POPULATION DYNAMICS OF STOCKED ADULT MUSKELLUNGE (*ESOX MASQUINONGY*) IN LAC COURT OREILLES, WISCONSIN 1961-1977

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COVER: *Capturing spawning muskellunge with a fyke net.*

ABSTRACT

We examined the long-term population dynamics of adult stocked muskellunge that occurred with an expanding northern pike population in Lac Court Oreilles, Sawyer County, Wisconsin. Using data collected from 1961 to 1977, we estimated population size, mortality, angler exploitation, and recruitment using POPAN-2 (a multiple mark-recapture model). Accurate estimates of these parameters are necessary if current muskellunge populations are to be maintained and managed effectively.

From 1961 to 1977, muskellunge were marked and recaptured during spring spawning, and these data were supplemented with voluntary tag returns from anglers. We analyzed population parameters for a homogenous subset—stocked adult muskellunge age VI or older—to: (1) compare and contrast the population dynamics of male and female adult muskellunge, (2) examine the influence of angler exploitation on the mortality of adult muskellunge, and (3) determine whether increases in northern pike abundance influenced population parameters of adult muskellunge.

We found that male and female adult stocked muskellunge differ in population size and probably recruitment to age VI and harvest, but not in mortality and exploitation rate. For both sexes combined, annual mortality averaged 34% and showed no trends over time. Angler exploitation is clearly the main source of the mortality of adult stocked muskellunge in Lac Court Oreilles. Voluntary tag returns by anglers were positively related to muskellunge population size. Coupled with the constant exploitation rate, this finding suggests that total harvest was positively related to muskellunge abundance.

Recruitment to age VI was highly variable from year to year, and was not significantly related to the number of fish stocked 6 years before. Inaccuracy in recruitment estimates was partially responsible for this lack of relationship between stocking and recruitment.

Adult muskellunge numbers declined over the study period, primarily because stocking was suspended from 1966 through 1970. Apparently the large increases in northern pike population size during the study period did not contribute substantially to this decline. Northern pike population size was not correlated with adult stocked muskellunge mortality or recruitment, and the naturally reproduced component of the muskellunge population did not decline as northern pike numbers increased.

KEY WORDS: Muskellunge, population size, mortality, exploitation, recruitment, mark-recapture model, POPAN-2, northern pike

Population Dynamics of Stocked Adult Muskellunge (*Esox masquinongy*) in Lac Court Oreilles, Wisconsin 1961-1977

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INTRODUCTION

Because adult muskellunge (*Esox masquinongy*) are typically found at low densities and are often difficult to capture, limited information is available on their population dynamics in most lakes (Porter 1977). However, accurate estimates of population size, mortality, and recruitment are necessary if current muskellunge populations are to be maintained and managed effectively (Klingbiel 1981; Bimber 1982; Inskip, in press). In particular, the effects of angling and expanding northern pike (*Esox lucius*) populations on these three parameters need to be clarified.

From 1961 to 1977, a detailed mark-recapture program was conducted on spawning muskellunge and northern pike in Lac Court Oreilles, Sawyer County, Wisconsin. Coupled with voluntary angler tag returns, the results of this program provided a valuable opportunity to examine the long-term dynamics of an exploited muskellunge population that occurred with an expanding northern pike population. Johnson (1981) summarized the results of the mark-recapture program and estimated the population size and mortality of muskellunge greater than 20 inches total length. This paper extends the Johnson (1981) analysis, using a more sophisticated method for estimating population parameters, and focuses specifically on a subset of the data, stocked muskellunge age VI or older. This subset was chosen because the ages of the fish could be accurately determined based on fin clips given them the year they were stocked. All fish were probably mature and were large enough (30 inches or more) to be legally harvested.

Johnson's analysis considered all stocked, naturally reproduced, legal-sized, sub-legal sized, mature, immature, known-aged, and unknown-aged muskellunge together. Since muskellunge population parameters are influenced by age, size, and maturity, we restricted our analysis to stocked muskellunge age VI or older, a more clearly defined and homogenous subset. Our objectives are to: (1) compare and contrast the population dynamics of male and female adult muskellunge, (2) examine the influence of angler exploitation on the mortality of adult muskellunge, and (3) determine whether increases in northern pike population size influenced adult muskellunge population parameters.

METHODS

The study was conducted in Lac Court Oreilles, a soft water drainage lake (5,083 acres) in Sawyer County, northwestern Wisconsin (Fig. 1). From 1956 to 1972, the lake was stocked annually with fingerling muskellunge, except 1966-70, when stocking was discontinued as part of a research project (Johnson 1981). Muskellunge are native to the lake and naturally reproduced individuals were present in all years. Northern pike are not native to the lake and were first reported in 1945. Johnson (1971, 1981) provides more detailed descriptions of the physical, chemical, and biological characteristics of the lake.

Marking, Capturing, and Tagging Procedures

Muskellunge fingerlings were fin clipped when stocked to distinguish them from naturally reproduced muskellunge. The fin that was clipped varied from year to year, to permit a separation of year classes and an accurate determination of the age of mature stocked muskellunge.

Muskellunge and northern pike were captured with fyke nets during the muskellunge spawning run (late April-early May) from 1961 through 1978. The nets were 2-inch stretch mesh with 5 x 6-ft frames, 5-ft hoops, and 65-100 ft leads. All fish were captured in Musky Bay, the lake's primary muskellunge spawning area. All spawning muskellunge in the lake were thought to use this bay (Johnson 1981). Weight, total length, and sex were determined for all muskellunge captured. Untagged individuals had a 5 mm-wide numbered aluminum strap tag locked loosely around their preopercle (Johnson 1971). For recaptured tagged fish, tag numbers were recorded and damaged tags were replaced. Tag loss was not observed and was, therefore, assumed to be zero for population parameter calculations. All northern pike caught were fin clipped and measured for total length. Johnson (1981) provides details on field methods.

Population Parameter Estimates and Analysis

Only stocked muskellunge age VI or older (hereafter referred to as adult stocked muskellunge) were considered in calculations of population size, mortality, exploitation, and recruitment. (For this study, recruitment is defined as the number of age VI muskellunge entering the population each year.) These parameters were estimated for each year, from 1961 through 1977, using the POPAN-2 computer program (Arnason and Baniuk 1978). This program requires data from multiple mark-recapture experiments in which each marked animal is uniquely identified (e.g., with numbered tags) and uses methodologies first developed by Jolly (1965) and Seber (1965). In this study, each marking interval was 1 year, and parameters were determined for all ages (VI or older) of stocked adults combined. During each year, parameters for males, females, and both sexes combined were estimated separately. Each of these estimates was based on a different portion of the data and used a different maximum-likelihood estimator. Therefore, the sum of male and female estimates does not always equal the estimate for both sexes combined.

The exploitation rate for stocked muskellunge age VI or older was estimated from voluntary tag returns by anglers. Exploitation rate was determined by dividing the number of tag returns during a year by the number of tagged muskellunge estimated by

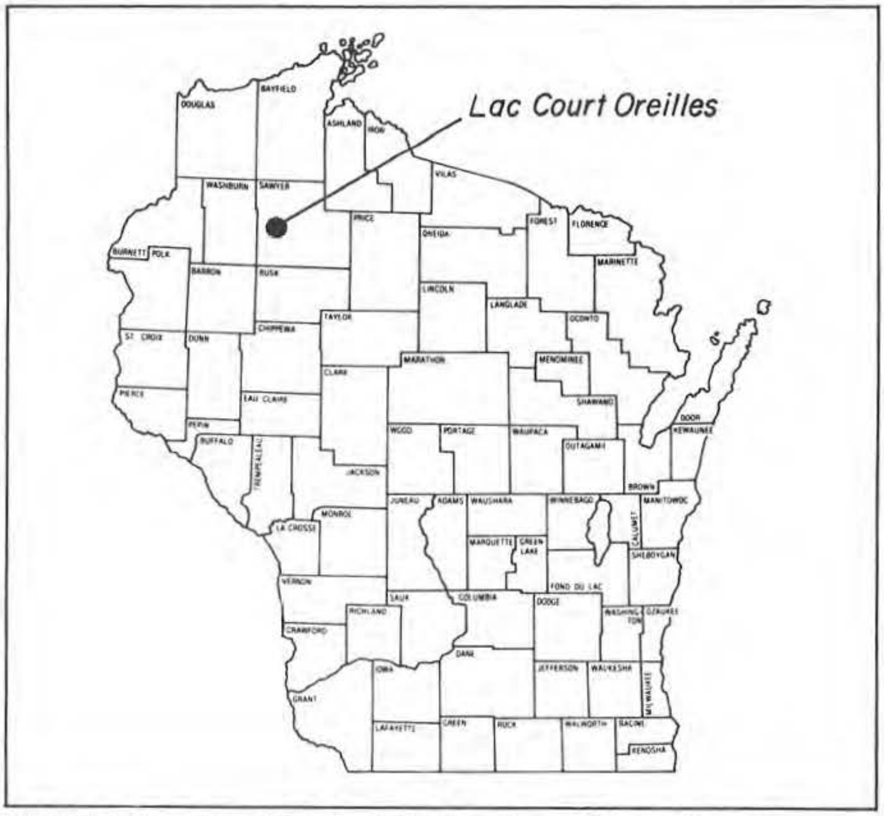
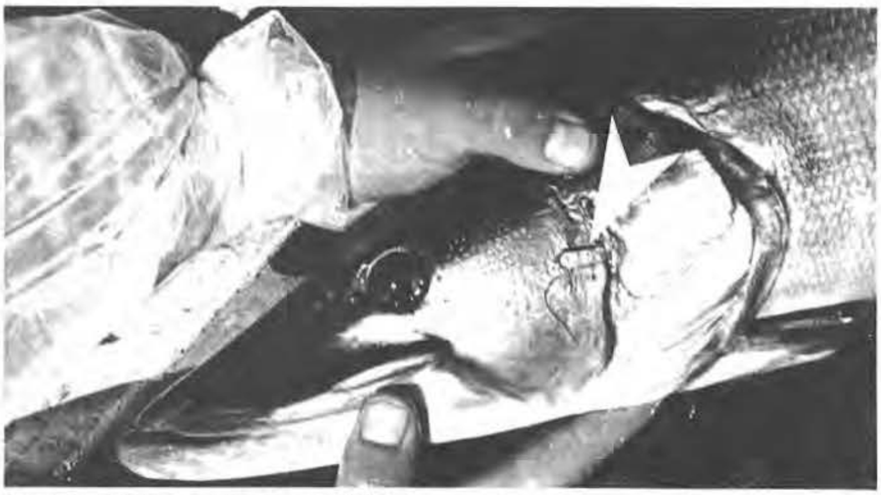


FIGURE 1. *Location of Lac Court Oreilles, Sawyer County, Wisconsin.*

Fin clipping a fingerling muskellunge before stocking.



Adult muskellunge with preopercle tag.

POPAN-2 to be present at the beginning of that year's fishing season. Because we assume that not all tagged adult muskellunge stocked and later harvested by anglers were reported, total exploitation was probably underestimated. All fish considered in this study were probably large enough to be legally harvested (Johnson 1971). Chapman's modification of the Peterson mark-recapture method (Ricker 1975) was used to estimate northern pike population size for fish greater than 15 inches total length (Johnson 1981).

Population parameters for male and female muskellunge were compared using 2 methods. First, parameters were compared for individual years by using point estimates (the actual estimate of population size, mortality, etc., for each year) and variances generated by the POPAN-2 program. The following statistic was calculated (Box et al. 1978):

$$z = \frac{\text{male point estimate} - \text{female point estimate}}{\sqrt{\text{variance of male point estimate} + \text{variance of female point estimate}}}$$

The value of this statistic (z) was compared with values in a unit normal distribution table to determine significance. A unit normal distribution has a mean of zero and a standard deviation of one. This statistic was not calculated for exploitation rate, since the variance of this parameter was unknown. For population size, mortality, and recruitment, this statistic was calculated 16 times each (once for each year). With 16 comparisons and a probability level for statistical significance of 0.05 (i.e., 1 in 20), significant differences could be detected that might be the result of chance rather than a real difference between the sexes. To minimize the possibility of this error, differences were only considered significant if $P < 0.003$(i.e., $0.05 \div 16$). This probability level is conservative and might fail to detect some real differences between the sexes. However, this level is unlikely to identify as real those differences that actually occurred because of chance (Snedecor and Cochran 1967).

The second method to compare population parameters used point estimates from all years. For each population parameter, male and female point estimates for all years were compared using a paired t-test (Stat. Anal. Syst. 1982); differences were considered significant if $P < 0.05$. This method could not be used for population size, because population sizes in each year were dependent on population sizes in previous years. Muskellunge are long-lived fish, and individuals might be part of population estimates for many years.

Factors influencing muskellunge population dynamics were investigated using correlation and regression analysis of yearly point estimates (Stat. Anal. Syst. 1982). Correlations and regressions were considered significant if $P<0.05$. The following variables were considered: muskellunge population size, percent annual mortality, recruitment, number of tags returned by anglers, minimum exploitation rate, and northern pike population size. Muskellunge population size, mortality, recruitment, and minimum exploitation rate could not be related to each other, because estimates of each were statistically dependent on the others (Arnason and Baniuk 1978). Other pairs of variables were related to each other in 2 ways: using Spearman rank correlation coefficients (a nonparametric correlation) and using simple linear regression analysis. Generally, the 2 analyses gave similar qualitative results, so unless otherwise noted, only results from regression analyses are presented.

For regression analyses, residual plots were examined for evidence of lack of fit (Draper and Smith 1981). None was observed, so nonlinear or higher order linear regression models were not fitted to the data. Simple linear regressions were also run on log and arc-sine transformed data, giving qualitatively the same results as regressions on untransformed data.

Analysis of variance (ANOVA) was used to examine the effects of the number of muskellunge stocked on muskellunge population size and recruitment. Each year was assigned to 1 of 3 groups, based on the number of fingerling muskellunge stocked 6 years before (under 500, 500-1,500, and over 1,500). Population sizes and recruitment were compared among groups by using one-way ANOVA (Stat. Anal. Syst. 1982); differences were considered significant if $P<0.05$.

RESULTS

Population Size

While the population size of stocked adult muskellunge age VI or older varied, it generally decreased during the period 1961-77 (Table 1). Numbers were lowest 4 years after the period when no muskellunge were stocked (1966-70). However, only a marginally significant relationship was observed between the population size of adult stocked muskellunge and the number of fingerlings stocked 6 years previously ($F=3.30$; $P=0.067$).

In most years, males outnumbered females (Table 2). Male population sizes were significantly greater than female population sizes in 1962 and 1964-68 ($z=2.98$-4.18; $P=0.0028$-<0.001). Males had higher point estimates of population size in 12 of 17 years. A significant positive relationship was observed between male and female population sizes ($F=6.38$; $P=0.024$; $r^2=0.31$), indicating that when male population size was low, female population size also tended to be low and vice versa.

Mortality

Muskellunge annual mortality varied and showed no obvious trends over time (Table 1), averaging 34% (range 16-51%) over all years. Male and female annual mortality (Table 2) did not differ significantly for single years or when all years were combined. However, male and female mortality rates were not significantly correlated with each other.

Exploitation

For both sexes together, the minimum angler exploitation of age VI and older stocked muskellunge averaged 24% (range 13-35%, Table 1). At least 71% of observed annual mortality was caused by angler harvest (calculated by dividing average exploitation by average mortality). No obvious trends were observed in exploitation, over time, even though the number of marked fish present (as well as population size) generally declined between 1961 and 1977. This finding suggests that fishing harvest was positively related to population size. Accordingly, the number of tags returned by anglers and the population size of muskellunge were positively correlated ($F=12.90$; $P=0.003$; $r^2=0.48$) (Fig. 2).

No significant difference was observed between males and females in exploitation rate, which averaged 24% for each sex (Table 2). However, exploitation rates were also not significantly correlated between males and

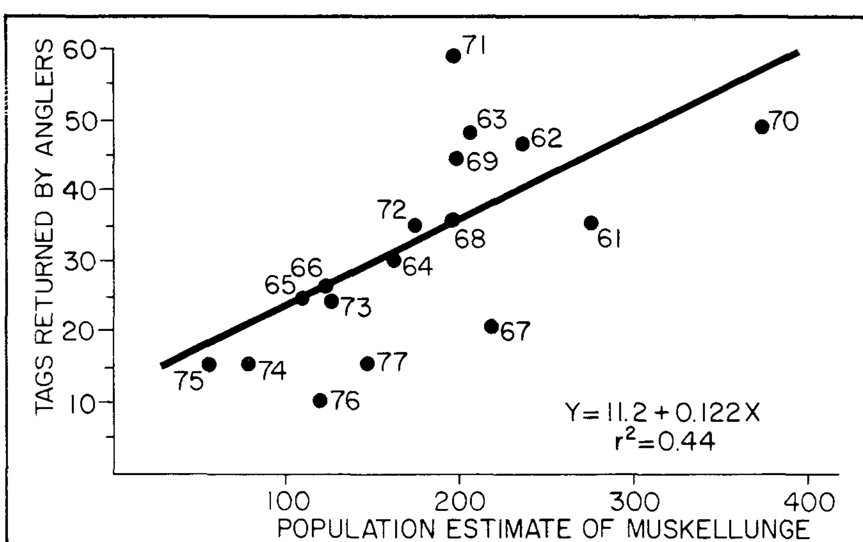


FIGURE 2. *Number of tags returned by anglers vs. population size of adult stocked muskellunge during each year of the study.*

TABLE 1. *Population parameters for all stocked muskellunge age VI or older in Lac Court Oreilles and population size of northern pike longer than 15 inches.*

Year of Estimate	Muskellunge: Stocked No.*	Stocked Year	Population Size	Annual Mortality (%)	Minimum Exploitation (%)	Voluntary Tag Returns	Recruitment	Northern Pike Population Size
1961	1,321	1955	271 (216) **	35 (6)	28	35	57 (144)	4,200
1962	1,015	1956	234 (17)	28 (6)	24	47	35 (14)	2,060
1963	965	1957	204 (15)	34 (6)	27	48	25 (8)	4,300
1964	1,000	1958	159 (10)	39 (6)	21	30	10 (5)	5,800
1965	1,000	1959	108 (7)	34 (8)	23	24	50 (10)	4,500
1966	1,000	1960	121 (13)	35 (7)	28	27	137 (16)	5,300
1967	1,958	1961	216 (17)	30 (6)	15	21	39 (14)	7,800
1968	1,000	1962	191 (16)	33 (8)	23	37	68 (13)	6,300
1969	1,000	1963	195 (18)	40 (8)	27	44	252 (45)	4,900
1970	1,000	1964	370 (53)	51 (6)	22	49	11 (24)	9,270
1971	2,000	1965	194 (17)	39 (8)	35	58	52 (15)	12,620
1972	0	1966	171 (23)	23 (15)	27	35	0 (13)	16,500
1973	0	1967	124 (23)	42 (14)	22	24	6 (8)	10,700
1974	0	1968	77 (14)	37 (13)	24	16	5 (6)	17,000
1975	0	1969	54 (7)	28 (12)	33	16	79 (17)	15,000
1976	0	1970	119 (18)	16 (9)	13	11	45 (18)	13,000
1977	1,002[a]	1971	145 (16)		14	16	No estimate	14,000

*Fingerlings (9-11 inch).
**Standard error given in parentheses.
[a]10,000 3-inch (76-mm) fingerlings also stocked.

TABLE 2. *Population parameters for male and female adult stocked muskellunge age VI or older.*

Year	Population Size: Male	Population Size: Female	Annual Mortality (%): Male	Annual Mortality (%): Female	Minimum Exploitation (%): Male	Minimum Exploitation (%): Female	Voluntary Tag Returns: Male	Voluntary Tag Returns: Female	Recruitment: Male	Recruitment: Female
1961	77 (41)*	117 (—)**	29 (8)	41 (7)	32	25	19	16	90 (36)	20 (—)
1962	145 (17)	89 (8)	28 (7)	29 (8)	21	29	24	23	13 (13)	20 (7)
1963	118 (11)	83 (9)	31 (8)	38 (8)	28	27	28	20	16 (7)	10 (5)
1964	97 (8)	61 (6)	41 (8)	35 (10)	19	24	17	13	11 (4)	0 (2)
1965	68 (6)	39 (4)	22 (12)	51 (11)	17	33	11	13	27 (8)	20 (5)
1966	80 (12)	40 (6)	45 (9)	20 (12)	26	30	17	10	85 (10)	48 (11)
1967	130 (10)	80 (12)	30 (8)	30 (10)	12	11	14	7	39 (11)	4 (8)
1968	131 (15)	60 (8)	40 (8)	28 (19)	23	22	25	12	40 (9)	27 (10)
1969	119 (11)	77 (17)	43 (7)	35 (19)	23	33	24	20	129 (25)	142 (54)
1970	198 (29)	192 (61)	50 (7)	55 (9)	19	28	25	25	15 (13)	0 (25)
1971	114 (11)	78 (13)	51 (8)	15 (19)	36	34	37	21	3 (4)	72 (30)
1972	59 (7)	138 (37)	29 (17)	19 (26)	29	28	16	19	0 (3)	0 (23)
1973	42 (9)	83 (25)	26 (23)	56 (16)	32	16	13	11	5 (4)	0 (6)
1974	36 (9)	37 (10)	49 (15)	22 (22)	27	22	9	7	1 (2)	5 (6)
1975	20 (3)	34 (7)	28 (18)	26 (15)	47	24	9	7	73 (20)	18 (6)
1976	87 (30)	43 (6)	22 (11)	10 (17)	9	19	4	7	7 (23)	27 (10)
1977	75 (9)	66 (13)	—	—	15	12	10	6	—	—

*Standard error given in parentheses.
**Dash indicates no estimate.

females. An average of 69% of male mortality and 77% of female mortality could be attributed to angler exploitation; this difference between the sexes was not statistically significant. Despite similarities between males and females in exploitation rate, anglers returned significantly more tags from males than from females ($t=3.11$; $P=0.007$) during the study years. This difference probably occurred because males usually outnumbered females and because for both sexes the numbers of tags returned were positively related to population size ($F=9.33$ and 13.41; $P=0.009$ and 0.003; $r^2=0.40$ and 0.49 for males and females, respectively). These results suggest that over all years more males than females were harvested.

Recruitment

Recruitment of stocked muskellunge to age VI was highly variable (Table 1). Perhaps because of this variability, male and female recruitment estimates were not significantly different during the study, even though males had higher point estimates of recruitment in 10 out of 16 years (Table 2). Males had significantly higher estimates at the $P\leq0.015$ level in 1964, 1966, 1967, and 1975. Male and female recruitment estimates were significantly positively related ($F=9.973$; $P=0.007$; $r^2=0.42$).

Recruitment to age VI was not significantly related to the number of fingerlings stocked 6 years before. Inaccuracy in recruitment estimates was partially responsible for the absence of correlation. During 1975 and 1976, recruitment estimates were significantly greater than zero, even though actual recruitment had to be zero, since no fingerlings had been stocked in 1969 and 1970 (Table 2).

Influence of Northern Pike

Abundance of northern pike greater than 15 inches increased substantially between 1961 and 1977, while the population size of stocked muskellunge age VI or older generally declined (Table 1). However, northern pike population size and the population size of stocked adult muskellunge exhibited only a weak negative relationship (Fig. 3). A linear regression was not significant, although a Spearman rank correlation was marginally significant (coefficient = -0.48; $P = 0.051$). However, when muskellunge sexes were analyzed separately, northern pike population size was not significantly correlated with either male or female muskellunge abundance by either type of analysis.

Northern pike had little obvious influence on the population dynamics of adult stocked muskellunge. No significant correlations were found between northern pike population size and adult stocked muskellunge exploitation, mortality, or recruitment for both muskellunge sexes together or for males and females separately. A significant negative Spearman rank correlation existed between northern pike population size and muskellunge tag returns (coefficient = -0.49, $P = 0.046$), probably because of the significant Spearman rank correlations between northern pike population size and muskellunge population size and between muskellunge population size and tag returns (coefficient = 0.74; $P = 0.007$).

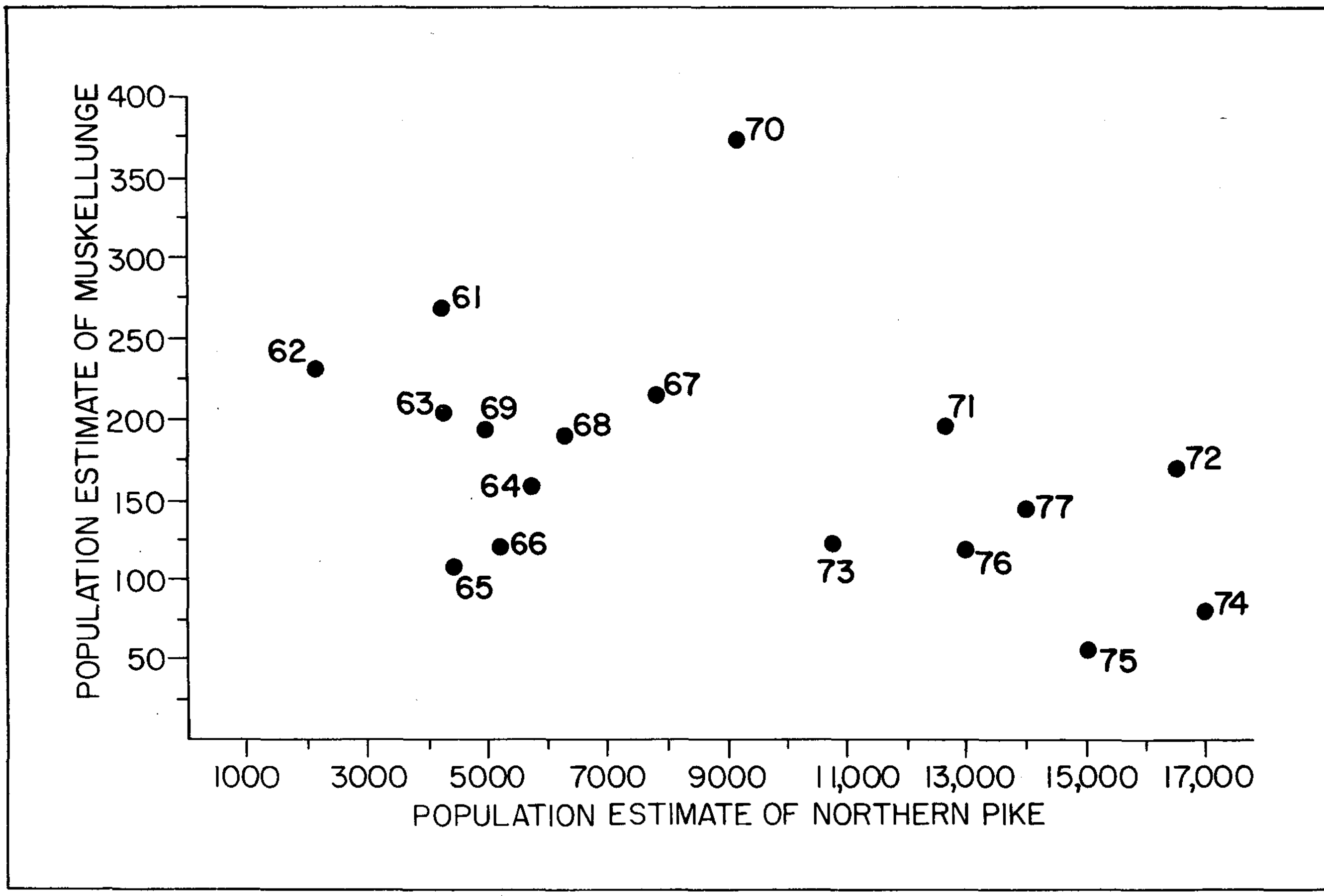


FIGURE 3. *Population sizes of adult stocked muskellunge vs. northern pike during each year of the study.*

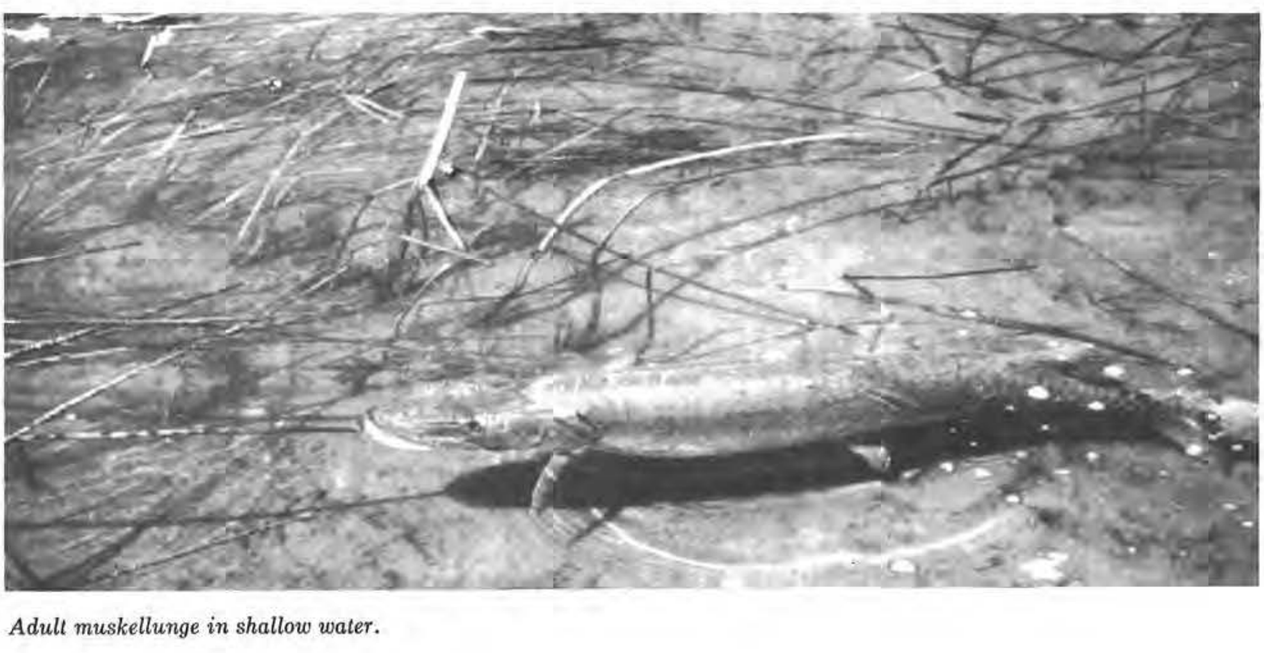
DISCUSSION

Population parameters for male and female adult muskellunge stocked in Lac Court Oreilles were similar in some respects. Percent annual mortality and minimum exploitation rates were similar for both sexes, but population sizes, tag returns, and probably recruitment to age VI and harvest were often greater for males, especially between 1962 and 1970. The differences between the sexes in these 4 population parameters were probably interrelated and were derived from differences in recruitment to age VI.

Only 2 potential factors, differences in recruitment to age VI or differences in adult mortality rates or both, could have caused the observed differences between the sexes in populations sizes. Although population size and recruitment could not be correlated because of their statistical dependence, greater recruitment by males is the only logical explanation for higher male population size. No significant differences were found between the sexes in annual mortality. The only year in which females had a substantially higher population size than males (1972) followed the only year in which female recruitment was substantially higher than male recruitment (1971). Greater recruitment of males could arise from a lower mortality rate before they reached age VI (pre-recruitment) or a greater number of males among the stocked fingerlings or both. Angler harvest might lead to greater mortality of females than males, for fish younger than age VI. Females in Lac Court Oreilles grow faster than males and usually reach legal size at an earlier age (Johnson 1971). Therefore, they are more likely to be harvested before they reach age VI.

The similarity in exploitation rates between males and females older than age VI, coupled with the greater number of tag returns for males, suggests that during the study years more adult stocked males were harvested than adult stocked females. Greater harvest of males was probably due to the greater population size of males in most years, which was probably the result of greater male recruitment. Since population sizes differed between the sexes but exploitation rates did not, males and females were probably similar in their vulnerability to harvest, and apparently the number of muskellunge present was important in determining harvest. However, other factors that might be independent of muskellunge population size, such as fishing pressure or availability of forage (Forney 1967), may have also influenced numbers harvested.

Angling is the major source of the mortality of adult stocked muskellunge in Lac Court Oreilles. Based on minimum exploitation estimates, an average of 71% of observed annual mortality was caused by angling. Since harvest estimates were based on voluntary tag returns and many tags were probably not returned by anglers, the true fraction of mortality caused by angling may have been much greater (Spangler 1968). In 8 northern Wisconsin lakes, voluntary registration of muskellunge averaged 52% of the estimated number of muskellunge actually harvested (range 3-100%) (Hanson, in press). For other species in other areas, voluntary tag returns have ranged from 18-64% of the estimated number of tagged fish caught (Rawstron 1971, Youngs 1974, Matlock 1981). The percentage of tag returns tends to increase with fish size (Rawstron 1971). The percentage of tag returns in Lac Court Oreilles had to be at least 70%, assuming that mortality estimates are accu-



Adult muskellunge in shallow water.

rate, since at a lower return rate exploitation rates would exceed observed mortality.

Total, fishing, and natural mortalities of stocked muskellunge age VI or older were relatively low in Lac Court Oreilles. Based on Ricker's equation (1975) for conditional mortality,

$$A = m + n - mn$$

where: A = total mortality,
m = mortality due to fishing, and
n = mortality due to other causes (natural mortality)

and assuming $A = 0.34$ and $m = 0.24$, then annual natural mortality averaged about 13%. This number is lower than any value we found in the literature (Table 3). Total and fishing mortality estimates in Lac Court Oreilles were also relatively low, although they were within the value ranges reported from other muskellunge populations (Table 3).

When angling significantly changes annual survival, annual exploitation is sometimes negatively correlated with survival rate (Youngs 1972). In this study, these 2 variables were not related, suggesting that angling may not significantly influence stocked muskellunge survival and hence not affect population size in Lac Court Oreilles. This implies that most of the fish captured by anglers would die anyway, i.e., natural mortality would be closer to 34% than 13%. Alternatively, angling may have had a major impact on survival and abundance, but a relationship between survival and exploitation might not have existed for 2 reasons. First, both natural mortality and percentage of tag returns varied substantially among years (Youngs 1972). Second, statistical dependence existed between survival and exploitation because both were partially based on the number of tagged fish in the lake.

We cannot conclude, based on analyses from this study as well as a re-examination of Johnson's data (1981), that increases in northern pike population size caused declines in muskellunge population size in Lac Court Oreilles during the 1960s and 1970s. Two lines of evidence lead to this view. First, no significant relationships between northern pike abundance and adult stocked muskellunge mortality or recruitment were found. Mortality did not show an increasing trend with time. Recruitment of stocked fish did decline during the early 1970s, but this was because no muskellunge were stocked between 1966 and 1970. Second, Johnson (1981) indicated that the number of naturally reproduced muskellunge recovered from each year class from 1958-78 (a measure of recruitment) also did not decline, even though northern pike population size increased by a factor of 3-4. No naturally reproduced muskellunge were captured in 1974-78 because sampling stopped in 1978, before many (if any) of the fish from these year classes were mature and vulnerable to capture (Johnson 1981). Thus, the decline in muskellunge numbers from this study and Johnson (1981) may be due to reduced muskellunge stocking rather than increased northern pike population size.

Still, northern pike and muskellunge may interact in Lac Court Oreilles. However, the data suggest that increases in northern pike population size were perhaps a response to reduced muskellunge numbers (which resulted from the cessation of stocking) rather than vice versa. Population sizes of both species were fairly stable during the early 1960s (Table 1). Major increases in northern pike only began in the late 1960s and 1970s, during and immediately after the period when muskellunge stocking was suspended. Northern pike population size stopped increasing by the late 1970s, several years after muskellunge stocking was resumed.

For the study of population dynamics, the POPAN-2 program used here is a useful tool, particularly when a relatively long time-series of data is available, but sample sizes from individual time periods are low. This program incorporates all available data, rather than subsets, as in some older techniques (e.g., Johnson 1981), and it usually produces more accurate and precise estimates. However, 2 things should be considered when using the POPAN-2 program. First, since population size, mortality, and recruitment are calculated together using the same data, estimates for the 3 parameters are not independent (Arnason and Baniuk 1978) and thus cannot be validly correlated with each other (e.g., stock-recruit curves cannot be generated). This characteristic is inherent in all multiple mark-recapture approaches. Second, as demonstrated with this data set, recruitment estimates can be inaccurate. Arnason and Baniuk (1978) suggested that this inaccuracy may be a general problem. This is unfortunate, but not surprising, since recruitment is typically the most difficult population parameter to estimate (Ricker 1975). Recruitment estimates from this study should be interpreted cautiously.

TABLE 3. *Comparison of mortality estimates for stocked adult muskellunge age VI or older from Lac Court Oreilles, Wisconsin, with published mortality estimates from other muskellunge populations.*

Location	Period	Annual Mortality (%) Total	Fishing	Natural	Comments	Reference
Lac Court Oreilles, WI	1961-77	34	24*	13**	Values are means of yearly estimates for stocked fish age VI or older.	This study
Winter Lake, WI	1979	—[a]	42	—	Based on creel census and voluntary registration; for all legal-sized fish (30 inches or longer).	Hanson (in press)
Sissabagama Lake, WI	1980	—	33	—	"	"
Little Arbor Vitae Lake, WI	1980	—	35	—	"	"
Big McKenzie Lake, WI	1981	—	14	—	"	"
Sand Lake, WI	1981	—	26	—	"	"
Day Lake, WI	1981	—	15	—	"	"
Big Lake, WI	1981	—	19	—	"	"
Big Arbor Vitae Lake, WI	1982	—	24	—	"	"
Corrine Lake, WI	1960-64	24	—	—	Average yearly mortality from ages VI-VIII for a single cohort stocked as fingerlings in 1956. Based on mark-recapture data.	Schmitz and Hetfeld (1965)
Escanaba Lake, WI	1946-81	—	28	—	Average for age IV and older (no size or bag limit). Based on complete creel census.	Hoff and Serns (in press)
South Central Ontario lakes (including Pigeon Lake)	1953	40	—	—	Average of 3 catch curves, which start at ages IV, V, and IX.	Crossman (1956)
Pigeon Lake, Ontario	1961-64	43	24.5*	24.5**	Age V or older. Based on catch curve.	Spangler (1968)
Upper Niagara River, NY and Ontario	1975-77	35	13	25**	For fish 30 inches or longer. Estimation method unknown.	Harrison and Hadley (1978)
Leesville Lake, OH	Pre-1971	43	32	16**	Stocked population. Estimation method and ages included unknown. Fishing mortality is maximum estimate.	Kenyon (1971), cited in Porter (1977)
Middle Island Creek, WV	1966-74	—	35*	—	All fish 22.5 inches or longer.	Miles (1978)
Chautauqua Lake, NY	1966-77	41	—	—	All fish.	Bimber (1982)
	1966-77	33	—	—	Stocked fish, 1961-67 year classes.	
					Both estimates from catch curve. Most fish included were adults.	
Noiges Creek, Ontario	1951-53	70	0	70	Age III and older.	Crossman (1956)
	1952-60	54	—	15	Age IV and older.	Muir (1964)
	1952-60	62	—	24	Age V or older.	
					All Noiges Creek estimates based on catch curves. No fishing was allowed, but between 1952 and 1960 25-40% of the population was removed annually with nets.	

*Based on voluntary tag returns (minimum estimate).
**Calculated from Ricker's equation ($A = m + n - mn$).
[a]Dash indicates no data.

SUMMARY AND MANAGEMENT CONSIDERATIONS

Male and female adult stocked muskellunge in Lac Court Oreilles differ in population size and probably recruitment to age VI and harvest, but not in mortality and exploitation rate. Differences between the sexes in population size and harvest probably result from differences in recruitment. Future efforts should compare mortality rates between male and female muskellunge younger than age VI and should determine the sex ratios of fingerlings stocked, to determine why recruitment to age VI differs between the sexes. Given the differences between the sexes in some population parameters, as well as in growth rates (Johnson 1971), the sexes should be considered separately when monitoring the population and setting management policies. However, it is statistically valid to consider the sexes together when estimating population parameters, since the sexes have similar mortality rates, a necessity if they are to be combined for POPAN-2 and most other mark-recapture models (Arnason and Baniuk 1978).

Angler exploitation is clearly the main source of the mortality of adult stocked muskellunge in Lac Court Oreilles. Total harvest, but not exploitation, probably increases with muskellunge population size, and population size is positively correlated with number stocked. Therefore, continued stocking is probably necessary to maintain the fishery at its current level. Exploitation rates showed no obvious trends over time, and angling may not substantially limit the abundance of stocked adult muskellunge. Good survival of stocked fish as adults, coupled with the failure of naturally reproduced fish to increase in number when stocking was suspended (Johnson 1981), suggests that muskellunge population size in Lac Court Oreilles is limited by reproductive success, survival of stocked and naturally reproduced juvenile fish, or both.

While northern pike have increased substantially in number in Lac Court Oreilles since 1960, they may not have caused the observed decline in muskellunge abundance. Northern pike abundance was not correlated with adult stocked muskellunge mortality and recruitment, and numbers of naturally reproduced muskellunge did not appear to decline as northern pike increased. However, increases in northern pike population size may have been a response to reduced muskellunge population size, which probably resulted from the cessation of stocking between 1966 and 1970.

The POPAN-2 program is a valuable tool for the long-term study of long-lived species such as muskellunge, which are difficult to catch in large numbers. POPAN-2 estimates of recruitment may be inaccurate, however, and should be interpreted cautiously.

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