

## Catchability of Walleyes to Angling in Escanaba Lake, Wisconsin, 1980–1995

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**Abstract.**—Angler catch rates were modeled as a nonlinear function of population density of adult walleyes *Stizostedion vitreum* to determine if walleye angling catchability was density dependent in Escanaba Lake, Wisconsin, during 1980–1995. Relations between angler catch rates (number fish/angler-hours) and catchability ( $q$ ) of walleyes were modeled from data derived from compulsory creel censuses and mark–recapture estimates of walleye abundance (number/acre). For age-3 and older walleyes combined and for individual ages 3–8, angler catch rate was linearly related to population density, whereas catchability was not significantly related to population density. We conclude that angling catchability of walleyes in Escanaba Lake is not density dependent and therefore that angling can safely be regulated using indirect management strategies such as creel limits, size limits, and closed seasons.

Effective fishery management relies on an understanding of the portion of a fish population that is removed by a single unit of fishing effort, defined as the catchability coefficient,  $q$  (Ricker 1975; Gulland 1988; Hilborn and Walters 1992; Quinn and Deriso 1999). Fishery catch rates are often assumed to be a relatively constant proportion of fish population density, described by the basic catch equation:

$$C/f = q \cdot N/A, \quad (1)$$

where  $C$  is the catch,  $f$  is fishing effort,  $q$  is the catchability coefficient,  $N$  is the number of fish, and  $A$  is the area occupied by the fish stock (Ricker 1975; Richards and Schnute 1986). The catch equation indicates that  $C/f$  is linearly related to  $N/A$ , with slope  $q$  (Peterman and Steer 1981). Catchability is often assumed to be constant but actually may vary with fish abundance or density (Peterman and Steer 1981; Shardlow et al. 1985; Winters and Wheeler 1985). Paloheimo and Dickie

(1964) predicted that  $q$  would vary inversely with fish density or abundance. If  $q$  varies inversely with fish density, the proportion of the population caught by each unit of effort increases as fish abundance decreases, thereby leading to overexploitation of a fish population (Shardlow et al. 1985).

Catchability may also vary with age or size of the fish in the catch (Arrenguín-Sánchez 1996). For example, rates of angler exploitation of walleyes *Stizostedion vitreum* in Escanaba Lake, Wisconsin, decreased from ages 3 to 7 (Serns and Kempinger 1981), which suggests that catchability decreased with age. Similarly, catchability of walleyes to angling in western Lake Erie increased from ages 2 to 5 (Isbell and Rawson 1989). Despite the importance of knowing the catchability of all ages and sizes of fish caught by anglers, studies of age- and size-specific catchability have rarely been undertaken (Arrenguín-Sánchez 1996).

Understanding the relationship between the rate at which fish are harvested and their population dynamics is important for the management of any fishery (Serns and Kempinger 1981; Winters and Wheeler 1985). Current management of walleye angling in Wisconsin assumes that walleye population densities regulate catch rates (Beard et al. 1997). Deriso and Parma (1987) found that catch rates of anglers varied directly with fish population

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density. Similarly, angling catch rates were directly related to abundance of age-2 to age-3 walleyes in Pool 4 of the Mississippi River (Thorn 1984), age-2 to age-5 walleyes in western Lake Erie (Isbell and Rawson 1989), and all walleyes in northern Wisconsin lakes (Beard et al. 1997).

Based on an analysis of data from 111 northern Wisconsin lakes, Hansen et al. (2000) found that angling catchability did not vary with walleye population density. We sought to complement that analysis by determining if catchability varied with walleye population density in a single lake over the long term. We also sought to determine if catchability varied with population density of individual age groups because Hansen et al. (2000) did not quantify catchability of individual ages of walleyes. To accomplish both objectives we modeled angling catch rates and catchability as functions of walleye population density in Escanaba Lake, Wisconsin, where mandatory creel census and mark-recapture estimates of walleye abundance have been obtained continuously since 1946.

### Study Area

Escanaba Lake is a 293-acre drainage lake in the Northern Highlands State Forest in central Vilas County, Wisconsin (latitude 46°04', longitude 89°35'). The lake has a 5.1-mi shoreline, a maximum depth of 26 ft, and an average depth of 13 ft. Shoreline and bottom contours are irregular and several small islands with rocky bars and shoals are situated throughout the lake. The outlet of the lake is regulated with a low-head dam that was built in 1963. Movement of fish across the dam is unlikely (Kempinger et al. 1972; Kempinger and Carline 1977).

Escanaba Lake usually stratifies during summer and ice generally covers the lake from mid-November through April. Dissolved oxygen concentrations often approach 0 mg/L near the bottom during summer stratification, but winterkill has never been observed. Total alkalinity is 16 mg/L, spring turnover nitrate nitrogen is 0.3 mg/L, Kjeldahl nitrogen is 0.6 mg/L, dissolved phosphate is 0.08 mg/L, total phosphate is 0.3 mg/L, and specific conductivity is 46  $\mu$ mhos/cm (Kempinger and Carline 1977). There are phytoplankton blooms in summer, and rooted vegetation is common in shallow areas (Kempinger et al. 1972).

Twenty-four species of fish have been reported from Escanaba Lake (Kempinger and Carline 1977; Serns 1982a). The predominant species in the sport fishery today include walleye, northern

pike *Esox lucius*, muskellunge *E. masquinongy*, yellow perch *Perca flavescens*, and rock bass *Ambloplites rupestris*. All species but walleye and northern pike are believed to be native to the lake (Serns 1982a, 1982b). Smallmouth bass *Micropterus dolomieu* were originally predominant in Escanaba Lake, but walleyes, introduced as fry in 1933, reproduced by 1943 and became firmly established after 1947 (Patterson 1953; Kempinger et al. 1972). Since 1946, only experimental groups of marked walleye fingerlings and muskellunge fingerlings and yearlings have been stocked (Kempinger et al. 1972).

Escanaba Lake was designated as an experimental lake in 1946, and since then, the sport fishery has been unregulated by size, bag, or season restrictions for all fish species except northern pike, which had a 56-cm minimum length limit from 1969 to 1973 (Kempinger and Carline 1977; Serns 1984). A mandatory creel census consisting of a compulsory permit system has been used to monitor angling since 1946 (Kempinger et al. 1972; Kempinger and Carline 1977). Permits are issued to anglers without charge. At the end of each fishing trip, anglers return permits to an attending creel clerk at the station who measures all game fish species (total length and weight), removes scales, and inspects fish for tags and fin clips. Although people fish year-round, most walleyes are caught between late April and late October (Serns and Kempinger 1981).

### Methods

The annual angler catch rate of age-3 and older walleyes in Escanaba Lake was modeled as a function of adult walleye density during 1980–1995. Walleye harvest was measured as the total number of walleyes caught and kept by anglers in each fishing season. Because there is no closed fishing season for walleye in Escanaba Lake, the annual fishing season was designated from ice-out in one year through ice-out in the following year. Fishing effort was measured as the total number of hours that anglers fished for all species in a given fishing season because most anglers target walleyes on Escanaba Lake. Catch of walleyes per unit of effort ( $C/f$ ) was computed as the harvest, divided by angler effort in each year. We defined catch rate in terms of harvest only, because angling catch may include fish not removed from the population (caught and released) that are of little importance in the estimation of catchability, i.e., the portion of the population removed by each unit of fishing effort (Ricker 1975).

Abundance of adult walleyes ( $N$ ) was estimated during spring spawning by mark-recapture (Hansen et al. 1998). Adult walleyes were captured in square-mesh (19-mm or 25-mm bars) fyke nets, tagged with Monel metal jaw tags, fin-clipped, and released. Scales or spines were collected from each walleye captured by angling or fyke nets. Recaptures were noted in conjunction with the compulsory creel census of all anglers. Ages of walleyes caught by anglers and in fyke nets were estimated from scales or spines (Serns 1986). Abundance of each age-group was estimated with the Petersen estimator (Ricker 1975). If no tagged fish were recaptured for an age-group in a particular year, the abundance of that age-group was estimated with Bailey's modification of the Petersen estimator (Ricker 1975).

To determine if the angler catch rate was linearly related to walleye population density, angling catch rate (number/h,  $C/f$ ) was modeled as a nonlinear function of walleye population density (number/acre,  $N/A$ ) for ages 3 and older combined and for individual ages 3–8 during 1980–1995:

$$C/f = \alpha(N/A)^{\beta+1}, \quad (2)$$

where  $\beta$  expresses the degree of curvature in the relation between  $C/f$  and  $N/A$ , and  $\alpha$  provides an estimate of  $q$  near the origin (Peterman and Steer 1981). Coefficients were estimated from the  $\log_e$ -transformed model:

$$\log_e(C/f) = b_0 + b_1 \log_e(N/A), \quad (3)$$

where the intercept  $b_0 = \log_e \alpha$  and the slope  $b_1 = \beta + 1$ . The degree of curvature in the relation between  $C/f$  and  $N/A$  (density dependence) was tested by determining if the slope ( $b_1 = \beta + 1$ ) differed significantly from 1 ( $\beta = 0$ ;  $P \leq 0.05$ ; Peterman and Steer 1981; Shardlow et al. 1985). Coefficients in equation (3) are biased (the slope is too low and the intercept is too high) when estimated by linear regression because  $N$  was estimated with error (Peterman and Steer 1981; Shardlow et al. 1985). So, we tested the significance ( $P \leq 0.05$ ) of coefficients by using the functional (geometric mean) regression of  $\log_e(C/f)$  on  $\log_e(N/A)$  (Ricker 1975; Sokal and Rohlf 1981). For individual ages 3–8, we first tested the homogeneity of slopes (degree of curvature) among ages by using the interaction between ages and  $\log_e(N/A)$  in an analysis of covariance (ANCOVA; Sokal and Rohlf 1981). If slopes were homogeneous ( $P > 0.05$ ), we dropped the interaction term, estimated the common slope of the functional re-

gression, and then tested it for significant departure from a value of 1 ( $P \leq 0.05$ ).

Dividing equation (2) by  $N/A$  allows walleye angling  $q$  to be modeled as nonlinear functions of  $N/A$ :

$$q = (C/f) / (N/A) = \alpha(N/A)^\beta, \quad (4)$$

where  $q$  is constant at all population densities when  $\beta = 0$ , decreases with population density when  $\beta < 0$ , and increases with population density when  $\beta > 0$ . Coefficients in equation (4) were estimated for the  $\log_e$ -transformed model:

$$\log_e q = b_0 + b_1 \log_e(N/A), \quad (5)$$

where the intercept  $b_0 = \log_e \alpha$  and the slope  $b_1 = \beta$ . As with catch rates, we estimated coefficients for equation (5) from the functional (geometric mean) regression of  $\log_e(q)$  on  $\log_e(N/A)$  because the parameters in equation (5) are biased when estimated by linear regression (Ricker 1975; Sokal and Rohlf 1981). The statistical significance of  $\beta$  in equation (5) cannot be tested directly because  $N$  appears on both sides of the equation,  $q = (C/f)/(N/A)$  (Peterman and Steer 1981; Shardlow et al. 1985). Therefore, we used equation (5) only to describe the functional relationship between  $q$  and  $N/A$ , and tested the significance of density dependence from the slope of equation (3), the relation between  $\log_e(C/f)$  and  $\log_e(N/A)$  (Peterman and Steer 1981; Shardlow et al. 1985). For individual ages 3–8, we tested the homogeneity of slopes among ages by using the interaction between ages and  $\log_e(N/A)$  in an ANCOVA (Sokal and Rohlf 1981). If slopes were similar ( $P > 0.05$ ), we dropped the interaction term, tested for significant differences in catchability among ages ( $P \leq 0.05$ ), and then estimated the adjusted (least-squares) means for each age. Significant differences ( $P \leq 0.05$ ) in catchability among ages were tested using Bonferroni-adjusted pairwise comparisons (SPSS 1997).

## Results

For walleyes of combined ages 3 and older, angling catch rate was linearly related to population density in Escanaba Lake during 1980–1995 (Figure 1). The slope of the functional regression between  $\log_e(C/f)$  and  $\log_e(N/A)$  was not significantly different from 1.0 ( $t = 0.60$ ,  $df = 14$ ,  $P = 0.56$ ):

$$C/f = 0.00546(N/A)^{1.122}.$$

Angling catch rate increased from 0.056 to 0.274 walleyes/h (3.65–17.76 h/walleye) as wall-

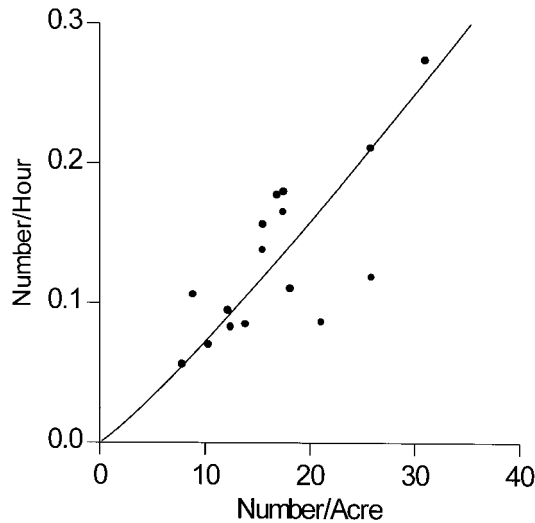


FIGURE 1.—Angling catch rate (number/h) versus population density (number/acre) for age-3 and older walleyes combined in Escanaba Lake during 1980–1995. The line depicts the functional (geometric mean) regression line.

eye population density increased from 7.8 to 31.0 walleyes per acre. The lack of significant curvature in the relationship between angling catch rate and population density suggests that catchability was independent of walleye population density in Escanaba Lake.

For walleyes of combined ages 3 and older, catchability appeared to be inversely related to population density in Escanaba Lake during 1980–1995 (Figure 2). However, the slope of the relationship was not significantly different from zero, because the slope of the relationship between angling catch rates and walleye population density was not significantly different from 1:

$$q = 0.0658(N/A)^{-0.779}.$$

Catchability varied erratically from 0.004 to 0.012 as walleye population density ranged from 7.5 to 31.0 walleyes per acre. The lack of significant curvature in the relationship between catchability and walleye population density again suggests that angling catch rate was independent of walleye population density in Escanaba Lake.

For individual ages 3–8, the degree of curvature in relationships between catch rate and density were similar among ages because the interaction between age and  $\log_e(N/A)$  in an ANCOVA was not significant ( $F = 1.56$ ;  $df = 5, 84$ ;  $P = 0.18$ ; Figure 3). Furthermore, catch rates of walleyes of individual ages 3–8 was linearly related to popu-

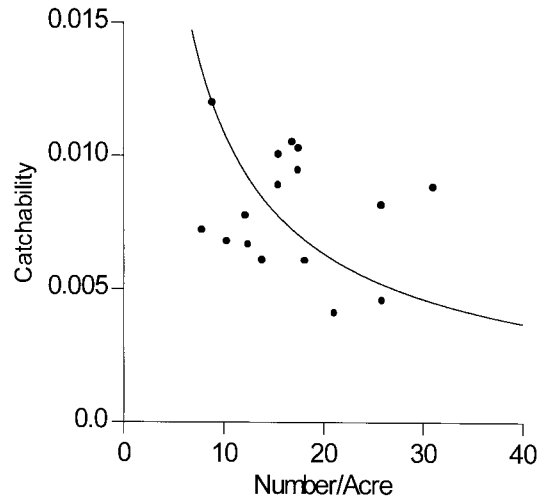


FIGURE 2.—Angling catchability coefficient,  $(C/f)/(N/A)$ , versus population density (number/acre) for age-3 and older walleyes combined in Escanaba Lake during 1980–1995. The line depicts the functional (geometric mean) regression line.

lation density because the common slope of the functional regression between  $\log_e(C/f)$  and  $\log_e(N/A)$  was not significantly different from 1 ( $b_1 = 0.904$ ,  $t = -1.75$ ,  $df = 89$ ,  $P = 0.08$ ). As with the aggregate of ages 3 and older, the lack of significant curvature in the relationship between walleye angling catch rates and population density of individual ages 3–8 suggests angling catchability was independent of walleye population density in Escanaba Lake.

For individual ages 3–8, the degree of curvature in relations between catchability and walleye population density was similar among ages because the interaction between ages and  $\log_e(N/A)$  in an ANCOVA was not significant ( $F = 1.56$ ;  $df = 5, 84$ ;  $P = 0.18$ ; Figure 4). As with aggregate ages 3 and older, catchability of individual ages 3–8 varied erratically, but not in relation to walleye population density. The catchability of walleyes varied significantly among ages 3–8 ( $F = 3.69$ ,  $df = 5, 89$ ,  $P = 0.004$ ) and generally declined with age (Figure 5). Mean walleye catchability ranged from 0.008 to 0.010 for ages 3–5 and from 0.004 to 0.006 for ages 6–8.

## Discussion

Our results suggest that angling catch rate increased linearly with walleye population density in Escanaba Lake, a relation reported in other studies (Thorn 1984; Isbell and Rawson 1989; Beard et al. 1997). In particular, Hansen et al. (2000)

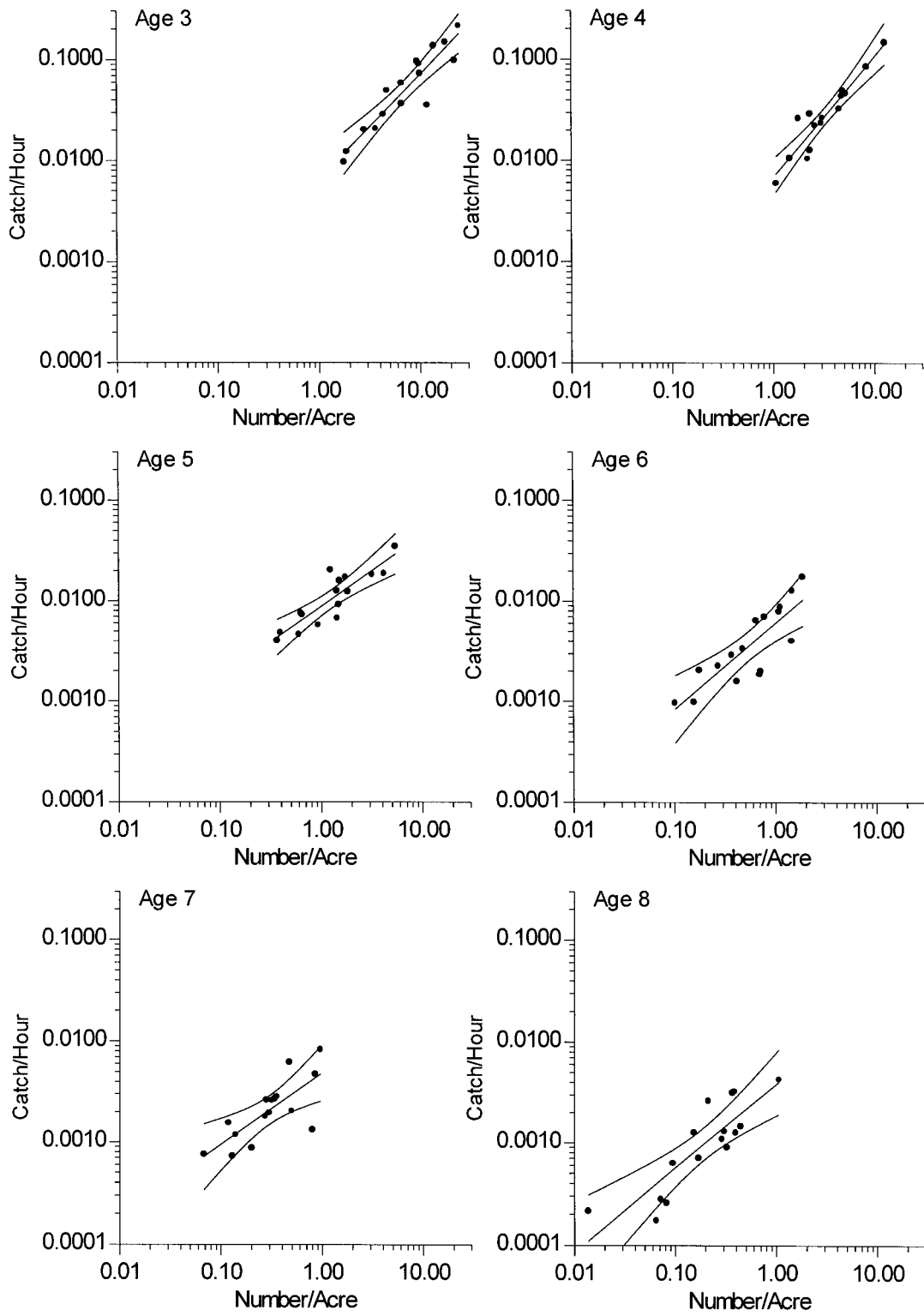


FIGURE 3.—Angling catch rate (catch/h) versus population density (number/acre) for walleyes by individual age-class, 3–8, in Escanaba Lake during 1980–1995. Upper and lower lines depict 95% confidence intervals.

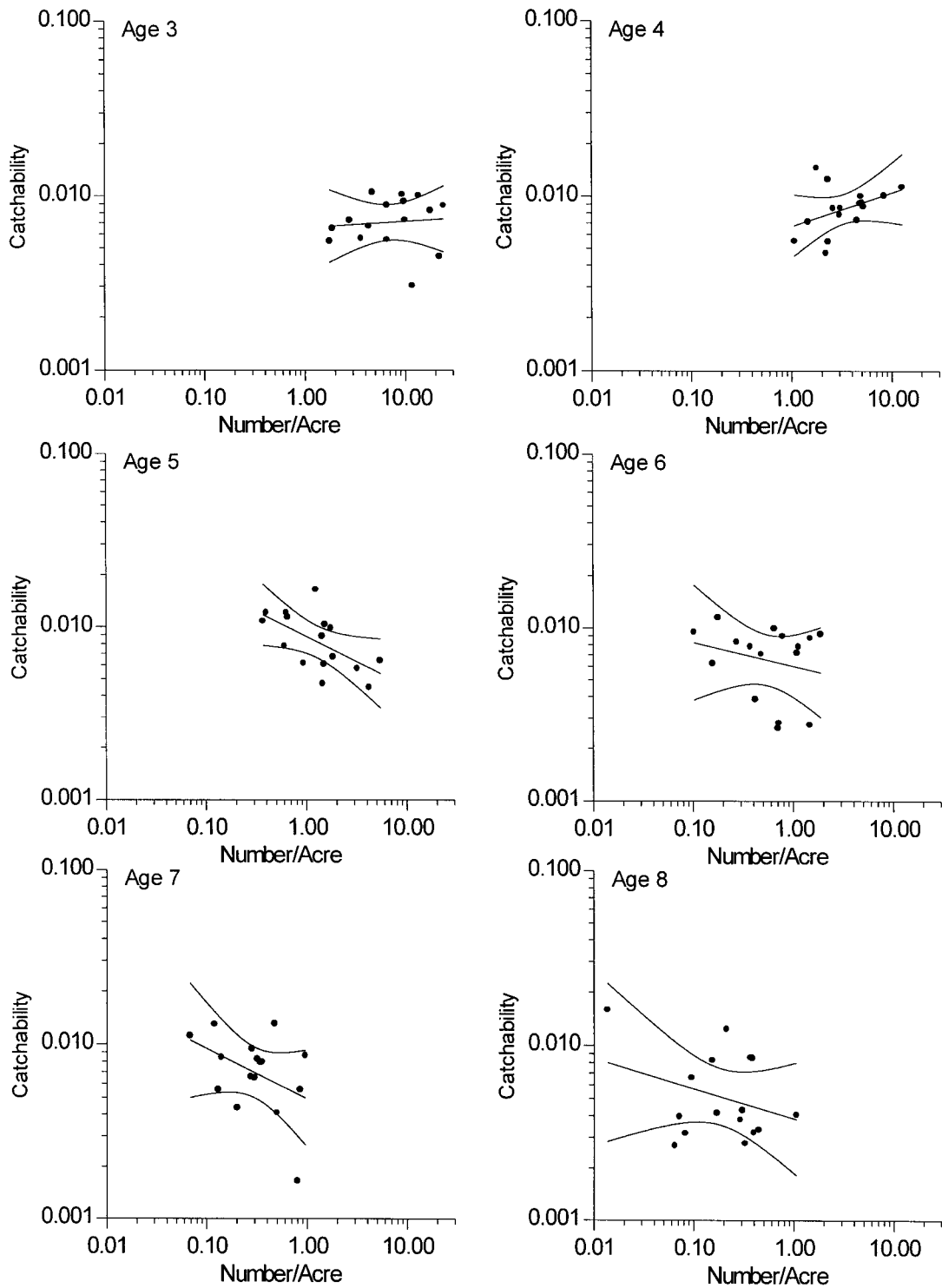


FIGURE 4.—Angling catchability coefficient,  $(C/f)/(N/A)$ , versus population density (number/acre) for walleyes by individual age-class, 3–8, in Escanaba Lake during 1980–1995. Upper and lower lines depict 95% confidence intervals.

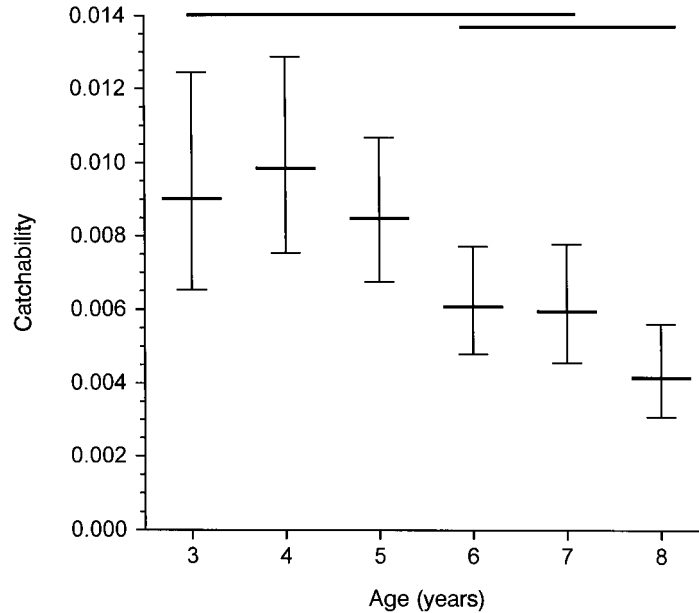


FIGURE 5.—Angling catchability coefficient,  $(C/f)/(N/A)$ , for walleyes by individual age-class, 3–8, in Escanaba Lake during 1980–1995. Error bars depict 95% confidence intervals around the mean. Horizontal lines above ages depict age-classes for which the catchability coefficients are not significantly different ( $P > 0.05$ ).

found that angling catch rate was linearly related to walleye population density in 111 northern Wisconsin lakes. The range of catch rate (0.0062–1.47/h) and walleye population density (0.696–43.3/acre) in the 111 lakes examined by Hansen et al. (2000) exceeded the range of catch rate (0.056–0.274/h) and walleye population density (7.79–31.0/acre) in Escanaba Lake in this study. Based on the similarity of findings from these two complementary studies, we conclude that angling success for walleyes does not change with population density, which is often assumed for such fisheries (Beard et al. 1997).

Our results suggest that catchability of walleyes to angling generally decreased from age 3 to age 8; other studies of walleye angling catch rates have been equivocal. Serns and Kempinger (1981) found that angling exploitation of walleyes decreased from age 3 to age 7 in Escanaba Lake, Wisconsin, which suggests that catchability decreased with age. In contrast, Isbell and Rawson (1989) reported that vulnerability of walleyes to angling increased from ages 2 to 5 in western Lake Erie. Anglers in Lac des Mille Lacs, Ontario, caught small walleye, primarily of ages 4–6 (Elsey and Thompson 1977), which suggests that younger walleye were more vulnerable to angling. Such changes in catchability with age or size are probably related to behavioral

changes associated with growth or sexual development (Arrenguín-Sánchez 1996).

Catchability of a fish is associated with the vulnerability of that fish to a particular fishing gear and vulnerability is the probability that a fish will encounter the fishing gear (Arrenguín-Sánchez 1996). Walleye anglers may not target the entire walleye population in Escanaba Lake with the fishing gear used; this could thereby decrease the vulnerability of older, larger walleyes. For example, Serns and Kempinger (1981) concluded that baits commonly used by Escanaba Lake anglers were a small fraction of the potential diet of larger walleyes and were mostly smaller than the preferred prey of larger fish. Angling exploitation of walleyes in Escanaba Lake therefore decreased as age and size increased (Serns and Kempinger 1981). Similarly, in Pike Lake, Wisconsin, walleyes longer than 508 mm were less vulnerable to angling than smaller walleyes (Mraz 1968). Walleyes are known to be size-selective in their prey selection (Campbell 1998), so size of baits or lures used by anglers may affect catchability.

Our results suggest that catchability of walleyes to angling did not vary with walleye population density in Escanaba Lake. In contrast, Paloheimo and Dickie (1964) predicted that catchability of fish would vary inversely with fish density. For

example, catchability was inversely related to abundance of chinook salmon *Oncorhynchus tshawytscha* (Peterman and Steer 1981) and density of lake trout *Salvelinus namaycush* (Shuter et al. 1998). Similarly, the catchability of Atlantic herring *Clupea harengus* in the commercial fishery was a density dependent function of stock abundance (Winters and Wheeler 1985). Angling catch rate may asymptote through gear saturation, which imposes an upper limit on the catch per hour, regardless of the population density (Deriso and Parma 1987). We found no evidence of such density dependence for walleye of ages 3–8 in Escanaba Lake. In fisheries where catchability varies inversely with fish density, the number of fish caught by each unit of effort increases as density decreases (Shardlow et al. 1985). The likelihood of overfishing a declining fish population therefore increases if catchability is inversely related to population density.

High variability in the relationship between angler catch rate and walleye population density limited the power of our test of density dependence. Based on the observed variation in our data, the exponent of the relationship between angler catch rate and walleye population density would have to have been at least 1.436–1.793 (rather than 1.122) for us to declare that the relationship was significantly nonlinear 50% to 95% of the time (Zar 1999). Therefore, it was possible that density dependence existed but was too small to be detected in Escanaba Lake. However, a similar analysis of 111 walleye lakes in northern Wisconsin, which covered a broader range of angler catch rates and walleye population densities, also failed to detect density dependence of angling catchability (Hansen et al. 2000). Based on the similarity of the results of these two analyses, we conclude that angling catchability does not vary with walleye population density.

### Management Implications

Knowledge of the relationship between the catch rate and fish population density is crucial to effective management of angling fisheries because angling harvest is only indirectly regulated through creel limits, size limits, seasons, closed areas, and gear restrictions (Noble and Jones 1993). Such indirect management assumes that angling catch rates vary in direct proportion to the population density (Beard et al. 1997) and therefore that catchability is constant at all population densities. However, catchability is inversely related to fish population density in some angling fish-

eries (Peterman and Steer 1981; Shuter et al. 1998). Our results for walleye angling in Escanaba Lake suggest that catchability does not increase at low population density and therefore that angling can be effectively managed through indirect methods.

Understanding the vulnerability of different ages of walleyes to angling could help fishery managers better predict the effects of length limits on walleye populations. If vulnerability declines with age, as in Escanaba Lake, a minimum length limit could be set to protect the most vulnerable age-class by setting the minimum length to include all lengths of fish in that age-class. If vulnerability increases with age, as in Lake Erie (Isbell and Rawson 1989), a maximum length limit could be set to protect the most vulnerable age-class to include all lengths of fish in that age-class. Slot limits could be used for populations where vulnerability does not change systematically with age.

To better explain variation in catchability, further studies of angling could include effects of different bait and lures, areas fished, prey density, fishing pressure, spring thermal fronts, and water conditions (Beard et al. 1997). For example, improvements in technology could cause catchability to increase through time. However, catchability of walleyes did not increase during 1980–1995 in Escanaba Lake ( $F = 2.63$ ;  $df = 1, 14$ ;  $P = 0.13$ ). Also, the vulnerability of walleyes to angling in Oneida Lake, New York, was inversely related to walleye growth and thereby to prey density (Forney 1980). Because walleye growth in Escanaba Lake is related to prey density (Serns 1984), walleye vulnerability to angling may be inversely related to prey density. These and other factors may help to explain variation in catchability not explained in this analysis.

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