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Movement Patterns of Brook Trout in a Restored Coastal Stream System in Southern Massachusetts

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MOVEMENT PATTERNS OF BROOK TROUT IN A RESTORED COASTAL STREAM SYSTEM IN SOUTHERN MASSACHUSETTS

A Thesis Presented

by

ERIN L SNOOK

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ABSTRACT

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Populations of anadromous brook trout can be found from northern Canada into New England. It is believed that the extent of anadromy exhibited by coastal brook trout populations decreases with latitude, but the ecology and movements of the more southern populations are less studied. A 33-month acoustic telemetry study of anadromous brook trout (*Salvelinus fontinalis*) was conducted in a restored coastal stream and adjacent marine system in southeastern Massachusetts. Movement and migration patterns of 54 brook trout were investigated for individual differences and common features. Individuals exhibited a range of movement patterns. Some were more resident and only moved short distances, while others moved great distances covering the entire stretch of the stream (7.25 km) and moving into the marine environment. General Additive Mixed Models revealed that date was the major influence on brook trout movement between habitats and predicted peaks in movement in the spring and fall. Downstream movement peaked in the spring and in the fall, suggesting post-spawning feeding migration. Fish transitioned between habitats more often at new and full moons and when stream temperature was between 8 and 12 °C. Upstream transitions peaked as temperatures declined in winter 2011. Fifty percent of tagged brook trout were detected in the estuary during the study, suggesting that it is an important habitat for the population. In summer 2012, 14 tagged brook trout (20% of active tags) resided near one receiver at the head of the tide, which contained a thermal refugium in the form of a cold-water spring seep. Of the 84 tagged brook trout, 9.5% moved to the marine environment. Warm temperatures in saline Buttermilk Bay in the summer and cold temperatures in winter probably discourage some individuals from entering the marine environment. Compared to more northern coastal populations of brook trout, the Red Brook population appears to be less anadromous.

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CHAPTER 1

GENERAL INTRODUCTION

Less than 1% of the world's fishes exhibit a specialized, regular migratory phenomenon known as diadromy (McDowall 1987). Fisheries biologists and resource managers are interested in diadromous fish species because many are exploited by humans and have high economic value, large numbers of fish are sometimes observed and caught during their migrations, and because migrations are fairly predictable on a seasonal basis (McDowall 1987). Anadromy is the most common type of diadromy, observed in 54% of diadromous species (McDowall 1987). It is perhaps also the most well-known form of diadromy due to the popularity of the Salmonid family of fish with recreational anglers. Anadromy was first formally defined by Myers (1949b). McDowall (1987) described a typical anadromous lifestyle as one that starts with larvae hatching in freshwater habitat and moving to sea soon after. Juvenile fish then spend several years at sea, feeding and growing. Mature adults return to freshwater river habitats to spawn and then die. However, there are many variations in this life cycle among species, populations, and even among individuals in a population (Gross 1987, Gross 1996). Although this rather simple pattern is observed in some anadromous species, there are varying degrees of all types of diadromy. For example, Rounsefell (1957) considered brook trout to be the least anadromous of salmonids, because migration is not obligatory for all individuals. Several authors have observed a greater degree of anadromy in brook trout and other salmonid species as latitude increases (Rousnefell 1958, Scott and Crossman 1973, Vladykov 1963, Nordeng 1961).

Maximizing fitness is at the core of evolving a diadromous life history strategy (Gross 1987). According to Gross (1987), fish are likely to become diadromous when they can obtain greater fitness from moving into a second habitat, migration costs included, than by staying in only one habitat. In temperate zones where the seas tend to be more productive than freshwater, anadromy has evolved as the dominant form of diadromy (Gross 1987, McDowall 1987). Although the costs of anadromy may be high due to energy expended during migration, osmoregulatory demands from switching between fresh and saltwater, and a higher risk of predation in estuaries and the sea, for some individuals the benefits of more rapid growth, larger body size, higher fecundity, and greater reproductive potential outweigh the costs (McDowall 2001).

1.1 Brook Trout Life History

For brook trout, there are several diversions from the previously described typical pattern of anadromy. Rousenfell (1958) developed a classification of anadromy among species by comparing extent of migration into the sea, duration of stay in the sea, state of maturity attained at sea, spawning habits, mortality after spawning, and the occurrence of freshwater resident forms. Species in the genus *Salvelinus* exhibit the lowest degree of anadromy among Salmonids (Rousenfell 1958, McCormick 1994). In iteroparous species such as brook trout, mature adults may live several years and spawn more than once (McDowall 1987). Most coastal brook trout populations have both individuals that move into brackish and saltwater and individuals that remain residents of the freshwater and do not migrate. Such populations are called “partially migratory” (Wysujack et al. 2009).

Brook trout are able to tolerate a wide range of salinities ranging from 1- 34 parts per thousand (Curry et al. 2006), but movement to seawater is ontogenetic, meaning that the timing of first downstream migration depends on age and growth rate (Theriault & Dodson 2003). Based on a number of physiological factors (including Na^+, K^+-ATPase activity and osmoregulatory ability), McCormick & Naiman (1985) concluded that while brook trout exhibit some outward changes such as silvering, they do not smolt (undergo metamorphic and physiological changes for seawater entry), so estuarine residence is important for them to acclimate to and eventually migrate to saltwater. For example, Castonguay et al. (1982) studied a population of brook trout in Quebec in which migratory individuals spent the first two to three years in the river, then one year in the estuary. When the brook trout finally moved to saltwater, they remained there for two to three months and then returned to the river (Castonguay et al. 1982). Transferring brook trout directly to sea water, Besner & Pelletier (1991) observed maximum production of Na^+, K^+-ATPase in June. Brook trout transferred to sea water in spring adapted better to salt water, with less osmoregulatory stress and higher survival rates than fish transferred to sea water in summer months (Besner & Pelletier 1991). McCormick & Naiman (1984) found that size was the primary determinant for brook trout survival in seawater, and after fish reached 140 mm FL the effect of seawater is reduced (i.e., stress from osmoregulation is lower for larger fish).

Feeding is considered the major advantage of migration for fish (Northcote 1978, Gross 1987). Greater food availability in the estuary and saltwater systems during certain times of the year is thought to be the main reason for brook trout to adopt an anadromous lifestyle. Testing the effects of food availability on development of migratory and non-migratory body morphologies in brown trout, Olsson et al. (2006) showed that most fish became migrants when food was scarce, and few migrated when it was plentiful. Anadromous forms of brook trout are larger on average, after returning from the sea, than their freshwater resident counterparts (Wilder 1952, Hutchings & Morris 1985, Jonsson & Jonsson 1993). Additionally, Hutchings (1991) found that greater food supply allows female brook trout to produce larger eggs. A positive relationship between egg size and juvenile survival was observed by Hutchings (1991) and Einum & Fleming (1999).

It is unclear why exactly some individuals in a population migrate but others remain residents. It is likely that both genetic and environmental factors play a role in the decision (Jonsson & Jonsson 1993). In general, it is believed that size and maturation determine whether a fish will migrate (Jonsson & Jonsson 1993). A threshold model developed by Fleming (1997) attempts to explain alternative migratory tactics in salmonids. In this model, individuals that are larger than a certain body size with fast growth rates and low metabolic costs remain residents. Those individuals with slower initial growth rates and high metabolic costs do not reach the body size threshold and therefore migrate to more productive marine habitats (Fleming 1997). Theriault & Dodson (2003) found that smaller 1-year old brook trout in the Sainte-Marguerite River in Quebec delayed migration to the following year, and that larger individuals either migrated as 1-year olds or remained resident for their lifetime. Consistent with the threshold theory, they also found that slow growth was associated with migration later in life at a bigger size (Theriault & Dodson 2003). Timing of migration within a season may also vary with size (Lenormand et al. 2004). Lenormand et al. (2004) observed that larger brook trout at sea returned to freshwater sooner in the fall than smaller individuals. Among brook trout that had migrated downstream in the Saint Marguerite River adults moved upstream to spawning areas from July to September, age 1 juveniles moved up into their natal rivers later in the fall, and age 0 juveniles stayed in the estuarine areas until October and overwintered outside their natal river (Lenormand et al. 2004). One early study on brook trout was conducted on five coastal streams in Cape Cod, MA using 92,100 marked individuals over seven years (Mullan 1958). Mullan (1958) found that brook trout age of age 2 years migrated downstream after spawning in October or November. Furthermore, while upstream movement occurred throughout the year in Cape Cod streams, it was most pronounced from May through June and in September (Mullan 1958). Using acoustic telemetry, Curry et al. (2006) detected brook trout entering the marine environment in May and June and returning to the Laval River in Quebec between late July and early September to spawn in October and November.

Studies suggest that there may be specific triggers that initiate migration for some species (Hutchings & Meyers 1994, Sykes et al. 2009, Hvidsten et al. 1995, Curry et al. 2006). Fish with adaptive phenotypic plasticity, such as the Atlantic salmon (*Salmo salar*), may have the ability to “choose” to migrate depending on population density and environmental conditions (Hutchings & Meyers 1994). Some differences in environmental conditions are food abundance, photoperiod, and water temperature. Sykes et al. (2009) showed experimentally that increasing temperature resulted in an earlier peak in downstream movement of Chinook salmon (*Oncorhynchus tshawytscha*) smolts. Zydlewski et al. (2005) found that rather than a single temperature threshold, for Atlantic salmon smolts downstream movement responded to temperature experience over time. On a shorter time scale, once a fish has made the “decision” to migrate, there may be optimum conditions under which it will move into the estuary or sea. Certain environmental factors can cause elevated levels of the hormone thyroxine, which are indicative of an increased tendency to migrate (Hoar 1976). Hvidsten et al. (1995) found that Atlantic salmon smolt downstream migration was related to water flow, decrease in water temperature, moon phase, and social interaction with other migrating smolts. Peaks in plasma thyroxine at new and full moon phases in coho salmon, Chinook salmon and steelhead were observed by Grau et al. (1982) who concluded that hormone peaks at lunar phases help to initiate migration. Mason (1975) found that coho salmon fry downstream movement peaked at the new moon and seaward migration of smolts peaked with the full moon. Plasma concentrations of thyroxine in masu salmon peaked at the new moon in April when downstream migration began (Yamauchi et al 1984, 1985). Castonguay et al. (1982) found that migration peaks in brook trout were synchronized with the new moon and that movements in the estuary were greater during spring tides than neap tides. Curry et al. (2006) observed a strong tidal periodicity to brook trout movements, noting that they would move into bays at high tide and back into rivers at low tide.

1.2 Habitat Fragmentation

Habitat fragmentation is a crucial issue in anadromous brook trout conservation (Nehlsen et al. 1991). Due to the nature of their migration between freshwater and marine habitats, anadromous fish are often subject to habitat fragmentation and destruction by humans (Nehlsen et al. 1991). While over-exploitation, naturally varying ocean and environmental conditions, and hatchery practices are factors that also affect these fish populations, habitat degradation including the destruction and modification of freshwater and estuarine habitats is the most common factor associated with declines in anadromous salmonids (Nehlsen et al. 1991). Examples of disturbances that can cause fragmentation are dam construction, channelization, urbanization, and inappropriately constructed stream crossings (Nehlsen et al. 1991). These alterations to aquatic systems can change the magnitude and frequency of flows, change sediment load, and cause channel erosion and temperatures changes (Poff et al. 1997).

Dams in particular can lead to many changes that are detrimental to fish populations. For aquatic migratory species, habitat fragmentation means interruption of passage between feeding and spawning habitat and changes in exchange of nutrients among ecosystems (Kline at al. 1990, Hall et al. 2011). Habitat fragmentation can lead to reduced biodiversity, cause decreases in population size and increase the risk of local extinction (Lande 1998, Pringle et al. 2000). When anadromous fish are unable to migrate back into freshwater to appropriate spawning habitat, they are essentially removed from their population. Also, fish upstream of a dam may be unable to migrate to the sea (Hall et al. 2011).

The potential for longer term genetic effects from habitat fragmentation are also of interest in the dialogue on conservation of anadromous brook trout. Species on the less anadromous end of the spectrum may not be affected immediately, but over several generations, if the tendency to migrate has a genetic basis, anadromy could be effectively bred out of the population (Mortita et al. 2009). Such isolated populations often experience a loss of migratory tendency, as observed in white-spotted char (*Salvelinus leucomaenis*) (Morita et al. 2009), which can reduce population size and increase the risk for local extinction. Local extinctions reduce dispersal to metapopulations thus increasing the risk for system-wide extinctions (Letcher et al. 2007). Among numerous threatened diadromous species on the east coast of the US, the Atlantic salmon (*Salmo salar*) and Atlantic sturgeon (*Acipenser oxyrinchus*) are currently listed as an endangered. In the northeast United States, brook trout (*Salvelinus fontinalis*) are one of the anadromous fish species whose populations have been severely impacted by dams and other habitat degradation (Nehlsen et al. 1991, Eastern Brook Trout: Status and Threats, Eastern Brook Trout Joint Venture 2006).

Fortunately for impacted diadromous fish species, interest in dam removal and stream restoration has increased in recent years (Bednarek 2001, Stanley & Doyle 2003). While there are short and long term ecological impacts associated with dam removal, there are significant benefits for diadromous fish species (Bednarek 2001). In a review of dam removals across the United States, Bednarek (2001) found that many post-dam removal sites that underwent a restoration of riffle-pool sequences experienced reappearance of gravel and cobble, increases in biotic diversity and improved fish passage. In addition, Hitt et al. (2012) found that American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) benefited from the removal of Embrey Dam in Shenandoah National Park. Furthermore, Hitt et al. (2012) observed an increase in American eel (*Anguilla rostrata*) populations nearly 100 miles away in headwater streams, which was attributed to the dam removal. A recent study in British Columbia by Godbout et al. (2011) documented sockeye salmon (*Oncorhynchus nerka*) populations reverting to anadromy of after removal of hydroelectric dams. After nearly 90 years, two rivers in western Canada where sockeye were thought to have been extirpated due to their impoundment, now support salmon that migrate both upstream and downstream (Godbout et al. 2011). All of these examples make a case for additional habitat restoration and continued research on fish migration.

1.3 Study Area

The location of my study site was Red Brook, a small coastal stream in southeastern Massachusetts (41°45'28.70"N, 70°37'20.77"W), and the adjacent Buttermilk Bay. There is considerable historical documentation by recreational anglers of large annual brook trout migrations, or sea-runs, between Red Brook and the Buttermilk Bay estuary near Bourne, Wareham and Plymouth, Ma (Theodore Lyman Reserve Management Plan, The Trustees of Reservations 2005). The system also supports several other diadromous fish species including American eel (*Anguilla rostrata*), and alewife (*Alosa pseudoharengus*). Striped bass (*Morone saxatilis*) are found in Buttermilk Bay from spring to fall (personal communication, B. Hoffman 2012, S. Hurley 2012).

As with many streams in southeastern New England, Red Brook was dammed in the 1800's to create cranberry bogs. The dams created a partial barrier for brook trout (M. Melchior, Inter-Fluve Inc. Concept Design Report on Red Brook, Ma. 2006) and limited sea runs for over

100 years. Theodore Lyman, an avid fisherman, bought much of the land around Red Brook in the 1800s in an attempt to preserve the brook trout. In the 1980s Theodore Lyman's descendents asked Trout Unlimited (TU), a non-governmental organization to help managethe property and restore the stream. TU then transferred ownership of the land to a land trust, The Trustees of Reservations (TTOR), which created the Lyman Reserve along lower reaches and Buttermilk Bay. The Massachusetts Division of Fisheries and Wildlife acquired land along the northern reaches of the stream, creating the Red Brook Wildlife Management Unit. From 2006-2009, with support from these multiple partnering organizations, four dams were removed along the stream and restoration to support the native brook trout populations began. Volunteers from TU and the Sea Run Brook Trout Coalition are active participants in the ongoing restoration and study of Red Brook.

Red brook has been studied informally by anglers for many years, and has been formally surveyed and monitored since 1984 (Theodore Lyman Reserve Management Plan, TTOR 2005). The Massachusetts Division of Marine Fisheries and TU have conducted studies measuring pH, dissolved oxygen, flow rate and temperature. Average daily stream temperatures in Red Brook range from 0 to 21°C (personal communication, S. Hurley 2011). Ground water springs in the stream create cold pools that satisfy brook trout preference for cold throughout the year. While restoration projects have restored habitat and opened passage to the bay, temperature and flow rate remain influenced by the upstream cranberry bog. A.D. Makepeace Co., owner of Century Bog at Red Brooks' headwaters, has agreed to stop cranberry harvest by 2014 to allow for complete restoration of the system.

Much of the published information about hydrology and bathymetry of Buttermilk Bay and Red Brook is from the late 1980's and early 1990's (e.g. Moog 1987, Valiela & Costa 1988, Hansen & Lapham 1992). Buttermilk Bay is located at the northern end of Buzzards Bay, bordered by the towns of Plymouth, Wareham and Bourne. The Plymouth Carver Aquifer lies in the Wareham Outwash Plain (Hansen & Lapham 1992). The land and the aquifer are therefore composed of glacial deposit from the Pleistocene era (Moog 1987, Valiela & Costa 1988) and much of the substrate in the area is sandy glacial till. The drainage area of the bay is from 70°35’W to 70°39’W longitude and 41°45’N to 41°51’N latitude (Valiela & Costa 1988). The area of the watershed is 16.2 km^2 (Valiela & Costa 1988). Sixty five percent of the drainage area was forested and the remainder was mostly residential and commercial cranberry bogs (Master’s thesis, Boston University, Moog 1987). The areas adjacent to the bay are densely populated by humans, especially on the western shore. Buttermilk Bay itself has a surface area of 2.14km^2 and mean low water depth of 0.9m (Valiela & Costa 1988). The bay experiences two tidal cycles per day with a range of 0.8 – 1.4m and a mean tidal range of 1m (Valiela & Costa 1988). All tidal flow is through Cohasset narrows at the south of the Buttermilk Bay (Valiela & Costa 1988). The bay is relatively shallow and has a high tidal range, so half of the volume of the bay leaves twice a day (Valiela & Costa 1988). Due to its shallow nature, there is significant wind-drive mixing (Valiela & Costa 1988). Valiela & Costa (1988) observed salinity stratification only near the mouth of streams or along beaches with groundwater discharge. Water in the center of Buttermilk Bay is fresher than the average salinity of 30.9 parts per thousand (Valiela & Costa 1988). In 1988, eelgrass was abundant in the bay and benthic micro- and macro-algae accounted for 60% of the primary production (Valiela & Costa 1988). Moog (1987) found that over three year the average freshwater discharge into Buttermilk Bay was 28,682,638m^3/yr. Red Brook is the largest source of this freshwater, discharging 8,360,255m^3/yr in 1985 and 14,311,866m^3/yr in 1986 (Moog 1987). The lower reaches of the brook behave like a typical salt wedge estuary, with saltwater along the bottom of the stream and freshwater on its surface forming a salt wedge.

1.4 Objectives

I focused my thesis on understanding the spatial ecology of a coastal brook trout population in a restored coastal stream. This involved monitoring movement and comparing movement patterns with environmental variables that may be factors in migration. My objective was to characterize brook trout movement patterns between Red Brook and the coastal waters of Buttermilk Bay, including where and when brook trout are found in the stream, estuary and bay. The null hypothesis was that there would be no significant difference in seasonal timing of brook trout movement between habitats. For environmental effects, the null hypothesis was that there would be no relationship between movement and moon phase, stream temperature or tide. Based on past studies, I expected that brook trout would move downstream in the spring as temperature warmed, remain resident in the stream in the summer when temperatures were highest and move upstream in the fall with colder temperatures. Furthermore, I expected to see more migratory movement occur at new and full moons. I also expected fish that moved from the estuary to the bay to do so at high tides.

1.5 References

Bednarek, A.T. 2001. Undamming rivers: A review of the ecological impacts of dam removal. Environmental Management. 27(6): 803-814.

Besner, M., & Pelletier, D. 1991. Adaptation of the brook trout, *Salvelinus fontinalis*, to direct transfer to sea water in spring and summer. Aquaculture. 97(2–3): 217-230.

Castonguay, M., FitzGerald, G.J., & Côté, Y. 1982. Life history and movements of anadromous brook charr, *Salvelinus fontinalis*, in the St-Jean River, Gaspé, Québec. Canadian Journal of Zoology. 60(12): 3084-3091.

Curry, R., van de Sande, J., & Whoriskey, F.J. 2006. Temporal and spatial habitats of anadromous brook charr in the Laval River and its estuary. Environmental Biology of Fishes. 76(2-4): 361-370.

Einum, S., & Fleming, I.A. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. Proceedings: Biological Sciences. 266(1433): 2095.

Fleming, I.A. 1997. Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in Fish Biology and Fisheries. 6(4): 379.

Godbout, L., Wood, C.C., Withler, R.E., Latham, S., Nelson, R.J., Wetzel, L., Barnett-Johnson, R., Grove, M.J., Schmitt, A.K., McKeegan, K.D., & Bradford, M. 2011. Sockeye salmon (*Oncorhynchus nerka*) return after an absence of nearly 90 years: a case of reversion to anadromy. Canadian Journal of Fisheries and Aquatic Sciences. 68(9): 1590-1602.

Grau, E.G., Specker, J.L., Nishioka, R.S., & Bern, H.A. 1982. Factors determining the occurrence of the surge in thyroid activity in salmon during smoltification. Aquaculture. 28(1): 49-57.

Gross, M.R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends in Ecology & Evolution. 11(2): 92-98.

Gross, M. 1987. Evolution of diadromy in fishes. *Edited by* Dadswell, M.J., Klauda, R.J., Moffitt, C.M., Saunders, R.L., Rulifson, R.A., Cooper, J.E. American Fisheries Society Symposium.

Hall, C.J., Jordaan, A., & Frisk, M.G. 2011. The historic influence of dams on diadromous fish habitat with a focus on river herring and hydrologic longitudinal connectivity. Landscape Ecology. 26(1): 95-107.

Hansen, B.P., & Lapham, W.W. 1992. Geohydrology and simulated ground-water flow, Plymouth-Carver aquifer, southeastern Massachusetts. US Department of the Interior, US Geological Survey.

Hartel, K., Halliwell, D., & Launer, A. 2002. Inland fishes of Massachusetts. Massachusetts Audubon Society, Lincoln, MA.

Hitt, N.P., Eyler, S., & Wofford, J.E. 2012. Dam removal increases American eel abundance in distant headwater streams. Transactions of the American Fisheries Society. 141(5): 1171-1179.

Hoar, W.S. 1976. Smolt transformation: evolution, behavior, and physiology. Journal of the Fisheries Board of Canada. 33(5): 1233-1252.

Hutchings, J.A., & Morris, D.W. 1985. The influence of phylogeny, size and behaviour on patterns of covariation in salmonid life histories. Oikos. 45(1): 118-124.

Hutchings, J.A. 1991. Fitness Consequences of Variation in Egg Size and Food Abundance in Brook Trout Salvelinus fontinalis. Evolution. 45(5): 1162-1168.

Hutchings, J.A., & Myers, R.A. 1994. The evolution of alternative mating strategies in variable environments. Evolutionary Ecology. 8(3): 256-268.

Hvidsten, N., Jensen, A., Vivaas, H., Bakke, O., & Heggberget, T. 1995. Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction. Nordic Journal of Freshwater Research. 70: 38-48.

Jonsson, B., & Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries. Volume 3, Number 4: 348-365.

Kline, T.C.,: Jr, Goering, J.J., Mathisen, O.A., Poe, P.H., & Parker, P.L. 1990. Recycling of elements transported upstream by runs of Pacific salmon: 1. [delta]15N and [delta]13C evidence in Sachin Creek, southeastern Alaska. Canadian Journal of Fisheries and Aquatic Sciences. 47(1): 136-144.

Lande, R., Engen, S., and Saether, B. 1998. Extinction times in finite metapopulation models with stochastic local dynamics. Vol. 83, pp. 383-389.

Lenormand, S., Dodson, J.J., & Menard, A. 2004. Seasonal and ontogenetic patterns in the migration of anadromous brook charr (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences. 61(1): 54-54-67.

Letcher, B.H., Nislow, K.H., Coombs, J.A., O'Donnell, M.J., & Dubreuil, T.L. 2007. Population response to habitat fragmentation in a stream-dwelling brook trout population. Plos One. 2(11): e1139-e1139.

Mason, J.C. 1975. Seaward movement of juvenile fishes, including lunar periodicity in the movement of coho salmon (*Oncorhynchus kisutch*) fry. Journal of the Fisheries Board of Canada. 32(12): 2542-2547.

McCormick, S.D., & Naiman, R.J. 1984b. Osmoregulation in the brook trout, *Salvelinus fontinalis,*—II. Effects of size, age and photoperiod on seawater survival and ionic regulation. Comparative Biochemistry and Physiology Part A: Physiology. 79(1): 17-28.

McCormick, S.D., Naiman, R.J., & Montgomery, E.T. 1985. Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences. 42(3): 529-538.

McCormick, S.D. 1994. Ontogeny and evolution of salinity tolerance in anadromous salmonids: hormones and heterochrony. Estuaries. 17(1): 26-33.

McCormick, S.D., & Naiman, R. 1984a. Osmoregulation in the brook trout, *Salvelinus fontinalis*. I. Diel, photoperiod and growth related physiological changes in freshwater. Comparative Biochemistry and Physiology Part A: Physiology. 79A(1): 7-7-16.

McCormick, S., & Saunders, R. 1987. Preparatory physiological adaptations for marine life of salmonids: Osmoregulation, growth, and metabolism. American Fisheries Society Symposium. 1(21):1-229.

McDowall. 2001. Anadromy and homing: two life-history traits with adaptive synergies in salmonid fishes? Fish and Fisheries. 2(1): 78-85.

McDowall, R. 1987. The occurrence and distribution of diadromy among fishes. American Fisheries Society Symposium. 1: 1-13.

Morita, K., Morita, S.H., & Yamamoto, S. 2009. Effects of habitat fragmentation by damming on salmonid fishes: lessons from white-spotted charr in Japan. Ecological Research. 24(4): 711-722.

Mullan, J.W. 1958. The sea-run or "salter" brook trout (*Salvelinus fontinalis*) fishery of the coastal streams of Cape Cod, Massachusetts. Massachusetts Division of Fisheries and Game.

Myers, G.S. 1949. Usage of anadromous, catadromous and allied terms for migratory fishes. Copeia, Ann Arbor. 1949: 89.

Nehlsen, W., Williams, J.E., & Lichatowich, J.A. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho and Washington. Fisheries (Bethesda). 16(2): 4-21.

Nordeng, H. 1961. On the biology of char (*Salmo alpinus L.*) in Salangen, North Norway. Norwegian Journal of Zoology. 10: 67-132

Northcote, T.G. 1978. Migratory strategies and production in freshwater fishes. *In* Ecology of Freshwater Fish Production. *Edited by* S. Gerking. John Wiley & Sons, New York, NY. pp. 326-359.

Olsson, I.C., Greenberg, L.A., Bergman, E., & Wysujack, K. 2006. Environmentally induced migration: the importance of food. Ecology Letters. 9(6): 645-651.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., & Stromberg, J.C. 1997. The natural flow regime. Bioscience. 47(11): 769-784.

Pringle, C., Freeman, M., & Freeman, B. 2000. Regional effects of hydrologic alterations on riverine macrobiotain the New World: tropical-temperate comparisons. Bioscience. 50(9): 807-823.

Rounsefell, G.A. 1957. Fecundity of North American Salmonidae. Fishery Bulletin, United States Fish and Wildlife Service. 57: 451-468.

Rounsefell, G.A. 1958. Anadromy in North American Salmonidae. Fishery Bulletin, United States Fish and Wildlife Service. 62: 171-185.

Ryther, J.H., & Trout Unlimited. 1997. Anadromous brook trout : biology, status and enhancement. Trout Unlimited, Arlington, VA.

Scott, W.B., & Crossman, E.J. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin. 184.

Stanley, E., & Doyle, M. 2003. Trading off: the ecological effects of dam removal. Frontiers in Ecology and the Environment. 1(1): 15-22.

Sykes G.E., Johnson C.J., & Shrimpton J.M. 2009. Temperature and flow effects on migration timing of chinook salmon smolts. Transactions of the American Fisheries Society. 138(6): 1252-1265.

Theriault, V. 2003. Body size and the adoption of a migratory tactic in brook charr. Journal of Fish Biology. 63(5): 1144-1144-1159.

Valiela, I., & Costa, J.E. 1988. Eutrophication of Buttermilk Bay, a Cape Cod coastal embayment: concentrations of nutrients and watershed nutrient budgets. Environmental Management. 12(4): 539-553.

Vladykov, V.D. 1963. A review of salmonid genera and their broad geographical distribution. Transactions of Royal Society of Canada. 1 (series 4, section 3): 450-504.

Wilder, D. 1952. A comparative study of anadromous and freshwater populations of brook trout (*Salvelinus fontinalis* (Mitchill)). Journal of the Fisheries Research Board of Canada. 9: 169-203.

Wysujack, K., Greenberg, L.A., Bergman, E., & Olsson, I.C. 2009. The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. Ecology of Freshwater Fish. 18(1): 52-59.

Yamauchi, K., Koide, N., Adachi, S., & Nagahama, Y. 1984. Changes in seawater adaptability and blood thyroxine concentrations during smoltification of the masu salmon, *Oncorhynchus masou*, and the amago salmon, *Oncorhynchus rhodurus*. Aquaculture. 42(3): 247-256.

Yamauchi, K., Ban, M., Kasahara, N., Izumi, T., Kojima, H., & Harako, T. 1985. Physiological and behavioral changes occurring during smoltification in the masu salmon, *Oncorhynchus masou*. Aquaculture. 45(1): 227-235.

Zydlewski, G.B., Haro, A., & McCormick, S.D. 2005. Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior of Atlantic salmon (*Salmo salar*) smolts. Canadian Journal of Fisheries & Aquatic Sciences. 62(1): 68-78.

CHAPTER 2

MOVEMENT PATTERNS OF BROOK TROUT IN A RESTORED COASTAL STREAM SYSTEM IN SOUTHERN MASSACHUSETTS

2.1 Abstract

Populations of anadromous brook trout can be found from northern Canada into New England. It is believed that the extent of anadromy exhibited by coastal brook trout populations decreases with latitude, but the ecology and movements of the more southern populations are less studied. A 33-month acoustic telemetry study of anadromous brook trout (*Salvelinus fontinalis*) was conducted in a restored coastal stream and adjacent marine system in southeastern Massachusetts. Movement and migration patterns of 54 brook trout were investigated for individual differences and common features. Individuals exhibited a range of movement patterns. Some were more resident and only moved short distances, while others moved great distances covering the entire stretch of the stream (7.25 km) and moving into the marine environment. General Additive Mixed Models revealed that date was the major influence on brook trout movement between habitats and predicted peaks in movement in the spring and fall. Downstream movement peaked in the spring and in the fall, suggesting post-spawning feeding migration. Fish transitioned between habitats more often at new and full moons and when stream temperature was between 8 and 12 °C. Upstream transitions peaked as temperatures declined in winter 2011. Fifty percent of tagged brook trout were detected in the estuary during the study, suggesting that it is an important habitat for the population. In summer 2012, 14 tagged brook trout (20% of active tags) resided near one receiver at the head of the tide, which contained a thermal refugia in the form of a cold-water spring seep. Of the 84 tagged brook trout, 9.5% moved to the marine environment. Warm temperatures in saline Buttermilk Bay in the summer and cold temperatures in winter probably discourage some

individuals from entering the marine environment. Compared to more northern coastal populations of brook trout, the Red Brook population appears to be less anadromous.

2.2 Introduction

Anadromous populations of brook trout (*Salvelinus fontinalis*), also known as brook charr, occur in northeast North America along the coast from Long Island, NY to northern Canada (Ryther 1997). According to Gross (1987), species are likely to evolve this life history trait when they can obtain greater fitness from moving into a second habitat, migration costs included, than by staying in only one habitat. The brook trout is a partially migratory anadromous species. Migration for brook trout is not obligatory, occurring only in populations with access to the marine environment, and even then only in certain individuals within populations (Rounsefell 1957, Power 1980). Brook trout are thought to be the least anadromous of salmonids because of factors including total time spent at sea, extent of migration into the sea and occurrence of freshwater forms (Rounsefell 1957). Several authors have observed a lesser degree of anadromy in brook trout and other salmonid species populations as one moves southward in the northern hemisphere (Rounsefell 1958, Scott & Crossman 1973, Vladykov 1963, Nordeng 1961). Although not all individuals move into the marine environment, brook trout are able to tolerate a wide range of salinities ranging from 1- 34 parts per thousand (Curry et al. 2006). Based on a number of physiological factors (including Na^+, K^+-ATPase activity and osmoregulatory ability), McCormick & Naiman (1985) concluded that brook trout do not smolt (undergo metamorphic and physiological changes for seawater entry), so estuarine residence is important for them to acclimate to and eventually migrate to saltwater. For example, Castonguay et al. (1982) studied a population of brook trout in Quebec whose migratory individuals spent the first two to three years in the river, then one year in the estuary. When they finally moved to saltwater, brook trout remained there two to three months and then returned to the river (Castonguay et al. 1982). Besner & Pelletier (1991) found that brook trout survival in saltwater was least likely in the summer and most likely in the spring.

It is unclear why exactly some individuals in a population migrate but others remain residents. It is likely that both genetic and environmental factors play a role in the decision (Jonsson & Jonsson 1993). In general, it is believed that size and maturation status determine whether a fish will migrate (Jonsson & Jonsson 1993). Studies suggest that there are specific triggers that initiate migration for some salmonids (Hutchings & Meyers 1994, Sykes et al. 2009, Hvidsten et al. 1995, Curry et al. 2006). Atlantic salmon smolt downstream migration is related to water flow, decrease in water temperature, moon phase, and social interaction with other migrating smolts (Hvidsten et al. 1995). Peaks in plasma thyroxine, which is indicative of an increased tendency to migrate (Hoar 1976), at new and full moon phases have been observed in coho salmon (*Oncorhynchus kisutch*), chinook salmon (*Oncorhynchus tshawytscha*), steelhead (*Oncorhynchus mykiss*) and masu salmon (*Oncorhynchus masou*) at the initiation of migrations (Mason 1975, Grau et al. 1982, Yamauchi et al. 1984, 1985). Castonguay et al. (1982) found that brook trout migration peaks were synchronized with the new moon and that movements in the estuary were greater during spring tides than neap tides. Curry et al. (2006) observed a strong tidal periodicity to brook trout movements, noting that they would move into bays at high tide and back into rivers at low tide.

One early study on brook trout migration was conducted on five coastal streams in Cape Cod, MA using 92,100 marked individuals over seven years (Mullan 1958). Mullan (1958) found that brook trout of age 2 years migrated downstream after spawning in October or November. Furthermore, while upstream movement occurred throughout the year in Cape Cod streams, it was most pronounced from May through June and in September (Mullan 1958). Brook trout were observed moving between freshwater and the brackish estuary throughout the year on Prince Edward Island, with downstream peaks in movement occurring from October to December and upstream peaks from April to July (Smith & Saunders 1958). Among brook trout that had migrated downstream in the Saint Marguerite River, Quebec, adults moved upstream to spawning areas from July to September (Lenormand et al. 2004). Using acoustic telemetry, Curry et al. (2006) detected brook trout entering the marine environment in May and June and returning to the Laval River in Quebec between late July and early September to spawn in October and November. Total time spent in the marine environment has been documented from an average 65 to 150 days, but is highly variable among brook trout populations and seems to decrease in more southern populations (White 1942, Naiman et al. 1987, Curry et al. 2006)

Habitat degradation including the destruction and modification of freshwater and estuarine habitats is the most common factor associated with declines in anadromous salmonids (Nehlsen et al. 1991) and impacts more than 50% of Massachusetts sub-watersheds (Eastern Brook Trout: Status and Threats, Eastern Brook Trout Join Venture 2006). These alterations to aquatic systems can change the magnitude and frequency of flows, change sediment load, and cause channel erosion and temperatures changes (Poff et al. 1997). Anadromous fish populations that become isolated due to dams often experience a loss of migratory tendency, as observed in white-spotted char (*Salvelinus leucomaenis*) (Morita et al. 2009), which can reduce population size and increase the risk for local extinction. Local extinctions reduce dispersal within metapopulations thus increasing the risk for system-wide extinctions (Letcher et al. 2007).

Red Brook in southeastern Massachusetts is an example of a coastal stream impacted by dams and habitat degradation since the 1800s and whose brook trout population is a concern to recreational anglers and managers. There is considerable historical documentation by recreational anglers of large annual brook trout migrations, or sea-runs, between Red Brook and the Buttermilk Bay estuary near Bourne, Wareham and Plymouth, Ma (Theodore Lyman Reserve Management Plan, The Trustees of Reservations 2005). From 2006-2009, with support from multiple partnering organizations, four dams were removed along the stream and restoration to support the native brook trout populations began, however, the degree of anadromy of Red Brook's brook trout population after dam removal was unknown.

The purpose of this study was to quantify brook trout movement patterns within Red Brook and the coastal waters of Buttermilk Bay and to examine potential factors that influence their movements. I employed acoustic telemetry to facilitate the contiguous monitoring of fish among freshwater, estuarine, and marine habitats (Curry et al. 2006). Most studies on the migration of brook trout have been in the northern parts of their range where anadromous forms are more common and the populations have incurred less human-caused degradation (Castonguay et al. 1982, Curry et al. 2002, Theriault & Dodson 2003, Lenormand et al. 2004, Curry et al. 2006). My study site is in a region with relatively few anadromous brook trout populations, most of which are challenged by the habitat degradation and fragmentation inherent to areas with high human population densities. Studying the movements of anadromous brook trout will help to characterize the biology and ecology of this species at its southern coastal range. Furthermore, the results of this study will help to inform management decisions as more degraded coastal streams are restored to promote brook trout. My objective was to describe brook trout movement patterns between Red Brook and the coastal waters of Buttermilk Bay and to examine potential factors that influence that movement.

2.3 Methods

2.3.1 Study Site

The study site was a small coastal stream in southeastern Massachusetts called Red Brook, (41°45'28.70"N, 70°37'20.77"W) and the adjacent Buttermilk Bay. Red Brook is a 7.25 km, low-gradient stream with an average width of 2 m and average depth of 1 m. Red Brook's headwaters are in cranberry bog and it empties into Buttermilk Bay. Average daily stream temperatures in Red Brook range from 0 to 21°C (personal communication, S. Hurley 2011). Substrate in the area is mainly glacial till through which groundwater seeps from the Plymouth Carver Aquifer (Master's thesis, Boston University, Moog 1987, Valiela & Costa 1988). Springs in the steam create cold pools that satisfy brook trout preference for cool water temperatures throughout the year. Red Brook is the largest source of freshwater input into Buttermilk Bay (with discharges of 8,360,255 m^3/yr in 1985 and 14,311,866 m^3/yr in 1986) (Moog 1987).

Buttermilk Bay is located at the northern end of Buzzards Bay, bordered by the towns of Plymouth, Wareham and Bourne, which are densely populated by humans. Buttermilk Bay has a surface area of 2.14km^2, a mean low water depth of 0.9m, and it experiences two tidal cycles per day with a range of 0.8 – 1.4m and a mean tidal range of 1m (Valiela & Costa 1988). All tidal flow is through Cohasset narrows at the south of the Buttermilk Bay (Valiela & Costa 1988). Valiela & Costa (1988) observed salinity stratification only near the mouth of streams or along beaches with groundwater discharge and noted that water in the center of Buttermilk Bay is fresher than the average Buttermilk Bay salinity of 30.9 ppt.

2.3.2 Acoustic Receiver Array

Acoustic telemetry is the most practical technique for tracking fish that use both freshwater streams and marine environments (see Koehn 2003, Cooke et al. 2012). Sixteen

VR2W stationary acoustic receivers (Vemco Inc., Halifax, NS) were deployed throughout Red Brook, the estuary, and Buttermilk Bay (Figure 1). Initially, nine receivers were deployed on 07 June 2010 (referred to as R01-09, Figure 1). The region of greatest interest to this study is the zone where fish move from freshwater to saltwater, so receivers were first placed in the lower part of the stream and estuary. Coverage of the mouth of the estuary opening into Buttermilk Bay was essential, because it is the entrance to the marine environment. To obtain greater coverage of migration patterns, two receivers (R10 and 11) were added upstream in potential spawning and overwintering areas on 17 February 2011. Two more receivers (R12 and 13) were added on 05 October 2011, another two (R14 and 15) on 21 October 2011, and a final receiver (R16) on 07 February 2012 (Figure 2). In total, one receiver was placed at the headwaters of Red Brook, just below the cranberry bog, three receivers were placed at the mid to lower reach of the stream, four were located in the estuary and, eight were placed in the marine environment, which includes Buttermilk Bay, Little Buttermilk Bay (a smaller, shallow bay connected to eastern Buttermilk Bay), and the channel to Buzzards Bay.

Receivers were moored to navigation aids or attached to metal bars affixed to cement paving stones. Receivers were placed with the transducer end pointing upward. A line attached to a buoy allowed for easy location of and access to receivers in the estuary and bay. Because brook trout are likely to remain in shallow (<1.7m), near-shore (<500m) areas in marine environments (Curry et al. 2006) where they can take cover from predators and are likely to find the most suitable prey items, most of the receivers in Buttermilk Bay were placed near the shore as detection nodes. Depth of stationary receivers in the Buttermilk Bay ranged from 1.2 to 2.6 m. Two receivers were placed in the channel from Buttermilk to Buzzards Bay to record fish leaving the system, though it is uncommon to find brook trout beyond the headlands of coastal bays (Curry et al. 2006).

Receivers were checked every three to six months to download detection data. Several receivers were removed by persons external to the study or lost due to wear on moorings or excessive winter icing. Therefore, there are varying periods of time for which some receivers were not collecting data. The final downloads of receivers occurred on 14 March 2013. A detection limit test for a subset of receivers was conducted in 50 m intervals up to 350 m in each of the four cardinal directions from a receiver. Detection limits (distance at which 100% of transmitter pings were heard in 3 minutes) for bay receivers ranged from 0-150 m and detection limits in the stream ranged from 5 -20 m.

2.3.3 Brook Trout Tagging Procedures

Brook Trout were captured using backpack electrofishing unit (FS 1001A-24DC Pelican Products, Torrance CA, USA) in Red Brook on five separate occasions in the spring or the fall (avoiding spawning times). Beginning 30 m upstream of Head of the Bay Road Bridge, approximately 500 m upstream of the mouth, the stream was divided into 21 sections (each 40 m in length), which were shocked individually. The sampling area of approximately 900 m of stream represents about 13% of Red Brook’s length. Sampling sections 1 to 5 are in areas where saltwater has been detected. The head of the tide is believed to be between sections 4 and 5. Fish from each section were retained in separate labeled holding tanks prior to tagging.

Brook trout greater than 160 mm fork length (FL) were tagged. McCormick & Naiman (1984) found that brook trout greater than 140 mm FL are able to survive seawater. Therefore, our size criteria was biased towards those fish that could physiologically exhibit anadromy. Fish to be tagged were transferred from the stream to a tagging station less than 5 m away from the stream bank. Fish condition (e.g. coordinated movements, equilibrium and opercular movements) was continuously monitored. Brook trout were handled using wet soft-mesh nets and wetted hands to minimize injuries related to transfer. Individual fish were anesthetized and considered ready for processing and surgery after being unresponsive for 30 seconds. Once anesthetized, fish were transferred to a wetted measuring board where fork length was measured (to the nearest mm). Fish were then weighed (to the nearest mg) using a wetted metal cradle scale (Scout Pro, Ohaus Corp, Parsippany, NJ).

Fish selected for tagging were then placed on a wetted, wedged sponge for the surgical procedure. Transmitters and surgical tools were disinfected with isopropyl alcohol. A 20 mm incision was made using a scalpel on the ventral surface between the pectoral and anal fin. Once the incision was made, a Vemco V9 acoustic transmitter (weighing 11 g in air, with a random delay of 120 to 240 seconds at a frequency of 69 kHz, estimated tag life 407 days, Vemco Inc., Halifax, NS) was inserted. A PIT tag was also implanted in each fish as part of a separate study. The incision was closed with two to three interrupted sutures (Ethicon 3-0, 2 mm diameter monofilament synthetic absorbable suture with a CP-2 26 mm curved, reverse cutting needle, Johnson and Johnson, New Jersey). Total surgery time for each fish was two to three minutes. Fish were then placed in an aerated recovery tank and monitored until fish regained equilibrium and displayed coordinated fin movements for at least 10 min, after which they were released back into the section of stream where they were captured.

2.3.4 Environmental Data Collection

Temperature/light data loggers (HOBO Pendant Temperature/Light Data Logger 64K - UA-002-64, Onset Corp, Onset MA) were attached to eight receivers in the estuary and bay to record hourly water temperatures (eight total loggers located at receivers R03-09 and R13). Temperature from the logger at R09 from 05 September 2011 to 21 December 2011 was used as a separate environmental variable because it is the closest bay temperature logger to the mouth of Red Brook. Stream temperature was collected for the entire study period from a water level and temperature data logger (HOBO U20, Onset Corp., Onset, MA) approximately 60 m upstream of R10, where there is no influence by tide. Moon phase has been shown to influence movements of many animal species including fish (Curry et al. 2006). Moon phase data for the study period was obtained for the Eastern Standard time zone from the United States Naval Observatory website (http://aa.usno.navy.mil/data/docs/MoonFraction.php). The geocentric data represents the fraction of the moon that is illuminated on each day, and is a quantitative way of describing the moon's phases.

Tidal data was collected using a water level logger (HOBO U20, Onset Corp, Onset MA), which measures absolute pressure, was deployed at the mouth of Red Brook for 13 days. An identical logger on land was used to compensate for barometric pressure changes and to produce accurate water level data. These data were then compared to NOAA tide predictions from the Onset, Massachusetts station to obtain an estimate of average lag time in the tidal cycles. The estimated difference of five minutes at low tide and six minutes at high tide was applied to the Onset data to obtain a tidal history for Red Brook for the entire study period.

2.3.5 Manual Tracking

In spring 2012, I used active manual tracking telemetry to locate tagged brook trout on about 1.2 km of Red Brook from the estuary to lower reaches of the stream. Manual tracking distance was limited by overgrown vegetation that blocked passage of tracking equipment. The acoustic receivers were stationary, so they only provided data points when a tagged brook trout passed within the detection range of receivers. Manually tracking individuals using a Vemco VR100 and omni-directional hydrophone over the course of several hours provided more information about movements and location of fish that reside mostly between receivers.

2.3.6 Data Analysis

Individual fish movements were examined using VUE software (Vemco Inc., Halifax, NS). In the Quality Assurance/Quality Control process, a tag was considered to be transmitting false detections when there were consistent, regular detections (i.e. every 120 to 240 seconds) at one receiver over at least a three-week period and no subsequent detections at other receivers (except possibly at a nearby downstream receiver where continuous, regular detections were also seen, indicating that the tag washed downstream). False detections indicating that a fish had died near a receiver or had shed its tag near a receiver were flagged for four individuals and removed from the data.

To compare movements of detected fish between habitats, receivers were grouped into four “nodes” by habitat type: 1) upper reach of the stream, 2) lower reach of the stream, 3) estuary, and 4) bay. Transition matrix plots were constructed to show when fish move between nodes. An initial transition matrix was used to look at movement over the entire study period, then reduced matrices were used to illustrate periods when important movements occurred. Detections were manipulated into transitions by selecting unique combinations of individual, date, and node. A transition required that a fish was detected in more than one node in the same day or was detected on more than one day. We first examined the empirical data for relationships between transition and temperature and moon phase. Then, individual fish detections were plotted over time (Appendix A). To address the hypothesis related to anadromy, detections for all receivers in the bay were combined for the individual brook trout plots.

Generalized additive mixed models (GAMM) using the gamm4 package in R (R version 3.0.1, http://cran.r-project.org/) were used to investigate the relationship between environmental variables and transitions between nodes (Swartzman 1997, Murase 2009, Yee

2010). Covariates tested as fixed and random effects included stream temperature, moon phase and day of year. Moon phase and stream temperature were selected for modeling against transitions as they were the most complete environmental variables available and other temperature variables were determined to be highly correlated. Models were chosen based on p-values (significant when $p < 0.05$) of covariates, by examining plots of residuals, and using Akaike's information criterion (AIC) to compare candidate models.

2.4 Results

A total of 84 brook trout was tagged over five sampling occasions from 2010 to 2012 (Table 1). There was no significant difference in fish length among the different sampling occasions (ANOVA, p=0.5). Following inspection of the raw detection data, 62 individuals (73.8%) yielded valid detections with a mean number of days tacked (between first and last detection) of 171 ± 140 SD (Table 1). Brook trout were detected from one to 45,942 times on one to nine receivers. Twelve of the detected brook trout (19.4%) were detected at some point during the study in the upper reaches of the stream, 44 (71%) were detected in the lower reaches of the stream, 42 (67.7%) were detected in the estuary, and eight (12.9% of detected) were detected in the bay. Manual tracking confirmed that two additional fish that had not been detected by VR2W acoustic receivers were in the stream and alive. Twenty one fish were not detected at any time during the study. In total, five tags produced unreliable detections at some point during the study. Only detections when those fish were expected to be alive were used in the analysis. One tag was determined to have been expelled or a mortality from initial deployment, so the data from this fish were removed from the analysis. During the last sampling, one fish that had previously been tagged was re-tagged because inspection for acoustic and PIT tags did not register the tag identification numbers. The fish was later found dead on the shore by a fisherman, and a necropsy revealed the two acoustic tags but no PIT tag (the original PIT tag had likely been expelled and the first acoustic tag battery had expired). The second acoustic tag detections for this fish were removed from the data.

2.4.1 Individual Movement Patterns

Movement patterns varied greatly among individuals, with some brook trout remaining non-migratory residents and others migrating from fresh to salt water and back. Some individuals moved little within the stream while a few made long distance movements as long as the head of the stream to the bay (7.25 km). Forty-two individuals (50% of tagged populations) were detected in the estuary, and eight brook trout made transitions from the estuary into Buttermilk Bay, representing 9.5% of the tagged sample. Brook trout were detected in Buttermilk Bay mostly in the fall and winter (Table 3). Half of the individuals that moved into the bay (n=4) made repeat trips between the estuary and bay and half moved directly from the estuary to the bay without returning to the estuary. The maximum time that an individual was detected in the marine environment ranged from 30 minutes to 54 days (one tag was detected only in the bay for 377 days and was likely an expelled tag or mortality, but could not be assigned based on QA/QC criteria). Only two of the eight brook trout were detected back in the estuary or stream after moving out into Buttermilk Bay and had only spent 30 minutes and two days in the bay. We cannot confirm the fate of individuals that did not return to Red Brook, but we know that three of the tags likely lost battery function (Vemco estimated tag life is 407 days) while the fish were at sea (Table 3). These individuals may have returned to Red Brook, but we were not able to detect the expired tags. Of course, it is also possible that these fish died in the marine environment. One individual (33398) was last detected at R08 heading out of the system and its tag was recorded for the next three days on a receiver in a separate acoustic tag array on the west side of the Cape Cod Canal.

Four individuals were selected as representatives of the distinctly different movement patterns (Figure 2). Fish 5516 recorded the maximum number of detections (45,942) for all brook trout tagged as part of this study, and registered an above average detection time span length (283 days). However, this individual's movement patterns are representative of many of the tagged brook trout as it was detected on an average number of receivers (3, mean= 2.61) and in an average number of nodes (2, mean= 2). It spent the majority of its time in the estuary, did not make long distance movements, and did not migrate into Buttermilk Bay. After tagging on 30 May 2012, Fish 5516 spent the summer at R14 near the head of the tide. In September it moved downstream to R01 where it stayed until December when it made a relatively quick upstream movement past the head of the tide and into the lower stream where it was detected on three consecutive days. Fish 5516 then moved back downstream to R01 where it overwintered, except for one short excursion up to R14 in January.

Fish 40111 spent most of its time in the estuary in the fall and winter but frequently moved between receivers. It recorded a slightly above average number of detections (5,343) and registered a slightly above average detection time span (235 days). It was detected on six receivers and in three nodes including Buttermilk Bay. Fish 40111 was tagged on 01 June 2011 and was first detected in the estuary in September 2011. In October and November, it moved up to the lower stream. In December 2011, this individual made an initial downstream movement from R14 all the way to R09 in Buttermilk Bay in three days. In late December 40111 continued to move between the estuary and bay receivers until January when it remained in the estuary, but continued moving between three receivers (Figure 2).

Fish 3066 moved long distances between habitats and changed from moving upstream in one fall to downstream in the next. It recorded a slightly above average number of detections (6,896) over a relatively long detection time span (406 days). Fish 3066 was detected on seven receivers and was the only brook trout to be detected in all four nodes. This individual was tagged on 20 September 2011 and was first detected at R14 in the estuary in October. In November, fish 3066 moved from the lower stream to the upper stream, covering approximately 3.6 km in less than 38 hours. In April 2012, this individual made another quick migration, this time back downstream to R14 where it spent the summer. In the second fall of its deployment, fish 3066 made a quick migration down through the estuary and into Buttermilk Bay. It was last detected several times on two receivers in Buttermilk Bay (R05 and R13) in early November 2012 (Figure 2). The battery in tag 3066 likely died while the individual was at sea, so whether the individual returned to Red Brook is not known.

Fish 33414 slowly moved downstream from fall to spring as it moved from the lower stream to the bay. It recorded an above average number of detections (23,434) over a nearly average detection time span (190 days). It was detected on six receivers, but remained within the lower stream and estuary, thus visiting the average number of nodes (2). Fish 33414 was tagged on 20 September 2011 just below R10 and was first detected at R10 in the lower stream in November. This individual made more of a gradual downstream movement through the estuary during the winter, registering numerous consecutive detections at R01 from January to March 2012. In the beginning of March, fish 33414 was detected mostly on R01, making excursions down to R12. Throughout March, it was detected mostly on R12, making excursions down to R02 (Figure 2).

2.4.2 Movement by Date and Environmental Factors

Of the 54 individuals in the transition analysis that were detected in more than one node or were detected on two or more days across the study period, 33 made transitions between nodes. Downstream transitions were made by 25 individuals and accounted for 70 of the 142 transitions (mean=2.5 transitions per individual). Upstream transitions were made by 32 individuals and accounted for 72 (50.7%) of the total transitions (mean=2.8 transitions per individual). Downstream transitions from the upper stream to lower stream (n=4) occurred in April and May while upstream transitions from the lower stream to upper stream (n=7) occurred in March, April, October and November. Downstream and upstream transitions between the lower stream and the estuary (n=75) occurred most frequently in October and November (mean transitions per month in Dec. and Nov. = 18.75, as compared to mean transitions in all other months = 1.8). Between estuary and the bay, the greatest number of transitions (n=17) occurred in December, fewer transitions between occurred during the late winter to summer months (mean=4.43 transitions per month), and no transitions occurred from April-June, August, and October (Figure 3).

Three transition matrices were selected to illustrate important periods when movement occurred. Across two years of the study, there were autumn peaks in the total number of individuals in the lower stream and the estuary, as well as an increased number of individuals moving between the lower stream and estuary (Figure 4). From 21 October 2011 – 03 January 2012, 14 individuals (20.29% of total tags deployed at the time) completed 37 downstream transitions from the stream to the estuary, with a maximum of seven transitions per individual. This peak is visible in November 2010 in the estuary, but was not seen in the lower stream in 2010 because receivers were not placed in the lower stream until February 2011. There were several days in spring and summer 2012 when an increased number of individuals were residing in the estuary (Figure 5). The majority of fish detected in the estuary during this time (Figure 6) were detected at one receiver (R14), which is located in the area that is believed to be the head of the tide (personal communication, S. Hurley 2011). Fourteen brook trout were detected between 30 May 2012 and 20 September 2012. Three of these fish had been tagged at previous sampling periods and 11 were tagged on 30 May. Of the latter group, six had been initially captured and released in the estuary below R14 (up to 190 m downstream) and five had been captured and released in the two sampling sections above R14 (up to 75 m upstream). Seven fish out of the 14 (50%) were detected on other receivers during the May -September period in addition to R14 (mean= 2.43 receivers/fish), and 10 of the 14 fish were detected on other receivers after the period (mean=2.22 receivers/fish), proving their continued viability. Three of the 14 fish were only detected on R14 during the period and were not detected afterward. However, their detections were not regular, so they could not be considered mortalities or dropped tags. After September, four individuals moved upstream and six moved further into the estuary with one transitioning into Buttermilk Bay.

Fish were detected more often throughout the system at new and full moon phases. Downstream and upstream transitions also occurred more frequently during new and full moons (Figure 7). Migration from the estuary to bay occurred almost exclusively during new moon and full moons. Mean daily stream temperature over the study period was 11°C (±4.8) while mean daily temperature in Buttermilk Bay just outside the mouth of Red Brook was 13.1°C (±6.4) over 411 days (06 October 2011 – 20 December 2012). In fall and spring, Buttermilk Bay temperatures were just above stream temperature, in the winter the bay was colder, and in the summer the bay was much warmer than the stream (Figure 8). Average mean daily temperature across all loggers in Buttermilk Bay was 10.6 °C (±5.2) over 264 days (06 October 2011 – 28 June 2012).

Fifty percent of downstream transitions by brook trout occurred when stream temperature was between 7.9 and 12.0 °C (Figure 9). The maximum number of fish moving downstream per day (n=5) occurred at a temperature of 10.9 °C.

2.4.3 GAMM models

The best fit GAMM models for upstream (Figure 10) and downstream (Figure 11) transitions had date (centered on median date) as the sole smoothed fixed effect. In this model, centered moon (percent illuminated) and centered stream temperature by Fish ID were set as random effects and helped to account for more of the variation in the model, suggesting that they play an important, but less crucial role in transition. Transitions by day of year, stream temperature and moon phase varied by year (Figure 12), indicating that fish responded differently to these variables each year. Both models predicted that brook trout are most likely to transition in the spring and in the fall. Brook trout moved upstream in winter 2010 - spring 2011, followed by a spring peak in downstream transitions. Downstream and upstream transitions peaked around the same time in fall 2011. A small peak in downstream movement was then closely followed by a spring upstream peak in 2012. While the movement peaks were much smaller in latter part of 2012, downstream movement did occur in early fall followed by late fall-winter upstream movement.

2.5 Discussion

Seasonal movements of brook trout in Red Brook with spring and fall peaks in transitions are consistent with past studies that have generally seen upstream movement in the spring and fall and downstream movement mainly in the fall and winter (Mullan 1958, Smith & Saunders 1958). Downstream movement peaked most clearly in November, which is likely a post-spawning migration to richer feeding grounds (Smith & Saunders 1958, Castonguay et al. 1982, Swanberg 1997, Curry et al. 2002). Fall and winter were also the periods of greatest presence by numbers in the estuary. From the small sample size of brook trout that moved into Buttermilk Bay, it appears that there can be movement into the bay at almost any time of year. However, given the clear seasonal patterns of movement in the rest of the system, more data would be necessary to make a conclusion about estuary to bay movement patterns.

Individual movement patterns provided important insights into variation in residential and migratory strategies. A wide range of movement patterns among individuals was observed in Red Brook and Buttermilk Bay systems, as seen in several other movement studies (Curry et al. 2002, 2006). Both residency with little movement and rapid descent of rivers toward the sea, as seen in fish 3066 (Figure 2), are common in brook trout and other salmonids (Naiman et al. 1987). Individuals responded to season differently in their habitat choices and when they moved. The same individual's movement strategy changed from one year to the next as seen in fish 3066 (Figure 2), which ascended rapidly from the estuary to the upper stream in fall 2011, but in fall 2012 instead descended rapidly from the estuary into Buttermilk Bay. This may be an example of an individual that waited until age 2 or 3 to travel to saltwater, as suggested by Mullan (1958) and Castonguay et al. (1982).

The fact that 9.5% of tagged brook trout moved into Buttermilk Bay suggests that for those individuals that choose to initiate the anadromous lifestyle by entering the estuary, either 1) the estuary is an area with sufficient food resource, 2) physiological constraints to the environment discourage travel further into the bay or, 3) they are residing in the estuary to acclimate to and eventually migrate to saltwater, which did not occur within the time of our study. Smith & Saunders (1958) observed a greater percentage of migrating brook trout in

Prince Edward Island, which varied annually (over six years) but ranged from 12 – 35%. They attributed brook trout movement out of saltwater back into the river to adverse sea temperatures (Smith & Saunders 1958). In a study by Curry et al. (2002) in a New Brunswick, Canada, only one acoustic tagged brook trout out of six choose to enter the marine environment even though it was accessible to all, potentially indicating that brook trout must be restricted by their physical environment which limits saltwater migration.

High occupancy of the estuary by coastal brook trout could be related to high prey availability. Half of the tagged brook trout in Red Brook were detected in the estuary, suggesting that this area is important. It is well documented that feeding is the main reason for fish to migrate (Northcote 1978, Gross 1987) and that anadromous brook trout obtain greater fitness through richer marine food resources than their resident counterparts (Wilder 1952, Hutchings & Morris 1985, Hutchings 1991, Jonsson & Jonsson 1993, and Einum & Fleming 1999). For adult brook trout marine prey items are larger than freshwater prey items, consisting mostly of fish and marine crustaceans (Power 1980, Morinville & Ramussen 2006), and are more abundant (Thorpe 1994). Olsson et al. (2006) showed that most brown trout became anadromous migrants when food was scarce and few migrated when it was plentiful and Smith and Saunders (1958) found that construction of a freshwater pond at the head of a coastal stream eventually eliminated brook trout movement to saltwater.

Brook trout residing in the Red Brook estuary may also have been preparing for seaward movement through a period of saltwater adaptation. Brook trout have been observed in other studies concentrating in small areas in channels that are mixing zones between fresh and saltwater (Castonguay et al. 1982, Curry et al. 2002). This is likely because brook trout do not smoltify like other salmonids and therefore require a period of adaptation in the estuary before they move to the marine environment (McCormick 1994).

The fact that many of the individuals that moved into Buttermilk Bay did so only for brief periods might be related to physiological restrictions imposed by temperature and salinity. Temperature preferences for brook trout vary by study location, but range from 11 - 19°C (Smith & Saunders 1958, Power 1980, Power 1999, Hartel et al. 2002). That said, Curry et al. (2006) found brook trout in temperatures from 5 - 18°C, and they are known to perform adequately from 5 - 20°C (Power 1980). Lethal temperature for brook trout yearlings is 25.5°C (Fry et al. 1946) and die-offs of adults have been observed when river temperatures rose to 31.4°C (Huntsman 1946) and when air temperatures in the Hudson Bay rose above 30°C (Gunn & Snucins 2010). While brook trout are able to tolerate the salinity of seawater after a period of estuarine residence (McCormick & Naiman 1985), ability to adapt to saltwater is severely inhibited at temperatures <3 °C (Claireaux & Audet 1999). This suggests that as temperature varies, there is a limit to the habitats available to brook trout.

Although water temperature as measured in Red Brook did not directly trigger brook trout movement in the model, variation in water temperature on smaller spatial scales may have influenced the way brook trout select seasonal habitats. In the New Brunswick brook trout population, Curry et al. (2002) documented increased movement when river temperatures rose above 15 °C, whereas in Red Brook, transitions between habitats occurred mostly when mean daily stream temperatures were between 8 and 12 °C. Water temperature is a controlling factor in within-stream habitat selection (Baltz et al. 1987) and brook trout may aggregate in areas of cooler groundwater springs as water temperatures warm (Power 1999). Fish seek thermal refugia because when the optimal temperature range for physiological processes is exceeded, activity, appetite and enzyme efficiency are affected, reducing growth rate (Power 1999). In Buttermilk Bay, water temperature warms faster than Red Brook and stays warmer through the summer due to the bay's shallow nature. Therefore, it may be that Red Brook provides the thermal refugia with its cold water springs and the warmer Buttermilk Bay temperatures (sometimes 9 °C warmer, with mean daily temperature reaching 25.6 °C in summer) create a barrier that many brook trout are reluctant to cross. In the winter, Buttermilk Bay mean daily temperature just outside the mouth of the estuary is often colder than stream temperatures (up to 3.3 °C colder) and reaches 2.4 °C, which is below the acceptable temperature for saltwater adaptation (Claireaux & Audet 1999).

Thermal refugia may explain the summer residency observed in 14 individuals in summer 2012 near the head of the tide. During this period, these individuals moved between the stream and the estuary regardless of moon phase. When these transition observations are removed from the data, the overall relationship between transition and moon phase becomes stronger. This suggests that there was some other factor, probably temperature or food, with a stronger influence on habitat selection during this period. This receiver near the head of the tide may be the site of a recently enlarged groundwater spring, providing a cold water pool (which may have been deepened by 4.4 cm above normal summer rainfall) that served as refuge from the above average summer temperatures (air temperature was 0.8 °C above the 30 year average, UMass East Wareham weather station data, http://www.umass.edu/cranberry/cropinfo/weather_2012.html). Habitat selection at fine spatial scales within Red Brook is an area worth further investigation and could be accomplished with the use of stream thermographs and temperature loggers at known sites of brook trout aggregation.

Anadromy may be less developed in the Red Brook population than for other more northern brook trout populations due to differences in geographical location and climate. Most individuals that moved into Buttermilk Bay were detected there for a few hours to a few days. This is vastly different than migrations seen in Canadian coastal streams where brook trout typically spend 65 to 150 days in the marine environment (White 1942, Naiman et al. 1987, Curry et al. 2006). This seems to reinforce the idea that anadromy in salmonids decreases with decreasing latitude (Rounsefell 1958, Nordeng 1961, Vladykov 1963, Scott & Crossman 1973) because the Red Brook population is near the southern extent of the anadromous brook trout range. It may be that the costs of moving fully into the marine environment outweigh the benefits.

Predation, an example of the costs related to the anadromous life history, may have been the fate of non-returning sea-run brook trout. Six out of eight migratory brook trout were not detected back in Red Brook after moving into Buttermilk Bay. Striped bass, a likely predator, are expected to be absent from Buttermilk and Buzzards Bay by mid-November (B. Hoffman, Massachusetts Division of Marine Fisheries, personal communication), after which the four individuals moved into Buttermilk Bay. However, other local predators could include double-crested cormorants (*Phalacrocorax auritus*), common loons (*Gavia immer*), and grey seals (*Halichoerus grypus*).

Other possible explanations for the brook trout that did not return to Red Brook could include expired tag batteries and movement to a different river. At least three of the tags likely lost battery function while the fish were at sea. This means that they may have returned to the stream but could not be detected by receivers. Another possibility is that some of the brook trout may have moved to a nearby river. In general brook trout at sea stay close to their natal rivers and have a strong homing tendency, however Curry et al. (2002) recorded one member of an otherwise river resident population swimming through the freshwater lens of a brackish estuary to visit another river <5km away. One of the Red Brook acoustic tagged brook trout was detected on a receiver that was a part of a separate acoustic tracking study on the west side of the Cape Cod Canal, 3.4 km from the mouth of Red Brook. Brook trout in Cape Cod rivers are known to travel through saltwater to return to their home stream after being experimentally placed in a neighboring river (S. Hurley, unpublished data).

Although the environmental variables measured in this study did not contribute strongly to transitions models, temperature and lunar cycle do explain part of the variation in brook trout movement. Movements throughout the system seem to be influenced by moon phase. One area where moon phase influence was quite clear is during movements from the estuary to Buttermilk Bay, which were undertaken especially at new and full moons. In addition to the physiological effects that moon phase has on fish, higher spring tides as a result of the new and full moons may be encouraging movement (Castonguay et al. 1982).

Other environmental variables not measured in this study could play a role in triggering migratory movements of brook trout in Red Brook. Including other variables such as photoperiod, stream flow rate, diel period, and tidal cycle and height, which have been shown to influence salmonid migration (Castonguay et al. 1982, McCormick & Naiman 1984, Curry et al. 2006), may create a stronger model and clearer picture on migration triggers. Smith & Saunders (1958) suggested that maturation and spawning over-ride other stimuli that would otherwise influence movement. The current study was also limited to the adult life stage of brook trout due to the size of acoustic tags used. Incorporating PIT tag data or otherwise tracking juveniles and younger individuals could help to inform whether the population behaves more like that described by Mullan (1958) and Castonguay et al. (1982) in which brook trout wait until they have reached age 1 or 2 to travel to saltwater or if juveniles also move down into the estuary as observed by Lenormand et al. (2004). Examining body size and growth rate of resident versus migratory individuals would require a larger sample size, but would provide more information about how this southern anadromous brook trout population might differ from others in the way and to what extent individuals exploit the marine environment.

Table 1. Summary of brook trout tagged and released at Red Brook

Date	n	FL mm (± 1 SD)	Min (mm)	Max (mm)
08 June 10	10	230 ± 35	195	305
16 Sept 11	20	222 ± 22	201	285
01 June 11	20	216 ± 31	167	290
16 Sept 11	20	215 ± 43	177	312
30 May 12	14	217 ± 33	173	274

Table 2. Acoustic tag detection summary including days tracked, total detections, detections per days tracked, and number of receivers detected on

	Days tracked	Total detections	Detections per days tracked	Total no. of receivers detected on
Mean	171.6	4116.0	27.8	2.6
Median	141.0	238.5	3.4	2.0
SD	140.9	9819.0	70.3	1.9
Max	498.0	45942.0	374.5	9.0
Min	1.0	1.0	0.003	1.0

Table 3. Summary of individuals that transitioned into Buttermilk Bay including the months that the tag was detected in the bay, whether the individual made repeat trips from the estuary to the bay, whether the tag was detected back in the stream (Red Brook) after having been in the bay, the maximum time the tag was detected in the bay or at sea, and the number of days from tagging to last detection.

Transmitter ID	Month(s) in bay	Repeat trips	Final return to stream	Max. time at sea (days)	Days from tagging to last detection
3066	Nov	N	N	< 1 (8 hrs)	406†
33398	Dec	N	N	4*	98
33420	Sep-Nov	Y	N	54	411†
33427	Nov, Dec	Y	N	4	78
40111	Dec	Y	Y	2	235
40116	July	Y	N	377**	411†
60666	Jan	N	Y	<1 (30 min)	369
60669	Aug-Sep	N	N	32	86

*this tag was then detected on Mass Maritime receiver in cape cod canal, 1 day in RBBB system 3 days in canal

**probable expelled tag or mortality, however this tag did not meet QA/QC criteria for false detections

†acoustic tag batteries probably died while individual was at sea, estimated tag life is 407 days

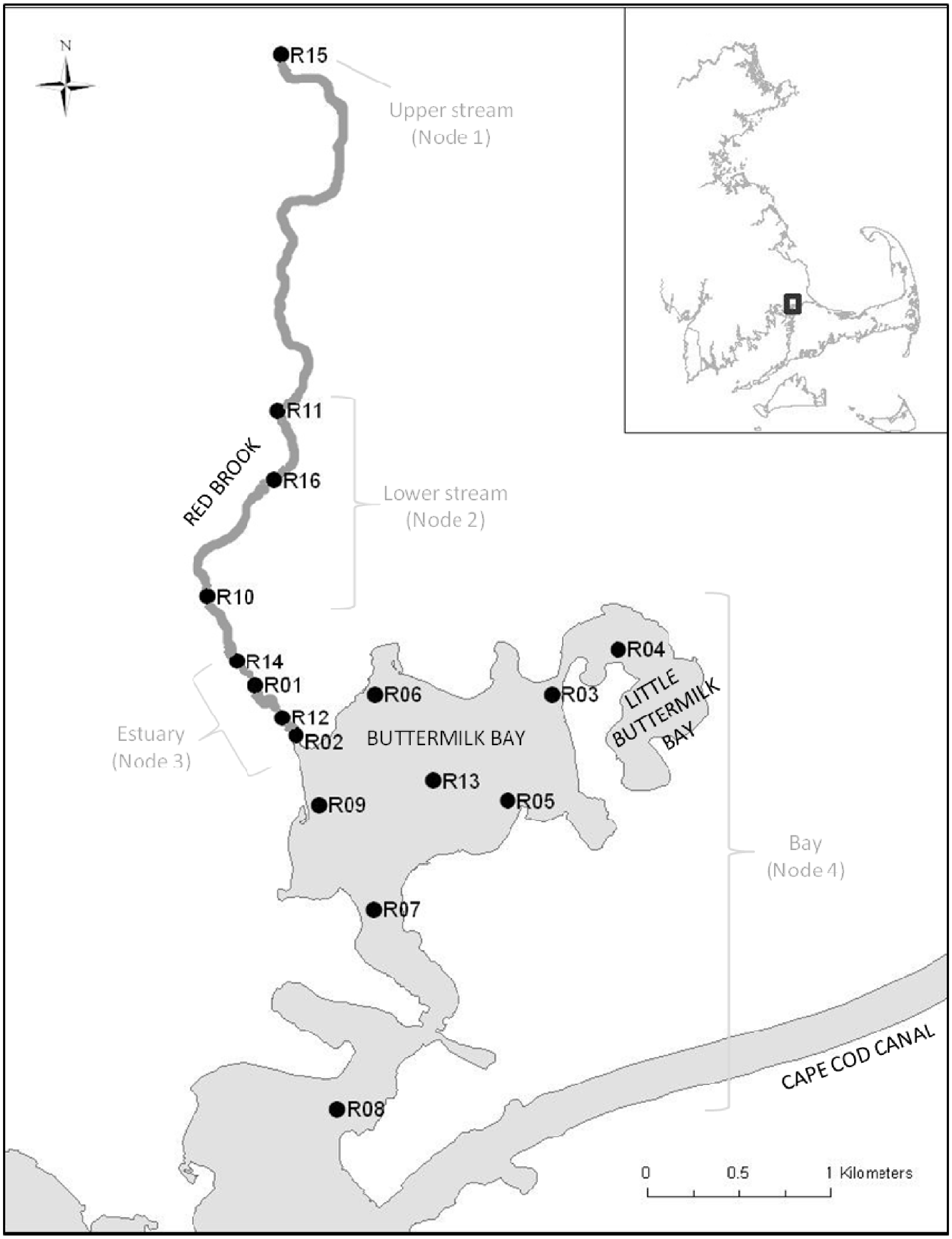


Figure 1. Receiver locations in Red Brook and Buttermilk Bay. Red Brook is located in southeastern Massachusetts at the western end of Cape Cod as indicated by the dark rectangle in the inset.

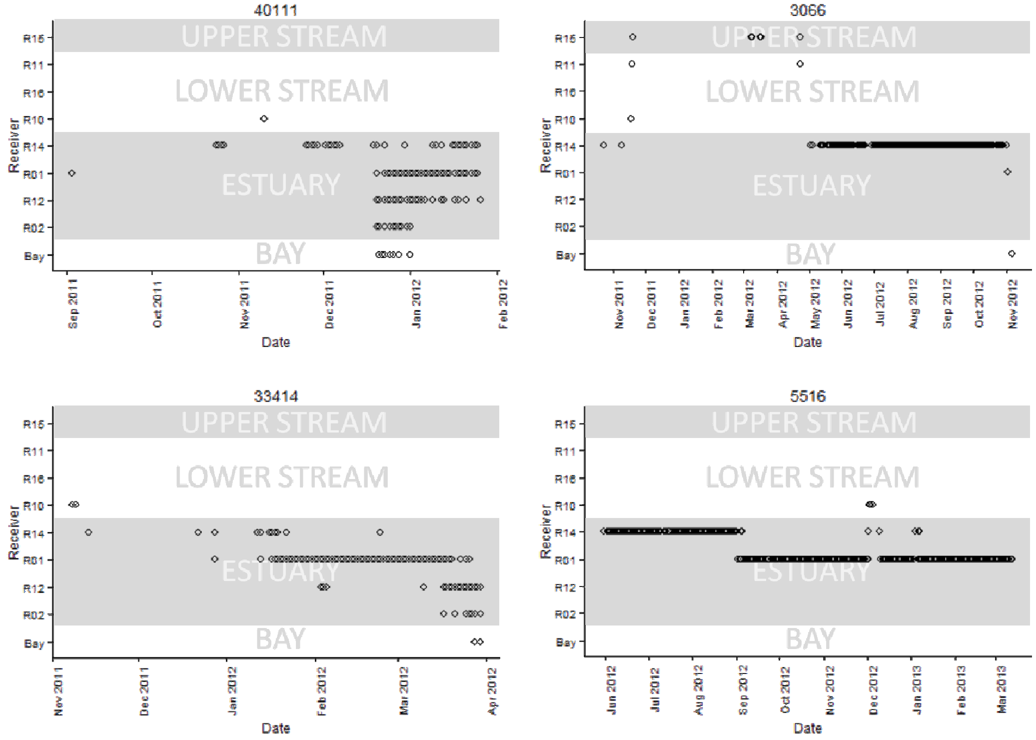


Figure 2. Detection histories of four representative brook trout (40111, 3066, 33414, and 5516) for the entire periods over which they were each tracked. On the y axis are the receivers ordered upstream to downstream (Bay receivers are grouped).

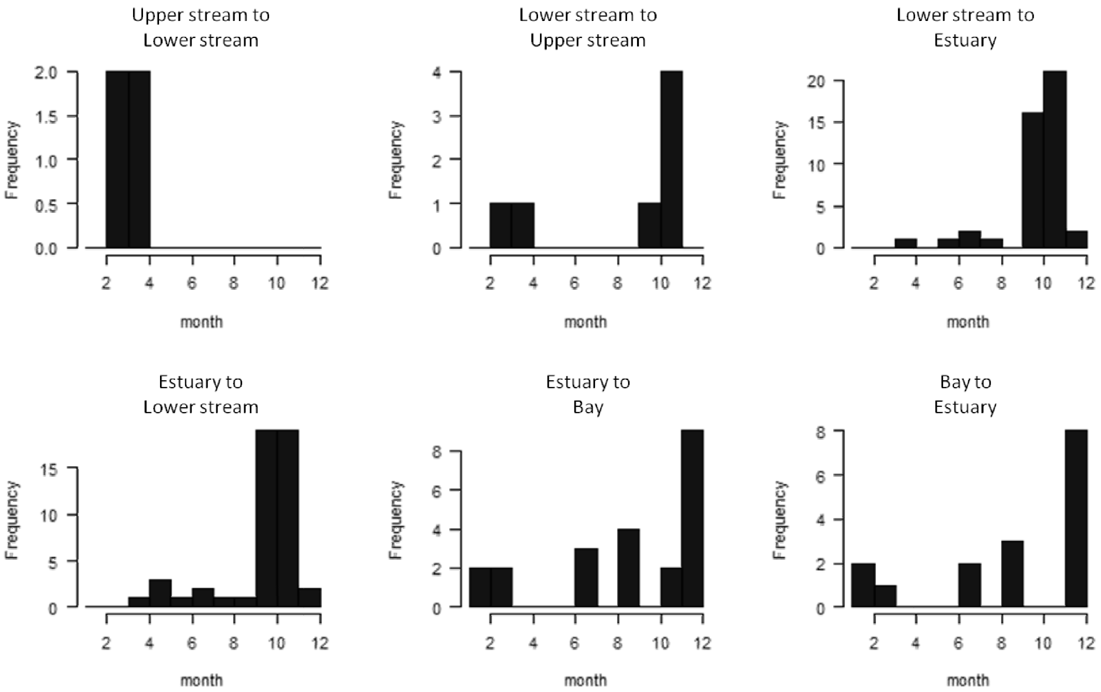


Figure 3. Histograms of transitions by month for each transition possibility.

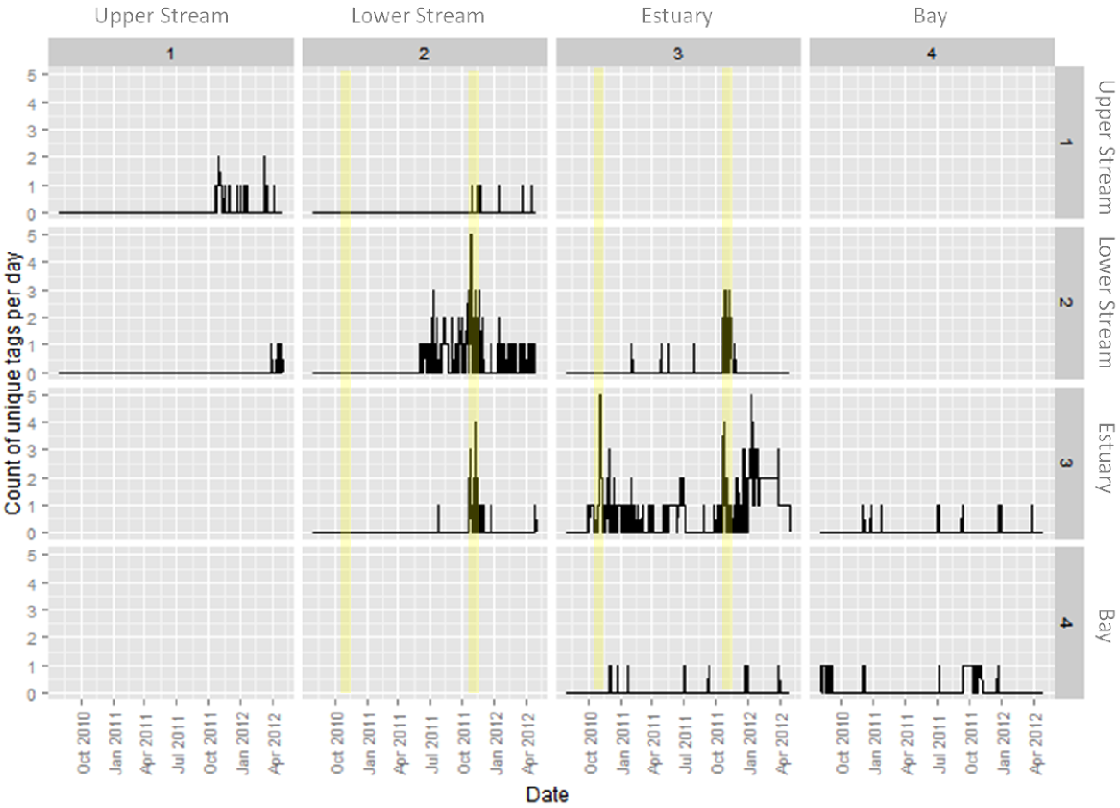


Figure 4. Transition matrix from July 2010 to May 2012. Fish movement between habitats (nodes) over time in terms of unique individuals completing a particular transition per day. The x-axis is median date between detections at each node and the y-axis is the count of unique individuals performing each transition per day. Labels across the top of the matrix represent the node where the fish started and labels on the right side represent the node to which the fish moved. Panels on the diagonal from the top left to bottom right are the residence panels where fish stayed within one node. Highlighted are two periods of interest when there was a peak in the total number of individuals in the lower stream and the estuary as well as an increased number of individuals moving between the lower stream and estuary.

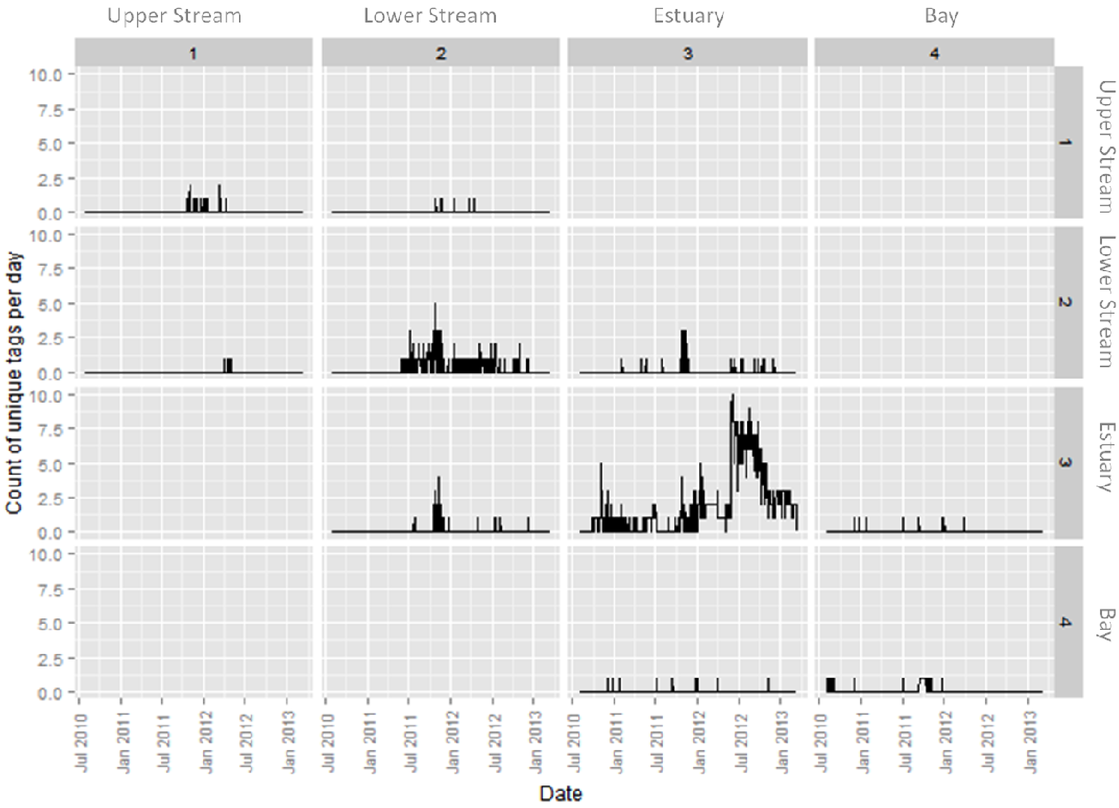


Figure 5. Transition matrix for the entire study period from July 2010 to March 2013. Fish movement between habitats (nodes) over time in terms of unique individuals completing a particular transition per day. Labels across the top of the matrix represent the node where the fish started and labels on the left side represent the node to which the fish moved. Panels on the diagonal from the top left to bottom right are the residence panels where fish stayed within one node. Note the increased number of individuals in panel 3_3.

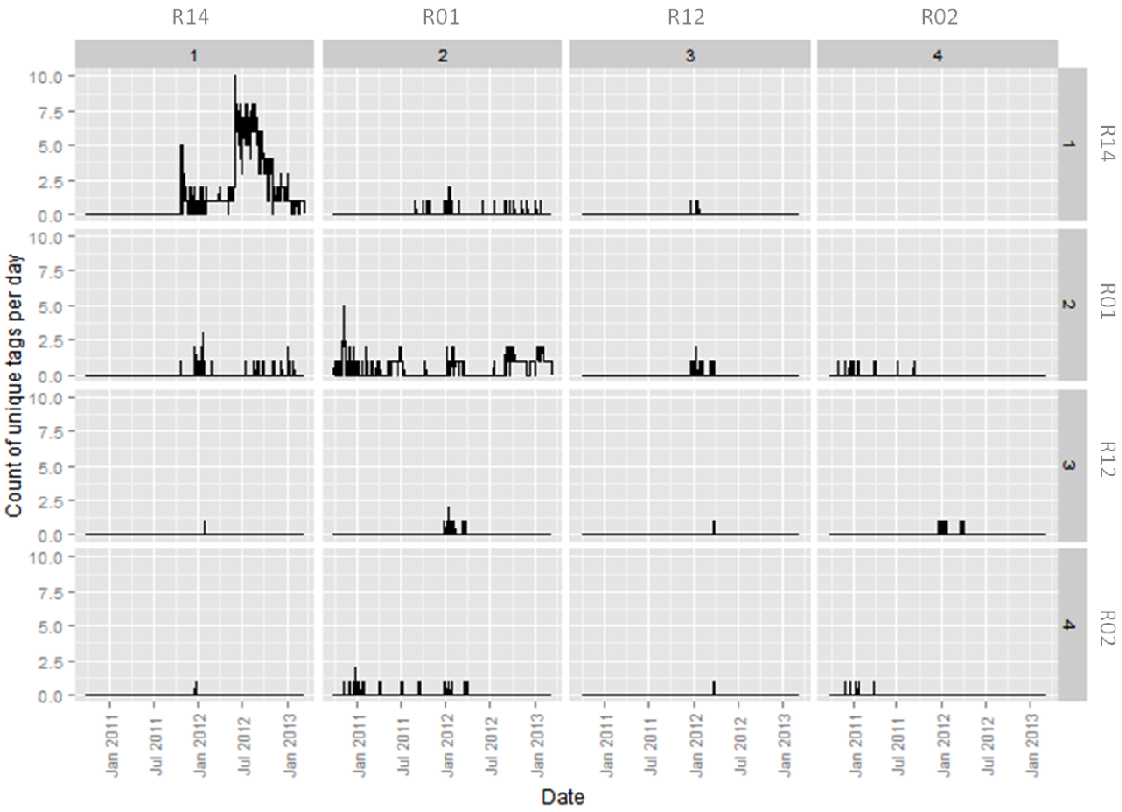
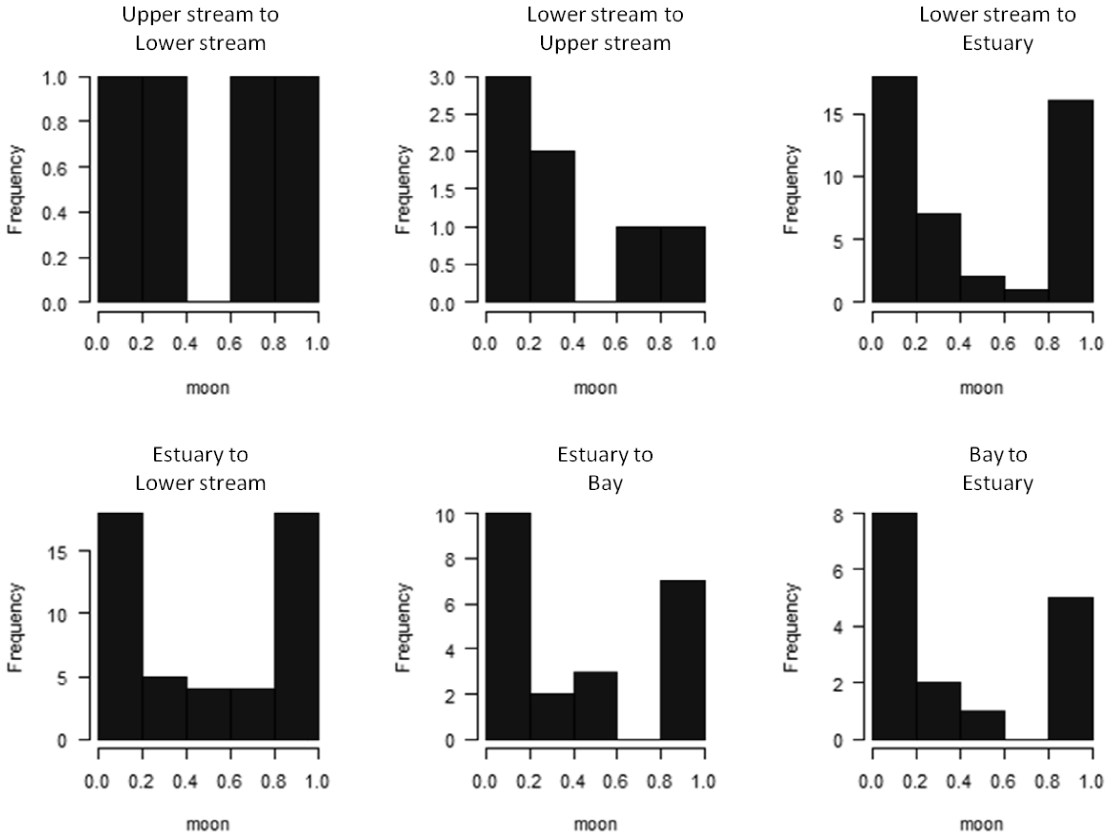


Figure 6. Transition matrix between receivers in the estuary. The receivers are labeled one to four, ordered from upstream to downstream. Labels across the top of the matrix represent the receiver where the fish started and labels on the left side represent the receiver to which the fish moved. Panel s on the diagonal from the top left to bottom right, then, are the residence panels where fish stayed within one node. Note panel 1_1, which shows the residency by several individuals at R14.


Upper stream to Lower stream

Lower stream to Upper stream

Lower stream to Estuary

Estuary to Lower stream

Estuary to Bay

Bay to Estuary

Figure 7. Histograms of transitions by moon phase for each node to node transition possibility.

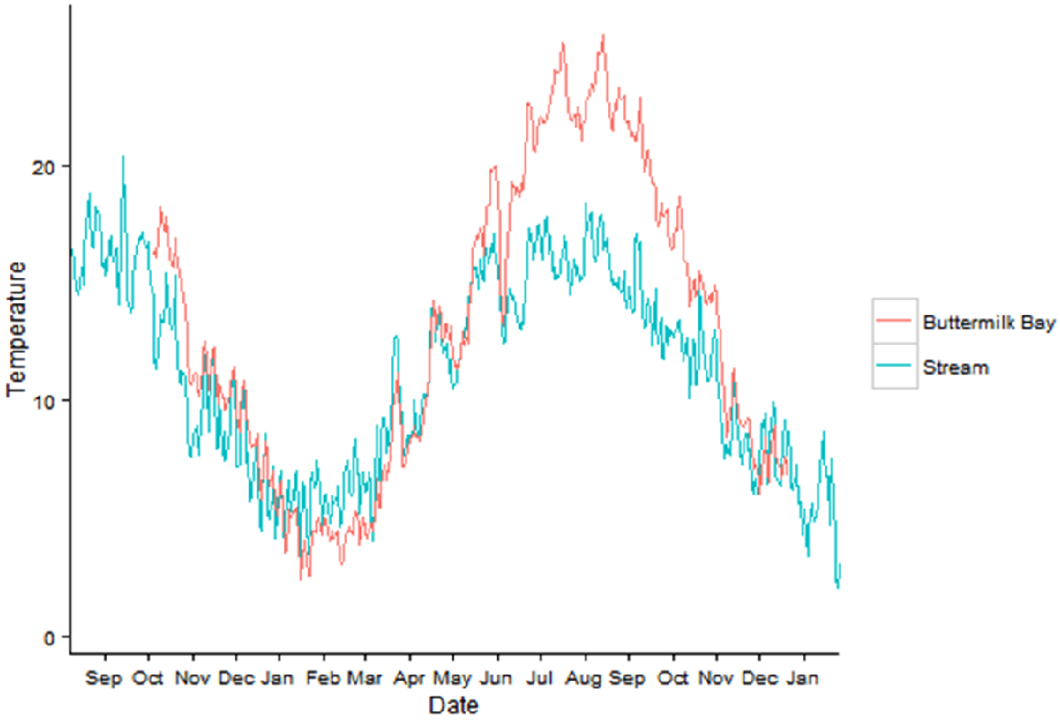


Figure 8. Mean daily temperature for Red Brook (stream) and Buttermilk Bay from fall 2011 to winter 2012

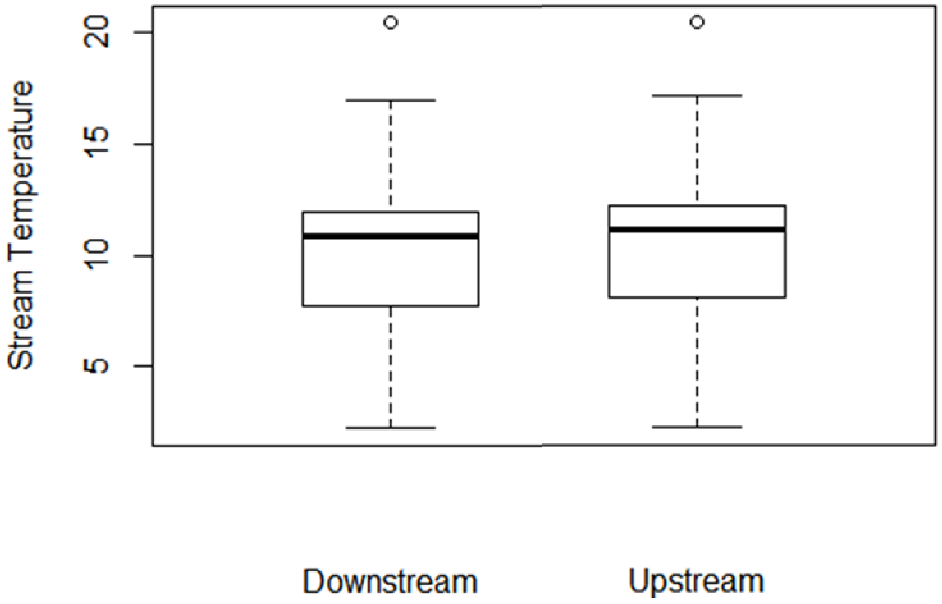


Figure 9. Box and whisker plots of mean daily stream temperature during downstream and upstream transitions

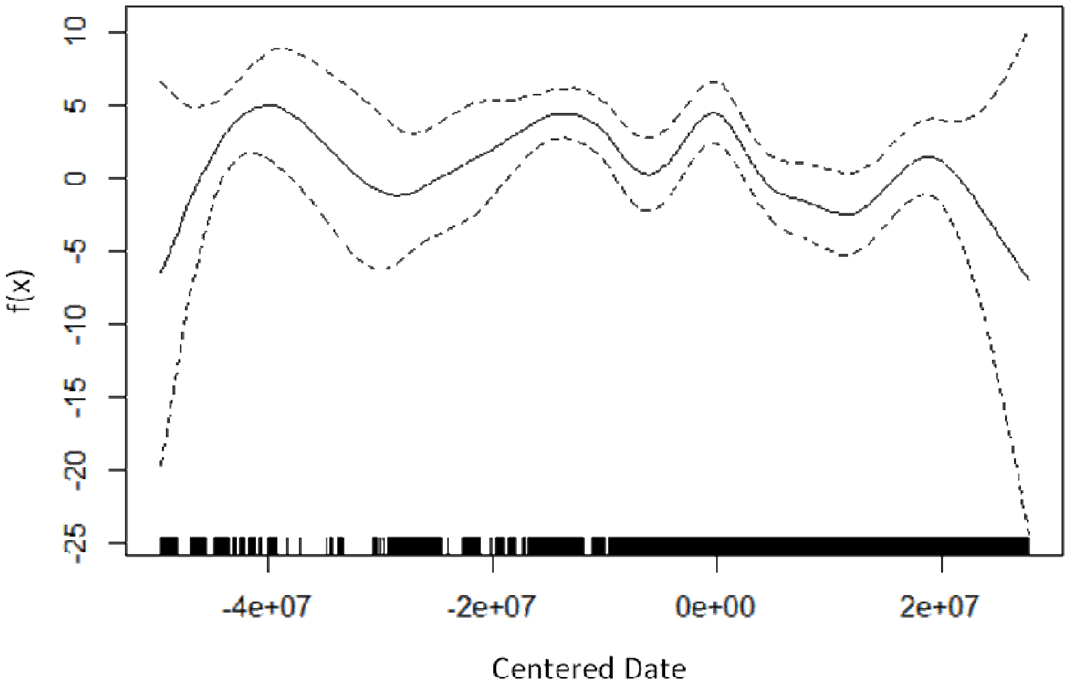


Figure 10. Smoothed fit of GAMM for centered day of year modeling downstream transitions-residencies over the entire study period. The x axis is centered date (units are difference from the median date) while the y-axis represents the spline function. Tick marks on the x-axis are observed data points. Dashed lines are the 95% confidence bounds.

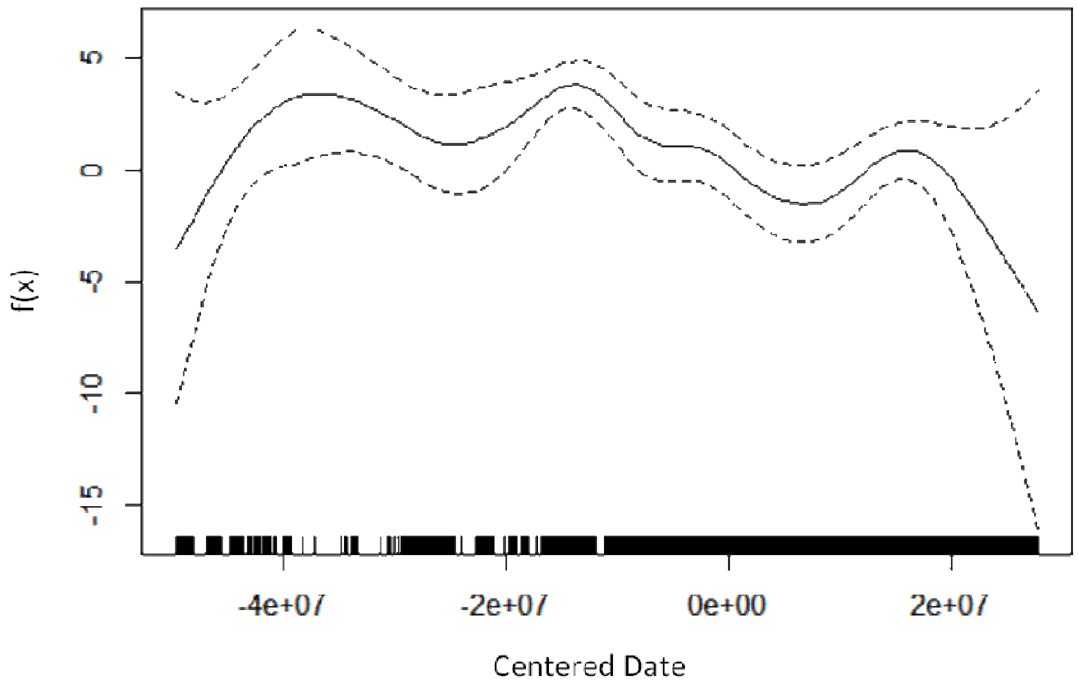


Figure 11. Smoothed fit of GAMM for centered day of year modeling upstream transitions-residencies over the entire study period. The x axis is centered date (units are difference from the median date) while the y-axis represents the spline function. Tick marks on the x-axis are observed data points. Dashed lines are the 95% confidence bounds.

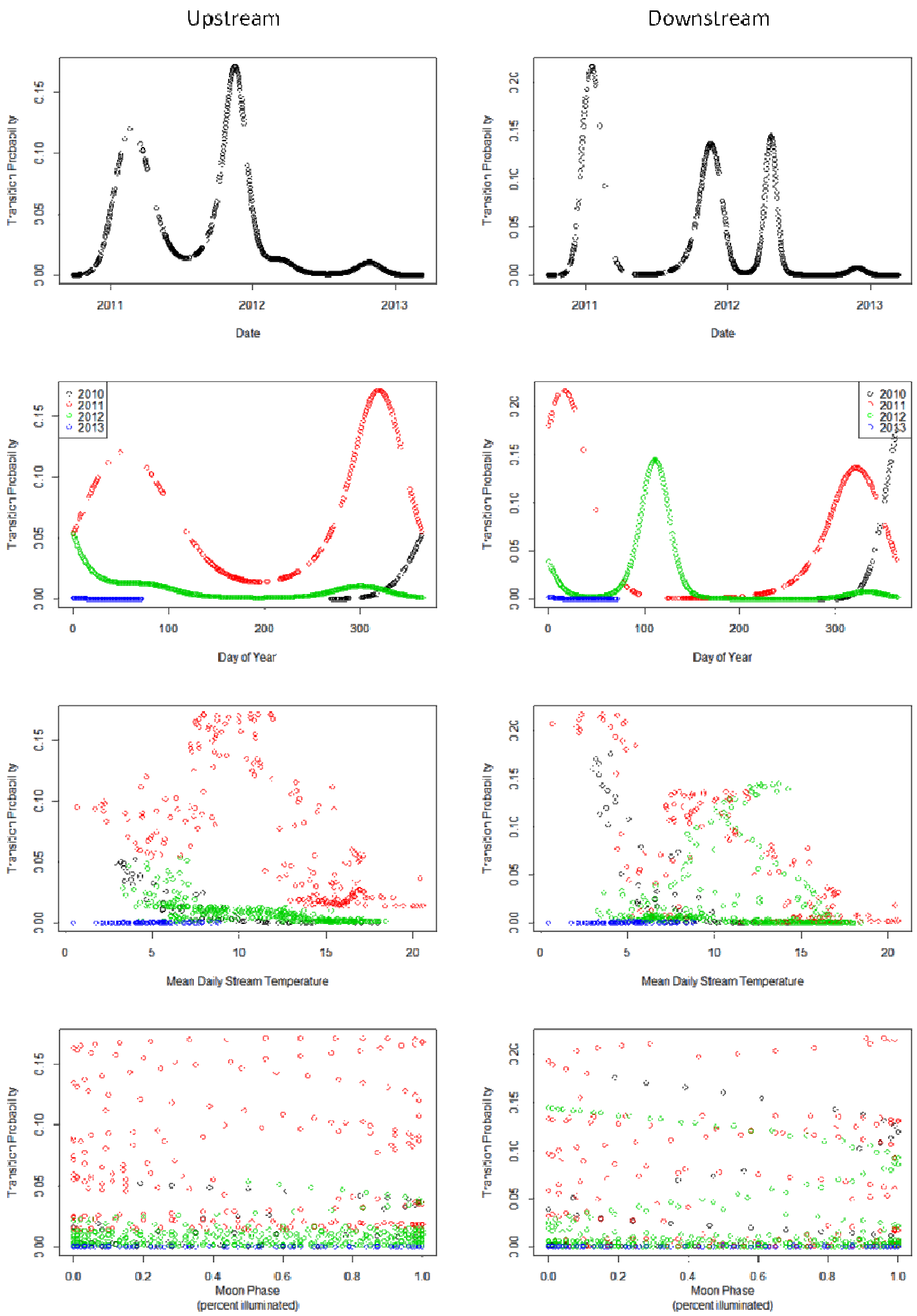
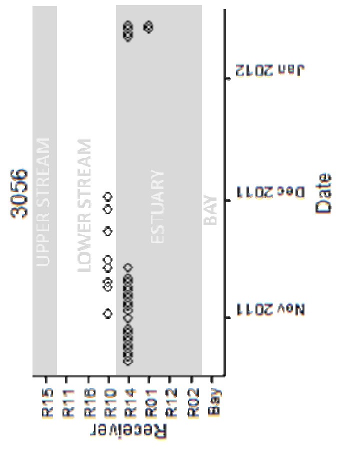
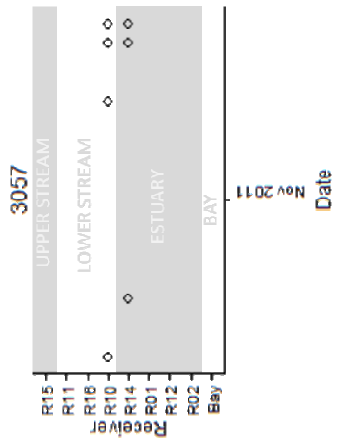


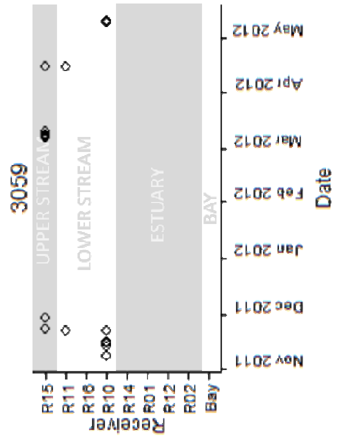
Figure 12. Comparison of GAMM Models. The first upstream and downstream plots show the expected probabilities of transitions by date, including all of the effects from the models. The bottom six plots are the fitted variables in the upstream and downstream GAMM models including date, the smoothed variable, as well as day of year and the random effects variables mean daily stream temperature and moon phase. The y-axis is the probability of a brook trout transitioning between nodes. Colors on the bottom six plots represent the year from 2010 to 2013.

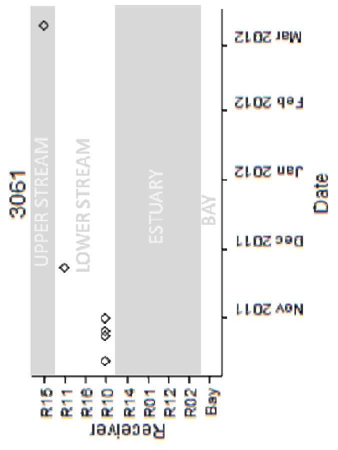
APPENDIX

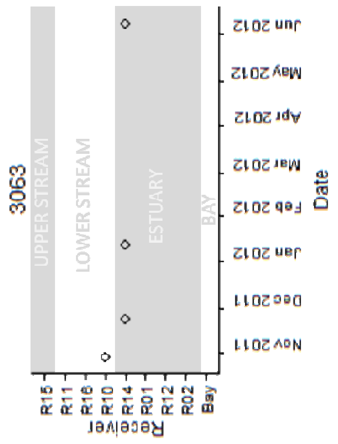
INDIVIDUAL MOVEMENT PLOTS FOR 54 BROOK TROUT INCLUDED IN TRANSITIONS ANALYSIS

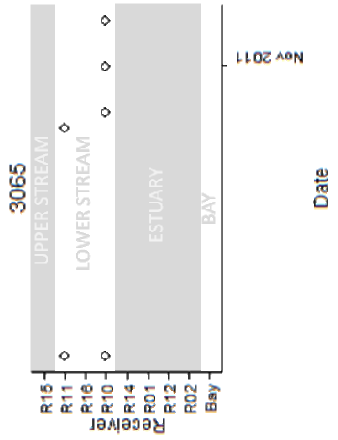


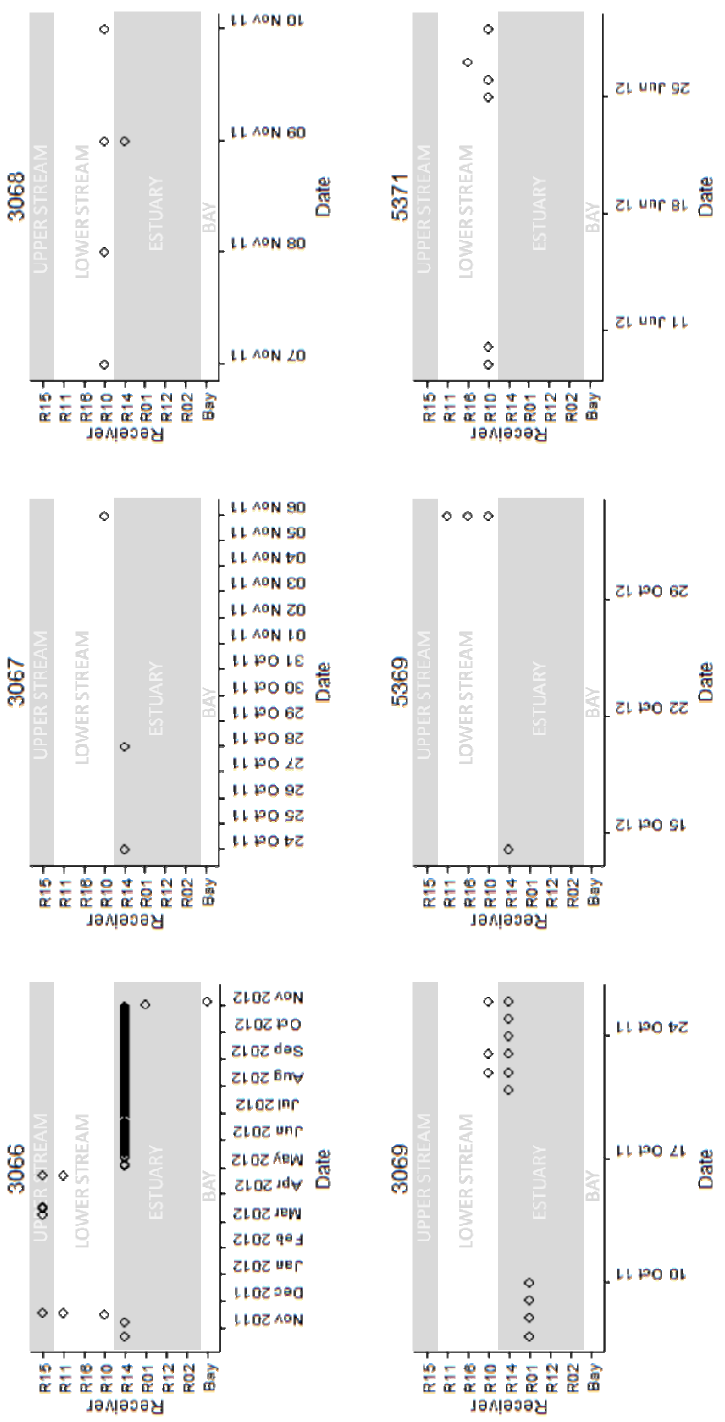








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UPPER STREAM
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BAY
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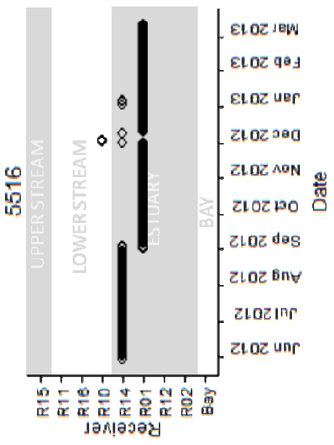
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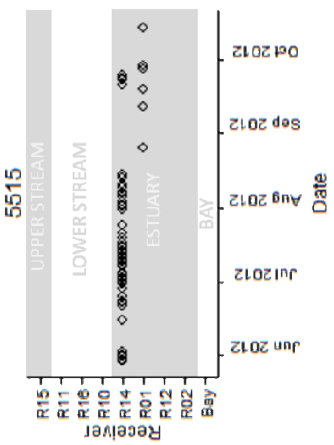
5515
UPPER STREAM
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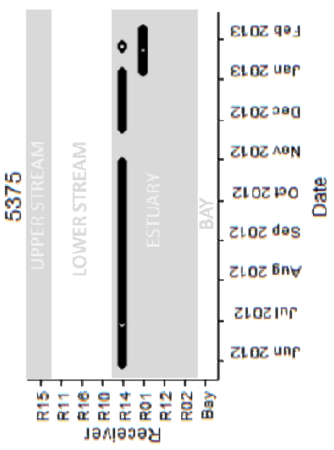
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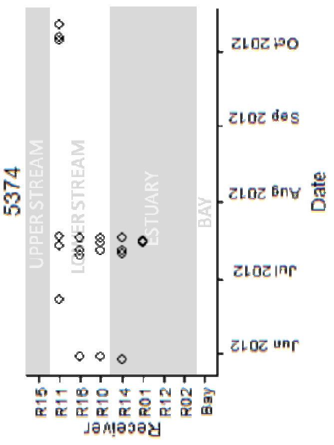
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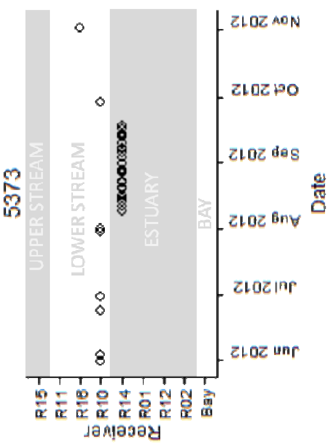
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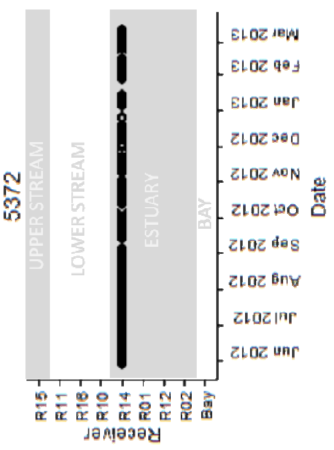
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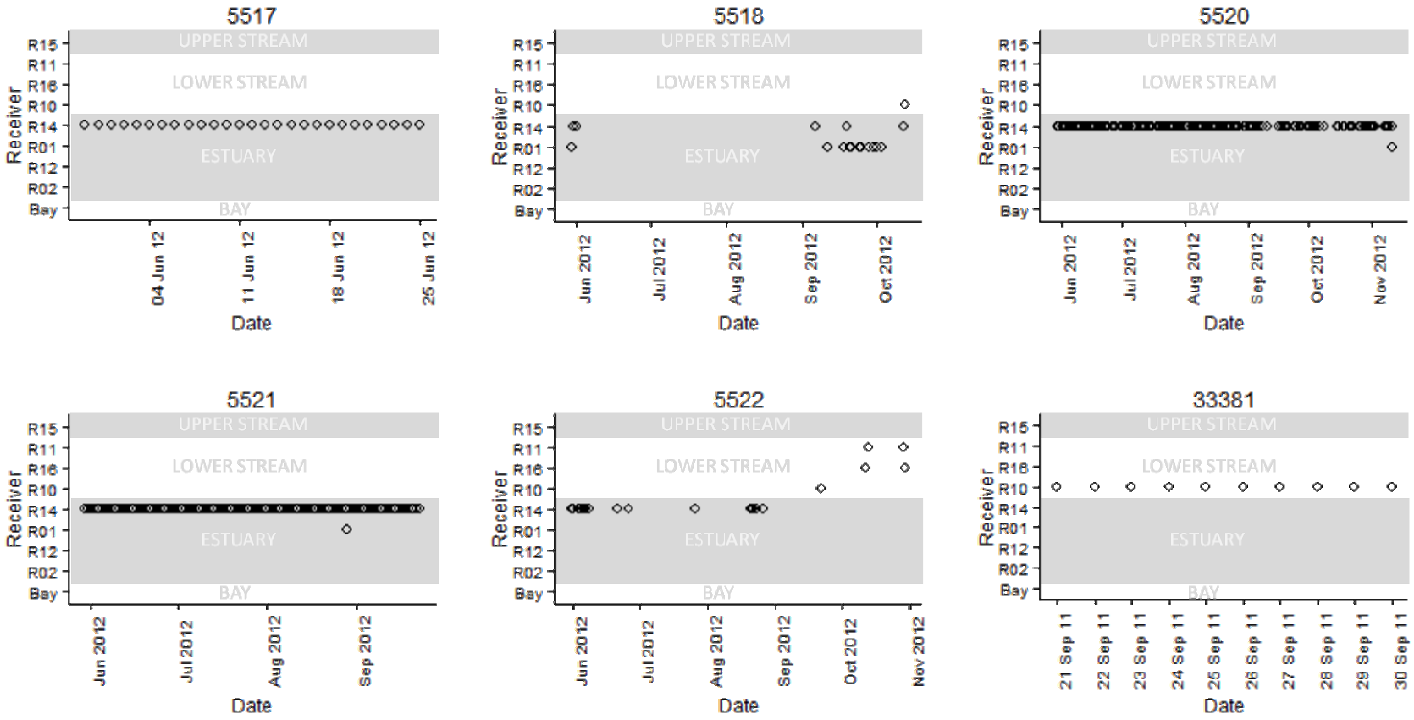
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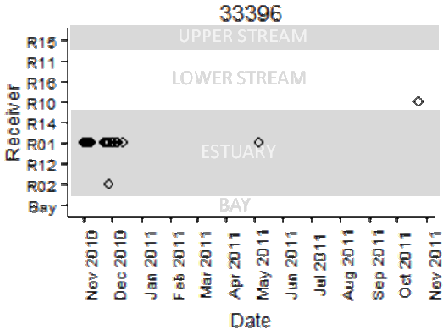
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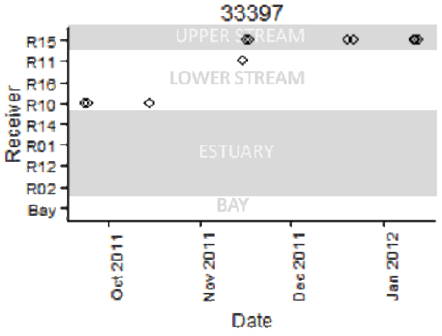
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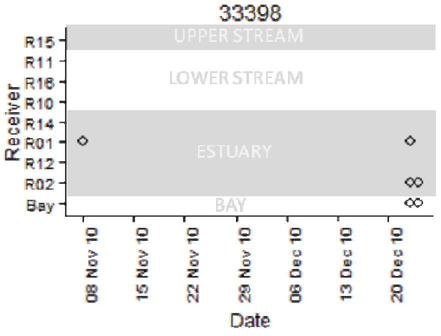
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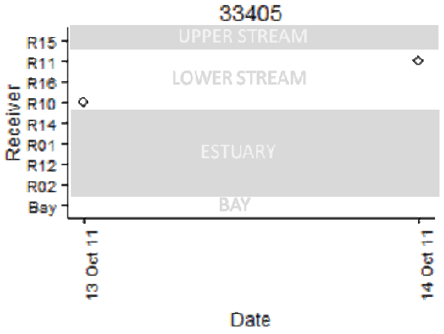
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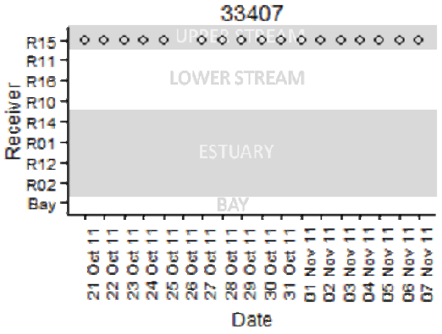
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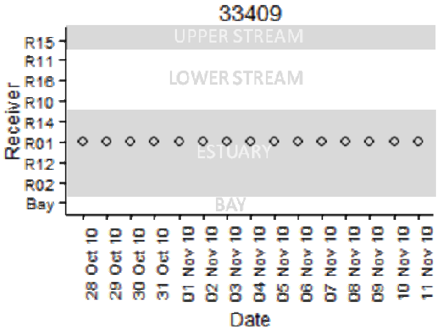
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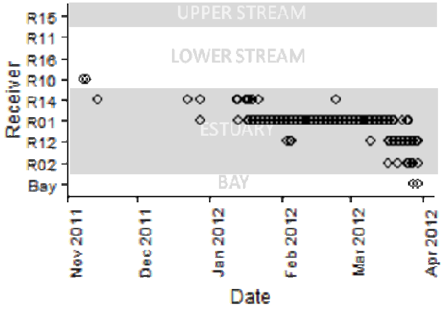

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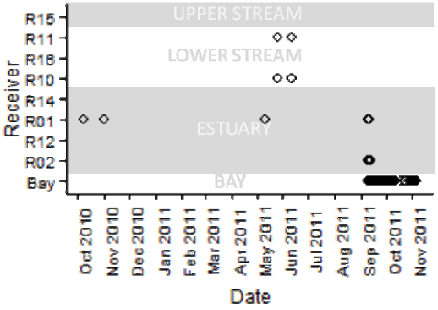

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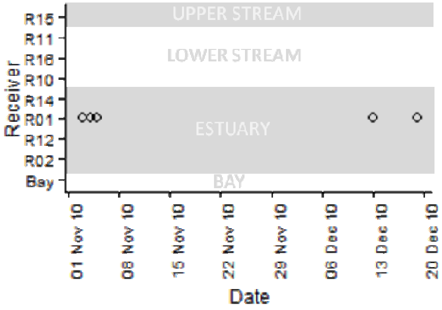

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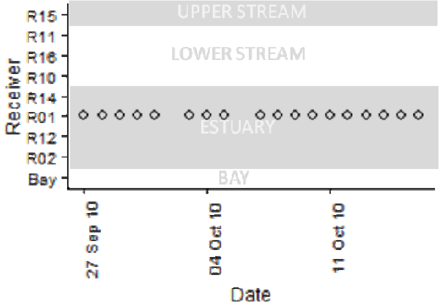

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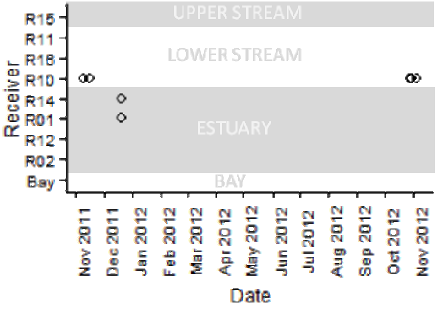

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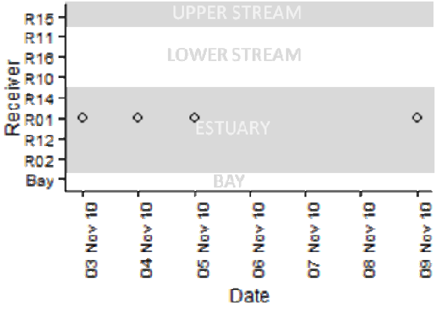

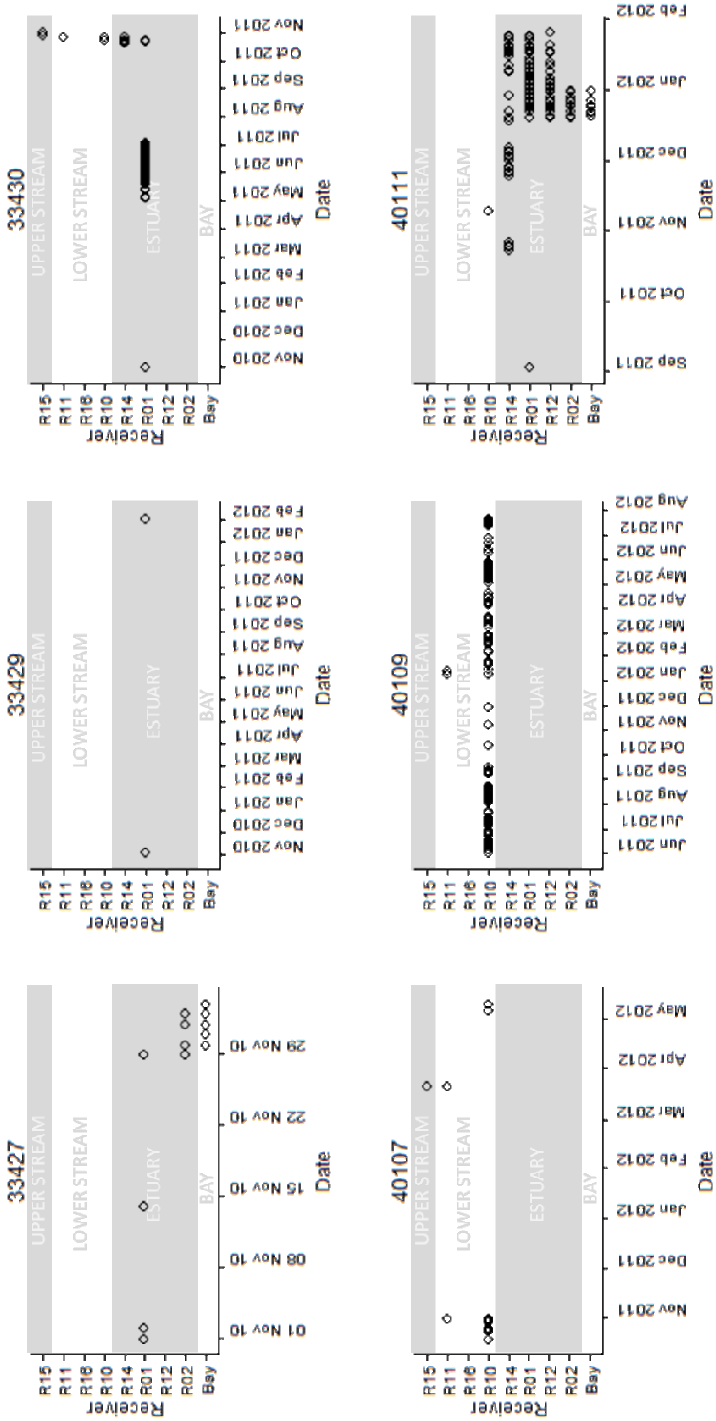
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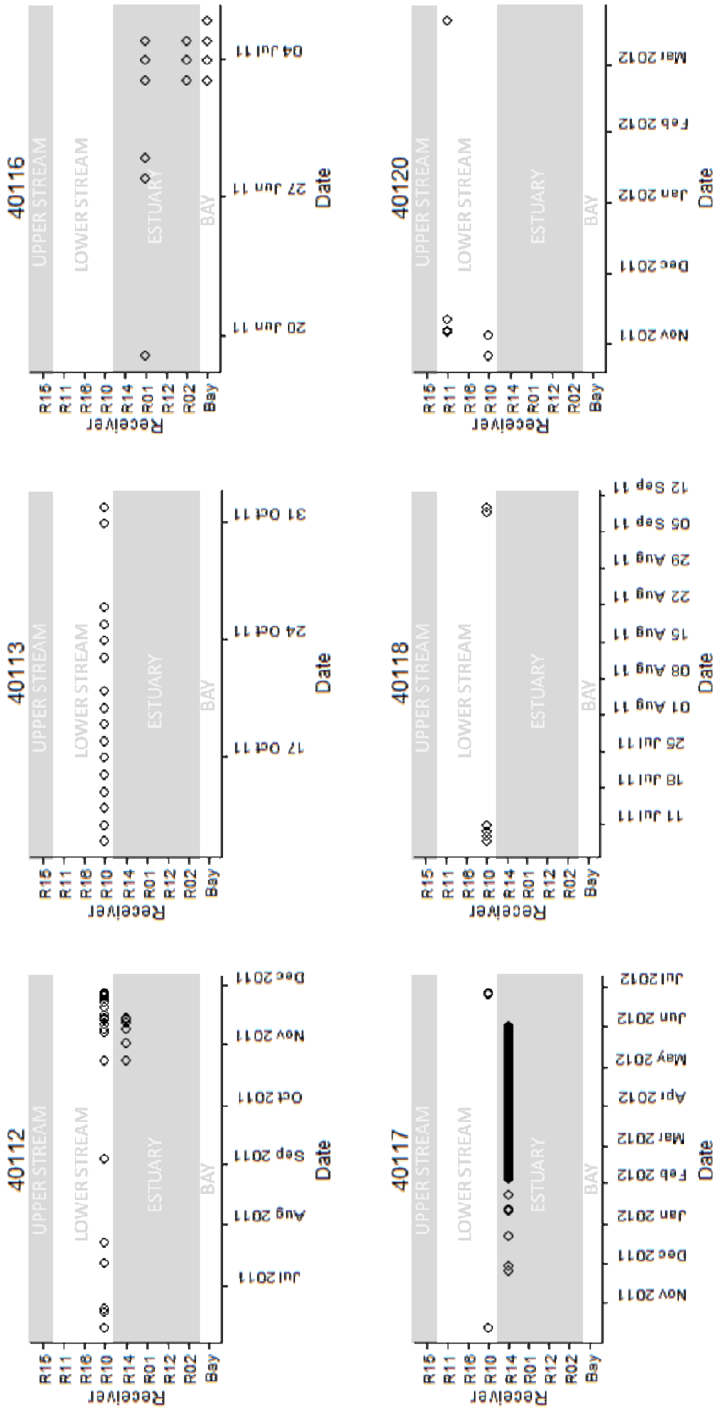
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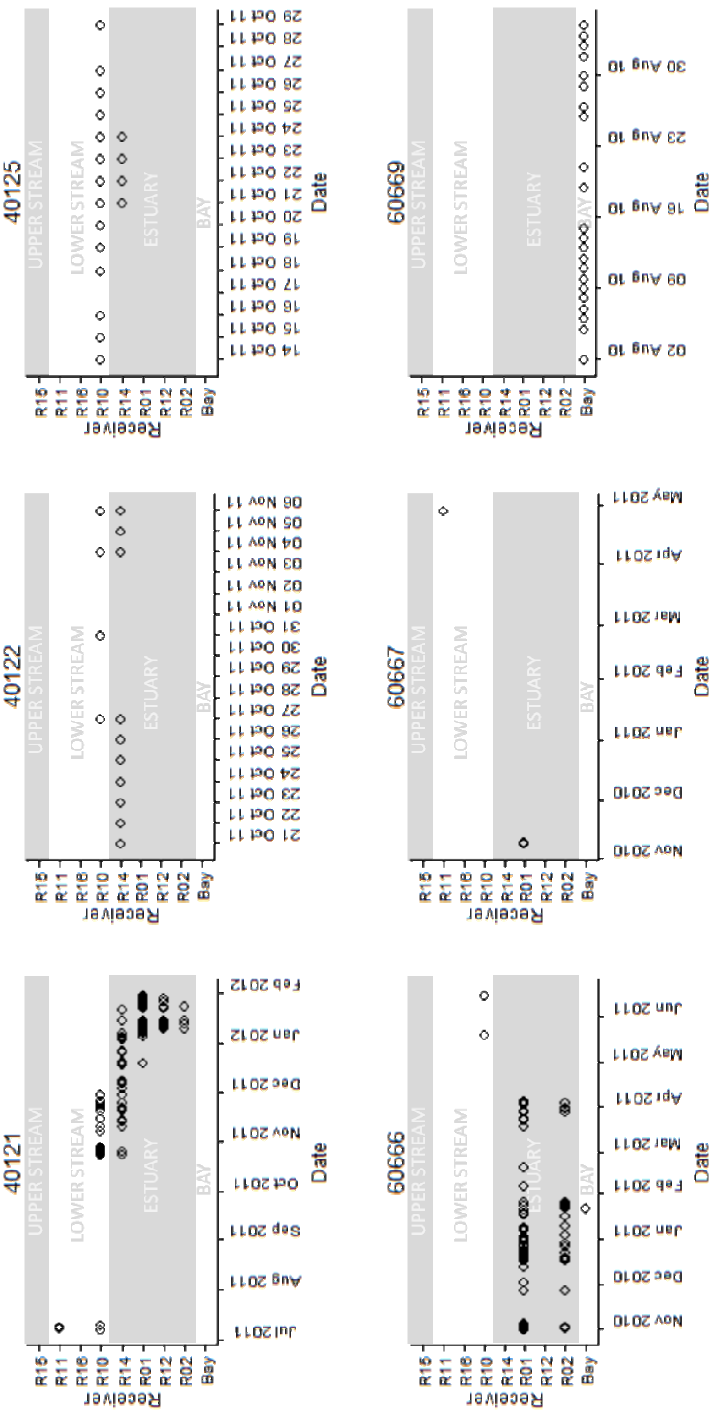
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REFERENCES

Baltz, D.M., Vondracek, B., Brown, L.R., & Moyle, P.B. 1987. Influence of temperature on microhabitat choice by fishes in a California stream. Transactions of the American Fisheries Society. 116(1): 12-20.

Castonguay, M., FitzGerald, G.J., & Côté, Y. 1982. Life history and movements of anadromous brook charr, *Salvelinus fontinalis*, in the St-Jean River, Gaspé, Québec. Canadian Journal of Zoology. 60(12): 3084-3091.

Claireaux, G., & Audet, C. 1999. Seasonal changes in the hypo-osmoregulatory ability of brook charr: the role of environmental factors. Journal of Fish Biology. 56(2): 347-373.

Curry, R.A., Sparks, D., & van de Sande, J. 2002. Spatial and temporal movements of a riverine brook trout population. Transactions of the American Fisheries Society. 131(3): 551-560.

Einum, S., & Fleming, I.A. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. Proceedings: Biological Sciences. 266(1433): 2095.

Fry, F.E.J., Hart, J.S., & Walker, K.F. 1946. Lethal temperature relations for a sample of young speckled trout, *Salvelinus fontinalis*. Pulications of the Ontario Fisheries Research Laboratory. 54: 9-35.

Grau, E.G., Specker, J.L., Nishioka, R.S., & Bern, H.A. 1982. Factors determining the occurrence of the surge in thyroid activity in salmon during smoltification. Aquaculture. 28(1): 49-57.

Gross, M. 1987. Evolution of diadromy in fishes. *Edited by* Dadswell, M.J., Klauda, R.J., Moffitt, C.M., Saunders, R.L., Rulifson, R.A., Cooper, J.E. American Fisheries Society Symposium.

Gunn, J., & Snucins, E. 2010. Brook charr mortalities during extreme temperature events in Sutton River, Hudson Bay Lowlands, Canada. Hydrobiologia. 650(1): 79-84.

Hartel, K., Halliwell, D., & Launer, A. 2002. Inland fishes of Massachusetts. Massachusetts Audubon Society, Lincoln, MA.

Hayes, D.B., Dodd, H., & Lessard, J.A. 2008. Effects of small dams on coldwater stream fish communities. American Fisheries Society, Bethesda MD.

Hitt, N.P., Eyler, S., & Wofford, J.E. 2012. Dam removal increases American eel abundance in distant headwater streams. Transactions of the American Fisheries Society. 141(5): 1171-1179.

Hoar, W.S. 1976. Smolt transformation: evolution, behavior, and physiology. Journal of the Fisheries Board of Canada. 33(5): 1233-1252.

Huntsman, A. 1946. Heat stroke in Canadian maritime stream fishes. Journal of the Fisheries Board of Canada. 6(7): 476-482.

Hutchings, J.A., & Morris, D.W. 1985. The influence of phylogeny, size and behaviour on patterns of covariation in salmonid life histories. Oikos. 45(1): 118-124.

Hutchings, J.A. 1991. Fitness Consequences of Variation in Egg Size and Food Abundance in Brook Trout Salvelinus fontinalis. Evolution. 45(5): 1162-1168.

Hvidsten, N., Jensen, A., Vivaas, H., Bakke, O., & Heggberget, T. 1995. Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction. Nordic Journal of Freshwater Research. 70: 38-48.

Jonsson, B., & Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries. Volume 3, Number 4: 348-365.

Kenward, R.E. 2001. A manual for wildlife radio tagging. Academic Press, London.

Koehn, J.D. 2012. Designing studies based on acoustic or radio telemetry. *In* Telemetry Techniques: A User Guide for Fisheries Research. *Edited by* Adams, N.S., Beeman, J.W., & Eiler, J.H. American Fisheries Society, Bethesda, MD. pp. 21-44.

Letcher, B.H., Nislow, K.H., Coombs, J.A., O'Donnell, M.J., & Dubreuil, T.L. 2007; 2007. Population response to habitat fragmentation in a stream-dwelling brook trout population. Plos One. 2(11): e1139-e1139.

Mason, J.C. 1975. Seaward movement of juvenile fishes, including lunar periodicity in the movement of coho salmon (*Oncorhynchus kisutch*) fry. Journal of the Fisheries Board of Canada. 32(12): 2542-2547.

McCormick, S.D., & Naiman, R. 1984a. Osmoregulation in the brook trout, *Salvelinus fontinalis*. I. Diel, photoperiod and growth related physiological changes in freshwater. Comparative Biochemistry and Physiology Part A: Physiology. 79A(1): 7-7-16.

McCormick, S.D., & Naiman, R.J. 1984b. Osmoregulation in the brook trout, *Salvelinus fontinalis,*—II. Effects of size, age and photoperiod on seawater survival and ionic regulation. Comparative Biochemistry and Physiology Part A: Physiology. 79(1): 17-28.

McCormick, S.D., Naiman, R.J., & Montgomery, E.T. 1985. Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences. 42(3): 529-538.

McCormick, S.D. 1994. Ontogeny and evolution of salinity tolerance in anadromous salmonids: hormones and heterochrony. Estuaries. 17(1): 26-33.

Morinville, G.R., & Rasmussen, J.B. 2008. Distinguishing between juvenile anadromous and resident brook trout (*Salvelinus fontinalis*) using morphology. Environmental Biology of Fishes. 81(2): 171-184.

Mullan, J.W. 1958. The sea-run or" salter" brook trout (*Salvelinus fontinalis*) fishery of the coastal streams of Cape Cod, Massachusetts. Massachusetts Division of Fisheries and Game.

Murase, H., Nagashima, H., Yonezaki, S., Matsukura, R., & Kitakado, T. 2009. Application of a generalized additive model (GAM) to reveal relationships between environmental factors and distributions of pelagic fish and krill: a case study in Sendai Bay, Japan. ICES Journal of Marine Science: Journal Du Conseil. 66(6): 1417-1424.

Naiman, R., McCormick, S., Montgomery, W., & Morin, R. 1987. Anadromous brook charr, *Salvelinus fontinalis*: Opportunities and constraints for population enhancement. Marine Fisheries Review. 49(4): 1-13.

Nordeng, H. 1961. On the biology of char (*Salmo alpinus L.*) in Salangen, North Norway. Norwegian Journal of Zoology. 10: 67-132

Northcote, T.G. 1978. Migratory strategies and production in freshwater fishes. *In* Ecology of Freshwater Fish Production. *Edited by* S. Gerking. John Wiley & Sons, New York, NY. pp. 326-359.

Olsson, I.C., Greenberg, L.A., Bergman, E., & Wysujack, K. 2006. Environmentally induced migration: the importance of food. Ecology Letters. 9(6): 645-651.

Power, G. 1980. The brook charr, *Salvelinus fontinalis*. *In* Charrs: salmonid fishes of the genus Salvelinus. *Edited by* E. Balon. Dr. W. Junk Publishers, The Hague, pp. 141-203.

Power, G., Brown, R., & Imhof, J. 1999. Groundwater and fish—insights from northern North America. Hydrological Processes. 13(3): 401-422.

Rounsefell, G.A. 1958. Anadromy in North American Salmonidae. US Government Printing Office.

Rounsefell, G.A. 1957. Fecundity of North American Salmonidae. US Government Printing Office.

Scott, W.B., & Crossman, E.J. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin. 184.

Smith, M., & Saunders, J. 1958. Movements of brook trout, *Salvelinus fontinalis* (Mitchill), between and within fresh and salt water. Journal of the Fisheries Board of Canada. 15(6): 1403-1449.

Swanberg, T.R. 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. Transactions of the American Fisheries Society. 126(5): 735-746.

Swartzman, G. 1997. Analysis of the summer distribution of fish schools in the Pacific Eastern Boundary Current. ICES Journal of Marine Science: Journal Du Conseil. 54(1): 105-116.

Thorpe, J. 1994. Salmonid fishes and the estuarine environment. Estuaries. 17(1): 76-93.

Vladykov, V.D. 1963. A review of salmonid genera and their broad geographical distribution. Transactions of Royal Society of Canada. 1 (series 4, section 3): 450-504.

White, H. 1942. Sea life of the brook trout (*Salvelinus fontinalis*). Journal of the Fisheries Board of Canada. 5(5): 471-473.

Wilder, D. 1952. A comparative study of anadromous and freshwater populations of brook trout (*Salvelinus fontinalis* (Mitchill)). Journal of the Fisheries Research Board of Canada. 9: 169-203.

Yamauchi, K., Koide, N., Adachi, S., & Nagahama, Y. 1984. Changes in seawater adaptability and blood thyroxine concentrations during smoltification of the masu salmon, *Oncorhynchus masou*, and the amago salmon, *Oncorhynchus rhodurus*. Aquaculture. 42(3): 247-256.

Yamauchi, K., Ban, M., Kasahara, N., Izumi, T., Kojima, H., & Harako, T. 1985. Physiological and behavioral changes occurring during smoltification in the masu salmon, *Oncorhynchus masou*. Aquaculture. 45(1): 227-235.

Yee, T.W. 2010. VGLMs and VGAMs: an overview for applications in fisheries research. Fisheries Research. 101(1): 116-126.

Zydlewski, G., Haro, A., & McCormick, S. 2005. Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior of Atlantic salmon (*Salmo salar*) smolts. Canadian Journal of Fisheries and Aquatic Sciences. 62: 68-78.