Summer Movements of Sub-Adult Brook Trout, Landlocked Atlantic Salmon, and Smallmouth Bass in the Rapid River, Maine

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ABSTRACT

Summer movement patterns and spatial overlap of native sub-adult brook trout (*Salvelinus fontinalis*), non-native landlocked Atlantic salmon (*Salmo salar*), and non-native smallmouth bass (*Micropterus dolomieu*) in the Rapid River, Maine, were investigated with radio telemetry in 2005. Fishes were captured by angling, surgically implanted with radio transmitters, and tracked actively from June through September. Most brook trout (96%) and landlocked salmon (72%) displayed long distance movements (>1 km) to open water bodies (28 June to 4 July) followed by periods of time spent in presumed thermal refugia (5 July to 16 September). Summer water temperature rose above 25 °C, near the reported lethal limits for these coldwater species. In contrast, the majority of smallmouth bass (68%), a warmwater species, did not make long distance movements from areas of initial capture, remaining in mainstem sections of the river (28 June to 16 September). Spatial overlap of smallmouth bass and brook trout in the summer is unlikely because brook trout presumably move to thermal refugia during this time. However, interspecific competition between brook trout and landlocked salmon may occur since they select similar habitats June through September.

INTRODUCTION

Brook trout (*Salvelinus fontinalis*) is a coldwater species native to northeastern North America, originally extending along the Appalachian mountains in the Carolinas to Atlantic Canada and westward to the Great Lakes (Karas 1997, Bonney 2006). Correlative evidence has implicated the introduction of non-native fishes (Dunham et al. 2002, Peterson and Fausch 2003, NCWRC 2003, Dunham et al. 2004) in the decline of brook trout abundance and distribution across its native range (Hudy et al. 2005). For example, species composition in a Minnesota stream changed from nearly 100% native brook trout to predominantly non-native brown trout (*Salmo trutta*) over 15 years (Waters 1983). Similar declines in brook trout populations have been documented in the southern Appalachians following introduction of rainbow trout (*Oncorhynchus mykiss*) (Larson and Moore 1985). Effects of non-native fish introductions on native brook trout populations in other waters are less clear (Ricker 1968).

The Rapid River in western Maine (Fig. 1) is a premier wild brook trout recreational fishery (Boucher 2005, Bonney 2006), but juvenile recruitment data (Boucher 2005) and observations by anglers suggest a decline in brook trout abundance since 1998. This decline has been coincident with the illegal introduction of a warmwater species, smallmouth bass (*Micropterus dolomieu*), in Umbagog Lake during the mid-1980s (Boucher 2005). Over the past 10 years, the smallmouth bass has become

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abundant, expanding its range into the Rapid River and Pond in the River.

While predation has been implicated as the primary effect of smallmouth bass populations on native salmonid populations, the evidence is equivocal. Smallmouth bass consumed an estimated 7-9 % of migrating salmonids in a Columbia River watershed (Reiman et al. 1991, Angela 1997). In other systems, however, smallmouth bass consumed few salmonids, and direct predation may have a minor impact on salmonid populations (Lachner 1950, Warner et al. 1968, Martin and Fry 1972). Predation of smallmouth bass on salmonids may be stream-specific, where other mechanisms, such as direct competition during sub-adult life history stages, may play a role in declining salmonid population trends.

Non-native landlocked Atlantic salmon (*Salmo salar*) was introduced to the Rapid River system in 1875 (Ritzi 1968, Sherrifs 1995, Karas 1997). Although this fish provides an ancillary sport fishery, it is hypothesized that competition with Atlantic salmon may be contributing to the decline of Rapid River brook trout (Boucher 2005). Based on snorkeling and SCUBA surveys during 2003-2005 (Murphy 2005), brook trout and landlocked Atlantic salmon use the same sections of the Rapid River during the spawning season (Murphy 2006), and superimposition of many brook trout redds by Atlantic salmon was documented. Furthermore, in other river systems, Atlantic salmon compete with brook trout for habitat (Gibson 1973, Bley 1986) through territorial conflict (Kalleberg 1958) at juvenile and sub-adult life stages.

Native brook trout may compete with non-native landlocked Atlantic salmon and smallmouth bass during sub-adult life stages in the Rapid River. Documenting temporal and spatial overlap of sub-adults (fish between age 1 and their reproductive life stage) of these species is a first step to assessing such interactions in the wild. Sub-adult habitat for brook trout may be limited in the summer when water temperature is elevated and flow in this regulated system is variable. The objectives of this study were to (1) characterize summer movements of sub-adult brook trout, sub-adult landlocked Atlantic salmon, and sub-adult smallmouth bass, and (2) determine spatial overlap of river and lake use by these three species during the summer.

METHODS AND MATERIALS

Characterization of study area

The Rapid River is a small river between Lower Richardson Lake and Umbagog Lake, part of the Rangeley Lakes in western Maine, USA (Fig. 1). The Rapid River encompasses Pond in the River and flows through Middle Dam and Lower Dam. Middle Dam is a hydropower generating facility without fish passage, and Lower Dam was removed from the river in August 2005, during this study. Daily water temperature and discharge data were collected by Florida Power Light and Energy (FPLE). Flow data were collected at Middle Dam. A HOBO Temp™ data logger, placed mid-stream at Lower Dam (mean depth of 2.0 m), recorded daily temperatures. Average water depths in Pond in the River and Umbagog Lake were collected by Maine Department of Inland Fisheries and Wildlife (MDIFW).

Capture and tagging

Brook trout (n=27), landlocked Atlantic salmon (n=24), and smallmouth bass (n=22) were angled 20-22 June 2005 at five sites along the Rapid River (Figs. 2a, 2c and 2e). Water temperature ranged from 14.8 to 20.2 °C. We anesthetized the captured fish [MS-222 (100 mg L^{-1}, 20 mM Na_2CO_3), pH=7.0, in source water] and recorded length and mass. Scales were removed from above the lateral line, posterior to the dorsal fin, to determine age.

We targeted sub-adults (based on size) for this study. Fish > 40 g were selected for implantation of small tags (Lotek "nano-tag", 148-150 kHz, 3 sec pulse rate, 1.4 g,

dia. 7.6 mm). Fish > 70 g were selected for larger radio tags (Lotek "nano-tag", 148-150 kHz, 3 sec pulse rate, 2.1 g, dia. 8.3 mm). Sub-adults were defined *a priori* as 40-260 g. No fish < 40 g could accommodate the tags used in this study, and fish > 260g likely were adult fish (Boucher 2005).

The skin on the ventral surface was swabbed with 10% povidone-iodine, and an incision of ~ 12 mm in length was made through the skin and peritoneal wall. The antenna of the tag was threaded through the body cavity and pushed through the right lateral wall of the peritoneal cavity anterior to the anus with a sterile septum needle. The sterilized tag was inserted into the peritoneal cavity, and the incision was sutured with 5-0 coated Vicryl absorbable sutures (Ethicon, Inc., Somerville, New Jersey). The surgical procedure took less than three minutes to complete. Tagged fish were allowed to recover until normal swimming behavior was observed and then were released in slow flow near the capture site.

Radio tracking

For the life of the tags (approximately 45 or 90 days), the movements of the radio-tagged fish were tracked actively with a Lotek SRX-400 portable receiver and a handheld three-element directional yagi antenna. Tracking on the upper and lower river sections was carried out twice weekly by foot and on Umbagog Lake and Pond in the River twice monthly by boat. All tracking events occurred during daylight hours and were not standardized for weather conditions. Georeferenced locations (±1 m) were obtained at each vantage using a Global Positioning System unit. Locations were accurate within 20 m^2 (based on the successful location of hidden transmitters before this study).

Age determination

Ages of tagged fish were estimated by scale impression analysis (Smith 1954). Annuli were identified according to criteria specified by Jearld (1983). Age of each fish was estimated independently by two readers. When there was disagreement between the

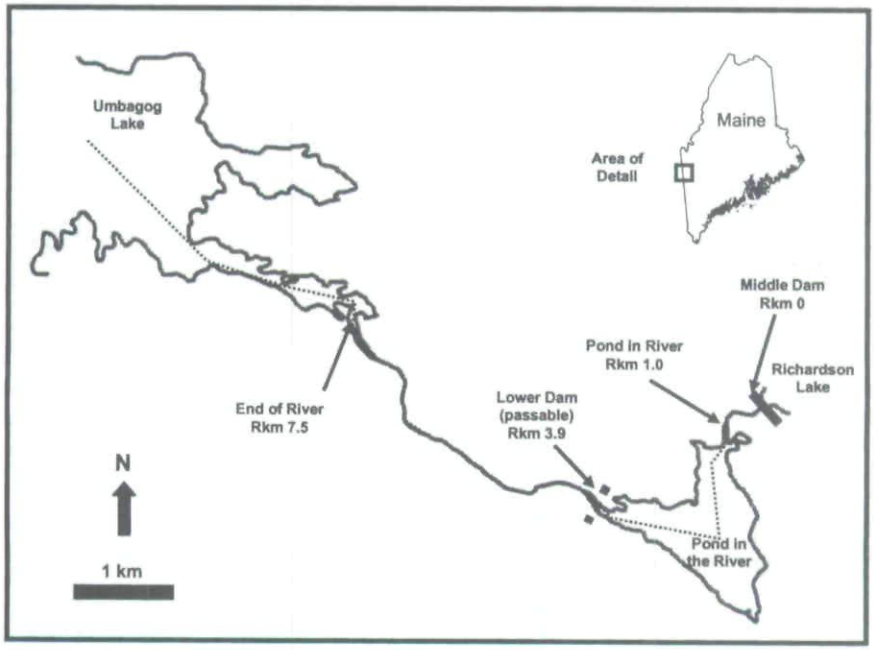

Figure 1. Rapid River, Maine, study area. The dotted line is the reference centerline used to calculate river kilometer as a descriptor of movement.

two readers (12/76), the scale was examined by a third person. When there was disagreement among all three readers, age was reported as "unknown."

Calculations

In order to describe movements in the Rapid River system, fish locations were converted to linearized river kilometers (Rkm) by calculating a position orthogonal to an idealized series of centerlines (Fig. 1). Individual fish movements were estimated by measuring the distance between consecutive locations (in Rkm) and computed as the "minimum distance" moved from the original tagging location. Average minimum distance moved for each species was calculated as the average of all individual values for each species. The telemetry season was divided into "early summer" and "mid-summer" (20 June – 4 July, and 5 July – 16 September, respectively) to describe and compare movements within and between species.

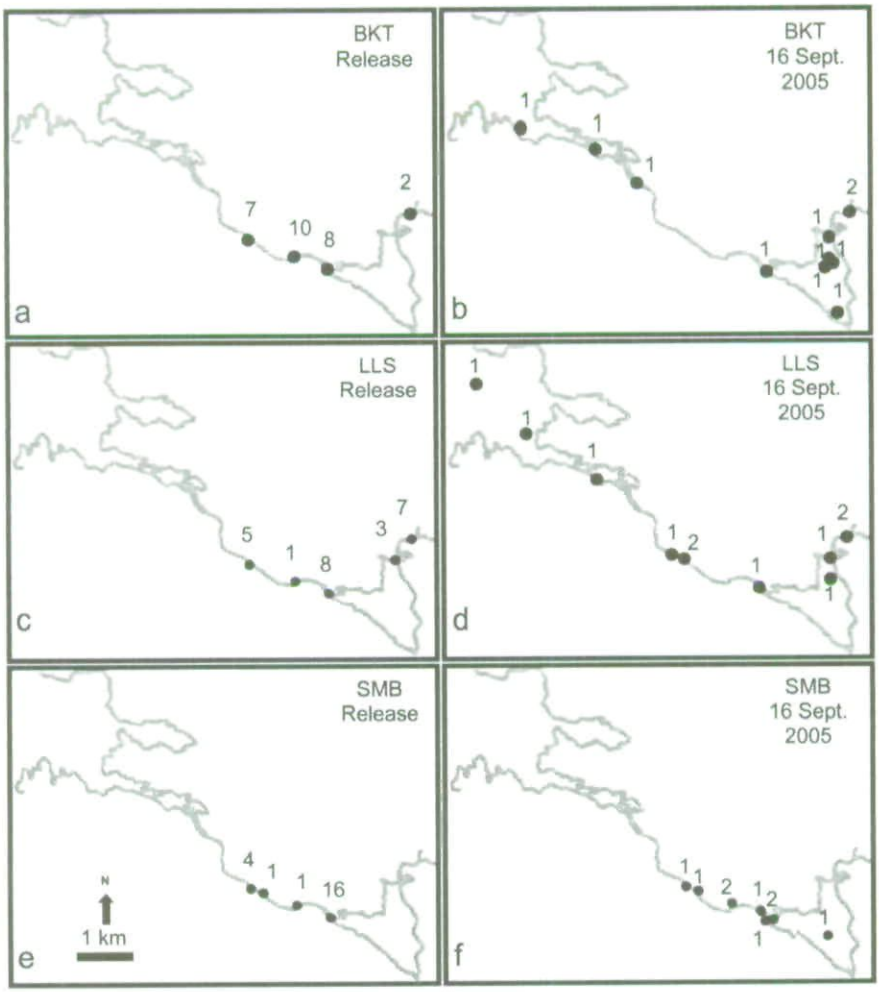

Figure 2. Initial release locations (a,c,e) and fish positions at the end of the three-month study, 16 September 2005, (b,d,f) for sub-adult brook trout (BKT), landlocked Atlantic salmon (LLS), and smallmouth bass (SMB). Number of fish at each location is indicated.

Analysis of interspecific sub-adult movement

Minimum distances moved were compared among species with a Kruskal-Wallis test; post-hoc comparisons were conducted with Mann-Whitney U-tests. Fish movements were compared with fork length, mass and age using simple linear regressions and Chi-squared analysis. The relationship between regulated discharge and daily temperature range was assessed using a linear regression using data from 1 July to 31 August, 2005. Significance of statistical analyses are reported at the $p < 0.05$ level.

RESULTS

Tracking was conducted from 28 June to 16 September. Of tagged fish, 24 brook trout, 18 salmon, and 22 smallmouth bass were successfully located at least once (88, 75, and 100%, respectively). A total of 412 fish locations was used to describe fish movements.

Brook trout movements

Over the three month study, 96% of the radio-tagged sub-adult brook trout (23/24) made large movements (>1 km), with only one fish remaining within 1 km of its initial release (Fig. 3). The average minimum distance traveled from the site of capture was 3.76 km (SE = 1.64, range= 0.12-6.7 km, n = 24), with much of this movement occurring during early summer.

In early summer, all but one brook trout (96%, n = 23) had left the sites of their initial release, and 42% of them left the mainstem sections of the river entirely and could be found in Pond in the River or Umbagog Lake (Fig. 3). Movement declined during mid-summer. Brook trout were observed in Pond in the River (58%) and Umbagog Lake (21%) throughout mid-summer. Brook trout use of these two water bodies appeared to be concentrated in the deepest locations (12 m in Pond in the River and 14 m in Umbagog Lake, based on MDIFW depth maps). Relative strength of tag signals indicated that many of these fish were deep in the water column. At the last location event, 16 September, three brook trout had moved back into the river (Figs. 2 and 3).

For fish successfully located during early summer (54%) the mean rate of movement was 0.41 km/day (range= 0.01-0.97 km/day, n = 19), whereas the mean rate of movement during mid-summer was 0.05 km/day (range= 0.00-0.68 km/day, n = 83).

Landlocked Atlantic salmon movements

Over the three month study, 72% (13/18) of landlocked Atlantic salmon made large movements (>1km). The remaining 28% did not move more than 1 km from their initial release sites (Figs. 2 and 3). The average minimum distance traveled from the initial site of release was 3.0 km (SE= 3.1, range= 0.01-12.4 km, n = 18).

Many of the salmon (9/18) moved from their initial release sites during early summer. Unlike brook trout, however, these salmon did not move directly into either Pond in the River or Umabgog Lake. Instead some (6/18) remained in mainstem sections of the river until mid-summer, at which point they then moved to either Pond in the River or Umbagog Lake. Of the salmon located during this study, 67% were observed using either Pond in the River, Umbagog Lake, or both. Some 33% of salmon remained in the mainstem sections of the river for the duration of the study.

Of the fish located during early summer (50%), the mean rate of movement was 0.23 km/day (range= 0.0-0.75 km/day, n = 12). The mean rate of all radio-tagged landlocked Atlantic salmon movements during mid-summer was 0.15 km/day (range= 0.00-6.72 km/day, n = 89). Salmon found in Pond in the River and Umbagog Lake during mid-summer were observed moving within these water bodies more than brook trout. Average minimum distances traveled by sub-adult brook trout and landlocked Atlantic salmon were significantly different from those traveled by smallmouth bass ($\chi^2 = 19.6$, $P < 0.002$).

Smallmouth bass movements

Over the three-month study, 68% (15/22) of smallmouth bass moved <1 km from the initial site of release. The remaining 32% moved >1 km (Figs. 2 and 3). The average minimum distance traveled from the initial site of release for radio-tagged smallmouth bass was 1.10 km (SE= 1.7, range= 0.01-6.7 km, n = 22).

Of the fish successfully located during early summer, only one smallmouth bass

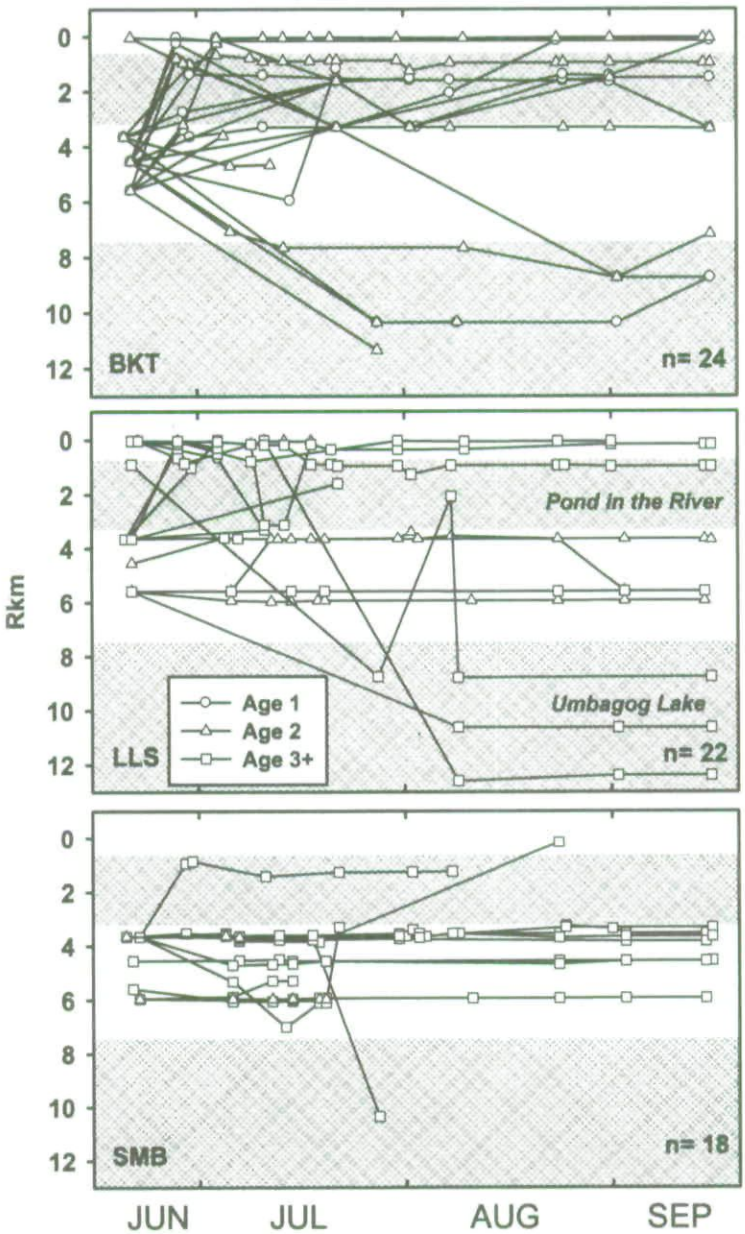

Figure 3. Movement data for sub-adult brook trout (BKT), landlocked Atlantic salmon (LLS), and smallmouth bass (SMB) implanted with radio tags in the Rapid River, Maine. Individual fish movements are presented over time with respect to calculated river kilometer positions. Middle Dam is defined as Rkm 0. Pond in the River and Umbagog Lake are indicated as gray shaded regions.

had moved away from the initial site of release, and 28% moved from their initial site of release during mid-summer. Throughout this study, 12% of the smallmouth bass used either Pond in the River (two) or Umbagog Lake (one). For fish successfully located during early summer (13/22) the mean rate of movement was 0.04 km/day (range= 0.00-0.39 km/day, n = 15), whereas the mean rate of movement during mid-summer was 0.05 km/day (range= 0.00-1.36 km/day, n = 120).

Age, fork length and mass

Brook trout ranged from 46 to 260 g and were age 1 and age 2 in near equal proportions (Table 1). Salmon ranged from 45 to 260 g, and were ages 1-5 (79% were ages 2 - 4). Smallmouth bass ranged from 43 to 262 g and were ages 2 - 6, but the majority (73%) were age 3. Within each species, age and size did not correlate with average minimum distance traveled.

Water temperature and flow

Regulated water discharge from Middle Dam fluctuated more than three-fold over the study period, from less than 14 m^3/sec to more than 45 m^3/sec, in one day. Periods of low flow were punctuated with periods of elevated flow through the summer. Daily river water temperature fluctuated greatly during periods of low flow (Fig. 4), ranging more than 7 °C in a 24 h period. Water flow directly influenced the daily range of temperature in the river ($R^2 = 0.14$, $p = 0.003$). Average water temperature increased (June 19-June 30) and remained high (20-25 °C) until the end of August.

Changes in water temperature and river discharge coincided with the initiation of large scale movements of brook trout and landlocked Atlantic salmon (June 28-July 4; Figs. 2 and 4). At the time that fish were tagged and released, water discharge at Middle Dam ranged 65 -80 m^3. In the days immediately following tagging (June 21-June 22), water was withheld at Middle Dam and water flows declined (mean flow rate = 27 m^3, range = 11 – 51 m^3, var = 246) and remained lower than the initial observed range of

Table 1. Mean fork length and mass of sub-adult brook trout, landlocked Atlantic salmon, and smallmouth bass (by age) implanted with radio tags in 2005. Values in parentheses are standard deviations.

Species	Age	n	Fork Length (mm)	Mass (g)
Brook trout	1	11	176 (16)	65.7 (20.0)
	2	16	249 (21)	187.8 (44.1)
	All	27	219 (41)	138.1 (70.8)
Atlantic salmon	1	2	183 (47)	74.9 (41.9)
	2	5	237 (42)	154.1 (65.1)
	3	10	271 (18)	213.5 (34.3)
	4	4	270 (13)	195.9 (51.0)
	5	1	285	157.8
	Unknown	2	192 (78)	218.8 (51.2)
	All	24	250 (43)	184.7 (59.1)
Smallmouth bass	2	2	162 (23)	64.4 (30.3)
	3	16	181 (25)	92.7 (50.1)
	4	1	197	93.9
	6	1	262	262.2
	Unknown	2	214 (38)	146.9 (81.8)
	All	22	187 (31)	102.8 (61.4)

water flow for the remainder of the study. This decrease in river discharge at Middle Dam resulted in temperatures that reached 26 °C in the river. Brook trout and landlocked salmon began moving immediately following this change in flow as average daily water temperature rose above 20°C.

DISCUSSION

Brook trout movements reflected water temperature fluctuations. In early summer the majority of brook trout traveled an average minimum distance of 3.8 km to areas in Pond in the River or Umbagog Lake. The initiation of movement was coincident with increased river temperature which also was related to dam operation. By July, average daily water temperature in the Rapid River had exceeded 20°C, near the lethal limit for brook trout (Fry et al 1946, McCormick et al. 1972). Increased temperature in early summer was coincident with decreased flow caused by dam operation. While changes in flow may have affected movement of brook trout, the factors covaried, which obscured any potential relationship. Flow did directly influence the daily range of temperature in the river, and periods of regulated low flow had the greatest daily fluctuation. Though discharge explained only 14 % of the variation in temperature observed, it should be noted that flow data are point estimates rather than averaged daily discharge.

Brook trout that reached Pond in the River and Umbagog Lake remained there through the summer months and exhibited little movement. Weak radio signals from tagged fish indicated that brook trout were not near the water surface. Deep areas in these water bodies remain significantly cooler than the river during summer months (K. Murphy, FPL, unpublished data).

Landlocked Atlantic salmon made similar movements toward deep water bodies, though some fish remained in the river through the summer. In early summer, many of the salmon had moved from the river an average minimum distance of 3.0 km to deep areas in Pond in the River or Umbagog Lake. This summer movement pattern is generally consistent with other studies of landlocked Atlantic salmon movement in Maine (Warner 1959, DeSandre et al. 1977).

Unlike brook trout, a higher proportion of Atlantic salmon (28%) remained in the river through the summer. Additionally, the mean rate of movement of landlocked Atlantic salmon during mid-summer was greater than for brook trout. This variability in movement of Atlantic salmon is consistent with exploratory behavior observed in

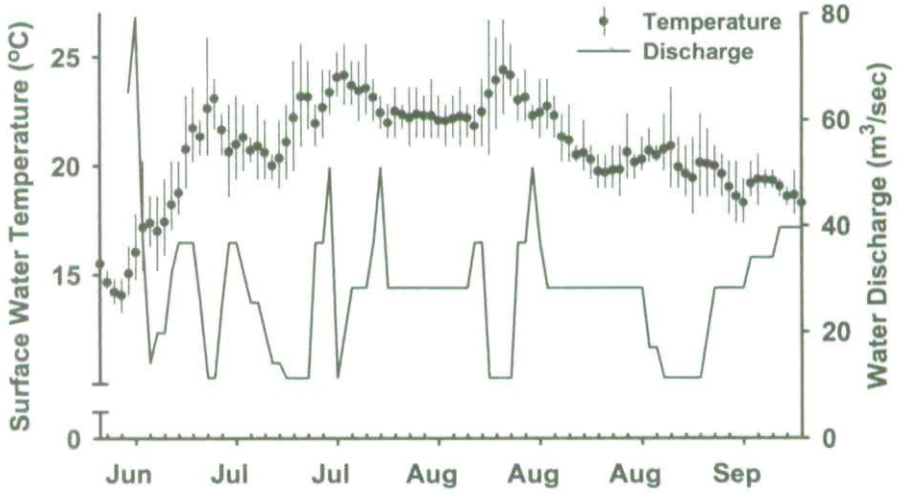

Figure 4. Daily water discharge (m³/sec) at Middle Dam and average daily water temperature (°C) and range during summer 2005.

juvenile Atlantic salmon (Armstrong et al. 1997) and juvenile Pacific salmonids (Kahler et al. 2001) during summer months. The greater use of the river and greater movement during the summer by landlocked salmon likely reflects a greater thermal tolerance of the species with respect to brook trout. The lethal temperature for Atlantic salmon has been reported to be 28 °C (Elliot 1991). Water temperature that might typically displace brook trout do not necessarily cause landlocked Atlantic salmon to move (Sayers 1990).

Only five of the 18 located landlocked Atlantic salmon were age 1 or age 2. Therefore, the seasonal movement and behavior patterns of landlocked Atlantic salmon observed in this study may not be entirely representative of the sub-adult population in the Rapid River but may also reflect behavior of reproductive individuals. Three of the five salmon used either Pond in the River or Umbagog Lake and two moved from the initial sites of release but remained in mainstem sections of the river. Because behaviors were comparable between sub-adults (age 1 or age 2) and adults, we believe that the observed movements of landlocked Atlantic salmon were not related to developmental stage.

In contrast to the general patterns observed for brook trout and landlocked salmon, smallmouth bass radio-tagged in the mainstem sections of the Rapid River exhibited little tendency to move from the area of capture. Most smallmouth bass (68%) traveled less than 1 km from the release site. Only three individuals were observed moving into either Pond in the River or Umbagog Lake. These results are consistent with previous findings that smallmouth bass is a sedentary species with a small home range and, generally, does travel long distances (Funk 1955, Munther 1977, Todd and Rabeni 1989, VanArnum 2004). Summer water temperature in the Rapid River was within the preferred temperature range for smallmouth bass (Coble 1975). There was no apparent pattern to suggest flow or temperature conditions caused the observed movements.

While it was the goal of this study to document behavior of sub-adult fish in the Rapid River, it is likely that many of the smallmouth bass could have been reproductively mature. Only two of the radio-tagged smallmouth bass were age 2, whereas 16 were age 3. Maturity for male smallmouth bass generally begins at age 2-4 for males and 3-4 for females (Coble 1975). The consistency of the pattern of movement, however, suggests that smallmouth bass movement is unrelated to developmental stage.

Overlap between species

Based on observations of spatial segregation during the summer, it is unlikely that brook trout and smallmouth bass are competing for resources in the Rapid River system. The majority of brook trout moved into Pond in the River and Umbagog Lake. Radio-tagged smallmouth bass that moved into Pond in the River (9%, n=2) and Umbagog Lake (5%, n=1) did not use the same areas of the water bodies.

Though radio-tagged brook trout and smallmouth bass did not overlap extensively, no smallmouth bass were tagged in the large water bodies. Smallmouth bass presence has been documented extensively in both Pond in the River and Umbagog Lake (Boucher 2005, Murphy 2006). Based upon thermal preferences, interaction between brook trout and smallmouth bass in these large water bodies is unlikely. At warm summer temperatures smallmouth bass are likely in shallow edge habitat (Coble 1975), whereas the brook trout and salmon select deeper and cooler waters.

Some evidence suggests that brook trout and landlocked salmon compete for space during summer months when brook trout are already confined to few thermal refugia. Young-of-the-year brook trout aggressively defend cool water microhabitats, which affects their daytime feeding. Thermal refuges are a potential limiting resource during periods of high temperature (Biro 1998). Limiting such areas would increase competition between con-specifics and between life history stages that may otherwise have limited interactions.

Whereas smallmouth bass in the river may not overlap spatially with brook trout, the fact that they remain in the areas evacuated by brook trout may be significant. As brook trout begin to move back into the river as temperature falls, areas previously held as territories will have been occupied and exploited by smallmouth bass. There is ample evidence that establishment of non-native bass can adversely affect littoral prey abundance and diversity in north-temperate lakes and streams (Chapleau et al. 1997, Vander Zanden et al. 1999, MacRae and Jackson 2001, Jackson 2002). Through predation, smallmouth bass can reduce prey fish abundance and diversity (Power et al. 1985, Harvey et al. 1988, Chapleau et al. 1997, Whittier et al. 1997) which can negatively affect food resources of native salmonids. Furthermore, the brook trout is less successful in the presence of littoral species with which it must compete for food (Bourke et al. 1999). If competition for food resources or for territory occurs in the Rapid River, then it is possible that growth and fecundity would be affected.

The movement data suggest that a proportion of landlocked salmon remains in the river during the summer. These salmon likely exploit areas that might otherwise be selected by brook trout under different thermal conditions. Atlantic salmon can successfully compete with brook trout for habitat, often resulting in exclusion from part of their fundamental niche (Gibson 1973, Bley 1984). In other systems, Atlantic salmon affected shifts in habitat use by brook trout but without a reduction in fitness (Sayers 1990). Where larger brook trout were present, however, brook trout may displace Atlantic salmon to the detriment of salmon growth (MacCrimmon et al. 1983).

Based on observations of spatial segregation during the summer, it is unlikely that landlocked Atlantic salmon and smallmouth bass interact with each other in the Rapid River system. The landlocked Atlantic salmon that moved into Pond in the River and Umbagog Lake were concentrated in areas of deep water, whereas radio-tagged smallmouth bass that moved into Pond in the River and Umbagog Lake did not use these same deep waters. In the mainstem sections of the river, landlocked Atlantic salmon did not overlap with smallmouth bass.

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