Growth, Survival, and Vulnerability to Angling of Three Wild Brook Trout Strains Exposed to Different Levels of Angler Exploitation Over Time

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Abstract.—It has been suggested that the genetic growth potential of trout may be degraded, over time, by differential angler harvest of the faster-growing fish of each cohort. To test this hypothesis young-of-the-year wild brook trout from two branches of the Au Sable River and from the East Branch of the Fox River were stocked in three experimental lakes to determine their relative growth and survival after 2 years of residence. Brook trout populations from the Au Sable River were believed to have been historically exploited more intensively than that from the East Branch of the Fox River. The relative vulnerability to angling for the three strains was estimated in two of the lakes. Further, mean sizes of angler-caught trout were compared to mean sizes of trout captured by intensive gill netting to determine if anglers caught the larger trout in the population, and to ascertain possible correlations between growth rate and vulnerability to angling. Some differences in growth were found, suggesting that strains differed genetically. Brook trout from the East Branch Fox River exhibited significantly greater increases in length and weight than fish from either the North Branch Au Sable or the Mainstream Au Sable. Growth was similar for both Au Sable River strains. A habitat or lake effect on brook trout growth was evident. Highest growth for all strains occurred in Hemlock Lake and lowest in South Twin Lake. The superior growth performance of East Branch Fox River brook trout was most evident in Hemlock Lake, where all strains grew best. Mature males were significantly longer and heavier than mature females when data were pooled across strains for each lake. East Branch Fox River mature females allocated relatively less energy to gonadal weight than mature females of the Au Sable River strains. East Branch Fox River and Mainstream Au Sable brook trout had the highest and lowest survival, respectively, in all three lakes. The difference in survival between East Branch Fox River and Mainstream Au Sable strain trout was greatest in Hemlock Lake, where all strains exhibited relatively low survival; the difference was least in North Twin Lake, where all strains demonstrated relatively high survival. A significantly higher percentage of the population of East Branch Fox strain brook trout were caught, during 3 days of experimental angling, than either of the Au Sable River strains indicating greater vulnerability to angling for this strain. The mean lengths and weights of brook trout caught by angling from North Twin Lake were significantly higher than the means for trout caught with nets. In South Twin Lake, where all strains were more similar in size, no significant differences were detected between lengths or weights of angler and net-caught trout. The results of this study suggest that the intensity of angler exploitation, over time, may have altered the genetic potential for growth and catchability of these wild brook trout strains.

Biologists and anglers have hypothesized that some growth differences observed among brook trout (*Salvelinus fontinalis*) populations may be due to genetic differences in their growth potential as well as to the productivity of their environment. It has been further suggested that the genetic growth potential of trout has been degraded by differential angler harvest of the faster-growing fish of each cohort, over time, thus leaving the slower growers to reproduce the stock. Cooper (1952) showed that anglers differentially exploited the faster-growing brook trout in the Pigeon River. Further evidence that growth and angler catchability are positively related was reported by Brauhn and Kincaid (1982) and Dwyer and Piper (1984), who found that rainbow trout strains genetically selected for faster growth were more vulnerable to angling than slower-growing strains. The probability of angler capture also appears to increase with fish size for brown trout, largemouth bass, and small-mouth bass (Favro et al. 1986; Burkett et al. 1986; Clapp and Clark 1989). Circumstantial evidence suggests that selective harvest of the faster-growing fish of a cohort by commercial or sport fisheries may reduce the genetic growth potential of fish stocks (Handford et al. 1977; Ricker 1981; Alexander 1987). Other possible evolutionary responses to size-selective exploitation include reductions in fish age and size at first reproduction (Handford et al. 1977; Healey 1975; Kennedy 1953). Modification of phenotypic variation by exploitation imposes the risk of a reduction of genotypic diversity, which in turn could result in a lower level of fitness (Kapuscinski and Lannan 1986).

The impetus for this study was provided by the finding of Alexander (1987) that wild brown trout populations which were believed to have been exposed to high levels of size-selective exploitation grew more slowly than more lightly exploited stocks. The greater vulnerability to angling of brook trout, compared to brown trout could theoretically result in more intense selection for slower growth, or changes in other traits like catchability.

The primary purpose of the present study was to determine if wild brook trout from the East Branch Fox River, Michigan, which have been exposed to relatively low angling exploitation over time, differ in their growth potential from wild brook trout from two branches of the Au Sable River which have been subject to more intense exploitation. Secondary objectives were to estimate survival, measure gonadal energy storage, measure vulnerability to angling, determine if anglers caught the larger members of the populations, and determine if growth rate and angling vulnerability were correlated.

Methods

Young-of-the-year wild brook trout were collected with continuous current 230-volt DC electrofishing gear in October 1987 from three Michigan rivers. Two rivers were located in Crawford County; the Mainstream Au Sable River (T26N, R2W, Section 5, and T26N, R3W, Section 12), and the North Branch Au Sable River (T28N, R1W, Section 19, and T27N, R1W, Section 8. The third trout stock was collected from the East Branch Fox River in Schoolcraft County (T47N, R13W, Sections 21 and 28). We believe strongly that the Au Sable River stocks have been subject to more intensive harvest over the past 100 years than the stock in the East Branch of the Fox River. The estimated annual fishing pressure for the North and Mainstream Au Sable rivers ranged from 371 to 1065 hours per ha during the time period 1958-76 (Alexander et al. 1979). It can be safely assumed that fishing pressure prior to this time was also high due

to the river's long-standing reputation as a good trout stream and its accessibility to anglers from Michigan's population centers. No creel census surveys have been conducted on the East Branch Fox River, but fishing pressure is believed to be relatively lower because it is in a remote area, is more difficult to fish due to heavy cover within and along the stream, is more distant from population centers, and has a lesser reputation as a trout stream.

Trout collected from the above rivers were planted in three experimental lakes in the Pigeon River Country State Forest, Otsego County, Michigan (Table 1). No sorting or selection of trout to be transplanted was done. Thus, trout caught and transplanted were as close as possible to a random sample of the young-of-the-year cohorts. Upon capture, all trout were measured and fin clipped for permanent identification. Trout from both the Mainstream Au Sable River and North Branch Au Sable River were stocked in the experimental lakes on the same days they were collected. Brook trout from the East Branch Fox River were held in a wire-mesh live crate in the river for a maximum of 2 days before being transported and stocked. Stresses due to collection, holding, transporting, fin clipping, and planting were believed to be similar for both Au Sable River groups and no mortalities occurred. East Branch Fox River trout were held longer prior to stocking and 30 trout were dead upon arrival at the stocking sites. However, only live and apparently vigorous trout were stocked. Each experimental lake was stocked with a total of 247 trout per ha (to allow for comparisons with previous studies of brook trout conducted in these lakes). Equal numbers of each of the three wild brook strains were stocked in each lake. The experimental lakes were closed to fishing and patrolled at random times to look for possible poaching. Information on the morphometry, chemistry, and minnow species present in the study lakes can be found in Gowing (1986).

After planting, trout were allowed to grow for 2 years and their incremental growth gain and survival were used to judge the relative performance of the three stocks. Sampling was begun in mid-October 1989 to obtain population estimates using mark-and-recapture techniques. A portion of the trout population in Hemlock Lake was captured by electrofishing and marked by clipping the bottom tip of the caudal fin. Trout in North and South Twin lakes were captured for marking by angling using artificial lures. All angler-caught trout were held in fine-mesh nylon-holding nets for 48 hours after capture to determine if there was any hooking mortality before they were marked and released. All trout captured by electrofishing and angling were measured to the nearest 0.25 cm, weighed to the nearest gram, and identifying fin clips were recorded. Two days after these marked trout were released we began the near-complete removal of trout from the lakes using gill nets. Mesh sizes ranged from 5.7- to 8.9-cm stretched mesh. Approximately 600 m of gill nets were set in each lake on each day that netting was conducted. Netting continued through October and early November 1989 until daily catches declined to near zero. All trout were weighed, measured, and fin clips were recorded in the same manner as stated above. In addition, gonadal tissues were weighed to the nearest 0.1 g and sex was recorded.

Population estimates and variances were computed using the Petersen mark-and-recapture method (Ricker 1975). The gill-net samples provided recapture ratios for Petersen population estimates. Differences between brook trout strain averages for length increments, total weight, gonad weight, and the ratio of gonad weight to total

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weight were analyzed for each lake using one-way analysis of variance. The Scheffè multiple comparison procedure was used to compare all possible combinations of strain means (Scheffè 1959). Differences were judged to be significant for $P < 0.05$. The assumption of homogeneity of variance was tested using the Bartlett test (Neter and Wasserman 1974). The hypothesis that the populations had the same variance was rejected if both tests had $P > 0.05$. Effects of strain, sex, and lake on growth were tested using a three-way analysis of variance. Survival was computed as the Petersen population estimate divided by the number of trout stocked. Confidence limits (95%) for survival estimates were then computed and examined for overlap to determine significant differences. Average lengths and weights of trout caught by angling and gill nets were compared using a two-sample t-test.

Results

Growth

The data for all lakes showed that East Branch Fox River brook trout increased significantly more in length (length increments) during the 2 years than either Au Sable strain in every lake ($P < 0.05$) (Figure 1). There were no significant differences in length increments between the two Au Sable strains. All strains of trout exhibited the best growth in Hemlock Lake and the slowest growth in South Twin Lake. The difference between the growth increment of the East Fox Branch River strain and the slowest-growing strain in Hemlock Lake was 3.1 cm, approximately twice the analogous difference found in North Twin and South Twin lakes (Figure 1).

East Branch Fox River brook trout also exhibited significantly greater mean body weight than both Au Sable strains when recovered at the end of the study ($P < 0.05$) (Figure 1). The mean weight for brook trout (all strains combined) was more than twice as high in Hemlock Lake, where growth in weight was greatest, than in South Twin Lake, where growth was slowest. There was more than a fourfold greater weight difference between the fastest- and slowest-growing strains in Hemlock Lake (126 g) than in South Twin Lake (29 g). Thus, in lakes where growth in weight was higher, the absolute differences between East Branch Fox and Au Sable trout were larger.

Although mature male brook trout of all strains had a greater mean length increment than mature females in every lake (Figure 2), the differences between the sexes were not significant ($P > 0.05$). Mean weight of males versus females paralleled results for length increments but likewise were not significantly different (Figure 2). A three-way analysis of variance for incremental length with strain, sex, and lake indicated that all three variables had highly significant effects on growth ($P < 0.001$). Females were significantly smaller than males based on pooled-strain mean lengths and weights in each of the three lakes ($P < 0.01$).

Survival

In all three test lakes East Branch Fox River trout exhibited the highest survival, Mainstream Au Sable trout had the lowest survival and North Branch Au Sable trout survival was intermediate (Table 1). Survival ranged from 6.1% for Mainstream Au Sable trout in Hemlock Lake up to 68.1% for East Branch Fox trout in North Twin Lake. East Fox Branch strain survival was 1.6 times higher than survival of Mainstream Au Sable fish in North Twin Lake, 2.4 times higher in South Twin Lake, and 3.5 times higher in

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Hemlock Lake. Thus, in lakes where survival of all strains was lower the differences in survival between the strains was higher.

Gonad growth

Mean gonadal weight for mature males and females and the percentage of total weight comprised of gonads varied between lakes and strains (Figure 3). For mature females the percentage ranged from 13.1 to 19.1. The analogous percentage for mature males ranged from 1.9 to 3.7. In North Twin Lake, East Branch Fox River strain mature females had a significantly lower percentage gonad weight than either Au Sable strain whereas mature East Fox Branch River males had a significantly higher percentage gonad weight ($P < 0.05$). In South Twin Lake ovarian tissues of East Branch Fox trout comprised a significantly smaller percentage of total weight than both Au Sable strains and North Branch Au Sable percent gonad weight for females was significantly smaller than those for Mainstream Au Sable fish ($P < 0.05$). There were no significant differences among strains in the amount of energy allocated to gonadal tissue by mature males recovered from South Twin Lake. In Hemlock Lake, East Branch Fox River females had significantly lower percent-age gonad weight than Mainstream Au Sable females while East Branch Fox males apportioned significantly more energy to gonads than North Branch Au Sable males. Other comparisons between strains in this lake were not significant at $P < 0.05$.

Vulnerability to angling

Experimental anglers caught a significantly higher percentage ($P < 0.05$) of the population of East Branch Fox River strain brook trout in North Twin Lake during 3 days of angling than either of the Au Sable strains (Table 2). In South Twin Lake a significantly lower percentage of North Branch Au Sable trout were caught by angling compared to East Branch Fox trout. No significant differences in vulnerability to angling (percent of population caught) were detected between the Au Sable strains in either lake.

The brook trout caught by angling (all strains combined) were 1.1 cm longer than those caught with gill nets in North Twin Lake and the difference was significant ($P < 0.001$). Angler-caught brook trout (all strains combined) were also significantly heavier (15 g) than those taken with gill nets in North Twin Lake ($P < 0.02$). Although angler-caught trout of each of the three individual strains were larger than gill-netted trout there were no significant differences at the 95% level between lengths and weights in North Twin Lake. However, the 0.6 cm greater length of East Branch Fox River strain trout caught by angling versus those caught in gill nets was marginally significant at $P = 0.059$. In South Twin Lake, where all strains were more similar in size, there were no significant length or weight differences between angler and gill- net-caught trout either for combined or within individual strains.

Discussion

Growth

The East Branch Fox River trout stock grew better than both the North Branch Au Sable and Mainstream Au Sable stocks. Although there was a habitat (lake) effect on growth the relative growth ranking of the three trout strains was consistent over all three lakes. There were essentially no

growth differences between brook trout from either of the Au Sable River stocks.

A number of possible explanations can be offered for the varying growth rates of these wild brook trout stocks. First, the hypothesis that growth potential has been altered by angler exploitation of faster-growing trout is supported to the extent that growth rates measured in this study seem to be inversely correlated with historical harvest rates on the donor populations. Moreover, the relatively larger ovaries found in Au Sable River brook trout are consistent with the hypothesis that a trout population subject to high exploitation of reproductive-age fish may increase its fitness by increasing fecundity thereby enhancing the probability of successful reproduction.

Breeding of captive trout stocks indicates that growth is heritable and can be enhanced through selection (Donaldson and Olson 1955; Donaldson and Menasveta 1961; Aulstad et al. 1972; Gjedrum 1976; 1983; Kincaid et al. 1977; Kinghorn 1983). Thus, selection for slower growth is also possible, particularly under controlled conditions where selection intensity can be high. In wild populations evidence of selection for either fast or slow growth is largely circumstantial since neither the selection intensity nor heritability of growth for these populations can be readily estimated. Trout predators are a natural selection force which would favor faster-growing trout since predators selectively harvest smaller fish (Alexander 1977). Thus, the slower-growing trout of a cohort are within the predators' preferred prey size range for a greater period of time than fast growers. Since angler harvest usually is subject to minimum size limit regulations, the faster-growing members of a cohort reach the legal size quicker and are therefore cropped more intensively than the slow-growing individuals. Under these circumstances selective pressures for changes

in growth potential would be expected to be partially compensatory. The findings reported for this study and a similar study reported by Alexander (1987) provide circumstantial evidence that the net selection is in the direction of slower growth. However, Behnke (1989) argues that the selection for fast growth by predators coupled with factors such as multiple spawning opportunities and greater fecundity and dominance of larger fish would favor fast growth genes even in populations subject to angling exploitation.

A second possible reason for differing growth potentials in these wild brook trout stocks is that they may have been founded by different parental stocks. Accounts of early settlers in Michigan around 1840 indicate that there were no brook trout in the northern part of the Lower Peninsula with the possible exception of a few streams at the northern tip. During the same time period they were recognized as widely dispersed in Upper Peninsula streams (Westerman 1961). The principal salmonid formerly in these waters was the Arctic grayling (*Thymallus arcticus*), since extirpated. Thirty years later brook trout were widely established in most coldwater streams of the Lower Peninsula as a result of state and private stocking efforts. Both the East Branch Fox and Au Sable rivers received plants of hatchery-reared brook trout over the years between 1900 and 1960. None of the rivers is currently stocked near the areas where test fish for this study were collected. Thus, the present stocks represent an unknown mixture of founder brook trout stocks which may differ in their growth characteristics for many reasons other than size-selective angling exploitation.

A third possible interpretation of growth differences is that natural selection over time has resulted in a divergence in growth potential. Presumably, mortality due to

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predacious fish and birds would represent selection for fast growth of trout in river systems since smaller trout are more vulnerable to predation. Variation in growth potential or other stock characteristics could still occur due to differences in the intensity of selection or the amount of additive genetic variance for growth traits (Kapuscinski and Jacobson 1987). Although estimates of selection intensity or additive genetic variance are not available for the brook trout stocks tested in this study, one may reasonably postulate that the Au Sable River stocks which were originally established from hatchery plants may be less genetically variable than stocks in the East Branch Fox River which have a native fish component. Early fish culturists had little knowledge of the negative effects on genetic diversity and fitness which ensue when small numbers of parents are used for breeding purposes. In theory, even in the absence of exploitation of the larger trout by man, natural selection could have more rapidly "used up" the additive genetic variance for growth in an originally less variable Au Sable stock resulting in fixation of growth potential at a lower level than East Branch Fox stocks.

A fourth possible explanation for the higher growth potential of East Branch Fox River brook trout is that this stock is better adapted to a lake environment. Such adaptation could be a consequence of greater genetic diversity as discussed above, or the result of environmental selection. Large segments of the lower reaches of the East Branch Fox River are characterized by deep, slow-moving water. In these regions the river has a more lake-type habitat. Local fisheries biologists and anglers report that the brook trout in this area grow to exceptionally large size. Further, when these trout migrate upstream to smaller and faster waters with appropriate spawning substrate, they probably have a competitive advantage due to their large size, higher fecundity, and larger egg size, relative to trout which are residents of areas of faster and smaller waters. This could be expected to propagate traits which are more adaptive to lakes.

Finally, the greater growth in length and weight exhibited by East Branch Fox trout may be due, in part, to the fact that East Branch Fox females allocated relatively less energy to gonadal growth thereby enhancing somatic growth. Study design did not permit measure-ment of percentage maturity after one growing season in the lake so it is also possible that relatively more individuals of the Au Sable stocks matured earlier and hence grew less over the 2-year test period. Virtually all trout were mature after two growing seasons in the lakes. Differences in the amount of energy allocated to gonads by males cannot readily account for the larger East Branch Fox male growth increment measured in all three test lakes since East Branch Fox male gonads comprised a greater percentage of body weight than gonads of males of both Au Sable River strains in two of the three test lakes. In addition, the difference between the growth increments of mature males of the East Branch Fox trout versus growth increments for males of the Au Sable strains were generally larger than the analogous increments for mature females. If energy allotted to gonad growth had a major influence on strain differences in somatic growth the opposite relationship would be expected since percent gonad weight for mature males of the three strains usually differed by less than 1% whereas percent gonad weight for females differed by as much as 5.7% (Figure 3).

It cannot be determined from this study why the growth potentials varied among the wild stocks tested. This study showed that there was only a 1.9 cm difference in mean length increment over 2 years between brook trout from the East Branch Fox River versus

the average for North Branch Au Sable and Mainstream Au Sable brook trout (averaged over all three lakes). If we assume that differential cropping by anglers occurred only on the Au Sable River over a period of 100 years the degradation rate per 10 years was only 0.19 cm. In light of the fact that growth differences between strains were less in lakes where growth was slower for all strains, we would expect differences in growth between strains to be very small in typical Michigan riverine habitats where growth is usually much slower than in lakes.

Survival

Although differences in survival between strains were not statistically significant, the consistent top ranking of East Branch Fox strain survival rates in all three lakes suggests that there were true differences in survival potential. Higher survival of East Branch Fox versus Au Sable trout cannot be readily explained on the basis of differences in mortality due to handling stresses at the time young of the year were collected and stocked since the East Branch Fox trout were subject to longer holding times in a live crate in the river and were transported a much greater distance to the lakes.

If East Branch Fox brook trout were more adapted to lake environments, as discussed above under growth differences, their superior survival in the three lakes may also reflect this adaptation. Such adaptation could also be the result of greater genetic diversity and/or different environmental selection of parental stocks. In view of the good survival, particularly in North and South Twin lakes, illegal cropping of trout was apparently a negligible source of bias. No evidence of illegal angling was observed during the course of the study. Moreover, as discussed below, East Branch Fox trout were

apparently more vulnerable to angling, yet they had the best survival in all lakes.

Vulnerability to angling

The hypothesis that growth rate and angling vulnerability are positively correlated was supported by the fact that East Branch Fox River brook trout in North Twin Lake were significantly more vulnerable to capture by angling than either of the Au Sable River stocks. The significantly greater mean length of brook trout caught by angling (all strains combined) versus mean length of trout caught with gill nets in North Twin Lake likewise supports this hypothesis. The apparent lower catchability of Au Sable River brook trout could also be a response to selection against less wary individuals or they may have been less catchable simply because they were smaller. Numerous mark-and-recapture estimates of brook and rainbow trout populations conducted in sequential years in Michigan trout lakes have conclusively demonstrated that a larger proportion of the same cohort can be caught by the same amount of angling effort as the fish grow older and larger (Michigan Department of Natural Resources, unpublished data). Other investigators have also observed that probability of angler capture appears to increase with fish size for brown trout, largemouth bass, and smallmouth bass (Favro et al. 1986; Burkett et al. 1986; Clapp and Clark 1989). Brauhn and Kincaid (1982) and Dwyer and Piper (1984) observed that faster-growing rainbow trout strains were more readily captured by anglers than slower- growing strains. Differences in catchability may also be related to behavioral differences. Trojnar and Behnke (1974) attributed differential vulnerability to angling between cutthroat trout strains to ecological segregation which

made one strain more available to surface-fishing fly fishermen. Catchability ranks of the different stocks in South Twin Lake were the same as those observed in North Twin Lake but were not significantly different, possibly because the sample size was smaller.

Management implications

If the superior growth rate exhibited by the East Branch Fox River strain brook trout is due primarily to angler selection, regulations which give greater protection to larger, faster-growing trout should reduce further changes to the genetic character of wild stocks and may even result in increases in growth rates and catchability over time because the faster-growing trout of a cohort are likely to have greater natural survival rates and spawning success. However, such responses will probably be slow and cannot be assured since the frequency of genes which provide the basis for fast growth may have become extremely reduced over time.

Managers can utilize strain performance differences due primarily to greater genetic diversity by making greater use of select wild broodstocks for stocking purposes.
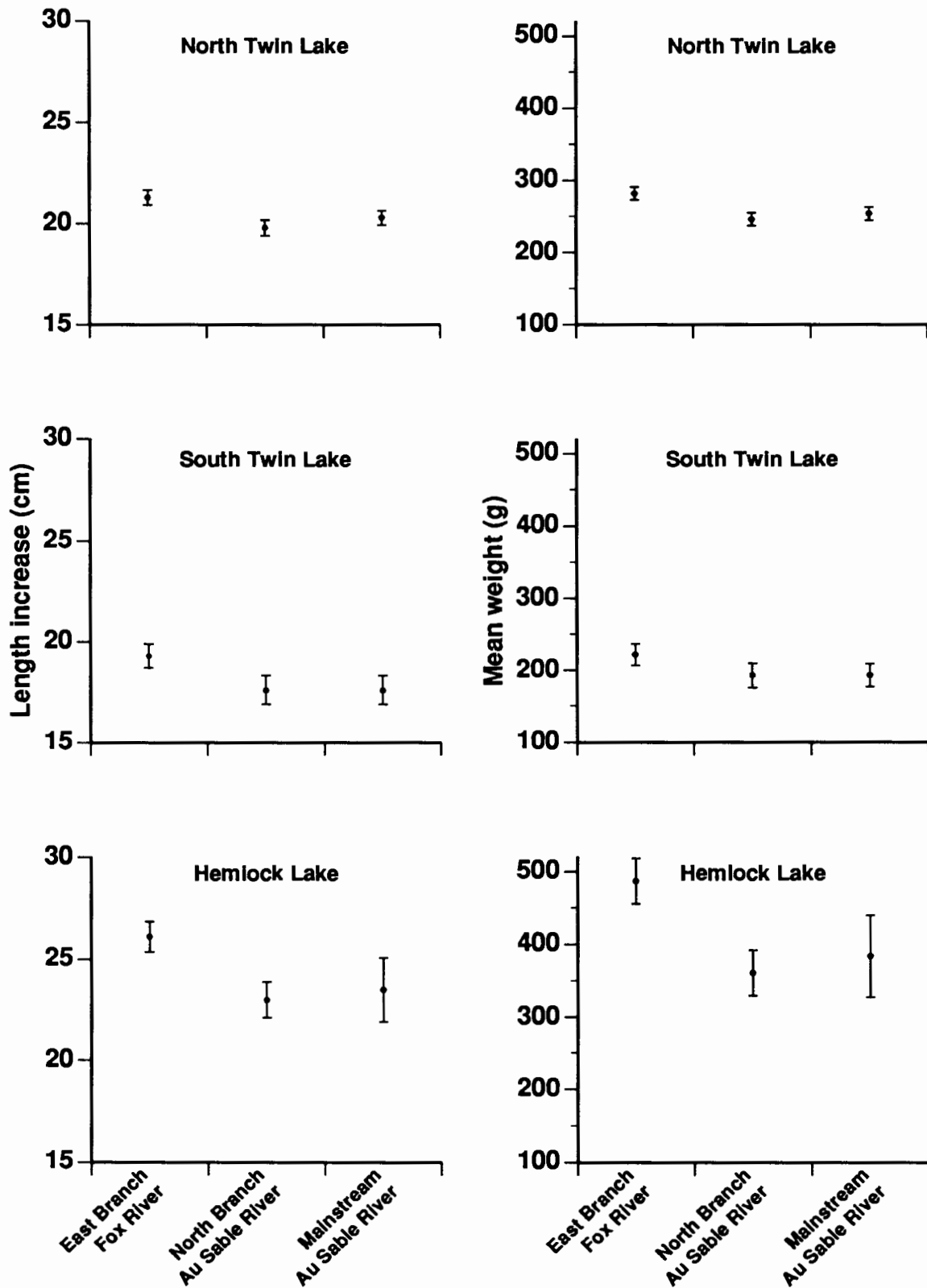
Figure 1.—Mean 2-year length increase, mean weight after 2 years, and 95% confidence limits for three strains of brook trout in three experimental lakes.
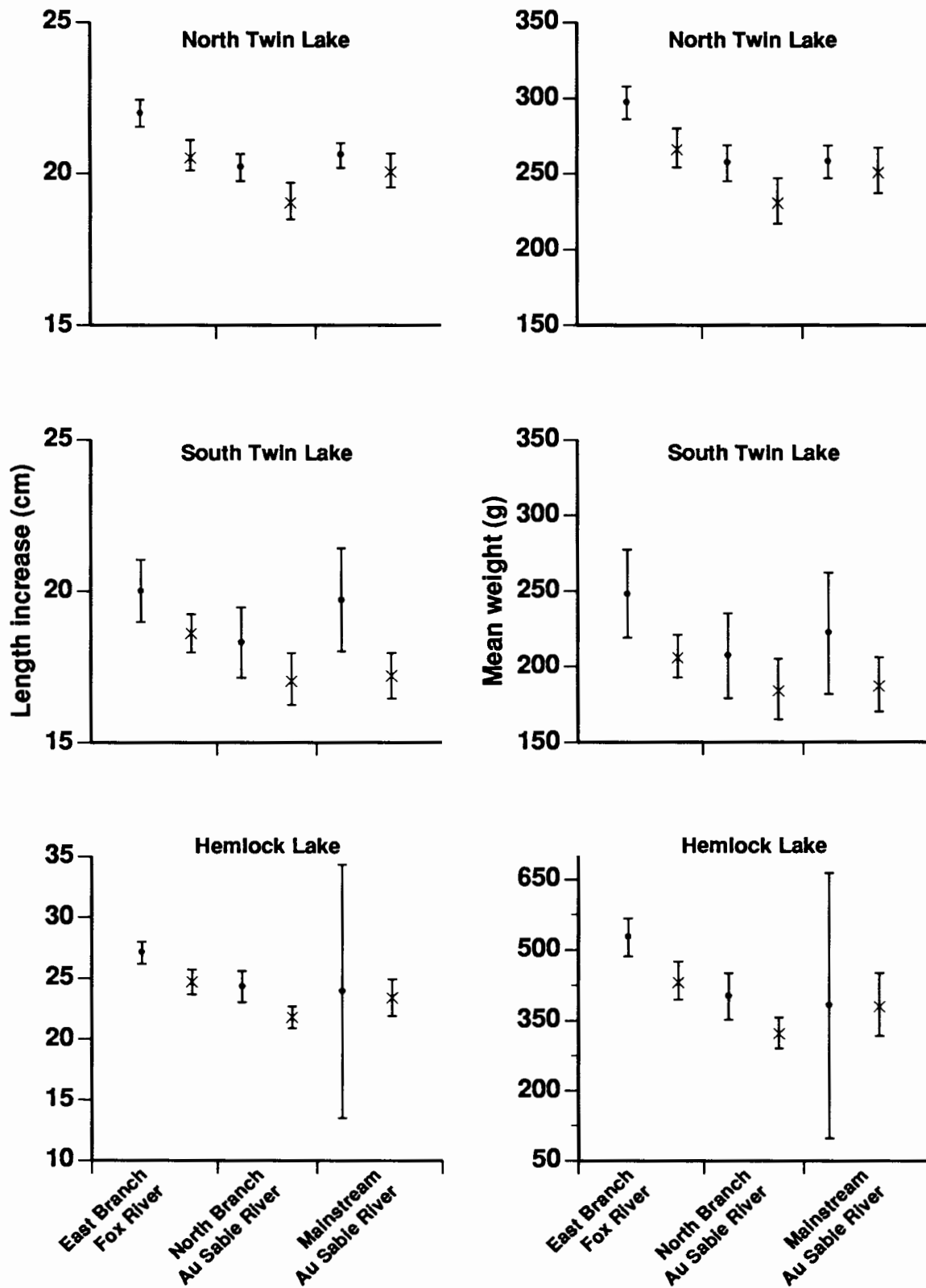
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Figure 2.—Mean 2-year total length increase, mean weight after 2 years, and 95% confidence limits for male (•) and female (x) brook trout of three strains recovered from three experimental lakes.
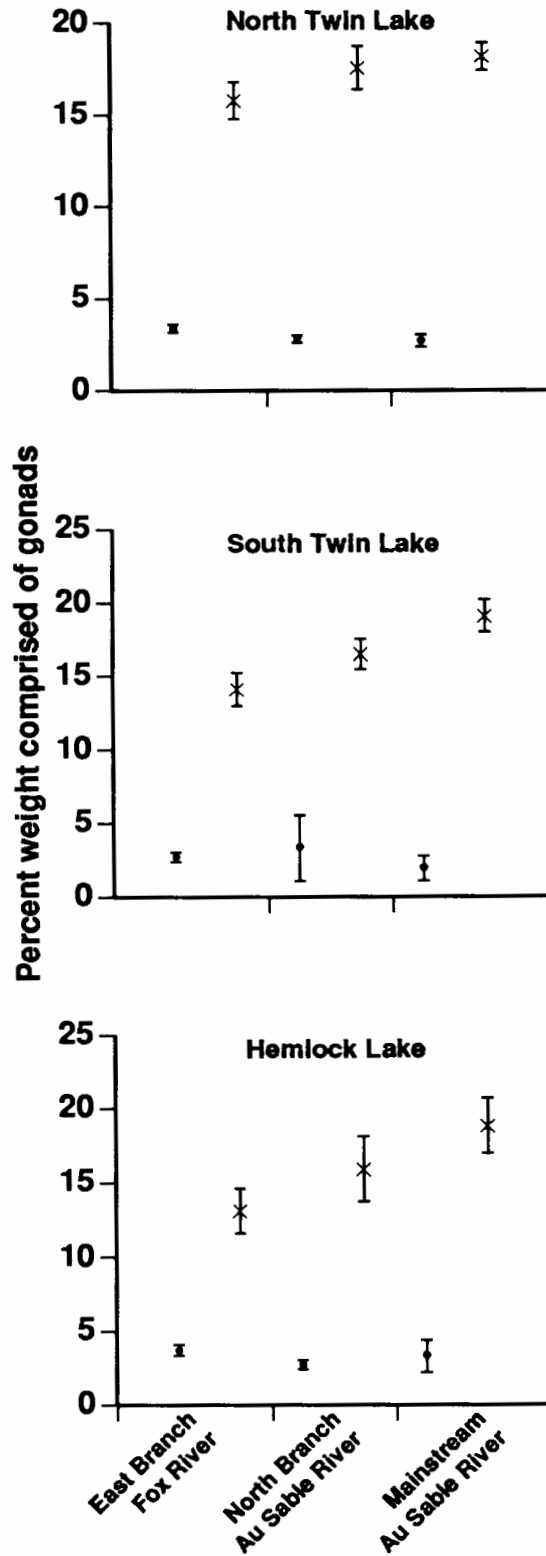
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Figure 3.—Percentage of mean weight comprised of gonads, and 95% confidence limits for male (•) and female (x) for three strains of brook trout from three experimental lakes.

Table 1.—Planting-and-recovery data for three wild brook trout strains planted in three experimental lakes. Shown are the number and mean total length of fish planted in October 1987; and the number recovered in gill nets, the estimated population, and the percent survival as of October 1989.

| Experimental Lake (area in ha) | Planting data | | | Recovery data | | |
	Strain	Number	Length in (cm)	Number netted	Estimated population	Percent survival
North Twin Lake	East Branch Fox River	160	9.0	96	109	68.1
(1.94)	North Branch Au Sable River	160	8.6	85	85	53.1
	Mainstream Au Sable River	160	8.4	70	70	43.8
South Twin Lake	East Branch Fox River	130	9.0	67	76	58.5
(1.59)	North Branch Au Sable River	130	8.6	39	52	40.0
	Mainstream Au Sable River	130	8.4	28	32	24.6
Hemlock Lake	East Branch Fox River	197	9.0	42	42	21.3
(2.39)	North Branch Au Sable River	197	8.6	29	29	14.7
	Mainstream Au Sable River	197	8.4	12	12	6.1
All lakes	East Branch Fox River	487	9.0	205	229	47.0
(combined)	North Branch Au Sable River	487	8.6	153	162	33.3
	Mainstream Au Sable River	487	8.4	110	114	23.5

Table 2.—Percentage of the trout population caught during 3 days of angling and mean lengths (cm) and weights (g) of angler-caught trout. Two standard errors shown in parentheses.

| Strain | North Twin Lake | | | South Twin Lake | | |
	Percent	Length	Weight	Percent	Length	Weight
East Branch Fox River	38.5 (9.92)	31.0 (0.50)	288 (12.90)	34.2 (11.52)	28.4 (0.86)	207 (22.56)
North Branch Au Sable River	11.8 (7.42)	29.3 (0.98)	260 (24.06)	7.7 (8.54)	26.4 (3.06)	170 (41.20)
Mainstream Au Sable River	18.6 (9.30)	28.9 (0.78)	257 (22.92)	28.1 (16.54)	25.6 (1.54)	180 (21.88)

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