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Movement patterns of Brook Trout in a restored coastal stream system in southern Massachusetts

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Abstract – Coastal Brook Trout (*Salvelinus fontinalis*) populations are found from northern Canada to New England. The extent of anadromy generally decreases with latitude, but the ecology and movements of more southern populations are poorly understood. We conducted a 33-month acoustic telemetry study of Brook Trout in Red Brook, MA, and adjacent Buttermilk Bay (marine system) using 16 fixed acoustic receivers and surgically implanting acoustic transmitters in 84 individuals. Tagged Brook Trout used the stream, estuary (50% of individuals) and bay (10% of individuals). Movements into full sea water were brief when occurring. GAMM models revealed that transitions between habitat areas occurred most often in spring and fall. Environmental data suggest that use of the saline environment is limited by summer temperatures in the bay. Movements may also be related to moon phase. Compared to more northern coastal populations of Brook Trout, the Red Brook population appears to be less anadromous overall, yet the estuarine segment of the system may have considerable ecological importance as a food resource.

Key words: Brook Trout; salvelinus; anadromy; migration; acoustic telemetry

Introduction

Anadromous populations of Brook Trout (*Salvelinus fontinalis*), also known as brook charr, occur along the coast of northeast North America from Long Island, NY, to northern Canada (Ryther 1997). 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; Hutchings & Morris 1985). 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). Evolutionarily, this partial-facultative anadromy in brook trout is likely the result of freshwater forms emerging from anadromous individuals (Curry et al. 2010). Several studies have indicated a lesser degree of anadromy in Brook Trout and populations of other salmonid species as one moves southward in the Northern Hemisphere (Rounsefell 1958; Nordeng 1961; Vladykov 1963; Scott & Crossman 1973).

Adoption of the resident or anadromous life history appears to be highly environmentally sensitive (Curry et al. 2010), and growth rate and growth rate efficiency appear to be the most important proximate factors linked to their expression (Morinville and Rasmussen 2003; Theriault et al. 2007). Once migration to the ocean is initiated, specific triggers, such as water flow, decrease in water temperature and moon phase, and social interaction have been reported for some salmonids (Castonguay et al. 1982; Hutchings & Myers 1994, Sykes et al. 2009, Hvidsten et al. 1995; Curry et al. 2006). Past studies have found that Brook Trout movement has seasonal peaks. Upstream movement is most pronounced from April through June (Mullan 1958; Smith & Saunders 1958) and from July to September as Brook Trout move upstream to spawning grounds (Lenormand et al. 2004, Curry et al. 2006). Total time spent in the marine environment has been documented from an average of 65 to 150 days, but is highly variable among Brook Trout populations, and evidence suggests it

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decreases in more southern populations (White 1942; Naiman et al. 1987; Curry et al. 2006).

Understanding the degree of anadromy for Brook Trout in coastal streams is imperative for their conservation and management. Life-history diversity in populations of an individual species, such as migratory tendency in Brook Trout, provides greater resilience for a species and enhances ecosystem services that species provides (Schindler et al. 2010). Considering that worldwide rates of population extinction are three times greater than species extinction (Hughes et al. 1997), documenting and preserving life-history diversity is worthwhile. 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 subwatersheds (Eastern Brook Trout: Status and Threats, Eastern Brook Trout Join Venture 2006). Anadromous fish populations that become isolated by dams often experience a loss of migratory tendency, as observed in white-spotted char (*Salvelinus leucomaenis*; Morita et al. 2009). This can reduce population size, increase the risk for local extinction and possibly increase the risk for system-wide (metapopulation) extinctions (Letcher et al. 2007).

Red Brook in south-eastern 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 (Fig. 1) near Bourne, Wareham and Plymouth, MA (Theodore Lyman Reserve Management Plan, The Trustees of Reservations 2005). From 2006 to 2009, four dams were removed along the stream and restoration to support the native Brook Trout populations began. However, the degree of ocean use of Red Brook's Brook Trout population after dam removal was unknown.

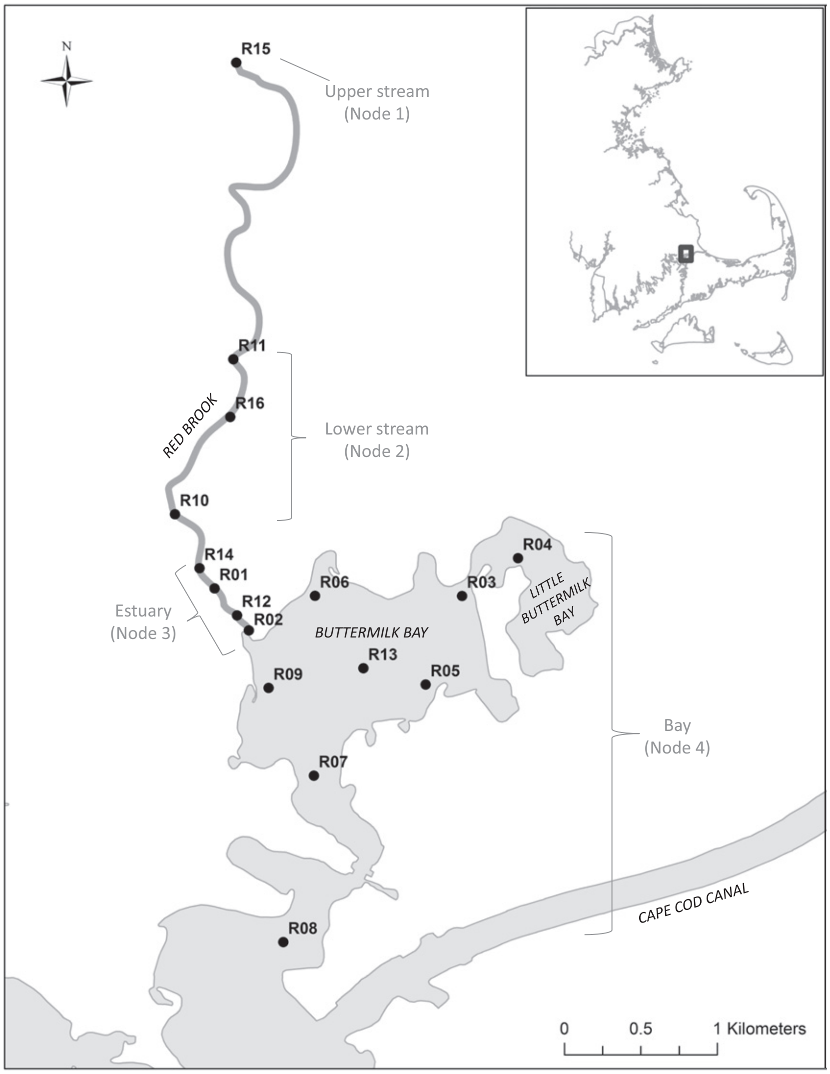

Fig. 1. Receiver locations in Red Brook and Buttermilk Bay. Red Brook is located in south-eastern Massachusetts at the western end of Cape Cod as indicated by the dark rectangle in the inset.

The purpose of this study was to quantify Brook Trout movement patterns within Red Brook and the coastal waters of Buttermilk Bay. We employed acoustic telemetry to facilitate the contiguous monitoring of Brook Trout among freshwater, estuarine and marine habitats (Curry et al. 2006). Studying the movements of anadromous Brook Trout will help to characterise 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 populations.

Methods

Study site

Red Brook is a small coastal stream in south-eastern Massachusetts (41°45′28.70″N, 70°37′20.77″W) that flows into Buttermilk Bay. It is a 7.25-km, low-gradient stream with an average width of 2 m and average depth of 1 m. The headwaters of Red Brook are in a cranberry bog where the water flow is partially regulated. Average daily stream temperatures in Red Brook range from 0 to 21 °C. Substrate in the area is mainly glacial till through which groundwater seeps from the Plymouth Carver Aquifer (Moog 1987, Valiela & Costa 1988). Springs in the stream create cold pools throughout the year. Red Brook is the largest source of freshwater input into Buttermilk Bay (with discharges of 8,360,255 $m^3 \cdot year^{-1}$ in 1985 and 14,311,866 $m^3 \cdot year^{-1}$ in 1986) (Moog 1987).

Buttermilk Bay is located at the northern end of Buzzards Bay, bordered by the towns of Plymouth, Wareham and Bourne and densely populated by humans. Buttermilk Bay has a surface area of 2.14 km^2 and a mean low water depth of 0.9 m, and it experiences two tidal cycles per day with a mean tidal range of 1 m (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 centre of Buttermilk Bay is fresher than the average Buttermilk Bay salinity of 30.9 ppt.

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 (Fig. 2). 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).

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 fixed acoustic receivers (VR2W, Vemco Inc., Halifax, NS) were deployed throughout Red Brook, the estuary and Buttermilk Bay (Fig. 1). The region of greatest interest to this study is the zone where fish move from freshwater to salt water, 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

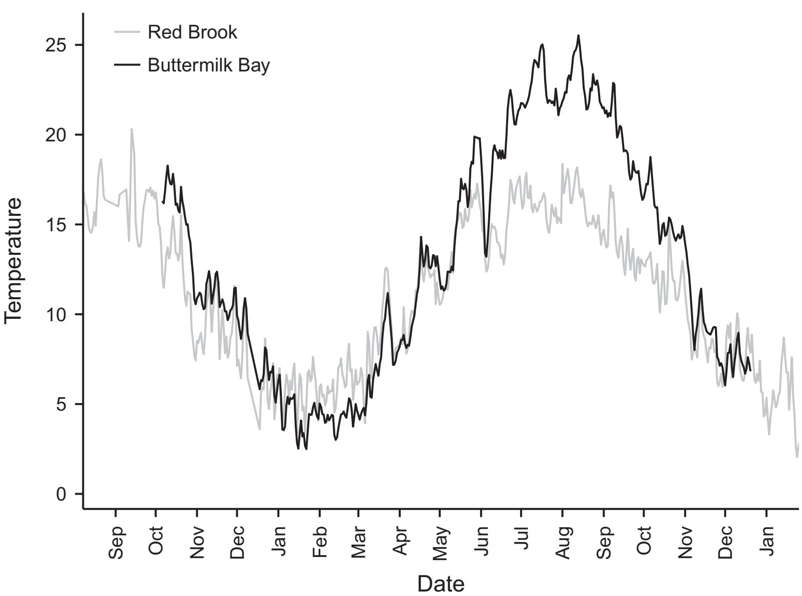

Fig. 2. Mean daily temperature for Red Brook (stream) and Buttermilk Bay from fall 2011 to winter 2011.

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 (Fig. 1). 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 placed 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 and 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 (<1.7 m), near-shore (<500 m) 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 Buttermilk Bay ranged from 1.2 to 2.6 m from the bottom. Two receivers were placed in the channel from Buttermilk to Buzzards Bay to record fish leaving the system. Receivers were inspected every 3–6 months, and detection data were downloaded. A detection limit test was conducted to determine possible overlap in receiver detection ranges. Several receivers were inadvertently removed or were lost due to wear on moorings or excessive winter icing. They were replaced at the same site as soon as possible. As such, there are varying periods of time for which some receivers were collecting data. The final downloads of receivers occurred on 14 March 2013.

Brook Trout tagging procedures

Brook Trout were captured using a 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 approximately 500 m upstream of the mouth, the stream was divided into sections that were individually fished. The sampling area of approximately 900 m of stream represents about 13% of Red Brook's length. Sampling sections 1–5 are in areas where salt water has been detected (the head of the tide is usually between sections 4 and 5, near Receiver 14). Fish from each section were retained in separate labelled holding tanks prior to tagging.

Adult Brook Trout greater than 160 mm fork length (FL) were retained for tagging with acoustic transmitters. This size threshold was used to reduce tag weight burden on Brook Trout. In addition, larger Brook Trout greater than 140 mm FL are able to survive sea water (McCormick & Naiman 1984b). Fish to be tagged were transferred from the stream to a tagging station <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 minimise injuries related to transfer. Brook Trout were anesthetized using MS-222 (100 mg l^{-1}), until stage 4 anaesthesia was achieved, and fork length and mass were measured (to the nearest mm and 0.1 g).

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 4.7 g in air, with a random delay of 120–240 s 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 2–3 min. Fish were then placed in an aerated recovery tank and monitored until they 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.

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). 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. Because 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 represent the fraction of the moon that is illuminated on each day, and are a quantitative way of describing the moon's phases.

Data analysis

Individual fish movements were examined using VUE software (Vemco Inc., Halifax, NS). Detections of Brook Trout were used from the time they were released into the stream after tagging until the end of the study or until the tag failed. We conducted quality assurance/quality control to determine whether a tag was transmitting false detections. We defined false detections as consistent, regular detections (i.e., every 120–240 s) 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: (i) upper reach of the stream, (ii) lower reach of the stream, (iii) estuary and (iv) bay. Transition matrix plots were constructed to show when fish move between nodes. Movement between nodes is referred to as a 'transition'. 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 1 day. We examined the empirical data for relationships between transition and temperature and moon phase. Then, individual fish detections were plotted over time. To address the hypothesis related to anadromy, detections for all receivers in the bay were combined for the individual Brook Trout movement plots (Fig. 3).

Generalised 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 et al. 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 modelling 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.

Results

A total of 84 Brook Trout were 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 tracked (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. Mean total detection for all individuals was 4116 (SD = 9819). The mean number of days tracked (from tag deployment to last detection) was 171.6 (SD = 140.9), and the mean number of detections per days tracked was 27.8.

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 were 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. We concluded that two tags had been expelled or the fish died, so the data from this tag were removed from the analysis.

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 min) for bay receivers ranged from 0 to 150 m, and detection limits in the stream ranged from 5 to 20 m. This test showed that at times there was an overlap in detection ranges of R05, R06 and R13 as well as R02 and R09. There was no overlap in receiver detection range within Red Brook. Data were examined for these overlaps, and dual detections within 1 min were discounted.

Individual movement patterns

Movement patterns varied greatly among individuals, with some Brook Trout remaining in the stream and others migrating from fresh to salt water and back. Some individuals moved little within the stream, while a few made long-distance movements from the head of the stream to the bay (7.25 km). Forty-two individuals (50% of tagged Brook Trout) 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 2). 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 min 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 min and 2 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 2). 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 was last detected at R08 heading out of the system, and its tag was recorded for the next 3 days on a receiver in a separate acoustic tag array on the west side of the Cape Cod Canal (unpublished data, B. Hoffman, MA Division of Marine Fisheries).

Four individuals were selected as representatives of distinctly different movement patterns observed (Fig. 3). Fish A 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 (5343) 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 A 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 3 days. In late December, fish A continued to move between the estuary and bay receivers until January when it remained in the estuary, but continued moving between three receivers.

Fish B 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 (6896) over a relatively long detection time span (406 days). Fish B 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 B moved from the lower stream to the upper stream, covering approximately 3.6 km in less than 38 h. 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 B 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 (Fig. 3). The battery in tag B likely died while the individual was at sea, so whether the individual returned to Red Brook is not known.

Fish C 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 C 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

Table 1. Summary of Brook Trout tagged and released at Red Brook.

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

Table 2. 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 h)	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.
**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, and estimated tag life is 407 days.

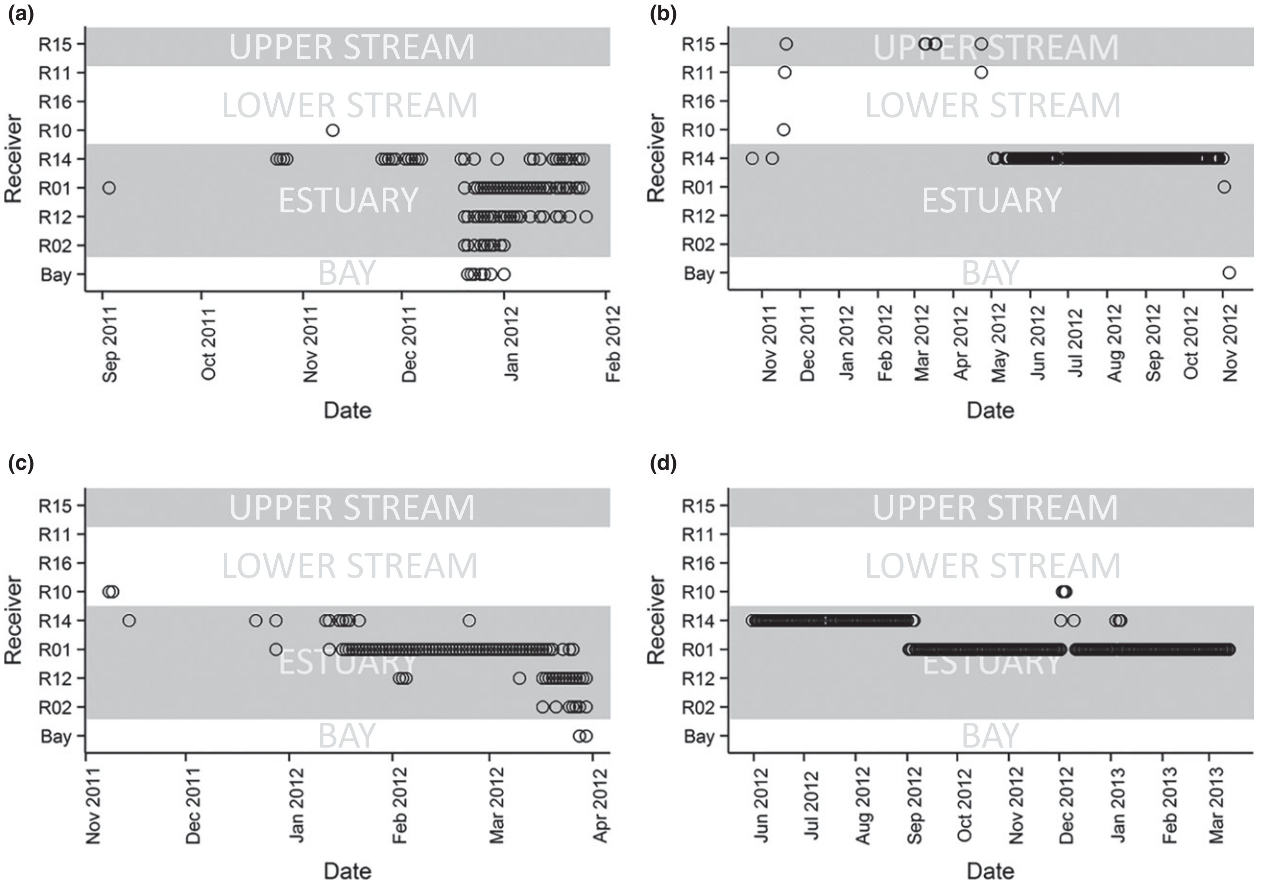

Fig. 3. Detection histories of four representative Brook Trout for the entire periods over which they were each tracked. On the *y*-axis are the receivers ordered upstream to downstream (Bay receivers are grouped).

at R01 from January to March 2012. In the beginning of March, fish C was detected mostly on R01, making excursions down to R12. Throughout March, it was detected mostly on R12, making excursions down to R02 (Fig. 3).

Fish D 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 pattern is 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 D spent the summer at R14 near the head of the tide (Fig. 3). 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 D then moved back downstream to R01 where it overwintered, except for one short excursion up to R14 in January.

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 December and November = 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 occurred during the late winter to summer months (mean = 4.43

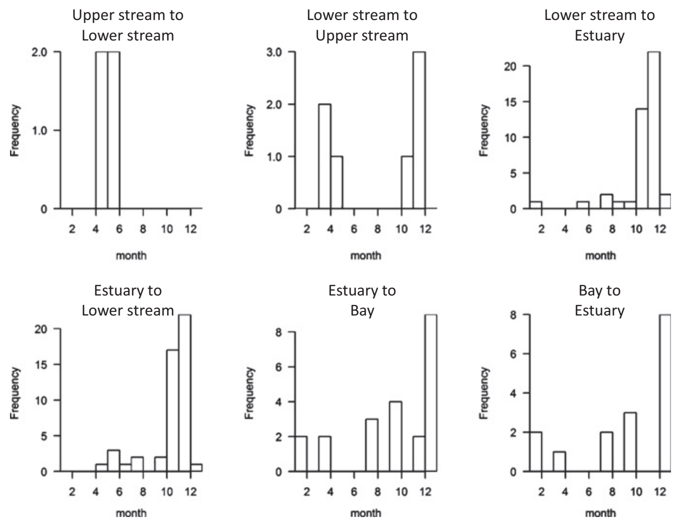

Fig. 4. Histograms of transitions by month for each transition possibility.

transitions per month), and no transitions occurred from April to June, August and October (Fig. 4).

Two transition matrices were selected to illustrate important periods when movement occurred. Across 2 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 (Fig. 5). From 21 October 2011 to 03 January 2012, 14 individuals (20% 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 (Fig. 6). The majority of fish detected in the estuary during this time were detected at one receiver (R14). 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 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), verifying their continued viability. Three of the 14 fish were only detected on R14 during the period and were not detected afterwards. 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 (Fig. 7). Migration from the estuary to bay occurred almost exclusively during new moon and full moons. Fifty per cent of downstream transitions by Brook Trout occurred when stream temperature was between 7.9 and 12.0 °C. The maximum number of fish moving downstream per day (n = 5) occurred at a temperature of 10.9 °C.

GAMM models

The best-fit GAMM models for upstream and downstream (Fig. 8) transitions included date (centred on median date) as the sole smoothed fixed effect. In this model, centred moon (per cent illuminated) and centred 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 (Fig. 8), 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 to 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 the latter part of 2012, downstream movement

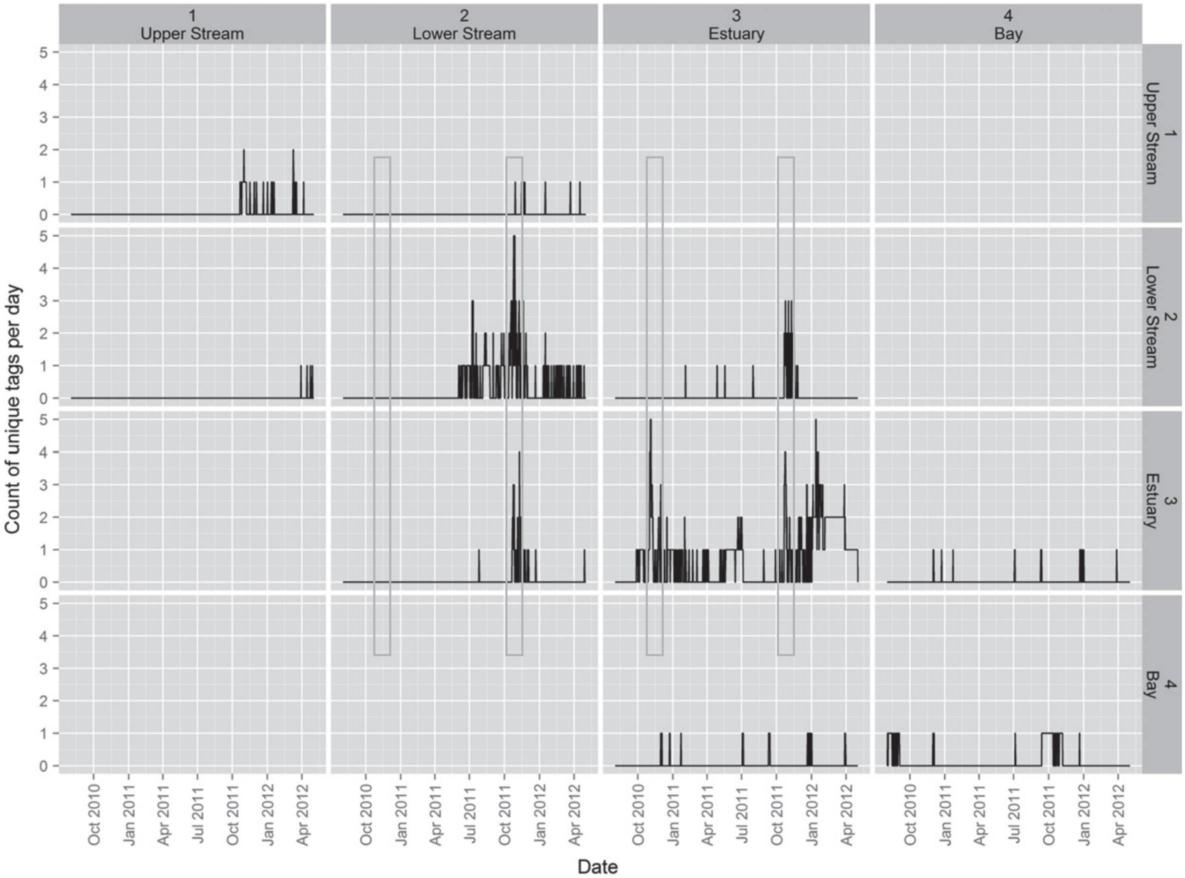

Fig. 5. Transition matrix from July 2010 to May 2012. Fish movement between habitats (nodes) over time in terms of unique individuals completing a particular transition per day. The *x*-axis is median date between detections at each node, and the *y*-axis is the count of unique individuals performing 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 with elongated boxes 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.

occurred in early fall followed by late fall-winter upstream movement.

Discussion

Seasonal movements of Brook Trout in Red Brook with spring and fall peaks in transitions between habitats 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 postspawning travel 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 numerical presence by numbers in the estuary. From the small sample size of Brook Trout that moved into Buttermilk Bay, movements may occur 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 movement strategies. We observed a wide range of movement patterns among individuals in Red Brook and Buttermilk Bay systems. While it is uncommon to find Brook Trout beyond the headlands of coastal bays (Curry et al. 2006), as observed in one individual, both residency with little movement and rapid descent of rivers towards the sea, as seen in fish B (Fig. 3), are common in Brook Trout and other salmonids (Naiman et al. 1987; Curry et al. 2002, 2006). Individuals responded to season differently in their habitat choices and when they moved. Sometimes, an individual's movement strategy changed from 1 year to the next as seen in fish B (Fig. 3), 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.

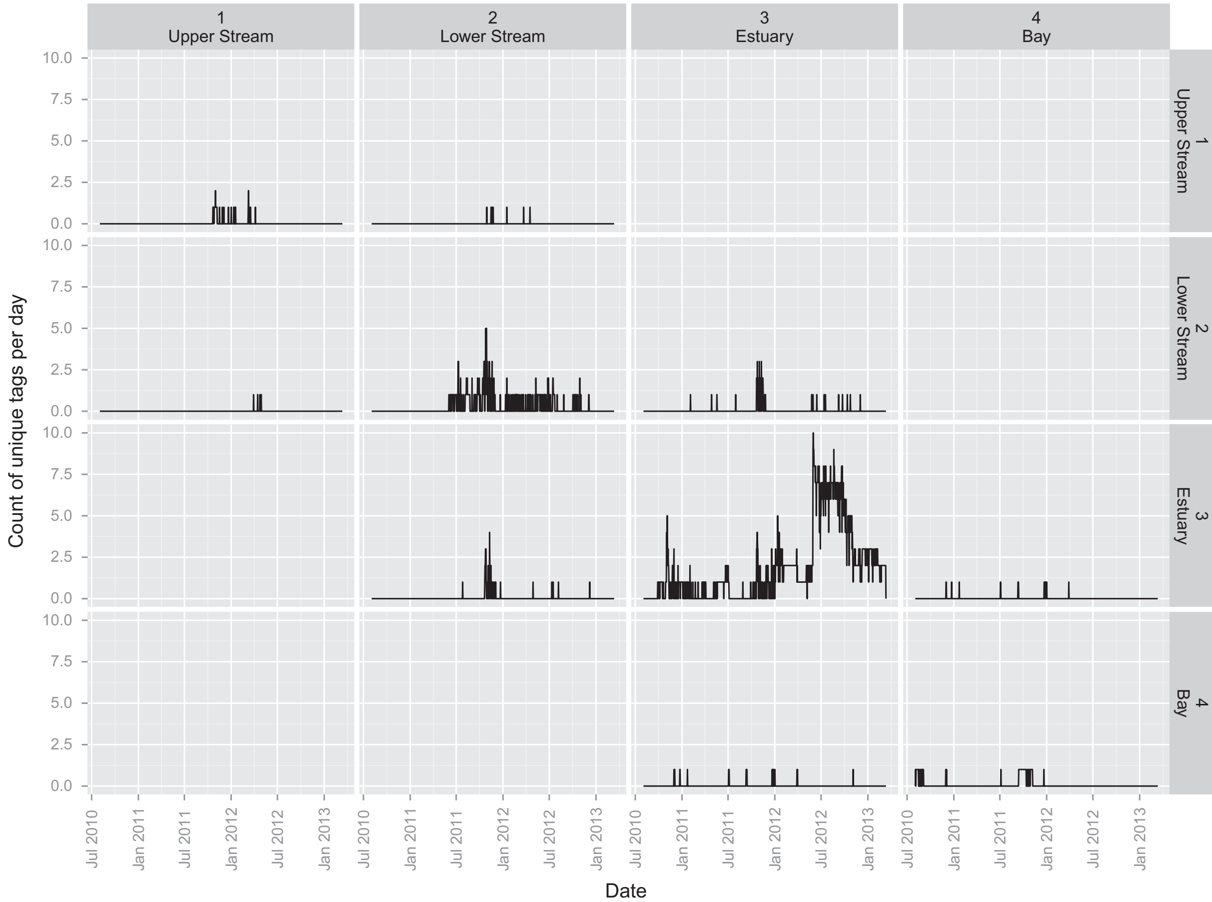

Fig. 6. Transition matrix for the entire study period from July 2010 to March 2013. Fish movement between habitats (nodes) over time in terms of unique individuals completing a particular transition per day. Labels across the top of the matrix represent the node where the fish started, and labels on 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.

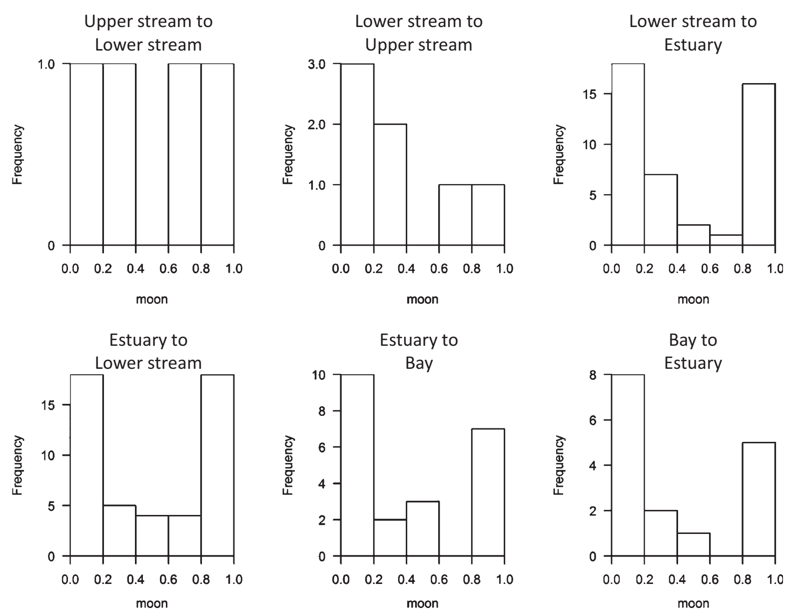

Fig. 7. Histograms of transitions by moon phase for each node to node transition possibility. Moon phase is represented in per cent illuminated where 0 is a new moon and 1 is a full moon.

This may be an example of an individual that waited until age 2 or 3 to travel to salt water, as suggested by Mullan (1958) and Castonguay et al. (1982).

The observation that 9.5% of tagged Brook Trout moved into Buttermilk Bay suggests that for those individuals that choose to enter the estuary, either (i)

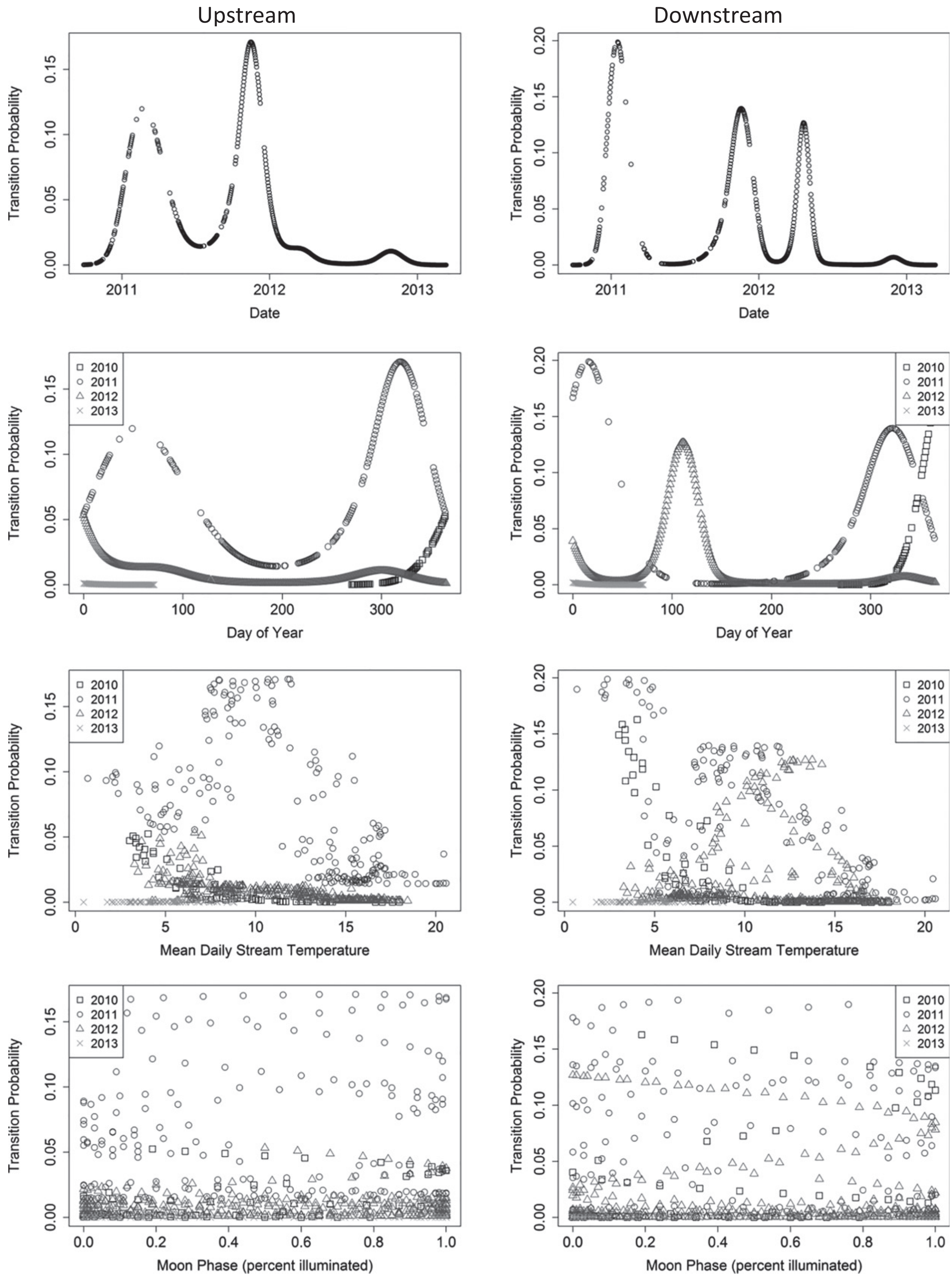

Fig. 8. Comparison of GAMM models. The first upstream and downstream plots show the expected probabilities of transitions by date, including all of the effects from the models. The bottom six plots are the fitted variables in the upstream and downstream GAMM models including date, the smoothed variable, 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. Colours on the bottom six plots represent the year from 2010 to 2013.

the estuary is an area with sufficient food resource, (ii) physiological constraints to the environment discourage travel further into the bay, or (iii) they are residing in the estuary to acclimate to and eventually move to salt water, which did not occur within the time of our study. Smith & Saunders (1958) observed a greater percentage of Brook Trout migrating to sea in Prince Edward Island, which varied annually (over 6 years) but ranged from 12% to 35%. They attributed Brook Trout movement out of salt water back into the river to adverse sea temperatures (Smith & Saunders 1958). In a study in New Brunswick, Canada, only one acoustic tagged Brook Trout of six choose to enter the marine environment even though it was accessible to all, potentially indicating that Brook Trout are restricted by their physical environment, which limits saltwater migration (Curry et al. 2002).

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 anadromous Brook Trout obtain greater fitness through richer marine food resources (larger and more abundant prey) than their resident counterparts (Wilder 1952; Power 1980; Hutchings & Morris 1985; Hutchings 1991; Jonsson & Jonsson 1993; Thorpe 1994; Einum & Fleming 1999; Morinville & Rasmussen 2006). When food is scarce in freshwater, most individuals of a partially anadromous population tend to become migrants, but few or none migrate when food is plentiful (Smith & Saunders 1958; Olsson et al. 2006).

Brook Trout residing in the Red Brook estuary may also have been preparing for seaward movement through a period of saltwater acclimation. In other studies, Brook Trout have been observed concentrating in small areas in channels that are mixing zones between fresh and salt waters (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. As discussed by Curry et al. (2010), the environment dictates how sea-running behaviour is expressed. Temperature preferences for Brook Trout vary by study location, but range from 11 to 19 °C (Smith & Saunders 1958; Power 1980; Power et al. 1999; Hartel et al. 2002). That said, Curry et al. (2006) found Brook Trout in temperatures from 5 to 18 °C, and they are known to perform adequately from 5 to 20 °C (Power 1980). Die-offs of adult Brook Trout 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 sea water after a period of estuarine residence (McCormick et al. 1985), ability to adapt to salt water 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. Castonguay et al. (1982) studied a population of Brook Trout in Quebec whose migratory individuals spent the first 2–3 years in the river, then 1 year in the estuary. When they finally moved to salt water, Brook Trout remained there 2–3 months and then returned to the river (Castonguay et al. 1982). Besner & Pelletier (1991)) found that Brook Trout survival in salt water was least likely in the summer and most likely in the spring.

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 a 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, or thermal refugia, as water temperatures warm to avoid detrimental effects on activity, appetite and enzyme efficiency that reduce growth rate (Power et al. 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 that 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. Furthermore, 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. In summer 2012, air temperature was 0.8 °C above the 30-year average and rainfall was 4.4 cm above normal. Increased water volume could have increased the appeal of a groundwater spring at the receiver near the head of the tide (R14), providing refugia from heightened surface water temperatures (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. There are life-cycle variations from the classical example of anadromy on the species, population and individual level (Power 1980; Gross 1987). Riverine fish populations have both stationary or resident individuals and migratory or mobile individuals (Jonsson & Jonsson 1993; Radinger & Wolter 2013), as seen in the current study. In comparison to other coastal salmonids such as salmon in the Pacific Northwest which are obligatory migrators, the Red Brook population has fewer migratory individuals that travel shorter distances and spend less time at sea. Noncoastal, stream-resident Brook Trout lack access to rich marine habitats, but may still exhibit facultative movement, travelling several kilometers in search of feeding or spawning areas (Gowan & Fausch 1996). Adfluvial Brook Trout have a life history similar to anadromous forms, migrating between streams and lakes instead of marine habitats. Lacustrine Brook Trout, such as those in Lake Superior, on the other hand, spend most of their life cycle within a lake's nearshore habitats (up to 400 m from shore) and move into streams for an average of 46 days to spawn in the fall (Mucha & Mackereth 2008). Anadromy may be less developed in the Red Brook population than for other more northern coastal 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 65–150 days in the marine environment (White 1942; Naiman et al. 1987; Curry et al. 2006, 2010) and reinforces the idea that anadromy in salmonids decreases with decreasing latitude (Rounsefell 1958; Nordeng 1961; Vladykov 1963; Scott & Crossman 1973).

After moving into Buttermilk Bay, six of eight Brook Trout were not detected back in Red Brook. Predation, an example of the costs related to the anadromous life history, may have been the fate of nonreturning sea-run Brook Trout. Other possible explanations for Brook Trout not returning 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 fish 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 <5 km 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 salt water to return to their home stream after being experimentally placed in a neighbouring river (S. Hurley, unpublished data).

Prior to restoration, informal observers believed that brook trout were not able to access the estuary or bay and return to the stream. We have shown that, postrestoration, brook trout can indeed access these habitats. If the restoration of Red Brook is consistent with other dam-removal projects, brook trout are likely to continue make use of this habitat that was once available to their species before dams were constructed (Bednarek 2001; Hitt et al. 2012). As movement distances increase over time for riverine fish species (Radinger & Wolter 2013), habitat exploration and dispersal can be expected to increase for populations near newly rehabilitated habitats such as Red Brook.

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. Moon phase seems to influence movements throughout the system, but that influence was particularly clear during movements from the estuary to Buttermilk Bay, which were undertaken especially at new and full moons (Fig. 7). Brook Trout may be further encouraged to move by higher spring tides that result from new and full moons phases (Castonguay et al. 1982).

Other environmental variables not measured in this study could play a role in triggering movements of Brook Trout in Red Brook. 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 1984a,b; Curry et al. 2006), may create a stronger model and clearer picture of migration triggers. The current study was also limited to the adult life stage of Brook Trout due to the size of acoustic tags used, but it has been suggested that maturation and spawning override other stimuli that would otherwise influence movement (Smith & Saunders 1958). 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 salt water or whether 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 coastal Brook Trout population might differ from others in the way and to what extent individuals exploit the marine environment.

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