

**FISHING, WATER REGULATION, AND COMPETITION: THE PAST,
PRESENT, AND FUTURE OF BROOK TROUT IN THE RAPID RIVER, MAINE**

By

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Thesis Advisor: Dr. Joseph Zydlewski

An abstract of the Thesis Presented
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The Rapid River, located in western Maine, has been renowned as a premiere native brook trout (*Salvelinus fontinalis*) fishery in the eastern United States since European settlement in the late 1800s. Since this time the Rapid River fishery has declined due to over harvest, heavy fishing pressure, introductions of non-native fish species, and habitat degradation from logging activities, including construction of dams. Currently, the greatest threat to the Rapid River brook trout is speculated to be the introduction of non-indigenous smallmouth bass (*Micropterus dolomieu*). In addition to these impacts, the Rapid River brook trout population also may be influenced by the continued high angling pressure, and more regional (e.g. acid rain) and global (e.g. climate change) environmental conditions. Increasing concerns about management and preservation of this brook trout population prompted this review of eastern brook trout

and the history of the fishery in the Rangeley Lakes region. Knowledge of both the historical and current factors that may limit brook trout is important in informing management decisions for the restoration and recovery of this important native species.

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. Fish were captured by angling, surgically implanted with a radio transmitter, 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 temperatures rose above 25 °C, near the reported lethal limits for these cold water species. In contrast, the majority of smallmouth bass (68%), a warm water species, did not make long distance movements (< 1km) from areas of initial capture, remaining in main stem 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.

As populations of wild brook trout (*Salvelinus fontinalis*) decline across their native range in the North America angling regulations such as fly-fishing-only and catch and release are being used by management agencies to conserve fish while maintaining angling opportunities. Post release mortality may significantly impact age and size structure of populations. In order to assess the possible impacts of catch and release

fishing on brook trout population structure, I applied data from several sources to build a deterministic population model in which age classes up to 5 years occurred. To assess the potential impact of fishing, I examined the changes in population characteristics at varying levels of angler effort (0-240 rod·hours·ha⁻¹·yr⁻¹) and post release hooking mortality rates (0-14%). A “trophy” brook trout fishery was sustainable only at low levels of angling intensity (<120 rod·hours·ha⁻¹·yr⁻¹). As angling effort increased, the proportion of older aged fish (3, 4, and 5 years old) declined significantly. At higher levels of angling effort, 4, and 5 year old fish were no longer part of the population. Increases in post release mortality rates resulted in similar declines of older age classes. The results of this simulation indicate that post release mortality rates, as might be common in catch and release fisheries, may significantly shift the age structure of a population, reducing trophy angling potential.

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TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	vi
LIST OF TABLES	ix
LIST OF FIGURES	x
CHAPTER 1: THE RAPID RIVER BROOK TROUT: PAST, PRESENT, AND FUTURE OF A MAINE NATIVE	1
Introduction	2
Life history of brook trout	6
Influence of environment of brook trout	9
Factors for Rapid River brook trout decline	11
Rapid River brook trout – looking to the future	20
References	23
CHAPTER 2: SUMMER MOVEMENTS OF SUB-ADULT BROOK TROUT, LANDLOCKED ATLANTIC SALMON, AND SMALLMOUTH BASS IN THE RAPID RIVER, MAINE	29
Introduction	30
Methods	33
Results	38
Discussion	45
References	54

CHAPTER 3: ASSESSING THE EFFECTS OF CATCH AND RELEASE	60
REGULATIONS ON AN ADFLUVIAL BROOK TROUT	
POPULATION USING AN AGE-STRUCTURED MODEL	
Introduction	61
Methods	63
Results	73
Discussion	79
References	85
BIOGRAPHY OF THE AUTHOR	90

LIST OF TABLES

Table	Page
2.1. Mean and range of fork lengths, masses, and radio tag types.	36
2.2. Mean fork lengths (mm), masses (g), condition factors (CF) and ages of sub-adult brook trout (BKT), landlocked Atlantic salmon (LLS), and smallmouth bass (SMB).	43
3.1. Age specific parameter set for an age-structured fishery model representing an adfluvial "trophy" brook trout population.	66
3.2. Age specific natural annual mortality rates (m) as reported in literature.	67
3.3. Non-age specific parameter set for an age-structured fishery model representing an adfluvial brook trout population.	70

LIST OF FIGURES

Figure	Page
1.1. Map of the Rangeley Lakes, Maine.	3
1.2. Time-table (chronological) of events that likely affected the Rapid River brook trout population over the past 150 years.	4
2.1. Rapid River, Maine, study area.	31
2.2. Initial release locations and fish positions at end of 3-month study.	34
2.3. Movement data for sub-adult brook trout, landlocked Atlantic salmon, and smallmouth bass implanted with radio tags in the Rapid River, Maine.	40
2.4. Daily water discharge (m^3/sec) at Middle Dam and average daily water temperatures ($^{\circ}C$), and range, during summer 2005.	44
3.1. Simplified structure of an adfluvial “trophy” brook trout fishery as simulated in STELLA®.	65
3.2. Stock-recruitment relationship.	70
3.3. Simulated population characteristics of a brook trout fishery.	74
3.4. Sensitivity and elasticity of population characteristics to changes in life-history parameters.	75
3.5. Simulated population characteristics of a brook trout fishery under angling pressure.	78

Chapter 1

THE RAPID RIVER BROOK TROUT: THE PAST, PRESENT, AND FUTURE OF A MAINE NATIVE

Abstract

The Rapid River, located in western Maine, has been renowned as a premiere native brook trout (*Salvelinus fontinalis*) fishery in the eastern United States since European settlement in the late 1800s. Since this time the Rapid River fishery has declined due to over harvest, heavy fishing pressure, introductions of non-native fish species, and habitat degradation from logging activities, including construction of dams. Currently, the greatest threat to the Rapid River brook trout is speculated to be the introduction of non-indigenous smallmouth bass (*Micropterus dolomieu*). In addition to these impacts, the Rapid River brook trout population also may be influenced by more regional (e.g. acid rain) and global (e.g. climate change) environmental conditions. Increasing concerns about management and preservation of this brook trout population prompted this review of the life history of the eastern brook trout and the history of the fishery in the Rangeley Lakes region. Knowledge of both the historical and current factors that may limit brook trout is important in informing management decisions for the restoration and recovery of this important native species.

Introduction

Once plentiful in streams and rivers from Maine to South Carolina, brook trout (*Salvelinus fontinalis*) have been greatly reduced by human activities throughout their native range in North America. Self-sustaining populations of brook trout remain in just 5% of the areas inhabited in pre-colonial areas of the United States (Hudy et al. 2006). Maine is now considered the “last stronghold” for brook trout in the eastern United States. Maine has as many intact brook trout populations as all other states in the eastern range combined. Even so, only 14% of brook trout populations in Maine remain wild and intact (Hudy et al. 2006, Bonney 2006).

The Rapid River connects the most southern water bodies in the Rangeley Lakes system (Figure 1.1). This system is illustrative of the plight of native brook trout in Maine. The Rapid River supports a wild population of brook trout and is one of the most heavily fished rivers in the state (Boucher 2005; Bonney 2006). The brook trout in this system, however, are feared to be on the decline. Preliminary juvenile recruitment data (Boucher 2005) and anecdotal evidence from local anglers suggest an overall reduction in abundance since 1998. This brook trout population is also genetically distinct from populations in connecting waters (Fraser et al. 2004), emphasizing the evolutionary significance of the Rapid River brook trout.

The ecology of the Rapid River has been and remains heavily impacted. Over the past 150 years, over fishing, degradation of habitat by land clearing, log driving, dam construction, and fish introductions have all likely contributed to the decline of the Rapid River brook trout (Table 1.1; Sherrifs 1995; Karas 1997).

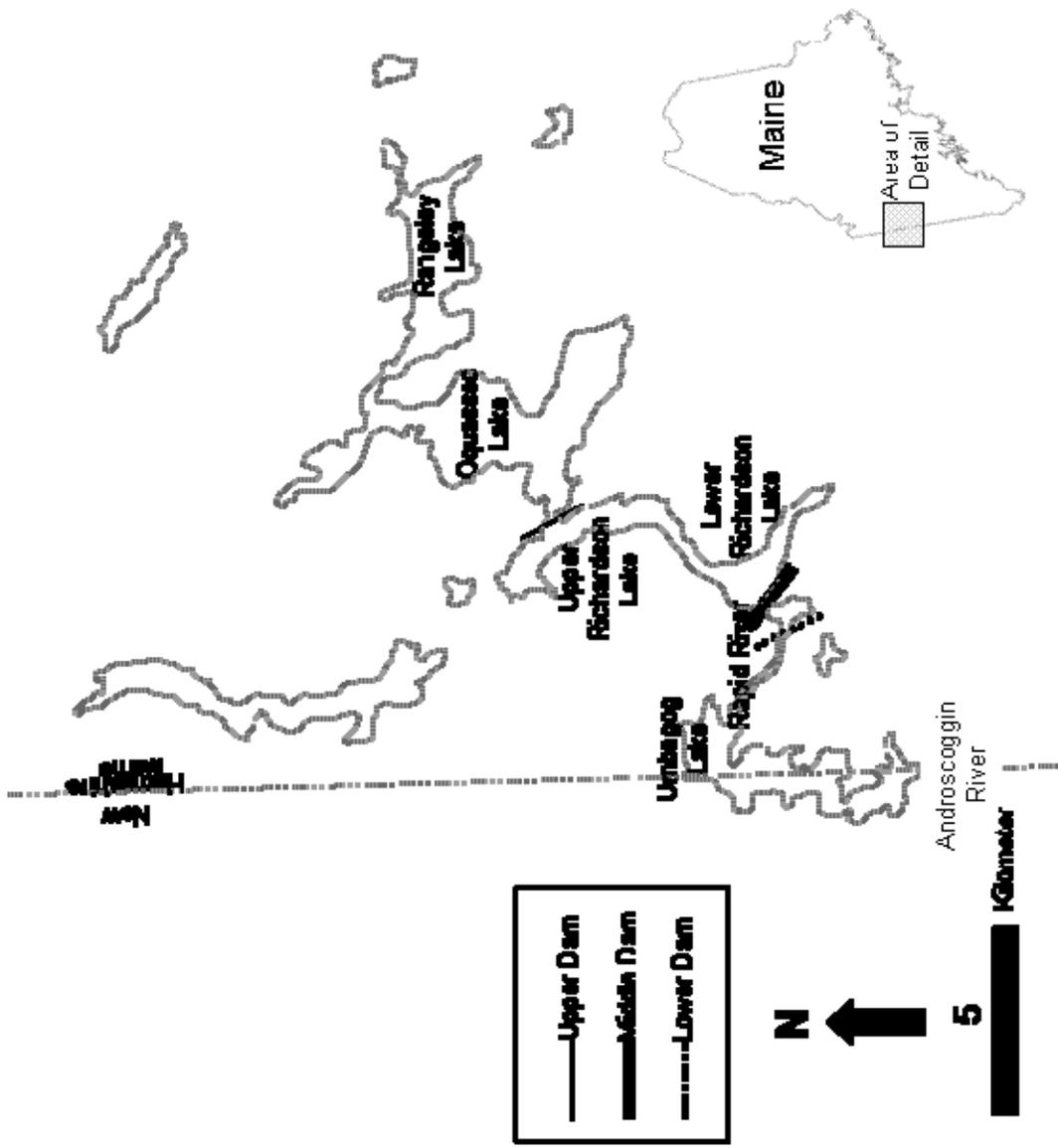


Figure 1.1. Map of the Rangeley Lakes, Maine. Prior to the building of upper, middle, and lower dams, brook trout would have had unobstructed access to each area within the Rangeley Lakes Region.

Management efforts have recently focused on the colonization of the Rapid River by an exotic species, smallmouth bass (*Micropterus dolomieu*). As with many other systems in Maine, anthropogenic effects sometimes mask the influence that a single factor may have on the brook trout population. In this article, the life history and status of the brook trout is explored in the context of both the history and ecology of the Rapid River of the Rangeley Lakes region as a case study. A more thorough understanding of the many factors that likely influence the Rapid River brook trout may provide a foundation upon which managers can make informed decisions about population management, habitat improvement, and guide the direction of future research.

Life History of Brook Trout

Brook trout generally occur under conditions described as “clean, pure, and aesthetically desirable” (Power 1980). Pristine freshwater ecosystems provide rearing areas for all life history stages. The life cycle of brook trout begins in the fall with spawning. Females dig an egg pit (“redd”) and deposit eggs concurrent with a vibrant display of courting behavior by the male (Everhart 1976). The process of spawning is energetically demanding, and adult brook trout actively feed prior to moving into overwintering areas. The eggs are deposited under the surface of the gravel, developing through the winter. Brook trout emerge from their eggs in May (as “alevin” or “sac fry”) and remain in, or near, the redd until their yolks sacs are absorbed. Fry will then begin actively feeding in shallow waters and defending a territory (Griffith 1972; Power 1980). As they develop a series of dark vertical bands (parr marks) appear along their sides. These marks become less obvious as these juveniles become subadults and then adults.

Temperature is the single most important factor limiting brook trout distribution, growth and production (McCormick et al. 1972). In general, brook trout are a cold water species capable of surviving over only a narrow range of temperatures (5-24°C; Power 1980) with an upper lethal temperature of 25°C which limits its distribution (Ricker 1934; Fry et al. 1946 MacCrimmon and Campbell 1969; Magnuson et al. 1979). Thermal tolerance ranges and growth optima are specific to life history stage. Optimal embryonic development and hatching, for example, occurs over a range of 4.5-11.5°C (Davis 1961; MacCrimmon & Campbell 1969). Juvenile optimal growth occurs over a range of 11-16°C (Raleigh 1982). Growth rate increases with increasing temperatures through this narrow interval (Hokanson et al. 1972).

At these temperatures, less energy is required for maintenance of basal metabolic processes resulting in more energy that can be allocated to the brook trout's growth (Power 1980). As water temperatures increase beyond the optimal range, available energy for growth decreases. As temperatures approach the upper, or lethal limit, their capacity to function properly diminishes, resulting in poor body condition, reduced cardiac performance, and even mortality (Brett 1965; Fry 1967). Water temperatures are negatively related to latitude, as well as altitude. More suitable habitat is found in northern states and in higher elevations. Due to this clinal variation, brook trout in northern populations can reach 8-10 years of age and be 4.5 kg. In southern populations, brook trout rarely survive past 3-4 years and reach a lesser size (0.1 kg; Behnke 1980).

Like many salmonids, brook trout exhibit great variation in life-history expression. Throughout much of its geographic distribution three life-history strategies are common: adfluvial, fluvial, and stream-resident. The adfluvial life-history strategy

involves spawning migrations from lakes or reservoirs to rivers or streams (Ryther 1997). The fluvial life-history strategy involves spawning migrations from large rivers to smaller rivers or streams. In contrast, the stream-resident strategy consists of life history completion in small streams. The least common or, perhaps, the least studied life-history strategy is the anadromous, or sea run. The anadromous life-history strategy involves spawning migrations from marine or estuarine habitats to rivers or streams (Ryther 1997).

Because of the diversity of life-history strategies, generalizing age and size structures of brook trout populations is difficult. Brook trout growth rates are influenced heavily by productivity and temperature of the water, size of the water body, and diet (Hutchings 1993). Migratory strategies generally allow individuals to take advantage of productive environments that are habitable only during certain parts of the year, seek thermal refuge to avoid exposure to extreme water temperatures, and avoid other stressful environmental conditions (Dingle 1996). Greater productivity and less exposure to stressful conditions enable higher growth rates, larger size-at-age, and greater energy stores (Dingle 1996; Hendry et al. 2004). Consequently, migratory individuals will exhibit delayed sexual maturity, increasing their reproductive output. Due to homogeneity in their environment, stream-resident brook trout tend to have shorter life spans, slower growth rates, greater annual mortality, and early sexual maturity (Power 1980; Josephson & Young 1996) than adfluvial, fluvial, and anadromous brook trout. Due to the higher proportion of accessible productive habitat and thermal refuge (from high summer and freezing winter temperatures), adfluvial, fluvial, and anadromous brook trout tend to live longer, delay sexual maturity, and experience greater growth rates over their lifetime (Power 1980).

Influence of environment on brook trout

Changes in temperature initiate movements of brook trout throughout their life (Power 1980; Romig 1990). Spawning activity (movement of reproductive individuals to spawning habitat) is associated with a decrease in water temperature ($<16^{\circ}\text{C}$; Hokanson et al. 1972). On a seasonal basis, many observed movements to thermal refugia are also associated with changes in water temperature (Bjornn 1971; Chapter 2, Jackson & Zydlewski, submitted). During summer months, brook trout in the Rapid River move to presumed thermal refuges when water temperatures exceed 20°C , near the lethal limit for brook trout (Jackson & Zydlewski, submitted).

Throughout their life cycle, water flow affects brook trout indirectly. During summer months, when stream flows are typically lowest, groundwater fed thermal refugia can be vital habitat for brook trout. Stream flow, or discharge, and water velocities also directly define brook trout habitat. Adult brook trout typically spawn in areas with moderate water flow ($0.09 - 0.64$ m/sec; Greenley 1978) and prefer areas with upwelling groundwater (Webster and Eiriksdottier 1976; Curry et al. 1995). Low water flows during development of brook trout embryos may result in a lack of oxygen and sedimentation which, in turn, reduces survival (Harshberger 1975; Waters 1995). Young brook trout avoid fast water, preferring low water velocities of about 0.01 to 0.02 m/sec (Griffith 1972). As they grow, they move into areas of faster moving water for feeding, but also utilize velocity refuges such as pockets of slow moving water behind rocks and other structures (Griffith 1972; Gibson 1978).

Concentrations of suspended solids, or turbidity levels, are directly related to stream flows in conjunction with stream bank erosion. Increased turbidity can restrict brook trout distribution and production (Curry & MacNeill 2004). Survival of brook trout eggs to hatching can be reduced by as much as 50% when suspended solids accumulate on redds (Curry & MacNeill 2004). Indirectly, high or persistent water turbidity can interfere with visual feeding (>30 Jackson Turbidity Units; Raleigh 1982).

Brook trout are more tolerant of low pH than other salmonid species, but this remains a key factor in distribution and production. Optimal pH range for brook trout is 6.5 – 8.0 while a range of 4.0 – 9.5 is tolerable (Raleigh 1982). Like other habitat conditions, tolerances vary with life history stage. Brook trout embryos and fry are more sensitive to low pH than are adult fish. While embryos can survive a pH as low as 4.5 (Power 1980) continued exposure to pH below 6.5 results in decreased hatching success and poor growth (Menendez 1976).

The acidity, or pH value, of Maine's waters has historically been suitable for brook trout (mean pH = 7.2, range 6.0-8.2; Peckenham et al. 2002). However, there has been concern about the possibility of substantial declines in pH values in Maine due to acid rain, which would result in decreased river and stream productivity levels. As of the year 2000, the most acidic rain in the United States had a pH of 4.3 (EPA 2002). Maine's location downwind from major industrialized region of the United States results in precipitation estimated to be two to four times more acidic than the pre-industrial average (Kahl and Scott 1994). At low pH levels, brook trout hatching success (Menendez 1976), growth, and fecundity (Mount et al. 1988) are all negatively affected.

Factors for Rapid River Brook Trout Decline

Early accounts document the presence of some of North America's largest brook trout in the Rangeley Lakes (Karas 2005), and the region is still renowned for its "trophy" brook trout fishery. However, historical data demonstrate that the body size of brook trout has declined significantly in the Rangeley Lakes since exploitation began in the middle of the 19th century (Kendall 1918; Bonney 2006). There have been no authenticated brook trout weighing more than 2.3kg caught from the Rangeley Lakes region since the early 1900s (Karas 2005). Many factors have likely contributed to this decline.

Angling and exploitation

Angling for brook trout in the Rangeley Lakes system is a long-standing tradition. The Rangeley Lakes region was settled during 1814-1825, and records of an important fishery date from 1840 (Sherrifs 1995). By 1860, a tourist boom had begun, and hotels and fishing camps dotted the lake shores. With no regulations placed on fishing and harvesting, native fish became heavily exploited. Despite its current reputation as a premier fly fishery, catching and harvesting of brook trout was accomplished by bait, seine and hoop netting in the 1800s (Sherrifs 1995). Spear fishing was also used and described as a "rare excitement" by J. G. Rich (1883) who, with a friend, took more than six hundred pounds of brook trout in one night by spear. There are reports that workers at the dams also took brook trout in great numbers right from the spawning beds by spear and dynamite (MacCrimmon & Gots 1980).

In the late 1800s, the first harvest restrictions were implemented for brook trout in the Rangeley Lakes region, though these were often ineffective, liberal, and poorly enforced. The Oquossoc Angling Association placed a limit of one brook trout per day on its members in Rangeley streams, but lake fishing, which was more frequent, remained unrestricted (Karas 1997). In 1872, Maine introduced legal seasons for both landlocked salmon and brook trout. This season was shortened to today's May through September fishing season in 1878. In 1882, the State of Maine passed the first brook trout minimum length limit (5 in). The bag limit however was 50-pounds and had no restriction on the number of fish (MacCrimmon & Gots 1980). Through the 1900s, regulations on brook trout fishing progressively became more restrictive and enforcement improved. Minimum length limits increased through the early 1900s, however, the changes were relatively small (2 in over nearly 90 years). Weight limits remained unchanged until 1951, when it was reduced to 5 pounds (Bonney 2006). It is in the early 1970s that we see the first special regulations being placed on specific brook trout waters, instead of statewide implementation.

Based on observations in the late 20th century of shifting size and age structure in the Rangeley Lakes brook trout populations (MacCrimmon & Gots 1980; Karas 2000), new regulations have been developed (Boucher 2005) but the population remains one of the premiere brook trout fisheries in the U.S. In 1994, the Maine Department of Inland Fisheries and Wildlife (MDIFW) restricted angling on the Rapid River to fly-fishing-only (1994) and imposed a catch-and-release (C&R) regulation on brook trout in 1996 (Boucher 2000).

The obvious and most profound effect that human harvest can have on a fishery is extirpation of the population. Less obvious effects of both over harvest and continued angling pressure are changes to phenotypic traits and the age and size structure of the exploited population (Longhurst 2000; Dairmont et al. 2009). Tendency of anglers to target and harvest large, reproductive-aged adults may result in shifts in population life history traits (e.g., reproduction at earlier ages and smaller sizes, and an overall truncation of the natural pyramid of age classes; Longhurst 2000; Darimont et al. 2009). Even when harvest is prohibited (i.e., C&R), significant hooking mortalities and sublethal effects may shift the age class structure and eliminate larger age classes from a population (Chapter 3).

Fish Introductions.

Fishery managers introduced several non-native species to the Rangeley Lakes region with great and unanticipated impacts on native brook trout since the 1800s. Landlocked Atlantic salmon were introduced into the Rangeley Lakes in 1875 (Ritzi 1968; Sherrifs 1995; Karas 1997) and the Androscoggin (below Umbagog Lake; Figure 1.1) in 1880 (American Angler 1890; Boucher 2005). Smelt (*Osmerus mordax*) were introduced in 1891 to provide forage for landlocked salmon (Sherrifs 1995; Karas 1997; Boucher 2005). Pickerel (*Esox niger*) were introduced (sometime before 1883) into Umbagog Lake (Rich 1883; Ritzi 1968), brown bullhead (*Ameiurus nebulosus*) in 1900 (Ritzi 1968), and lake trout (*Salvelinus namaycush*) (sometime before 1905) into the Richardson Lakes (Sherrifs 1995; Karas 1997; Boucher personal communication). Yellow perch (*Perca flavescens*) were introduced around 1953 into a tributary to

Rangeley Lake (Ritzi 1968), and most recently smallmouth bass (in the early 1980s) into southern Umbagog Lake (Boucher 2005).

Coinciding with the introduction of salmon and subsequently smelt; blueback trout (*Salvelinus alpinus spp.*, a.k.a. *Salvelinus oquassa*) disappeared from the Rangeley Lakes region and were considered extinct by 1905 (Nile 1948; Ritzi 1968; Sherrifs 1995; Karas 1997, Bonney 2006). Blueback trout, now found in only 11 Maine waters, once existed in the Rangeley Lakes in tremendous numbers (Nile 1948; Kircheis 1980; Karas 1997). In the Rangeley Lakes, brook trout historically foraged on blueback trout; this prey base is hypothesized to have supported great growth, resulting in “legendary sizes” (Karas 1997; Bonney 2006). Kendall (1918) ...The disappearance of blueback trout likely forced brook trout to shift their diets to smaller prey items subsequently limiting their growth potential.

Early anecdotal evidence suggests these numerous introductions affected brook trout rapidly and precipitously. J. G. Rich (1883) expressed concern for the brook trout in the Rapid River, stating that after introduced, pickerel “filled the lake... and now run up the Rapid River clear to the dam”. In “Tales of the Rangeley Lakes”, Nile (1948) stated that wherever salmon were planted, the brook trout “seemed to be diminishing”. After a ten year assessment of the Rangeley fishery, and the introduction of both Atlantic salmon and yellow perch, Ritzi (1968) concluded that salmon had replaced brook trout as the dominant fish species. Large brook trout were to be considered a rarity. Interestingly, he asserted that brook trout populations in the Rangeley’s suffered from the yellow perch introduction, not the salmon.

Introduction of competing fish species (Dunham et al. 2002; Peterson and Fausch 2003; NCWRC 2003; Dunham et al. 2004) is recognized as one of the primary threats to native brook trout populations across their native range (Hudy et al. 2006). Of the seven nonnative fish that were introduced into the Rangeley Lakes, landlocked Atlantic salmon, pickerel, yellow perch, and smallmouth bass are still present and self-sustaining in the Rapid River (Murphy 2005). Each of these four introduced species is likely to impact brook trout in this system.

Chain pickerel may compete with brook trout for habitat, but their impact through predation is more significant (Warner et al. 1968; Brokaw 2001). Where brook trout and yellow perch co-occur, brook trout growth rate is reduced and survival is poor (Eschmyer 1938; Fraser 1978). These effects can be observed even when total yellow perch biomass is small (<5% of total fish biomass; Flick & Webster 1992), though the mechanism is poorly characterized.

Atlantic salmon and brook trout directly compete for habitat at many life history stages (Gibson 1973; Bley 1986; Sayers 1990; Murphy 2006). In the presence of landlocked Atlantic salmon, juvenile brook trout shift their habitat use and consequently suffer a decrease in growth (Bley 1986). Such a shift has been observed in other displaced species (Morse 1974; Fausch and White 1981). Spatial overlapping of spawning by brook trout and Atlantic salmon also occurs in the Rapid River (Murphy 2006). In 2003-2005, divers observed brook trout and landlocked Atlantic salmon utilizing the same habitats in the Rapid River for spawning (Murphy 2006). Extensive superimposition of brook trout redds by Atlantic salmon was documented and may significantly affect brook trout recruitment (Boucher 2005).

Of the non-native fish introductions, the establishment of a smallmouth bass population has been the most publicized and feared (Boucher 2005; Carpenter 2005; Sherwood 2005; Shirley 2006; Bonney 2006). Little information on bass-salmonid interactions and competition is available in the Rapid River. However, introduced smallmouth bass actively prey on native salmonids in other systems. Reiman et al. (1991) estimated that smallmouth bass in the Columbia River were responsible for 9% of fish predation on juvenile salmonids near the John Day Dam. Similarly, smallmouth bass consumed 7% of juvenile fall Chinook salmon (*Oncorhynchus tshawytscha*) in the Lower Granite Reservoir of the Snake River (Angela 1997). The potential for predation by smallmouth bass is highest when juvenile salmonids utilize littoral areas that overlap the preferred habitat of smallmouth bass (Gray & Rondorf 1986). During spring and early summer, when their habitat use overlaps with that of smallmouth bass, juvenile salmonids made up 59% of smallmouth bass diet and were present in 65% of the stomachs of smallmouth bass in the Columbia River (Tabor et al. 1993). In the Rapid River, brook trout emerge in early spring and rear in littoral areas (Murphy 2006). This overlap with smallmouth bass may make brook trout particularly vulnerable to predation (Munther 1970).

Timber Harvest and Log Driving. The harvesting of forest products drove much of the habitat degradation of the Rangeley region. Agricultural impacts (land clearing) were initially modest for early European settlements. Timber harvests were small as logging was confined to winter when the ground was frozen. With the advent of mechanized timber harvest and increased demands from urban areas in the 1940s, year

round cutting was established (Shirrefs 1995). Cutting changed the landscape and the waterways through which logs were moved to reach mills down river. Timber harvesting resulted in increased fires and sediment loads, widespread erosion, and exacerbated flooding (Verry et al. 1983).

Log driving is a means of log transport that makes use of a river's current to move floating logs downstream. This practice forcibly changed the lakes and rivers throughout the Rangeley Lakes system. Timber harvested in the Rangeley Lakes region would be "driven" through the river-lake system, down the Rapid River, and eventually to sawmills located on the Androscoggin River (Figure 1.2). Log driving scoured the river's bottom, removing naturally occurring structures, increased the river's width and reduced natural sinuosity. The resulting river habitat had less diverse channels, fewer pools, and wide shallow streambeds (Karas 1997; Bonney 2006). Spawning grounds utilized by brook trout were often scoured out by log driving or smothered by silt and debris flowing down the river. The last log drive on the Rapid River occurred in 1951 (Sherrifs 1995).

The timber industry also shaped the ecology of the region by building dams. These structures limited previously available rearing and spawning habitat for brook trout. Middle Dam and Lower Dam (Figure 1.1) are the lowermost dams on the Rangeley Lakes built in 1851 (Sherrifs 1995; Karas 1997). The dams were built to intentionally enlarge the lakes of the Rangeley's, including Pond in the River, to produce large bodies of water over which logs could be floated in great numbers during the log drives (Sherrifs 1995). Brook trout were able to spawn successfully in the short, tail water rapids below each reservoir (Karas 1997) but eventually beds were scoured out and no longer suitable for spawning.

These impoundments eliminated connectivity between these regions for more than 150 years. Middle dam is currently owned by Florida Power and Light Energy and functions as a hydropower generating dam. A fish ladder was added at Middle dam in 1957 (Ritzi 1968) but it was ineffective. The fish ladder was removed from Middle dam in 1968 (Boucher personal communication) and there are no plans to rebuild. While the current impassable dam is believed to prevent upstream movement of the non-native smallmouth bass into the other Rangeley waters, brook trout are also prevented from reaching previously accessible habitats.

Lower Dam was heavily damaged by a major log jam and decommissioned in 1940 (Sherrifs 1995) becoming passable to brook trout. The dam remained, in parts, in the river until 2005. In 2005, the last remnants of the impoundment were removed through a grant from Rangeley Lakes Heritage Trust.

The Rapid River remains a highly manipulated system. Water flow in the Rapid River is controlled at Middle Dam and provides water to a variety of downstream industrial and municipal interests. Water levels on Umbagog Lake are maintained during the loon nesting period (June – July). Flow through Middle Dam is maintained at low levels (approximately 8.5 to 14 m³/sec) during August and September except for two-day periods during which flows are increased 3-fold (to 42 m³/sec) within a 12 hour period. This extreme change in flow is orchestrated to provide white water rapids for kayakers and rafters and is a greater and more rapid change than would occur naturally with rain.

Such artificial fluctuations in discharge are likely to negatively impact brook trout in the Rapid River. Growth and survival have been demonstrated to be reduced in rainbow trout (*Oncorhynchus mykiss*), Atlantic salmon (*Salmo salar*), and brown trout

(*Salmo trutta*) experiencing similar fluctuations (Jensen & Johnson 1999; Fausch et al. 2001). For brook trout, summer survival of young of the year is strongly influenced by ground water levels and river discharge (Latta 1965). Coble (1961) found that at decreased water levels, water velocity and dissolved oxygen concentrations also decreased resulting in an overall decrease of survival of brook trout eggs to hatching.

Flow fluctuation at Middle Dam can also indirectly affect brook trout by influencing the thermal regime. Low flows in the Rapid River during the summer months are associated with large daily water temperatures fluctuations, with peak temperatures of 27°C measured in 2006 (Chapter 2, Jackson & Zydlewski, submitted), higher than the lethal limit for brook trout (Fry et al. 1946). Rapid River brook trout move to thermal refuges in Pond in the River and Umbagog Lake where they remain throughout the summer until waters temperatures decrease (Chapter 2, Jackson & Zydlewski, submitted). When thermal refuges are limited, brook trout may crowd into such areas and may increasingly suffer from physiological and competitive stress, becoming more vulnerable to diseases, predation, and, ultimately, further population decline (Zalewski et al. 1985). Brook trout may also be less competitive with co-occurring non-native species at sub-optimal temperatures (Raleigh 1982).

Additional manipulations to the water flow in the Rapid River are likely. In 2005, Kleinschmidt, Inc., in collaboration with Trout Unlimited, Maine Department of Inland Fisheries and Wildlife, Florida Power and Light Energy, and the Rapid River Coalition, initiated studies to evaluate the feasibility of manipulating flow velocities in the Rapid River during key smallmouth bass life history periods as a means of reducing smallmouth bass recruitment and growth. The goal of this effort is to identify target flow pulses that

can be released from Middle Dam that could directly impair smallmouth bass fry survival without threatening brook trout production.

Rapid River brook trout-looking to the future

Rapid River brook trout have survived many direct and indirect anthropogenic challenges. Some of these impacts such as the introduction of non-native fish species, extirpation of blueback trout and habitat alteration are irreversible. The introduction of smallmouth bass poses a significant threat to Rapid River brook trout through predation interactions.

Climate change will not favor this cold water species. The distribution and performance of brook trout is strongly governed by temperature as discussed above. Global climatic change (Hengeveld 1990), will likely affect distributions of coldwater fish species and may shift geographic distributions of some species northward and to higher altitudes (Magnuson et al. 1990; Meisner 1990; Shuter and Post 1990). Climate models predict average air temperatures will increase 1.25 – 5.2°C by 2100 (IPCC 2001). New England climate models predict similar increases (NERA 2001). Winter and early spring temperatures are expected to change the most, having already increased an average of 0.75°C in the last century (NERA 2001). As water temperatures increase, abundance of brook trout will decline and distribution will shift northerly (Meisner 1990, Schuter and Post 1990, Eaton and Scheller 1996). In systems whose temperatures already approach the brook trout's upper thermal preference or tolerance, such as occurs in the Rapid River system, extirpation may be possible.

Other threats to Rapid River brook trout, however, can be mitigated. Harvest impacts have been eased by strong management actions, including the restriction of angling to C&R fly-fishing-only. The tremendous summer flow fluctuations and associated increases in river water temperatures remains a significant impact that reflects a choice in management. With less erratic water regulation, brook trout would be subjected to lower thermal fluctuations. The future of the Rapid River brook trout will be determined how this species responds to both the influences of the past and their protection in the future.

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References

- Angela, S. A. 1997. Abundance and food habits of smallmouth bass and distribution of crayfish in Lower granite Reservoir, Idaho – Washington. Master's Thesis. University of Idaho, Moscow.
- Bartholomew, A., and J. A. Bohnsack. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries*. 15:129–154.
- Behnke, R.J. 1980. A systematic review of the genus *Salvelinus*. In: Balon, E.K. *Charrs Salmonid Fishes of the Genus Salvelinus*. The Hague: Junk, pp. 441–480.
- Bjornn, T. C. 1971. Trout and Salmon Movements in Two Idaho Streams as Related to Temperature, Food, Stream Flow, Cover, and Population Density. *Transactions of the American Fisheries Society*: Vol. 100, No. 3 pp. 423–438
- Bley, P. W. 1986. Seasonal habitat selection of juvenile brook trout (*Salvelinus fontinalis*) and landlocked Atlantic salmon (*Salmo salar*) in streams: evidence of competition. M. S. Thesis, University of Maine.
- Bonney, F. 2006. Maine brook trout: biology, conservation, and management. Maine Department of Inland Fisheries and Wildlife. Augusta, Maine.
- BOUCHER, D. P. 2000. RAPID RIVER FISHERY MANAGEMENT. JOBS F-104 AND F-103. PROGRESS REPORT SERIES NO. 1. MAINE DEPARTMENT OF INLAND FISHERIES AND WILDLIFE. AUGUSTA, MAINE.
- Boucher, D. P. 2005. Rapid River and Pond in the River fishery investigations. Fishery Progress Report Series No. 05-1. Maine Department of Inland Fisheries and Wildlife. Augusta, Maine.
- Clark, R. D., G. R. Alexander, and H. Gowning. 1981. A History and Evaluation of Regulations for Brook Trout and Brown Trout in Michigan Streams. *North American Journal of Fisheries Management*: Vol. 1, No. 1 pp. 1–14
- Cooper, E. L. 1952. Rate of Exploitation of Wild Eastern Brook Trout and Brown Trout Populations in the Pigeon River, Otsego County, Michigan. *Transactions of the American Fisheries Society*: Vol. 81, No. 1 pp. 224–234
- Cooper, E. L. 1967. Growth and Longevity of Brook Trout (*Salvelinus fontinalis*) in Populations Subjected to Light Exploitation. *Transactions of the American Fisheries Society*: Vol. 96, No. 4 pp. 383–386
- Curry, R. A. & D. L. G. Noakes. 1995. Groundwater and the selection of spawning sites by brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic*

- Sciences. 52: 1741-1749.
- Curry, R. A., and W. S. MacNeill. 2004. Population-level responses to sediment during early life in brook trout. *Journal of the North American Benthological Society* 23: 140-150.
- Darimont et al. 2009. *Proceedings of the National Academy of Sciences*. vol. 106 no. 3.
- Eaton, J. G., and R. M. Scheller. 1995. Effects of climate warming on fish thermal habitat in streams of the United States. Duluth, MN: U.S. Environmental Protection Agency, Mid Continent Ecology Division.
- EPA 2002. Quality Criteria for Water 2002, US Environmental Protection Agency, Washington. D.C. EPA 440/5/-02-001.
- Eschmeyer, R. W. 1938. Experimental Management of a Group of Small Michigan Lakes. *Transactions of the American Fisheries Society*: Vol. 67, No. 1 pp. 120-129
- Everhart, W. H. 1976. Fishes of Maine. Maine Department of Inland Fish and Game, Augusta, Maine (4 th Edition 1976, 3 rd Ed. 1966, 2 nd Ed. 1958, 1 st Ed. 1950).
- Fausch, K. D. Taniguchi, Y. Nakano, S. Grossman, G. D. Townsend, C. R. 2001. Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. *Ecological Applications* Vol. 11, No. 5 : 1438-1455.
- Fausch, K. D., and R. J. White. 1981. Competition between brook trout and brown trout for positions in a Michigan Stream. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1220-1227.
- Flick, W. A., and D. A. Webster. 1992. Standing Crops of Brook Trout in Adirondack Waters before and after Removal of Non-trout Species. *North American Journal of Fisheries Management*: Vol. 12, No. 4 pp. 783–796
- Fraser, J. M. 1978. The Effect of Competition With Yellow Perch on the Survival and Growth of Planted Brook Trout, Splake, and Rainbow Trout in a Small Ontario Lake. *Transactions of the American Fisheries Society*: Vol. 107, No. 4 pp. 505-517
- Fry, F. E. J., J. S. Hart, and K. F. Walker. 1946. Lethal temperature relations for a sample of young speckled trout (*Salvelinus fontinalis*). University of Toronto Studies, Biological Series 54. (Publication of the Ontario Fisheries Research Laboratory 66: 9-35.
- Gibson, R. J. 1973. Interactions of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*). pp.181-202. In: Proc. Int. Atl. Salmon Symposium.

- St. Andrews, N. B. 1972. Int. Atl. Salmon. Found. Spec. Publ. 4.
- Greenely, J. C. 1978. Stream flow investigations: stream resource maintenance flow determinations on Idaho streams. Project Report F-69-R-3. Idaho Department of Fish & Game.
- Griffith, J. S. 1972. Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarkii*) in small streams in Northern Idaho. Journal of the Fisheries Research Board of Canada. 29(3):265-273.
- Harshberger, T. J. 1975. Factors affecting regional trout stream productivity in USDA (U.S. Department of Agriculture) Forest Service, Southeastern Forest Experimental Station, Proceedings of the Southeastern Trout Resource: Ecology and Management Symposium, Asheville, North Carolina, p. 11-27.
- Hengeveld, H. D. 1990. Global Climate Change: Implications for Air Temperature and Water Supply in Canada. Transactions of the American Fisheries Society: Vol. 119, No. 2 pp. 176-182.
- Hendry, A.P., Bohlin, T., Jonsson, B., Berg, O.K. (2004). To Sea or Not to Sea? Anadromy Versus Non-anadromy in Salmonids. In Evolution Illuminated: Salmon and Their Relatives (Hendry, A.P. & Stearns, S.C., eds.), pp. 93-125. Oxford University Press, New York.
- Hokanson, K. E. F., J. H. McCormick, B. R. Jones & J. H. Tucker. 1973. Thermal requirements for maturation, spawning and embryo survival of brook trout, *Salvelinus fontinalis*. Journal of Fish. Res. Board of Canada. 30:975-984.
- Hudy, M., T. M. Thieling, N. Gillespie, and E. P. Smith. 2006. Distribution, status and threats to brook trout within the eastern United States. Eastern Brook Trout Joint Venture.
- Houghton, J. T. 2001. Climate Change 2001 the scientific basis. Geneva, Switzerland: International Panel on Climate Change.
<http://www.grida.no/climate/ipcc%5Ftar/wg1/index.htm>.
- Jensen, A. J., and B. O. Johnson. 1999. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and Brown Trout (*Salmo trutta*). Functional Ecology 13: 778.
- Josephson, D. D., and W. D. Young. 1996. Association between emigration and age structure in populations of brook trout (*Salvelinus fontinalis*) in Adirondack lakes. Canadian Journal of Fisheries and Aquatic Sciences 53:534-541.
- Kahl, J. S., and M. Scott. 1994. The aquatic chemistry of Maine high elevation lakes, 1986-89: Results from the HELM Project. Final Report. Maine Department of

- Environmental Protection. 61p.
- Karas, N. 1997. Brook trout. Lyons and Buford, New York.
- Keenleyside, M. H. A. 1962. Skin-diving observations of Atlantic salmon and brook trout in the Miramichi River, New Brunswick. *Journal of Fisheries Resources Board of Canada*. 19:625-634.
- Kendall, W. C.. 1918. The Rangeley Lakes Maine: With special reference to the habits of the fishes, fish culture, and angling. Document No. 861, *Bulletin of the Bureau of Fisheries*, Volume XXXV, 1915-16. U.S. Department of Commerce.
- Kircheis, F. W. 1980. The landlocked charrs of Maine: the sunapee and blueback. *In* Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk bv Publishers, The Hague, The Netherlands, pp. 749-755.
- Latta, W. C. 1965. Relationship of young-of-the-year trout to mature trout and groundwater. *Transactions of the American Fisheries Society* 94:32-39.
- MacCrimmon, H. R., and J. C. Campbell. 1969. World distribution of brook trout, *Salvelinus fontinalis*. *Journal of Fisheries Resources Board of Canada*. 26: 1699-1725.
- MacCrimmon, H.R. and B.L. Gots, 1980. Fisheries for charrs. *In* Charrs: salmonid fishes of the genus *Salvelinus*, edited by E.K. Balon. The Hague, Dr W. Junk bv. Publishers, pp. 797-839.
- Magnuson, J. J., J. D. Meisner, and D. K. Hill. 1990. Potential changes in the thermal habitat of great lakes fish after global climate warming. *Transactions of the American Fisheries Society*: Vol. 119, No. 2 pp. 254-264
- McCormick, J. M., K. E. F. Hokanson & B. R. Jones. 1972. Effects of temperature on growth and survival of young brook trout, *Salvelinus fontinalis*. *J. Fish. Res. Board. Can.* 29:1107-1112.
- Meisner, J. D. 1990. Effect of climate warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. *Journal of the Fisheries Research Board of Canada* 24:1425-1459.
- Menendez, R. 1976. Chronic effects of reduced pH on brook trout *Salvelinus fontinalis*. *Journal of Fisheries Resources Board of Canada*. 33:118-123.
- Morse, D. H. 1974. Niche breadth as a function of social dominance. *American Naturalist* 108: 818-830.
- Mount, D. R., C. G. Ingersoll, D. D. Gulley, J. D. Fernandez, T. W. LaPoint, and H. L.

- Bergman. 1988. Effort of long-term exposure to acid, aluminum, and low calcium on adult brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1623-1632.
- Murphy, K. 2006. FPL Energy Maine Hydro LLC Rapid River fishery assessment for the upper and middle dams storage project, FERC no. 11834-000. Lewiston, Maine.
- North Carolina Wildlife Resources Commission (NCWRC). 2003. Brook trout management in North Carolina: supplement to a plan for management of North Carolina's trout resources. North Carolina Wildlife Resources Commission, Raleigh, North Carolina.
- NERA (New England Regional Assessment). 2001. Preparing for a Changing Climate. The New England Regional Assessment Overview. U.S. Global Change Research Program, University of New Hampshire, Durham, NH. Available online at <http://www.necci.sr.unh.edu/2001-NERA-report.html>
- Nile, L. 1948. *Tales of the Rangeley Lakes*. The Knowlton & McLeary Co. Farmington, Maine.
- Peckenham, J.M., Kahl, J.S., Mower, B. 2003. Background mercury concentrations in river water in Maine, U.S.A. *Environmental Monitoring and Assessment* 89: 129-152.
- Peterson, D. P., and K. D. Fausch. 2003. Upstream movement by nonnative brook trout (*Salvelinus fontinalis*) promotes invasion of native cutthroat trout (*Onchorhynchus clarki*) habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 60(12): 1502-1516.
- Post J. R., C. Mushens, A. Paul, and M. Sullivan. 2003. Assessment of alternative harvest regulations for sustaining recreational fisheries: model development and application to bull trout. *North American Journal of Fisheries Management*: Vol. 23, No. 1 pp. 22-34
- Power, G. 1980. The brook charr, *Salvelinus fontinalis*. In *Charr: salmonid fishes of the genus Salvelinus*. Dr. W. Junk bv Publishers, The Hague, The Netherlands, pp. 141-203.
- Raleigh, R. F. 1982. Habitat suitability index models: Brook trout. U.S. Department of the Interior, Fish and Wildlife Service. FWS/Obs-82/10.24. p.42.
- Reiman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 111: 255-266.

- Rich, J. G. 1883. The trout of Maine waters. *The American Angler*. IIL: 227-230.
- Ricker, W. W. 1934. Studies of speckled trout (*Salvelinus fontinalis*) in Ontario. University of Toronto, Student Biological Services. 36 *Publ. Ont. Fish. Res. Lab.* 44:67-110.
- Ritzi, C. F. 1968. The Rangeley Lakes and the management of their salmon and trout fisheries. *Maine Fish and Game*. 10:4-8.
- Romig, G. P. 1990. Habitat use and selection by juvenile salmonids in New Hampshire and Vermont streams. M. S. Thesis, University of Maine.
- Ryther, J. H. 1997. Anadromous brook trout: biology, status and enhancement. Trout Unlimited, Inc. pp. 34.
- Sherrifs, H. P. 1995. The Richardson Lakes: Jewels in the Rangeley chain. Bethel Historical Society. Bethel, Maine.
- Shutter, B. J., and J. R. Post. 1990. Climate, population viability and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* 119:316-336.
- Tabor R. A., R. S. Shively, and T. P. Poe. 1993. Predation on juvenile salmonids by smallmouth bass and northern squawfish in the Columbia River near Richland, Washington. *North American Journal of Fisheries Management*: Vol. 13, No. 4 pp. 831-838
- Verry, E. S., J. R. Lewis, and K. N. Brooks. 1983. Aspen clearcutting increases snowmelt and storm flow peaks in north central Minnesota. *Winter Resources Bulletin* 19(1):59-67.
- Warner, K., R. P. Auclair, S. E. DeRoche, K. A. Havey, and C. F. Ritzi. 1968. Fish predation on newly stocked landlocked salmon. *Journal of Wildlife Management*. 32(4): 712-717.
- Warner, K. 1970. Age and growth of brook trout, *Salvelinus fontinalis*, in some northern Maine streams. *Copeia* 2: 358-360.
- Webster, D. A. & G. Eiriksdottir. 1976. Upwelling water as a factor influencing choice of spawning sites by brook trout (*Salvelinus fontinalis*). *Trans. Amer. Fish. Soc.* 105:416-421.
- Zalewski M., P. Frankiewicz, and B. Brewinska. 1985. The factors limiting growth and survival of brown trout, *Salmo trutta m.fario* L. introduced to different types of streams. *Journal of Fish Biology*. 27:59 – 73.

Chapter 2

SUMMER MOVEMENTS OF SUB-ADULT BROOK TROUT, LANDLOCKED ATLANTIC SALMON, AND SMALLMOUTH BASS IN THE RAPID RIVER, MAINE

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. Fish were captured by angling, surgically implanted with a radio transmitter, 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 temperatures rose above 25 °C, near the reported lethal limits for these cold water species. In contrast, the majority of smallmouth bass (68%), a warm water species, did not make long distance movements (< 1km) from areas of initial capture, remaining in main stem 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*) are a cold water 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 (Figure 2.1) is one of Maine's premier wild brook trout recreational fisheries (Boucher 2005; Bonney 2006). Juvenile recruitment data (Boucher 2005) and observations by anglers suggest a decline in brook trout abundance since 1998. This decline has been coincident with illegal introduction of a warm water species, smallmouth bass (*Micropterus dolomieu*), in Umbagog Lake (Figure 2.1) during the mid-1980s (Boucher 2005). Over the past 10 years, smallmouth bass have become abundant, expanding their range into the Rapid River and Pond in the River (Figure 2.1).

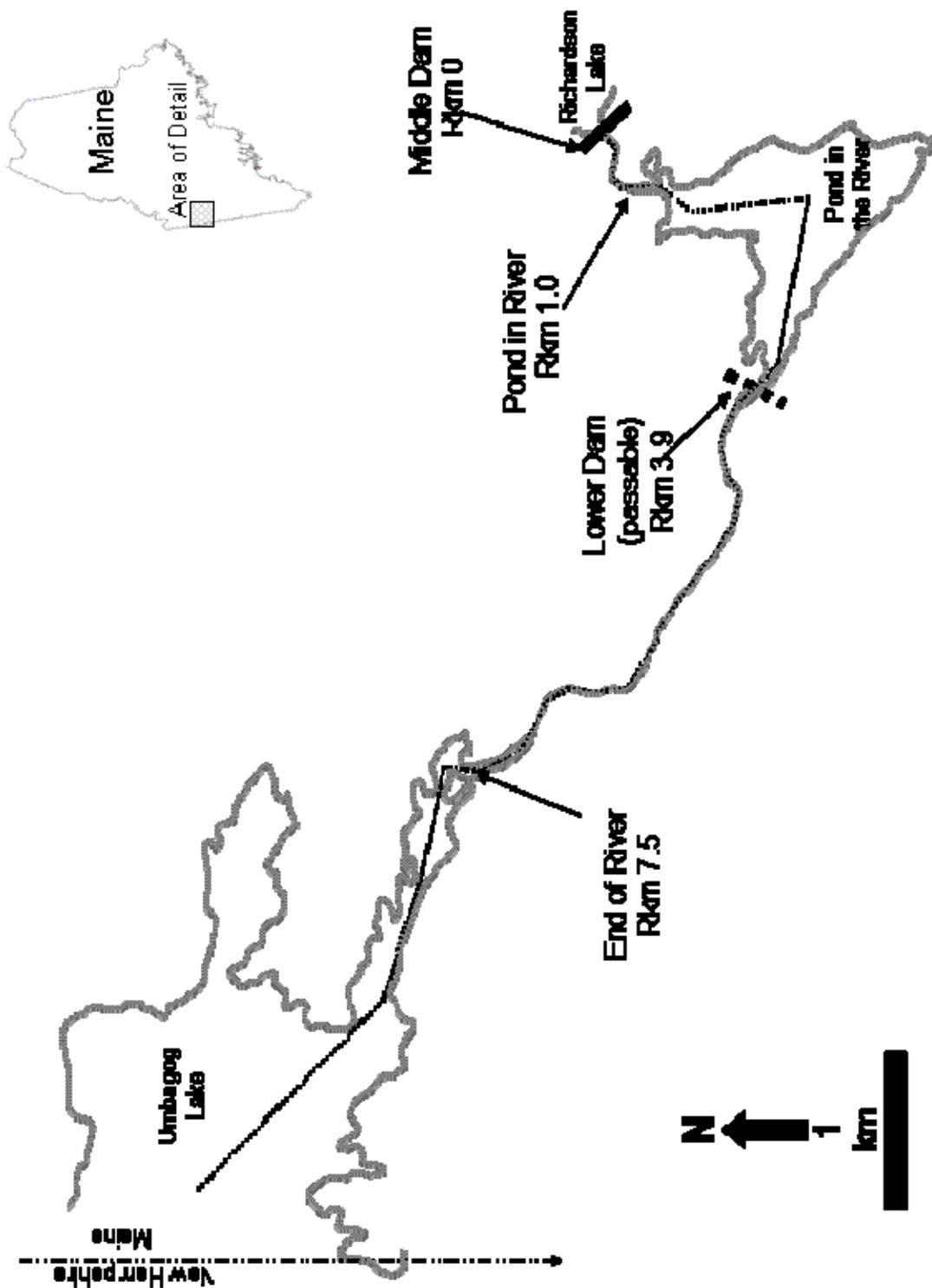


Figure 2.1. Rapid River, Maine, study area. The dotted line is the reference centerline used to calculate “river kilometer” as a descriptor of movement.

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 affect on salmonid populations (Lachner 1950; Warner et al. 1968; Martin and Fry 1972). Predation effects 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*) were introduced to the Rapid River system in 1875 (Ritzi 1968; Sherrifs 1995; Karas 1997). Although these fish provide 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 temperatures are greater and flows in this regulated system are 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 in the Rapid River with radio telemetry.

Methods

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 (Figure 2.1). The Rapid River encompasses Pond in the River and flows through Middle and Lower Dams. Middle Dam is a hydropower generating facility without fish passage, and Lower Dam was removed from the river in August 2005, during this study.

Physical characteristics of Rapid River

Daily water temperature and discharge data were collected by Florida Power Light and Energy (FPLE). Flow data were collected at Middle Dam. A HOBO TempTM 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, landlocked Atlantic salmon, and smallmouth bass were angled 20-22 June 2005 at five sites along the Rapid River (Figure 2.2). Water temperatures ranged

I 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) (Table 2.1). Sub-adults were defined *a priori* as 40-260 g. No fish < 40g 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 Betadine (10% povidone-iodine) and an incision of ~ 12 mm in length was made through the skin and peritoneal wall with a sterilized scalpel. 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 sutured with 5-0 coated Vicryl absorbable sutures (Ethicon, Inc., Somerville, New Jersey). The surgical procedure took less than 3 minutes to complete. Both the wound and exit site of the antenna were swabbed with Betadine prior to the fish being allowed to recover in aerated source water. Tagged fish were allowed to recover until normal swimming behavior was observed and then released in slow flow near the capture site.

Table 2.1 – Mean and range (min-max) fork lengths (mm), masses (g), and radio tag type implanted in sub-adult brook trout (BKT), landlocked Atlantic salmon (LLS), and smallmouth bass (SMB) in 2005. NTC-4-2S corresponds to the small tag (battery life ~ 45 days) and NTC-4-2L corresponds to the large tag (battery life ~90 days).

Species	Tag Type (n)	Fork Length (mm)	Mass (g)
BKT	Small 13	209 (158 - 274)	121.5 (45.5 - 244.7)
	Large 14	289 (182 - 280)	153.5 (69.6 - 259.8)
LLS	Small 10	237 (136 - 294)	181.1 (45.3 - 260)
	Large 14	260 (192 - 299)	187.4 (90.3 - 257.8)
SMB	Small 13	175 (145 - 252)	82.8 (43 - 256.2)
	Large 9	260 (182 - 262)	134.1 (87.2 - 262.3)

Radio tracking

For the life of the tags (approximately 45 and 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, primarily on the northern bank, 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. Positions of tagged fish were estimated by maximizing signal strength from at least two

vantages and a compass bearing. Georeferenced locations (± 1 m) were obtained at each vantage using a Global Positioning System (GPS) unit (Garmin 12XL). Locations were accurate within 20 m² (based on the successful relocation of hidden transmitters before this study).

Age determination

Age classes of tagged fish were estimated by scale impression analysis (Smith 1954). Scale samples were pressed onto cellulose acetate, 0.51 mm thick, with the use of a heated hydraulic press (100 °C, 2300 kg). Scale impressions were projected on a microfiche screen and annuli were identified according to criteria specified by Jearld (1983). Age classes of tagged fish were estimated, independently, by 2 readers. When there was disagreement between the 2 readers (12/76), the scale was examined by a third. When there was disagreement by 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 (Figure 2.1). 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.

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, condition factor 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 – 31 August, 2005. Significance of statistical analyses are reported at the $p < 0.05$ level.

Results

In summer 2005, movement patterns of sub-adult brook trout ($n = 27$), sub-adult landlocked Atlantic salmon ($n = 24$), and sub-adult smallmouth bass ($n = 22$) were documented. Fish were tagged and released in the river (Figure 2.2; a, c and e for each species). No attempt was made to capture fish from either Pond in the River or Umbagog Lake.

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

Brook trout movements

Over the 3-month study, 96% of the radio-tagged sub-adult brook trout (23/24) made large movements (>1 km) with only one fish remaining within a kilometer of its initial release (Figure 2.3). 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 site of their initial release and 42% (n = 10) of them left the mainstem sections of the river entirely and could be found in Pond in the River or Umbagog Lake (Figure 2.2). Movement declined during mid-summer. Brook trout were observed in Pond in the River (58%, n = 14) and Umbagog Lake (21%, n = 5) 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 relocation event, 16 September, three brook trout had moved back into the river.

For fish successfully relocated during early summer (54%, n = 13) 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).

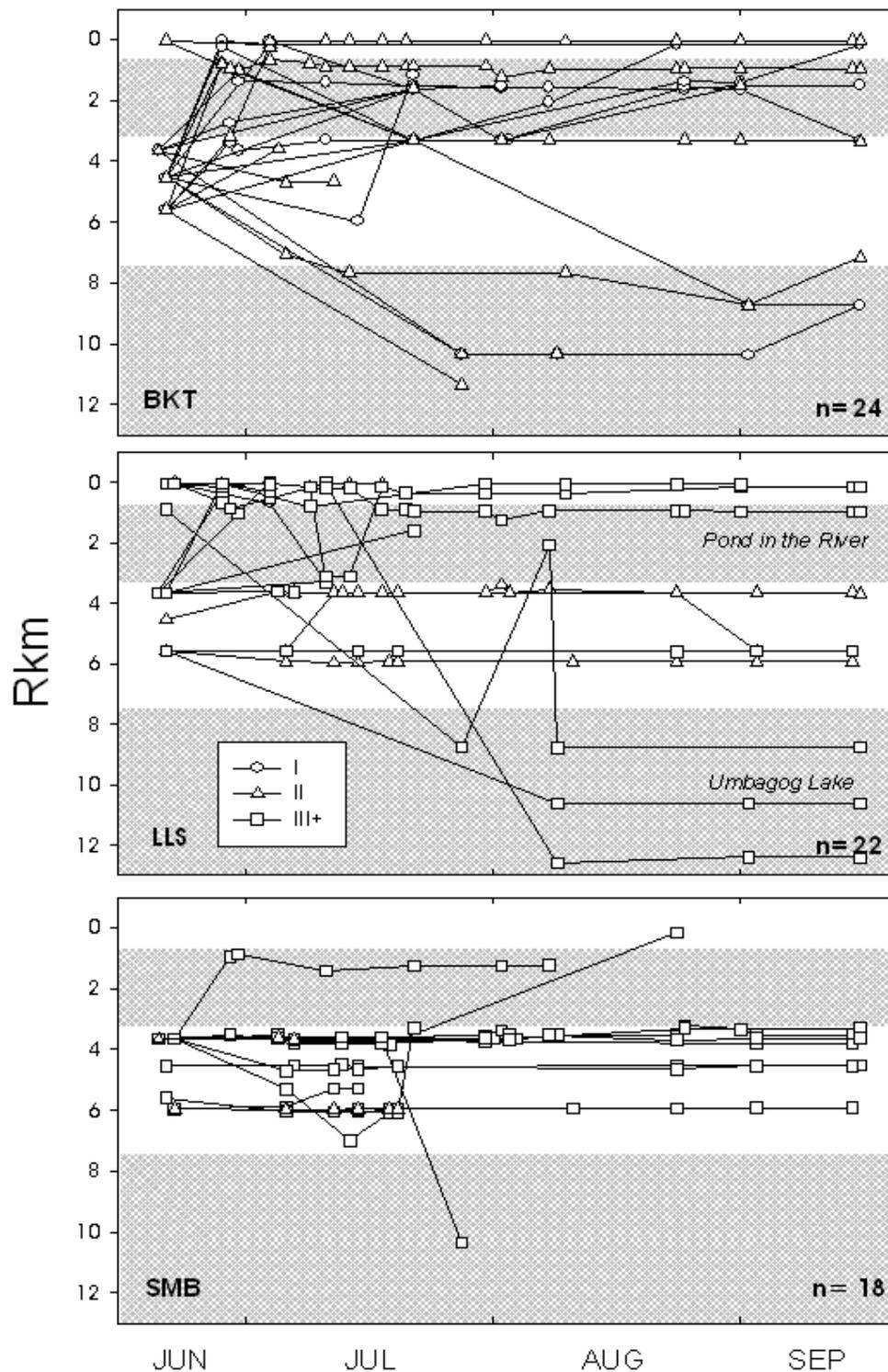


Figure 2.3. Movement data for sub-adult brook trout (BKT), landlocked Atlantic salmon (LLS), and smallmouth bass (SMB) implanted with radio tags in the Rapid River, Maine. Individual fish movements are presented over time with respect to calculated river kilometer positions. Middle Dam is defined as Rkm 0. Pond in the River and Umbagog Lake are indicated as gray shaded region.

Landlocked Atlantic salmon movements

Over the 3-month study, 72% (13/18) of landlocked Atlantic salmon made large movements (>1km). The remaining 28% (5/18) did not move more than 1 kilometer from their initial release sites. 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) of the salmon 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 relocated during this study, 67% (12/18) of salmon were observed using either Pond in the River, Umbagog Lake, or both; and 33% (6/18) of salmon remained in the mainstem sections of the river for the duration of the study.

Of the fish relocated during early summer (50%, 9/18) 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 than those traveled by smallmouth bass ($\chi^2= 19.6, P < 0.002$).

Smallmouth bass movements

Over the 3-month study, 68% (15/22) of smallmouth bass moved <1 km from the initial site of release. The remaining 32% (7/22) moved >1km (Figure 2.2 and 2.3). 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 relocated during early summer, only one smallmouth bass had moved away from the initial site of release and 28% (6/22) smallmouth bass moved from their initial site of release during mid-summer. Throughout this study, 12% (3/22) smallmouth bass were observed using either Pond in the River (2/22) or Umbagog Lake (1/22). For fish successfully relocated 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, size and condition factor

Brook trout ranged 46-260 g (Table 2.1) and were ages 1 - 2 in near equal proportions (Table 2.2). Salmon ranged 45 - 260 g, and were ages 1-5 (79% were ages 2 - 4). Smallmouth bass ranged 43-262 g and were ages 2 - 6, but the majority (73%) were age 3. Within each species, age, size, and condition did not correlate with average minimum distance traveled.

Table 2.2 – Mean fork lengths (mm), masses (g), condition factors (CF) and ages of sub-adult brook trout (BKT), landlocked Atlantic salmon (LLS), and smallmouth bass (SMB) implanted with radio tags in 2005. Values are mean (SD).

Species	Age (n)	Fork Length (mm)	Mass (g)	CF ((g/mm ³)*100,000)
BKT	I 11	176 (16)	65.7 (20.0)	1.2 (0.1)
	II 16	249 (21)	187.8 (44.1)	1.2 (0.1)
	All 27	219 (41)	138.1 (70.8)	1.2 (0.1)
LLS	I 2	183 (47)	74.9 (41.9)	1.2 (0.2)
	II 5	237 (42)	154.1 (65.1)	1.1 (0.1)
	III 10	271 (18)	213.5 (34.3)	1.1 (0.1)
	IV 4	270 (13)	195.9 (51.0)	1.0 (0.1)
	V 1	285	157.8	0.7
	Unk 2	241 (8)	218.8 (51.2)	1.6 (0.5)
	All 24	254 (36)	184.7 (59.1)	1.1 (0.2)
SMB	II 2	162 (23)	87.3 (2.1)	1.5 (0.1)
	III 16	181 (25)	92.7 (50.1)	1.5 (0.1)
	IV 1	197	93.9	1.2
	VI 1	262	262.2	1.5
	Unk 2	214 (38)	146.9 (81.8)	1.4 (0.1)
	All 22	258 (31)	186.3 (55.7)	1.1 (0.2)

Water temperature and flow

Regulated water discharge from Middle Dam fluctuated more than 3 fold over the study period, from less than 14 m³ to more than 45 m³ in one day. Periods of low flow were punctuated with periods of elevated flow through the summer. Daily river water temperatures fluctuated greatly during periods of low flow (Fig 4), ranging more than 7 °C in a 24 h period (var = 4.68). Water flow directly influenced the daily range of temperature in the river (R² = 0.14, p= 0.003). Average water temperatures 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; Figures 2.2 and 2.4). At the time that fish were tagged and released, water discharge at Middle Dam ranged 65 -80 m³. In the days immediately following tagging (June 21-June 22), water was withheld at Middle Dam and water flows declined (mean flow rate = 27 m³, range = 11 – 51 m³, var = 246) and remained lower than the initial observed range of 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 temperatures rose above 20°C.

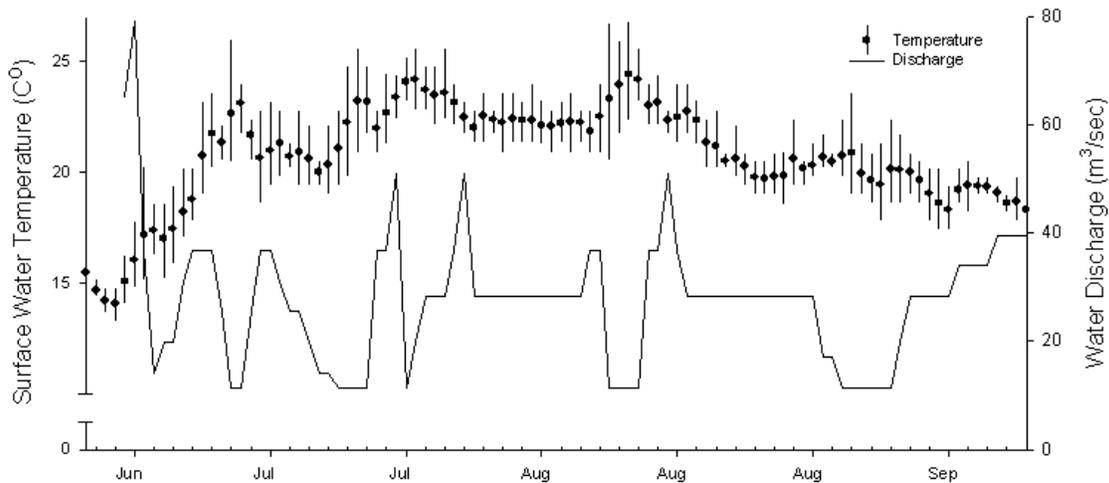


Figure 2.4. Daily water discharge (m³/sec) at Middle Dam and average daily water temperatures (°C), and range, during summer 2005.

Discussion

Brook trout movement

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 temperatures in the Rapid River had exceeded 20°C, near the lethal limit for brook trout (Fry et al 1946; McCormick et al. 1972). Brook trout will seek refuge from water temperatures above 20°C (Fry 1951; Meisner 1990; Curry et al. 1997; Biro 1998).

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 obscuring 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. Whereas discharge explained only 14 % of the variation in temperature fluctuation observed, it should be noted that flow data represented semi-quantitative point estimates, rather than integrated 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 indicate 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 movement

Landlocked 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 (Figure 2.2). 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 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 temperatures that might typically displace brook trout do not necessarily cause landlocked Atlantic salmon to move (Sayers 1990).

Only five of the 18 relocated landlocked Atlantic salmon were “sub-adult” (age I-II; Table 2.2). 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 sub-adults used either Pond in the River or Umbagog Lake and the others

moved from the initial sites of release, but remained in mainstem sections of the river. Because behaviors were consistent between sub-adults and adults, we believe that movement of landlocked Atlantic salmon was not related to developmental stage (sub-adult versus adult).

Smallmouth bass movements

In contrast to the general patterns observed for brook trout and landlocked salmon, smallmouth bass radio-tagged in the main-stem 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 tagging site. Only three individuals were observed moving into either Pond in the River or Umbagog Lake. These results are consistent with previous studies finding that smallmouth bass are a sedentary species with a small home range and, generally, do not travel long distances (Funk 1955; Munther 1977; Todd & Rabeni 1989; VanArnum 2004).

Summer water temperatures in the Rapid River were 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. This suggests that factors influencing these few movements were probably very local in scale (microhabitat) rather than a river-wide effect.

Warm water and cold water fish differ in both their optimal range, and lethal temperatures. For brook trout and landlocked Atlantic salmon, both cold water species, their optimal temperatures range 5-20°C (Power 1980) and 15 -19°C (Berg 1988), respectively. For smallmouth bass, a warm water species, the optimal temperatures range

19.4 – 21.7°C (Coble 1975). During this study, average water temperatures in the Rapid River ranged 20-25 °C. Temperature increases beyond the optimal range for any species can influence the capacity to function properly and result in diminished swimming ability (MacNutt et al. 2004), poor body condition, and reduced cardiac performance (Brett 1965; Fry 1967). Brook trout, Atlantic salmon, and smallmouth bass also differ in their upper lethal temperatures. For brook trout, landlocked Atlantic salmon, and smallmouth bass these limits are 23°C (Power 1980), 28°C (Elliot 1991), and 36.7°C (Currie et al. 1998), respectively.

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 (sub-adult versus adult).

Affect of tagging

The patterns of movement observed in these three species are unlikely to have been a result of the tagging process. In other studies, implantation of transmitters had no observable long-term effect on survival, growth, and swimming and feeding behavior in young Atlantic salmon (Moore et al. 1990) and rainbow trout (Martin et al. 1995). Healing of surgical incisions is complete within weeks, depending upon temperature (Young 1994). Transmitters in this study never exceeded 2% of body weight, as

recommended by Winter (1983). It can be assumed, however, that surgical tagging is likely to affect short term performance and may have contributed to vulnerability to predation (Adams 1998). Relocation data collected during the five days following tagging was omitted. At least one smallmouth bass is suspected to have been removed from the system by a predator.

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) were not observed using 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, affecting their daytime feeding, and 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 temperatures fall, 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 have been shown to reduce prey fish abundance (Power et al. 1985; Harvey et al. 1988) and decrease prey fish diversity in the fish community (Chapleau et al. 1997; Whittier et al. 1997) negatively affecting food resources that were once available to native salmonids. Furthermore, brook trout have been shown to be less successful in the presence of littoral species with whom they 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 remain 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 have been observed to 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 were not observed using these same deep waters. In the mainstem sections of the river landlocked Atlantic salmon did not overlap with smallmouth bass.

Conclusion

The distinct movements made by sub-adult brook trout to presumed thermal refuges suggest that these areas represent essential summer habitat for this native species. Regulated low flows in the summer months result in a greater daily temperature variation than would naturally occur. In conjunction with overall high temperatures, brook trout are precluded from residing in the river during summer months based on thermal tolerance. The potential for direct competition between landlocked salmon exists in thermal refugia, but smallmouth bass are less likely to compete directly with brook trout through these months. The evacuation of river habitat by brook trout due to thermal tolerance, however, may place these fish at a competitive disadvantage with non-native smallmouth bass and landlocked Atlantic salmon which also relocate to cooler water.

Landlocked salmon and smallmouth bass in the Rapid River system may displace native brook trout occurring in the same river reaches near their limit of thermal tolerance. Additionally, low water flow, regulated at Middle Dam, results in greater daily water temperature variation than would naturally occur during the summer months, potentially limiting habitat for brook trout in the Rapid River. A logical next step in future research should focus on (1) the effects that competition for food and space between brook trout, landlocked Atlantic salmon, and smallmouth bass may have on the Rapid River brook trout; and (2) the effects of regulated water flow on brook trout populations in the Rapid River.

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References

- Adams, N. S., D. W. Rondorf, S. D. Evans, and J. E. Kelly. 1998. Effects of surgically and gastrically implanted radio transmitters on growth and feeding behavior of juvenile chinook salmon. *Transactions of the American Fisheries Society* 127:128-136.
- Angela, S. A. 1997. Abundance and food habits of smallmouth bass and distribution of crayfish in Lower Granite Reservoir, Idaho–Washington. Master's thesis. University of Idaho, Moscow.
- Armstrong, J. D., V. A. Braithwaite, and F. A. Huntingford. 1997. Spatial strategies of wild Atlantic salmon parr: exploration and settlement in unfamiliar areas. *Journal of Animal Ecology* 66:203-211.
- Beamesderfer, R. C. P. 2000. Managing fish predators and competitors: deciding when intervention is effective and appropriate. *Fisheries* 25(6):18-23.
- Biro, P. A. 1998. Staying cool: behavioral thermoregulation during summer by young-of-year brook trout in a lake. *Transactions of the American Fisheries Society* 127:212-222.
- Bley, P. W. 1986. Seasonal habitat selection of juvenile brook trout (*Salvelinus Fontinalis*) and landlocked Atlantic salmon (*Salmo salar*) in streams: evidence of competition. Master's Thesis. University of Maine, Orono.
- Bonney, F. 2006. Maine brook trout: biology, conservation, and management. Maine Department of Inland Fisheries and Wildlife, Augusta.
- Boucher, D. P. 2005. Rapid River and Pond in the River fishery investigations. Maine Department of Inland Fisheries and Wildlife, Fishery Progress Report 05-1, Augusta.
- Bourke, P., P. Magnan, and M. A. Rodriguez. 1999. Phenotypic responses of lacustrine brook charr in relation to the intensity of interspecific competition. *Evolutionary Ecology* 13:19-31.
- Brett, J. R. 1956. Some principles in the thermal requirements of fishes. *The quarterly Review of Biology* 31:75-88.
- Chapleau, F., S. C. Findlay, and E. Szensay. 1997. Impact of piscivorous fish introductions on fish species richness of small lakes in Gatineau Park, Quebec. *Ecoscience* 4:259-268.
- Coble, D. W. 1975. Smallmouth bass. Pages 21-23 in R. H. Stroud, and H. Clepper,

- editors. Black bass biology and management. Sport Fishing Institute, Washington, District of Columbia.
- Currie, R. J., W. A. Bennett, and T. L. Beiting. 1998. Critical thermal minima and maxima of three freshwater game-fish species acclimated to constant temperatures. *Environmental Biology of Fishes* 51: 187-200.
- Curry, R. A., C. Brady, D. L. G. Noakes, and R. G. Danzmann. 1997. Use of small streams by young brook trout spawned in a lake. *Transactions of the American Fisheries Society* 126:77-83.
- Curry, R. A., D. Sparks, and J. van de Sande. 2002. Spatial and temporal movements of a riverine brook trout population. *Transactions of the American Fisheries Society* 131:551-560.
- DeSandre, R. A., C. F. Ritzi, and W. L. Woodward. 1977. Rangeley Lake fishery management. Maine Department of Inland Fisheries and Wildlife, Fisheries Research Bulletin 10:64, Augusta.
- DeSandre, R. A. 1986. Rapid River report. Maine Department of Inland Fisheries and Wildlife, Augusta.
- Dunham, J. B., S. B. Adams, R. E. Schroeter, and D. C. Novinger. 2002. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and their potential impacts on inland cutthroat trout. *Reviews in Fish Biology and Fisheries* 12:373-391.
- Dunham, J. B., D. S. Pilliod, and M. K. Young. 2004. Assessing the consequences of nonnative trout in headwater ecosystems in western North America. *Fisheries* 29(6):18-26.
- Elliot, J. M. 1991. Tolerance and resistance to thermal stress in juvenile Atlantic salmon, *Salmo salar*. *Freshwater Biology* 25:61-70.
- Fausch, K. D., and R. J. White. 1981. Competition between brook trout and brown trout for positions in a Michigan stream. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1220-1227.
- Fry, F. E. J., J. S. Hart, and K. F. Walker. 1946. Lethal temperature relations for a sample of young speckled trout (*Salvelinus fontinalis*). *Ontario Fisheries Research Laboratory* 66:9-35.
- Fry, F. E. J. 1951. Some environmental relations of the speckled trout (*Salvelinus fontinalis*). *Proceedings of the Northeast Atlantic Fisheries Conference* 1:29.
- Funk, J. L. 1955. Movement of stream fishes in Missouri. *Transactions of the American*

- Fisheries Society 85:39-57.
- Gibson, R. J. 1966. Some factors influencing the distributions of brook trout and young Atlantic salmon. *Journal of the Fishery Research Board of Canada* 23(12):1977-1980.
- Gibson, R. J. 1973. Interactions of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*). Pages 181-202 in *Proceedings of the International Atlantic Salmon Symposium*. International Atlantic Salmon Foundation Special Publication 4, St. Andrews, N. B.
- Griswold, B. L. 1967. Some aspects of the shore spawning of brook trout (*Salvelinus fontinalis*). Master's thesis. University of Maine, Orono.
- Harvey, B. C., R. C. Cashner, and W. J. Matthews. 1988. Differential effects of largemouth and smallmouth bass on habitat use by stoneroller minnows in stream pools. *Journal of Fish Biology* 33:481-487.
- Jackson, D. A. 2002. Ecological effects of *Micropterus* introductions: the dark side of black bass. *American Fisheries Society Symposium* 31:221-232.
- Jearld, Jr., A. 1983. Age Determination. Pages xx-xx in L. A. Nielsen, and D. L. Johnson editors. *Fisheries Techniques*, American Fisheries Society, Bethesda, Maryland.
- Kahler, T. H., P. Roni, and T. P. Quinn. 2001. Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1947-1956.
- Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *Salmo trutta* L.). Institute of Freshwater Research, Report 39:55-98, Drottingholm.
- Karas, N. 1997. Brook trout. Lyons and Buford, New York.
- Larson, G. L., and S. E. Moore. 1985. Encroachment of exotic rainbow trout into stream populations of native brook trout in the southern Appalachian Mountains. *Transactions of the American Fisheries Society* 114(2):195-203.
- MacCrimmon, H. R., T. A. Dickinson, and R. J. Gibson. 1983. Implications of differences in emergent times on growth and behaviour of juvenile Atlantic salmon (*Salmo salar*) and brook charr (*Salvelinus fontinalis*) in sympatric stream populations. *Naturaliste Canada* 110:379-384.
- MacNutt, M. J., S. C. Hinch, A. P. Farrell, and S. Topp. 2004. The effect of temperature and acclimation period on repeat swimming performance of cutthroat trout.

Journal of Fish Biology 65:342-353.

- MacRae, P. S. D., and D. A. Jackson. 2001. The influence of smallmouth bass (*Micropterus dolomieu*) predation, and habitat complexity on the structure of littoral-zone fish assemblages. Canadian Journal of Fisheries and Aquatic Sciences 58:342-351.
- Martin N.V. and F.E.J Fry. 1972. Lake Opeongo: Effects of exploitation and introductions on the salmonid community. Journal of Fish Research Board of Canada 29:795-805.
- McCormick, J. K., K. E. F. Hokanson, and B. R. Jones. 1972. Effects of temperature on growth and survival of young brook trout, *Salvelinus fontinalis*. Journal of the Fisheries Research Board of Canada 29: 1107-1112.
- Meisner, J. D. 1990. Effect of climate warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. Journal of the Fisheries Research Board of Canada 24:1425-1459.
- Moore A., I. C. Russell, and E. C. E. Potter. 1990. The effects of intraperitoneally implanted dummy acoustic transmitters on the behaviour and physiology of juvenile Atlantic salmon, *Salmo salar* L. Journal of Fish Biology 37(5): 713–721.
- Morse, D. H. 1974. Niche breadth as a function of social dominance. American Naturalist 108:818-830.
- Munther, G. L. 1977. Movement and distribution of smallmouth bass in the middle Snake River. Transactions of the American Fisheries Society 99:44-53.
- Murphy, K. 2006. Rapid River fishery assessment of the upper and middle dams storage project. Florida Power and Light Energy, Maine, FERC no. 11834-000, Lewiston.
- Naughton, G. P., D. H. Bennett, K. B. Newman. 2004. Predation on juvenile salmonids by smallmouth bass in the Lower Granite reservoir system, Snake River. North American Journal of Fisheries Management 24: 534-544.
- North Carolina Wildlife Resources Commission (NCWRC). 2003. Brook trout management in North Carolina: supplement to a plan for management of North Carolina's trout resources. North Carolina Wildlife Resources Commission, Raleigh.
- Peterson, D. P., and K. D. Fausch. 2003. Upstream movement by nonnative brook trout (*Salvelinus fontinalis*) promotes invasion of native cutthroat trout (*Onchorhynchus clarki*) habitat. Canadian Journal of Fisheries and Aquatic Sciences 60(12): 1502-1516.

- Pflug, D. E., and G. B. Pauley. 1984. Biology of smallmouth bass (*Micropterus dolomieu*) in Lake Sammamish, Washington. Northwest Science 58:118-130.
- Power, G. 1980. The brook charr, *Salvelinus fontinalis*. Pages 141-203 in E. Balon, editor. Charrs. Dr. Junk Publishers, The Hague, The Netherlands.
- Reiman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Transactions of the American Fisheries Society 111: 255-266.
- Ritzi, C. F. 1968. The Rangeley Lakes and the management of their salmon and trout fisheries. Maine Fish and Game report 10:4-8, Augusta.
- Romig, G. P. 1990. Habitat use and selection by juvenile salmonids in New Hampshire and Vermont streams. Master's Thesis. University of Maine, Orono.
- Sayers, R. E. Jr. 1990. Habitat use patterns of native brook trout and stocked Atlantic salmon: Interspecific competition and salmon restoration. Doctoral Dissertation. University of Maine, Orono.
- Sherrifs, H. P. 1995. The Richardson Lakes: Jewels in the Rangeley chain. Bethel Historical Society. Bethel, Maine.
- Swanberg, T. R., and D. R. Grist. 1997. Effects of intraperitoneal transmitters on the social interactions of rainbow trout. North American Journal of Fisheries Management 17: 178-181.
- Tabor, R. A., R. P. Shively, and T. P. Poe. 1993. Predation of Juvenile salmonids by smallmouth bass and northern squawfish in the Columbia River near Richland, Washington. North American journal of Fisheries management 13: 831-838.
- VanArnum, C. J. G., G. L. Buynak, and J. R. Ross. 2004. Movement of smallmouth bass in Elkhorn Creek, Kentucky. North American Journal of Fisheries Management 24: 311-315.
- Vander Zanden, M. J., J. M. Casselman, and J. B. Rasmussen. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature (London) 401: 464-467.
- Warner, K. 1956. Aroostook River salmon restoration and fisheries management. Maine Department of Inland Fisheries and Game Atlantic Salmon Commission. Fishery Research Bulletin No. 4: 66.
- Warner, K. 1970. Age and growth of brook trout, *Salvelinus fontinalis*, in some northern

- Maine streams. *Copeia* 2: 358-360.
- Warner, K., R. P. Auclair, S. E. DeRoche, K. A. Havey, and C. F. Ritzi. 1968. Fish predation on newly stocked landlocked salmon. *Journal of Wildlife Management*. 32(4): 712-717.
- Waters, T. F. 1983. Replacement of brook trout by brown trout over 15 years in a Minnesota stream: production and abundance. *Transactions of the American Fisheries Society* 112: 137-146.
- Winter, J. D. 1983. Underwater Biotelemetry. Pages 371-395 *in* L. A. Nielsen and D. L. Johnson, editors. *Fisheries techniques*. American Fisheries Society, Bethesda, Maryland.
- Young, M. K. 1994. Mobility of brown trout in south central Wyoming streams. *Canadian Journal of Zoology* 72: 2078-2083.

Chapter 3

ASSESSING THE EFFECTS OF CATCH AND RELEASE REGULATIONS ON AN ADFLUVIAL BROOK TROUT POPULATION USING AN AGE- STRUCTURED MODEL

Abstract

As populations of wild brook trout (*Salvelinus fontinalis*) decline across their native range in the North America angling regulations such as fly-fishing-only and catch and release are being used by management agencies to conserve fish while maintaining angling opportunities. Post release mortality may significantly impact age and size structure of populations. In order to assess the possible impacts of catch and release fishing on brook trout population structure, we applied data from several sources to build a deterministic population model in which age classes up to 5 years occurred. To assess the potential impact of fishing, I examined the changes in population characteristics at varying levels of angler effort (0-240 rod·hours·ha⁻¹·yr⁻¹) and post release hooking mortality rates (0-14%). A “trophy” brook trout fishery was sustainable only at low levels of angling intensity (<120 rod·hours·ha⁻¹·yr⁻¹). As angling effort increased, the proportion of older aged fish (3, 4, and 5 years old) declined significantly. At higher levels of angling effort, 4, and 5 year old fish were no longer part of the population. Increases in post release mortality rates resulted in similar declines of older age classes. The results of this simulation indicate that post release mortality rates, as might be common in catch and release fisheries, may significantly shift the age structure of a population, reducing trophy angling potential.

Introduction

Throughout their native range, many populations of brook trout (*Salvelinus fontinalis*) have been negatively effected by a combination of habitat degradation, the introduction of exotic species, and over-exploitation (Hudy et al. 2006). Today, Maine contains more than twice the number of intact subwatersheds for brook trout as the other 16 states in the eastern range combined (Hudy et al. 2006). Wild brook trout populations in Maine are declining (Hudy et al. 2006; Bonney 2006). The vast majority of large rivers that historically produced brook trout are no longer self-sustaining (Hudy et al. 2006), and the quality of the fisheries are diminished (Bonney 2006). In systems like the Rapid River in the Rangeley Lakes region of Maine, brook trout that were once renowned as “world-class” or “trophy” fisheries have now been depicted as “threatened,” “vulnerable,” or “endangered” (Hudy et al. 2006; Karas 2007; Bonney 2006; Boucher 2005).

The Rapid River is emblematic of the plight of native brook trout in Maine. The Rapid River is considered to be one of Maine’s premiere wild brook trout fisheries and contributes significantly to the region’s economy drawing in hundreds of anglers during the open water fishing season, annually (Boucher 2005). In response to this high fishing pressure, Maine Department of Inland Fisheries and Wildlife (MDIFW) has relied upon more restrictive fishing regulations (i.e. fly-fishing-only, and catch and release) to provide protection and maintain sustainability of this resource (Boucher 2005).

Management agencies have increasingly relied upon catch and release (C&R) fishing regulations to promote sustainable fisheries where the exploited populations are at risk of severe decline or collapse (Quinn 1996; Bartholomew & Bohnsack 2005; Cook

and Suski 2005). The ultimate success of this type of fishing regulation depends on ensuring high release survival rates by minimizing injury and mortality (Bartholomew & Bohnsack 2005).

Several field assessments have examined post release mortality of C&R angling on salmonids, but the results are equivocal and reported mortality rates vary greatly. Conventional wisdom of management agencies has been that fish caught on flies suffer lower mortalities rates than those caught on artificial lures or bait (Schisler & Bergensen 1996; Bachman 2000). In his review of hooking mortality literature, Wydoski (1977) reported a mean hooking mortality of fish caught on artificial flies of 4% (range 0-11.3%) and artificial lures of 6.1% (range 1.7-42.6%). A second study by Mongillo (1984), based on much of the same literature but excluded studies involving non-salmonid fish species, concluded that there was no difference in hooking mortality between trout caught on flies and lures (range 5-10%), but hooking mortality of trout caught on bait was significantly higher (30-50%). More recently, Schisler and Bergensen (1996) reported post release mortalities for rainbow trout (*Oncorhynchus mykiss*) of 3.9% (range 1-14%) for fly-caught fish, 21.6% (range 9-29%) for fish caught on artificial baits that were fished actively, and 32.1% (range 19-45%) for fish caught on artificial baits fished passively. They also concluded that the length of time played and length of time out of water contributed to mortality, as did increasing water temperatures and bleeding intensity.

Few post release hooking mortality studies reflect the effects of common angling practices on wild trout. Many involved hatchery fish (Warner 1976; Hulbert & Engstrom-Heg 1980, Schisler & Bergensen 1996), fish that were electrofished and held in

hatchery raceways (Warner & Johnson 1978). Others used fasted fish (Hulbert & Engstrom-Heg 1980), or fish intentionally allowed to swallow the bait (Mason and Hunt 1967). The limited studies comparing the hooking mortality of wild stream-caught trout on flies suggest that mortality is very low (Shetter & Allison 1955; 1958; Pavol & Klotz 1996). Other data, however, indicate that brook trout may be more sensitive to hooking mortality than other trout species (Shetter and Allison 1958; Taylor & White 1992).

In heavily fished areas, even small changes in post release mortality rates may alter the age and size structure of a fishery, truncating its natural pyramid of age classes and reducing its longevity (Longhurst 2002). Such populations have unstable population dynamics and are more vulnerable to stochastic events that could lead to a collapse of a fishery (Longhurst 2002; Anderson et al. 2008). The purpose of this work is to assess the potential impacts of C&R fishing on an adfluvial brook trout population. An individual-based brook trout population model (Power and Power 1995) was constructed to examine age class structures at increasing mortality rates as might be experienced under fly-fishing-only and C&R regulations.

Methods

Design

An individual based model was constructed using the software package STELLA[®] (Richmond 1985). Specific life history (see Figure 3.1 for a conceptual diagram) input parameters included length at age, critical life stage recruitment relations, juvenile survival, adult survival, and size-fecundity relation. The fishery component consisted of age specific vulnerability to hooking, angling effort, and post-release

hooking mortality. Data were scaled to a representative 1.0 ha. Parameters were estimated as described below.

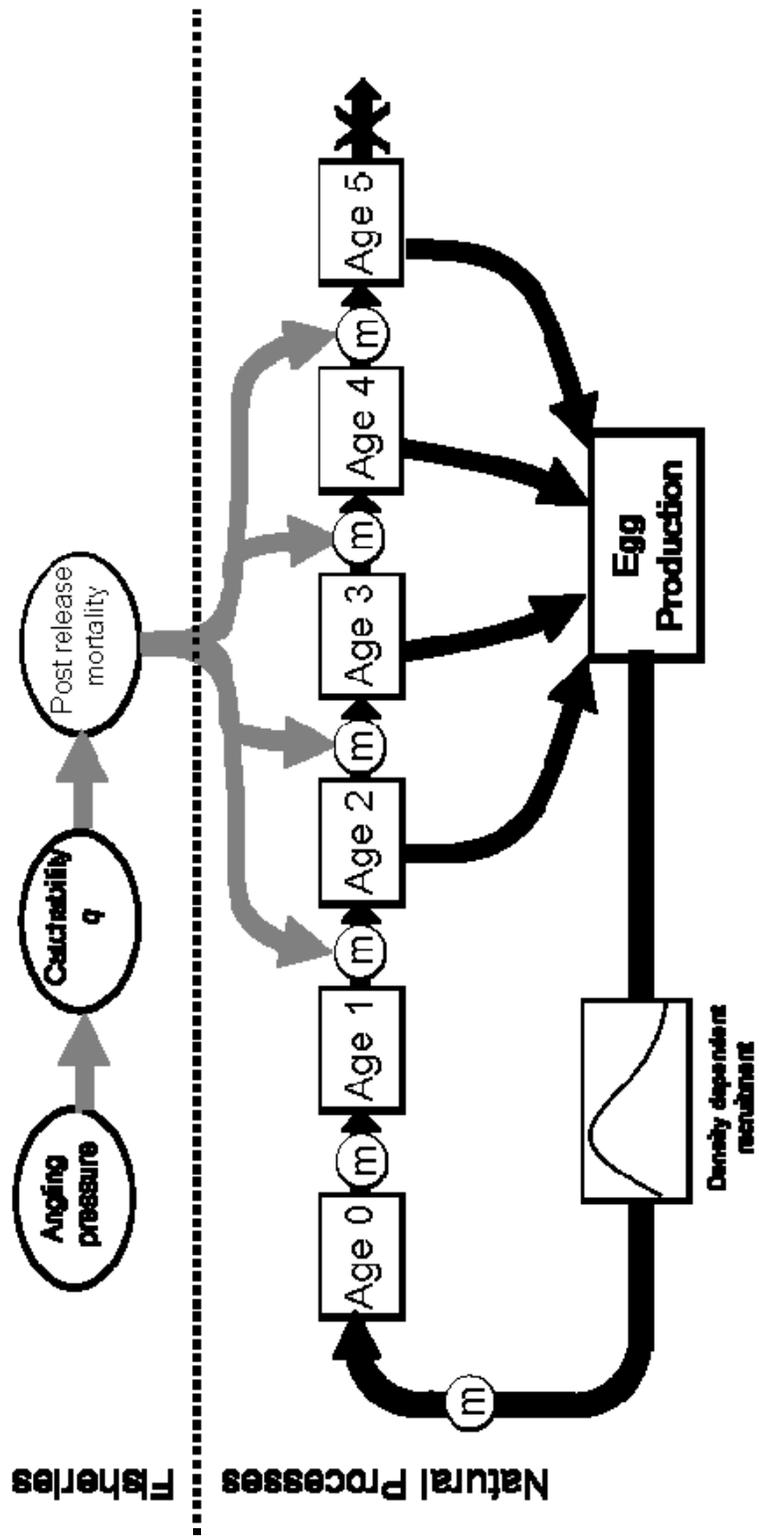


Figure 3.1. Simplified structure of an adfluvial “trophy” brook trout fishery.

Life history

I developed an age-structured population model with a maximum age of 5 years and an age at maturity of 2 years, typical of adfluvial brook trout in Maine supporting a fishery for large, or “trophy” brook trout (Figure 3.1; Bonney 2006). All processes modeled are based on an annual time step from spawning period in the fall. At each time step, individuals of the maximum age (5) spawn and die, whereas, individuals of all other ages, if mature, spawn and then experience a constant per capita mortality rate (natural mortality “ m ”, Table 3.1). Age-0 individuals recruit into the population annually as detailed later.

Table 3.1 – Age specific parameter set for an age-structured fishery model representing an adfluvial "trophy" brook trout population. See text for definitions.

Parameter	Value						Source
	Age						
	0	I	II	III	IV	V	
Initial population	3771	1565	279	100	69	55	a
Natural annual mortality (m)	0.4	0.5	0.55	0.55	0.55	1.0	a
Proportion of reproductive individuals (e)	0	0.9	0.9	0.9	0.9	0.8	a
Hooking vulnerability (q)	0	0.01	0.05	0.05	0.01	0.01	b
Mean length (mm) (L)	82	135	176	253	281	314	a

^a Parameters were heuristically chosen such that with zero mortality due to angling, age structure and total population fluctuated normally about an equilibrium similar to that observed in a quality brook trout population (McFadden et al. 1967).

^b Parameters developed to approximate contribution of each age class to the annual catch statistics observed from a catch-and-release brook trout river (Clark, Jr. et al. 1981).

The initial population and age structure (Table 3.1) was primarily based on age class data from a 14 year study of brook trout in Hunt Creek, Michigan (McFadden et al. 1967). The adult distribution in this system was dominated by age 2 and 3, with very few fish at age 4 and 5 (Table 3.1). In order to begin with a modeled age distribution that supported these older classes, these proportions were increased to reflect proportions consistent with other self-sustaining populations (Table 3.2). This age structure is observed in the Rapid River, Maine where age 4 and 5 are commonly observed year classes (Murphy 2006).

Table 3.2 – Age specific natural annual mortality rates (m) as reported in literature.

Parameter	Value						Source
	Age						
	0	1	2	3	4	5+	
Natural annual mortality (m)	0.54	0.63	0.59	0.74	0.90	0.99	McFadden et al. 1967
	(0.25-0.65)	(0.43-0.75)	0.51	0.51	0.51	0.51	Hatch & Webster 1961
			0.45	0.45	0.45	0.45	Hunt 1969
	0.41	0.41	0.53	0.53			Brasch et al. 1973
			0.45	0.45	0.45	0.45	Hutchings 1993
			0.33	0.45	0.45	0.45	Nuhfer & Alexander 1994
			0.29	0.35	0.82	0.90	1.00
0.54	0.54	0.62	0.62	0.62			Curry et al. 2003
							Petty et al. 2005

Size at age

Length of fish at age- a were constant variables (Table 3.1) and obtained directly from McFadden et al. (1976) and in accord with other data reported in literature (Clark et al. 1981; Hutchings 1993; Paul et al. 2003) and with data obtained from the Rapid River,

Maine (Murphy 2006). I tested the sensitivity of the model to the length at age- a variable over a range 0.7-1.5 of the static values, referred to from here on out as growth factor.

Maturity rate

Contributions to reproduction (or maturity rates) were also constant variables (Table 3.1) estimated from Halfyard et al. (2008) and consistent with average egg content at length data from McFadden et al. (1976). Sensitivity of the model to these variables was also tested over the range 0.0-1.0 for each age class (2-5) separately.

Fecundity

Egg production was calculated as a function of individual female length with a size fecundity relationship. Fecundity was calculated by assuming that one-half of the population was female (a 1:1 sex ratio) and mature age-2 and older fish would spawn annually (Table 3.3; Halfyard 2008; McFadden et al. 1976):

$$E = \sum_{a=2}^5 [N_a (eL_a^f) \cdot 0.5]$$

where E is egg number calculated by summing over all mature eggs, e is the proportion of mature (spawning) adults, f is a coefficient describing the fecundity of an individual of length L_a at age a , and N_a is the total number of age- a fish.

Table 3.3 – Non-age specific parameter set for an age-structured fishery model representing an adfluvial brook trout population. See text for definitions.

Parameter	Value	Source
Fecundity	$E = \sum [N_a (eL_a^f)*0.5]$	c
<i>e</i>	3.0×10^{-3}	
<i>f</i>	2.2	
Recruitment	$R = \alpha P e^{-\beta P}$	d
α	0.162202	
β	1.77394×10^{-5}	
Hooking mortality (<i>r</i>)	0.05 (0, 0.14)	e
Angler effort (A)	0-60 rod hours ha ⁻¹ year ⁻¹	f

^c Parameters developed to approximate observations of a quality brook trout population in a major tributary system (Halfyard et al. 2008).

^d Recruitment is modeled using a Ricker stock recruitment (1975) and recruitment data from a quality brook trout population from Hunt Creek (McFadden et al. 1967).

^e Hooking mortality rates used here vary over the range of hook-and-release mortality rates for salmonids reported in literature (Shetter & Allison 1955; Warner 1978; Dotson 1982; Schisler & Bergersen 1996).

^f I varied angler effort over the range of 0-60, which is the range observed in brook trout fisheries in western Maine (Boucher 2006).

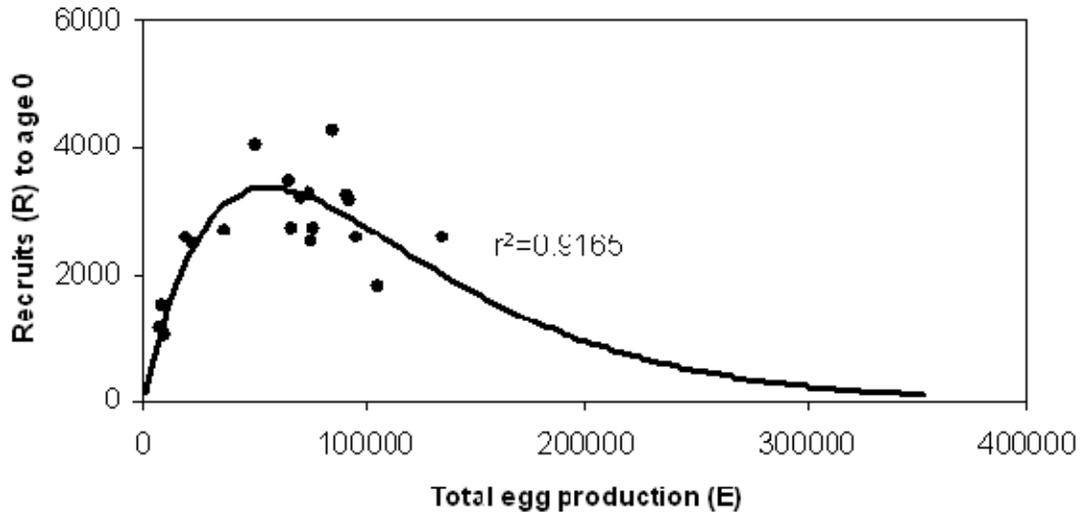
Recruitment

For salmonids, population density is regulated chiefly by density-dependent survival in early life-stages and is often best described by a dome-shaped, stock-recruitment curve (Elliot 1989). Recruitment from population fecundity to age-0 juveniles was modeled by using a Ricker (1975) stock-recruitment relationship (Table 3.3; Figure 3.2):

$$R = \alpha E e^{-\beta E}$$

where R is recruitment of age-0 fish, α and β are parameters determining the shape of the stock-recruitment relationship, and E is total number of eggs. The necessary data to

derive such a stock-recruitment relationship was obtained directly from McFadden et al. (1976) and scaled to produce a stable age class structure as defined above. Sensitivity of the model to the stock-recruitment relationship was tested at $\alpha \pm 1$ S.D., and $\beta \pm 1$ S.D.



3.2. Stock-recruitment relationship with Ricker (1975) curve fitted for brook trout. Solid line represents the fitted Ricker curve where $\beta = 1.77394e^{-05}$, $\alpha = 0.162202$. Data from McFadden et al. (1967).

Natural Mortality

Natural mortality (m) is represented as constant instantaneous rates for ages 1, 2-4, and 5 of 0.5, 0.55, and 1.0, respectively (Table 3.1). Natural mortality for age 0 fish is determined by two components, the stock-recruitment relationship (Figure 3.2) and a constant rate of 0.4 (Table 3.1). The stock-recruitment relationship, as described previously, determines the number of young brook trout that survive hatching to the fall fingerling stage. These fall fingerlings are then subject to a mortality rate of 0.4 before

recruiting into the population as age class 1 the following year. This is in accord with reported mortality rates of brook trout in literature (Table 3.2; Hutchings 1993; van Zyll de Jong 2000; Curry et al. 2003; Paul et al. 2003) but higher mortality rates for brook trout were reported by McFadden et al. (1976; Table 3.2). As stated above, the age class structure in this model includes a greater proportion of 3, 4, and 5 year old fish than were observed by McFadden (in order to be representative of Maine adfluvial populations). Stabilizing this population structure required that survival between age classes increased from those calculated by McFadden et al. (1976; Tables 3.1, and 3.2). Sensitivity of the model to mortality rates was tested over the range 0.0-0.9 separately for ages 0, 1, and 2-4. It is assumed that there is no immigration or emigration in this population.

Fishing Parameters

The vulnerability to hooking (v) of individual age-classes to the fishery were constant rates scaled from 0 (completely invulnerable) to 1.0 (completely vulnerable) and were age class specific (Table 3.1). Based on data reported by McFadden et al. (1967) and Boucher (2005) for the Rapid River, Maine, age 0 fish are invulnerable to angling ($v=0.0$). Size dependent vulnerability for brook trout indicate that they first become vulnerable to angling at 125 mm, therefore age 1 and older fish are completely vulnerable ($v=1.0$) to angling. Catchability (q) of individuals age classes to the fishery were constant rates and age class specific. However, the number of fish that are actually caught is determined by the equation

$$\text{Catch} = qAv$$

where v is the total vulnerable population at age- a , q is the catchability of the total population at age- a , and A is angler effort ($\text{rod}\cdot\text{hours}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$). I assumed catchability rates that were lower than those reported in literature (range 0.07-0.12; Quinn et al. 1994; van Zyll de Jong et al. 2000; Curry et al. 2003) to be conservative with respect to its effect on the model and to examine the effects of angler effort and post release mortality rates on the population characteristics.

Assuming that the practice of fly-fishing results in lower post release hooking mortalities than the use of other common angling gear, I used a base line hooking mortality rate of 5%. The sensitivity of the population to this parameter was tested over the range 0-14%, which is the range reported in literature (Shetter & Allison 1955; Warner 1978; Dotson 1982; Schisler & Bergersen 1996).

Angler effort is applied in the model by defining the number of persons angling for brook trout in one season (one year). I assumed that each angler who “visits” the system will spend 4 hours fishing. Therefore, when the input is 10 persons, the actual angling effort in fishery management terminology is $40 \text{ rod}\cdot\text{hours}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. To assess the effects of C&R angling on a brook trout population, I examined the population characteristics over range 0-60 persons (or $0\text{-}240 \text{ rod}\cdot\text{hours}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) at increments of 10 persons (Table 3.3). While the upper extent of this range is beyond angler effort commonly applied to brook trout fisheries (Quinn et al. 1994; Paul et al. 2003), this is the range observed in brook trout fisheries in western Maine (Boucher 2005).

Running the model

At the end of one time step (one year), the model censuses the existing population in each age class and calculates the required summary statistics, including total number, adult number, number of each age class (0, 1, 2, 3, 4, and 5) total mortality, and total egg production. The model then repeats all calculations for the next year. Population statistics were calculated for 30 years. Data from years 1-10 were omitted from calculation to allow the population to reach equilibrium. Sensitivity of the model to the estimated life-history variables was assessed by comparing proportional changes of mean population density and proportional changes in the range of population density at a 10% increase in life-history variables. Sensitivity analysis was conducted on life-history parameters when angler effort was set to zero. To assess the effect of varying levels of angling pressure on the simulated brook trout population, post release hooking mortality was set to 5% and life-history parameters were set as described in Tables 3.1 and 3.3. Effect of post release mortality rate was assessed when angler effort was set to 10 persons ($40 \text{ rod}\cdot\text{hours}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) and life-history parameters were set at values as discussed (Tables 3.1 and 3.3).

Results

The model was run with life-history parameters as described (Tables 3.1 and 3.3) with angler effort set to zero to establish the baseline population characteristics of our model brook trout fishery (Figure 3.3). Mean and range (averaged over 20 years) of total density, adult density, total egg production, and proportion of age-*a* fish were generally consistent with the mean and ranges reported by McFadden et al. (1967).

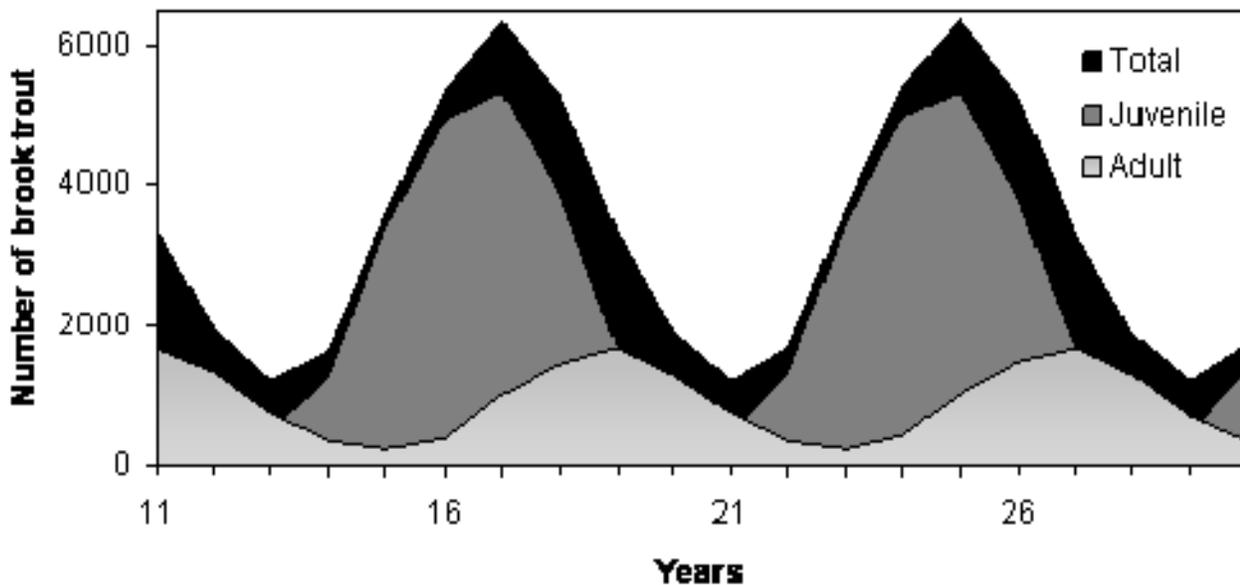


Figure 3.3. Simulated population characteristics of a brook trout fishery when angling effort is set to zero and biological parameters are set at baseline estimates (Tables 3.1 & 3.3).

Sensitivity analyses

Changes in natural mortality rate at each age class (0, 1, and 2-4) affected population characteristics similarly. As mortality rates increase, the equilibrium adult density and proportion of older age classes decrease (Figure 3.4). Changes in the natural mortality rate of age class 1 had a greater effect on the population characteristics than mortality rates of the other age classes. For example, a 10% increase in juvenile mortality rate and adult mortality rate resulted in a negative change in equilibrium total density of 5, and 3%, respectively (Figure 3.4). Equilibrium total density was positively related to natural mortality rates, increasing with higher mortality. Increases in mortality rate for each age class resulted in a proportional decrease in the amplitude of oscillation about the mean population characteristics over the simulated 20 years (Figure 3.4). Despite this change in amplitude, the general trend in total density, adult density, total egg production, and proportion of age-*a* fish were the same.

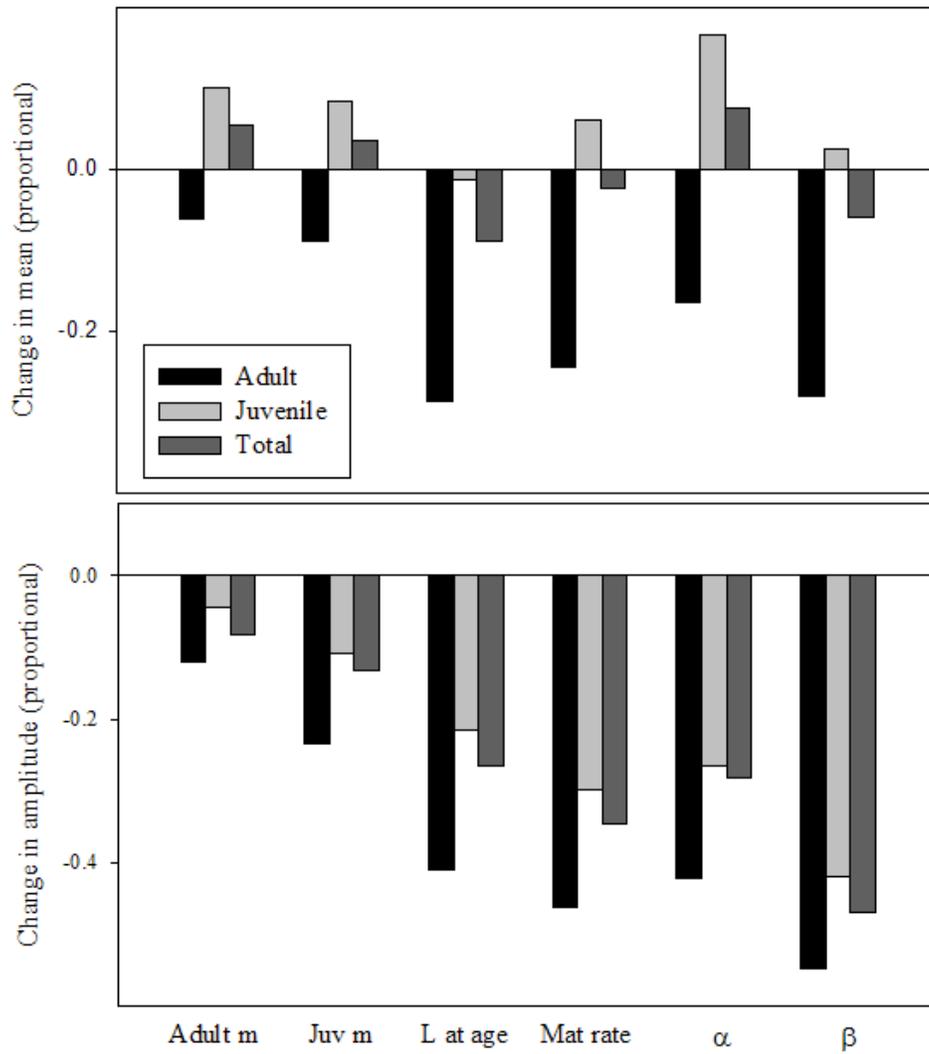


Figure 3.4. Sensitivity of population characteristics of a brook trout fishery to changes in adult mortality rate (ages 2-4), juvenile mortality rate (ages 0-1), length at age a , maturity rate of adult fish (ages 2-4), α , the y-intercept of the stock-recruitment relationship, and β , the slope of the stock-recruitment relationship (f).

Increases in the proportion of reproductive individuals (maturity rate) by age class (2, 3, 4, and 5) decreased both the proportion of older age classes and adult density (Figure 3.4). These increases were of a low magnitude. A 10% increase in maturity rate resulted in a negative proportional change in equilibrium total density of 2% (Figure 3.4). Increases in maturity rate had a fairly more significant effect of the amplitude of oscillation about the population mean, relative to the effect of other variables (i.e. mortality rate; Figure 3.4).

Equilibrium adult density and total density was negatively related to length at age- a , the model's sensitivity to this variable, however, was small. The proportion of each older age classes (2, 3, 4, and 5) increased, slightly, with an increase in length (Figure 3.4). A 10% increase in length at age- a resulted in a negative proportional change in equilibrium total density of 9% (Figure 3.4). Increases in length at age- a had a more significant effect of the amplitude of oscillation about the population mean, relative to the effect of other variables (i.e. mortality rate; Figure 3.4).

Parameters α and β determine the shape of the stock-recruitment relationship where α represents the y-intercept controlling the height of the curve, and β is the slope of the curve (Figure 3.2). Equilibrium total and adult density, and total annual egg production were positively associated with an increase in the value of α (Figure 3.4). A 10% increase in the value of α resulted in a positive proportional change in equilibrium total density of 7% (Figure 3.4). Increases in the value of α had a fairly more significant effect of the amplitude of oscillation about the population mean, relative to the effect of other variables (i.e. mortality rate; Figure 3.4). Despite this change in amplitude, the general trend in total density, adult density, total egg production, and proportion of age- a

fish were the same. Equilibrium total and adult density, and total annual egg production were negatively related to an increase in the value of β (Figure 3.4). A 10% increase in the value of β resulted in a negative proportional change in equilibrium total density of 6% (Figure 3.4). Increases in the value of β had a fairly more significant effect of the amplitude of oscillation about the population mean, relative to the effect of other variables (i.e. mortality rate; Figure 3.4). Proportion of age classes (0, 1, 2, 3, 4, and 5) were relatively unaffected by changes in either α or β .

Impact of angling

Adult density and proportion of older age classes (3, 4, and 5) decreased as post release hooking mortality rate increased (Figures 3.5a and 3.5b). The hooking mortality rate was set at 5% for baseline simulations. Increases in hooking mortality rate beyond 7%, however, resulted in age classes 4, and 5 accounting for 1%, and <1% of the total population, respectively. An increase in hooking mortality rate was positively associated with an increase in equilibrium total density, however, the population was mostly comprised of age 0, 1, and 2 year old fish (Figure 3.5a). An increase in post release mortality rate resulted in an increase in the amplitude of oscillation about the mean population characteristics over the simulated 20 years.

Angler effort (measured in persons fishing) had a strong negative relationship to adult density and proportion of older age classes (3, 4, and 5; Figure 3.6a and 3.6b). At an effort of 30 persons fishing, 5 year old fish were no longer present in the population. At an effort of 40 persons fishing, 4 and 5 year old fish were no longer present and at 50 persons fishing, 3, 4, and 5 year old fish were no longer present in the population. Angler

effort was positively related to equilibrium total density, however, at high levels of angler effort, the population was comprised of only 0, 1, and 2 year old fish. An increase angler effort resulted in an increase in the amplitude of oscillation about the mean population characteristics over the simulated 20 years.

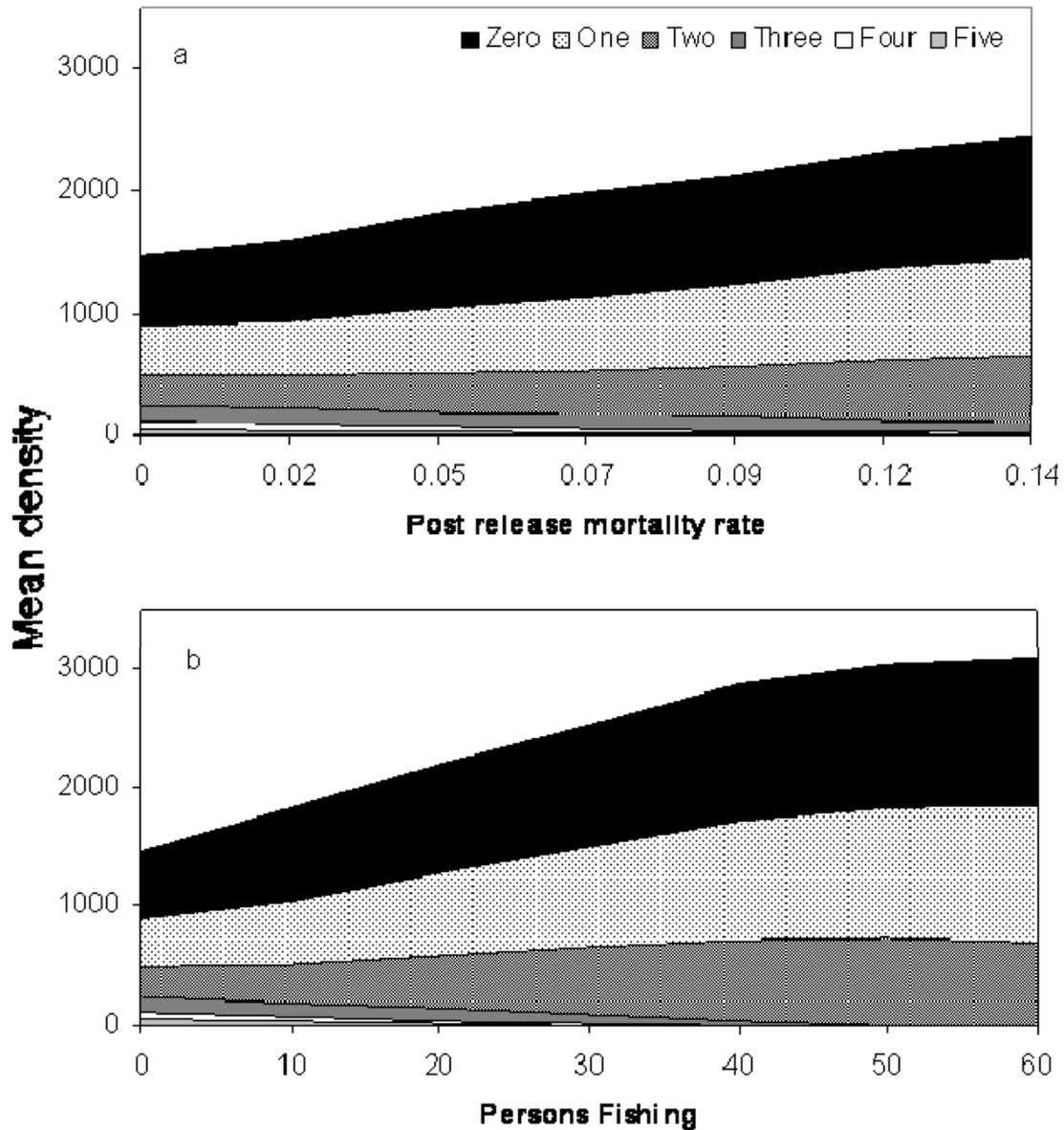


Figure 3.5. Simulated population characteristics of a brook trout fishery when post-release mortality rates are varied (a), and at varying levels of angler effort (b).

Discussion

The results of this modeling study indicate that modest increases in mortality rate as might be associated with C&R fisheries are sufficient to strongly impact the age structure of a brook trout population. In this model, angler effort (Figures 3.6a and 3.6b), and post-release mortality (Figures 3.5a and 3.5b) all affected the observed age structure in a parallel fashion. Increases in mortality (through either of these variables) resulted in a shift away from older age classes and domination by early age classes. These results are consistent with trout systems that experience high fishing pressure. Mean age, and age diversity of brown trout (*Salmo trutta*) is reduced with increased fishing pressure (Almodovar & Nicola 2004). Even when the fishery is restricted to C&R native salmonid populations (cutthroat trout and bull trout) may decline (Paul et al. 2003).

The angling pressures used in this model are consistent with the angling pressures I see for many “trophy” brook trout fisheries in Maine, namely the Rapid River (Boucher 2005). However, our results indicate that angling pressures of only 30 persons (120 rod-hours·ha⁻¹·yr⁻¹) would be sufficient to cause a decline in the density of older, or larger, fish (<5% of the total population). Angling pressures of 40 persons (160 rod-hours·ha⁻¹·yr⁻¹) would be sufficient to reduce age 4, and 5 year old fish to zero.

The catchability of brook trout used in this model was conservative. Clearly catchability links the vulnerable fish population to the fishery, and the magnitude of

catchability contributes to the level of impact (e.g., Quinn et al. 1994; Shuter et al. 1998). In this model, catchability was a constant rate within each age class (Table 3.1). If the more appropriate relationship was inverse density dependent as suggested by Shuter et al. (1998), then our loss due to hooking mortality may be over-estimated for each age class. The relationship is ambiguous, however, as other research has suggested that this relationship is random (Curry et al. 2003) or constant (Ricker 1975). Regardless, the values used for this model (0-5%) are conservative when compared to other estimates of catchability for salmonids (range 0.07-0.86; Anderson and Nehring 1984; Post et al. 2003) and for brook trout in particular (range 0.07-0.12; Quinn et al. 1994; van Zyll de Jong et al. 2000; Curry et al. 2003).

Of the variables that influence angling related mortality, post release hooking mortality has the greatest range of reported values. Empirical estimates of post release hooking mortality vary widely (range 0-14%) for fly-caught fish. Mortality is higher for artificial lure caught fish (2-43%), and 9-50% for bait caught fish (Wydoski 1977; Mongillo 1984; Schisler & Bergensen 1996). While our baseline hooking mortality rate (5%) was conservative with respect to this range of mortality rates for C&R fly-fishing-only, a small error would significantly influence the magnitude of the results, but not the trends. This is similar to results obtained by model simulations of bull trout, and cutthroat trout populations where hooking mortalities exceeding 2.5% resulted in declines the total abundance of both native species (Paul et al. 2003). For lure and bait fishing, the impact is greater.

The actual post release mortality rate is dependent upon many factors, including length of time “played” and length of time out of water (Schisler & Bergensen 1996;

Cook and Suski 2005). Angling, or playing time, is essentially a combination of aerobic and anaerobic exercise that results in a series of physiological changes including depletion of energy stores and an accumulation of lactate, as well as acid/base changes and osmoregulatory disturbances (Wood 1991). During the period of recovery after a hooking event, elevated metabolic rates increase the chance of metabolic rate dependent mortality and reduce the ability of the fish to respond to other stressors such as air exposure or predator avoidance (Priede 1985). Because the size of the fish is positively correlated with the duration of the angling event (Thorstad et al. 2003) larger age classes, may be at an increased risk of post release mortality. Effort by anglers to intentionally prolong the angling event through the use of light line or rods could also increase both the post release mortality rate and sub-lethal physiological effects.

Air exposure occurs upon capture when anglers remove hooks, weigh and measure fish, or hold fish for photo opportunities. During this time out of water, gill lamellae collapse leading to the adhesion of the gill filaments (Boutilier 1990) and several major physiological changes occur. In rainbow trout, blood oxygen tension and the amount of oxygen bound to hemoglobin both fell over 80% during brief air exposure, causing severe anoxia, compared to fish that were exercised but not removed from water (Ferguson & Tufts 1992). Further, when trout were caught by artificial lure and exposed to air for 30 or 60 s following the angling event, mortality increased to 38 and 72%, respectively.

Studies of the consequences of angling related stress on fecundity and spawning are relatively few (Cook & Suski 2005). However, because successful spawning is essential for generating offspring to contribute to the populations, it is only logical that

sub-lethal effects must be minimized during the spawning season to allow the maximum contribution of offspring to subsequent year classes. In aquaculture, there is evidence that salmonids exposed to acute and chronic stressors exhibit endocrine alterations that depress fitness and reduce gamete quality (Campbell et al. 1992). Largemouth bass exposed to angling stress prior to spawning produced fewer and smaller offspring than control fish (Ostrand et al. 2004).

Post release hooking mortality is also correlated with temperature (Dotson 1982; Schisler & Bergersen 1996). Angling at especially high water temperatures is associated with increased physiological disturbances and the probability of mortality increases exponentially (Cook and Suski 2005) especially as water temperatures approach the species' lethal limit (Thorstad et al. 2003). For cold water fish species, such as the brook trout, any angling pressure, including C&R, may pose a severe risk impact in fisheries that experience high temperature. Brook trout have a lethal limit of $\geq 23^{\circ}\text{C}$ (Power 1980). Many brook trout rivers are exposed to higher than optimal temperature regimes due to habitat degradation and global climactic change (Magnuson et al. 1990; Meisner 1990; Shutter and Post 1990). Rivers such as the Rapid River in Maine are thermally impacted due to flow regulation approaching 25°C during the summer (Jackson and Zydlewski, submitted; Chapter 2).

While increased mortality has a strong effect on older age classes, the population persisted with a lower age structure; the population shifted from six age classes to a population comprised of only 0, 1, and 2 year old fish (Figures 3.6a and 3.6b). Interestingly, the total number of fish in this model population increased due to the density dependent survival of egg to age class 0. Donald and Alger (1989) also found

that recruitment to age 1 increased under exploitation, offsetting increased mortality from exploitation. While not accounted for in this model, compensatory mechanisms may also come into play. Jensen (1971) and Donald and Alger (1989) observed that exploited populations of brook trout exhibited altered fecundity and maturity schedules that compensated for increased mortality of older individuals. These results suggest that brook trout, relative to other trout species, may be extremely resilient to angling, given their ability to mature at small sizes and early ages (Paul et al. 2003). Further application of this model would likely require more site- and species- specific estimations of the recruitment relationship and nature of population regulation during early life stages.

The purpose of this study was to construct a testable model system rather than describe the population of a specific site. The dome-shaped stock-recruitment relationship I used in this model allowed for total brook trout abundance to increase due to a decrease in egg production (a density-dependent relationship; Ricker 1975). Density-dependent mortality has been suggested for salmonid early life stages in streams (McFadden et al. 1967) and is often best described by a dome-shaped, stock-recruitment curve (Elliot 1989). However, not all stream populations exhibit this type of density-dependence (Grant and Kramer 1990). The biological parameters used to define the recruitment relationship are poorly characterized for most species, including brook trout (Quinn et al. 2003). While derived from the best available data, uncertainty, (and error) in this relationship will greatly affect the outcome. Indeed such relationships are site specific and with great annual variation (Elliot 1989).

In spite of these caveats, our results suggest post release hooking mortality can be significant for brook trout fisheries. This mortality can have unanticipated impact and

shift the age structure to younger and smaller fish. While C&R fly fishing has been implemented in wild brook trout fisheries such as the Rapid River in Maine, heavy angling may limit trophy potential. Though the Rangeley system has historically supported such fisheries (Boucher 2005, Bonney 2006) this work demonstrates that it may be sustainable only at low intensities of angling impact. Reducing impact in this C&R model requires reduction of catchability, fishing pressure, or post release mortality; the first of which is not readily managed. In addition to limiting season, managers may wish to reduce mortality through engaging anglers. Education of anglers in the importance of limiting playing times, and exposure to air (especially at high temperatures) may represent a low effort management action that would decrease post release mortality rates of C&R angling effort.

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References

- Almodovar, A. and G. G. Nicola. 2004. Angling impact on conservation of Spanish stream-dwelling brown trout *Salmo trutta*. *Fisheries Management and Ecology*. 11:173-182.
- Anderson, C. N. K., C. Hsieh, S. A. Sandin, R. Hewitt, A. Hollowed, J. Beddington, R. M. May, G. Sugihara. 2008. Why fishing magnifies fluctuations in fish abundance. *Nature*. 452:835-839.
- Bachman, R. A. 2001. Closing plenary presentation: Integrating the ecological and human dimensions of trout management. Pages 85-90 in R. DuBois, K. Kayles, M. Ebbers, and S. Turner, editors. *Trout and the Trout Angler II*. American Fisheries Society, North Central Division, Salmonid Technical Committee, St. Paul, Minnesota.
- Bartholomew, A., and J. A. Bohnsack. 2005. A review of catch-and-release angling Mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries*. 15:129–154.
- Behnke, R.J. 1980. A systematic review of the genus *Salvelinus*. In: Balon, E.K. *Charrs Salmonid Fishes of the Genus Salvelinus*. The Hague: Junk, pp. 441–480.
- Bendock, T., and M. Alexanders Dottir. 1993. Hooking mortality of Chinook salmon released in the Kenai River, Alaska. *North American Journal of Fisheries Management*. 13:33, 540-549.
- Bonney, F. 2006. Maine brook trout: biology, conservation, and management. Maine Department of Inland Fisheries and Wildlife. Augusta, Maine.
- Boucher, D. P. 2005. Rapid River and Pond in the River fishery investigations. Fishery Progress Report Series No. 05-1. Maine Department of Inland Fisheries and Wildlife. Augusta, Maine.
- Brobbel, M. A., M. P. Wilkie, K. Davidson, J. D. Kieffer, A. T. Bielak, and B. L. Tufts. Physiological effects of catch and release angling in Atlantic salmon (*Salmo salar*) at different stages of freshwater migration. *Canadian Journal of Fisheries and Aquatic Sciences*. 53:9 2036-2043.
- Clark, R. D., G. R. Alexander, and H. Gowning. 1981. A History and Evaluation of Regulations for Brook Trout and Brown Trout in Michigan Streams. *North American Journal of Fisheries Management* 1:1 1–14.
- Cook, S. J., and C. D. Suski. 2005. Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve the diverse fishery resources? *Biodiversity and Conservation* 14:5 1195-1209.

- Donald, D. B., and D. J. Alger. 1989. Evaluation of exploitation as a means of improving growth in a stunted population of brook trout. *North American Journal of Fisheries Management*. 9:2 177-183.
- Dotson, T. 1982. Mortalities in trout caused by gear type and angler-induced stress. *North American Journal of Fisheries Management*. 2:1 60-65.
- Elliot, J. M. 1989. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. I. The critical time for survival. *The Journal of Animal Ecology*, 58:3 987-1001.
- Gigliotti, L. M., and R. B. Peyton. 1998. Values and behaviors of trout anglers, and their attitudes toward fishery management, relative to membership in fishing organization: A Michigan case study. *North American Journal of Fisheries Management*. 13:3 492-501.
- Grant J. W. A., and D. L. Kramer. 1990. Territoru size as a predictor of the upper limit to population density of juvenile salmonids in streams. *Canadian Journal of Fisheries and Aquatic Sciences*. 47:9 1724-1737.
- Halfyard, E. A., J. L. MacMillan, R. J. Madden. 2008. Fecundity and sexual maturity in select Nova Scotia trout populations. Nova Scotia Salmon Association & Nova Scotia Department of Fisheries and Aquaculture, Inland Fisheries Division, Pictou, Nova Scotia.
- Hudy, M., T. M. Thieling, N. Gillespie, and E. P. Smith. 2006. Distribution, status and threats to brook trout within the eastern United States. *Eastern Brook Trout Joint Venture*.
- Hulbert, P. J., and R. Engstrom-Heg. 1980. Hooking mortality of worm-caught hatchery brown trout. *New York Fish and Game Journal* 27:1-10.
- Hutchings, J. A. 1993. Adaptive life histories effected by age-specific survival and growth rate. *Ecology* 74:3 673-684.
- Jensen, A. L. 1971. Response of brook trout (*Salvelinus fontinalis*) populations to a fishery. *Journal of the Fisheries Research Board of Canada* 28:458-460.
- Karas, N. 1997. *Brook trout*. Lyons and Buford, New York.
- Kendall, K. 1978. Hooking mortality of Lake-dwelling landlocked Atlantic salmon, *Salmo salar*. *Transactions of the American Fisheries Society* 107:4 518-522.
- Longhurst, A. 2002. Murphy's law: longevity as a factor in recruitment to fish

- populations. *Fisheries Research* 56:2 125-131.
- Magnuson, J. J., J. D. Meisner, and D. K. Hill. 1990. Potential changes in the thermal habitat of great lakes fish after global climate warming. *Transactions of the American Fisheries Society*: Vol. 119, No. 2 pp. 254–264.
- Mason, J. W., and R. L. Hunt. 1967. Mortality rates of deeply hooked rainbow trout. *The Progressive Fish-Culturist* 27:87-91.
- Meisner, J. D. 1990. Effect of climate warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. *Journal of the Fisheries Research Board of Canada* 47:1425-1459.
- Mongillo, P. E. 1984. A summary of salmonid hooking mortality. Washington Department of Game, Fisheries Management Division, Olympia.
- Nelson, T. C., M. L. Rosenau, N. T. Johnston. 2005. Behavior and survival of wild and hatchery-origin winter steelhead spawners caught and released in a recreational fishery. *North American Journal of Fisheries Management* 25:931-943.
- S. J. Cook, and D. H. Wahl. 2004. Effects of stress on largemouth bass reproduction. *North American Journal of Fisheries Management* 24:1038.
- Paul A. J., J. Post, and J. D. Stelfox. Can anglers influence the abundance of native and nonnative salmonids in a stream from the Canadian Rocky Mountains? *North American Journal of Fisheries Management* 23:109-119.
- Pavol, K. W., A. W. Klotz. 1996. Gear type and the associated hooking mortality of wild trout in the Savage River tailwater. Federal Aid Project F-48-R, Study VI, Job 2. Final Report. Maryland Department of Natural Resources.
- Power, G. 1980. The brook charr, *Salvelinus fontinalis*. In *Charr: salmonid fishes of the genus Salvelinus*. Dr. W. Junk by Publishers, The Hague, The Netherlands, pp. 141-203.
- Power, M., and G. Power. 1995. A modeling framework for analyzing anthropogenic stresses on brook trout (*Salvelinus fontinalis*) populations. *Ecological Modelling* 80:171-185.
- Quinn, N. W. S, R. M. Korver, F. J. Hicks, B. P. Monroe, and R. R. Hawkins. 1994. An empirical model of lentic brook trout. *North American Journal of Fisheries Management* 14:692-709.
- Quinn, S. 1996. Trends in regulatory and voluntary catch-and-release fishing.

- American Fisheries Society Symposium 16:152-162.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of Fisheries Research Board of Canada* 191:382.
- Schisler, G., and E. P. Bergersen. 1996. Post release hooking mortality of rainbow trout caught on scented artificial bait. *North American Journal of Fisheries Management* 16:570-578.
- Shetter, D. S., and L. N. Allison. 1955. Comparison of mortality between fly-hooked and worm-hooked trout in Michigan streams. Michigan Department of Conservation, Institute for Fisheries Research, Misc. Publication No. 9 12, Ann Arbor.
- Shuter, B. J., M. L. Jones, R. K. Korver, and N. P. Lester. 1998. A general, life history based mode for regional management of fish stock: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2161-2177.
- Shuter, B. J., and J. R. Post. 1990. Climate, population viability and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* 119:316-336.
- STELLA[®] Version 9.1, Isee Systems, Inc. Copyright 1985-2009. Richmond. <http://www.iseesystems.com/>.
- r, J.T., and K.R. White. 1992. A meta-analysis of hooking mortality of nonanadromous trout. *North American Journal of Fisheries Management* 12:760-767.
- Thera, T. M., A. J. Paul, P. J Hvenegaard, and J. R. Post. 2001. Identification of research priorities for a fluvial bull trout (*Salvelinus confluentus*) population using a quantitative life-cycle model in a simulation modeling framework. Pages 105-107 in M. K. Brewin, A. J. Paul, and M. Monita, editors. Bull trout II conference proceedings. Trout Unlimited, Calgary, Alberta.
- Thorstad, E. B., T. F. Naesje, P. Fiske, and B. Finstad. 2003. Effects of hook and release on Atlantic salmon in the River Alta, northern Norway. *Fisheries Research* 60:293-307.
- Warner, K. 1976. Hooking mortality of landlocked Atlantic salmon, *Salmo salar*, in a hatchery environment. *Transactions of the American Fisheries Society* 105:365-369.
- Warner, K., and P. R. Johnson. 1978. Mortality of landlocked Atlantic salmon (*Salmo salar*) hooked on flies and worms in a river nursery area. *Transactions of the American Fisheries Society* 107:772-775.

Wydoski, R. S. 1977. Relation of hooking mortality and sublethal hooking stress to quality fishery management. Pages 43-87 *in* R. A. Barnhart and T. D. Roelofs, editors. Catch-and-Release fishing as a management tool. California Cooperative Fishery Research Unit, Humboldt State University, Arcata.

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