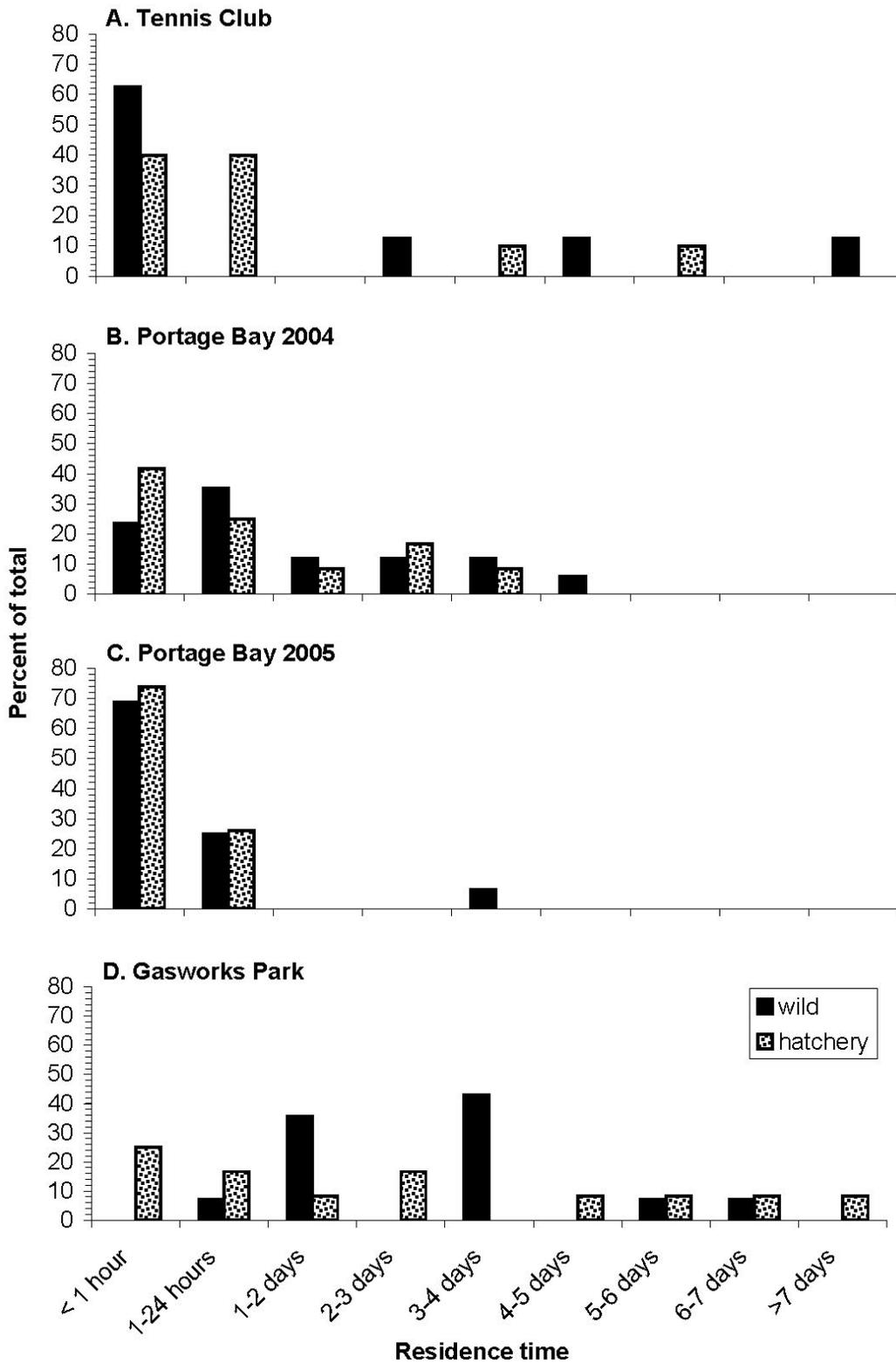


FIGURE 11. Site area residence times of tagged Chinook salmon smolts at the Portage Bay site, May-June, 2004, and the Seattle Tennis Club, Portage Bay, and Gas Works Park sites, May-June, 2005.

of all wild and hatchery holding fish were much shorter than those observed in 2004. Median area residence times of holding fish were 30 and 4 h in 2004 and 2005, respectively. This difference was significant (pooled variance t-test: $P = 0.001$). As in 2004, patterns in meso-scale behavior were largely similar between wild and hatchery fish (Figure 10).

The Gas Works Park site functioned almost exclusively as a short- to long-term holding area. Holding behavior was observed in 100% and 67% of wild and hatchery fish, respectively (Figure 10). Conversely, behaviors associated with minimal site use were observed in only 17% of hatchery fish and no wild fish. The remaining 16% of hatchery fish could not be classified due to insufficient data. Fish generally remained at and near this site longer than the other sites (Figure 11). Median residence time was 77 and 89 h for wild and hatchery holding fish, respectively. This difference was not significant (pooled variance t-test: $P = 0.594$). Fish presence within the actual tracking area during this time was sporadic rather than continuous, indicating that the site was a small part of a larger general area that fish were using during this time. Again, meso-scale behavior patterns were largely similar between wild and hatchery fish (Figure 10).

Shoreline orientation and depth selection

Considerable differences in shoreline orientation and depth selection were evident between Lake Washington and the LWSC. Chinook salmon smolts at the Seattle Tennis Club site in Lake Washington were close to shore during the day, almost exclusively in water < 6 m deep. The substantial majority of daytime activity occurred at water column depths of 1-5 m along the entire length of the site (Figure 12). Both wild and hatchery fish showed the highest possible selection (median, 1.0) for the 2-4 m depth range (Figure 13). Median selection ratios were lower for the 0-2 m and 4-6 m ranges. There was substantial variability in selection ratios within all categories < 6 m, suggesting considerable use of all shallow water depths.

There were indications at the Seattle Tennis Club site of a shift from nearshore habitat during the day to off-shore limnetic areas at night. Two fish - one wild and one hatchery - were tracked at night. Both were observed in the deepest offshore areas of the site, and moved into or out from the site along the site's eastern edge 230 m from shore (Figure 14). At dawn these fish moved into shallower nearshore areas typical of daytime use. Fish at dawn were observed in both nearshore and offshore areas (Figure 15). Five fish - one wild and four hatchery - were tracked at dawn but not at night. Two hatchery fish were observed moving directly into the nearshore from deeper water offsite from the east. One hatchery fish entered and exited the site during dawn, traversing the site in water that was mostly > 8 m deep. The remaining one hatchery and one wild fish entered the site during dawn and were already close to shore. Only one fish was tracked at dusk, and this fish was in shallow water close to shore.

Further evidence for a diel horizontal shift in habitat use was also evident in fish that were not tracked at night, but for which movement patterns could be inferred. Four cycling fish - three wild and one hatchery - entered the site on the far south end and

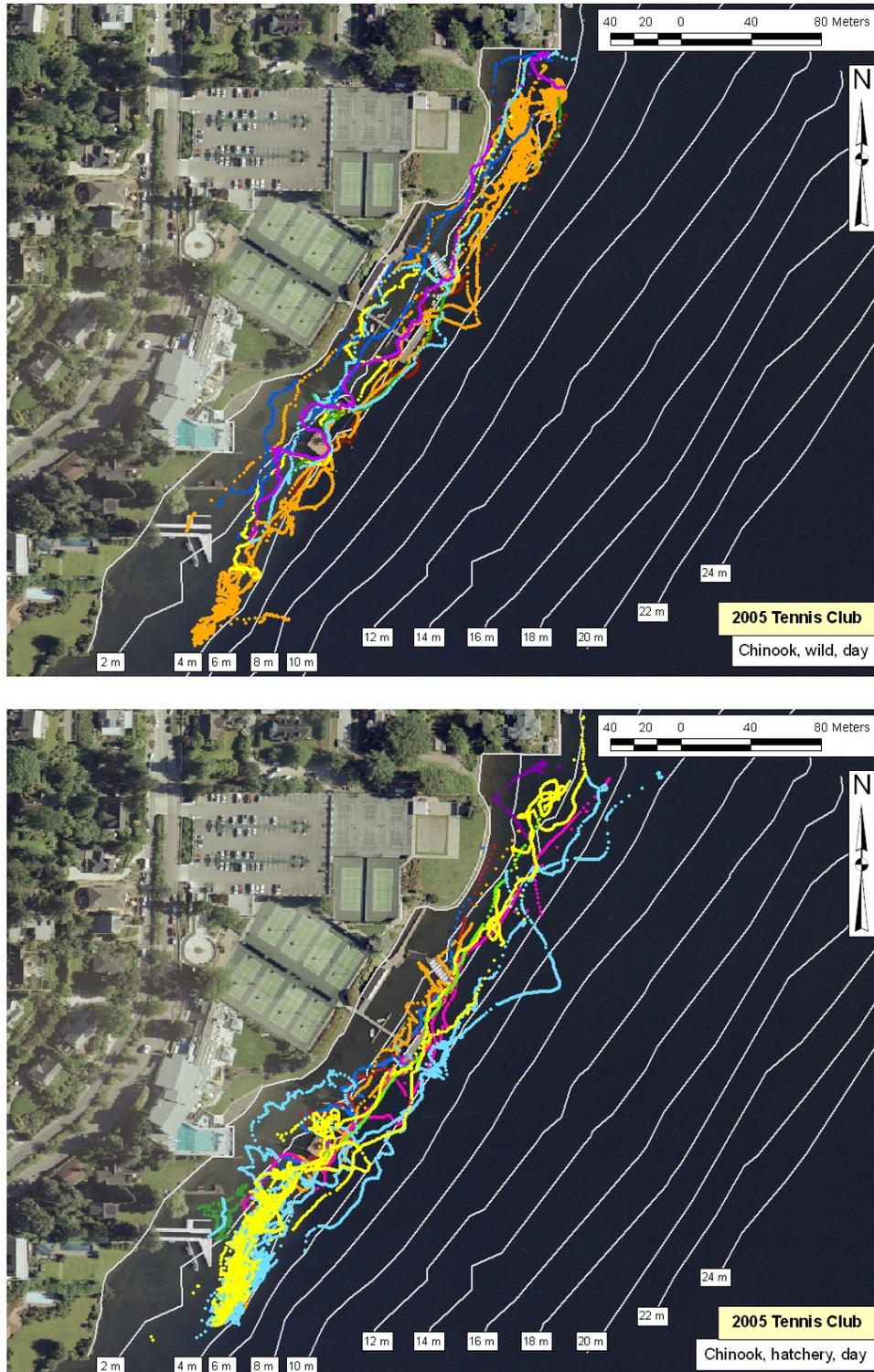


FIGURE 12. Movement pathways of wild (top) and hatchery (bottom) Chinook salmon smolts during the day at the Seattle Tennis Club site, June, 2005. Each color represents an individual fish.

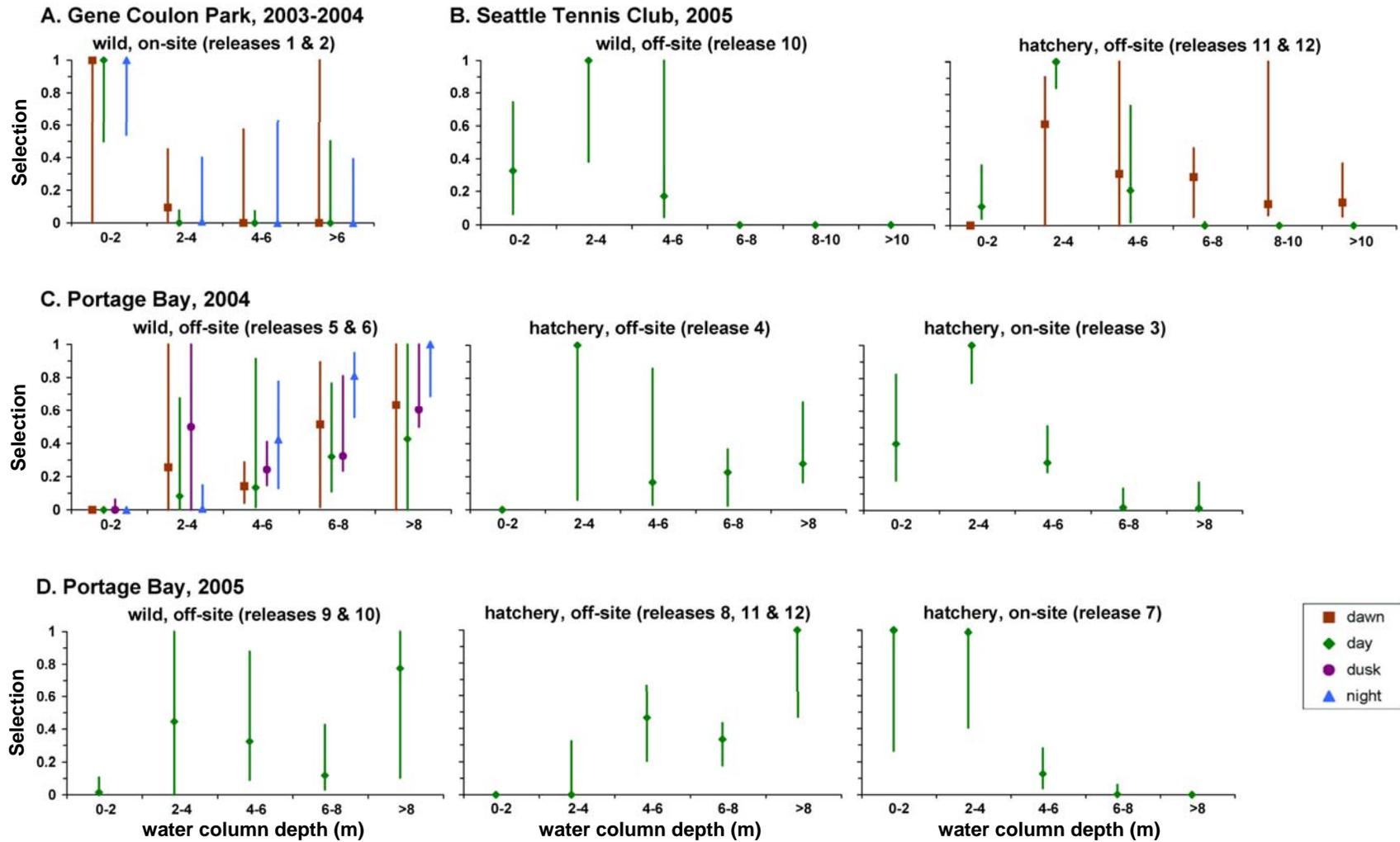


FIGURE 13. Diel depth selection of Chinook salmon smolts by site, year, and analytical unit. Symbols represent the median selection ratio of all fish in the analytical unit. Error bars represent the 1st and 3rd quartiles.

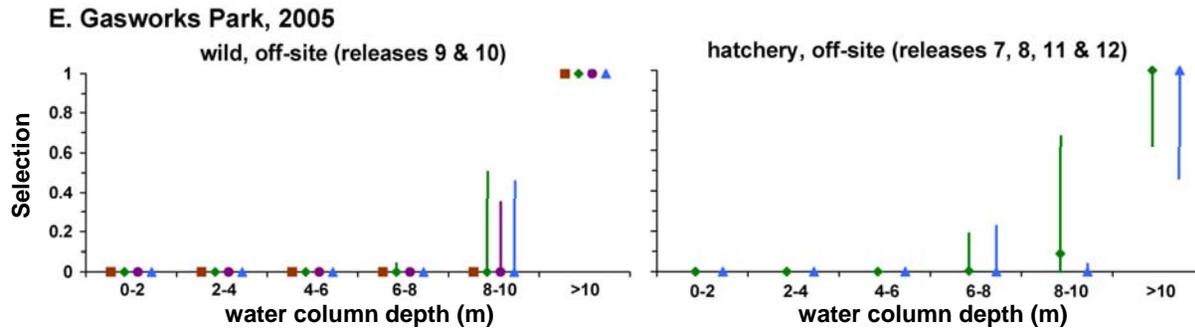


FIGURE 13. Continued.

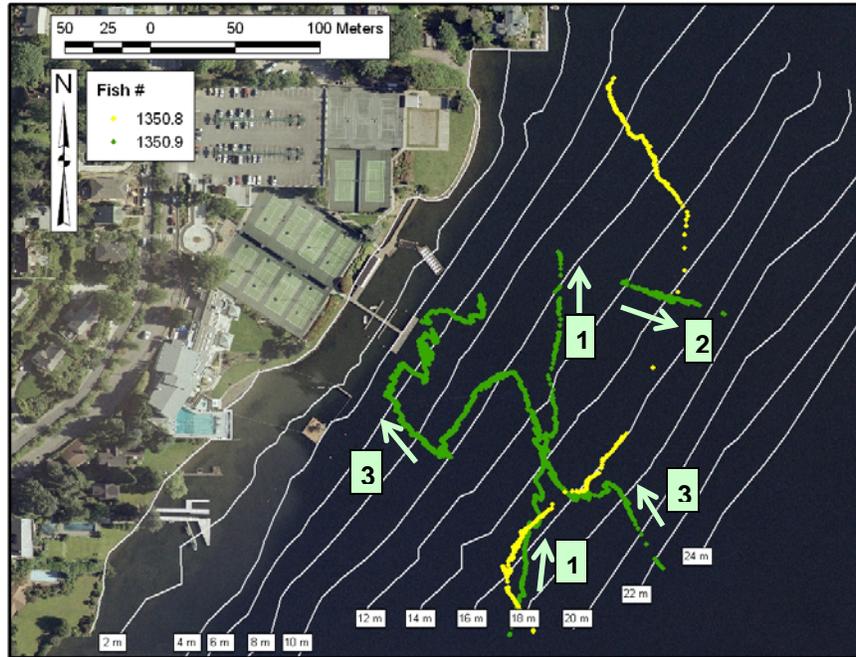


FIGURE 14. Movement pathways of Chinook salmon smolts at night at the Seattle Tennis Club site, June, 2005. Only two fish - one wild (#1350.8) and one hatchery (#1350.9) - were tracked at night. Direction of fish #1350.8 was toward shore. Fish #1350.8 moved toward (tracks 1 and 3) and away (track 2) from shore.

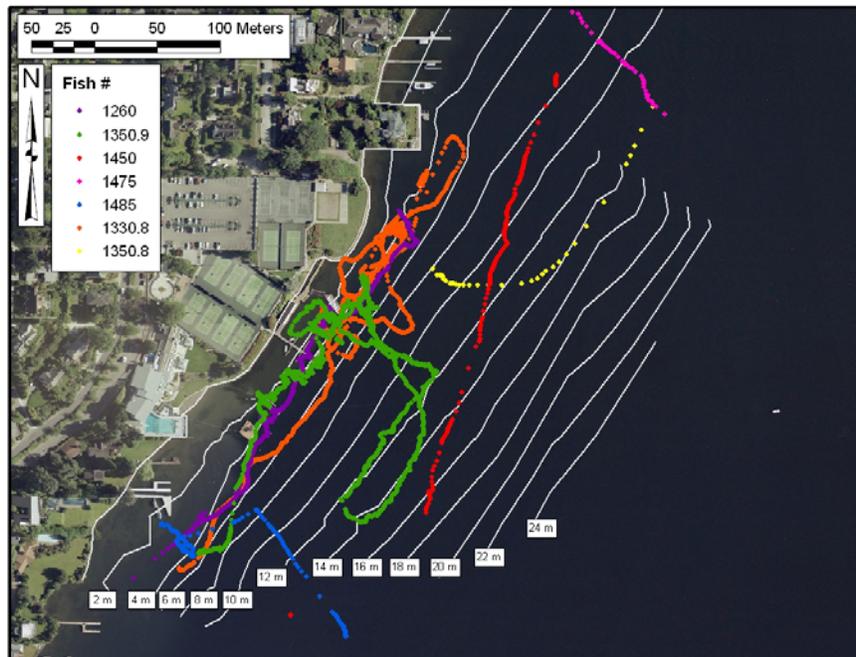


FIGURE 15. Movement pathways of Chinook salmon smolts at dawn at the Seattle Tennis Club site, June, 2005. Seven fish - two wild (#1330.8 and #1350.8) and five hatchery - were tracked at dawn. Directions of fish #1350.8, #1475, and #1485 were toward shore. Direction of fish #1450 was away from shore.

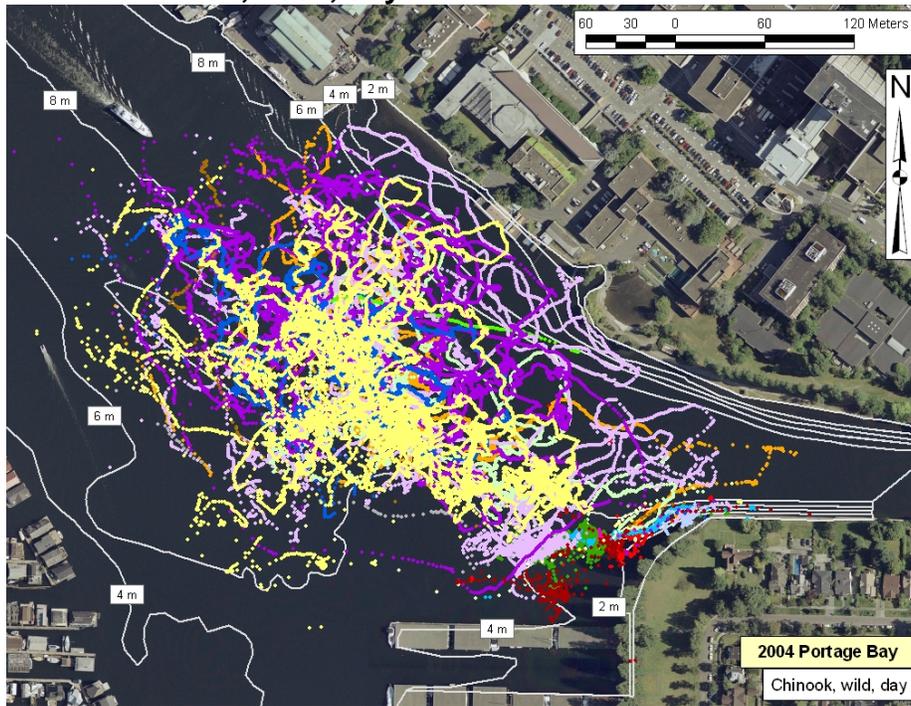
exited to the north on two or three different days without being tracked moving south. That is, after exiting north the first time, these fish returned south without being tracked moving south. Tracking equipment was fully operational during this time, with no malfunctions or other downtime events. Therefore, southward movement presumably occurred > 230 m off-shore beyond the detection boundaries of the equipment, and also presumably occurred during a diel period other than day (all daytime movements of all fish were exclusively in the nearshore well within the tracking boundaries of the array).

In contrast to the Seattle Tennis Club results, fish tracked at Portage Bay and Gas Works Park were broadly distributed across deeper, off-shore areas during all diel periods, including day. There was no diel shift such as that observed in Lake Washington. During the day, wild and hatchery fish tracked at Portage Bay in 2004 and 2005 broadly distributed across most or all the tracking area, primarily in water > 2 m deep (Figure 16). All groups except the 2004 hatchery group showed the highest median selection for water > 8 m deep (Figure 13). There was substantial variability in most selection ratios for depths > 2 m, suggesting notable use of all but the shallowest depths. This was also evident in the plotted fish tracks which showed considerable horizontal distribution across water column depths > 2 m. Fish were rarely detected in water < 2 m deep, and all groups of fish had the lowest possible selection ratio (median, 0.0) with little to no variability at 0-2 m depth (Figure 13).

Wild fish tracked in 2004 at Portage Bay showed similar patterns during all diel periods, although a subtle shift to deeper water was apparent at night. Depth selection during dawn and dusk was similar to that during the day: there was minimal use of water < 2 m deep, and the greatest selection was for water > 8 m deep. As with daytime observations, there was considerable use of all but the shallowest depths during both dawn and dusk. This was evident in the spatial distribution of plotted fish tracks (Figure 17), and the large variability in selection for depths > 2 m (Figure 13). Nighttime observations were largely similar, although a shift to deeper water was apparent. Unlike other diel periods, the 2-4 m water column depth was scarcely used at night (Figures 13 and 17). Also, the selection for deeper water (> 4 m) that was observed during all diel periods was more pronounced at night: nighttime selection ratios for all depths > 4 m were higher with less variability than other diel periods.

Movements of fish at Portage Bay during dawn, dusk and night could not be assessed for other analytical units (2004 and 2005 hatchery fish, and 2005 wild fish). There were too few fish observed during these other periods to provide meaningful analysis. However, plotted tracks of these fish showed similar patterns as those described above for the 2004 wild fish.

A. Wild Chinook, 2004, day



B. Hatchery Chinook, 2004, day

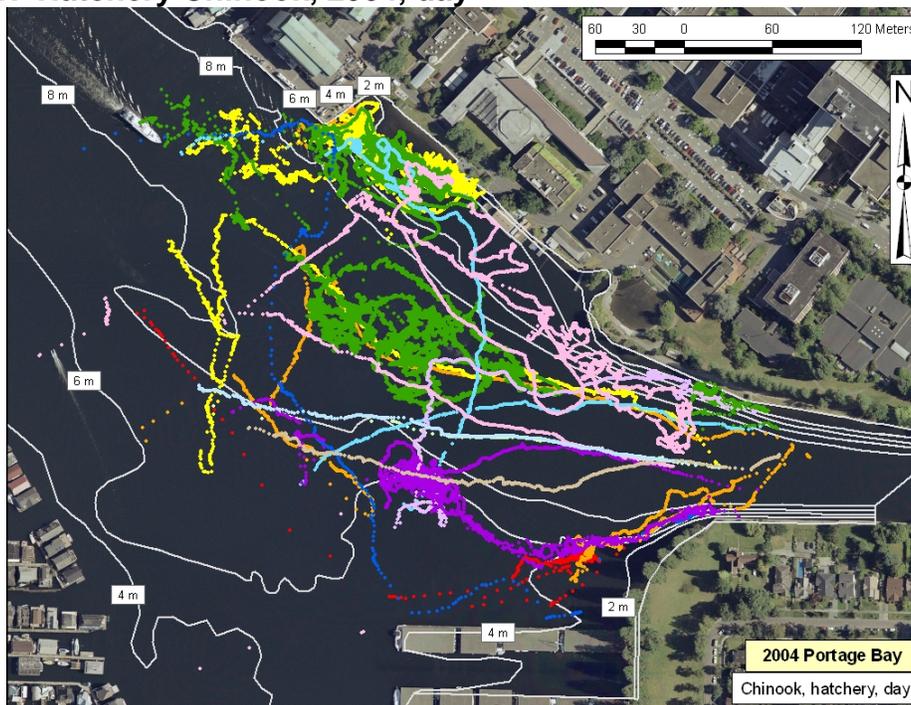
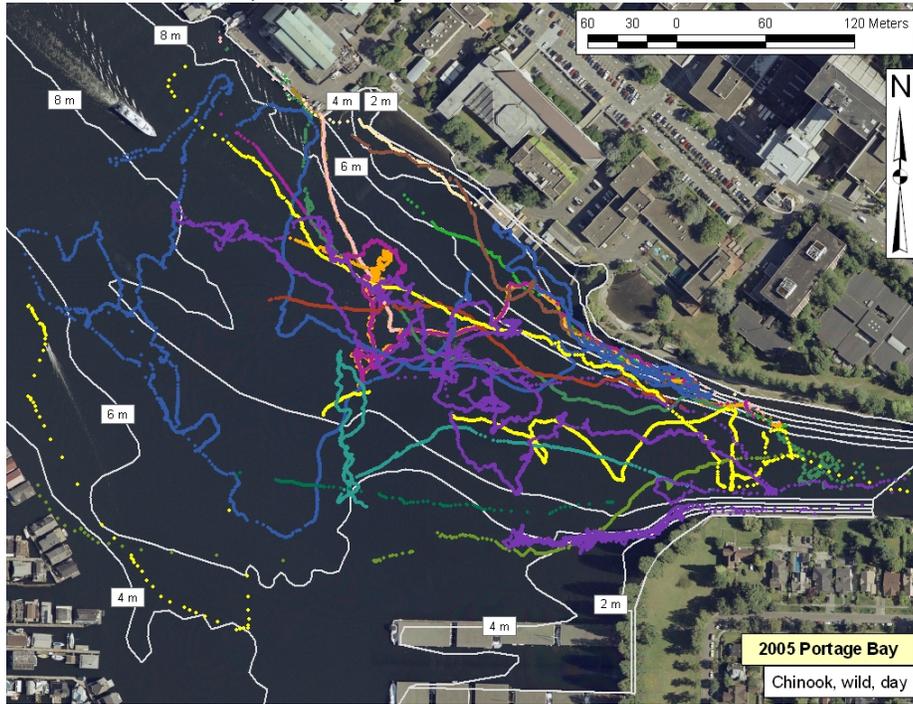


FIGURE 16. Movement pathways of Chinook salmon smolts during day at the Portage Bay site, May-June, 2004-2005: A) wild fish, 2004; B) hatchery fish, 2004; C) wild fish, 2005; and, D) hatchery fish, 2005. Each color represents an individual fish.

C. Wild Chinook, 2005, day



D. Hatchery Chinook, 2005, day

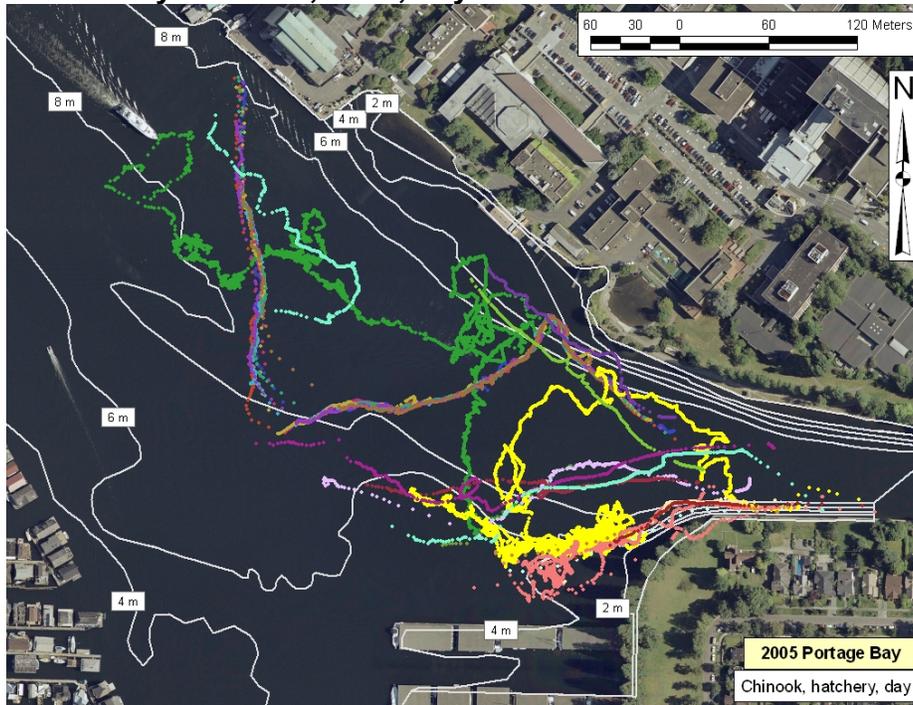
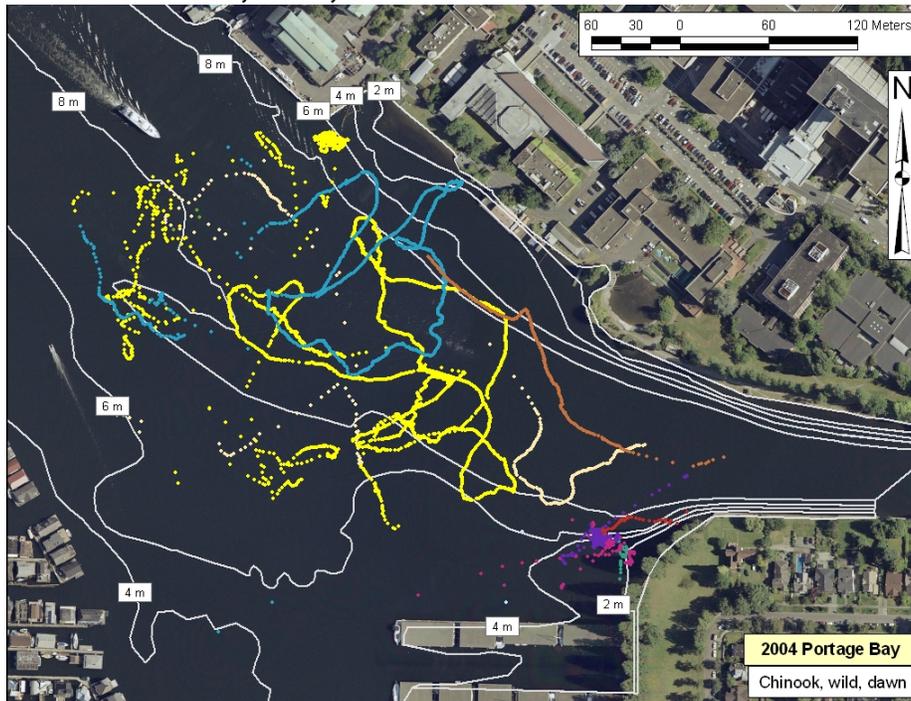


FIGURE 16. Continued.

A. Wild Chinook, 2004, dawn



B. Wild Chinook, 2004, dusk

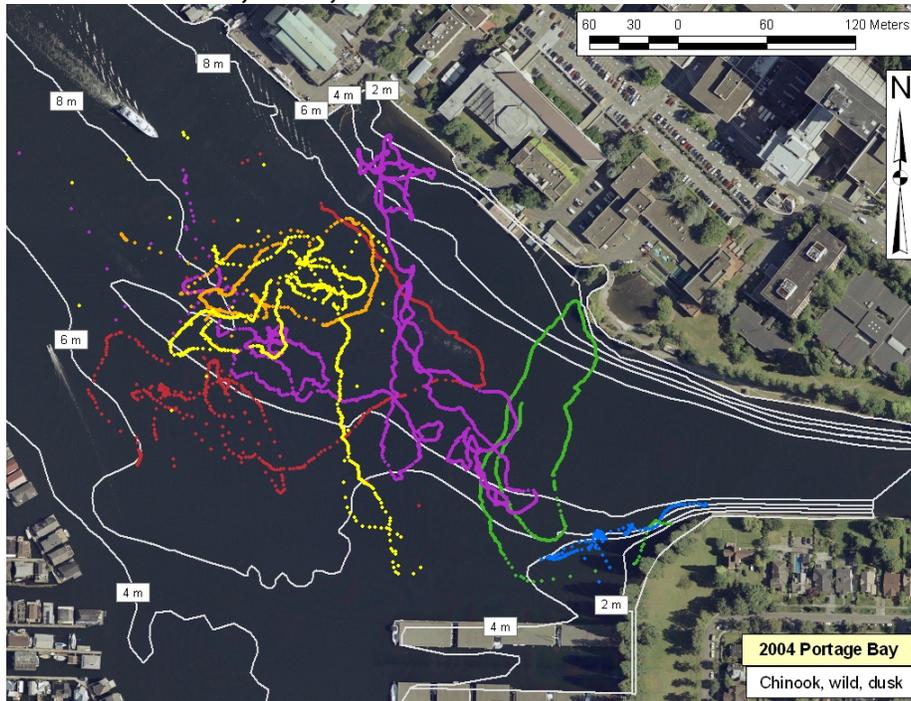


FIGURE 17. Movement pathways of Chinook salmon smolts at the Portage Bay site, May-June, 2004: A) dawn; B) dusk; and, C) night. Each color represents an individual fish.

C. Wild Chinook, 2004, night

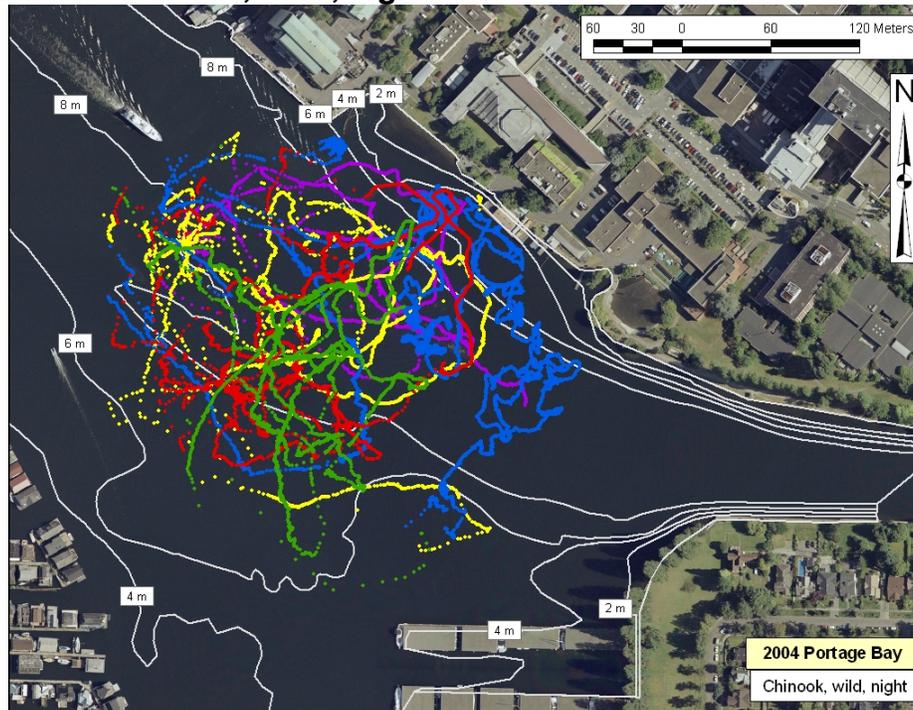
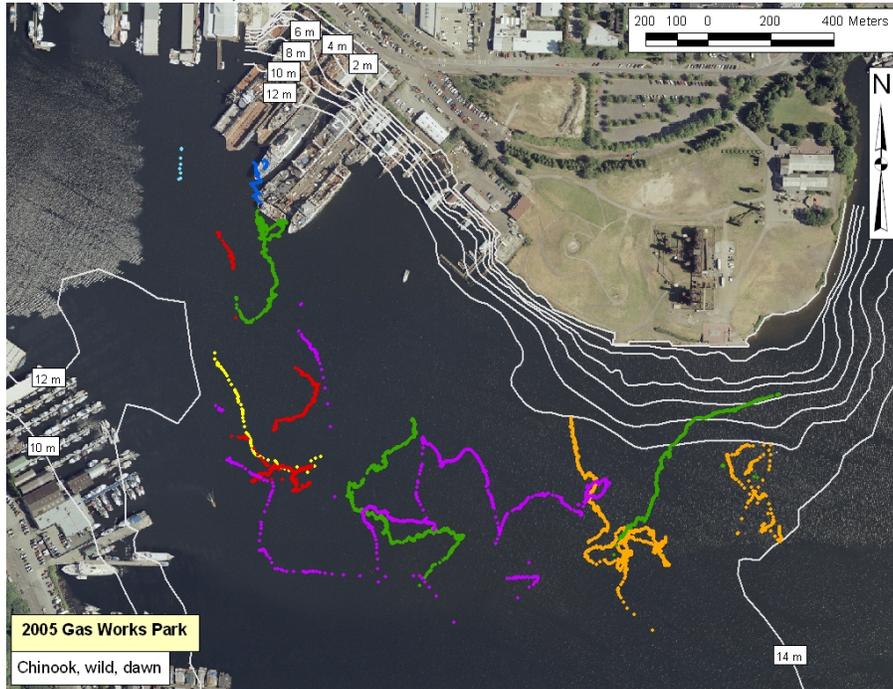


FIGURE 17. Continued.

Fish at Gas Works Park were similar to those at Portage Bay in having a broad spatial distribution, an off-shore orientation, and no apparent horizontal diel shift. However, fish at Gas Works Park showed a much stronger selection for deeper water. Fish were broadly distributed across nearly the entire tracking area during dawn, day, dusk, and night (Figure 18). Plotted tracks showed that fish rarely entered shallower water, and those that did exited shortly after entering. This was also reflected in depth selection calculations. During each diel period, fish showed the strongest possible selection (median, 1.0) for water > 10 m deep (Figure 13). There was a notable lack of variability in selection ratios at this depth, suggesting that most fish strongly preferred deep water column depths. Conversely, water < 10 m deep was rarely used, with fish showing the lowest possible selection (median, 0.0) and little to no variability at these depths. There was no evidence of any diel horizontal shift given the nearly identical patterns in spatial distribution, shoreline orientation, and depth selection across all diel periods.

A. Wild Chinook, dawn



B. Wild Chinook, day

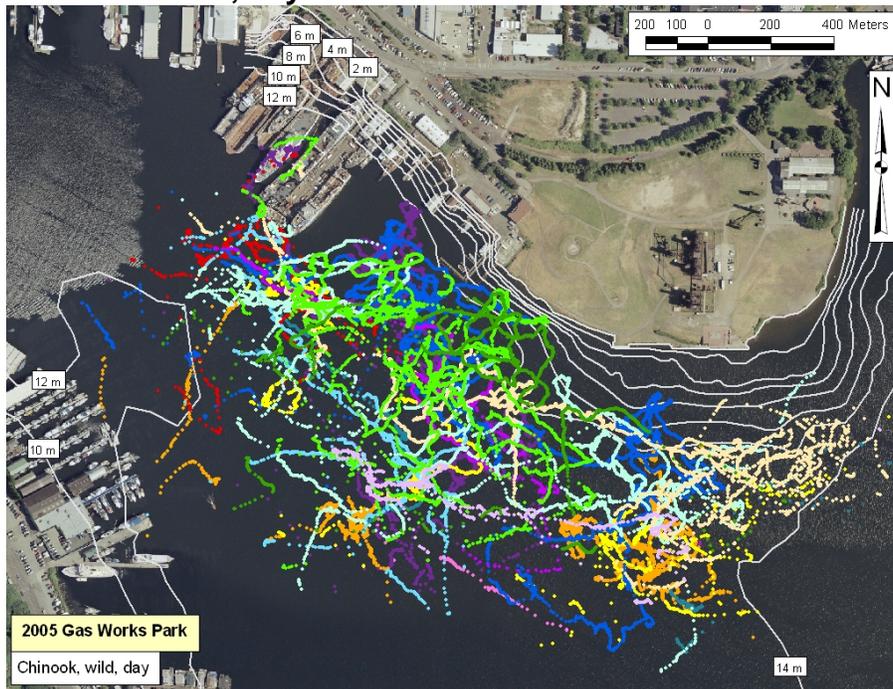
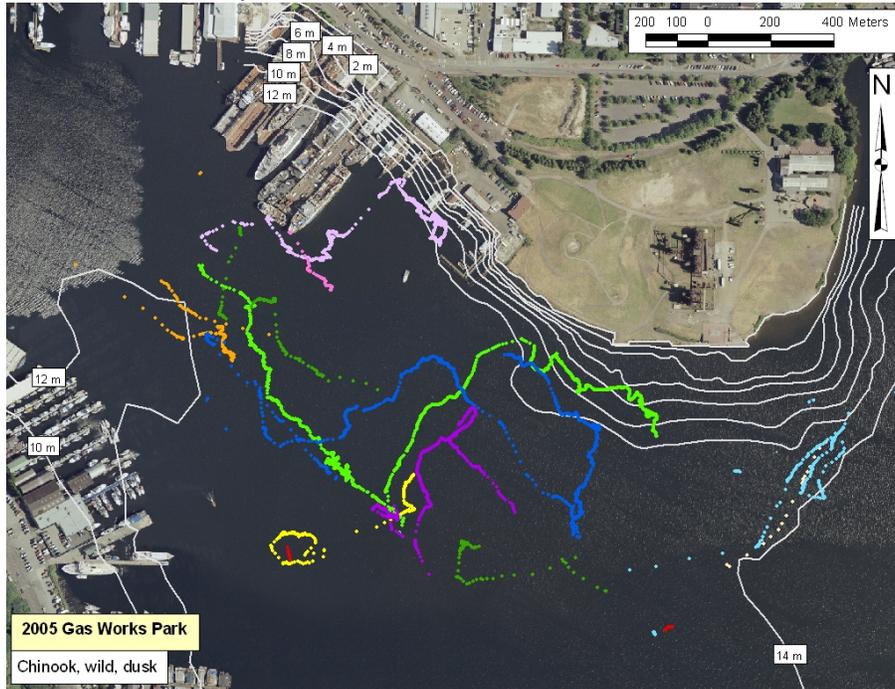


FIGURE 18. Movement pathways of Chinook salmon smolts in north Lake Union at the Gas Works Park site, May-June, 2005: A) wild fish, dawn; B) wild fish, day; C) wild fish, dusk; D) wild fish, night; E) hatchery fish, day; and, F) hatchery fish, night. Each color represents an individual fish.

C. Wild Chinook, dusk



D. Wild Chinook, night

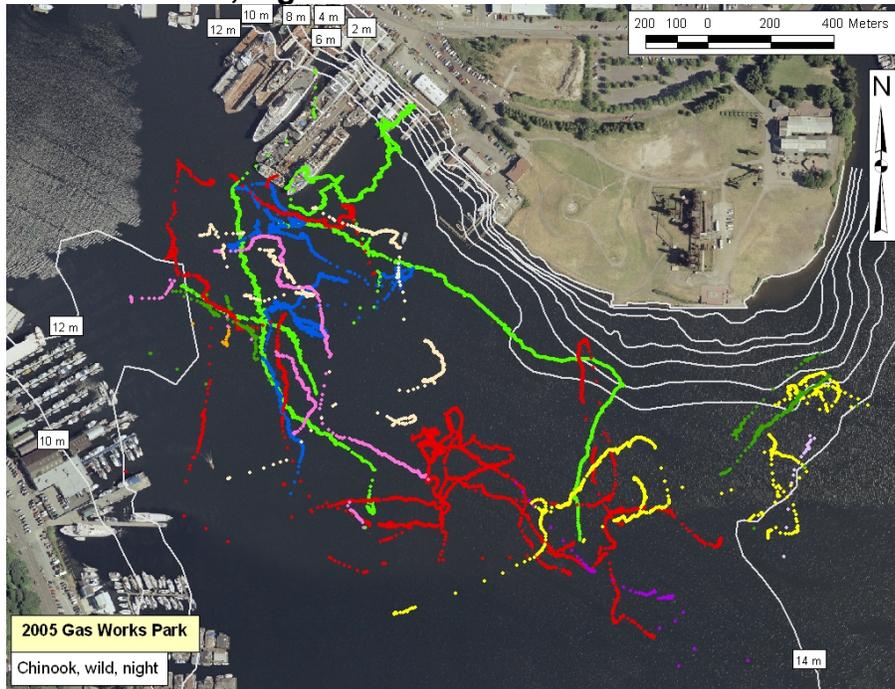
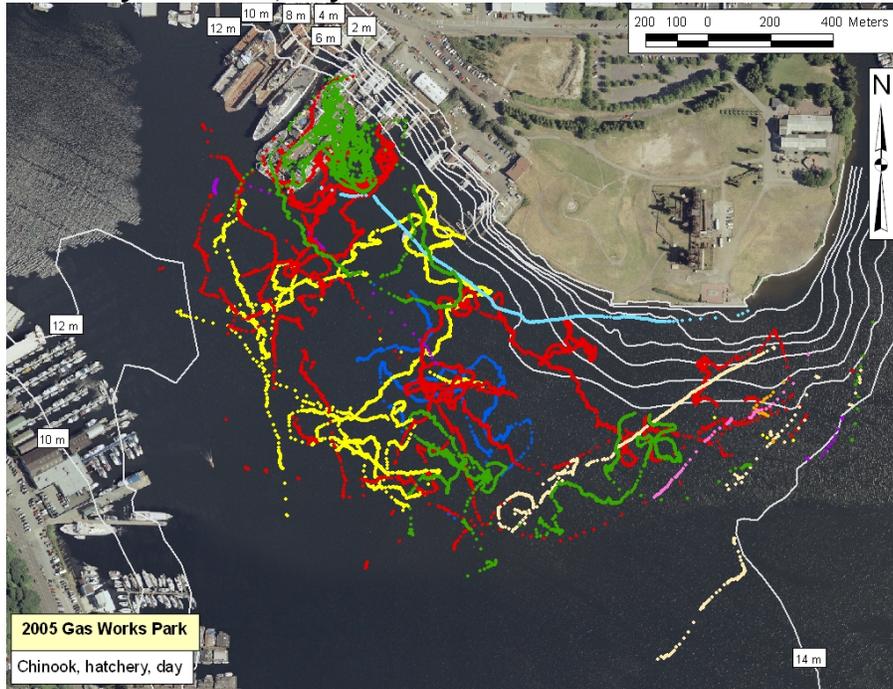


FIGURE 18. Continued.

E. Hatchery Chinook, day



F. Hatchery Chinook, night

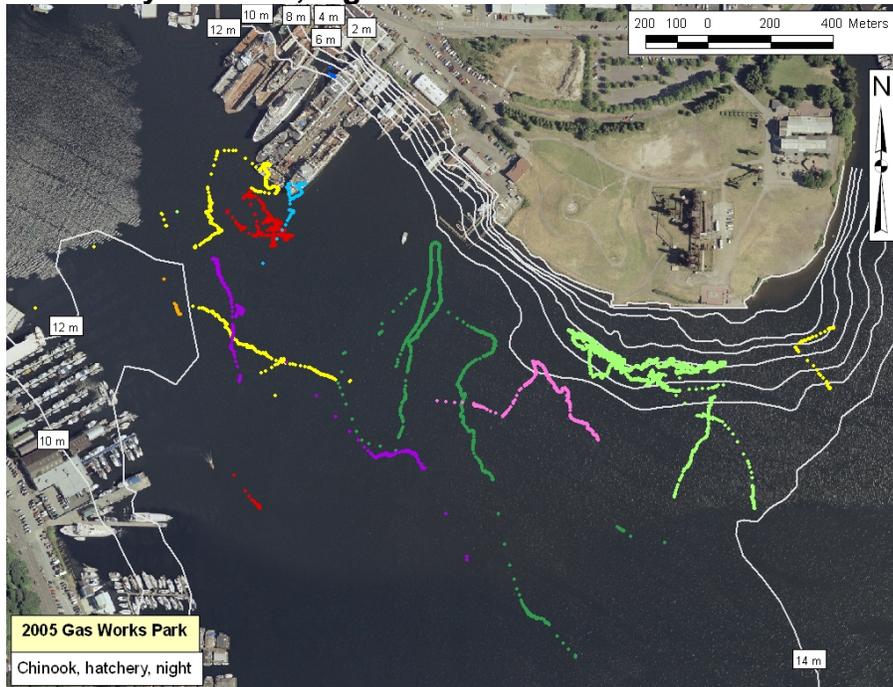


FIGURE 18. Continued.

Spatial distribution and localized habitat use

The Seattle Tennis Club site showed areas of low to moderate relative use throughout the daytime migrational corridor of 1-5 m water column depth for both wild and hatchery fish (Figure 19). Areas of high and moderate relative use areas appeared where two or more fish followed a common migrational pathway (scenario 2). The highest use areas occurred around overwater structures where fish followed similar pathways around the edges of the structures. Fish did not linger in these areas, but rather migrated through along similar pathways. Other areas of higher use were caused by crossing-over of tracks from different fish (scenario 3). One area of moderate use was observed at the south end of the site where two hatchery fish milled about for extended periods of time (scenario 1).

The Portage Bay site in 2004 showed areas of moderate to high use in the southeast corner of the site near the elodea bed during the day (Figure 20). Several wild ($n = 7$) and hatchery ($n = 3$) fish lingered in these areas for extended periods of time (scenario 1). Additional wild ($n = 6$) and hatchery ($n = 1$) fish passed through these areas but did not stay long (scenario 3). Hatchery fish in 2005 also showed higher use in this area, although much of this was from only two fish that milled here (scenario 1), and four fish that passed through (scenario 3). In contrast, wild fish in 2005 did not use this area any more than other areas of the site. Another highlighted area appeared in the northwest corner of the site near the restored shoreline. This area showed moderate use by hatchery fish in 2004, and moderate to high use by wild fish in 2005. In 2004, four hatchery fish milled around in this area (scenario 1), two of which stayed for prolonged periods. An additional fish passed through but did not stay long (scenario 3). In 2005, two wild fish milled about in this area for extended periods (scenario 1), and an additional three fish meandered through at different times (scenario 3). Most other highlighted areas of the site during the day in 2004 and 2005 were caused by either: fish that migrated along common pathways (scenario 2), including some groups that appeared to migrate through in a school; or, crossing-over of tracks from different fish (scenario 3).

Relative use of the Portage Bay site during other diel periods was evaluated only with wild 2004 fish. Other analytical units had too few observations. The same southeast corner highlighted during the day was also highlighted at dawn when several fish either used ($n = 3$) or passed through ($n = 1$) this area (scenarios 1 and 3, respectively; Figure 21). The southeast corner was also highlighted at dusk, however this mostly from one fish with relatively few data points (scenario 5). A similar situation was observed in the northwest corner of the site at night. This highlighted area was from one fish that resided here for a prolonged period (scenario 4). All other highlighted areas during dawn, dusk and night were caused by crossing-over of tracks from different fish (scenario 3).

Fish at the Gas Works Park site distributed throughout the deeper portions of the tracking area, and did not appear to use any particular area of the site more than others (Figure 22). This was true of wild and hatchery fish and all diel periods. Areas highlighted by Tecplot as being more heavily used were due to one or more of the following: crossing-over of tracks from different fish (scenario 3), localized use by a single fish (scenario 4), and fish with few data points (scenario 5).

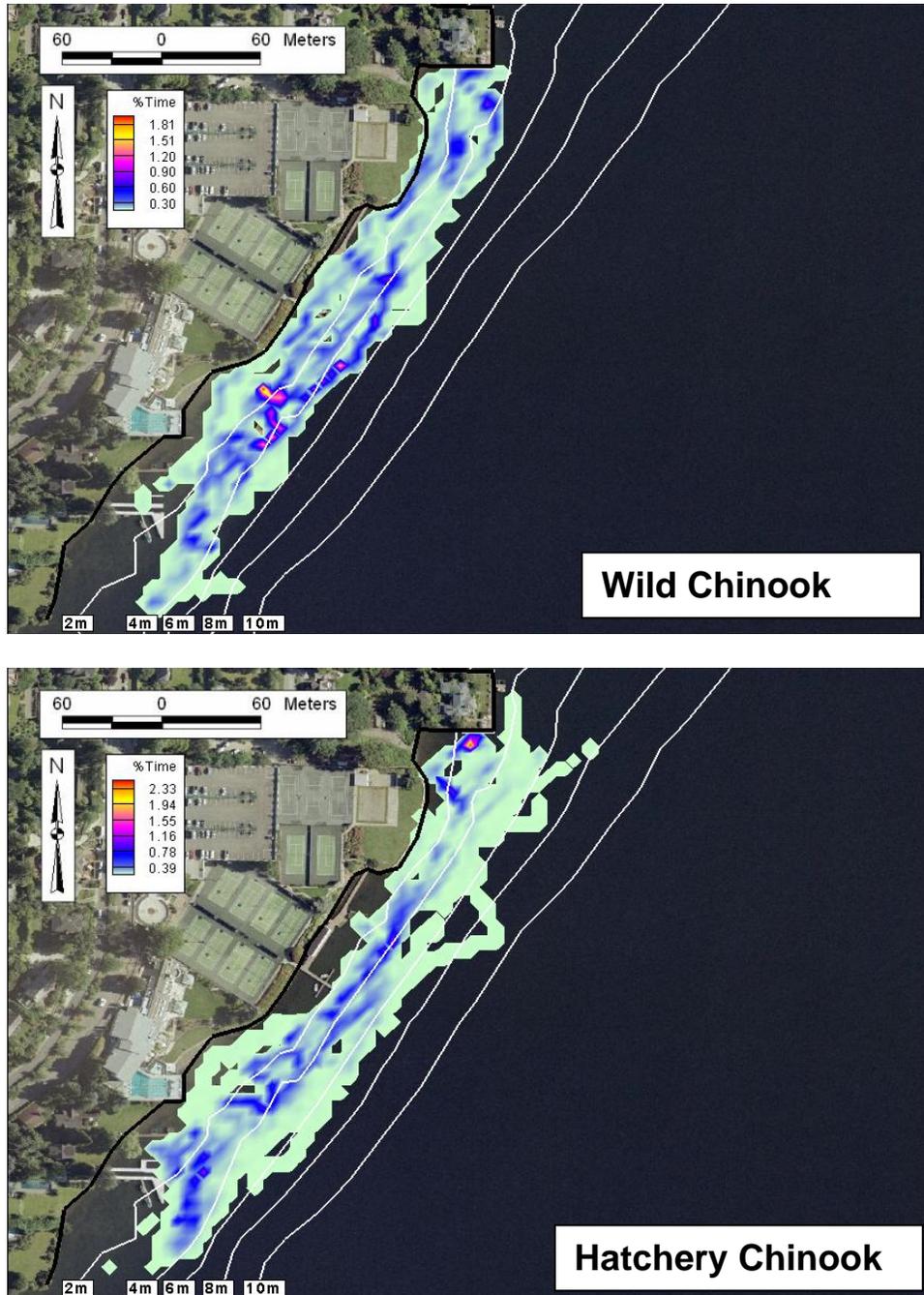
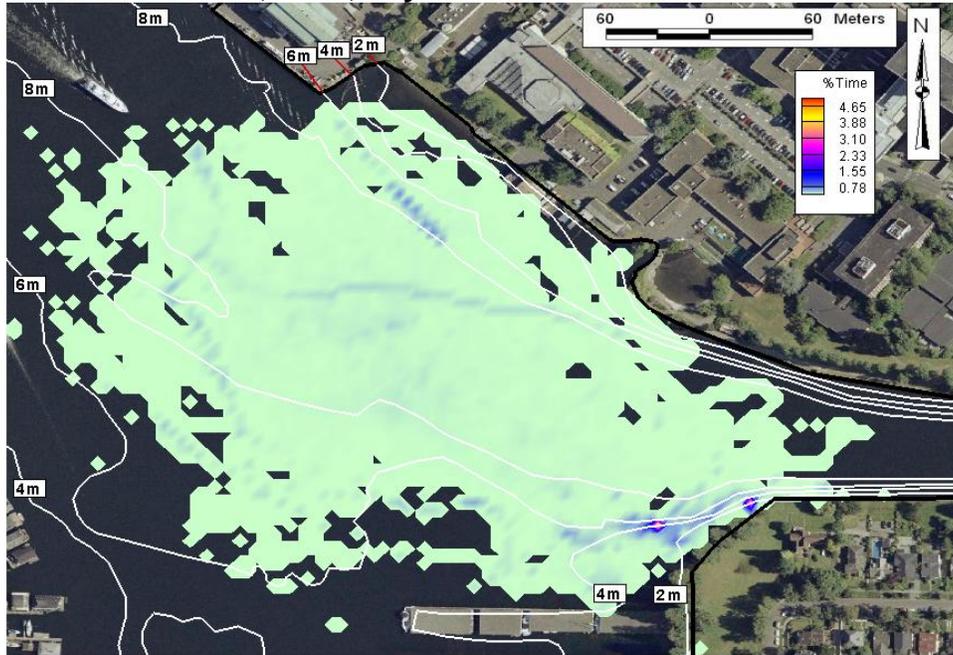


FIGURE 19. Relative daytime use of the Seattle Tennis Club site by wild and hatchery Chinook salmon smolts, June 2005. Relative use increases from light blue (lowest relative use) to red (highest relative use). Each fish was weighted equally.

A. Wild Chinook, 2004, day



B. Hatchery Chinook, 2004, day

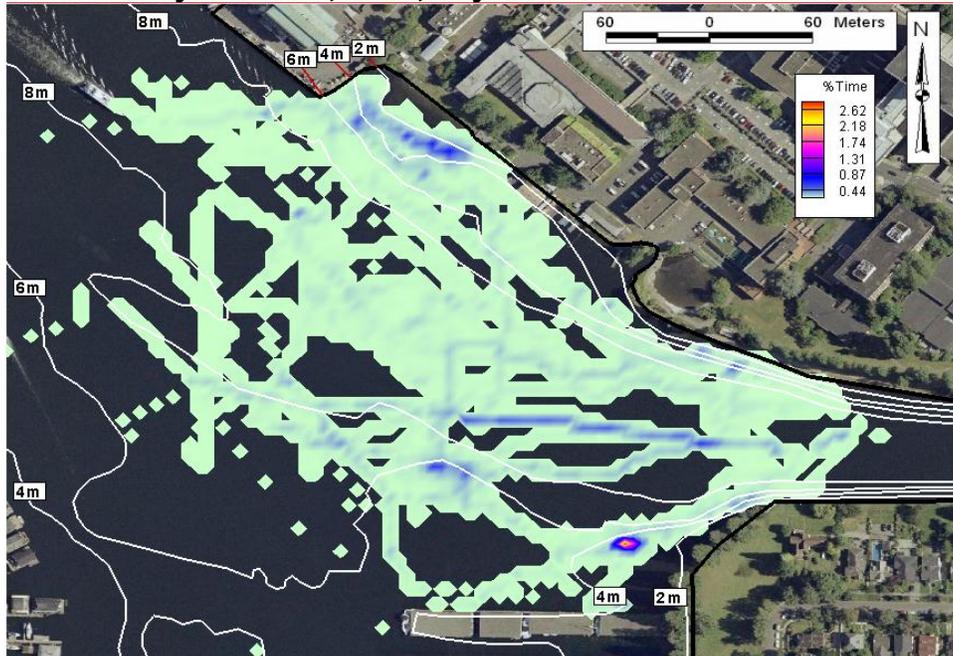
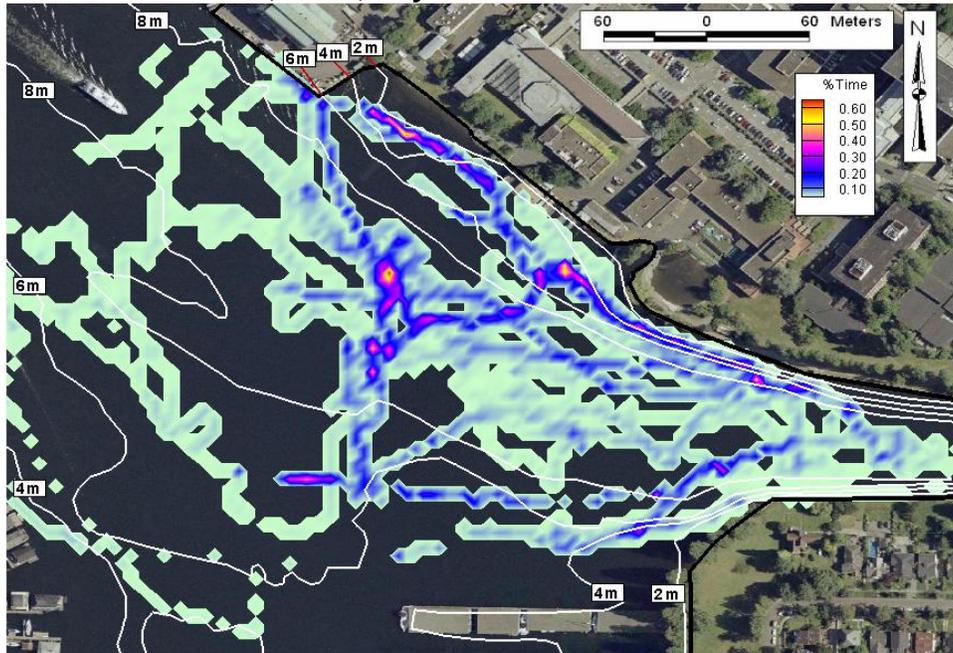


FIGURE 20. Relative daytime use of the Portage Bay site by Chinook salmon smolts, May-June, 2004-2005: A) wild fish, 2004; B) hatchery fish, 2004; C) wild fish, 2005; and, D) hatchery fish, 2005. Relative use increases from light blue (lowest relative use) to red (highest relative use). Each fish was weighted equally.

C. Wild Chinook, 2005, day



D. Hatchery Chinook, 2005, day

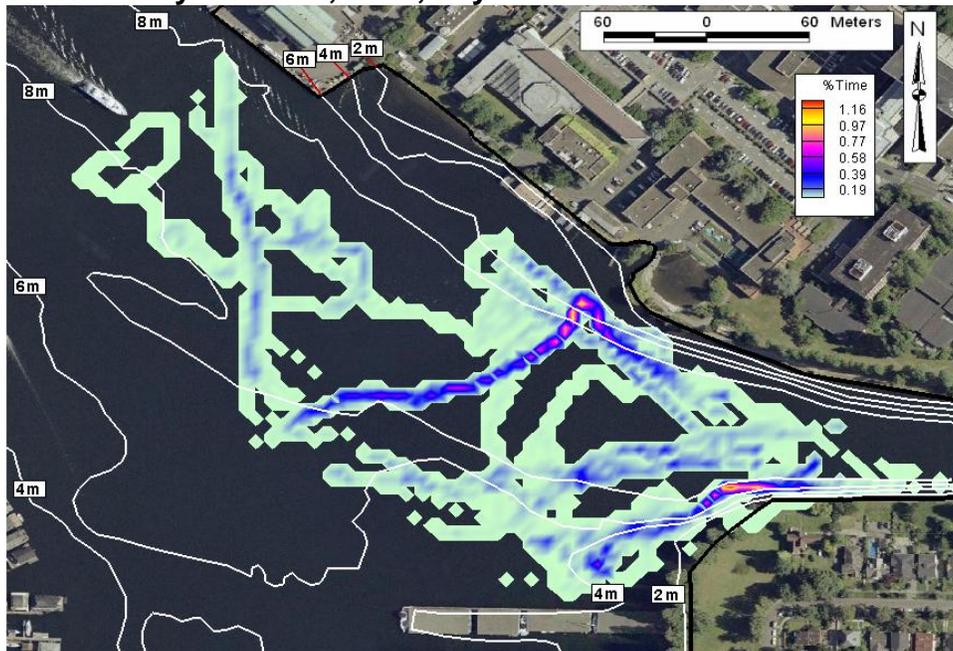
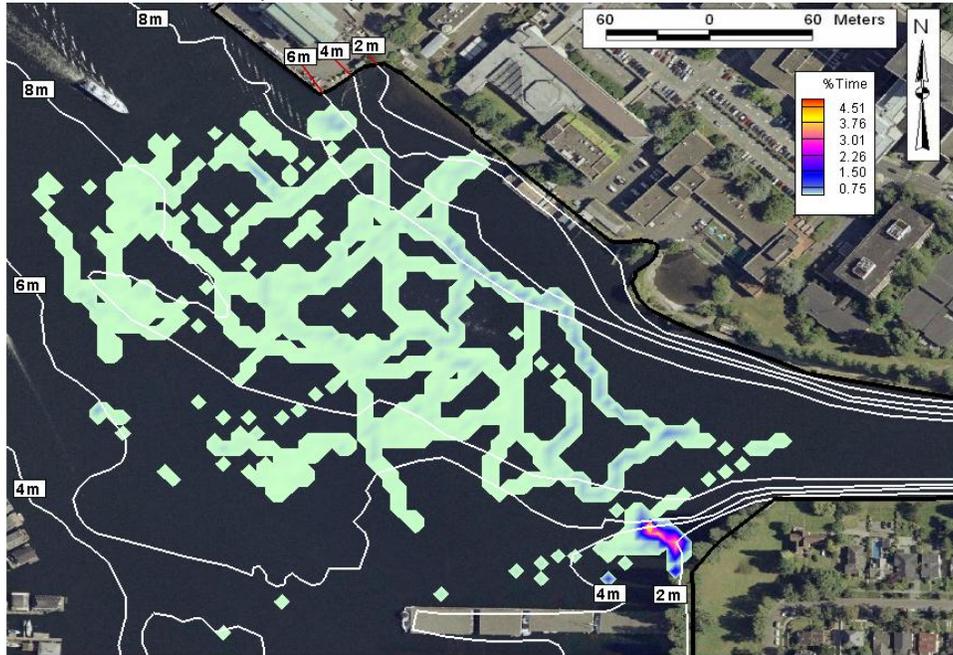


FIGURE 20. Continued.

A. Wild Chinook, 2004, dawn



B. Wild Chinook, 2004, dusk

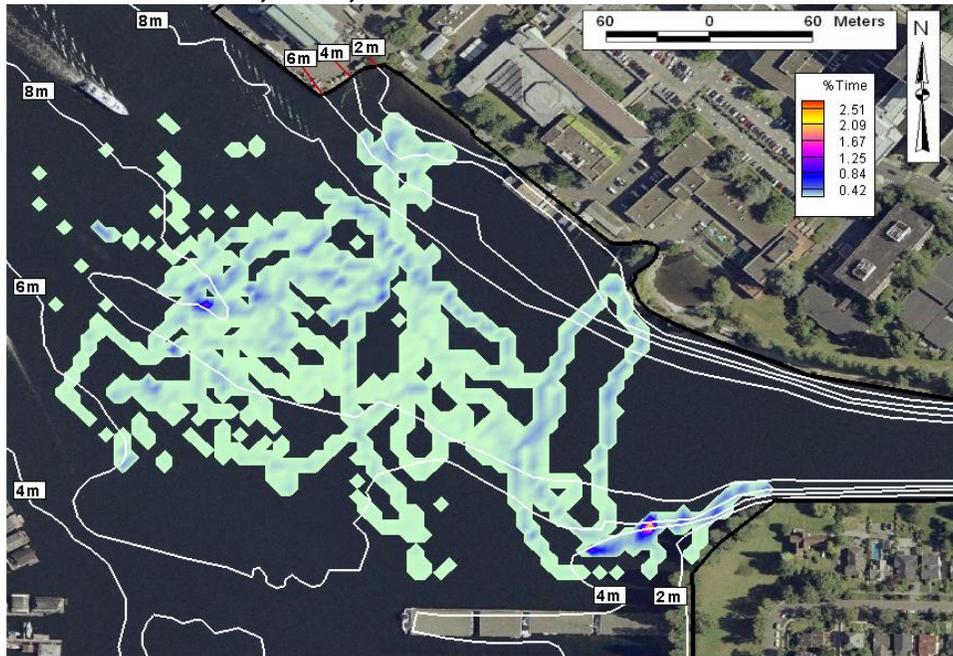


FIGURE 21. Relative use of the Portage Bay site by wild Chinook salmon smolts, May-June, 2004: A) dawn; B) dusk; and, C) night. Relative use increases from light blue (lowest relative use) to red (highest relative use). Each fish was weighted equally.

C. Wild Chinook, 2004, night

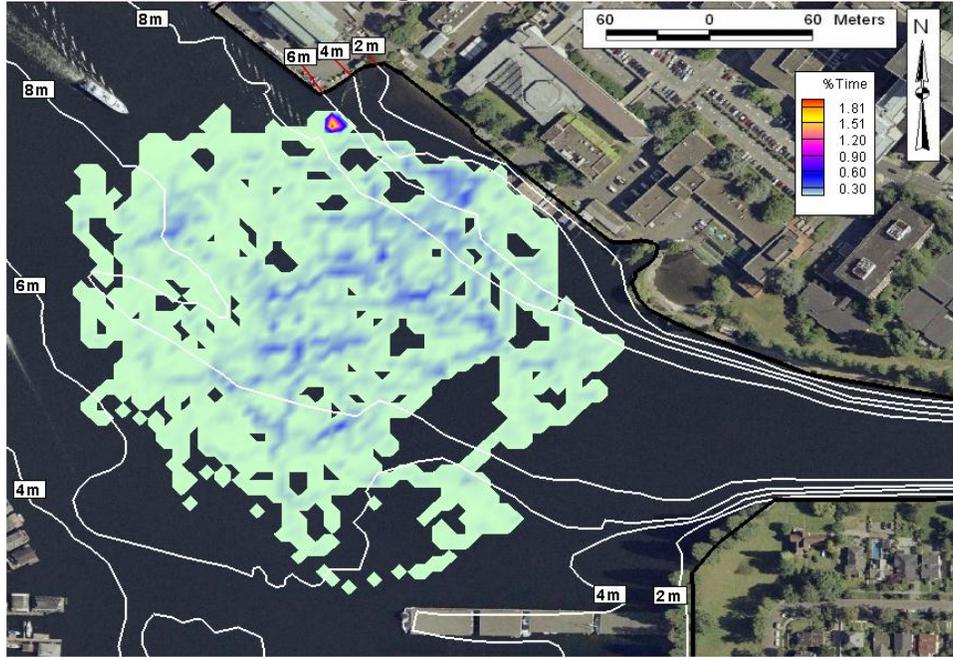
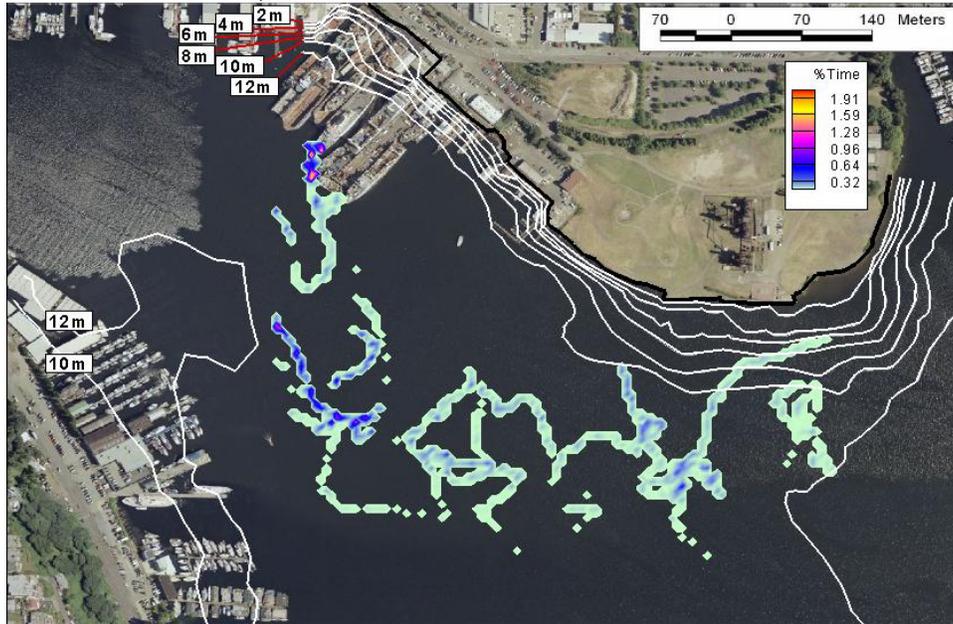


FIGURE 21. Continued.

A. Wild Chinook, dawn



B. Wild Chinook, day

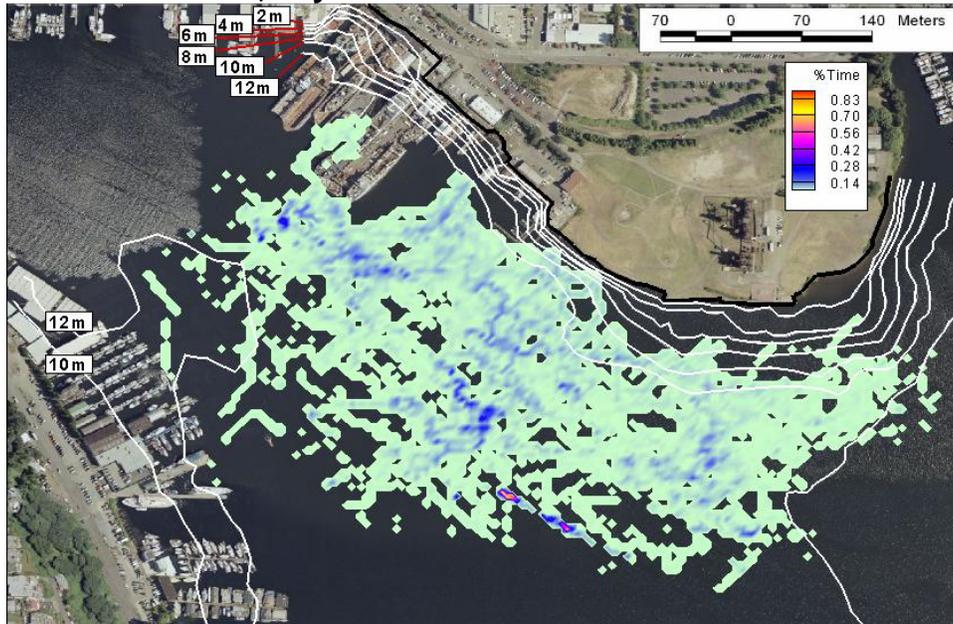
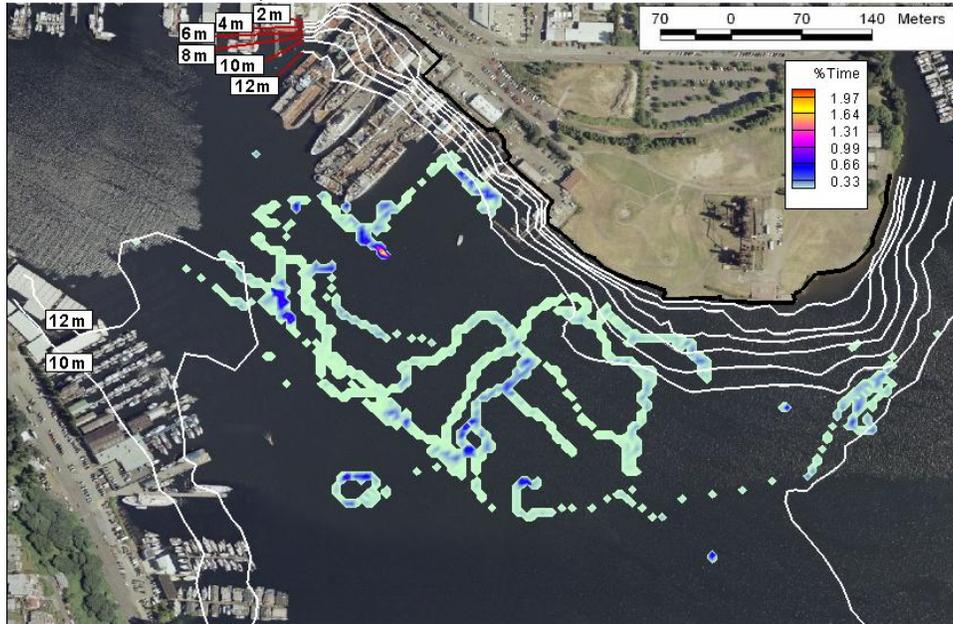


FIGURE 22. Relative use of the Gas Works Park site in north Lake Union by Chinook salmon smolts, May-June, 2005: A) wild smolts at dawn; B) wild, day; C) wild, dusk; D) wild, night; E) hatchery, day; and, F) hatchery, night. Relative use increases from light blue (lowest relative use) to red (highest relative use). Each fish was weighted equally.

C. Wild Chinook, dusk



D. Wild Chinook, night

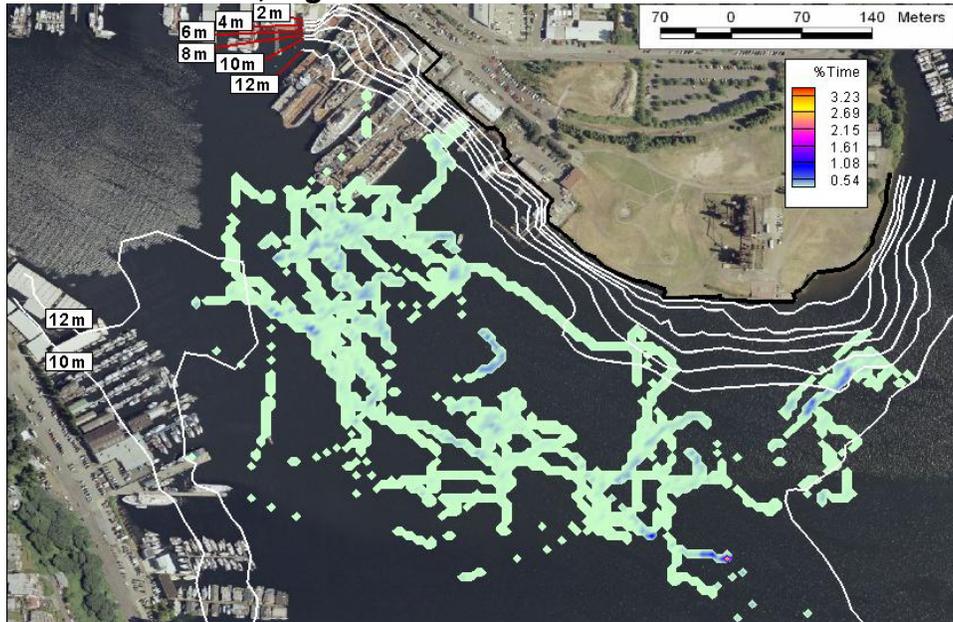
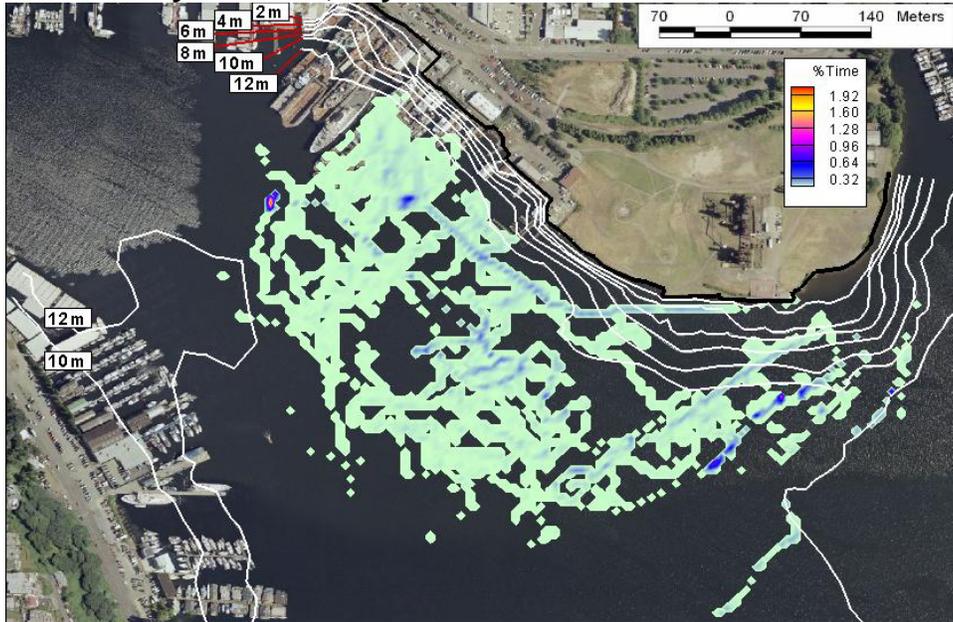


FIGURE 22. Continued.

E. Hatchery Chinook, day



F. Hatchery Chinook, night

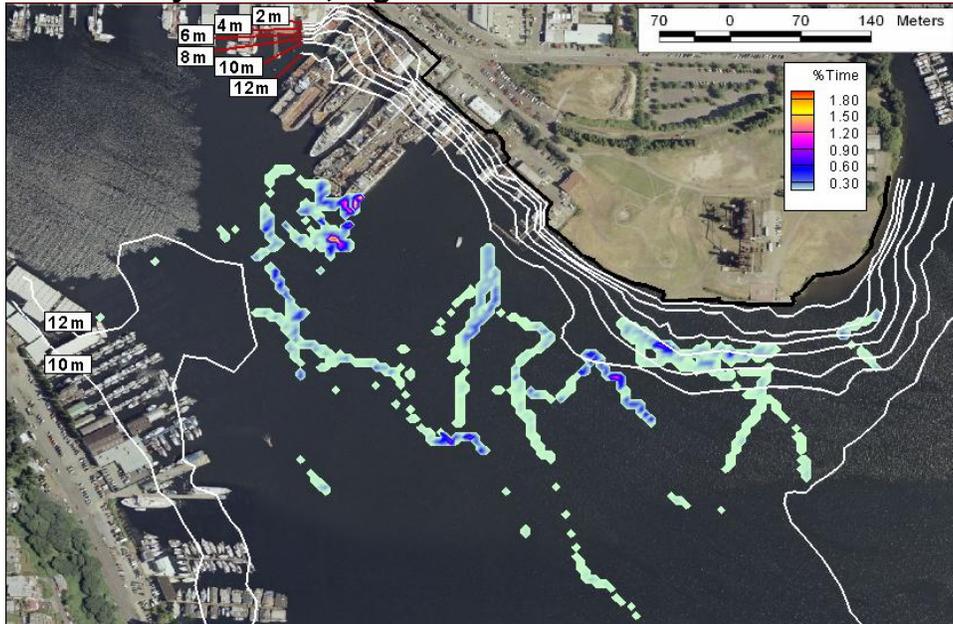


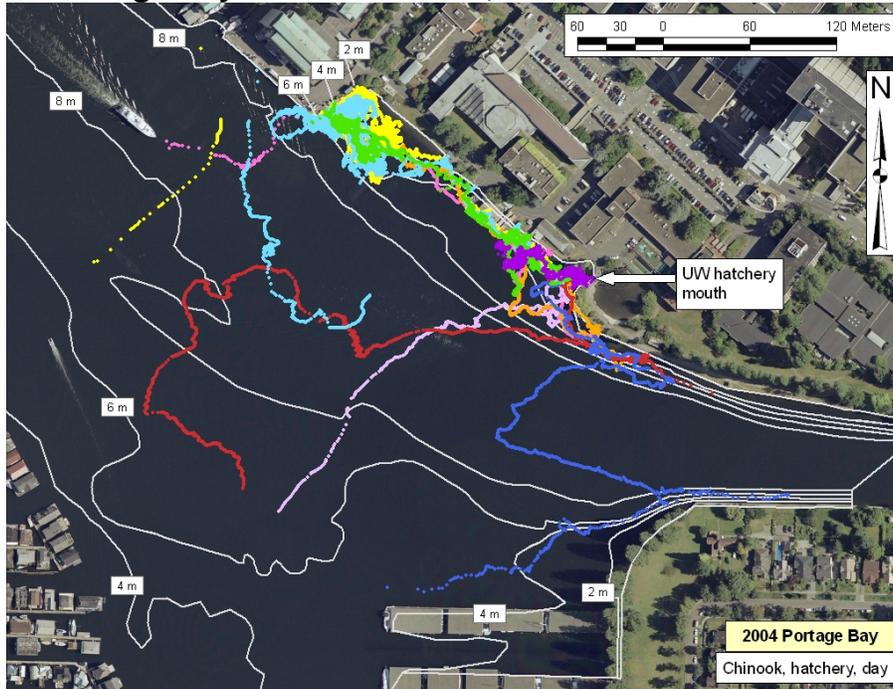
FIGURE 22. Continued.

On-site releases

Fish released on-site at the Portage Bay site showed markedly different patterns in behavior, shoreline orientation, depth selection, and spatial orientation than fish that entered the site volitionally. On-site releases of hatchery fish in 2004 and 2005 showed similar patterns to one another. Most fish milled around at slow speeds close to shore near the hatchery mouth release site for 0.5-11 hours before leaving the site (Figure 23). In both years, most fish were released early in the day and left the site later the same day. As such, there were few fish tracked during dawn, dusk or night. Greatest relative use occurred along the north shore where water was < 6 m deep between the hatchery mouth and the west bulkhead (Figure 24). In contrast, off-site releases were primarily off-shore and deep water oriented. A small degree of overlap in spatial distribution between on- and off-site releases was evident, but was minimal (compare Figures 20 and 24). Corresponding differences in depth selection ratios were also observed. Daytime depth selection for on-site releases was highest at water column depths < 4 m, and fish showed little use of or selection for water column depths > 6 m (Figure 13). Off-site releases were essentially opposite, showing much higher selection for deeper water, particularly in 2005. Shallow water was hardly used by fish released off-site: least selected depths were < 4 m in 2005, and < 2 m in 2004. Swim velocities were also different between on-site and off-site releases. Mean daytime swim velocities of on-site releases were 2.3 BL/s (SD, 0.7 BL/s) in 2004, and 2.7 BL/s (SD, 0.5 BL/s) in 2005. These were significantly slower than fish that volitionally entered the site (2004: pooled variance t-test, $P = 0.040$; 2005: pooled variance t-test, $P = 0.002$), and more closely matched those of holding fish in general regardless of site (Table 3).

Fish released at Gene Coulon Park showed similar patterns as fish released on-site at Portage Bay. Fish at Gene Coulon Park milled about at slow speeds close to shore in shallow water near the release site for several hours before leaving the tracking area. Most fish at Gene Coulon Park were released at night and left the site during the following dawn and day. Residence time was 1.7-18 hours for 9 of the 11 tracked fish. Mean nighttime swim velocity was 1.1 BL/s (SD, 0.3 BL/s), which was comparable to nighttime swim velocities of holding fish at other study sites (Table 3). Fish dispersed across and milled about much of the tracking area enclosed by the overwater walkway (Figure 25). Shallow depths < 2 m were strongly selected for during all diel periods, although there was considerable variability among tagged fish (Figure 13). Tecplot images showed moderate to heavy use along the shore in water < 2 m deep (Figure 26). Nine of the 11 tracked fish spent a substantial proportion of their time in these shallow nearshore areas. One fish milled extensively beneath a 40 m length of the boardwalk on the northwest side during the day (Figure 25). This was a drastically different behavior than the other fish, and may be indicative of predation. That is, the tagged Chinook salmon may have been consumed by a predator. The observed tracks would then represent the predator's movement.

A. Portage Bay on-site releases, 2004



B. Portage Bay on-site releases, 2005

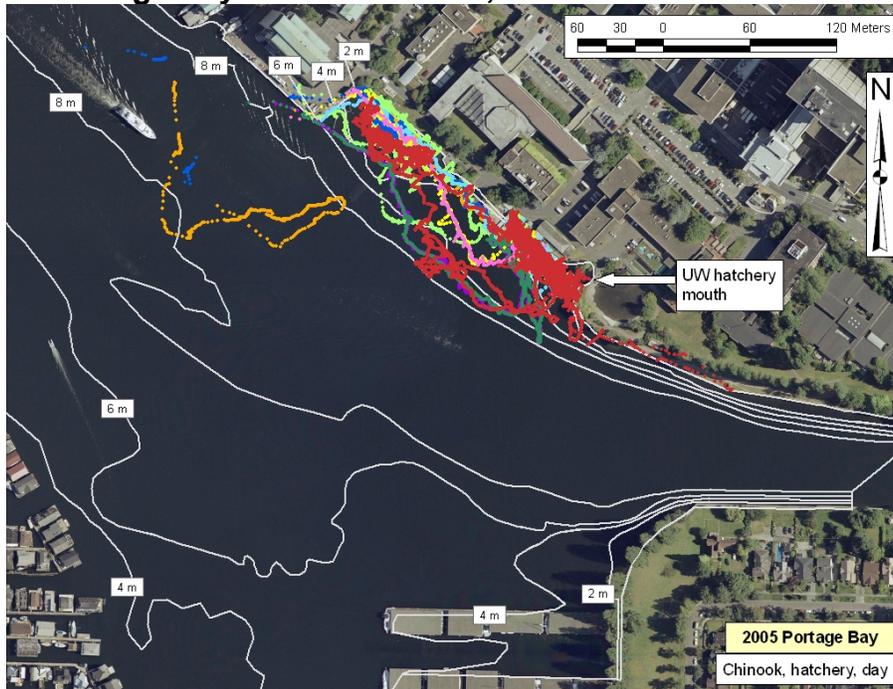
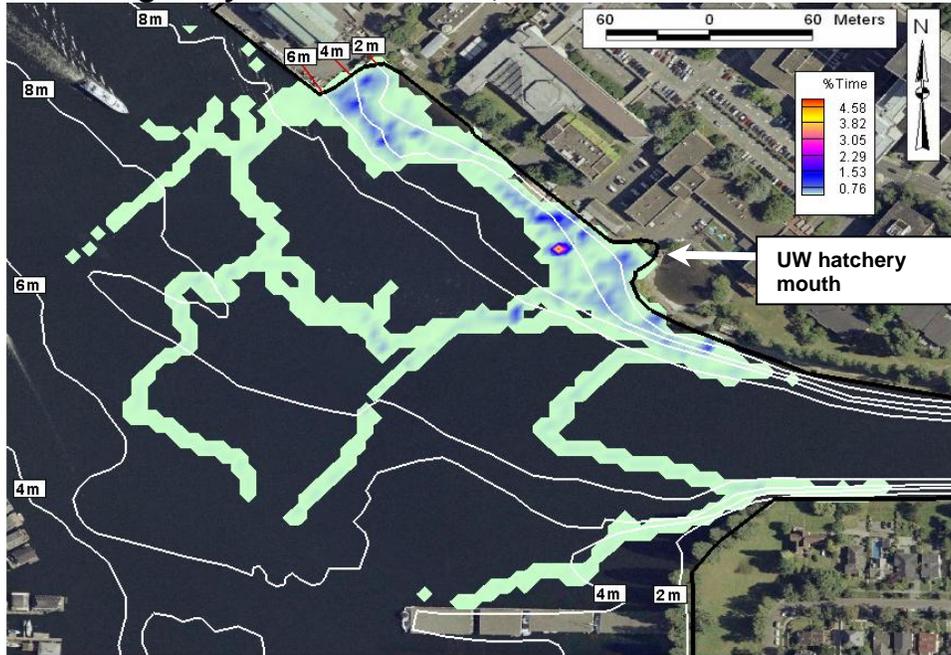


FIGURE 23. Daytime movement pathways of Chinook salmon smolts released on-site at the University of Washington hatchery mouth in Portage Bay, May, 2004-2005. Each color represents an individual fish.

A. Portage Bay on-site releases, 2004



B. Portage Bay on-site releases, 2005

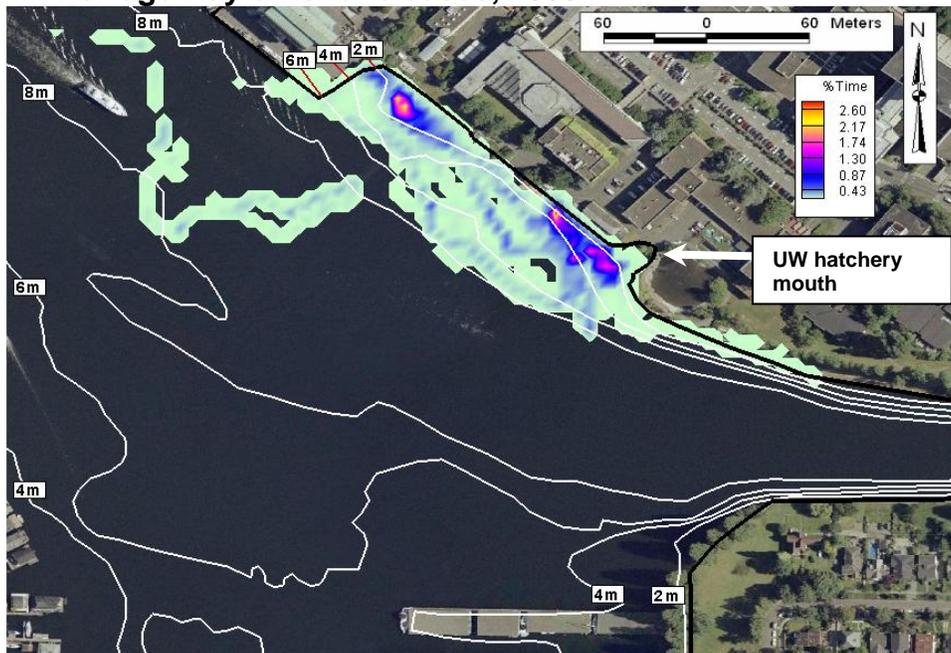
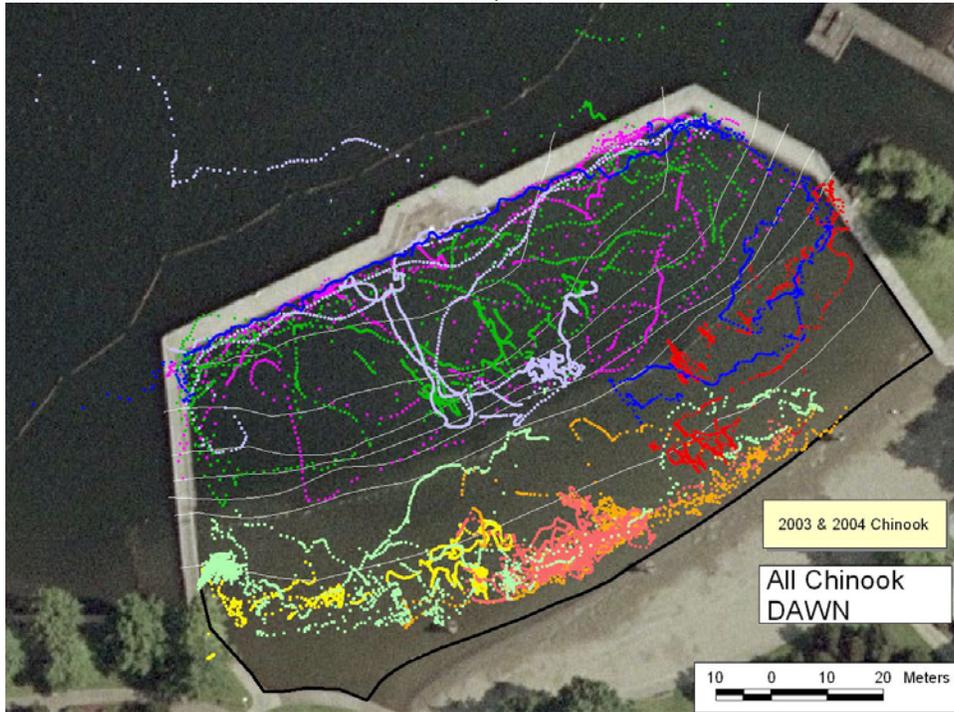


FIGURE 24. Relative daytime use of the Portage Bay site by Chinook salmon smolts released on-site at the University of Washington hatchery mouth, May, 2004-2005. Relative use increases from light blue (lowest relative use) to red (highest relative use). Each fish was weighted equally.

A. Gene Coulon Park 2003-2004, dawn



B. Gene Coulon Park 2003-2004, day

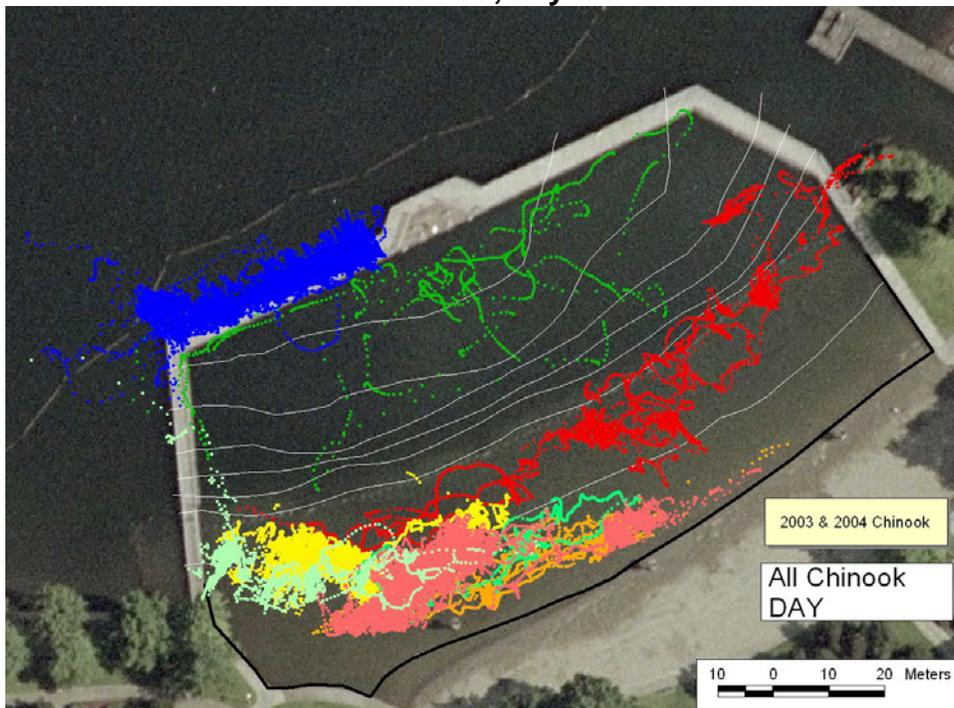


FIGURE 25. Movement pathways of wild Chinook salmon smolts released on-site at the Gene Coulon Park site, May-June, 2003-2004. A) dawn; B) day; and, C) night. Each color represents an individual fish.

C. Gene Coulon Park 2003-2004, night

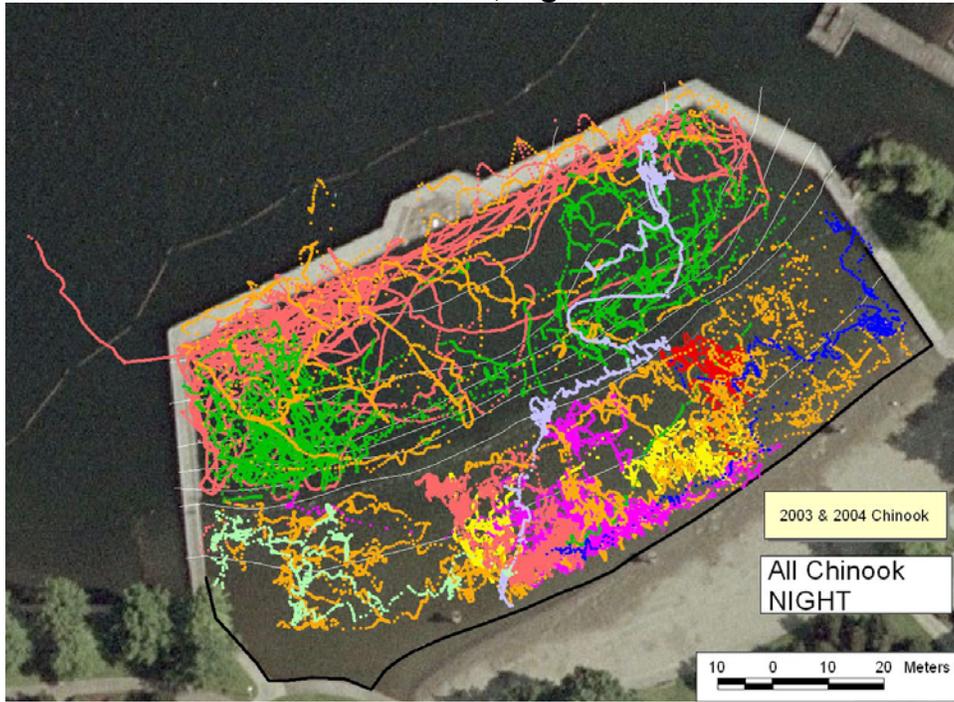


FIGURE 25. Continued.

A. Gene Coulon Park 2003-2004, dawn



B. Gene Coulon Park 2003-2004, day

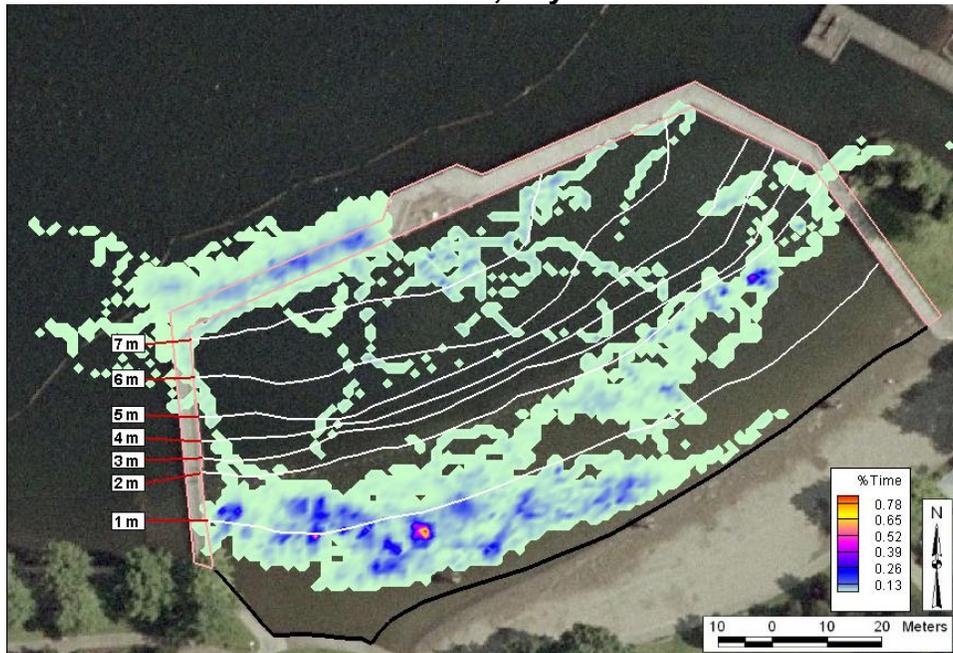


FIGURE 26. Relative use of the Gene Coulon Park site by wild Chinook salmon smolts released on-site, May-June 2003-2004. A) dawn; B) day; and, C) night. Relative use increases from light blue (lowest relative use) to red (highest relative use). Each fish was weighted equally.

C. Gene Coulon Park 2003-2004, night

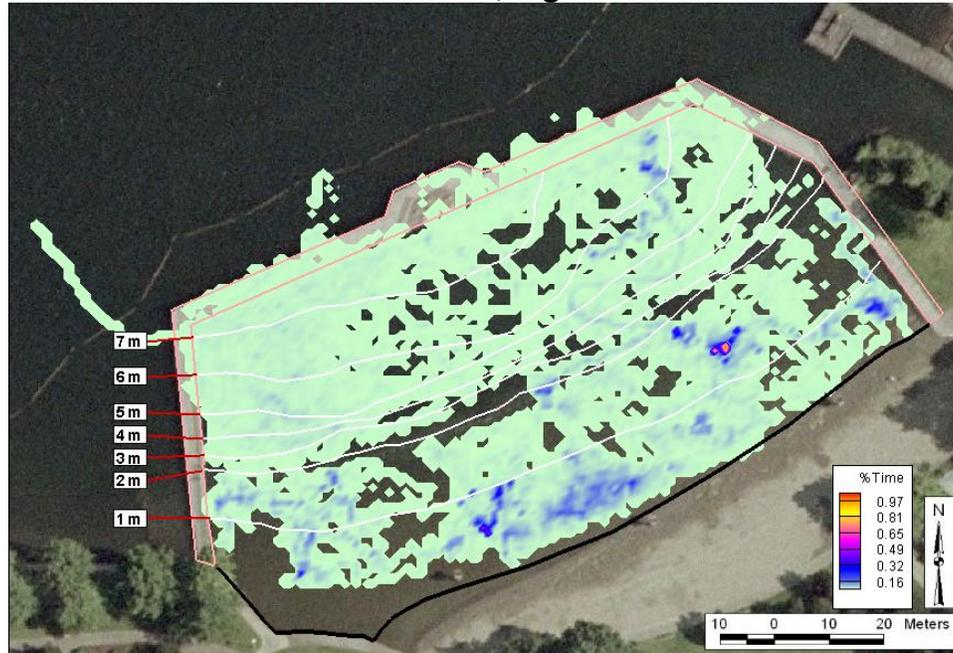


FIGURE 26. Continued.

Macro-scale movement patterns

In 2004, none of the nine fish released at Gene Coulon Park, and one of the four fish released in the Cedar River were detected at Portage Bay. The Cedar River fish was released on June 16 at 10:45 hours and was detected 5 days later on June 21 at 06:01 hours.

In 2005, Chinook salmon smolts traveling from the Seattle Tennis Club to Portage Bay showed two distinct behaviors, although these observations were based on relatively small sample sizes. Some fish (33%) appeared to actively migrate directly to Portage Bay within hours after leaving the Seattle Tennis Club site. Other fish (56%) appeared to hold between the sites for a day or more. Five wild and four hatchery fish were detected at both sites. Of these, one wild and two hatchery fish appeared at Portage Bay 3-4 hours after leaving the Seattle Tennis Club site. These fish travelled the 4.5 km shoreline distance between the sites at mean velocities of 3.0-3.5 BL/s. These velocities were likely underestimated because distance traveled was based on straight shoreline distance. Actual distance swam was probably greater due to natural tortuosity of fish swim paths, and additional distances required to move around structures and other obstacles. Therefore, swim velocities were likely greater and probably more closely matched those that we observed in actively migrating fish at the meso-scale. Conversely, four wild and one hatchery fish went undetected for 1-3 d after leaving the Seattle Tennis Club site. These fish presumably spent this time holding, resting or rearing between the two sites.

The remaining hatchery fish traveled from the Seattle Tennis Club to Portage Bay (16 h), back to the Seattle Tennis Club (11 h), then back to Portage Bay (3.2 h) and on to Gas Works Park. Fish size did not appear to be a factor in determining whether Chinook salmon actively migrated or held between the two sites. Release date relative to the nearest apogee may have influenced behavior. All actively migrating fish were released six days or less from the nearest apogee, and four of the five holding fish were released 13 days from the nearest apogee.

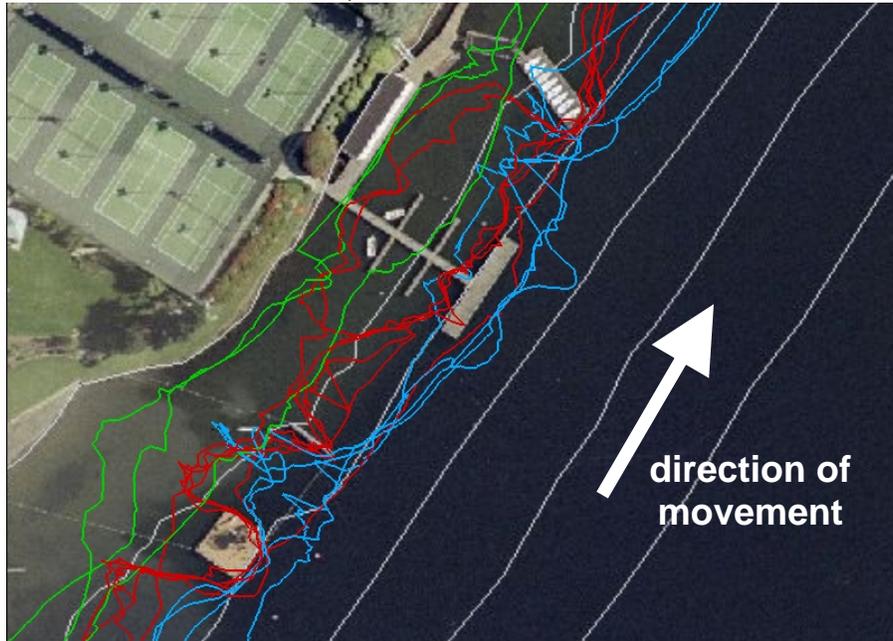
Fish traveled from Portage Bay to Gas Works Park relatively quickly, although these observations were based on relatively small sample sizes. Many fish were observed at both sites; however, substantial equipment downtime events lasting 4-5 d (two events at Gas Works Park, one at Portage Bay) obscured travel times for many fish. These fish were not considered in travel time calculations unless they left one site and appeared at the next during a time period unaffected by equipment problems. This left five wild and nine hatchery fish useable for travel time estimates. Of these, 57% (two wild and six hatchery) appeared to actively migrate from Portage Bay to Gas Works Park. These fish travelled the 2.5 km straight shoreline distance between the sites in 1.3-2.2 h at mean velocities of 2.5-4.5 BL/s (mean, 3.3 BL/s; SD, 0.6 BL/s). Again, actual distance traveled and swim velocities were likely underestimated, and actual velocities probably more closely matched those that we found for actively migrating fish at the meso-scale. The remaining three wild and three hatchery fish were all detected at Gas Works Park within 13 h of leaving Portage Bay. These fish appeared to move more slowly between sites; however, travel times may have been slightly inaccurate because tracking area boundaries did not cover the full width of either site at the ends closest to one another. Once detected at Gas Works Park, no fish were observed backtracking to Portage Bay.

Movement around overwater structures

Juvenile Chinook salmon generally avoided areas directly beneath overwater structures. However, areas along the edges of structures (within about 2 m horizontal distance) were sometimes used for prolonged periods (up to 2 hours in one case). This use of edges was primarily observed in fish released on-site at the Portage Bay and Gene Coulon Park sites. These observations may be representative of holding fish near structures in general, but may not be an accurate indication of how untagged Chinook salmon would generally behave upon volitionally entering these specific areas. Actively migrating fish (i.e., most fish released off-site and observed at the Seattle Tennis Club site) often appeared to change course as they approached a structure. Structure width and water depth appeared to influence degree of avoidance. Fish appeared less hesitant to pass beneath narrow structures. Fish also appeared to move into deeper water to travel beneath or around structures.

The Seattle Tennis Club site had three main structures extending into the migrational corridor used by tracked fish (Figure 27). An 11 m square diving platform was located on the south side of the site. In the center of the site was a boat dock with a 2 m wide walkway extending perpendicular to shore. Extending out from this main walkway were

A. Seattle Tennis Club, structures



B. Seattle Tennis Club, after structures

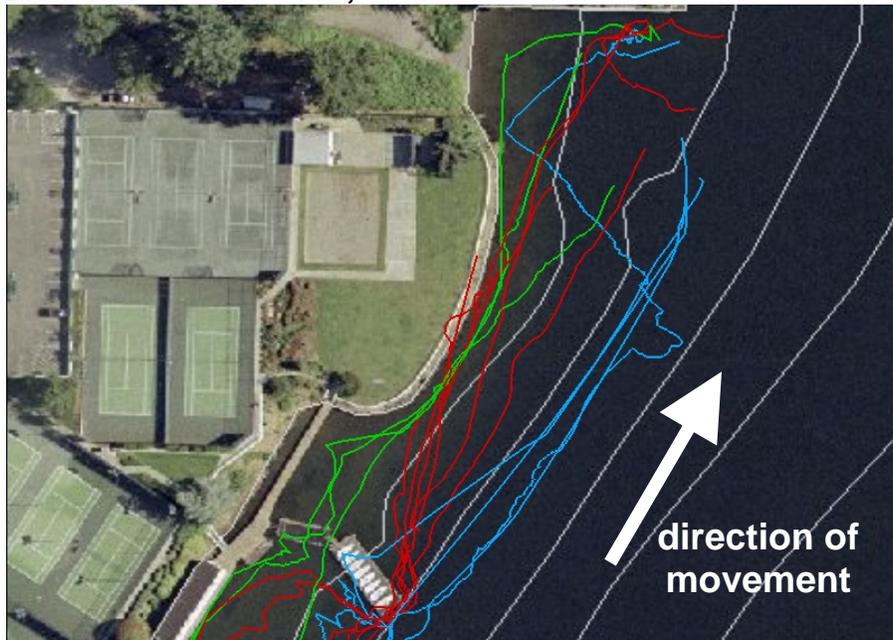


FIGURE 27. Movement of Chinook salmon smolts around overwater structures at the Seattle Tennis Club site, June, 2005. A) movement around the structures themselves; and, B) movement after passing the last structure. Each line is a different fish. Colors represent predominant water column depths used and degree to which structures appeared to influence movement: green fish (n=3) remained in shallow water (< 2 m) and were minimally affected by structures; red fish (n=6) were in deeper water (2-4 m) and responded substantially to structures; and blue fish (n=4) were in the deepest water (4-6 m) and responded moderately to structures.

four narrow (1 m wide) walkways. A 3.8 m wide walkway running parallel to shore was at the end. On the north side of the site was another boat dock. This dock was segmented into two parts: a 3.9 m wide section close to shore and a 5.0 m wide section farther from shore. These two sections were joined by a short narrow walkway that measured 1.0 m wide and 1.2 m long. There were also two minor structures between the diving platform and the center boat dock. In addition, there was a structure that ran parallel to the shore in shallow water and connected the two boat docks and a protruding shoreline to the north. This structure varied in width between 2 m and 4 m.

We evaluated 13 Chinook salmon smolt tracks through and around the dock structures at the Seattle Tennis Club site. These tracks were believed to be representative of actively migrating Chinook salmon through this site based on our results. Other fish were not included because they either were not tracked through this portion of the site, or because they showed behaviors other than active migration. Three fish (green lines in Figure 27) remained in shallow water < 2 m deep and did not appear to respond much to structures. Most other fish appeared to avoid the areas directly beneath the diving platform and the outer segment of the north boat dock. Upon approaching these structures, most tracks showed an obvious change in direction toward deeper water beyond the outer edge of the structure. Once beyond the structures, many fish appeared to move back closer to shore. Six fish (red lines in Figure 27) on the south end of the site appeared to respond to something else in addition to the dive platform. These fish were traveling parallel with the shore at 2 m depth where they would have passed between the shore and the dive platform. However, as these fish approached the buoy line that extended from the shore to the dive platform, they made an abrupt 90° turn toward deeper water. Four of these fish appeared schooled together, and two were not schooled with any other tagged fish. After moving around the platform, 5 of these fish abruptly turned back toward shallow water. All of these fish showed similar responses to the boat dock on the north end of the site. Four fish (blue lines in Figure 27) appeared primarily deep water oriented and appeared somewhat affected by the presence of the structures, but not as much as the six fish described above.

Behavior around aquatic macrophytes

Relatively large beds of aquatic macrophytes were present at the Seattle Tennis Club and Portage Bay sites (Figures 3 and 4). At the Seattle Tennis Club site there was considerable overlap between Chinook salmon smolt migration pathways and the milfoil bed that ran the length of the site (Figure 28). Fish migrated in shallow nearshore areas where milfoil was lacking, and over the milfoil bed to a depth of about 5 m. At Portage Bay, most Chinook salmon activity was off-shore away from macrophyte beds. However, some fish were observed migrating and holding near macrophyte beds (Figure 29). These fish did not appear to use macrophytes extensively, and were also observed in open water areas.

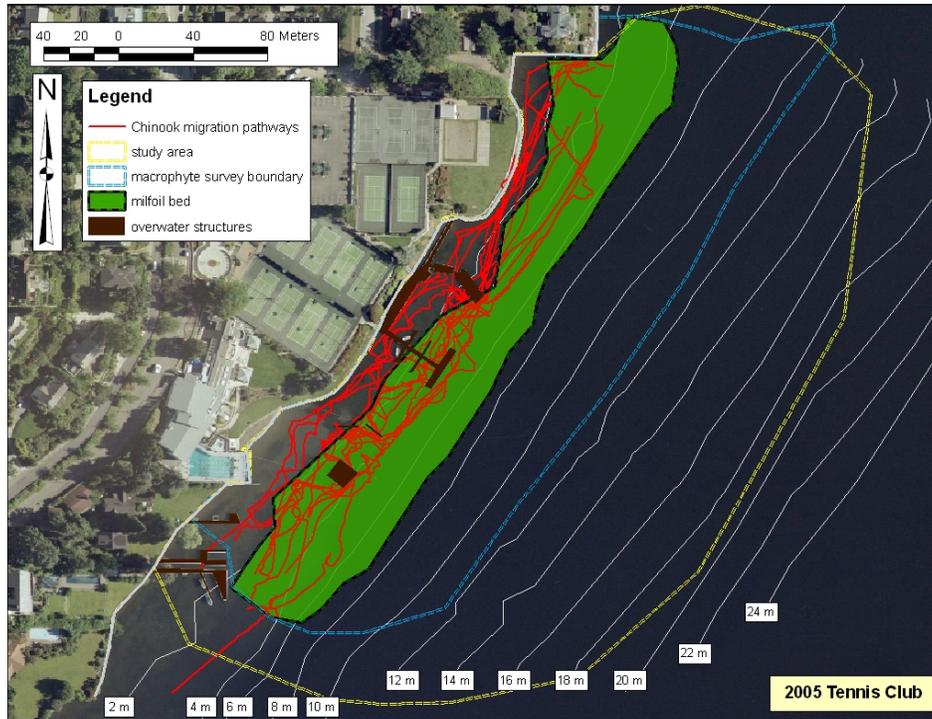


FIGURE 28. Migration pathways of Chinook salmon smolts in relation to milfoil bed at the Seattle Tennis Club site, June, 2005. Direction of Chinook salmon movement is from south to north.

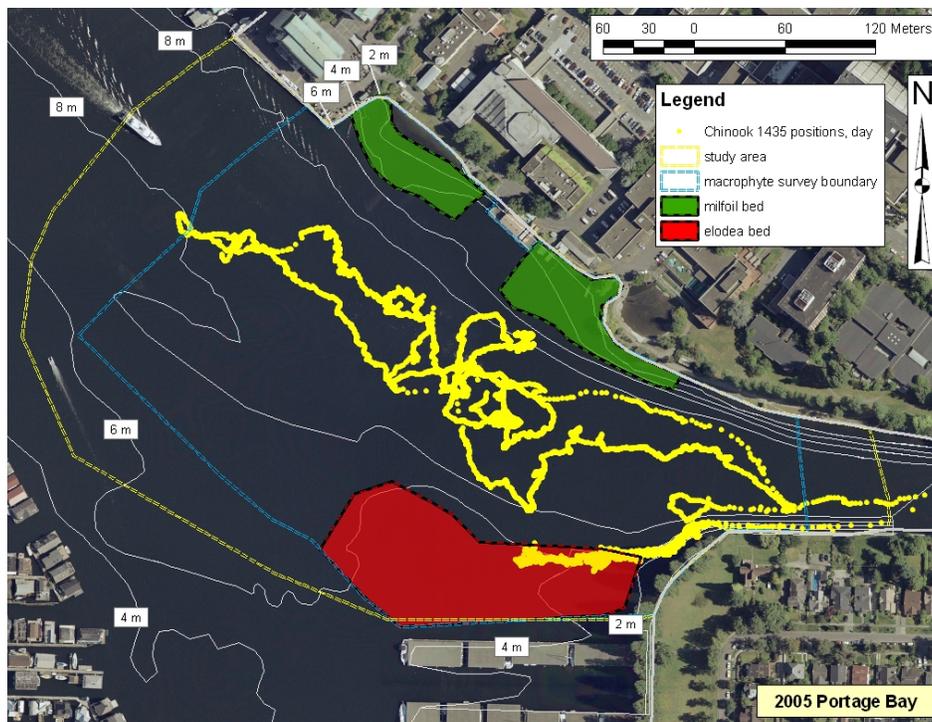


FIGURE 29. Example of a Chinook salmon smolt utilizing macrophyte and open water areas of the Portage Bay site, June, 2005.

Smallmouth bass

A wide range of sizes of smallmouth bass were captured and tagged (Table 5; range, 145-442 mm FL). Of the 24 tagged smallmouth bass (2004 and 2005 combined), we were able to get useful tracking information on 19. The remaining five fish were captured near the periphery of the array and were only tracked for a brief time and appeared to leave the array area. Altogether, we obtained over 500,000 data points of smallmouth bass.

Smallmouth bass were generally in water that was less than 4 m deep; however, there was large variability between individuals (Figure 30). Only one bass was observed to use water > 8 m to any extent. For most smallmouth bass, there was little difference between day, dusk, night, and dawn depth selection. However, some smallmouth bass appeared to make occasional forays into deeper water at dawn and dusk.

TABLE 5. Summary data of smallmouth bass tagged with acoustic tags at four locations; two in Lake Washington (Gene Coulon Park and Seattle Tennis Club) and two in the LWSC (Portage Bay and Gas Works Park), May-June 2004 and 2005. ND = no data. Number of data points after 24 h is the number after 24 h of the fish being released.

Year	Location	Tag period	Fork length (mm)	Date released	Date of last data point	Total # of data points	# of points after 24 h
2004	Gene Coulon Park	1260	160	5/25	6/3	2,791	2,503
	Gene Coulon Park	1270	145	5/25	ND	0	0
	Gene Coulon Park	1280	160	5/25	6/4	15	7
	Portage Bay	1970	390	6/9	6/30	7,476	6,070
	Portage Bay	1980	410	6/9	6/17	228,845	198,573
	Portage Bay	4007	300	5/17	6/19	3	0
	Portage Bay	4017	275	5/17	6/9	6,637	6,472
	Portage Bay	4027	400	5/17	6/8	13,762	13,140
2005	Tennis Club	5083	224	6/16	6/23	7,699	1,804
	Tennis Club	5088	173	6/16	6/30	38,649	35,203
	Tennis Club	5203	226	6/10	6/14	22,578	21,705
	Tennis Club	5293	195	6/23	6/30	4,342	656
	Tennis Club	5298	415	6/23	6/30	58,387	55,515
	Portage Bay	5008	442	5/11	5/29	36,761	30,512
	Portage Bay	5013	372	5/11	5/13	15,321	10,733
	Portage Bay	5014	374	5/13	5/19	13,901	12,619
	Portage Bay	5018	350	5/13	5/21	2,465	443
	Portage Bay	5103	308	5/26	6/15	863	497
	Gas Works Park	5108	270	5/26	6/20	99,611	96,632
	Gas Works Park	5118	222	5/26	6/3	4,654	14
	Gas Works Park	5123	215	5/26	6/20	5,740	679
	Gas Works Park	5128	244	5/26	6/8	66,089	60,544
	Gas Works Park	5133	220	5/26	6/8	9,708	4,788
	Gas Works Park	5138	310	5/26	5/27	2,392	0

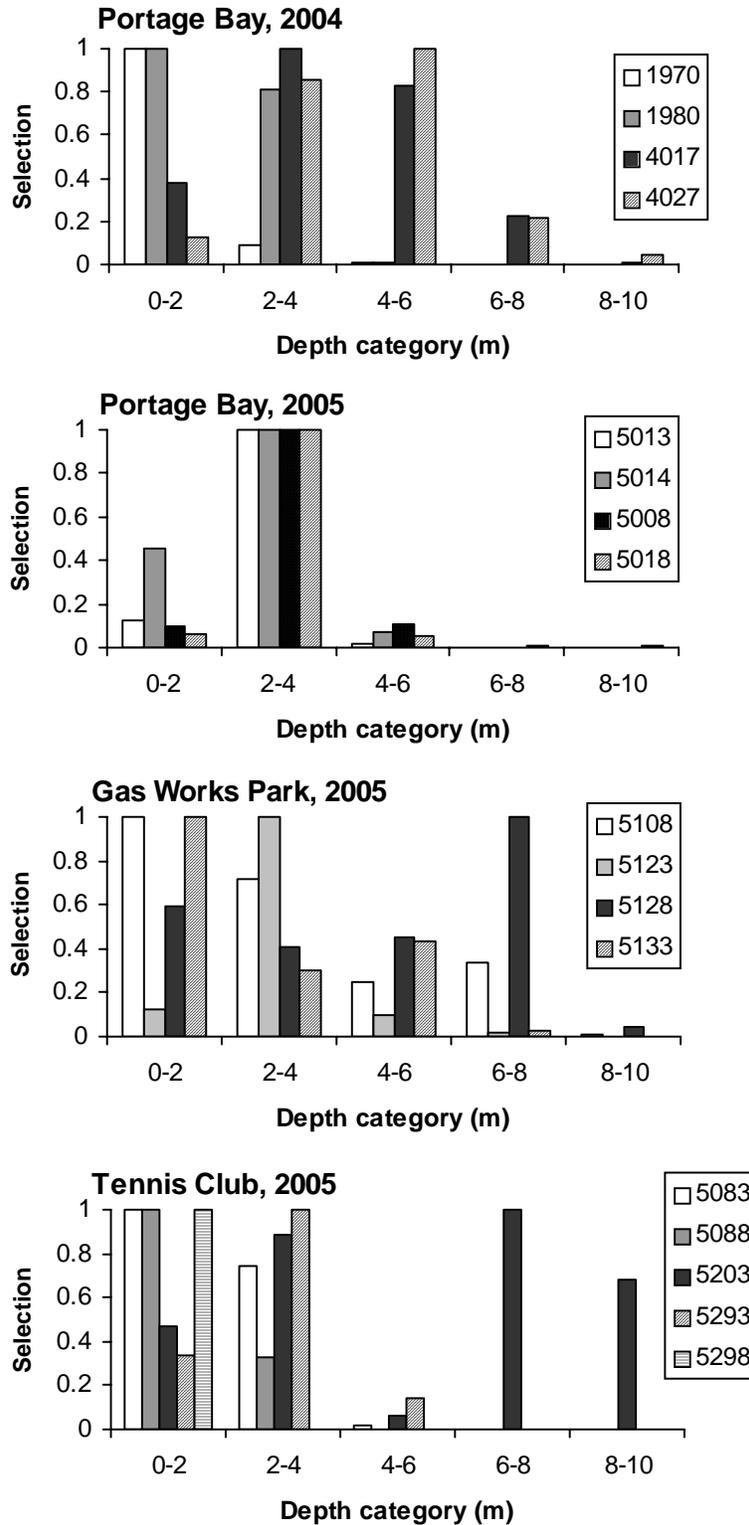


FIGURE 30. Depth selection (m, depth of entire water column) of individual smallmouth bass from two locations in the LWSC (Portage Bay and Gas Works Park) and one location in Lake Washington (Seattle Tennis Club), May-June 2004 and 2005. Labels represent the tag period for each smallmouth bass.

Smallmouth bass that infrequently used overwater structures tended to be in deeper water than bass that frequently used overwater structures. An average of 48% of the data points of bass that frequently used overwater structures were between 0 and 2 m deep. In contrast, only 28% of data points of bass that rarely used overwater structures were between 0 and 2 m deep. The mean depth selection for bass that frequently used overwater structures was highest at 0-2 m deep; whereas, it was 2-4 m for the other bass (Figure 31).

Intermediate-sized smallmouth bass (225-300 mm FL) tended to be in deeper water than either small-sized bass (150-225 mm) or large bass (> 300 mm) (Figure 32). The shallow depth selection of the small and large bass may have been due in part to their association with overwater structures. Half of both the small and large smallmouth bass frequently used overwater structures; whereas, only one of the six intermediate-sized bass frequently used overwater structures.

Smallmouth bass were usually closely associated with one of three habitat types, either an overwater structure (Figure 33), rocky shoreline including rip rap (Figure 34), or the offshore edge of aquatic macrophytes (Figures 35 and 36). At Portage Bay and the Seattle Tennis Club, where all three habitat features were present, some smallmouth bass appeared to move between the three habitat types. Seven of the 19 smallmouth bass were closely associated with an overwater structure throughout the tracking period. Overall, 10 of 19 smallmouth bass showed a selection for overwater structures. They were more often located near (within 2 m) an overwater structure than would be expected based on the percentage of the coverage area comprised of overwater structures (chi-square analysis, $\chi^2 > 3.8$, $P < 0.05$). The percentage of detections near overwater structures for one bass was similar to the amount available. The remaining six bass appeared to avoid overwater structures (chi-square analysis, $\chi^2 > 3.8$, $P < 0.05$).

Shoreline type selection also varied greatly between individuals; however, there was little use of beach shoreline by any smallmouth bass (Figure 37). Beach shorelines generally had a much lower gradient than the other shoreline types. The other four shoreline types (riprap, bulkhead, riprap with overwater structures, and bulkhead with overwater structures) were commonly used by smallmouth bass. There did not appear to be any strong trends among the other shoreline types. A larger sample size is probably needed to discern any difference.

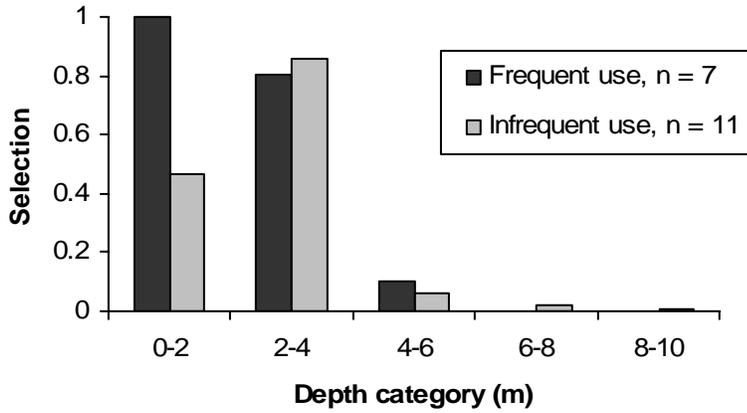


FIGURE 31. Median depth selection (m, depth of entire water column) of smallmouth bass with different levels of use of overwater structures. Frequent use = > 40% of data points are within 2 m or less of an overwater structure; Infrequent use = < 20%. N = number of tagged smallmouth bass.

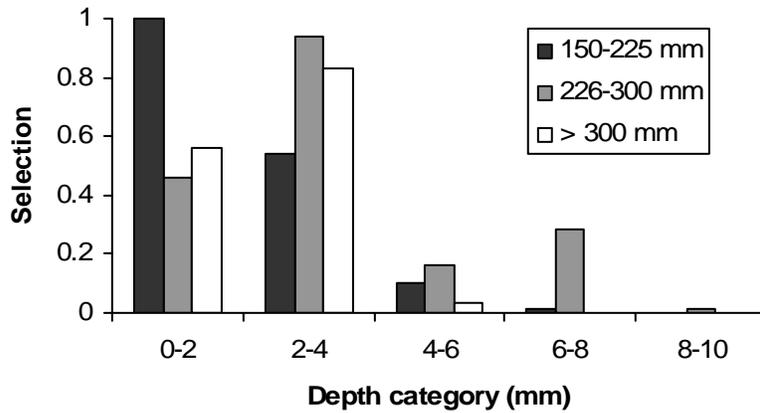


FIGURE 32. Median depth selection (m, depth of entire water column) of three size categories (mm, FL) of smallmouth bass. Sample size was six for each size category.

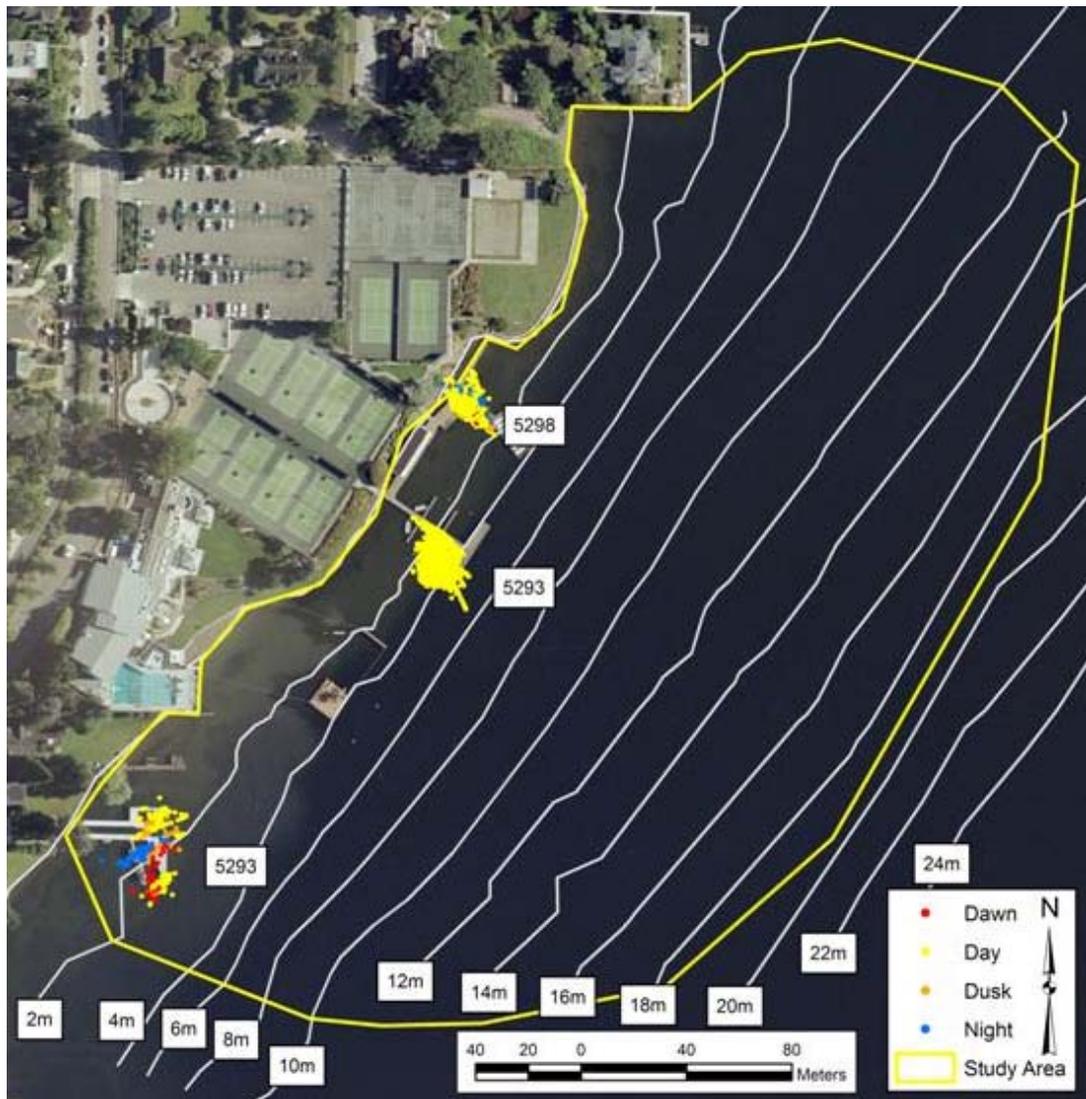


FIGURE 33. Locations of two smallmouth bass which were closely associated with overwater structures at the Seattle Tennis Club site, Lake Washington, June 2005. Fish #5298 spent the entire time (7 d) at one location while the other smallmouth bass spent 7 h at the more northerly structure and was detected periodically over the course of six days at the other structure.

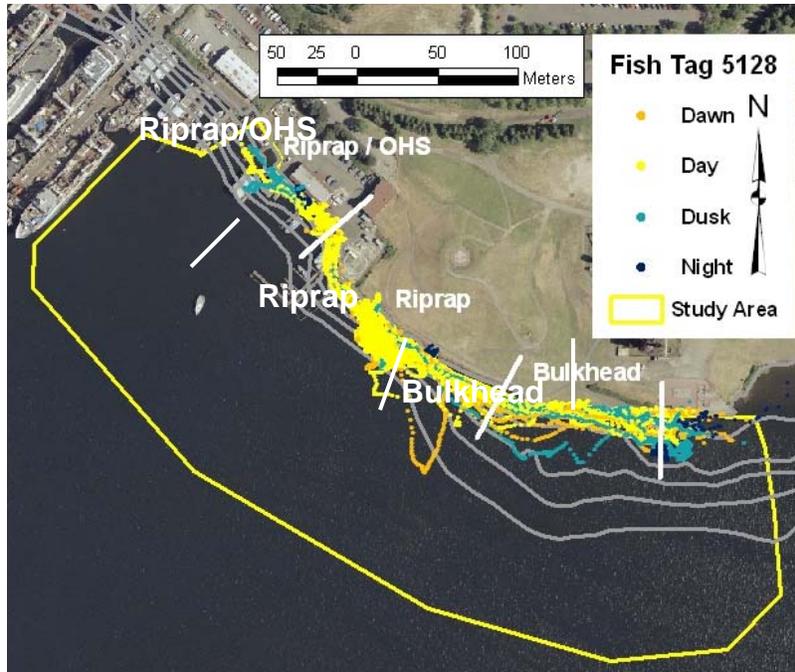


FIGURE 34. Locations of smallmouth bass #5128 (244 mm FL) which was closely associated with rip rap and other shoreline types at the Gas Works Park site, LWSC, June 2005. This smallmouth bass was tracked for 14 d. OHS = overwater structures

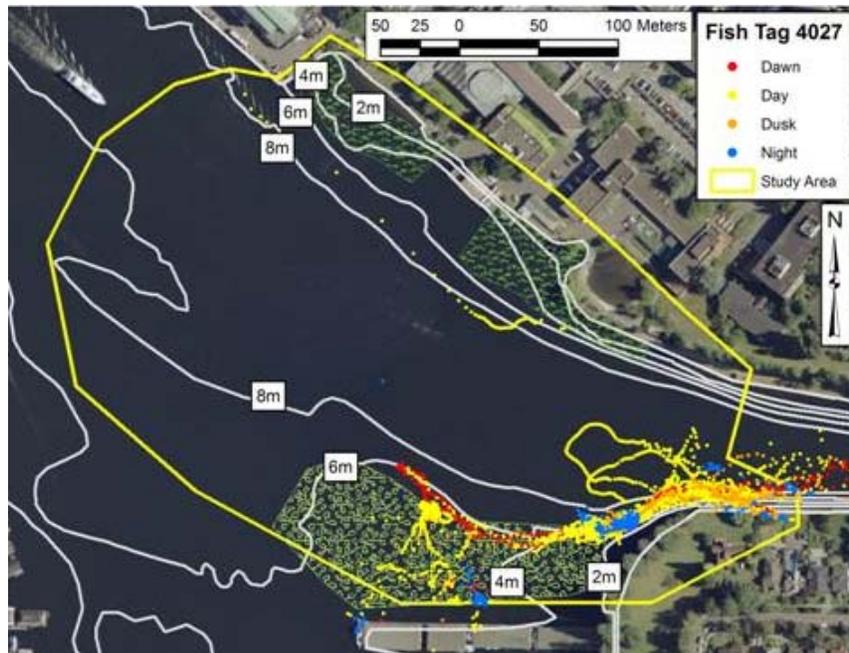


FIGURE 35. Locations of smallmouth bass # 4027 (400 mm FL) which was associated with the offshore edge of macrophytes (elodea) as well as rip rap and bulkhead shorelines at the Portage Bay site, LWSC, June 2005. Fish #4027 was tracked for 23 d.

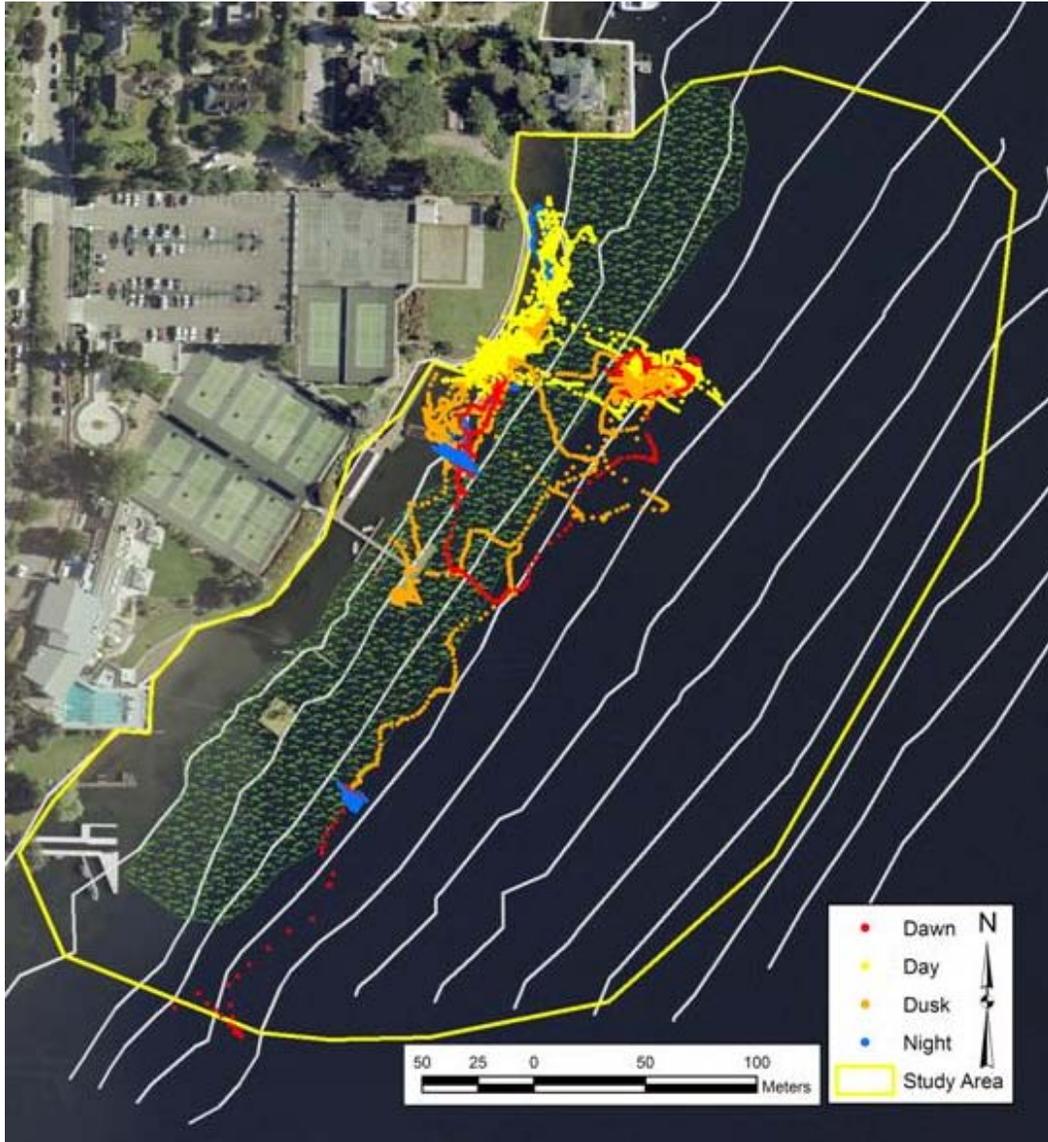


FIGURE 36. Locations of smallmouth bass #5203 (226 mm FL) which was associated with the offshore edge of macrophytes (milfoil) as well as rip rap shoreline and overwater structure at the Seattle Tennis Club site, Lake Washington, June 2005. Depth contours are in 2-m intervals. Fish #5203 was tracked for 14 d.

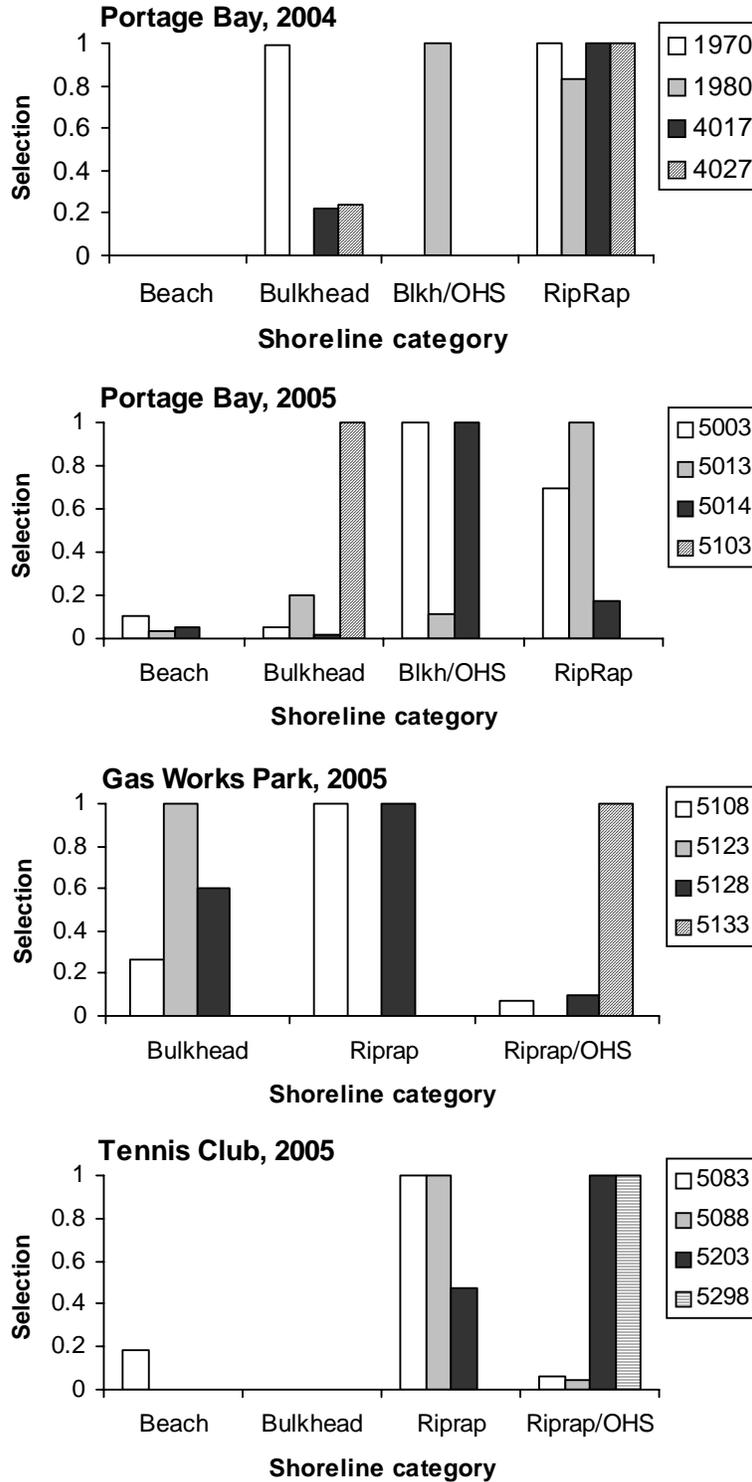


FIGURE 37. Shoreline selection of individual smallmouth bass from two locations in the LWSC (Portage Bay and Gas Works Park) and one location in Lake Washington (Seattle Tennis Club), May-June 2004 and 2005. Labels represent the tag period for each smallmouth bass. Selection was based on the number of detections in shoreline areas that was less than 4 m deep. OHS = overwater structures (e.g., piers and docks); Blkh = bulkhead.

Daytime and nighttime home range size of smallmouth bass varied considerably between individuals (Figure 38). Daytime home range size ranged from 31 to 16,578 m² and nighttime size ranged from 0.1 to 4,243 m². Daytime home range was larger than the night home range in 14 of 18 smallmouth bass. Some smallmouth bass, perhaps due to nearby artificial lighting, appeared to be active at night. However, bass often appeared to move little over the course of one night (Figure 36), thus indicating they were probably resting on the bottom, similar to what we observed during nighttime snorkel surveys. All three smallmouth bass less than 200 mm FL had relatively small home ranges (< 600 m²) and appeared to stay within the coverage area throughout the life of the tag. Home range size of larger smallmouth bass (> 200 mm FL) varied considerably, possibly due to differences in spawning activity (i.e., nest guarding by males).

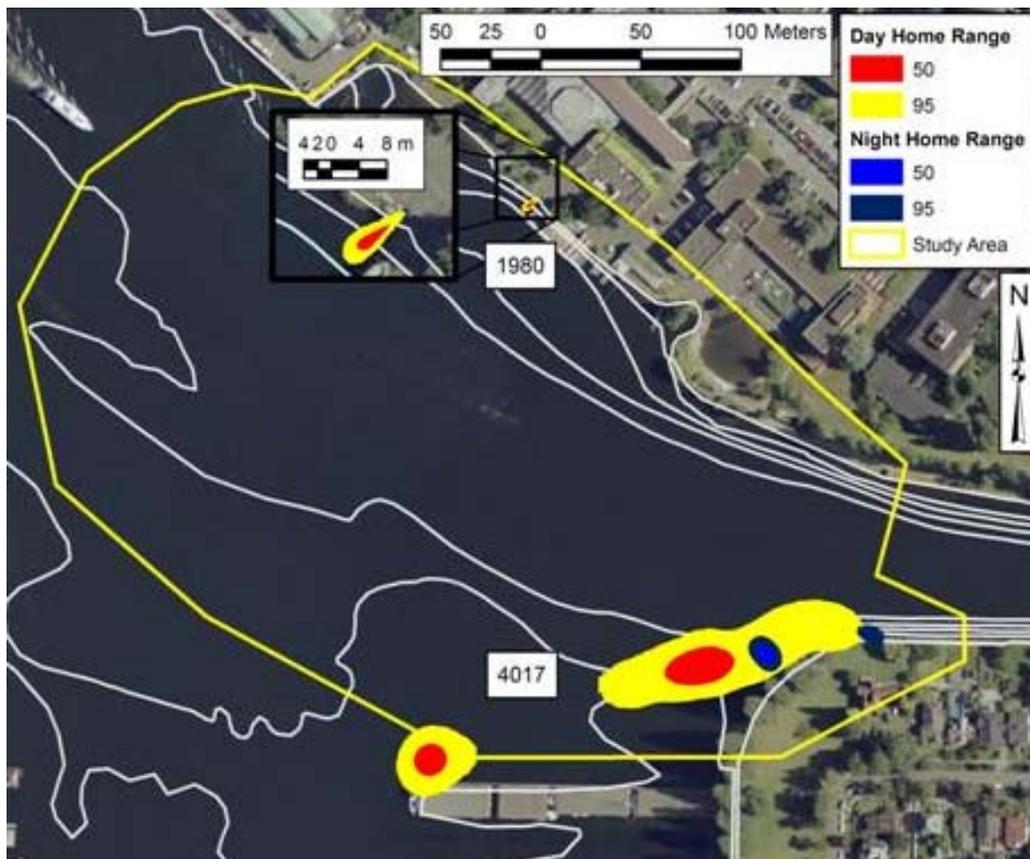


FIGURE 38. Daytime and nighttime Kernel home range size of two smallmouth bass in Portage Bay, May-June 2004. Both 50% and 95% home ranges are displayed.

Prickly sculpin

All eight prickly sculpin tagged in 2004 (five at Gene Coulon Park and three at the Portage Bay site) were successfully tracked. Six of the eight fish were tracked for more than eight days and the other two fish were tracked for 2-3 d. The average number of data points was 22,838 and ranged from 1,539 to 50,270 (Table 6). In contrast to 2004 results, few data points were obtained for the twelve prickly sculpin tagged at the Seattle Tennis Club in 2005. Most were tracked for less than three days. The average number of data points was only 1,231 and ranged from 0 to 7,405 (Table 6). This may have been caused by irregular bathymetry in some areas obstructing tag signal transmissions to hydrophones. Additionally, the tracking system was down on some days, which further reduced the number of possible data points. Prickly sculpin that were inshore had fewer data points, while prickly sculpin that moved offshore appeared to be tracked better.

TABLE 6. Summary data of prickly sculpin tagged with acoustic tags at three locations; two in Lake Washington (Gene Coulon Park and Seattle Tennis Club) and one in the LWSC (Portage Bay), May-June 2004 and 2005. ND = no data.

Year	Location	Tag period	Total length (mm)	Date released	Date of last data point	Number of days tracked	Number of data points
2004	Gene Coulon Park	1290	140	5/25	6/4	10	22,616
	Gene Coulon Park	1300	143	5/25	6/2	3	1,539
	Gene Coulon Park	1310	135	5/25	6/4	9	50,270
	Gene Coulon Park	1320	135	5/25	5/28	3	17,220
	Gene Coulon Park	1330	135	5/25	6/4	10	34,930
	Portage Bay	1960	145	6/9	6/18	7	15,489
	Portage Bay	2005	161	6/9	6/18	9	36,408
	Portage Bay	2015	147	6/9	6/18	9	4,231
2005	Tennis Club	5063	118	6/16	6/26	2	648
	Tennis Club	5073	128	6/16	ND	0	0
	Tennis Club	5078	133	6/16	6/28	2	1,353
	Tennis Club	5208	123	6/10	6/12	2	93
	Tennis Club	5213	115	6/10	6/24	3	356
	Tennis Club	5218	126	6/10	6/21	4	1,819
	Tennis Club	5223	118	6/10	6/12	2	520
	Tennis Club	5228	121	6/10	6/12	2	76
	Tennis Club	5233	135	6/10	6/10	1	11
	Tennis Club	5238	133	6/10	6/13	4	1,765
	Tennis Club	5243	125	6/10	6/25	3	728
	Tennis Club	5303	110	6/23	6/30	6	7,405

At Gene Coulon Park, all five prickly sculpin appeared to be primarily active at night and inactive during the day. The night home range size was substantially larger than the daytime home range for each fish. Less than 0.5% of the total data points for each of these fish were during the day. Four of the five fish were in shallow water and appeared to retreat to cover under the boardwalk at dawn. At dusk, the sculpin would reappear from their daytime refuge. Of the four shallow fish, three were in water that was 0-2 m deep and the other was in water that was 2-6 m deep. The fifth fish (#1320) was in deep water (6-8 m deep) during both day and night. The number of data points was similar between day and night for this fish; however, the home range size was substantially larger at night than during the day. Three days after release this fish moved to deeper water (> 8 m deep) during the morning and moved outside of the array and was not detected again. One of the four sculpin that remained in shallow water was only tracked on the first and seventh night after release; it probably spent most of its time outside of the array. The other three sculpin were each tracked more than nine days. Each fishes' movement pattern was similar between nights. Nightly home range size varied but the home range location overlapped strongly from night to night (Figure 39). Mean nightly home ranges sizes were 61.1, 144.4, and 193.4 m².

All three of the Portage Bay prickly sculpin remained within a localized area for most of the time they were detected. One of these sculpin remained in a localized area for the first eight days and then moved offshore at night to 6 m deep water for a few minutes and then moved approximately 75 m in 3 hours to shallow water (< 1 m deep) at the small gravel beach west of the release site. The sculpin remained at the beach site for an hour and was not detected again (most likely the tag battery died). The other two sculpin were primarily in water that was 0-2 m deep although there was some movement into 2-4 m deep water at night. In two of the three Portage Bay sculpin, the daytime home range size was similar to the night home range size.

Six of the eleven tagged sculpin at the Seattle Tennis Club remained inshore, albeit few data points were made of each fish. An average of 77.4% of the data points of the inshore sculpin were in water that was 0-2 m deep and 22.6 % were in water that 2-4 m deep. In contrast, 40.1% of the data points of sculpin that moved offshore were in water that was 8-10 m deep and 22.5% were in water that was > 10 m deep (Figure 40). These fish were in water as deep as 16 m. Some may have moved to deeper water outside of the array. These offshore sculpin did not appear to have specific home ranges; instead moved in a variety of directions without any discernable pattern. Most of the movements by offshore sculpin occurred at dusk, night, or dawn. An average of 80% of the data points of offshore sculpin were at dusk, night, or dawn. Compared to Gene Coulon Park and Portage Bay sculpin, Seattle Tennis Club sculpin moved a relatively long distance. For example, fish #5078 moved approximately 375 m in 2.4 hours.

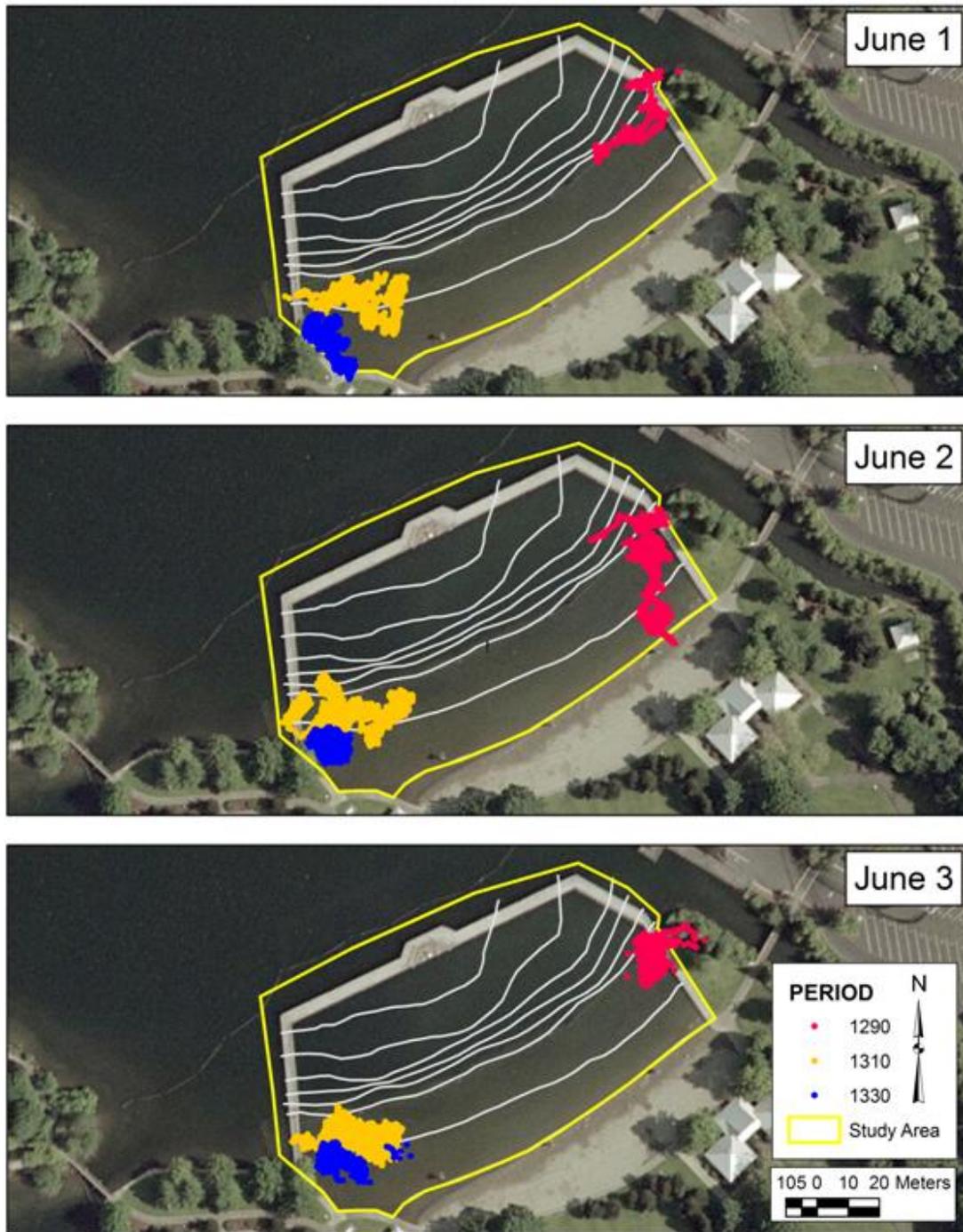


FIGURE 39. Locations of three prickly sculpin (140, 135, and 135 mm TL) at the Gene Coulon Park site, Lake Washington, June 1-3, 2004.

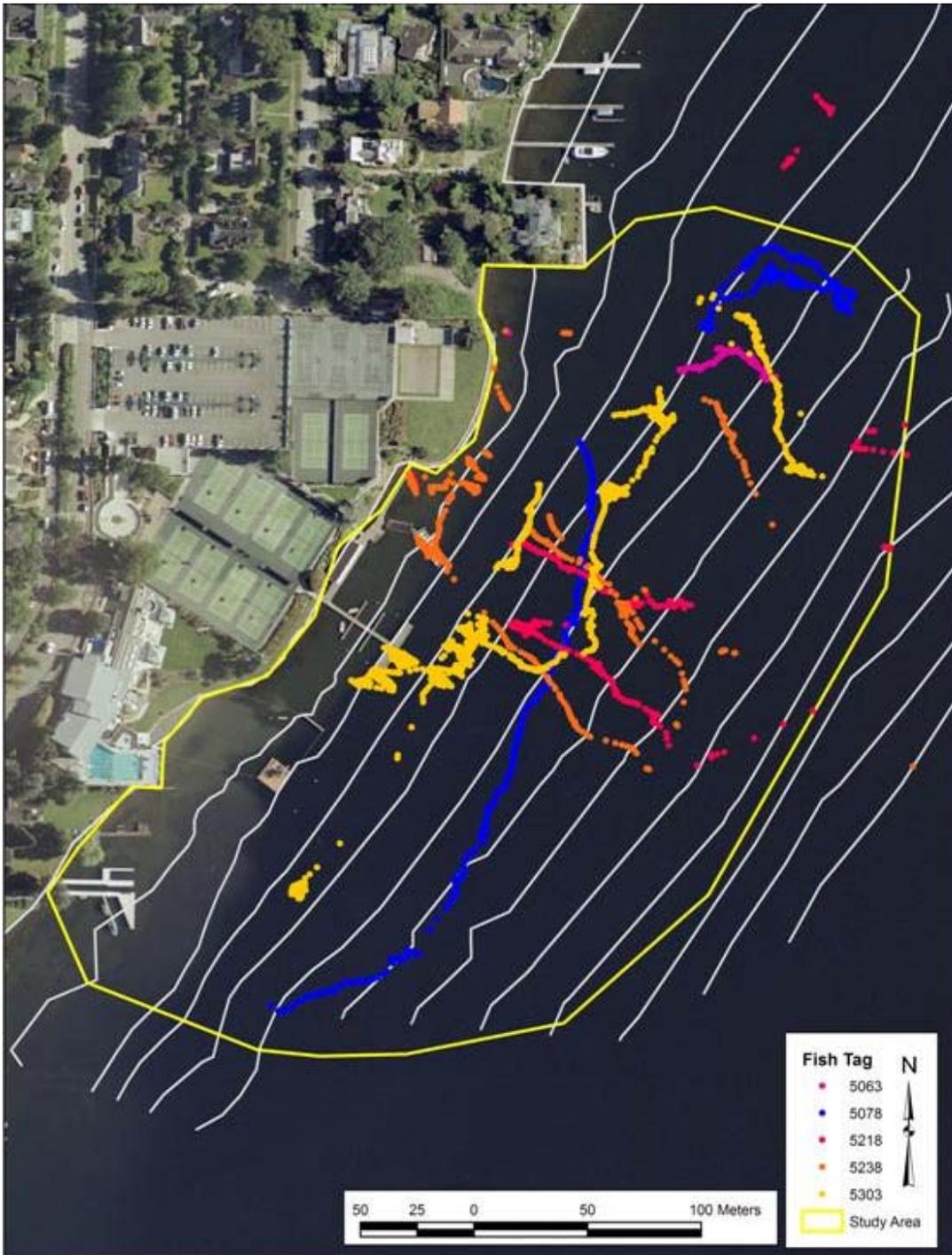


FIGURE 40. Locations of five offshore prickly sculpin at the Seattle Tennis Club site, June 2005. Depth contours are in 2-m intervals.

Other species

The two tagged northern pikeminnow were only tracked for a short time after they were released (Table 7). The pikeminnow released at the Portage Bay site was tracked for 27 h (232 data points) and was active in deep offshore areas during the daytime of the release day and the next day. No night data points were made. The other pikeminnow, which was released at Gas Works Park, was tracked for 12 h (397 data points). For the first 8 h, this fish was only detected in the shipyard immediately to the west of our tracking area and did not move appreciably. Afterwards, the pikeminnow was tracked at night for 40 minutes as it moved east along the shore. No further data points were made of this fish except a few nighttime data points three days later at the east edge of the array.

The only largemouth bass tagged was tracked for 8.5 d (Table 7) and spent the entire time near or under the boardwalk at the Gene Coulon Park. At night, the largemouth bass was close to shore in shallow water (0-2 m deep) and did not move appreciably. During the day, the bass had a larger home range (Figure 41) and was in shallow water (0-2 m deep water) much of the time but 11.3% of the data points were in water that was 2-4 m deep.

TABLE 7. Summary data of largemouth bass and northern pikeminnow tagged with acoustic tags in Lake Washington (Gene Coulon Park) in the LWSC (Portage Bay and Gas Works Park), May-June 2004 and 2005. Number of data points after 24 h is the number after 24 h of the fish being released.

Year	Species	Location	Tag period	Fork length (mm)	Date released	Date of last data point	Total # of data points	# of points after 24 h
2004	Largemouth bass	Gene Coulon Park	1250	135	5/25	6/4	49,092	49,022
2005	Northern pikeminnow	Portage Bay	5003	388	5/11	5/12	232	64
	Northern pikeminnow	Gas Works Park	5113	333	5/26	5/29	397	3

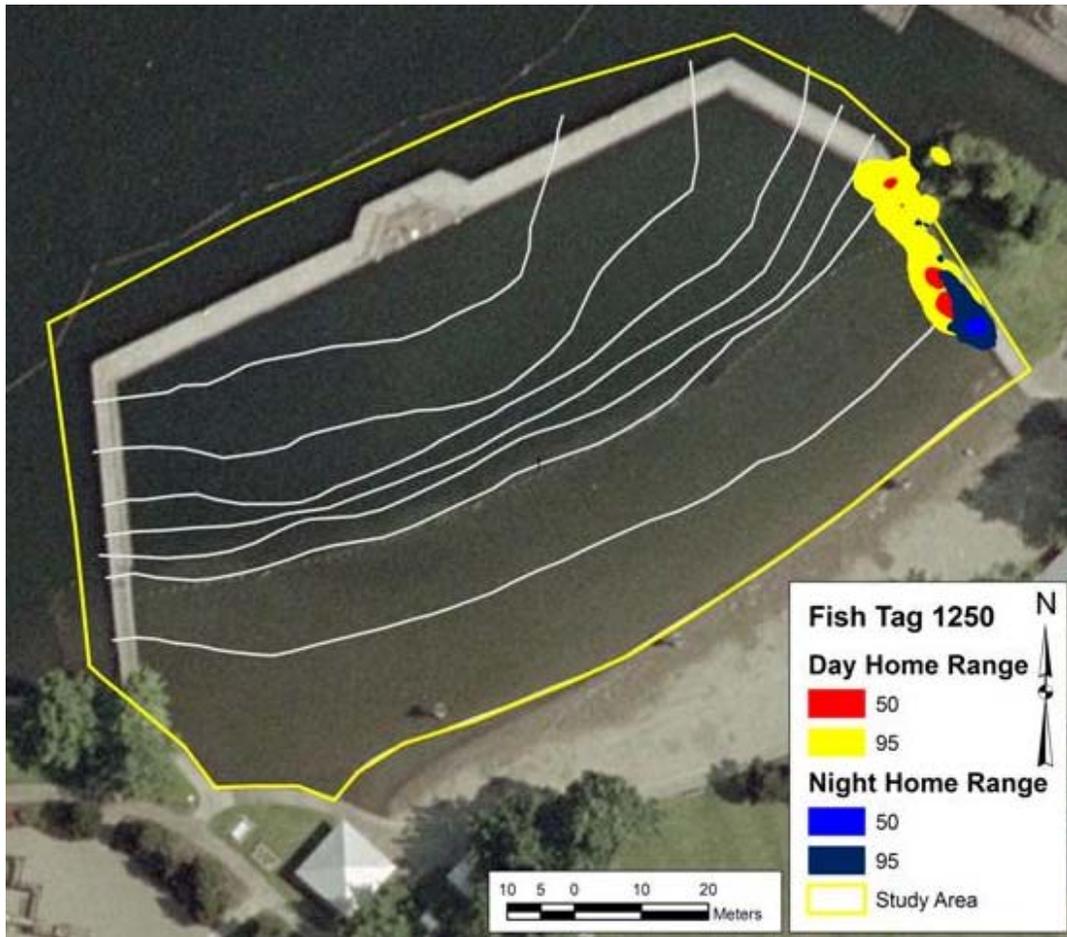


FIGURE 41. Kernel home range size of a largemouth bass (135 mm FL) at Gene Coulon Park, May-June 2004. Both 50% and 95% home ranges are displayed.

DISCUSSION

Chinook salmon

The ratio of tag weight to fish weight for most Chinook salmon in this study was $\leq 6\%$. Brown et al. (1999) argued that the 2% rule commonly advocated for biotelemetry studies is based primarily on theory and has little empirical basis, and found that a ratio of up to 12% did not affect swimming performance of juvenile rainbow trout *O. mykiss* (5-10 g). Similarly, Anglea et al. (2004) found that tags weighing up to 6.7% of juvenile Chinook salmon body weight (approximately 36 g) did not adversely affect swimming performance or susceptibility to predation. Adams et al. (1998a) observed that feeding activity and overall health was not impaired by tagging juvenile Chinook salmon (114-159 mm FL) with tags that weighed 2.3-5.5% of body weight, the only range of tag sizes used in the study. Hockersmith et al. (2003) observed that migration rate and survival of juvenile Chinook salmon (127-285 mm FL) implanted with radio-tags representing 1.3-7.0% of body weight were similar to those implanted with much lighter PIT tags. Conversely, Adams et al. (1998b) observed that swimming performance and susceptibility to predation were adversely affected by tagging juvenile Chinook salmon (< 120 mm FL) with tags weighing 4.6-10.4% of body weight. However, the tags used in the study had an antenna that was external to the body of the fish, and it is not clear whether the effects observed were due to the tag weight or the presence of an external antenna. The HTI tags used in our study had no external antenna, and were thus more comparable to those used by Anglea et al. (2004). Few if any studies have rigorously addressed tag volume as a potential factor influencing behavior, survival, and other properties of tagged fish. These findings suggest that the 6% ratio used in this study was appropriate, although there is still uncertainty regarding the full effects of tagging, tag weight, and tag volume on study fish.

Shoreline orientation and depth selection

We observed a distinct difference in shoreline orientation and depth selection between Lake Washington (Seattle Tennis Club) and the LWSC (Portage Bay and Gas Works Park). Fish in Lake Washington were observed close to shore in shallow littoral water (< 6 m) during the day, and in much deeper limnetic areas at night. This behavior – moving from shallow daytime habitat to deep water at night – corresponds with other observations in Lake Washington. Celedonia et al. (2008) observed similar patterns in a fine-scale acoustic tracking study of Chinook salmon smolts near the SR 520 bridge on the western shore of Lake Washington during June. Fish selected for depths < 6 m and made minimal use of deeper water during the day, but at night distributed throughout deeper water areas selecting for water > 6 m deep. Also, visual observations from docks on the western shore of Lake Washington have recorded large schools of Chinook salmon smolts migrating northward early in the day in June and July, typically in water 1.5-3.0 m deep (Tabor et al. 2006). Additionally, hydroacoustic surveys in pelagic areas of Lake Washington found Chinook salmon smolts in the upper 20 m of 65 m deep water at night (Koehler et al. 2004). Fish were not observed here during daytime surveys, and dusk appeared to be a transitional period.

Diel horizontal movement from littoral daytime habitat to limnetic areas at night is typical of planktivorous fishes in lacustrine habitats (Hall et al. 1979; Jacobsen and Berg 1998; Shoup 2003). Such shifts are largely attributed to food availability and predation risk. Open water limnetic areas often provide the best foraging opportunities, but also present the greatest predation risk from piscivorous fishes. Therefore, planktivores use these areas during crepuscular periods and at night when low light levels diminish predation risk from visual predators. During the day when predation risk is higher, planktivores take cover in shallow littoral areas often near macrophyte beds. Juvenile Chinook salmon in Lake Washington appear to selectively feed on zooplankton during June (Koehler et al. 2006), which corresponds with our study period. Visual predatory fishes that may prey on juvenile Chinook salmon in limnetic and deeper littoral areas of Lake Washington include cutthroat trout, northern pikeminnow, smallmouth bass, and largemouth bass.

The diel habitat shift observed in Lake Washington stood in stark contrast to observations in the LWSC, where fish showed no diel shift, but rather were broadly distributed off shore in deeper water (> 8-10 m) during all diel periods, not just at night. Diel activity patterns and habitat use in juvenile salmonids of similar size, condition and life history stage are quite plastic, and are largely influenced by habitat conditions, food availability, predation risk and other related factors (Fraser et al. 1995; Bradford and Higgins 2001; Reeb 2002; Vehanen and Hamari 2004; Railsback et al. 2005). For example, Bradford and Higgins (2001) observed different diel activity and habitat use patterns in juvenile Chinook salmon in two reaches of the same river. In one reach, fish were largely nocturnal and were rarely observed in the water column during the day. In the other reach, substantial proportions of fish were observed in the water column during the day. The authors excluded temperature and streambed features as possible causal factors for the difference, and speculated that differences in flow, drift rate, fish density and predation risk may have been influential.

The differences in diel spatial distributions we observed between Lake Washington and the LWSC may be related to differences in water clarity and perceived predation risk. King County water quality monitoring data indicated that water clarity was generally lower in the LWSC than along the western shore of Lake Washington during the study period (Figure 42). Turbidity and light intensity can substantially alter juvenile fish habitat use patterns (Gregory 1993; Miner and Stein 1996; Abrahams and Kattenfeld 1997; Reeb 2002). In general, predation risk declines in turbid conditions allowing prey species to abandon anti-predator behaviors. For example, in clear water small bluegill remain in shallow areas when predators are present, but spend substantial proportions of time (> 80%) in deepwater habitat under turbid conditions (Miner and Stein 1996). Similarly, Gregory (1993) observed that juvenile Chinook salmon concentrated in one part of a test arena under clear conditions, but that fish distributed more evenly throughout the arena under turbid conditions. Higher water clarity in Lake Washington may force Chinook salmon closer to shore, and diminished clarity in the LWSC may allow fish to utilize open water areas during the day and take advantage of presumably better foraging opportunities as well as lower, more favorable water temperatures. Future

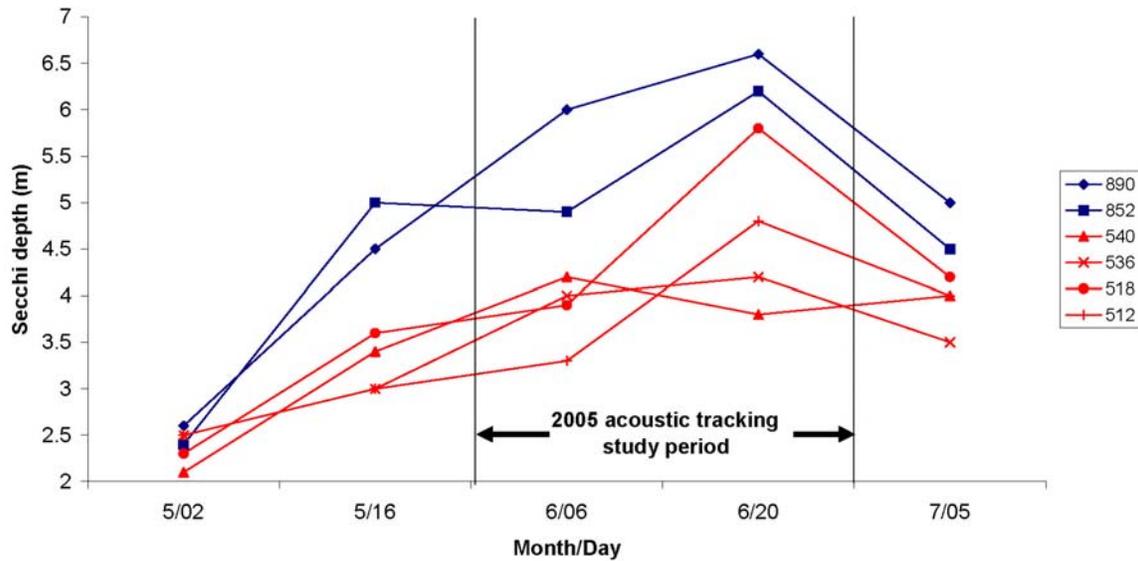


FIGURE 42. Water clarity (Secchi depth) in Lake Washington (blue) and the LWSC (red), May-July, 2005. Data was collected by King County. Symbol numbers represent King County monitoring sites.

studies should consider sampling site-specific water clarity and zooplankton distributions to confirm these relationships.

General migratory behaviors

Migrating animals in general, and salmonid smolts in particular, are faced with a complex array of ecological and physiological challenges (Berthold and Terrill 1991; Dingle 1996; Zabel 2002; Alerstam et al. 2003; Dingle 2006; Skagen 2006). Migration is energy-intensive and generally requires animals to rest and replenish energy reserves along the way. In doing so, migrants must balance the time demands brought on by migrational cues with the need to rest and refuel. This occurs within the context of continually moving into unfamiliar territory and the concomitant unfamiliarity with the habitat conditions and resource availability that lay ahead. Salmonid smolts have the additional burden of undergoing physiological transformations necessary to move from fresh into salt water. The behavior of salmonid smolts at any given site and time along the migration route is thus the culmination and expression of these often conflicting demands.

Lake Washington Chinook salmon smolts appear highly variable in how quickly they move through the lower basin. Extensive PIT tagging studies have observed that many smolts in Lake Washington move about 1-5 km/day, although a notable proportion move faster at speeds up to 20 km/day (DeVries et al. 2005; DeVries et al. 2007). Within this broader spatial and temporal context, we observed two main phases of Chinook salmon smolt migration in Lake Washington and the LWSC: an active migration phase where

fish move rapidly and directly toward the marine environment, and a holding phase where fish pause in their migration. Migrating animals, including fish, travel at speeds that maximize fitness (Pyke 1981; Zabel 2002). Swim speeds of 1.0 BL/s appear most efficient in terms of maximizing distance traveled while minimizing energy expended (Weihs 1973). However, such energetically optimum speeds are usually not observed in the field. For example, Weihs (1973) noted that “long range cruising speeds as inferred from tank tests are usually up to four lengths s^{-1} .” Also, migrating sockeye salmon smolts (86 mm FL) have been observed moving at sustained speeds of about 3.7 BL/s (Groot 1972; Ware 1978). Maximum sustained speeds of juvenile Chinook salmon coarsely approximated by critical swim speeds (U_{crit}) are on the order of 4.0-4.5 BL/s (Anglea et al. 2004). Actively migrating smolts in our study moved at mean speeds of 3.3 BL/s (site-to-site) and 4.5 BL/s (on-site). Actual site-to-site speeds were probably closer to measured on-site speeds: Measured site-to-site speeds were based on straight shoreline distance and thus excluded natural tortuosity of fish swim paths and movement around structures and other obstacles. These findings suggest that actively migrating Chinook salmon in Lake Washington and the LWSC maximize speed regardless of energy expenditure. We observed little evidence of what Venditti et al. (2000) termed “rearing migration,” whereby fish presumably move slowly downstream as they forage. Deeper level analyses of our data could be performed to provide further certainty in this regard.

Lake Washington Chinook salmon appear to migrate primarily during the day. We observed active migration predominantly during the day and never at night. Notable migratory movements were also observed during dawn. These patterns were consistent after accounting for release time bias. Other studies have also observed primarily daytime movement of Lake Washington Chinook salmon. In the SR 520 tracking study (Celedonia et al. 2008), movement of Chinook salmon smolts through the study site and into the LWSC occurred almost exclusively during the day. Passage at the Chittenden Locks also occurs predominantly during daylight hours and proportionally little passage is observed during other periods (DeVries et al. 2005). These findings stand in contrast to other results suggesting that juvenile salmonid migrations generally occur at night throughout much of their range (Quinn 2005), although daytime migration is not entirely uncommon. Beeman and Maule (2001) provide two references to unpublished data documenting equivalent migration rates during day and night through reservoirs on the Columbia and Snake Rivers. Numerous studies on Columbia and Snake River dams show that salmonid passage through the dams often occurs during night, but that daytime passage is also common under certain circumstances (Ferguson et al. 2005). In the Columbia River estuary, Ledgerwood et al. (1991) observed downstream movement of Chinook salmon juveniles primarily from sunrise to early afternoon, and decreased movement at night.

Holding fish in our study moved at speeds of 2.0 to 2.1 BL/s during dawn, day, and dusk. This corresponds closely with expected speeds of foraging fish under conditions of abundant food resources. Theory presented by Weihs and Webb (1983) suggest that optimal foraging speed of a 109 mm fish (the mean of our holding fish) at 15°C is 2.4 BL/s. Such theoretical calculations have been shown to correspond closely with actual

observations (Ware 1975; Ware 1978; Weihs and Webb 1983). Holding fish in our study showed reduced activity at night (1.5 BL/s). These findings suggest that holding fish may have been mostly foraging during dawn, day, and dusk, and resting more at night, particularly in the LWSC where most of the nighttime and crepuscular observations were made. Further study is needed to confirm actual diel foraging patterns. Also, given the considerable differences in diel and site-specific behaviors between Lake Washington and the LWSC, further study is needed to better evaluate nighttime and crepuscular swim speeds, activity levels, and foraging patterns in Lake Washington.

Behavioral variability between sites and between years

Expression of migratory behaviors appeared highly site-specific and subject to change from year to year. We had limited ability to discern how Chinook salmon smolts intersperse periods of active migration and holding through time and space in the broader lower Lake Washington basin. Hypothetically, interspersions of active migration and holding may take the following forms: 1) prolonged periods and distances of active migration only rarely punctuated by brief periods of holding; 2) short periods of active migration frequently interspersed with periods of holding; or, 3) something in between the two. Understanding the needs and patterns of Chinook salmon smolts throughout the lower Lake Washington basin is important for species management and recovery. For example, knowing precisely when and where holding habitat is used and/or needed can help focus restoration efforts to maximize benefits. Future studies should consider expanding fine-scale acoustic tracking to include more sites along the Lake Washington shoreline and in the LWSC to help address these important issues.

Causal factors contributing to the meso-scale behavioral patterns we observed could not be identified with certainty. For example, holding may be volitional as fish choose to rest, recover, replenish energy stores, and possibly adjust to changing physiological and ecological conditions before continuing their migration. Alternatively, holding may be triggered by an impediment to continued migration such as undesirable environmental or habitat conditions, physical barriers, or loss of migrational urge. For example, migrating Chinook salmon smolts encountering one Snake River dam delayed for several days in the forebay where they milled around and occasionally moved back upstream (Venditti et al. 2000). Behavior at each of our study sites and in each year was likely influenced by unique combinations of the following: site-specific environmental and habitat conditions (e.g., salinity, water clarity, temperature); perceived predation risk; position on migration route and proximity to potentially influential features (e.g., estuary, entrance to LWSC); timing of migrational cues, particularly moon apogee; degree of smoltification or desmoltification; and, release location bias (i.e., released near or far from site). Unique factors at each site make it difficult to extrapolate our findings to other specific areas of Lake Washington and the LWSC.

Relative to the other sites, the Seattle Tennis Club site had the strongest association with minimal site use. For most fish, this site functioned as a daytime migratory corridor. Reasons for this are uncertain. Fish may choose to spend little time here because conditions (e.g., temperature, prey availability, cover, predation risk) may not be

favorable. Conversely, migrational urges may take precedence and may drive fish to move through otherwise suitable habitat in order to get closer to the estuary. Proximity of the release site to the study site may have biased our results. Fish were released relatively near to the study site. Fish travelling a longer distance on a given day before reaching this site may behave differently on-site. This appears unlikely, however. Surface observations of migrating Chinook salmon (Tabor et al. 2006; R. Tabor, unpublished data) suggest similar patterns along much of the western shore of Lake Washington, whereby migrating smolts move quickly and directly through the site in shallow water parallel to the shore. The degree to which our results are representative of untagged migrating Chinook salmon smolts should receive further study. One possible study design could involve releasing equal sizes of tagged fish different distances from the release site, and comparing on-site behaviors between groups.

The cycling behavior we observed in Lake Washington was curious and may be an indicator of an inhibition to continue migration when considered with other evidence of delay or inhibition to enter the LWSC. Eleven of 18 fish (61%) tracked at the Seattle Tennis Club site were either never observed at Portage Bay (8 fish) or took two or more days to reach Portage Bay after last detection at the Seattle Tennis Club (3 fish). Four additional fish took 16-34 hours to reach Portage Bay after leaving the Seattle Tennis Club site. Celedonia et al. (2008) released tagged Chinook salmon on June 1, 14, and 28 south of the SR 520 bridge in Lake Washington. As June progressed, progressively fewer fish were observed at the University Bridge in the LWSC: 83%, 46%, and 38% from the June 1, 12, and 28 groups, respectively. The latter two groups also exhibited holding behaviors at and near the entrance to Union Bay, possibly representing an inhibition to continue migration. PIT tagging results by DeVries et al. (2005) also suggest a possible decline in Chinook salmon entrance into the LWSC during late-May and June. DeVries et al. (2005) observed that PIT tagged fish released at the east entrance to the LWSC on the west side of Union Bay showed a declining temporal trend in detections at the Ballard Locks from mid-May through late-June. Conversely, Chinook salmon released into Lake Union in the middle of the LWSC showed no such decline (DeVries et al. 2005), suggesting that fewer fish entered the LWSC as the season progressed. Given this apparent decline in LWSC entrance during June, it appears likely that at least some of our tagged fish did not enter the LWSC as opposed to entering after the tag battery expired.

Surface observations along the western shore of Lake Washington have documented both northerly and southerly movements of Chinook salmon schools (Tabor et al. 2006; R. Tabor, unpublished data). In 2003 and 2004, 36% and 15% of Chinook salmon schools were moving south along the western shore of Lake Washington away from the LWSC (Tabor et al. 2006). Southerly travel represents upstream movement away from the estuary. In the Columbia River, migrating Chinook salmon and steelhead encountering dams often reverse their direction of travel and move upriver several kilometers or more (Giorgi et al. 1994; Adams et al. 1995; Venditti et al 2000; Plumb et al. 2006). Venditti et al. (2000) argued that such movements amounted to dam-induced delay as opposed to some sort of beneficial "rearing migration," and Plumb et al. (2006) presented evidence that such upriver movements are likely deleterious. The southerly,

away-from-estuary movements we observed may thus be another indicator of an inhibition to enter the LWSC.

Reasons for declining entrance into the LWSC during June are uncertain. DeVries et al. (2005) speculated that a late-season thermal barrier may inhibit migration into the LWSC. This appears unlikely to have substantially influenced behavior of our study fish. Fish at the Seattle Tennis Club site showed the highest use of and selection for water that was 2-4 m deep, which varied from 17-20°C for most of the study period. Surface water temperatures during our study were similar in Lake Washington (Seattle Tennis Club) and in the LWSC (Portage Bay). Thus, migrating fish would likely not have encountered any appreciable thermal gradients as they approached the LWSC assuming their depth selection remained constant at 2-4 m. It therefore appears unlikely that temperature alone limited movement of our study fish into the LWSC.

Other factors that may contribute to a decline, reluctance, and delay in entering the LWSC may include physical characteristics of the LWSC entrance, food abundance and availability, thermal sum (i.e., degree days) and desmoltification, temporal changes in water clarity, and/or temporal changes in predation risk. This study and others (Tabor et al. 2006; Celedonia et al. 2008; R. Tabor, unpublished data) have found actively migrating Chinook salmon smolts in Lake Washington close to shore in shallow water 1-5 m deep. Such shallow water selection may be related to water clarity (Gregory 1993; Miner and Stein 1996; Abrahams and Kattenfeld 1997; Reeb 2002), and water clarity generally increases during late spring in Lake Washington (King County, unpublished data). It is conceivable then that lack of an adequate shallow water migrational corridor may inhibit migration. One characteristic of the Montlake Cut is that it is steep sided – there essentially is no shallow water migrational corridor. The hypothesis then is that under conditions of increasing water clarity Chinook salmon may become more reluctant to move into the steeply banked, deep water Montlake Cut.

Thermal sum (degree days), desmoltification, and residualism may also partially explain a seasonal decline in entrance into the LWSC. Desmolting, or parr-reversion, is a loss of physiological adaptations to seawater that may occur in salmonid smolts. The timing and severity of desmolting is at least partially temperature-dependent (Clarke and Hirano 1995). For example, Stefansson et al. (1998) found that desmolting in Atlantic salmon was a function of thermal sum, or degree-days, and that fish held at lower temperatures maintained smolt-like characteristics, but fish held at higher temperatures quickly passed through the “smolt window.” Chinook salmon experiencing desmoltification may be prone to residualizing in Lake Washington. Residualism in Lake Washington Chinook salmon has been observed in other studies (DeVries et al. 2005; DeVries et al. 2007). DeVries et al. (2007) observed that Chinook salmon appeared to residualize later in the outmigration season and also during years with warmer water temperatures in the LWSC during the outmigration season. However, the effects of desmoltification on movement and habitat use of Chinook salmon are uncertain. Typical smolt characteristics (i.e., elevated gill Na^+, K^+ -ATPase) are not always a predictor of seaward movement in Chinook salmon (Ewing et al. 1980; Tiffan et al. 2000). Conversely, Aarestrup et al. (2000) observed a notable switch from a migratory mode to

residency in desmoltling anadromous brown trout. Also, Giorgi et al. (1988) observed that susceptibility of Chinook salmon smolts to bypass systems at two Columbia River dams was influenced by degree of smoltification, suggesting that habitat use characteristics may be partially dependent on smolt status. Thus, differences in degree of smoltification or desmoltification resulting from prolonged exposure to elevated water temperatures may have contributed to some of the movement patterns we observed. For example, tagged fish that showed the cycling behavior in Lake Washington may have had less of a migrational urge than fish that actively migrated directly to Portage Bay. Cycling fish may not have been as far along in the smoltification process, or they may have been experiencing desmoltification. Future studies should consider measuring physiological parameters related to smoltification such as gill Na^+, K^+ -ATPase to better evaluate these influences.

Predation risk may also contribute to an inhibition to enter the LWSC. Predators such as smallmouth bass (Fresh et al. 2001) and northern pikeminnow (Olney 1975; Brocksmith 1999) inhabit shallow water areas during late-spring, and they consume more juvenile salmonids in both Lake Washington and the LWSC during this time (Tabor et al. 2004). Abundance of predators, predation rate, and overall predation risk to Chinook salmon near the entrance to the LWSC is currently unknown. Smallmouth bass (Fresh et al. 2001; Tabor et al. 2004) and northern pikeminnow (Olney 1975; Brocksmith 1999; Tabor et al. 2004) appear well distributed throughout Lake Washington and the LWSC. Northern pikeminnow have been shown to congregate in areas of Lake Washington (Olney 1975; Brocksmith 1999; Tabor et al. 2004) and in other systems (Collis et al. 1995) where prey is abundant. In the Columbia River, northern pikeminnow often move to areas where juvenile salmonids are concentrated, such as hatchery release sites (Collis et al. 1995) or near dams (Beamesderfer and Rieman 1991).

The shift in dominant behaviors and residence times at Portage Bay between 2004 and 2005 may have been caused by variation in timing of migrational cues and/or variation in habitat conditions. DeVries et al. (2004) discovered that lunar gravitation is a dominant migrational cue for Chinook salmon in Lake Washington, and that substantial seaward migration occurs one day after the lunar apogee when the moon is furthest from the earth and its gravitational pull the weakest. All of our wild and hatchery study fish in 2004 were released 7-8 d before the apogee. In 2005, however, many tracked wild (69%) and hatchery (43%) fish were released the day before or the day of the apogee. This could have resulted in a stronger urge to rapidly migrate through the site for 2005 fish, while 2004 fish were not subjected to similarly strong lunar gravitation cues. Variation in perceived predation risk may have also contributed to more rapid migration in 2005. In 2005, we observed many tagged fish migrating into and through the site in schools. For example, 8 of 9 tracked fish from one release group traveled together from one end of the site to the other. Smaller groups from other releases also entered the site together but often dispersed shortly after entering the site. No schooling was observed in 2004. Several studies have indicated that the degree of schooling can be influenced by perceived predation risk. Schooling appears to be an effective anti-predator behavior, and school cohesion increases in response to predation threats (Smith 1997). For example, schools of fathead minnows get tighter (Sullivan and Atchison 1978) and more

active (Moody et al. 1983) when predators are present and become more active. Conversely, qualitative observations indicate that school cohesion loosens when turbidity is high, which appears to lessen perceived predation risk (Vandenbyllaardt et al. 1991; Reid et al. 1999).

Our results confirm the findings of DeVries et al. (2005) that Chinook salmon smolts reside in the Lake Union area for several days. PIT tagging studies showed that smolts released in Lake Union took an average of 10 days to pass through smolt flumes at the Chittenden Locks (DeVries et al. 2005). The smolts we tracked in north Lake Union were usually observed on-site sporadically over a period of 1-7 days, and they were often observed entering and exiting the site to the south. Reverse movement to Portage Bay was not observed, suggesting that fish were limiting their residence to the immediate Lake Union area, and possibly also the LWSC west of Lake Union. Our estimates of residence time in this area were almost certainly underestimated. Our array did not cover the entire span of either the entrance into or the egress from Lake Union. Although we covered a large portion of this area, the southern-most parts of the channel on the west and east ends were undetectable by our array. Therefore, it is likely that at least some smolts entered prior to our first detecting them, and exited after we last detected them. In addition, the upper end of the residence times we observed approached the upper limit of the tag battery life. Also, a relatively small proportion of fish were released at the Seattle Tennis Club site and delayed for several days prior to entering the LWSC. Therefore, it is likely that the batteries of some tags expired prior to the fish exiting the area. Nonetheless, the close correspondence between our findings and those of DeVries et al. (2005) suggest that Lake Union functions as an extended holding, resting and/or foraging area for many Chinook salmon smolts.

Smolts may hold in Lake Union due to an inhibition to enter the Fremont Cut (the egress out of Lake Union), or because conditions were favorable for resting, foraging, and completing their physiological transition to saltwater. Lake Union appeared to have generally favorable conditions: relatively cool water ($\leq 17^{\circ}\text{C}$) lay at depths below about 6 m, and elevated turbidity seemingly minimized perceived predation risk allowing smolts to forage during the day in presumably more productive open water areas. Also, low salinity water is generally found along the bottom of north Lake Union due to saltwater intrusion through the Chittenden Locks. Such pseudo-estuarine conditions may be partially responsible for triggering smolt holding behaviors. Murphy et al. (1997) observed that Chinook salmon smolts migrating from the Taku River held for 1-3 weeks in the lower river/upper estuary transitional area. They speculated that this transitional area of low salinity (< 3 ppt) was important rearing habitat where migrants could complete smoltification. In the Smith River estuary, Quiñones and Mulligan (2005) observed that Chinook salmon smolt presence was most correlated with areas of low salinity (< 5 ppt), and that juvenile salmonids appeared to spend more time in the upper and middle estuary than lower areas. Shreffler et al. (1990) observed Chinook salmon smolts residing 5-38 d in a low salinity (0.14-7.2 ppt) restored estuarine wetland in the Puyallup River estuary. Miller and Sadro (2003) noted the importance of distinguishing different parts of the estuary based on salinity, tidal range and other parameters. They consequently observed that the low-salinity stream-estuary transitional area, or ecotone,

functioned as long-term rearing habitat for juvenile coho salmon. Finally, Magunsson and Hilborn (2003) documented the importance of estuarine habitat to the survival of Chinook salmon.

Differences in smolt size can contribute to differences in smoltification and seaward movement (Wagner et al. 1969; Dickhoff et al. 1997; Beckman et al. 1998; Beckman et al. 2003). For example, when the University of Washington hatchery released juvenile Chinook salmon in 2005, individuals we captured in a beach seine close to shore eight days after release were smaller relative to the overall release (Figure 43). Larger individuals either moved quickly from the site, or were further off shore. It is uncertain how similar our study fish were to untagged naturally-reared fish in the same areas at the same time. We tagged fish that were generally larger than 105 mm FL due to limitations of tag size. Thus our results may not be representative of smaller smolts. However, naturally-reared Chinook smolts (106-108 mm FL) and larger hatchery-reared fish (117-119 mm FL) showed similar overarching patterns in movement and habitat use, suggesting there may be a certain threshold related to movement or that factors other than size take precedence. As fine-scale acoustic tracking technology advances and smaller tags become available, future studies should consider tagging smaller smolts to better evaluate size effects.

Release proximity bias

Recently released fish may require a period of orientation and acclimation prior to engaging in more typical migratory behavior. Researchers often allow released fish prolonged periods at large prior to collecting or using tracking data (e.g., Paukert and Willis 2002; DeGrandchamp 2008), although the selected time periods appear to have little basis in empirical data. We assumed that providing a sufficient post-tagging/pre-

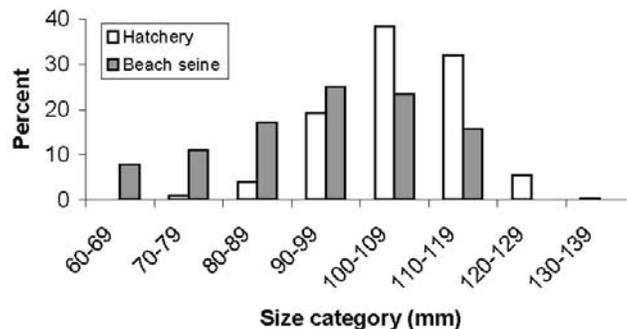


FIGURE 43. Size distributions of juvenile Chinook salmon released from the University of Washington hatchery on May 9, 2005 and those captured in a beach seine at night on May 17, 2005. Sample sizes were n = 64 and n = 350 for the beach seine and hatchery fish, respectively. Mean sizes of beach seine and hatchery fish were 94 and 106 mm FL, respectively. Difference in fork length was statistically significant (pooled variance t-test: $P < 0.001$).

release recovery period and releasing fish 300 m or more from a site would be sufficient for tagged fish to simulate site-specific behavior of untagged Chinook salmon smolts. Indications were that our methods were largely adequate, and that any bias from proximity of release site to tracking sites were minimal.

We observed stark differences in behavior, residence time, swim speed, and shoreline orientation between fish released on site at Portage Bay and those that volitionally entered the site. The behavioral differences we observed suggest that tagged and recently released Chinook salmon smolts orient and acclimate at and near the release site for several hours. At the Portage Bay site in 2005, there were no discernable differences between fish released 300 m away in the Montlake Cut, and those released 5.2 km away near the Seattle Tennis Club site, although sample sizes were limited. Of all sites, 300 m was the closest distance fish were released. It appears that this distance was adequate, and that fish were sufficiently oriented and acclimated as they volitionally entered each site.

Active migration was most prominent at the two sites - Seattle Tennis Club and Portage Bay - nearest release locations, suggesting a possible release proximity bias. However, indications were that any such bias was likely minimal. At Portage Bay in 2004, holding was more prominent than active migration despite these fish being released only 300 m away. If recently released fish had a tendency to actively migrate through nearby tracking areas, then we should have observed more active migration in 2004. Instead, the diversity of behaviors observed in 2004 suggest that other factors take precedence over proximity of release location as long as the release location is a certain minimum distance away from the tracking area.

We also did not observe any discernable differences between fish tracked the day of release and those tracked a day or more after release, except for first on-site detections of actively migrating fish. Fish first tracked the day of release entered almost exclusively during the day because they were released early in the day. Fish first tracked a day or more after release entered primarily during the day but notable numbers also entered at dawn. Based on these findings, we believe that proximity of release site did not substantially bias our results for volitionally entering fish, although further study is warranted. Furthermore, data obtained from fish released on-site are not suitable for studies intended to evaluate site-specific behaviors of untagged migrating smolts. On-site releases may provide useful information for evaluating general behavioral patterns, such as behaviors around structures, intended for extrapolation to other sites.

Overwater structures and aquatic macrophytes

Actively migrating Chinook salmon smolts appeared to avoid overwater structures, and forced some fish into deeper water. These findings concur with others (Kemp et al. 2005; Tabor et al. 2006; Celedonia et al. 2008) showing that migrating Chinook salmon avoid overwater structures. Such behaviors may increase the total distance traveled by migrating fish, and may expose them to increased predation by deep littoral zone predators such as cutthroat trout (Nowak and Quinn 2002) and piscivores attracted to

such structures like smallmouth bass (Fresh et al. 2001). Behavior at structures differed (i.e., swim beneath or travel around perimeter), and may have been related to such inter-related factors as: fish size, light levels beneath the structure, degree of contrast at the light-dark edge, width of the structure, height of the structure above the water surface, and water column depth beneath the structure. Further study is needed to conclusively determine how these and other factors interact to influence Chinook salmon behavior.

Holding Chinook salmon smolts also avoided areas beneath structures, but did not appear averse to residing near structure edges (within a few meters) for prolonged periods. In these cases, fish may choose to reside near structures because of their ability to provide cover from predation. Celedonia et al. (2008) observed many holding Chinook salmon smolts selecting for areas near the SR 520 bridge (within 20 m of the bridge edge) but not directly beneath the bridge. This behavior mimics that observed during estuarine residence of Chinook salmon smolts. For example, Toft et al. (2007) observed that Chinook and other salmonid smolt densities were highest near the edges of overwater structures in Puget Sound, and that areas directly beneath structures were avoided. The extent to which such behaviors benefit Chinook salmon smolts in freshwater is unknown. These behaviors could have an adverse impact by increasing exposure to predators such as smallmouth bass that are known to reside near overwater structures (Fresh et al. 2001).

The dense milfoil bed and overwater structures at the Seattle Tennis Club site may have confounded habitat selection observations. Submerged aquatic macrophytes appear to function as a false bottom to migrating salmonids, effectively shortening the perceived water column depth (Tabor et al. 2006). Thus, when utilizing areas above macrophytes, fish may be observed at deeper overall water column depths than they would be observed in areas without macrophytes. This may partially explain why our observations and those of Celedonia et al. (2008) found Chinook salmon smolts migrating in deeper water (1-6 m water column depth) compared to visual observations in areas free of macrophytes (1.0-2.5 m water column depth; Tabor et al. 2006). The upper canopy of the milfoil bed at the tracking site was generally 0.5-2.0 m below the water surface, which corresponds more closely with these other observations.

Smallmouth bass

Our results indicate smallmouth bass often have a defined home range. Several bass remained in a localized area during the duration of the tag life. However, the tags only lasted from 8 (0.75 g tag) to 20 d (1.5 g tag) and thus we only obtained information over a relatively short period of time. Studies conducted over several months have also shown smallmouth bass often have a defined home range (Gerber and Haynes 1988; Kraai et al. 1991; Ridgway and Shuter 1996; Hodgson et al. 1998; Cole and Moring 1997). Additionally, studies have shown that displaced smallmouth bass will often return to the original capture site (Pflug and Pauley 1983; Ridgway and Shuter 1996; Hodgson et al. 1998).

In contrast, some other studies have shown that smallmouth bass are often quite mobile and may not have a defined home range. Some bass we tagged were present in the array area for a few days and then left, which may indicate that some smallmouth bass do not have a well defined home range or their home range is transitory. Funk (1955) found there were two types of smallmouth bass in Missouri streams; sedentary and mobile (mostly intermediate-sized bass). Emery (1973) also found there were two types in Ontario lakes; a group with a small home range and another, more mobile group that may move a few kilometers in a day. Many smallmouth bass in the Snake River were also highly mobile (Petersen et al. 2000). In a Tennessee reservoir, smallmouth bass showed no tendency for home range establishment (Petersen and Myhr 1977).

Results of this study and other studies indicate the home range size can also vary considerably between lakes. Ridgway and Shuter (1996) found smallmouth bass in a large oligotrophic lake in Ontario had a mean home range size of 183 ha. Kraai et al. (1991) found smallmouth bass in a Texas reservoir had a home range of 1.3 to 43 ha. In contrast, Savitz et al. (1993) found their home ranges in a small Illinois lake were quite small, 0.07 to 0.2 ha. Although some of the differences may be due to the author's definition of home range and the methodology used to estimate it, there does appear to large differences between lakes. Large differences in home range size between lakes may depend largely on prey availability. Home range size of largemouth bass is substantially reduced when forage is more abundant (Savitz et al. 1983). Smallmouth bass home ranges in northern oligotrophic lakes may need to be large to meet daily foraging needs. Lake Washington is a mesotrophic lake with abundant prey (cottids, crayfish, and juvenile salmonids) and smallmouth bass may only need a relatively small home range. This may be particularly true in June when juvenile salmonids are abundant.

Within our study, home range size appeared to vary considerably between individual fish. One important factor that strongly influences home range size is nest guarding by males. During the spring, male smallmouth bass build a nest and after the female has laid the eggs, the male will guard the nest for several days. These male bass would be expected to have a small home range during this period. Two tagged smallmouth bass in particular had a small home range, fish #1980 and #5298. Fish #5298 appeared to be in the middle of nest when it was captured by a snorkeler. Savitz et al. (1993) also found that the smallest home range is for males that are guarding their nest.

Home range size may also be related to fish size. We did not observe a relationship between fish size and home range size; however, our results may have been confounded by other factors such as nest guarding, habitat conditions (i.e., presence of piers), and array size. In a Maine lake, smallmouth bass 406 to 520 mm had a total range (linear distance between the farthest two locations) of 2,427 m, while bass 305 to 356 mm had a total range of 1,426 m and bass 248-279 mm had a total range of 865 m (Cole and Moring 1997). Funk (1955) also found that smallmouth bass 214-330 mm were more mobile than bass 132-214 mm in Missouri streams; however, smallmouth bass greater than 330 mm were more sedentary than smaller smallmouth bass.

Although we were able to determine the home range of several smallmouth bass, some smallmouth bass quickly left the array area. These bass were collected close to the periphery of the array and their home range was largely outside of the array area. Even among bass that we were able to determine their home range, some appeared to have left the array area after a few days. Because we had a limited array size and the tags were only active for a few days, we may have underestimated the true home range size. Therefore, a 16-hydrophone or larger array is probably needed to more accurately determine the home range of smallmouth bass. Larger tags that can remain active longer would be beneficial. Also, only collecting bass near the middle of the array should reduce the likelihood of bass leaving the array area. Additionally, a large-scale tracking approach (i.e., Vemco VR2 hydrophone system) would be useful to determine the full extent of bass movements, both short term and seasonal.

In lakes, smallmouth bass occur almost exclusively in the epilimnion (Becker 1983) and are usually in water that is less than 12 m deep (Coble 1975). Within this area, their depth distribution may be related to habitat availability, water temperature, prey availability, and spawning activity. In the Lake Washington system, smallmouth bass may inhabit shallower water than in other systems because of the high availability of shallow water habitats (overwater structures and rip rap). Additionally, prey of smallmouth bass in Lake Washington and the LWSC consists primarily of crayfish, cottids, and juvenile salmonids; which all appear to be abundant in shallow waters. The high abundance of aquatic macrophytes (i.e., Eurasian milfoil) between 2 and 6 m deep may also keep many smallmouth bass in water less than 2 m deep. Additionally, smallmouth bass nests, which are guarded by males for several days, are usually in shallow water (Coble 1975; Becker 1983).

At each site, smallmouth bass were commonly found directly under piers. In natural conditions, smallmouth bass are often closely associated with cover types such as woody debris (Emery 1973; Hubert and Lackey, 1980; Brown et al. 2000). They are often located directly under woody debris and may use the overhead cover to ambush prey and avoid predators. Piers also provide overhead cover similar to woody debris. In a scuba survey of Lake Washington smallmouth bass, Fresh et al. (2001) found 49% of the bass were 2 m or less from a pier.

Smallmouth bass at each site were also often associated with rip rap, either in conjunction with overwater structure or by itself. In natural shoreline locations, smallmouth bass are most commonly associated with rocky shorelines with steep gradients. Rip rap shorelines is very similar to this habitat type and thus it would be expected that smallmouth would be commonly associated with rip rap. Additionally, the principal prey items (sculpin and crayfish) of smallmouth bass in Lake Washington and the LWSC are commonly found in rip rap. In a Tennessee reservoir, smallmouth bass catch rates were four to five times higher along rip rap shorelines than any other shoreline type (Sammons and Bettoli 1999).

Smallmouth bass typically prefer rocky shorelines and avoid thick beds of aquatic macrophytes (Becker 1983). Similar to other studies, we found smallmouth bass spent

little time in macrophytes beds but unlike other studies, we found they sometimes used the offshore edge of the macrophyte beds. The offshore edge typically had fine sediments, which is generally not preferred by smallmouth bass. The offshore edge appeared to be used primarily at dawn or dusk and thus may have been related to foraging since smallmouth bass often have a crepuscular feeding pattern (Vigg et al. 1991). This may be a valuable location to locate their preferred prey; crayfish and cottids. Dense aquatic vegetation generally decreases the foraging success of piscivores (Werner et al. 1983; Gotceitas and Colgan 1989) but they may be able to effectively forage along the edges.

At dawn and dusk, some smallmouth bass appeared to make forays along the shore or into deeper waters. These movements may have been movements to actively search for prey. Piscivores, such as smallmouth bass, are well adapted to feed in dim light and are often more active during crepuscular periods because they have the greatest advantage over prey species. In the Columbia River, smallmouth bass showed a crepuscular feeding pattern, but it was not pronounced (Vigg et al. 1991). An extended period of morning feeding was also observed. Emery (1973) also found peak feeding was at dawn and dusk and they fed opportunistically during the daytime. In the Snake River, smallmouth bass were most active in the early morning (Munther 1970). In laboratory experiments, Reynolds and Casterlin (1976) found smallmouth bass displayed a crepuscular activity pattern.

Most smallmouth bass did not appear to be active at night. Other studies have also found they are inactive at night and rest on the bottom near some type of cover such as large woody debris (Munther 1970; Emery 1973; Gerber and Haynes 1988). During our snorkeling in Lake Washington and the LWSC, we often encounter smallmouth bass that were motionless and appeared to be resting on the bottom. Some smallmouth bass appeared to be active at night and had relatively large night home ranges. Nighttime activity may be related to artificial lighting or moonlight. Some of the night-active smallmouth bass in Portage Bay and at the Seattle Tennis Club were near artificial lighting. In laboratory experiments, Reynolds and Casterlin (1976) found smallmouth bass were often active at night. Largemouth bass, which have similar crepuscular activity patterns (Reynolds and Casterlin 1976), can feed at night especially under full moon light conditions (McMahon and Holanov 1995).

Overlap in habitat between smallmouth bass and juvenile Chinook salmon appears to occur at each of the three main habitat types (piers, rip rap, and offshore edges of macrophytes) occupied by smallmouth bass. In Lake Washington, outmigrating Chinook salmon are in close proximity to smallmouth bass as they move along the shoreline and encounter piers. Juvenile Chinook salmon appear to react to the increased predation risk at piers by moving to deeper waters and either swimming under or around the pier. In the LWSC, Chinook salmon are further from shore but occasionally are near piers where they may be vulnerable to predation by smallmouth bass. At the Seattle Tennis Club, some juvenile Chinook salmon moved along a rip rap shore where their distribution would have overlapped with that of smallmouth bass. In the LWSC, juvenile Chinook salmon were generally further offshore and did not overlap closely with smallmouth bass along

rip rap shorelines (i.e., at Gas Works Park). Both smallmouth bass and juvenile Chinook salmon appear to use the offshore edge of macrophytes and they would be in close proximity to each other within this habitat type.

Prickly sculpin

In general, the acoustic array system appeared to work well to track prickly sculpin. Because prickly sculpin had a limited range, we were able to track most of them during the entire life of the tag. The system worked best at Gene Coulon Park swim beach, which is mostly a large sandy area with few macrophytes and few irregularities in the bottom topography. At the Portage Bay and Seattle Tennis Club sites, extensive macrophyte beds were present and the bottom topography was somewhat irregular and sculpin were not tracked as well. Future tracking efforts at other sites should take into account the amount of macrophytes and the bottom topography. Perhaps the hydrophones need to be placed closer together to increase the chance that four hydrophones receive the tag signal.

Results of acoustic tracking indicated prickly sculpin were active at night and were usually inactive during the day. Other observations of prickly sculpin indicate they hide underneath rocks and logs during the day and come out to forage actively at night (Moyle 2002). During day and night snorkel surveys of the nearshore area of south Lake Washington, 99% of prickly sculpin were observed at night (R. Tabor, unpublished data). Other species of freshwater sculpin in lake nearshore areas also appear to be more active at night (Emery 1973; Hoekstra and Janssen 1985).

Tracking results of prickly sculpin suggest they have a variety of movement patterns which may depend on habitat conditions and depth. At shallow sites with complex habitat and an adjacent sandy beach, such as Gene Coulon Park, prickly sculpin used the complex habitat as refuge during the day and then moved into the sandy beach area to forage at night. At large, complex shallow habitat sites, such as the Portage Bay site, prickly sculpin appeared to be primarily active at night but were occasionally active during the day. The Portage Bay and Seattle Tennis Club sites consists of a mosaic of different habitat types (i.e., riprap, aquatic vegetation, overwater structures, and pilings), which may allow prickly sculpin to be more active during the day and still avoid potential predators.

Prickly sculpin that moved into deeper water (> 5 m) were also mostly nocturnal but were often active during the day. In shallow, open water, large prickly sculpin would be vulnerable to piscivorous birds during the day and probably only occupy these habitats during the night. In deeper water, the light levels are reduced and prickly sculpin may be less vulnerable to piscivorous birds and too large to be consumed by most piscivorous fishes. Therefore, large prickly sculpin may be able to occupy open, deep areas throughout the day and night. In Lake Michigan, slimy sculpin in shallow areas were nocturnally active, whereas those in deep water show no diel pattern (Brandt 1986).

In comparison to other cottids, Lake Washington prickly sculpin appeared to have a relatively large home range. For example, the mean nightly home range area of the three prickly sculpin at Gene Coulon Park that we tracked for the entire tag life ranged from 61 to 191 m². In contrast, mottled sculpin in small North Carolina creeks were found to move less than 3 m over a 45 d period (Petty and Grossman 2004) and have a home range of less than 20 m in stream length over an 18 month period (Hill and Grossman 1987). Other studies have also shown that cottids in small lotic environments generally have a small home range (Bailey 1952; McCleave 1964; Brown and Downhower 1982; Greenberg and Holtzman 1987; Morgan and Ringler 1992). Petty and Grossman (2004) suggested the small home range of mottled sculpin in Coweeta Creek drainage, North Carolina was because food, refugia, and spawning habitat were all in close proximity to each other. Home ranges of cottids in lentic systems and large rivers have not been studied to any extent.

Six of our tagged sculpin appeared to move offshore, which may have been related to the seasonal movement of large prickly sculpin to deeper waters. In addition to extensive daily movements, prickly sculpin may also undergo extensive seasonal migrations; however, the extent of local migrations is poorly understood. Sampling of Gene Coulon Park indicated prickly sculpin greater than 100 mm are common in the nearshore area in the winter and spring but are no longer present in August when the water temperature is over 23°C (R. Tabor, unpublished data). Additionally, Rickard (1980) found prickly sculpin in Lake Washington moved offshore during the summer.

We documented the movements of prickly sculpin and juvenile Chinook salmon in May and June. Chinook salmon are over 75 mm FL during this period and are probably not vulnerable to prickly sculpin predation (Tabor et al. 2004). However, large prickly sculpin may influence their distribution and behavior. Prickly sculpin appear to be active at night and more abundant in the nearshore area (Figure 44) during this time period. Results of nighttime tracking at Gene Coulon Park, indicated juvenile Chinook salmon avoid the shallow areas near the boardwalk where sculpin are present. Instead, Chinook salmon were either active in deeper water or were inactive in shallow water in the middle of the swim beach. Thus, juvenile Chinook salmon appear to minimize their habitat overlap with large sculpin.

Our observations of prickly sculpin behavior may also provide insight into how sculpins may interact with small juvenile Chinook salmon when they are more vulnerable to sculpin predation in February, March, and April (Tabor et al. 2004). Night snorkel observations (February to June) indicate juvenile Chinook salmon are typically more abundant in the middle of the swim beach than on the outside edges, which are closer to the boardwalk. Juvenile Chinook salmon may prefer the middle of the beach to minimize their interaction with prickly sculpin. Typically, prickly sculpin were about 35 m or less from the boardwalk. The swim beach is 140 m long and thus the middle 70 m may be a low risk area for juvenile Chinook salmon at night. Predation of Chinook salmon by prickly sculpin is probably low during this time period because Chinook salmon inhabit open areas away from cover at night (Tabor and Piaskowski 2002). Predation rates are

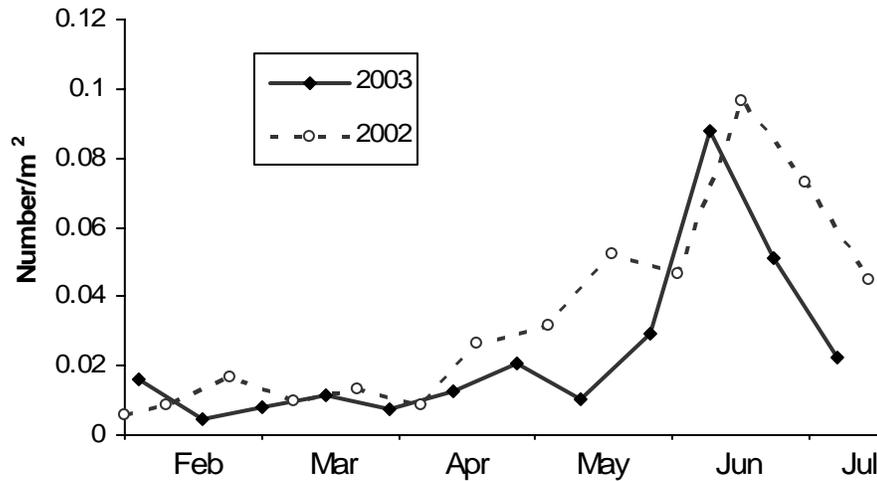


FIGURE 44. Density (number/m²) of large prickly sculpin (> 75 mm TL) at nine shoreline sites in south Lake Washington. Data were collected during nighttime snorkel transects along two depth contours; 0.4 and 0.7 m as part of a study to determine juvenile Chinook salmon spatial and temporal distribution (Tabor et al. 2006). Each site was a sand or gravel shoreline. Sculpin densities represent the total number of large prickly sculpin observed at all nine sites combined divided by the total area surveyed.

also low because sculpin are less active due to the low water temperatures and their abundance is reduced (Figure 44). Additionally, *Neomysis mercedis* are abundant in the nearshore area in the winter (Chigbu et al. 1998) and prickly sculpin may not need to undergo extensive movements to feed. *Neomysis* is the most important prey item in the winter diet of nearshore prickly sculpin (Tabor et al. 2007c).

Other species

In 2005, we tagged two northern pikeminnow with HTI acoustic tags and monitored their movements with fixed arrays but they appeared to be very mobile and the arrays were too small to provide much information about their movement patterns. Other studies have also found northern pikeminnow are often highly mobile (Martinelli and Shively 1997; Brocksmith 1999; Petersen et al. 2000); however, they will often congregate at locations where prey is abundant such as below dams (Beamesderfer and Rieman 1991) or near hatchery release sites (Thompson 1959; Collis et al. 1995) when juvenile salmonids are abundant. We originally had wanted to catch and release pikeminnow in Portage Bay before the UW hatchery salmonids were released but because of the close timing of the salmonid release date and Windermere Cup festivities (potential interference with hydrophone cables), pikeminnow were not tagged until after the salmonids had been released. In subsequent studies (2006-2008), we used Vemco acoustic tags to obtain information on macro-scale movements of northern pikeminnow. A series of independent hydrophones were placed strategically throughout the LWSC that

provided presence/absence information on each tagged fish. Additional movement information was obtained through mobile tracking surveys of the LWSC and Lake Washington. Analysis is underway and a report documenting results is forthcoming.

We were only able to capture and tag one largemouth bass, which appeared to have a small home range. Hodgson et al. (1998) found largemouth bass were less ranging and had more of defined home range than smallmouth bass. In a 3.4 ha Illinois pond, 96% of tagged largemouth bass were recaptured with 92 m of the original capture site (Lewis and Flickinger 1967). Savitz et al. (1983) found most largemouth bass had a home range less than 8 ha. Similar to smallmouth bass, a 16-hydrophone or larger array is probably needed to determine the home range of most largemouth bass.

The one tagged largemouth bass was always in close association with the boardwalk, an overwater structure. During snorkel surveys in Lake Washington and Lake Sammamish, largemouth bass have always been observed under some type structure (piers, water lilies, or overhanging vegetation) that provides overhead cover (R. Tabor, unpublished data). Other studies have also found that largemouth bass are commonly associated with overwater structures (Colle et al. 1989; Wheeler and Allen 2003). Wanjala et al. (1986) found that largemouth bass < 250 and > 380 mm in an Arizona reservoir were near cover in the littoral zone; whereas largemouth bass 250-380 mm occurred in open, limnetic waters. Additional largemouth bass of a variety of sizes need to be captured and tagged to better understand their relationship to overwater structures in Lake Washington and the LWSC.

SUMMARY OF FINDINGS

- Chinook salmon smolt migration in Lake Washington and the LWSC occurs in two primary phases: an active migration phase where fish move quickly and directly toward the estuary, and a holding phase where fish are temporarily paused in their migration. Active migration occurs primarily during the day, and sometimes at dawn. Holding occurs during all times of day and night, and is characterized by fish milling at reduced speeds over areas of about 10 ha and more. Details regarding duration and frequency of active migration and holding phases, factors that influence them, and effects on fitness and survival of Chinook salmon require further study.
- Different sites are used differently by Chinook salmon smolts. The Seattle Tennis Club site in Lake Washington was used mainly as a migration corridor. Portage Bay served as both a migration corridor and a short-term (< 1 day) holding area. North Lake Union functioned as a long-term (1-7 days) holding area.
- Factors influencing site use could not be identified with certainty, but some possibilities include: proximity to estuary, prey availability, water temperature, thermal sum (degree days), degree of smoltification, timing of migrational cues, predation risk, physical features of the migration corridor, and water clarity. Site use may vary seasonally and annually depending on the state of and interaction between these and possibly other factors.
- This study and others suggest that the ratio of Chinook salmon smolts entering the LWSC from Lake Washington declines during June. Reasons for this are uncertain but may be related to one or more of the following: desmoltification, elevated surface water temperatures, physical configuration of the entrance to the Montlake Cut (i.e., steep-sided with no shallow water migration corridor), increasing water clarity during June, increasing predation risk, increased predation, and increased prey availability in the lake. The degree to which smolt entrance into the LWSC declines during June, and factors that influence any such decline require further study.
- Chinook salmon smolt habitat use is markedly different between Lake Washington and the LWSC. In Lake Washington fish stay close to shore during the day (1-5 m water column depth), and move into deeper water at night (> 10 m water column depth; up to 230 m and more from shore). In the Ship Canal (Portage Bay and north Lake Union) smolts fan out across broad areas, mix across the channel during all times of day and night, and primarily use water greater than 8-10 m deep. Water clarity generally appears greater in Lake Washington than in the LWSC during June, and this may be the primary driver behind the differences observed.
- Actively migrating Chinook smolts often avoid passing beneath overwater structures. Anecdotally, avoidance behavior appears to be influenced by structure size and width, height of the structure above the water surface, light conditions beneath the structure, degree of contrast at the light-dark edge, and water depth beneath the structure.

Presence of predators (i.e., smallmouth bass) may also influence their behavior. Factors that influence behavior around overwater structures requires further study.

- Holding Chinook salmon smolts also avoided moving directly beneath structures, but often resided near structure edges (within 2 m) for prolonged periods (up to 2 hours). Structures may provide a source of cover from predation, but may also increase predation risk. These interactions require further study.
- Actively migrating Chinook salmon smolts did not avoid aquatic macrophytes. Instead, the migratory corridor used by smolts in Lake Washington (i.e., the Seattle Tennis Club site) substantially overlapped with the band of aquatic macrophytes. Macrophytes may function as a false bottom, causing smolts to use greater water column depths than they would otherwise use in the absence of macrophytes.
- Release location influences tagged Chinook salmon behavior. We observed markedly different patterns in movement and habitat use between fish released on-site and fish released off-site (> 350 m away from the study site).
- There is at least some spatial and temporal overlap between Chinook salmon and smallmouth bass habitat. The full extent and implications of this have yet to be explored (need larger sample sizes of bass).
- Smallmouth bass often had a defined home range. Home range size varied considerably between individuals. Male nest guarding, shoreline type, and presence of structures such as boat docks may have influenced home range size. Overwater structures may cause home ranges of smallmouth bass to decrease, thereby increasing density in the general area.
- Smallmouth bass were often associated with one or more of the following: areas directly beneath boat docks, rip rap shoreline, and offshore edges of aquatic macrophytes.
- Smallmouth bass were generally inactive at night, and appeared to forage during dawn and dusk. Elevated activity was also evident during the day.
- Prickly sculpin were active at night and usually inactive during the day. Habitat complexity and water column depth may influence daytime activity level. Limited daytime activity was observed at more complex sites, but prickly sculpin at simple sites showed no daytime activity. Prickly sculpin that moved into deeper water (> 5 m) were also often active during the day.
- Chinook salmon habitat overlap with large prickly sculpin was minimized at night. Chinook salmon at Gene Coulon Park avoided shallow areas near overwater structure where tagged prickly sculpin appeared active. Instead, Chinook salmon were found in deeper water and/or in shallow open areas away from overwater structure.

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