

Seasonal Fishery Dynamics of a Previously Unexploited Rainbow Trout Population with Contrasts to Established Fisheries

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Abstract.—Although predator–prey interactions between anglers and fish populations are well studied and understood, little is known about whether these interactions differ between lightly and fully exploited populations. Furthermore, within-season shifts in catch rates are poorly understood. These differences have been thought to be due in part to changes in fish behavior after catch and release, which reduces the overall catchability of the population. To address these questions, angling was introduced to a previously unexploited population of rainbow trout *Oncorhynchus mykiss* and the within-season fishery dynamics were contrasted with those of fully exploited populations. We found that catch rates rapidly decreased after the introduction of angling; moreover, once this had occurred, angler effort decreased. Catch per unit effort (CPUE) and catchability of the lightly exploited population were initially quite high compared with most exploited populations but quickly decreased throughout the summer to levels similar to those of fish populations that have been open to angling for decades. Therefore, the differences in catch rates are transitory and the unexploited population quickly becomes indiscernible from fully exploited populations. Seasonality in CPUE was observed in all lakes, with significant decreases in CPUE throughout the summer. These changes in CPUE reflected changes in catchability throughout the season. Although the relative effects of harvest and possible behavioral shifts in fish after catch and release accounted for some variation in catchability, the effects were insufficient to explain total seasonal decreases in catchability in the previously unexploited population. These findings demonstrate that any potential shifts in fish behavior subsequent to catch and release are inadequate to explain seasonal shifts in catch rates. Apparently, seasonal changes in CPUE are driven more by ecological processes than by the fishery.

Exploitation of freshwater fisheries can have pervasive impacts on populations through changes in abundance, size-structure, and life history traits (Healey 1978, 1980; McDonald and Hershey 1989; Rochet 1998; Paukert and Willis 2001). The interactions between anglers and fish can be thought of as predator–prey interactions in which the behavior of both predator and prey affect the qualitative and quantitative outcomes of the interaction (Johnson and Carpenter 1994; Post et al. 2002). These interactions can be characterized by the selective behavior of the predator, the efficiency of the predator, and the numerical response of the predator to abundance or catch per unit effort (CPUE) of the prey (Carpenter et al. 1994; Johnson and Carpenter 1994; Post et al. 2002). It is these characteristics of the interactions, as measured by rates, that drive the dynamics of the predator and prey populations.

Most North American freshwater fisheries of desirable species are fully established or overex-

ploited and the few that are lightly exploited or unexploited are protected by remoteness or access limitation (Post et al. 2002). Published findings on unexploited or lightly exploited populations are almost entirely based on studies from northern areas (e.g., Kennedy 1953; Johnson 1972, 1975, 1976; Power 1978; Johnson 1994) or in national parks or other protected areas (e.g., Donald and Alger 1986; Toetz et al. 1991; Mills et al. 2002; van Poorten 2003). Many life history traits in these unexploited populations often differ from those in their exploited counterparts (Goedde and Coble 1981; Paukert and Willis 2001; van Poorten 2003). Although angling has been introduced into some of these unexploited populations (Goedde and Coble 1981; McDonald and Hershey 1989), little information is available to determine whether lightly exploited fisheries differ fundamentally from the majority of fully exploited fisheries in the key processes of interaction between anglers (predators) and their prey fish populations.

The outcome of the interactions between anglers and fish populations, in terms of catch rates, is thought to be a function of both predator and prey behavior; this interaction controls not only the av-

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erage outcome but also the within-season dynamics of catch rates and harvest (Carpenter et al. 1994; Johnson and Carpenter 1994; Cox et al. 2002; Cox and Walters 2002). These hypotheses have been examined primarily in fully exploited populations; however, these interaction rates between anglers and fish populations can also be assessed by examining lightly exploited fisheries. Given the relative rarity of unexploited or lightly exploited populations, this latter set of studies has not been done. This calls into question whether lightly exploited populations differ from fully exploited ones in the interactions between angler behavior and fish populations.

Seasonality in angling catchability and resulting catch rates has been seen for decades (Lux and Smith 1960). Many studies avoid the problem of seasonal fluctuations in angler success either by assuming that catchability is constant through time or by analyzing fishery data on an annual time-scale (Carpenter et al. 1994; Johnson and Carpenter 1994). Previous works to identify potential biotic and abiotic factors leading to intraannual changes in angler success have examined such factors as prey availability, predator abundance, and water temperature (Lux and Smith 1960; Mills et al. 1986; Raat 1987). In addition, patterns of habitat use by fish often change seasonally because of reproductive behavior or prey distribution, which may affect catch rates (Cross et al. 1995; Cox et al. 2002; Cox and Walters 2002). Despite general conclusions that ecological interactions have some influence on the catchability of a population within a season, few researchers have examined the possibility that the fishery itself may cause the often-seen decline in catchability and catch rates within a fishing season (Cox 2000).

Cox (2000) hypothesized that there are three subunits within an exploited fish population. The first comprises fish that are unreactive to fishing gear because they are too small to react or because they are not present in an area that is being fished. The second comprises fish that are reactive to fishing gear and are available to be caught. The final subunit is made up of fish that have been caught and released but are then unavailable to be caught because of a behavioral shift after release, referred to as a refractory state. According to Cox (2000), fish do eventually recover from catch and release, but the exchange rate between this pool and the pool of reactive fish is unknown. Cox (2000) suggests that in fisheries where the proportion of catch that is harvested is low, catch rates will decrease because the pool of reactive fish available to be

caught will decrease as more fish become unreactive after catch and release. The existence of this third pool of fish, those in a "refractory state," has not been tested, either empirically or theoretically; however, it presents an interesting hypothesis to explain the often-decreasing catch rates within a season (Cox 2000).

We address two key questions in this paper. The first is whether the fishery dynamics of unexploited or lightly exploited populations differ fundamentally from those of fully exploited systems. The second question is whether within-season dynamics in catch-rates and angler behavior are driven by changes in the size of the reactive pool of fish, which may be a function of total harvest and behavioral shifts by fish after catch and release, as hypothesized by Cox (2000). We address these questions by experimentally introducing angling to a previously unexploited population and then describing the within-season dynamics of this fishery. We next contrast our results for the newly developed fishery with those for several fully exploited fisheries.

Methods

There are two components to this study: a detailed assessment of the angler dynamics during an experimental fishery on a previously unexploited population and comparisons of these assessments with those of the fully exploited fisheries for rainbow trout *Oncorhynchus mykiss* reported by Cox (2000). Cabin Lake in Jasper National Park, Alberta, Canada, was fishless before 1929; at which time it was stocked with rainbow trout (Lamontagne and Schindler 1994); it had never been open to angling because the lake was used as the main water supply for the town of Jasper, Alberta, Canada. Cabin Lake also contains a non-native population of lake chub *Couesius plumbeus*, which are believed to have been accidentally released into the lake in the 1950s (Lamontagne and Schindler 1994). Starting in 1988, however, Cabin Lake was no longer used as the source of drinking water for Jasper. In 2000, a new management plan was approved that outlined the need to shift angler pressure away from native stocks towards non-native stocks in the park. It was agreed at that time to open Cabin Lake to angling.

In 2000, a limited test fishery was approved to assess angling rates in Cabin Lake. The lake was opened to angling from 0800 to 2200 hours on July 29–30 and August 5–6. Anglers were required to report the times when they began and ended angling, the approximate size of each fish caught,

and the time at which each fish was caught. Anglers who participated in this test fishery are a representative sample of angler skill-types available in the park. Before the test fishery opened, 1,619 rainbow trout had been caught with fyke nets, trap nets, or a boat-mounted electrofisher. All were tagged with individually coded Floy FD-94 T-bar anchor tags as part of a mark-recapture analysis. Tag loss was found to be negligible, based on a double-tagging experiment in 2000 and 2001 (van Poorten 2003). If the anglers caught tagged trout, they recorded the number on the tag.

To facilitate sampling, all angler-caught fish were placed into a holding tube made of black plastic tubing. These holding tubes were 610 mm long, with an internal diameter of 103 mm. On either end a Plexiglas piece was fit into slots on opposite sides of the tube. One end piece was fixed; the other could be removed to allow fish to be placed into or removed from the tube. Holding tubes were perforated throughout to allow fish to be held with a free flow of water, yet in relative darkness. The purpose of the holding tubes was to help reduce stress while the angler waited for a researcher to relieve him or her of the fish for examination. Each holding tube could hold as many as five live fish. Tubes were emptied by researchers approximately every 30–45 min, to minimize both the time each fish was held and the number of fish in a holding tube. Harvest was not permitted in 2000. Once taken from anglers, fish were measured for fork length to the nearest millimeter and, if not previously tagged, were tagged with a Floy tag for later identification. Recaptured fish were not measured, but the Floy tag code was recorded. If a fish was caught, but escaped while being placed in the holding tube, it was considered landed, although no biological information could be obtained from the fish.

Cabin Lake was reopened for a larger test fishery in 2001. Specific angling policies were developed to ensure that data collected were as complete as possible. All anglers fishing in Cabin Lake were required to carry a prenumbered creel card with them at all times. On arriving at the lake, anglers were required to sign in, giving their name, Jasper Park fishing permit number, and creel card number. All creel cards were numbered and special care was taken to ensure that all anglers received a creel card. That way, whether or not an angler returned a creel card, the exact number of anglers on the lake was known. Specific information requested on the creel card included the time fishing began and ended, the number of fish caught, and the num-

ber of fish harvested. In addition to these policies, which were specific to Cabin Lake, no live bait was permitted and anglers were limited to a daily bag limit of two fish, according to the regular angling policies elsewhere in the park (Parks Canada 2001). Anglers not conforming to these policies risked receiving a fine. Noncompliance with these policies was negligible, based on observations by researchers who were stationed at access points to the lake at all times during the test fishery.

The Cabin Lake open season began June 15, 2001, and was open until September 15, 2001. Anglers were permitted to fish only between 0800 and 1200 hours and between 1700 and 2200 hours, Thursday to Monday. These hours and days were chosen because they incorporate all holidays and weekends, as well as peak fishing times of the day, as identified in the 2000 test fishery. During all open hours of the fishery, creel officers were present at the lake to collect information from anglers and to ensure that all information was properly reported. All harvested fish had fork length, mass, and Floy tag code recorded by researchers as anglers were preparing to leave the area.

The relative size-based vulnerability of rainbow trout to angling was determined by comparing the size structure of fish caught in the 2000 test fishery with that from an electrofishing survey conducted on the nights of July 11 and 12, 2000. Electrofishing began at dusk and continued until the entire shoreline of the lake had been sampled with a boat-mounted electrofisher. The electrofisher was run with 600 V of direct current, electricity being used for a total time of approximately 4,000 and 4,600 s on July 11 and 12, respectively. Captured fish were processed as above. Comparisons of the size structure of fish in electrofishing catch with that of an angling catch assume a negligible size-specific bias of the electrofishing gear for fish in the lake.

The size structure of the population in 2001 was assessed from fish caught in gill nets on September 29 and 30 and October 19 and 20. Nets were fished for 24 h from midday to midday the following day. Gill-net sets consisted of one floating and one sinking seven-panel gill net. Each gill net contained mesh sizes of 25, 32, 38, 51, 64, 76, and 89 mm. Each net was randomly divided into two nets of either three or four panels, to maximize coverage of available habitat. This gill-net configuration has been shown to accurately sample all sizes of fish present in the population (Post et al. 1999). Captured fish were processed as above.

To assess hooking mortality, we compared the

recapture rates of (1) fish caught and released during the 2000 test fishery, (2) fish caught and released during the summer electrofishing period in 2000, and (3) fish from each capture method that were recaptured during the fall gill netting. A chi-square test was used to test for a differential number of recaptures between (1) and (3) and between (2) and (3). All fish caught during electrofishing in the summer of 2000 were held for at least 12 h before release to ensure that mortality attributable to electrofishing was minimal. Any mortalities occurring after electrofishing were subsequently removed from analysis. Therefore, we assume that any differences in the number of recaptured fish from each capture method are attributable to hooking mortality.

During the creel census, we also counted the total angler effort, total number of fish caught, and total number of fish harvested. Results are summarized by week and for the complete 2000 test fishery, as well as for the early 2001 fishery (June 15 to June 29), the middle 2001 fishery (June 29 to July 12), and the late 2001 fishery (July 13 to September 15). A final summary is included for the 2 weeks in 2001 that corresponded to the 2000 test fishery (July 26 to August 6), referred to as the 2001 July–August time period.

The catch per unit effort over a given time is given as the number of fish caught, whether retained for harvesting or not, per unit of effort (Cox 2000), that is,

$$\text{CPUE} = \frac{\sum_{i=1}^n C_i}{\sum_{i=1}^n E_i}, \quad (1)$$

where C_i is the number of fish caught by angler i and E_i is the number of angler-hours spent per angler per trip to the lake. An angler who made a trip to the lake in the morning and again in the evening was counted as making two trips. Harvest-per-unit effort was measured the same way, but with harvested fish only.

Although every effort was made to get information on each angler who fished, some creel cards were not returned. Therefore, angler effort was estimated as

$$E = n_T \frac{\bar{e}}{n_s}, \quad (2)$$

where E is effort in a time period of interest, n_T is the total number of anglers fishing in that time

period (estimated as the number of creel cards used), \bar{e} is the mean angler effort of anglers who returned creel cards in the time period, and n_s is the number of anglers who returned creel cards in the time period. This assumes that anglers who return completed creel cards made the same mean effort as those who did not. We report angler effort for Cabin Lake in units of angler-hours/ha for ready comparison with other studies. Because estimation of the various fishery statistics that follow are carried out on the whole Cabin Lake population, the catch, effort, and population size estimates involve numbers, not density. Catch must be estimated on the basis of the number of completed creel cards as follows:

$$C = \text{CPUE} \cdot E. \quad (3)$$

Data on harvested fish are assumed to be complete, because it is likely that anglers who retained fish would be more willing to take the time to get them measured by researchers.

The number of fish caught at any given time is described by

$$C_t = E_t \cdot q \cdot \text{NV}, \quad (4)$$

where E_t is the total effort within the time interval of interest (angler-hours), q is the catchability (fish caught·vulnerable fish⁻¹·angler-hour⁻¹) and NV is the number of fish vulnerable to angling, referred to here as the vulnerable population. The size of the vulnerable population is described by the equation

$$\text{NV} = \sum_{j=1}^s \hat{N}_j \cdot v_j, \quad (5)$$

where \hat{N}_j is the estimated number of fish in each 10-mm size-class and v_j describes the size-dependent vulnerability of fish to angling gear. Vulnerability is described by the sigmoid relationship (Paul 2000)

$$v_j = (1 - e^{-\beta(\text{FL})^\gamma}), \quad (6)$$

where β and γ are fitted parameters and FL is the length of a fish in size-class j . Vulnerability ranges from completely invulnerable ($v_j = 0$) to completely vulnerable ($v_j = 1$). Data for vulnerability for each size-class were fitted by comparing the catch data from the test fishery in 2000 with the size structure assessed in the electrofishing catch earlier that year. This assumes equal vulnerability for all sizes to the electrofishing gear. Although probably not perfectly true, it will be approxi-

mately true for all fish of catchable size caught in moderate macrophyte cover (Bailey and Austen 2002). It is possible, however, that vulnerability to angling is slightly underestimated for larger fish if these fish are also more vulnerable to electrofishing than smaller fish are. This procedure for calculating vulnerability data allows for vulnerability to be greater than 1.0, although the model will never exceed 1.0. Observed vulnerability, therefore, can reflect differences in effort between the two capture methods, which may result in more fish within a size-class to be caught by angling. Intra-annual growth was assumed to be negligible for vulnerability purposes with regards to the 10-mm size-classes. Therefore, recaptured fish in 2000 for which size was not recorded were assumed to be approximately the same size as at initial capture earlier that summer, which allows them to be included in calculating vulnerability.

Maximum likelihood was used to estimate vulnerability and catchability in 2000, assuming a binomial distribution of the probability of capture. This allows for observed vulnerabilities to be weighted by the sample size in the electrofishing sample. Size-based vulnerability should be constant within a population over time (Paul 2000). Using the population size structure from the fall gill-net sampling and the abundance estimate for all fish in the population in 2001 (from van Poorten 2003), we calculated the size of the vulnerable population for that year. The multimesh gill nets used will capture fish at least 150 mm long with equal vulnerability (Post et al. 1999). Using estimates for C_p , E_p , and NV, we can then estimate the catchability coefficient for any time period of interest in 2001. Catchability was calculated on a weekly and monthly basis in 2001. Estimates were also made for the components of the early, middle, and late 2001 fishing season.

Catch inequality was calculated for the 2000 test fishery and the early, middle, and late 2001 fisheries by using the Gini coefficient (Baccante 1995). The Gini coefficient is calculated from the Lorenz curve, which is the cumulative percentage of fish caught over the cumulative percentage of anglers fishing. Perfect equality of catch between anglers would result in a 1:1 relationship. If the relationship falls below 1:1, then an increasing proportion of anglers are catching fewer fish. The Gini coefficient quantifies this pattern by calculating the area between the 1:1 relationship and the Lorenz curve as a proportion of the area under the 1:1 relationship

$$G = \frac{a_1 - a_2}{a_1}, \quad (7)$$

where G is the Gini coefficient, a_1 is the area under the 1:1 relationship, and a_2 is the area under the Lorenz curve. The area under the Lorenz curve (a_2) was estimated by constructing a series of triangles under the curve, calculating their respective areas, and summing (Baccante 1995). A Gini coefficient close to 0 represents nearly equal catches among anglers, whereas a coefficient close to 1.0 represents inequality in catch among anglers; that is, few anglers are catching the majority of the catch.

Data from the Cabin Lake fishery were compared with data on previously angled populations observed by Cox (2000). Catchability and CPUE were calculated from Cox (2000) by using estimates of abundance, catch, and effort on these lakes. Only lakes for which abundance estimates are available are considered so as to be able to estimate catchability for all lakes. Not all lakes were open during the same months Cabin Lake was. Unfortunately, effort in Cox (2000) is given in units of angler-days. Because daily effort on these exploited lakes is assumed to be 4 angler-hours (Cox 2000; Cox and Walters 2002), we multiplied by 4 the estimates of effort reported in Cox's (2000) exploited lakes to compare efforts at those lakes with that reported here for Cabin Lake. Both CPUE and catchability were calculated as the mean of each month for each lake. We separated the lakes in this comparison into lakes in which rainbow trout are the only fish species present (referred to as allopatric lakes) and those where rainbow trout co-occur with other fish species, species that are not targeted by anglers (referred to as sympatric lakes); this helped us identify whether differences in catch rates and catchability exist that may be the result of the presence of other species. In all sympatric lakes, including Cabin Lake, rainbow trout are the only species sought by anglers.

Seasonality was assessed by analyzing all exploited lakes for which measurements of catchability and CPUE were available from June to September. Repeated-measures analysis of variance (ANOVA) was used to test the hypotheses that both catchability and CPUE change significantly over time within a season and that this change will differ for allopatric and sympatric populations. Significance was assessed by using a type I error rate of 0.05.

To account for seasonal trends in catchability, we tested whether changes in angler skill through-

out the season would influence catchability appreciably. Because our data did not allow us to make judgments about angler skill, we assumed that throughout the summer there are two pools of anglers—either skilled or unskilled. Therefore, overall catchability was multiplied by an adjustment factor ranging from 1 to 0.2 that reflected the relative skill of skilled and unskilled anglers, respectively. These multipliers were not chosen randomly; instead, they were derived from the relative catchability of the 10th and 90th percentile from anglers in the 2000 test fishery. For this we used catch and effort data from all anglers in the 2000 test fishery who fished for more than 1.25 h, which eliminated any anglers who caught no fish during their angling trip. We then assumed that at the beginning of the angling season, all anglers present are of the skilled pool and their relative proportion of all anglers drops linearly throughout the summer, whereas the proportion of unskilled anglers increases linearly throughout the summer so that by the end of the season, all anglers present are of the unskilled group. In other words, the catchability multiplier decreased linearly from 1 to 0.2 throughout the season. To see what effect this may have had on catchability throughout the season in Cabin Lake, we calculated catchability with an assumed constant angler skill as follows:

$$q_{\text{const}} = [q_{\text{obs}} \cdot (1 - \text{adj})] + q_{\text{obs}}, \quad (8)$$

where q_{const} is catchability with a constant angler skill throughout the season, adj is the catchability multiplier, and q_{obs} is the observed catchability. Equation (8) adds the adjusted catchability to the observed catchability to estimate what the catchability of rainbow trout would have been if angler skill remained constant.

To quantify the potential relative effect of harvest, we calculated a refractory period (as suggested in Cox 2000) after catch and release, a change in mean angler skill, and the decrease in catchability from week 1 to week 14 for each effect relative to the observed decrease in catchability.

Results

The vulnerability of fish to angling gear varies in a size-dependent fashion for rainbow trout in Cabin Lake (Figure 1). The vulnerability curve approaches zero at a fish length of 80 mm and approaches full vulnerability at 450 mm. Some rainbow trout seen in Cabin Lake have a fork length of 435 mm, but this is rare. Although some individual length bins have raw vulnerability es-

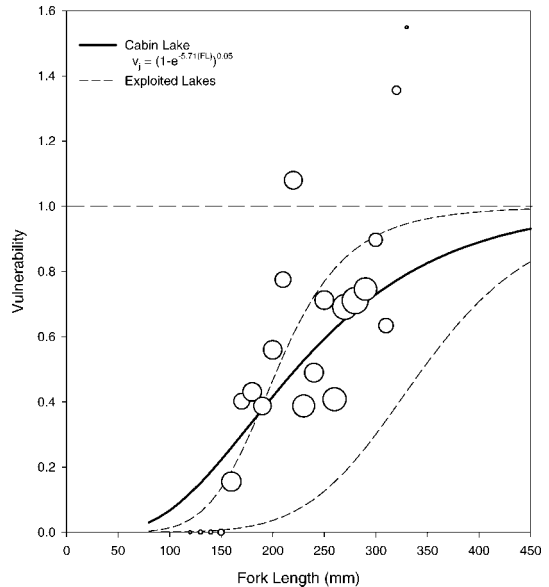


FIGURE 1.—Size-specific vulnerability of rainbow trout to the Cabin Lake fishery. The circles represent observed vulnerabilities (for 10-mm size bins) for fish caught in the 2000 test fishery relative to the size structure obtained from electrofishing on July 11 and 12, 2000. The diameter of each circle represents the sample size of the electrofishing catch, which ranged from 1 to 72 fish. The overall sample size for the electrofishing catch was 666 fish, compared with 254 fish in the 2000 test fishery. The solid sigmoid curve is the log-likelihood best-fit line of the size-structured vulnerability. The two dashed sigmoid curves represent the maximum variation in the vulnerability of rainbow trout to angling in Fawn and Hardcastle lakes, which have fish with higher and lower vulnerabilities at age, respectively (Cox 2000).

imates greater than 1, this can be expected if the number of fish in the electrofishing sample of this size were underrepresented or if anglers caught an unusually large number of fish in this size-class. Also, individual anglers might recatch the same fish, whereas fish that were obtained by electrofishing were held until all electrofishing was finished on the second night. Of the 343 fish caught in the 2000 test fishery, only 5 were captured more than once. All values with an observed vulnerability greater than 1.0 have low weighting because of the low number of sampled fish in electrofishing, represented by the size of the data point (Figure 1). All the rainbow trout described by Cox (2000) had increasing vulnerability over the same size range as trout in Cabin Lake. However, the trout described by Cox (2000) show a steeper increase in vulnerability than do the Cabin Lake trout (Figure 1). Asymptotic lengths of fish in Cox

(2000) were higher in all lakes than in Cabin Lake (van Poorten 2003), indicating that a higher proportion of populations in Cox (2000) are fully vulnerable to angling, whereas Cabin Lake rainbow trout are not.

Although hooking mortality was not measured directly, the relative returns of fish originally caught in the 2000 test fishery were compared with those of fish originally caught by electrofishing in July of the same year. The proportion of fish recaptured from each original capture method did not differ significantly (χ^2 : $df = 1$, $P > 0.05$). From this, we assume that hooking mortality is negligible.

Patterns in the distribution of observed catch among anglers differed between the test fishery in 2000 and the early 2001 fishery period. In the 2000 test fishery, catch was relatively evenly distributed among anglers, a maximum of 31 fish being caught per angler-day (Figure 2A); only a small proportion of anglers caught no fish. In the early 2001 fishery, however, 35% of anglers caught no fish, and fewer anglers caught larger numbers of fish than in 2000 (Figure 2B). This trend continued in the middle 2001 fishery, wherein 52% of anglers caught no fish (Figure 2C). In the late 2001 fishery, 68% of anglers caught no fish, the maximum caught per angler-day being 14 fish (Figure 2D). As the fishing season progressed in 2001, fewer anglers caught at least their bag limit of two fish (represented by a broken vertical line in the 2001 panels of Figure 2). The percentage of anglers who caught two or more fish per day dropped from 54% to 16% from the early to late fishery periods in 2001. These patterns in the distribution of catch among anglers are clear in the pattern of Gini coefficients through the development of the Cabin Lake fishery. In 2000 the Gini coefficient was 0.48 and continually increased through the early, middle, and late portions of the 2001 fishery (0.66, 0.73, and 0.81, respectively). Thus, the longer the lake was open, the more skewed the catch frequency relationship became, indicating that a larger proportion of the anglers were catching few or no fish.

The distribution of daily fishing effort changed between 2000 and 2001. In the 2000 test fishery, the number of hours fished per angler per day ranged from 40 min to 10.3 h (Figure 3A). The average angler-day in 2000 was 3.85 h. Few anglers fished for more than 5 h, even though the fishery was open for 14 h per day. Most anglers fished from 2 to 4 h per day. In 2001 the fishery was open for a maximum of 5 h at a time, an

artificial truncation of the length of angler-days. In the early 2001 fishery, a relatively even number of anglers fished from 1 to 4 h, their mean effort being 2.4 angler-hours (Figure 3B). In the middle 2001 fishery, a clear mode developed in the distribution at 2 h per fishing trip; mean effort was 2.4 angler-hours (Figure 3C). In the late 2001 fishery, most anglers fished for 2–3 h in a trip (Figure 3D); mean angler effort in late 2001 was 2.3 angler-hours.

Fisheries statistics varied greatly throughout the study (Table 1). Total fishing effort was high in the 4 days of the 2000 test fishery at 5.8 angler-hours/ha. In both the early and middle 2001 fisheries, efforts were similar in the 2-week periods, 17.7 and 15.9 angler-hours/ha, whereas effort in the late 2001 fishery was 28.9 angler-hours/ha over a 10-week period. That is, effort in 2001 was almost twice that during the same time period in 2000, given that there were only 4 days of fishing in 2000, relative to 10 days in 2001. Catch rates, measured as catch per unit effort, were highest in the test fishery in 2000, with anglers catching on average 1.84 fish per angler-hour, approximately 40 times that during the same time period in 2001. Catch rates dropped from 1.6 to 0.8–0.3 throughout the early, middle, and late 2001 fisheries (Table 1). Catchability was highest in the initial 2 weeks of the 2001 fishery, at 5.70×10^{-4} fish·fish⁻¹·angler-hour⁻¹, but rapidly decreased by half to 2.79×10^{-4} fish·fish⁻¹·angler-hour⁻¹ in the second 2 weeks, and finally to 1.07×10^{-4} fish·fish⁻¹·angler-hour⁻¹ in late 2001. Catchability in the 2000 test fishery was 4.20×10^{-4} fish·fish⁻¹·angler-hour⁻¹, compared to 0.97×10^{-4} fish·fish⁻¹·angler-hour⁻¹ during the same time period in 2001, and was nearly as high as in the initial 2 weeks in 2001 (Table 1). Harvest in 2000 was zero because the fishery was regulated as catch and release only. Harvest was relatively constant in 2001, with harvests of 11.6% and 18% of the fish caught in the initial and second 2 weeks, respectively, of the 2001 fishery; in comparison, 10.5% of fish caught in late 2001 were harvested.

Examining the changes in catch rates across all lakes allows for differences to be detected in fishery dynamics between the fully and lightly exploited populations. Mean CPUE in all lakes decreased from June to August and remained low in September (Figure 4). As the season progressed, CPUE became increasingly similar between lakes. Monthly estimates of CPUE are consistently lower in sympatric lakes. Catch per unit effort for Cabin Lake in June was higher than for all sympatric

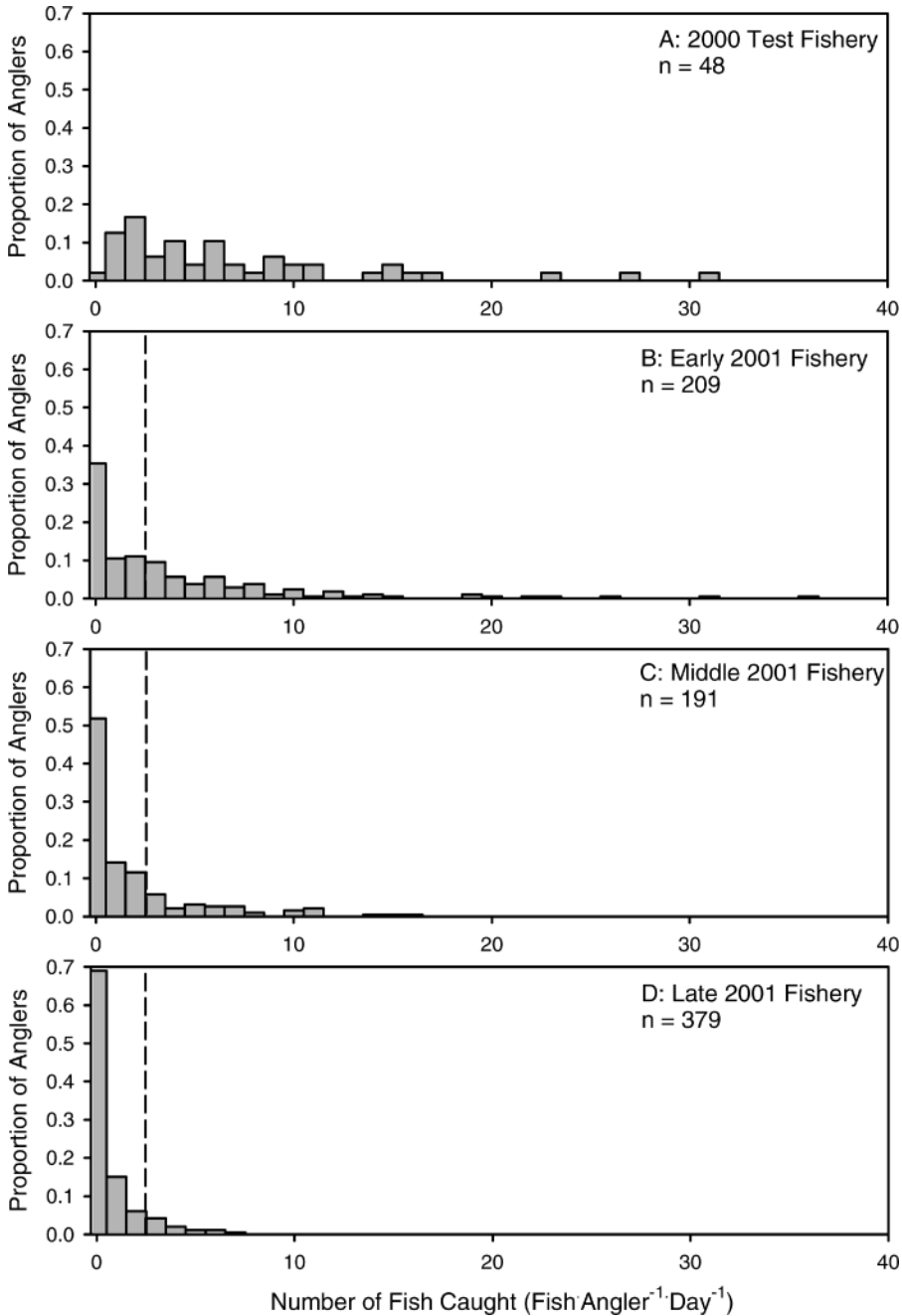


FIGURE 2.—Distributions of the number of fish caught per angler per trip to Cabin Lake as a proportion of all anglers during (A) the 2000 test fishery, (B) the early 2001 fishery, (C) the middle 2001 fishery, and (D) the late 2001 fishery. The broken vertical lines represent the bag limit of 2 fish per angler per day.

lakes and for most allopatric lakes (Figure 4A). However, for all remaining months, the CPUE in Cabin Lake does not deviate from those estimated for other sympatric lakes and was actually con-

sistently below the mean of the other sympatric lakes in August and September. In September, Cabin Lake had the third lowest CPUE of the 12 lakes for which data exist (Figure 4D). This suggests

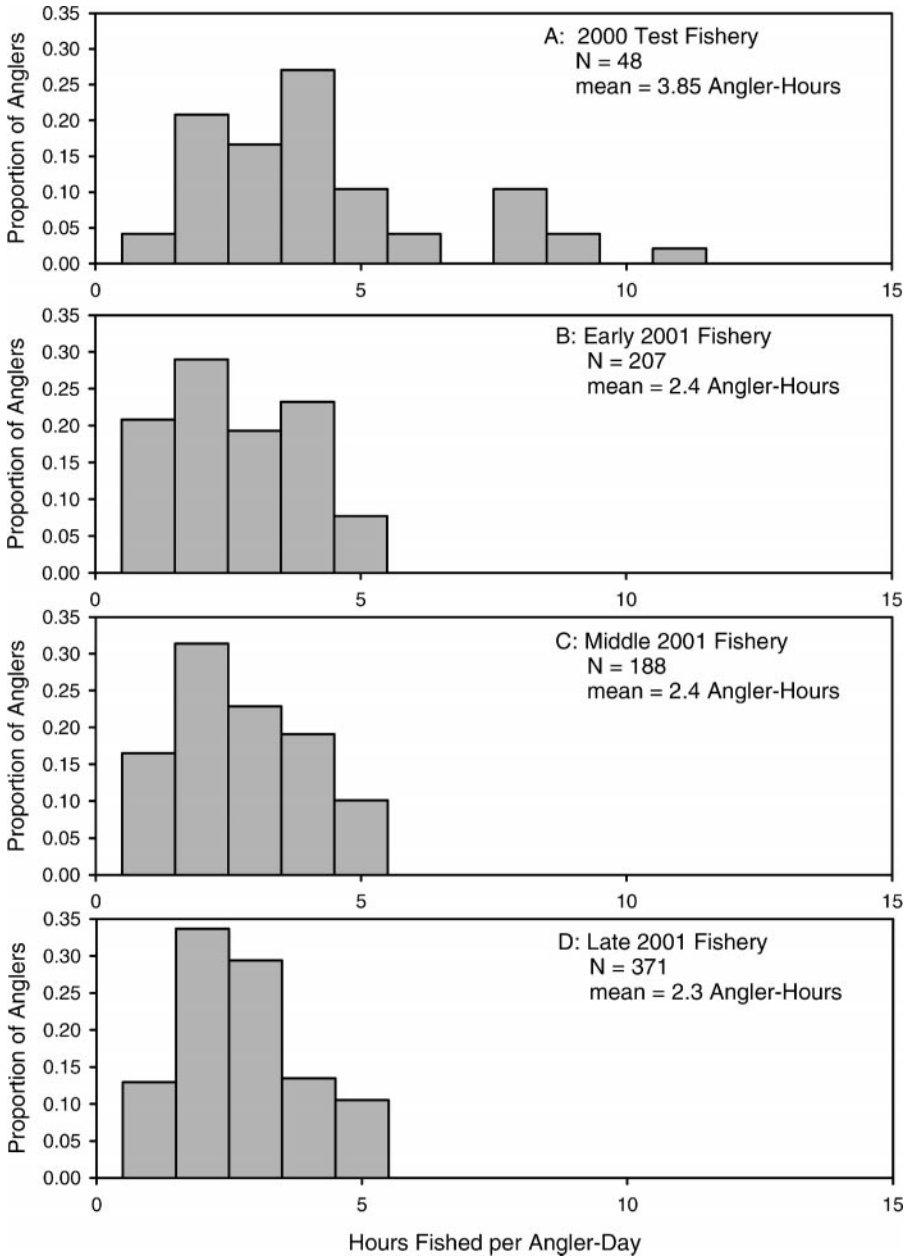


FIGURE 3.—Distribution of the number of hours fished per angler per trip to Cabin Lake as a proportion of all anglers during (A) the 2000 test fishery, (B) the early 2001 fishery, (C) the middle 2001 fishery, and (D) the late 2001 fishery.

that from the perspective of catch rates a lightly exploited population can be considered fully exploited after only a short period of time. Testing for seasonality in CPUE revealed a significant decrease in all lakes and an interaction between time and lake-type (allopatric or sympatric; repeated-measures ANOVA: $df = 1, 1, 8$; $F = 9.082$; $P <$

0.05). This indicates a significant decrease in CPUE throughout the summer angling season, which differs for allopatric and sympatric lakes.

Mean catchability for the allopatric lakes examined follows the same pattern as CPUE, where catchability decreases from June to August and remains low in September (Figure 5). In sympatric

TABLE 1.—Fishery statistics for the 2000 test fishery (July 29–30 and August 5–6), the early 2001 fishery (June 15–28), the middle 2001 fishery (June 29–July 12), the late 2001 fishery (July 13–September 15), the 2001 fishery corresponding to the 2 weeks of the 2000 test fishery (July 26–August 6), and the entire 2001 fishery.

Fishery	Total effort (angler- hour/ ha)	CPUE (fish/ angler- hour)	Number of anglers	Catchability (fish · vulnerable fish ⁻¹ · angler-hour ⁻¹)	Total harvest	Harvest per unit effort (fish/ angler-hour)
2000 test	5.77	1.84	48	4.20×10^{-4}	0	^a
Early 2001	17.67	1.58	242	5.70×10^{-4}	90	0.16
Middle 2001	15.92	0.77	215	2.79×10^{-4}	63	0.12
Late 2001	28.87	0.30	405	1.07×10^{-4}	29	0.03
All 2001	62.33	0.78	861	2.79×10^{-4}	182	0.09
Jul–Aug 2001	7.74	0.23	118	0.81×10^{-4}	7	0.03

^a Not applicable.

lakes, however, catchability increases slightly through the angling season. Although mean catchability in allopatric lakes is higher than in sympatric lakes in June and July, this pattern is reversed in August and September. Catchability observed in Cabin Lake was nearly three times the mean of other sympatric lakes in June but quickly fell below the mean of catchability for sympatric lakes in August and September (Figure 5C, 5D). In September, Cabin Lake had the second lowest catchability of all lakes examined (Figure 5D). These trends in catchability reinforce the concept of the similarity of lightly and fully exploited populations after only 1 month of angling. Testing for seasonality in catchability revealed a significant linear interaction between time and lake-type (repeated-measures ANOVA: $df = 1, 1, 5$; $F = 7.946$; $P < 0.05$). This indicates a significantly different change in catchability throughout the summer angling season between the two lake-types; however, sympatric lakes did not significantly decrease.

Examining the within-season fishery rates in the newly exploited Cabin Lake provides insight into how the population responds to the introduction of angling. Catch per unit effort declined almost immediately after the opening of the lake (Figure 6A), this measure declining after the first 4 weeks. Mean CPUE declined by approximately 79% over the first month of the open season and remained relatively constant for the remainder of the season (Figure 6A; closed circles). Harvest per unit effort was low throughout the season, dropping from 0.20 fish/angler-hour in week 1 to zero in the last 3 weeks of the season (Figure 6A; closed triangles).

Weekly measures of angler effort varied from 9.4 to 5.8 angler-hours/ha over the first month and declined continually for the rest of the season (Figure 6A; open circles). The number of anglers fishing per week decreased from a high of 117 anglers

in week 3 to 10 in week 13 (Figure 6B). The pattern in the number of anglers per week follows the same pattern as the angler effort, which demonstrates that the number of anglers was decreasing over time and the anglers were spending the same amount of time angling throughout the season on average (Figure 6B).

Within-season changes in catchability may result from several factors. After the introduction of angling on the Cabin Lake rainbow trout population, catchability declined by approximately 19% over the first 5 weeks and remained low for the remainder of the fishery (Figure 6C; closed circles). Possible reasons for this dramatic decrease in catchability include changes in population abundance because of harvest, recruitment, or natural mortality; shifts in mean angler skill over the course of the fishery; or a shift in fish behavior after catch and release. We explore each of these possibilities to assess which would be most likely to account for the observed pattern.

Changes in population abundance throughout the angling season will affect catch rates, which will be perceived as resulting from a change in catchability. When population size is adjusted for the limited harvest, there is virtually no difference in time-dependent catchability throughout the angling season relative to the unadjusted catchability. This is shown for a low annual harvest of 182 fish (Figure 6C; open circles). Although not shown here, recruitment of fish into the fishery throughout the year is low, because of both low growth rates and the low vulnerability of small fish (Figure 1; van Poorten 2003). Any recruitment into the fishery would exaggerate the pattern in Figure 6 by decreasing catchability even more as the season progressed because population size would increase with recruitment. Natural mortality will produce a decreasing catchability throughout the season if undetected. Although we have no quantitative es-

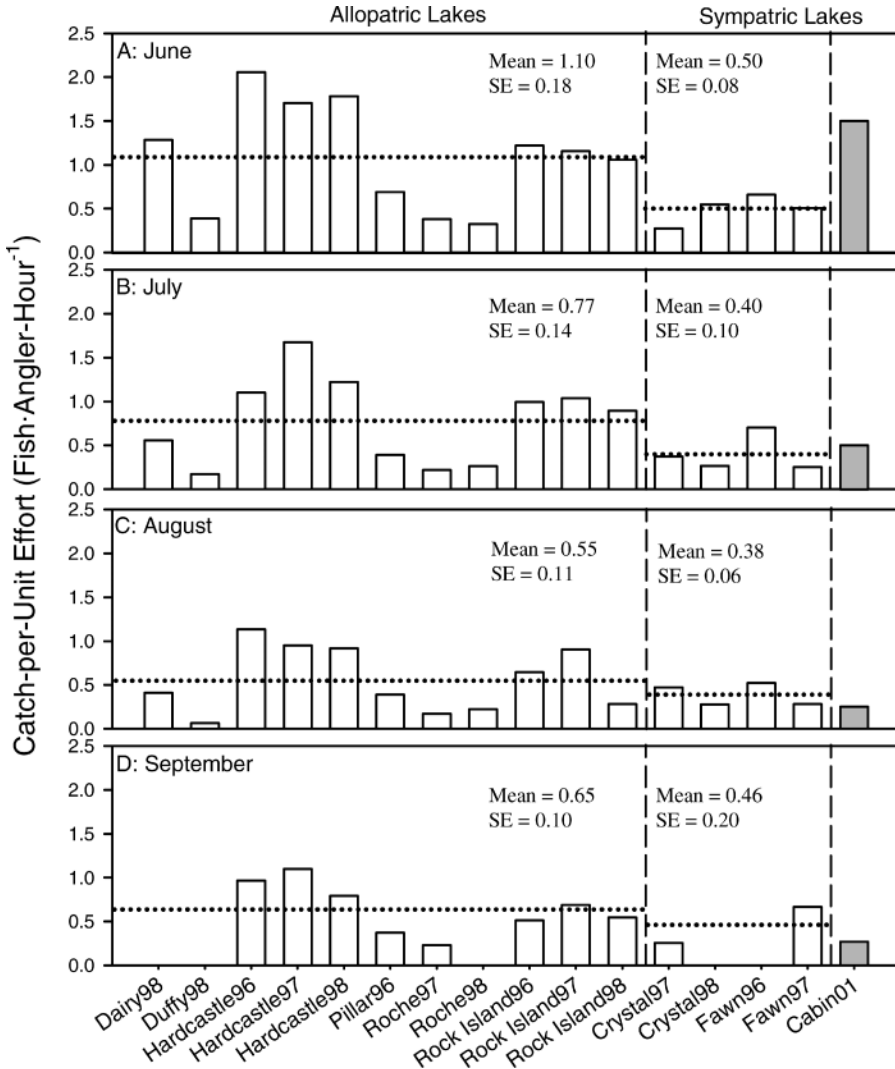


FIGURE 4.—Catch per unit effort of rainbow trout in Cabin Lake in 2001 (far right), compared with that of exploited populations from southern British Columbia (Cox 2000) in (A) June, (B) July, (C) August, and (D) September. Lake names are followed by the last two digits of the year in which they were sampled. Means are shown for each lake type in each month; overall means for the allopatric and sympatric populations are represented by dotted horizontal lines. Lake-months without bars represent missing data.

time of natural mortality, abundance would have to decrease by 86% to give the same decrease in catchability observed in Cabin Lake after the introduction of fishing. Such a change is unrealistic in a natural setting such as Cabin Lake. The dramatic changes in catchability throughout the growing season do not appear to be caused by changes in the abundance of catchable fish.

If the mean angler skill decreases throughout the fishing season, the resulting number of fish caught per unit effort will decrease, as will catch-

ability. A proportional decrease in skilled anglers is indicated by the decrease in Gini coefficients observed throughout the fishing season. Accounting for a change in angler skill results in an increase in catchability relative to the unadjusted catchability but still does not account for the pattern seen (Figure 6C; closed triangles). Thus, a decrease in mean angler skill probably is not the cause of the observed decrease in catchability in Cabin Lake after the introduction of angling.

If fish alter their behavior after catch and release

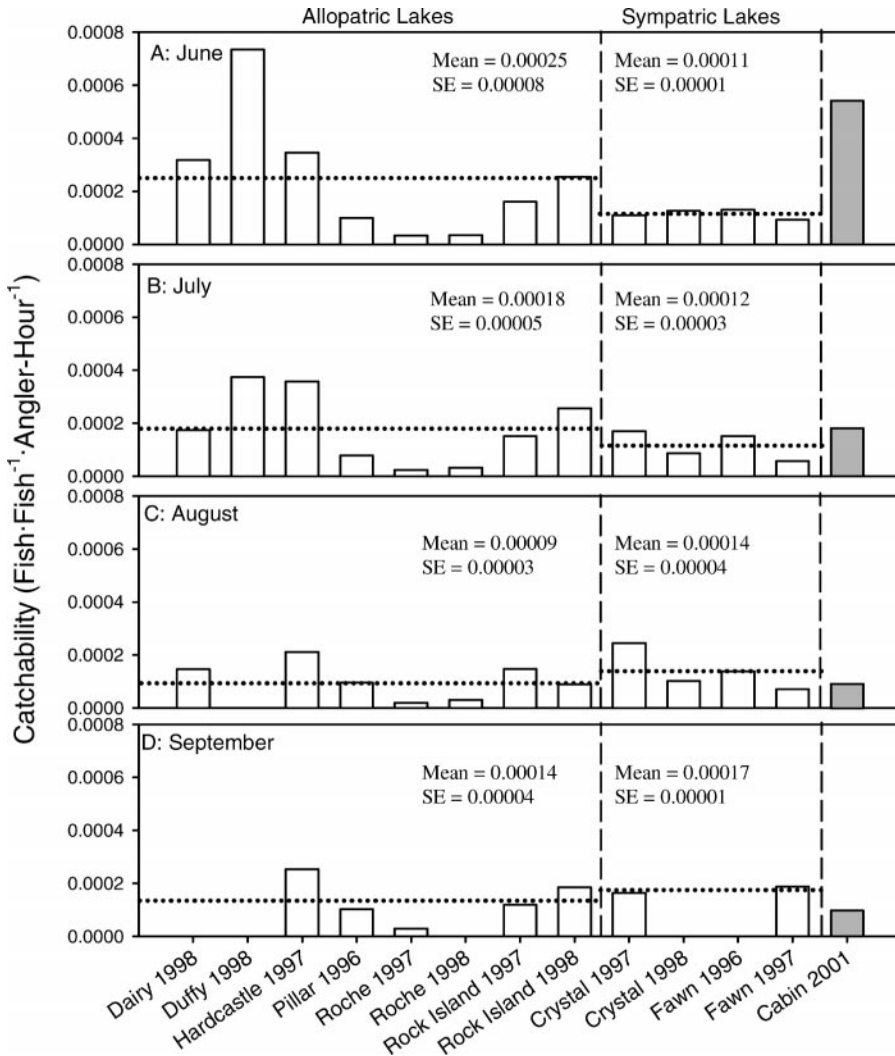


FIGURE 5.—Catchability of rainbow trout in Cabin Lake in 2001 (far right), compared with that of exploited populations from southern British Columbia (Cox 2000) in (A) June, (B) July, (C) August, and (D) September. Lake names are followed by the year in which they were sampled. Means are given for each lake type in each month; overall means for the allopatric and sympatric populations are represented by dotted horizontal lines. Lake-months without bars represent missing data.

so that they are no longer reactive to fishing gear, the observed catchability will decrease because of the decrease in the abundance of reactive fish. In theory, fish will eventually “recover” from being caught and will become as likely to take bait as before they were originally caught and released. When this happens, they will return to the reactive pool of fish. We adjusted the abundance of reactive fish to account for this hypothesized change in behavior after catch and release. Recovery time was assessed as taking either 2 weeks or the entire season. Assuming a 2-week recovery period pro-

duced catchability estimates higher than that observed in the first month while catch rates were high, but little difference was apparent later in the season because fewer fish were caught and released (Figure 6C; closed squares). Assuming a season-long recovery period resulted in catchability that did not decrease as much as the unadjusted catchability, but the same decreasing pattern was still followed (Figure 6C; open squares). Thus, behavioral changes in fish after catch and release are insufficient to account for the observed decrease in catchability in Cabin Lake.

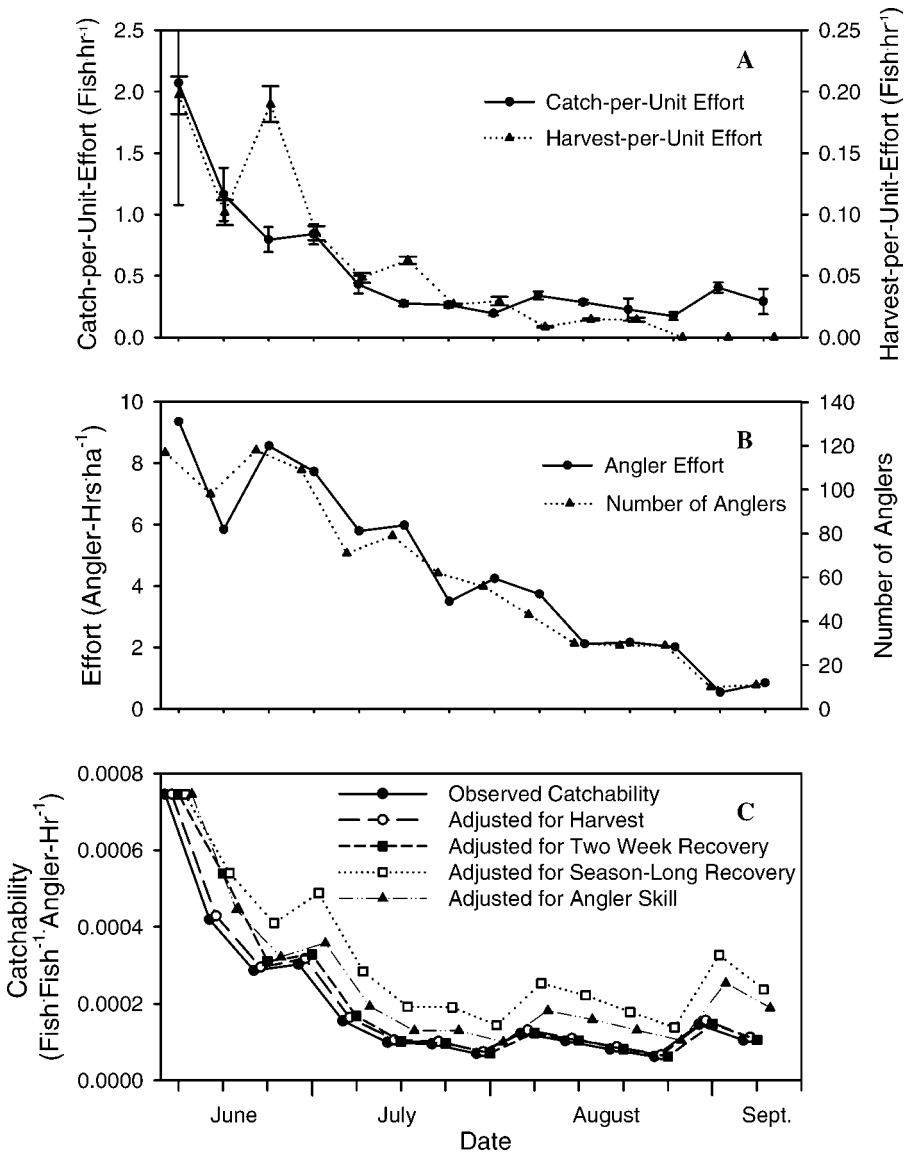


FIGURE 6.—Seasonal trends in (A) catch and harvest per unit effort, (B) angler effort and the number of anglers, and (C) catchability measures, each calculated for each week of the angling season in 2001 on Cabin Lake. The vertical bars in panel (A) represent standard errors. See the text for an explanation of the different catchability measures shown in panel (C).

Although none of the factors examined were found to have been the sole cause of the dramatic decrease in catchability, probably all played some part in the observed pattern. When we accounted for fish harvest, the decrease in catchability was 1.1% more than the decrease in unadjusted catchability. The assumption that mean angler skill decreased throughout the angling season accounted for 13.1% of the seasonal decrease in catchability.

Finally, refractory periods 2-weeks or season-long accounted for 0.0% and 20.6% of the change in catchability, respectively. Therefore, none of these processes alone can explain the seasonal decline in catchability we observed in Cabin Lake.

Discussion

Anglers play a key role in the dynamics of sport fish populations. The obvious and direct impact is

through both harvest and size-dependent catch-and-release mortality, in which large fish are more likely to be caught and harvested than small fish (Isbell and Rawson 1989; Paul et al. 2003; Post et al. 2003). Although angler motivations are varied and complex (Fedler and Ditton 1994; Connelly et al. 2001), angler effort clearly is influenced by catch rate (Johnson and Carpenter 1994; Cox and Walters 2002). In this way, the abundance of the fish population also influences angler behavior. Concordance between prediction from ideal free distribution theory and spatial distribution of fishing quality makes these dynamic linkages clear (Cox 2000; Post et al. 2002; Parkinson et al. 2004). These interactions between anglers and fish populations have been observed in fully exploited populations, which tend towards a dynamic equilibrium between effort and quality (Parkinson et al. 2004). On the other hand, newly developed fisheries such as the one we observed in Cabin Lake are probably in a transitory state marked by high catchability and high catch rates. A key question is whether this desirable state can be maintained.

The previously unexploited population of rainbow trout in Cabin Lake was not particularly dense in comparison with established exploited populations, at least in part because of competition for resources with lake chub (van Poorten 2003). But catchability was certainly higher than observed in many other fully exploited populations, at least early in the development of the fishery. Rainbow trout catchability was about 4.7 times higher than observed in other multispecies lakes and higher than the mean catchability observed in allopatric lakes. This difference in catchability disappeared within a few weeks after the population was opened to exploitation. This high catchability translated into high catch rates, but these high catch rates declined rapidly, in synchrony with decreases in catchability. Although our research on the population structure and fishery characteristics does not allow us to identify the process that gives rise to the pattern in catchability seen in this newly developed fishery, it does allow us to reject several commonly held explanations. First, inclusion of a complete creel census with precise estimates of total harvest and the total population estimate allows us to reject the hypothesis that our observed catchability pattern is biased as a result of rapid population reductions attributable to harvest. Although one could argue that a previously unexploited population might contain a proportion of naïve individuals that would be rapidly removed

when the fishery first opens, the harvest in Cabin Lake was sufficiently low that this process cannot explain the pattern of catchability we observed. One could also hypothesize that once a lake is opened to fishing, with a large catch-and-release component, individuals once released might become less catchable. Again, we know from our creel census conducted as part of the experimental fishery that the magnitude of catch and release was not sufficient to completely explain the initially high catchability and the subsequent rapid reduction to levels more typical of fully exploited rainbow trout fisheries. However, a behavioral change might be at least partially responsible for this rapid decrease in catchability early in the fishery. This helps explain the 5.2-fold difference in catchability in the test fishery time period (July–August) between years, despite a similar range in temperature each year (B. T. van Poorten, unpublished data). Direct behavioral observation will be needed to verify whether this behavioral shift after catch and release is a mechanism driving seasonal catchability.

Another interesting dynamic feature of the newly opened Cabin Lake rainbow trout fishery is the equity of catch among anglers. As is common in recreational fisheries, a small portion of the anglers catch the largest proportion of the catch and the largest portion of the anglers catch no or few fish (Baccante 1995). Early in the development of the Cabin Lake fishery, the catch was more evenly distributed among anglers, which is often indicative of high mean catch rates. This rapidly changed towards the highly skewed distribution of catches among anglers towards that more commonly seen (Baccante 1995).

Our detailed population and creel assessments also allow testing hypotheses of the mechanisms responsible for seasonal variation in catch rates in rainbow trout fisheries. It is a common observation that catch rates are highest in the spring, followed by substantial reductions in the summer and some recovery in the fall fishing season (Lux and Smith 1960; Johnson and Carpenter 1994; Cox 2000). Cox (2000) hypothesizes that this seasonal pattern reflects a combination of depletion of catchable-size fish as the fishing season progresses and an increasing pool of uncatchable individuals that have been caught and released. We observed a seasonal pattern in catch rate in Cabin Lake similar to that in Cox (2000) despite insignificant levels of depletion or catch and release of trout. Although a maximum of 21% of the reduction in catchability could be explained by a substantial shift in fish

behavior after catch and release, clearly an ecological rather than a fishery-dependent mechanism is primarily driving this commonly observed seasonal pattern.

This work has two important implications for fisheries management. First, maintaining high catchability and high catch rates in newly opened fisheries will be extremely difficult. Our experimental fishery, involving a pristine, previously closed population, suggests that very little fishing effort will drive newly developed fisheries to the dynamic status of fully exploited systems (Parkinson et al. 2004). The initially high catch rates seen in newly opened fisheries (Goedde and Coble 1981) apparently are transitory and quickly diminished by factors such as depletion (Cox 2000) or environmentally and fishery-induced behavioral changes. The second implication of this work to management is the inference that the seasonality in catchability is driven more by intrinsic factors than by the fishery. A common management technique is to control harvest by regulating for inefficiency. Techniques such as gear restrictions and spatial and temporal closures work by reducing the effectiveness per unit of effort (i.e., catchability) and therefore reducing harvest by a given effort density. Our analysis of seasonality of catchability in allopatric rainbow trout fisheries suggests that restricting fishing effort to July and August could support 13–130% more effort than a spring-only fishery, given the differences in catchability between those time periods. In contrast, there was no evidence of seasonality in catchability in fully exploited sympatric rainbow trout populations. Interestingly, catchability was similar during the summer months in sympatric and allopatric lakes and differed only in the spring.

Empirical and modeling studies have described the pattern and explored the mechanisms involved in the dynamic linkage between angler behavior and sport fish populations (Johnson and Carpenter 1994; Hansen et al. 2000; Newby et al. 2000; Cox et al. 2002; Post et al. 2002; Post et al. 2003; Parkinson et al. 2004). Studies on rainbow trout fisheries suggest that these interactions tend towards equilibrium, the mean regional catch rates differing as a function of travel time and variance being low within equivalent travel time regions (Cox and Walters 2002; Post et al. 2002; Parkinson et al. 2004). These positive deviations in fishing quality from equilibrium conditions may be due to factors such as inaccessibility (Parkinson et al. 2004). A newly developed fishery, such as the Cabin Lake fishery we studied, will also deviate

positively from this equilibrium. Our results suggest that not only is this transition a function of effort dynamics but also the duration of transition from a high catchability state towards the lower levels more typical of fully exploited systems is short (Goedde and Coble 1981). Additional study is needed to identify the mechanisms involved in supporting this desirable high catchability state and over what levels of effort it can be maintained.

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References

- Baccante, D. 1995. Assessing catch inequality in walleye angling fisheries. *North American Journal of Fisheries Management* 15:661–665.
- Bailey, P. B., and D. J. Austen. 2002. Capture efficiency of a boat electrofisher. *Transactions of the American Fisheries Society* 131:435–451.
- Carpenter, S. R., A. Munoz-del-Rio, S. Newman, P. W. Rasmussen, and B. M. Johnson. 1994. Interactions of anglers and walleyes in Escanaba Lake, Wisconsin. *Ecological Applications* 4:822–832.
- Connelly, N. A., B. A. Knuth, and T. L. Brown. 2001. An angler typology based on angler fishing preferences. *Transactions of the American Fisheries Society* 130:130–137.
- Cox, S. 2000. Angling quality, effort response, and exploitation in recreational fisheries: field and modelling studies on British Columbia rainbow trout (*Oncorhynchus mykiss*) lakes. Doctoral dissertation. University of British Columbia, Vancouver.
- Cox, S. P., T. D. Beard, and C. Walters. 2002. Harvest control in open-access sport fisheries: hot rod or

- asleep at the reel? *Bulletin of Marine Science* 70: 749–761.
- Cox, S. P., and C. Walters. 2002. Modeling exploitation in recreational fisheries and implications for effort management on British Columbia rainbow trout lakes. *North American Journal of Fisheries Management* 22:21–34.
- Cross, T. K., M. C. McInerney, and D. H. Shupp. 1995. Seasonal variation in trap-net catches of bluegill in Minnesota lakes. *North American Journal of Fisheries Management* 15:382–389.
- Donald, D. B., and D. J. Alger. 1986. Dynamics of unexploited and lightly exploited populations of rainbow trout (*Salmo gairdneri*) from coastal, montane, and subalpine lakes in western Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 43:1733–1741.
- Fedler, A. J., and R. B. Ditton. 1994. Understanding angler motivations in fisheries management. *Fisheries* 19(6):6–13.
- Goedde, L. E., and D. W. Coble. 1981. Effects of angling on a previously fished and an unfished warmwater fish community in two Wisconsin Lakes. *Transactions of the American Fisheries Society* 110:594–603.
- Hansen, M. J., T. D. Beard, Jr., and S. W. Hewett. 2000. Catch rates and catchability of walleyes in angling and spearing fisheries in northern Wisconsin Lakes. *North American Journal of Fisheries Management* 20:109–118.
- Healey, M. C. 1978. Fecundity changes in exploited populations of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*). *Journal of the Fisheries Research Board of Canada* 35: 945–950.
- Healey, M. C. 1980. Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* 37:255–267.
- Isbell, G. L., and M. R. Rawson. 1989. Relations of gill-net catches of walleyes and angler catch rates in Ohio waters of Western Lake Erie. *North American Journal of Fisheries Management* 9:41–46.
- Johnson, B. M., and S. R. Carpenter. 1994. Functional and numerical responses: a framework for fish–angler interactions? *Ecological Applications* 4:808–821.
- Johnson, L. 1972. Keller Lake: characteristics of a culturally unstressed salmonid community. *Journal of the Fisheries Research Board of Canada* 29:731–740.
- Johnson, L. 1975. Distribution of fish species in Great Bear Lake, Northwest Territories, with reference to zooplankton, benthic invertebrates, and environmental conditions. *Journal of the Fisheries Research Board of Canada* 32:1989–2004.
- Johnson, L. 1976. Ecology of arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, arctic char, *S. alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. *Journal of the Fisheries Research Board of Canada* 33:2459–2488.
- Johnson, L. 1994. Long-term experiments on the stability of two fish populations in previously unexploited arctic lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 51:209–225.
- Kennedy, W. A. 1953. Growth, maturity, fecundity, and mortality in the relatively unexploited whitefish, *Coregonus clupeaformis*, of Great Slave Lake. *Journal of the Fisheries Research Board of Canada* 10: 413–441.
- Lamontagne, S., and D. W. Schindler. 1994. Historical status of fish populations in Canadian Rocky Mountain lakes inferred from subfossil *Chaoborus* (Diptera: Chaoboridae) mandibles. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1376–1383.
- Lux, F. E., and L. L. Smith, Jr. 1960. Some factors influencing seasonal changes in angler catch in a Minnesota lake. *Transactions of the American Fisheries Society* 89:67–79.
- McDonald, M. E., and A. E. Hershey. 1989. Size structure of a lake trout (*Salvelinus namaycush*) population in an arctic lake: influence of angling and implications for fish community structure. *Canadian Journal of Fisheries and Aquatic Sciences* 46:2153–2156.
- Mills, C. P. R., G. A. T. Mahon, and D. J. Piggins. 1986. Influence of stock levels, fishing effort, and environmental factors on anglers' catches of Atlantic salmon, *Salmo salar* L., and sea trout, *Salmo trutta* L. *Aquaculture and Fisheries Management* 17:289–297.
- Mills, K. H., S. M. Chalanchuk, and D. J. Allan. 2002. Abundance, annual survival, and recruitment of unexploited and exploited lake charr, *Salvelinus namaycush*, populations at the Experimental Lakes Area, northwestern Ontario. *Environmental Biology of Fishes* 64:281–292.
- Newby, J. R., M. J. Hansen, S. P. Newman, and C. J. Edwards. 2000. Catchability of walleyes to angling in Escanaba Lake, Wisconsin, 1980–1995. *North American Journal of Fisheries Management* 20: 873–881.
- Parkinson, E. A., J. R. Post, and S. P. Cox. 2004. Linking the economics of harvest to recruitment dynamics in a spatially structured fishery. *Canadian Journal of Fisheries and Aquatic Sciences*. 61:1658–1670.
- Parks Canada 2001. Fishing regulations summary, April 1, 2001–March 31, 2002. Mountain national parks in Alberta and British Columbia. Ministry of Public Works and Government Services Canada, R63–259/2001E, Ottawa.
- Paukert, C. P., and D. W. Willis. 2001. Comparison of exploited and unexploited yellow perch *Perca flavescens* (Mitchill) populations in Nebraska sandhill lakes. *Fisheries Management and Ecology* 8:533–542.
- Paul, A. J. 2000. Recruitment dynamics of bull trout (*Salvelinus confluentus*): linking theory and data to species management. Doctoral dissertation. University of Calgary, Calgary, Alberta.
- Paul, A. J., J. R. Post, and J. D. Stelfox. 2003. Can anglers influence the abundance of native and non-native salmonids in a stream from the Canadian

- Rocky Mountains? North American Journal of Fisheries Management 23:109–119.
- Post, J. R., E. A. Parkinson, and N. T. Johnston. 1999. Density-dependent processes in structured fish populations: interaction strengths in whole-lake experiments. Ecological Monographs 69:155–175.
- Post, J. R., M. Sullivan, S. Cox, N. P. Lester, C. J. Walters, E. A. Parkinson, A. J. Paul, L. Jackson, and B. J. Shuter. 2002. Canadian recreational fisheries: the invisible collapse? Fisheries 27(1):6–17.
- Post, J. R., C. Mushens, A. Paul, and M. Sullivan. 2003. Assessment of alternate regulations for sustaining recreational fisheries: model development and application to bull trout. North American Journal of Fisheries Management 23:22–34.
- Power, G. 1978. Fish population structure in arctic lakes. Journal of the Fisheries Research Board of Canada 35:53–59.
- Raat, A. J. P. 1987. Effects of crowding and availability of food on growth and angling vulnerability in the two sexes of scaled and mirror patterned carp (*Cyprinus carpio* L.). Netherlands Journal of Zoology 37:1–25.
- Rochet, M.-J. 1998. Short-term effects of fishing on life history traits of fishes. ICES Journal of Marine Science 55:371–391.
- Toetz, D., M. Muoneke, and J. Windell. 1991. Age, growth, and condition of brook trout (*Salvelinus fontinalis*) from an unexploited alpine lake. Northwest Science 65:89–92.
- van Poorten, B. T. 2003. The impacts of angling on rainbow trout population dynamics. Master's thesis. University of Calgary, Calgary, Alberta.