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Structure, Abundance, and Movements of an Allacustrine Population of Rainbow Trout in the Naknek River, Southwest Alaska

Abstract

Allacustrine rainbow trout move downstream from Naknek Lake into the Naknek River to spawn, and become vulnerable to angling during the spawning season. Regulations, including an annual angling closure from 10 April through 7 June, have been implemented to protect spawning fish from angling mortality, but the synchrony of the angling closure to the time when sexually mature fish are present in the river was unknown. We describe (1) the length structure and abundance of sexually mature fish in the spawning population and (2) the post-spawning movements of sexually mature fish. We sampled sexually mature fish ranging from 424 to 860 mm fork length during 2000 and 2001. The spawning population was estimated to be ~ 3,000 fish. Of 70 radio-tagged fish, 80% moved from the river to the lake by 8 June 2001, but several fish remained in the river throughout the summer. More than half of the radio-tagged fish that moved to the lake returned to the river during the fall and early winter. A substantial portion of the spawning population was protected by the annual angling closure, but some fish were not protected because they remained in the river through the summer or returned to the river before it froze in the fall.

Introduction

Rainbow trout (*Oncorhynchus mykiss*) have a broad natural range in western North America extending north to the Kuskokwim River, Alaska (Behnke 1992). An unusual migration pattern among rainbow trout involves allacustrine movements or the migration of sexually mature fish that reside in a lake to the lake outlet for spawning (Northcote 1997). Such a migration pattern has been described among rainbow trout populations in British Columbia (Lindsey et al. 1959; Hartman et al. 1962; Northcote 1962, 1969) and Alaska (Minard et al. 1992), but information on the dynamics of these populations is limited. The allacustrine populations in British Columbia and Alaska tend to be composed of large, long-lived fish that are associated with large lakes with abundant prey fishes (Cartwright 1961, Minard and Dunaway 1991, Minard et al. 1992, Riffe 1994). The common prey species in these lakes is anadromous sockeye salmon (*Oncorhynchus nerka*) or kokanee, i.e., sockeye salmon that reside in freshwater systems through their life cycle (Burgner et al. 1969, Gwartney and Burger 1986, Dunaway and Sonnichein 2001).

Fisheries biologists need to know the population characteristics and movement patterns of allacustrine rainbow trout to manage populations. Because the large, sexually mature individuals within populations that display this migratory pattern become highly concentrated during the spawning period, they are particularly vulnerable to exploitation by anglers. Understanding the extent and timing of allacustrine movements by spawning populations can provide insight into the potential effectiveness of regulations designed to protect spawning fish from angling mortality.

Our goal was to describe selected aspects of the dynamics of the allascustrine population of rainbow trout that spawns in the Naknek River, Southwest Alaska. Our objectives were to describe (1) the length structure and abundance of sexually mature fish in the spawning population and (2) the post-spawning movements of sexually mature fish. The findings provide insight as to the potential effectiveness of special regulations for rainbow trout on the Naknek River designed to protect spawning fish from excessive exploitation as well as the

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physiological stress or latent mortality associated with being caught and released.

Study Area

Rainbow trout that spawn in the Naknek River of Southwest Alaska are believed to carry out allacustrine migrations, moving downstream from Naknek Lake to spawn in the Naknek River during the spring then returning to the lake. Rainbow trout in the spawning population are large with total lengths up to 920 mm total length (TL). They concentrate in a short reach of the Naknek River during the spring spawning period making them highly vulnerable to angling. Consequently, the Alaska Department of Fish and Game manages the Naknek River for trophy rainbow trout and protects the spawning population with a complete angling closure from 10 April to 7 June. Special regulations apply during the angling season: a maximum length limit of 45 cm TL, a creel limit of 1 fish/d from 8 June through 31 October and 5 fish/d from 1 November through 9 April, and use of only single-hook lures by anglers. The synchrony of the closure relative to the time when sexually mature fish are present in the river was unknown.

The Naknek River is near the northern limit of the natural range of rainbow trout (Behnke 1992). The river is formed by the outlet from Naknek Lake and flows past the town of King Salmon into Bristol Bay of the Bering Sea (Figure 1). Rainbow trout spawn within the upstream 14 km of the river that is not influenced by tides. Within this 14-km segment, rainbow trout spawning is concentrated in the downstream half where gravel bars and riffles are abundant. Discharge from Naknek Lake into the river is stable during the spawning period and rises gradually during late spring and early summer as snow melts in the mountains and contributes runoff into the lake.

Naknek Lake is oligotrophic with a surface area of ~ 610 km^2 and a maximum depth of 173 m (Burgner et al. 1969). Most of the lake is relatively turbid due to runoff from glaciers carried by the Savonoski River, with the exception of the Bay of Islands area (Figure 1).

Rainbow trout spawn in four streams around Naknek Lake: Idavain Creek, American Creek, Brooks River, and Naknek River. Mixing of rainbow trout from the Brooks River, Idavain Creek, and Naknek River within Naknek Lake during the nonspawning period has been identified by tagging studies. In addition to rainbow trout, the Naknek River drainage supports sockeye salmon, chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), chum salmon (*O. keta*), and pink salmon (*O. gorbuscha*), also Dolly Varden (*Salvelinus malma*), Arctic char (*S. alpinus*), lake trout (*S. namaycush*), Arctic grayling (*Thymallus arcticus*), and northern pike (*Esox lucius*). Sockeye salmon smolts are believed to be the primary prey for rainbow trout in the system.

Methods

Length Structure

Sampling was conducted over the upstream 14 km of the Naknek River (Figure 1). This segment of river was divided into four contiguous reaches of approximately equal length for sampling. All four reaches were sampled in 2000, but only the two downstream reaches were sampled in 2001 because almost all of the spawning habitat was in those two reaches. Sampling occurred at least 5 d each week from 20 March to 20 May 2000 and from 10 to 28 April 2001. Rainbow trout were captured with beach seines, drifting gill nets, and hook and line. The beach seine was 45.7 x 5.4 m with 2.54-cm^2 knotless nylon mesh, a lead line, and a float line. It was deployed by backing a boat from the shore and allowing it to drift downstream. The boat was used to move the outer end to the shore where the seine was retrieved from each end. The gill net was 15.2 x 3.0 m with 5.1-cm^2 multifillament mesh, a lead line, and a float line. The gill net was deployed so that it would drift with the current. When fish were entangled, the net was retrieved. Hook-and-line sampling was conducted by back trolling with diving lures and by fly fishing with an assortment of large, black streamers. Back trolling was conducted from a boat with a slow drift controlled by the power of an outboard motor. Diving lures were fished 5-10 m downstream as the boat moved slowly downstream.

Captured rainbow trout were measured to the nearest millimeter fork length (FL), categorized as sexually immature or mature, and the sex of sexually mature fish was determined. Sexually immature fish lacked secondary sexual features, whereas sexually mature fish were those fish believed to be capable of spawning during the spring of capture. Sexually mature males were dark, had

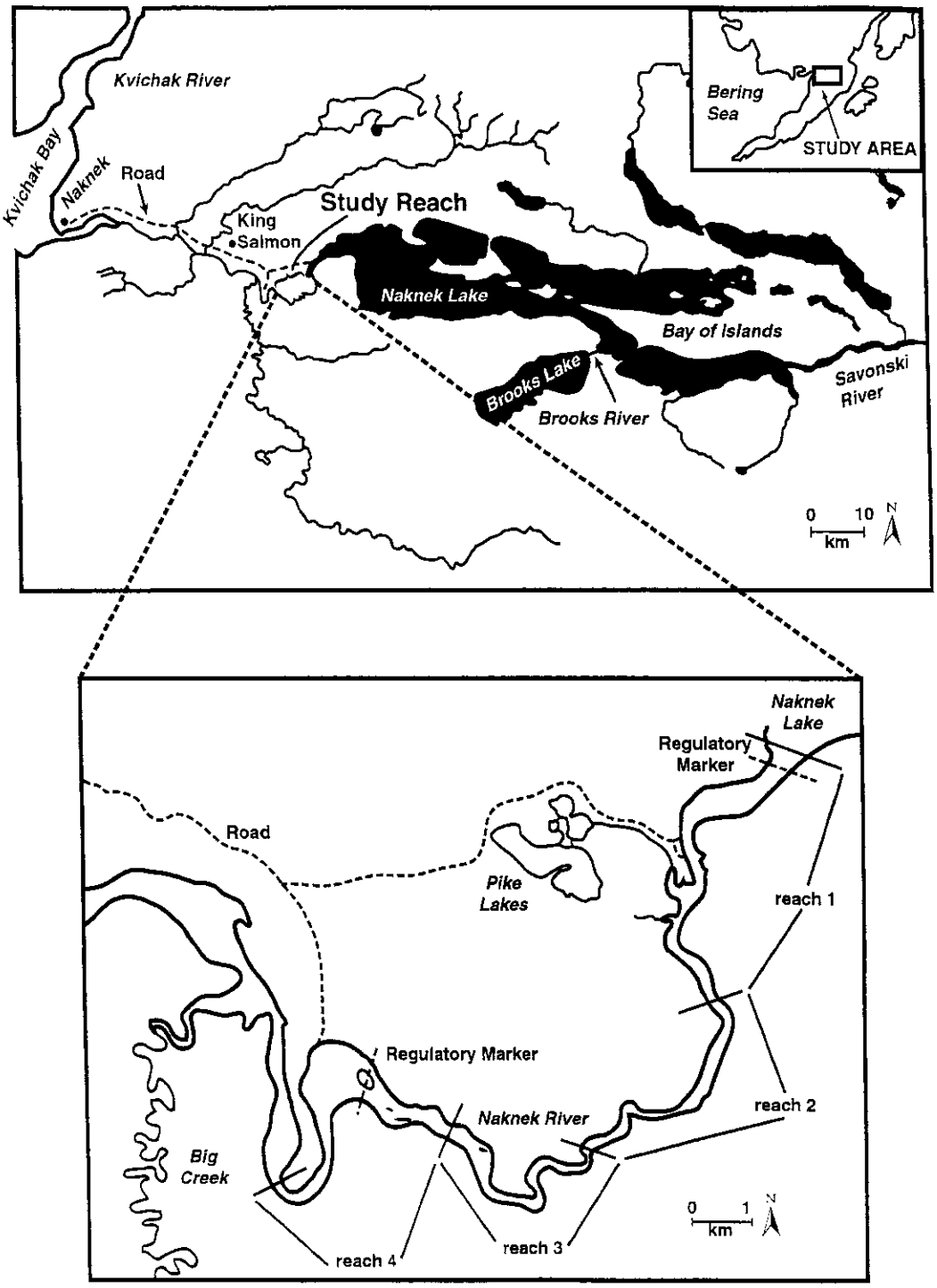

Figure 1. The study area is within the Naknek River watershed and southwest Alaska with the locations of the four sampling reaches.

a well-developed kype, and often exuded milt. Sexually mature females were silver, lacked a kype, had an extended abdomen with an ovipositor protruding from the vent, and sometimes exuded eggs. Differences between classes in the mean lengths of sexually mature fish were assessed using a two-sample *t*-test. Significance was determined at $P \leq 0.05$.

An individually numbered Floy T-Anchor tag, model FS-94, was inserted in the left side near the posterior base of the dorsal fin, a fin was clipped, and the fish were released near the point of capture. Markings enabled recaptured fish to be excluded from the data set describing population structure and allowed us to estimate abundance.

Abundance

A multiple mark-recapture technique was used to estimate the abundance of spawning rainbow trout. A capture history for each marked fish was created indicating the weeks during which each fish was marked and recaptured in order to model capture probabilities (Nichols 1992). Capture probabilities can vary due to time or trapping occasion (model M_t), behavioral responses (model M_b), variation among individual animals or heterogeneity (model M_h), or combinations of these factors (models M_{tb}, M_{th}, M_{bh}, and M_{tbh}) (Otis et al. 1972). The program CAPTURE was used to compute estimates of abundance from the capture histories (Rexstad and Burnham 1991). Likelihood-ratio and goodness-of-fit tests were used to identify the most appropriate model. Capture probabilities varied over time and among individual animals, so model M_{th} was used to estimate the abundance of spawning rainbow trout.

Movements

Post-spawning movements were assessed in 2001 using radio telemetry. Transmitters had frequencies of 152.610-153.990 Mhz, weighed 19 g, had a maximum life span of 1 yr, and were equipped with a mortality sensor that was activated by lack of movement for 8 hr. Transmitters were surgically implanted in the body cavity using the shielded-needle technique (Ross and Kleiner 1982) and surgical procedures of Summerfelt and Smith (1990). Transmitter weight was substantially less than 2% of fish weight (Winter 1996). Capture and implantation were conducted shortly after the fish completed spawning using fish captured in reach 4 (Figure 1). A beach seine, drifting gill net, or hook and line were used to capture spawned-out females and spawning males beginning 10 April 2001 and continuing for 5 wk. The number of fish implanted with transmitters during each week was based on the proportion of spawned-out fish sampled over that time period in 2000. The goal for transmitter implantations was 6, 10, 15, 30, and 13 fish each week, with approximately equal numbers of males and females. Our total sample-size goal was 74 fish, based on an estimate for a binomial proportion that fish would be in the river or lake on 8 June. We estimated that movements of 61 fish would have to be observed to determine the proportion of immigrants within 12.5% of the true value 95% of the time (Cochran 1997) and adjusting this value to account for 20% fish mortality and transmitter failure between implantation and early June when emigration was anticipated to be complete.

A continuously scanning receiver and data logger were placed near the regulatory marker at the lake outlet (Figure 1) to detect movement of radio-tagged fish from the river into the lake. Two antennas were used to detect the direction of movement of radio-tagged fish. We tracked fish from an airplane at least twice each month from May through December 2001, at an altitude of 500 m over both the lake and river. During each search several passes were made over the river between King Salmon Creek and the lake outlet and occasionally the river was searched downstream to Bristol Bay (Figure 1). The search routine for the lake was concentrated along the shoreline and around islands, and required over 3 hr to complete. The locations of individual radio-tagged fish were recorded with a global positioning system and marked on a map of the river and lake.

Results

Length structure

Fork lengths were measured for 820 immature and 892 sexually mature fish ranging from 196 to 830 mm FL in 2000 (Figure 2a). Fork-length measurements were obtained from 229 immature and 661 sexually mature fish ranging from 225 to 860 mm in 2001 when sampling was confined to reaches 3 and 4 (Figure 2b).

The minimum fork length of fish identified as sexually mature was 425 mm in 2000 and 424 in

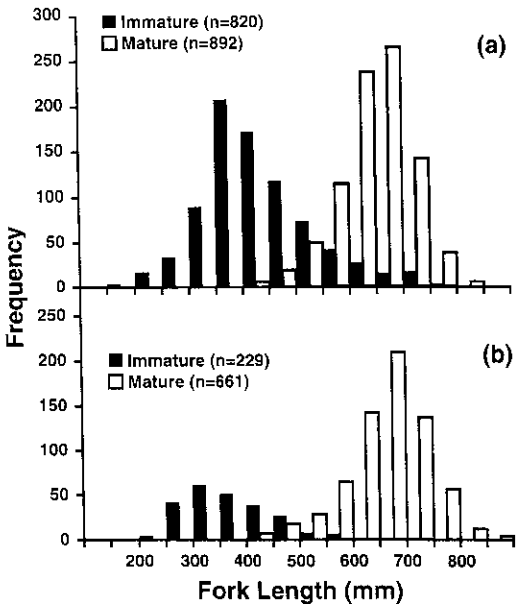

Figure 2. Length frequency distributions of sexually immature and mature rainbow trout captured in the Naknek River, Alaska, in 2000 (a) and 2001 (b).

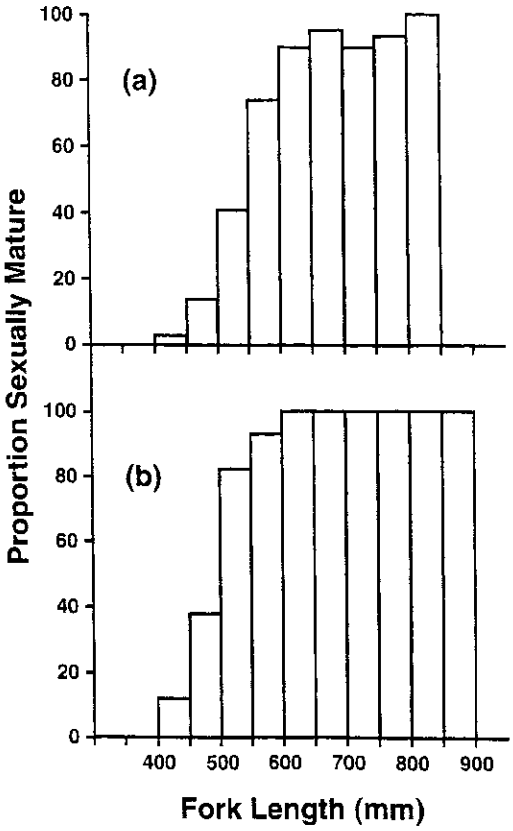

Figure 3. Proportions of sexually mature rainbow trout among length classes captured in the Naknek River, Alaska, in 2000 (a) and 2001 (b).

2001. The proportion of sexually mature fish increased as length increased (Figure 3), but a small proportion of immature fish was observed among even the longest length classes in 2000 when the entire study area was sampled. However, all fish over 650 mm FL were identified as sexually mature in 2001 when only reaches 3 and 4 were sampled.

Sexually mature males tended to be longer than sexually mature females in both 2000 and 2001 (Figure 4). Mean fork lengths of males (676 ± 2.9 mm) and females (617 ± 2.7 mm) differed significantly ($P < 0.001$) in 2000. Similarly, mean fork lengths of males (686 ± 3.7 mm) and females (630 ± 3.5 mm) differed significantly ($P < 0.01$) in 2001. Males represented 53% of the sexually mature fish sampled in 2000 and 59% in 2001.

Abundance

Nine, 1-wk capture events took place between 20 March and 21 May 2000 across all four reaches. A total of 983 sexually mature fish were marked with tags and fin clipped, and 115 were recaptured at least once. The first recaptures occurred during the fourth week (10-16 April). The percentage of marked fish increased from week 4 (5.6%) to week 8 (16.2%), but decreased during week 9 (15.1%) to indicate emigration of marked fish from the study area. Thus, week 9 was excluded in the abundance estimate. The estimated number of sexually mature fish in the Naknek River during the 2000 spawning period was 3,258 ± 389 (95% CI = 2,608-4,143). When limited to data from reaches 3 and 4, abundance was estimated to be 2,484 ± 429 (95% CI = 1,801-3,511) sexually mature fish.

Three, 1-wk capture events took place between 10 and 30 April 2001 in reaches 3 and 4. A total of 727 sexually mature fish were marked and 77 were recaptured at least once. The proportion of marked fish was 14.2% during week 2 and 12.2% during week 3. The estimated abundance of sexually mature fish in reaches 3 and 4 in 2001 was 2,413 ± 271 (95% CI = 1,956-3,029), similar to that obtained for the two reaches in 2000.

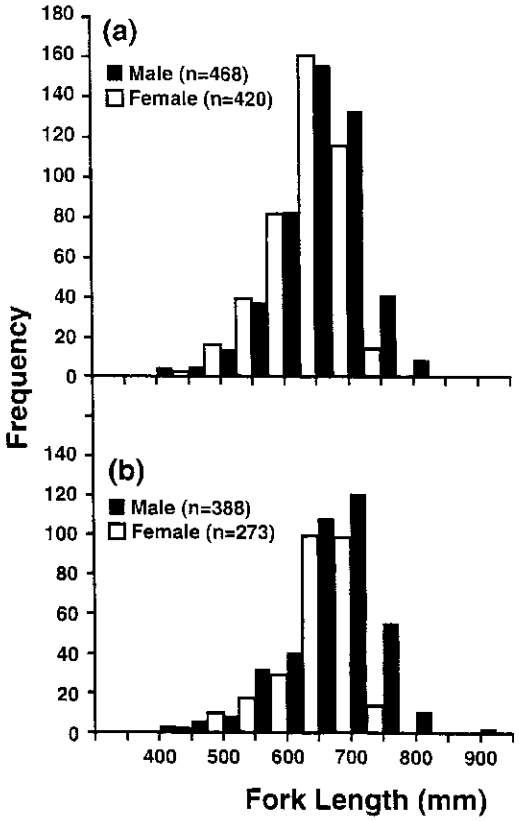

Figure 4. Length frequency distributions of sexually mature male and female rainbow trout captured in the Naknek River, Alaska, in 2000 (a) and 2001 (b).

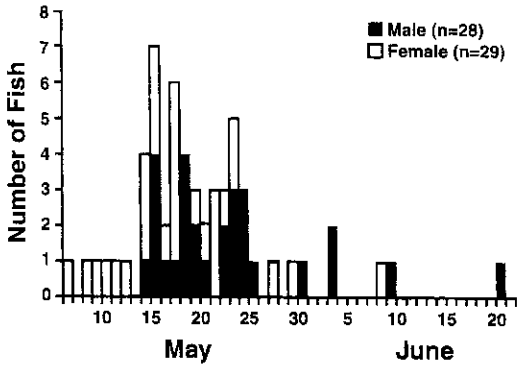

Figure 5. Date and sex of rainbow trout with radio transmitters that moved from the Naknek River to Naknek Lake during the spring 2001.

Movements

Transmitters were implanted in 38 males (mean FL = 674 ± 9 mm) and 36 females (mean FL = 638 ± 8 mm) between 10 April and 14 May 2001.

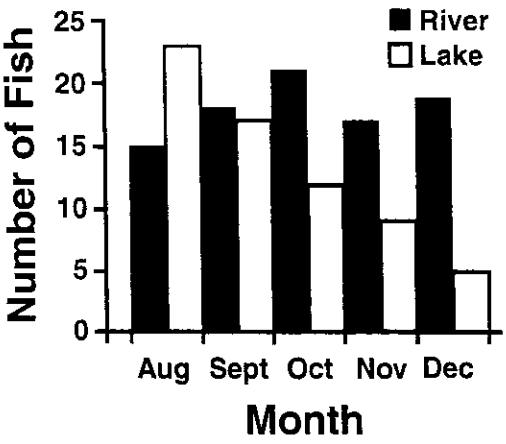

Figure 6. The numbers of rainbow trout with radio transmitters located in either the Naknek River or Naknek Lake from August through December 2001.

As of 8 June, 70 fish (35 of each sex) were alive with functioning transmitters. Of those 70 fish, 56 (27 males and 29 females) had moved from the Naknek River to Naknek Lake by 8 June, and 14 (7 of each sex) remained in the river (Figure 5). Movement to the lake was greatest in the middle of May. All of the fish that moved from the river into the lake did so by 19 June with the exception of one fish that did not enter the lake until 31 August. All of the fish that moved to the lake prior to 13 May were females. The mean fork lengths of males that remained in the river (635 ± 25 mm) and those that moved to the lake (685 ± 9 mm) differed significantly ($P = 0.026$). Similarly, the mean fork lengths of females that remained in the river (592 ± 27 mm) and those that moved to the lake (646 ± 7 mm) differed significantly ($P = 0.010$)

We located 64 radio-tagged rainbow trout during summer; 51 (80%) spent most of the summer in the lake and 13 remained in the river during the summer. Thirty-eight fish were located as of 1 September, 21 (55%) in the lake and 17 in the river. Five of the fish in the river on 1 September had returned to the river after spending the summer in the lake. Between 1 September and 19 December, 11 of the 21 fish in the lake on 1 September returned to the river (Figure 6).

Discussion

Rainbow trout sampled in the Naknek River in 2000 and 2001 were large, ranging up to 860 mm

FL (Figure 2). Age and growth studies of rainbow trout from the Naknek River (Minard and Dunaway 1991, Riffe 1994) indicated that fish in the spawning population lived up to 13 yr and attained fork lengths of 350-550 mm at age 5 and 550-700 mm at age 10. The minimum length at sexual maturity was 424 mm, but the majority of fish were sexually mature at 551-650 mm FL (Figure 3). Combining information from previous age and growth studies with our observations of lengths at sexual maturity suggest that rainbow trout in the Naknek River become sexually mature at 5-7 yr of age. The sex ratio of fish sampled from the spawning population averaged 56% males over the 2 yr of study. This structure was similar to what has been observed among allacustrine populations in the Kvichak River, Alaska (Steve Fleischman, Alaska Department of Fish and Game, personal communication); Lardeau River-Kootenay Lake, British Columbia (Cartright 1961); and Loon Lake, British Columbia (Hartman et al. 1962).

Length-frequency distributions for rainbow trout captured in the Naknek River during the spawning season showed bimodal patterns distinguishing sexually immature and mature fish (Figure 2). The length frequencies also indicated a low number of mid-length (~ 501-650 mm FL) fish. The low frequency of mid-length fish may have been due to poor recruitment of some cohorts, but it is more likely that sexually immature, mid-length fish reside primarily in Naknek Lake and were not sampled. In the Naknek River the proportion of sexually mature fish increased with downstream progression. Reaches 1 and 2 had little spawning habitat and immature fish were abundant, whereas reaches 3 and 4 had substantial amounts of spawning habitat and sexually mature fish were abundant. Segregation of sexually mature and immature fish during the spawning season is suggested by these observations.

Several > 650 mm FL rainbow trout collected from reaches 1 and 2 in 2000 lacked secondary sexual features and were identified as sexually immature. Consequently, some large fish in the Naknek River during spring were not part of the spawning population.

The estimated number of rainbow trout in the spawning population in the Naknek River was similar to estimates for spawning populations in the Kvichak River, Alaska (2,000-4,500 fish) (Minard et al. 1992) and the outlet of Loon Lake, British Columbia (3,200-7,900 fish) (Hartman et al. 1962), and substantially greater than the numbers in the Lardeau River-Kootenay Lake system (500-700 fish) (Hartman 1969), but the spawning area in the Lardeau River appeared to be much smaller than in the other systems.

Post-spawning movements of rainbow trout observed in the Naknek River indicated than an allacustrine migration occurred among a large proportion (80%) of the fish that spawned in the river (Figure 5). The post-spawning movements from the river to the lake may have been a feeding migration (Northcote 1997). Approximately 1.6 million sockeye salmon spawned in the Naknek River system and tributaries to Naknek Lake in 1999 (Dunaway and Sonnichein 2001), and the lake provides rearing area for the offspring of sockeye salmon that spawn in tributaries to the lake. The post-spawning migration of rainbow trout into Naknek Lake may be a response to the abundance of juvenile sockeye salmon available as food for large rainbow trout. However, rainbow trout that remain in the Naknek River feed on sockeye salmon smolts migrating downstream to Bristol Bay from June through July. Given the abundance of prey fishes in the river, it is not known why large rainbow trout migrate to the lake. Migration to the lake may be an avoidance behavior related to the large influx of adult salmon, most notably sockeye salmon, from June through August. Sockeye salmon become aggressive during spawning and agonistic encounters with rainbow trout are likely to occur (McPhail and Lindsey 1970, Morrow 1980, Groot and Margolis 1991).

Post-spawning female rainbow trout initiated movement into Naknek Lake before males (Figure 5). Females that spawned early tended to leave the river earlier, but males tended to remain in the river through the spawning period. Additionally, both males and females that moved to the lake tended to be larger than those that remained in the river. Rainbow trout that migrate may benefit from the abundant juvenile sockeye salmon prey, fewer aggressive encounters with adult salmon, or lower energy expenditure due to the lack of current in the lake.

Refuge responses among allacustrine salmonids have usually been described as movements to a lake to over-winter (Northcote 1997). However, more than half of the rainbow trout that spawned in the Naknek River and moved into the lake during the summer returned to the river during

the fall and early winter (Figure 6). These returning fish included essentially equal numbers of both sexes. Sexually mature rainbow trout may prefer the river as winter habitat or repeat spawners may stage in the fall for spawning the following spring. Over-wintering in rivers before spawning is common in many steelhead (*O. mykiss*) populations (Withler 1965, Behnke 1992, Begich 1999). Another mechanism that may attract fish to the river in the fall is the abundance of food in the form of deteriorating salmon carcasses.

Most of the rainbow trout that moved to Naknek Lake remained there at least through June and July, and were commonly found in a portion of the lake known as the Bay of Islands (Figure 1). Most of Naknek Lake is glacially turbid during summer due to inflow from the Savonoski River, but there is little or no glacial input by streams flowing into the Bay of Islands. Use of the Bay of Islands by rainbow trout may be due to their ability to more efficiently prey on juvenile sockeye salmon in this area (Gwartney and Burger 1986).

A management implication from this study is that the migration pattern of most of the rainbow trout that spawn in the Naknek River provides them protection from angling because there is little fishing on Naknek Lake. Consequently, fish that migrate to the lake survive longer and grow to large sizes. Spawning fish are protected by an angling closure on the river between 10 April and 7 June, and most of the migrating spawners appear to have moved to the lake by that time. Fish begin to move back to the lake during the fall, but angling on the river subsides in early October when the river freezes. Nevertheless, the segment (~ 20%) of the spawning population that remains in the river through the summer and the fish that return to the river in early fall are protected from harvest and angling mortality by a maximum length limit of 45-cm total length and the use of only single-hook lures by anglers. The combination of allacustrine migration and special regulations on the Naknek River appears to provide substantial protection of the rainbow trout spawning population from excessive angling mortality.

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