

Comparison of Angler and Cormorant Harvest of Walleye and Yellow Perch in Oneida Lake, New York

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Abstract.—Since at least the beginning of the last century, sport anglers and commercial fishers have often held cormorants responsible for declining catches. The recovery of double-crested cormorant *Phalacrocorax auritus* populations throughout the Great Lakes region since the late 1970s has rekindled efforts to assess their impact on sport fish populations. In this paper we compare the species and age composition of fish consumed by double-crested cormorants (diet study) and harvested by anglers (creel survey) with abundance estimates of walleyes *Stizostedion vitreum* and yellow perch *Perca flavescens* (mark–recapture and catch per unit effort). The numbers of walleyes consumed by cormorants were similar to those harvested by anglers; however, cormorants consumed only subadults, whereas anglers harvested only age-4 and older adults. Cormorants and anglers combined harvested 7% of age 1–3 walleyes and 14% of the adult walleye population. Cormorant consumption of adult yellow perch was similar to angler harvest, but cormorants consumed almost 10 times more age-2 yellow perch and only cormorants harvested age-1 yellow perch. Cormorants and anglers combined harvested 40% of age-1 and age-2 yellow perch and 25% of the adult yellow perch population. Total annual mortality of adult percids has not changed since cormorant colonization. Although cormorant consumption of adult percids has little effect on harvest by anglers, consumption of subadults will reduce future angler harvest of yellow perch and, to a lesser extent, walleyes.

Real or perceived conflicts between humans and cormorants for fish resources have been an issue in both Europe and North America since at least the beginning of the last century (Lewis 1929; Dieperink 1995; Milton et al. 1995; Callaghan et al. 1998). The resulting harassment and killings by fishermen, combined with decreased reproductive success due to contaminants, depleted populations of double-crested cormorants *Phalacrocorax auritus* in North America by the 1970s (Weseloh et al. 1983; Price and Weseloh 1986). The recovery of double-crested cormorant (hereafter, cormorant refers to double-crested cormorant) populations throughout the Great Lakes region since the late 1970s (Scharf and Shugart 1981; Price and Weseloh 1986) rekindled efforts to assess their impact on sport fish populations. Although cormorants consume fish species also used by anglers (Mendall 1936; Modde et al. 1996; Neuman et al. 1997)

and cormorant predation has the potential to reduce some sport fish populations (Modde et al. 1996; Schneider et al. 1999), most studies have concluded that double-crested cormorants have little or no effect on sport fisheries (Mendall 1936; Craven and Lev 1987; Campo et al. 1993; Shepard 1994; Trapp et al. 1995). These conflicting assessments may reflect real differences in size, scale, or fish assemblages between systems or differences in interpretation of the available data. Regardless, the information presented by these authors is not sufficient to conclusively assess the impact of cormorants on a fish population and a fishery. Such assessment requires concurrent quantitative information on three components: angler harvest, cormorant consumption, and fish population size. To our knowledge, studies combining these three components do not exist in the literature.

Oneida Lake is particularly well-suited for such an assessment because walleyes *Stizostedion vitreum* and yellow perch *Perca flavescens* are the predominant species in both the fish community and the angling catch. This 207-km² productive, shallow, polymictic lake in central New York (Mills et al. 1978) supports one of New York's most valuable warmwater sportfisheries for wall-

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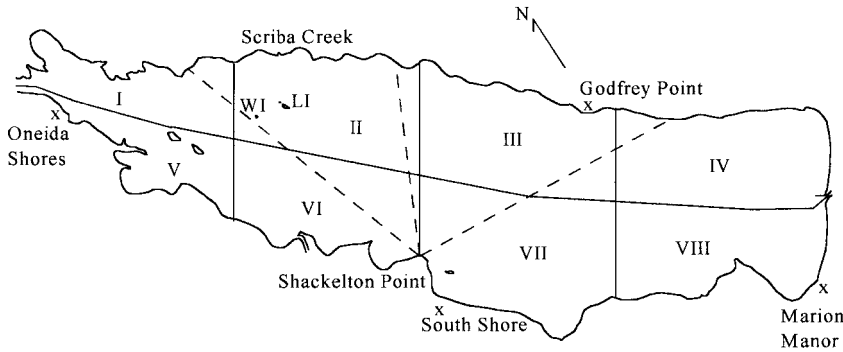


FIGURE 1.—Map of Oneida Lake, New York, showing Shackleton Point, where the boat counting tower was located, four public access sites (x), and double-crested cormorant colonies on Wanry (WI) and Long (LI) islands. The dashed lines indicate area borders for counting boats; the solid lines divide the lake into the eight areas (I–VIII) used for roving and aerial portions of the creel survey (east–west line is buoy line).

eyes, yellow perch, and smallmouth bass *Micropterus dolomieu* (Connelly and Brown 1991). Fish populations have been monitored since 1957 (Forney 1980). Because cormorants are opportunistic feeders, percids may predominate cormorant diets in Oneida Lake. Double-crested cormorants were first observed nesting on Oneida Lake in 1984 (Claypoole 1988). By 1997 the population had increased to over 300 nesting pairs. In addition, over 1,000 migrants typically used the lake from the middle of August through the middle of October (VanDeValk et al. 1998). Concurrent with the increase in double-crested cormorants, Oneida Lake experienced decreases in adult stocks of walleyes (Rutherford et al. 1999) and yellow perch (Mayer et al. 2000). Although percid stocks in the 1960s and 1970s varied annually in response to fluctuations in recruitment and angler harvest (Forney 1980), the decline in the 1990s was more prolonged than in earlier years.

The objectives of this study in Oneida Lake were to (1) compare the species composition and ages of walleye and yellow perch taken by anglers and double-crested cormorants during the 1997–1998 season, (2) compare predation by anglers and double-crested cormorants with abundance estimates of subadult and adult walleye and yellow perch to determine if cormorant predation coupled with exploitation could contribute to the decline in stock abundance, and (3) discuss the effects of cormorant consumption on the lake's sport fishery.

Methods

Percid abundance.—Numbers of adult walleyes (age 4 and older) and yellow perch (age 2 and older) were estimated by mark–recapture in 1997 and again in 1999 following methods described by

Forney (1967, 1980). Fish were fin-clipped in April during spawning runs at Scriba Creek on the north shore and Shackleton Point on the south shore (Figure 1). Recaptures were collected by electrofishing, gill netting, and trawling conducted throughout the lake during the summer and fall. Ages of fish marked and recaptured were determined from scales and population sizes calculated using a modified Petersen estimate (Ricker 1975). Error propagation is described in Van Den Avyle (1993).

Numbers of subadult walleyes (ages 1–3) and age-1 yellow perch present in the spring of 1997 were estimated from the catch and area swept by a 5.5-m bottom trawl. Ten fixed sites were sampled on three dates centered on May 1 (30 hauls) and then weekly from mid-July to mid-October (140 hauls). Each haul swept about 0.1-ha (Forney 1977). Lengths of age-1 and older fish were recorded and scales taken for age determination.

Efficiency of trawls in capturing walleyes was estimated by comparing mark–recapture estimates of numbers of age-4 and older walleyes in April with the mean number of age-4 and older walleyes caught per hectare swept by trawls in July–October (Cornell Biological Field Station, unpublished data). Walleye populations were estimated by mark–recapture in 9 years between 1988 and 1999. The trawl efficiency (ratio of trawl catch/ha to population density or number/ha), which averaged 0.22 (range, 0.08 to 0.32) for those years, was used to adjust estimates of density from the trawl catch. Corrected densities were multiplied by the surface area of the lake (20,700 ha) to estimate population sizes of subadult walleye age-classes (ages 1–3) in 1997. These numbers are considered to represent abundances on September 1 (the middle of

the trawling season) for each age-class. We adjusted the September 1 values back to May 1 based on observed adult annual natural mortality ($M = 0.05$; Forney 1967).

Abundance of age-1 yellow perch on May 1, 1997, was based on area swept by trawls centered on May 1 and expanded to the whole area of the lake. We assumed a trawl efficiency of 1.0, based on evidence that the catch of age-0 yellow perch per hectare swept by trawls during late summer in earlier years approximated the actual density of young estimated from the reconstruction of cohorts from piscivorous fish consumption (Forney 1977). Age-2 abundance was calculated from mark-recapture (see above). Abundance of age-0 yellow perch was not included in this analysis because of their absence in angler harvest and scarcity in cormorant diets in this study.

Biannual survival, S , of adult walleyes from April 1997 to April 1999 was estimated with the formula:

$$S = R_{12}M_2/M_1R_{22}, \quad (1)$$

where M_1 and M_2 are numbers of walleyes marked in 1997 and 1999 and R_{12} and R_{22} are recaptures in 1999 of fish marked in 1997 and 1999, respectively (Ricker 1975). For adult yellow perch, biannual survival was estimated by dividing numbers of age-5 and older fish in 1999 by the population estimate of age-3 and older fish in 1997 because the recovery of marked fish after 2 years was too low to justify use of equation 1. Annual survival was calculated as the square root of the biannual survival rate (assuming equal survival both years).

Angler harvest.—A stratified random creel survey was used to estimate angler harvest for three periods during the 1997–1998 walleye season (the first Saturday in May through March 15). Periods were open-water daytime, open-water nighttime, and winter daytime. Results from these three periods were pooled to estimate total annual harvest of walleyes and yellow perch. Data required for these estimates are measurements of angling effort and harvest rates.

Daytime angling effort during the open-water and winter seasons was measured daily before and after each survey period (see below). Fishing boats (individual anglers and shelters during the winter) were counted using a 20–60× spotting scope mounted on a 10-m tower at Shackelton Point. The lake was divided into four triangular areas with the apex at the tower and channel buoys marking

the boundaries of each area (Figure 1). In each area, all visible fishing and nonfishing boats were counted. For the open-water period, a boat was considered fishing unless it was (1) showing a visible wake, (2) in an area frequented by recreational boaters (inshore sand bars), (3) tied up with other boats (a common recreational practice on Oneida Lake), or (4) a watercraft not traditionally used for fishing (e.g., jet ski, sailboat).

Counts were adjusted to compensate for anglers not visible from the tower. Oneida has an irregular shoreline and several islands that prevent viewing the entire lake from a single fixed point. To account for unseen anglers, aerial counts from an airplane were conducted simultaneously with tower counts on 20 (18 open water and 2 winter) randomly selected dates and times. For aerial counts, the lake was divided into eight areas (Figure 1) and all fishing and nonfishing boats were counted. The same criteria used for tower counts were used to distinguish between fishing and nonfishing boats. Aerial counts were assumed to represent the absolute instantaneous fishing effort. A regression based on log-transformed count data were used to adjust tower counts (hereafter referred to as “adjusted tower counts”) and expressed as

$$\log_e(a) = 0.703 \cdot \log_e(b) + 1.88, \quad (2)$$

where a is the predicted aerial count and b is the tower count ($N = 20$, $r^2 = 0.86$, $P < 0.01$). The log-log regression provided a better fit to data (higher r^2) than a power equation or polynomial equations with zero intercepts. A zero intercept is required to avoid overestimating harvest during times of low fishing activity. Fishing effort and its associated variance were estimated as described by Pollock et al. (1994).

Effort at night was estimated from the number of fishing boats counted during a roving survey or a count of trailers at four boat access areas on nights when strong winds restricted travel by boat. Counts, scheduled for 1 night for weekdays and 1 night for weekends, were expanded to estimate weekly effort.

Monthly estimates of boat hours during the open-water season were multiplied by the mean number of anglers (established from interviews) per boat for each month to determine monthly daytime effort in angler-hours. Winter effort also was estimated in angler hours.

A stratified random design was adopted for surveys in each fishing period. For the daytime period, surveys were conducted on both weekdays and

nonweekdays (weekends and holidays); during the open-water season, surveys were further stratified by time categories: morning (0800–1400 hours), afternoon (1400–2000 hours), and night (2000–0200 hours). Only one time slot (0900–1600 hours) was used during the winter season because of the short daylight hours. Total effort was divided about evenly between weekends and weekdays in 1957–1959 (i.e., total weekday boat hours = 75–84% of total weekend day boat hours in 1957–1959; Grosslein 1961). Similar proportions of boating trips to the Oneida Lake South Shore boat launch were calculated in 1990 (3,720 weekday trips and 4,350 weekend trips; Connelly et al. 1997). Nighttime surveys were conducted twice each week on randomly selected nights (once on a weekday and once on a nonweekday) during the open-water season only. During the winter, nighttime angling was assumed to be negligible (Grosslein 1961).

Harvest rates (fish/h) were estimated using angler interviews following the methods of Pollock et al. (1994). Estimates were primarily based on roving surveys, but access point interviews also were conducted when weather conditions made travel on the lake unsafe. Roving surveys, conducted by boat during the open-water season and by snowmobile or foot during the winter, were stratified by the same eight areas used for aerial counts. Starting point and direction of travel were randomly selected for each survey. Upon arrival at each area, the clerk counted the number of fishing units (boats during the open-water season and individuals and shelters in the winter) using 10 × 40 binoculars (5 × 42 night vision binoculars for night surveys). A maximum of nine angling parties were interviewed, and after 45 min the clerk proceeded to the next area. Information collected at each interview included the date, time of day, area, number of anglers, the numbers of each species caught and kept, the number of legal fish released, the time fishing began, the time they anticipated ending their trip, and the targeted species. Complete trip (access point) surveys were conducted on anglers returning to public access points at four locations around the lake (Figure 1); 90 min were spent at each location. Interviews were identical to those used in roving surveys, except that the time the party finished fishing was known.

Total harvest was estimated by pooling results from all surveys. Daily estimates of effort and harvest were pooled by month to determine the total number of fish removed during the open-water season. Simultaneous access point interviews and

roving surveys on 18 dates indicated the two methods were not significantly different for estimating walleye ($t = 0.43$, $df = 17$, $P = 0.67$) or yellow perch ($t = 0.31$, $df = 17$, $P = 0.76$) harvest rates. Daily estimates for the winter season were pooled for the whole period. Harvest rates for dates when interviews were not conducted were estimated by averaging estimates from the dates before and after and then multiplying by the measured effort for that date. Estimates of annual harvest were the sum of the daytime open-water, nighttime open-water, and winter estimates. Lengths of 108 yellow perch harvested by anglers were measured and age composition of the angling catch were estimated from the length at age relationship developed from 503 yellow perch caught in gill nets during the summer of 1997.

Standard errors for harvest estimates were obtained for each month (Carpenter 1984) by using the observed variance of angling effort and harvest rates of walleyes and yellow perch. Variance for annual harvest is the sum of the variances for each period. Additional information on creel survey methods are provided by VanDeValk et al. (1999).

Cormorant consumption.—Estimates of consumption by cormorants were made using information on cormorant abundance and diet. Cormorants were surveyed by boat on the two nesting islands on Oneida Lake several times weekly from April through October. Most counts were made at dusk or just before cormorants left the colony soon after dawn. For each survey, the colony was counted three times, and the average of the counts was the estimate of abundance for that day. During spring and fall migration, numbers of cormorants were expected to vary daily as birds entered and left the area.

During the nesting season, the number of breeding adults was estimated by doubling the maximum number of simultaneously active nests (peak nesting). Nonbreeders were not considered in this analysis because very few were observed during the study. From June onward, fledgling recruitment was estimated by direct counts of birds on the colony and nesting surveys. Fledged chicks plus number of breeding adults composed the total number of resident cormorants on Oneida Lake. Cormorant days were calculated weekly for adults by multiplying the mean count for that week by 7. Chick days were calculated by multiplying the total number of chicks fledged that year by 56 (7 d/week for 8 weeks).

Cormorant diet was determined by examining pellets collected from May through September

1997. Pellets were dissected and fish species were identified based on otoliths and other diagnostic bones (Hansel et al. 1988). The number of individual fish consumed was determined by counting paired bones. Remaining unpaired bones were also considered to represent individual fish. The proportion of different fish species consumed was calculated for spring (April–May), summer (June–July), and fall (August–October). Unidentified fish were apportioned to species according to the proportions identified.

Otolith sizes were used to determine the proportion of different age-classes of walleye and yellow perch consumed by cormorants. Otoliths of yellow perch and walleye were measured (longest dimension) and classified by a degree-of-wear scale (1 = little or no wear, 6 = extreme wear; Suter and Morel 1996; Adams et al. 1998). Otoliths with wear ratings of 5 or 6 were not used for determining age composition because they were significantly smaller ($t = 1.96$, $df = 35$, $P < 0.05$) than otoliths with less wear. For yellow perch, otolith measurements provided a size distribution with peaks that could be identified as ages 0, 1, 2, and 3 and older. The proportion of otoliths in each age-class was determined (using SYSTAT; Wilkinson 1990) by nonlinear best fit for a combination of normal curves for the summer and fall seasons separately. We assumed the spring age composition was the same as the summer. Too few walleye otoliths were obtained from cormorant diets for a similar analysis. Walleye lengths were therefore calculated from otolith size by using species-specific regressions (Schneider and Adams 1999). This may underestimate the size of walleyes consumed by cormorants because of erosion of the otoliths (Suter and Morel 1996; Carss 1997).

Daily consumption was estimated by examining individual pellets and from published data on cormorant bioenergetics. The pellet method assumed that one pellet represented the daily intake of a single bird (Craven and Lev 1987; Derby and Lovvorn 1997). The daily intake was calculated as the average number of fish found per pellet for spring, summer, and fall multiplied by the number of cormorant days for each period. We assumed nestlings consume the same prey as adults (C. M. Adams, unpublished data from 1994 to 1996).

The bioenergetic method assumed adult cormorants consume 20% of their body weight/d (the lower value in a review by Dunn 1975). Oneida Lake adult double-crested cormorants weighed an average of 2.28 kg (SE = 0.032, $N = 112$; C. M. Adams, unpublished data from 1994 to 1996) re-

sulting in a daily consumption of 0.456 $\text{kg}\cdot\text{d}^{-1}\cdot\text{bird}^{-1}$. Chicks in Lake Champlain consumed 0.327 $\text{kg}\cdot\text{d}^{-1}\cdot\text{bird}^{-1}$ (mean consumption during the 8 week nestling period; Fowle 1997). Once chicks fledged at 8 weeks of age (Mendall 1936), they were assumed to be feeding at the adult rate (Madenjian and Gabrey 1995). Total consumption (kg) by adults and chicks was estimated for spring, summer, and fall by multiplying the number of cormorant days during the period times the daily consumption rate (kg/bird). Biomass consumed during each period was apportioned among species and age-classes in the same ratio we estimated from pellets. Numbers of individual fish found in pellets were multiplied by their mean age-specific weight and divided by the total weight. For walleyes and yellow perch, average weights were calculated for each age-class each season from data collected in standard sampling gears (gill nets and trawls, VanDeValk et al. 1998). For other species, average weights were derived from regurgitates collected in 1998 and 1999 and were kept constant throughout the study (J. Coleman, A. J. VanDeValk, and M. Richmond, unpublished data). Finally, the number of yellow perch and walleyes of different age-groups consumed by cormorants was calculated for each period by dividing the biomass of these consumed groups (proportion by weight multiplied by the total biomass consumed) for each period by the mean weights of the fish in that age-group.

Standard errors for the pellet method were obtained for each period (Carpenter 1984) by using the observed variance for the number of different fish groups found in pellets and for the numbers of cormorants observed on the lake. Variance for annual consumption is the sum of the variances for each period. These calculations do not account for unknown biases associated with the number of pellets produced per day per bird (Duffy and Laurenson 1983; Johnstone et al. 1990; Carss 1997) or the possibility that all otoliths are not recovered (Duffy and Laurenson 1983; Johnstone et al. 1990). Standard errors for the bioenergetic method were not calculated but would be larger because of added uncertainties associated with fish weight and daily intake by cormorants.

Results

Percid Abundance

A total of 20,922 age-4 and older walleyes and 11,187 age-2 and older yellow perch were marked in the spring of 1997. Subsequent examination of

TABLE 1.—Abundance estimates of walleye and yellow perch subadults and adults in Oneida Lake, New York, as of May 1, 1997.

Species	Age-class				Total
	1	2	3	Adult ^a	
Walleye	122,800	104,300	85,900	259,000	572,000
Yellow perch	1,511,000	1,246,000		808,000	3,565,000

^a Adults are age 3 and older for yellow perch and age 4 and older for walleyes.

1,177 walleyes and 2,753 yellow perch in 1997 yielded 94 walleye and 14 yellow perch recaptures. The resulting population estimates for spring 1997 were 259,000 (SE = 25,400) adult walleyes and 2,054,000 (SE = 512,100) age-2 and older yellow perch, of which 808,000 were age-3 and older (based on the age distribution of 1,392 yellow perch examined for marks; Table 1). Corrected trawl catches of walleye age-groups 1–3, backcast to estimate spring subadult abundances, resulted in an estimate of 313,000 age-1–3 walleyes in Oneida Lake in 1997. Age-1 yellow perch abundance for this same time was estimated at 1,511,000 (Table 1). Annual survival (*S*) of adults from 1997 to 1999 was estimated to be 75% for walleyes and 58% for yellow perch.

Angler Harvest

Harvest estimates were based on 635 tower counts and 3,287 interviews. Total effort during the 1997 fishing season was estimated at 354,800

angler hours. Open-water daytime effort was estimated from 515 tower counts resulting in 151,900 boat hours or 298,000 angler hours. Open-water daytime effort was low in May, probably due to persistent inclement weather; effort increased to more than 32,000 boat hours each month from June through August and then decreased steadily the rest of the season. Total nighttime effort was estimated at 9,200 boat hours (18,700 angler hours) and winter effort was estimated at 38,100 angler hours based on 120 tower counts.

Harvest rate estimates were based on 2,728 roving interviews and 559 access-point interviews during 217 sample periods. Harvest rates (fish/angler hour) for walleyes increased from 0.11 in May to 0.13 in June and 0.16 in July and then declined to 0.10 in August and to less than 0.03 for the remainder of the season; the winter harvest rate was 0.02. Yellow perch harvest rates started low (≤ 0.05 for May–August) but increased quickly to 0.5 in September, 1.4 in October, 2.3 in November, and 4.8 for the few anglers fishing in December; the winter harvest rate was 1.4.

Percids accounted for 95% of all fish harvested by anglers in 1997. Anglers creel an estimated 35,400 walleyes and 127,300 yellow perch during the 1997 season (Figure 2; Table 2). Most of the walleye harvest (82%) occurred during the first 4 months of the open-water season. Yellow perch harvest was divided about evenly between the open-water and winter seasons. All walleyes harvested were considered to be age-4 or older because none of those age-3 or younger caught in gill nets during the 1997 season exceeded the 380-mm minimum length limit for Oneida Lake. Comparison of the lengths of yellow perch retained by anglers and lengths of yellow perch aged from the gill-net catch indicated that about 26% (33,600 fish) of the yellow perch harvested were age 2 and the remaining 74% (93,700) were age 3 or older. Anglers did not retain any yellow perch under 170 mm, and no age-1 yellow perch caught in gill nets exceeded 170 mm.

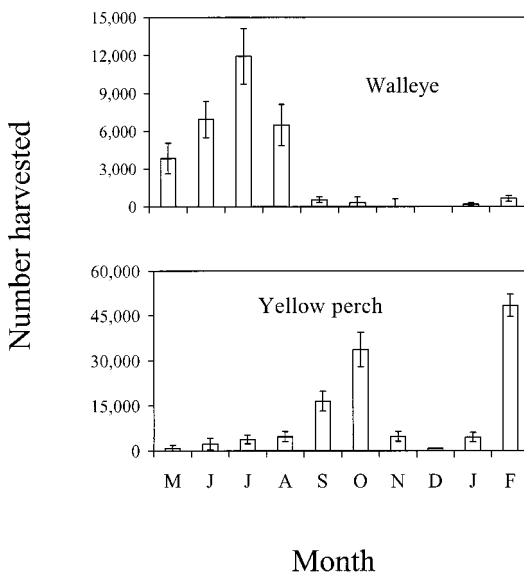


FIGURE 2.—Angler harvest of walleyes and yellow perch in Oneida Lake, New York, by month, in 1997. Error bars represent two standard errors.

TABLE 2.—Angler harvest and consumption by cormorant of walleyes and yellow perch in Oneida Lake, New York, in 1997, by age-class and estimation method.

Species	Age				Total (SE)
	0	1	2	≥3	
Angler (creel survey)					
Walleye	0	0	0	35,400	35,400 (2,700)
Yellow perch	0	0	33,600	93,700	127,300 (13,000)
Cormorant (pellet method)					
Walleye	5,800	13,700	3,900	3,900	27,300 (6,300)
Yellow perch	24,600	638,700	296,000	97,000	1,056,300 (138,400)
Cormorant (bioenergetics method)					
Walleye	8,400	16,300	4,000	4,000	32,700
Yellow perch	35,600	832,400	363,600	112,600	1,344,200

Cormorant Consumption

In 1997 the total number of cormorant days for Oneida Lake was 176,244 (159,500 adult days and 16,744 chick days). The first cormorant survey (April 15) enumerated 158 adults (Figure 3). Chicks were first observed on May 27. Most of the 299 chicks counted in 1997 were fledged by August, increasing the resident adult population to about 800 individuals. Migrant cormorants, presumably from Lake Ontario, began to appear on August 5. The mean count for August was 1,300 birds, increasing to 1,993 in September. As cormorants continued their migration south in October, counts decreased to 756 for the first half of the month and to only 10 for the remainder of the month.

Cormorant diet was determined from 138 pellets collected from the beginning of May through mid-September. Yellow perch was the species most frequently consumed (Table 3), accounting for 71, 69, and 62% of the total number of individual prey

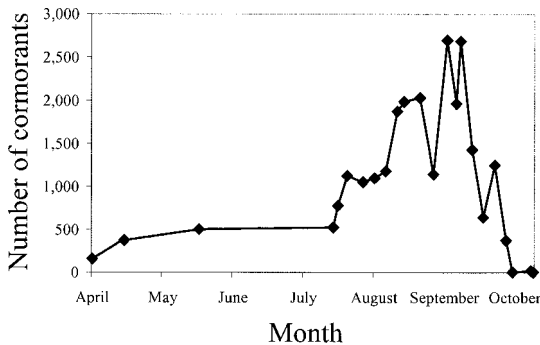


FIGURE 3.—Number of cormorants using Oneida Lake, New York, during 1997, as estimated from counts at colonies. The number of adult birds present during the nesting season (June–July) was estimated from the number of active nests.

items for spring, summer, and fall, respectively. Walleyes were fairly infrequent in the pellets, accounting for less than 5% of the diet by number; all walleye consumed were subadults. Fourteen other fish species were also identified in the pellets.

A combination of three normal curves (representing age-1, -2, and -3 and older yellow perch) fitted to the otolith length distribution of samples collected during the summer yielded relative proportions of 0.50 for age-1, 0.35 for age-2, and 0.15 for age-3 and older yellow perch (Figure 4). Similar analysis for the fall diet, using a combination of four curves, yielded relative proportions of 0.04 for age-0, 0.68 for age-1, 0.23 for age-2, and 0.05 for age-3 and older yellow perch. These proportions were applied to both the pellet and bioenergetic estimates of yellow perch consumed.

TABLE 3.—Number of fish by species occurring in double-crested cormorant pellets in spring, summer, and fall 1997, Oneida Lake, New York. Centrarchids include pumpkinseed sunfish *Lepomis gibbosus*, bluegill *L. macrochirus*, black crappie *Pomoxis nigromaculatus*, and rock bass *Ambloplites rupestris*; cyprinids are predominantly emerald shiners *Notropis atherinoides*; clupeids include alewife *Alosa pseudoharengus* and gizzard shad *Dorosoma cepedianum*; and others include trout-perch *Percopsis omiscomaycus*, white perch *Morone americana*, burbot *Lota lota*, white suckers *Catostomus commersoni*, tessellated darters *Etheostoma olmstedii*, and logperch *Percina caprodes*.

Species	Spring	Summer	Fall	Total
Walleye	2	21	3	26
Yellow perch	179	439	159	774
Smallmouth bass	0	6	6	12
Centrarchids	22	77	39	138
Cyprinids	35	67	23	125
Clupeids	0	1	2	3
Other	15	29	24	68
Unidentified	5	75	72	152

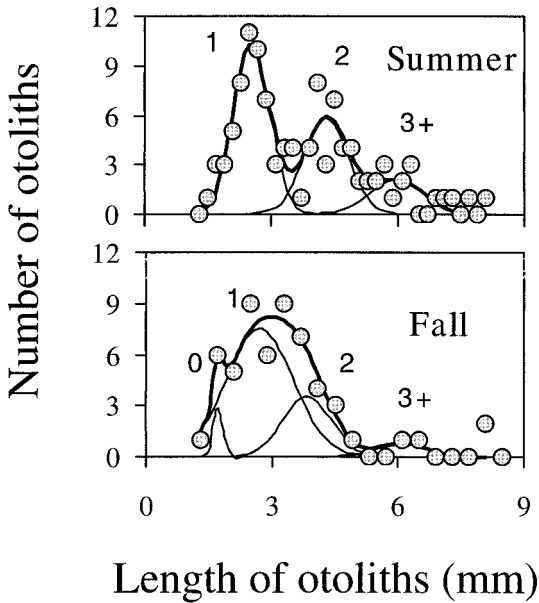


FIGURE 4.—Distribution of sizes (longest dimension, mm) of yellow perch otoliths recovered from cormorant pellets in summer (June–July) and fall (August–September) 1997. Distributions are based on 110 measured otoliths in the summer and 55 in the fall. The single bold line in each plot is the composite fit to the data (symbols) and the light lines represent normal curves for each age-class (three in the summer, four in fall).

Based on analysis of pellets, cormorants consumed 1,056,300 (SE = 138,400) yellow perch and 27,300 (6,300) walleyes in 1997; the bioenergetic method yielded estimates of 1,344,200 yellow perch and 32,700 walleye consumed (Table 2). Total consumption including nonpercids was 1.6 million fish (pellets) and 2.1 million fish (bioenergetics model). Estimates by the two methods were in close agreement in the spring and summer but diverged in the fall. The bioenergetic method assumed consumption at 20% body weight. The pellet method resulted in consumption at 18% body weight in the spring and summer and 14% in the fall.

Discussion

Both cormorants and anglers are top piscivores in lakes where they co-occur, and real or perceived competition between the two predators is the cause of current controversies in both North America and Europe, which are home to several species of cormorants (Craven and Lev 1987; Ewins and Weseloh 1994; Callaghan et al. 1998). However, data comparing the magnitude of predation by these two predators are rare. In Oneida Lake in 1997,

cormorant piscivory (hereafter expressed as the mean of pellet and bioenergetic estimates) was numerically similar to angler harvest of walleyes and higher than angler harvest of yellow perch. Also, there were important differences in both the seasonality and size of fish removed by anglers and cormorants.

Cormorant consumption of adult yellow perch was similar to angler harvest (104,800 versus 93,700 fish), but cormorants also consumed a large number of subadult yellow perch. Age-1 and older yellow perch were consumed by cormorants throughout the year with no marked seasonal pattern. Although anglers did harvest some age-2 yellow perch, cormorant consumption was almost 10 times higher than the angler take of this age-class, and only cormorants consumed age-1 yellow perch. Age-0 yellow perch did appear in fall diets after these fish reached a size of approximately 60 mm. Few age-0 yellow perch were consumed in 1997 but density of age-0 yellow perch was very low compared with the previous 10 years (Hall and Rudstam 1999). Harvest of age-3 and older yellow perch was similar between anglers and cormorants. All walleyes taken by cormorants in 1997 were subadults and smaller than the 380-mm size limit regulating angler harvest in the lake. However, the number of subadult walleyes taken by cormorants was similar to the number of age-4 and older walleyes harvested by anglers.

Seasonality of percid consumption differed between the two predators in 1997. Cormorant piscivory was confined to spring through the middle of October, with peak consumption during August and September when large numbers of migrants used the lake. Angler harvest of walleyes was highest during May through July and decreased in late summer through winter because of a decrease in catch rate and angling effort. Angler harvest of yellow perch was distributed approximately equally between summer and winter. Winter ice fishing often accounts for more than 50% of yellow perch harvest in northern lakes (Green 1972; Johnson and Staggs 1992) and this pattern was similar to observations in Oneida Lake in 1959–1961 (Groslein 1961). The winter fishery may typically account for more of the total yellow perch harvest on Oneida Lake than we observed in this study because the period of ice cover in 1998 (55 d) was the shortest on record since 1975 (mean = 96 d, range 55–121 d; Cornell Biological Field Station, unpublished data).

Cormorant piscivory and angler harvest together removed 29% of the age-2 and 25% of the age-

3 and older yellow perch population in 1997. Losses attributable to anglers and cormorants approached the mean total annual mortality (*A*) of Oneida Lake yellow perch from 1969 to 1977 (mean = 35% as calculated from sequential mark-recapture estimates of abundance; Forney 1980) but was lower than the 42% total annual mortality calculated from biannual survival from 1997 to 1999. However, statistical uncertainty in the yellow perch population estimates in recent years has been relatively high, resulting in relatively high uncertainty in the biannual survival rate. Therefore, piscivory by cormorants and harvest by anglers may have accounted for most of the adult yellow perch total annual mortality in Oneida Lake in 1997. For adult walleyes, total annual mortality from 1997 to 1999 (25%) also was higher than losses attributable to anglers (14%; cormorants were not observed feeding on adult walleyes in 1997) and was similar to 1957–1968 (28%; Forney 1980). Because cormorants do feed on older walleyes (based on regurgitates from Oneida Lake in other years; C. M. Adams and A. J. VanDeValk, unpublished data), it is possible that cormorants could contribute to the remaining mortality of adult walleyes.

Even with the recent addition of cormorants, adult percid total annual mortality was comparable to observations for Oneida Lake in the 1960s and 1970s (Forney 1980) and for other systems without cormorants. Estimates of total annual mortality from 22% to 84% have been reported for adult walleyes (Colby et al. 1979) and from 39% to 60% for adult yellow perch (Nakashima and Leggett 1975; Thorpe 1977). Total annual mortality also may vary substantially among years because of the relative popularity of the fishery (Johnson and Staggs 1992) or changes in catchability associated with abundance of prey fish (Forney 1967, 1980).

Because of uncertainties associated with estimating subadult fish abundance, comparisons of percid numbers consumed and subadult population size should be interpreted cautiously. Our best estimates suggest that cormorants removed 49% of age-1 and 26% of age-2 yellow perch and 7% of age-1–3 walleyes in 1997. Estimated losses of yellow perch are substantially higher than expected without cormorant piscivory, and estimates for walleyes are slightly higher.

Although natural mortality (*M*) was not estimated for subadult walleyes in years before cormorants were observed nesting on Oneida Lake, a value of 0.05 for age-4 and older walleye (Forney 1967) suggests low natural mortality at ages 2–3,

TABLE 4.—Percent of walleye and yellow perch age-classes harvested by double-crested cormorants and anglers from Oneida Lake, New York, in 1997.

Age-class	Cormorants (%)	Anglers (%)	Total (%)
Walleye			
2	7	0	7
3	7	0	7
≥4	0	14	14
Yellow perch			
2	26	3	29
≥3	13	12	25

which are not harvested by anglers. Low natural mortality is supported by the literature from other lakes predominated by percids (Olson 1958; Mraz 1968). Before cormorants, natural mortality for age-1 yellow perch was substantial because of walleye predation but was restricted to the first few months of their second year (Forney 1974, 1977; Nielsen 1980). Age-1 and older yellow perch were seldom found in walleye stomachs after June, when age-0 yellow perch of the following year-class became vulnerable to walleye predation (Nielsen 1980). Losses of age-2 yellow perch were probably minimal because yellow perch in Oneida Lake typically outgrew vulnerability to walleye predation by the end of their second year (Nielsen 1980). The effect of other predators on juvenile yellow perch populations was believed to be insignificant (Forney 1977). Year-class strength of both walleyes and yellow perch was set by their second fall (age 1) in Oneida Lake (Forney 1980; Rutherford et al. 1999). Therefore, additional mortality by cormorants of these subadult fish should directly affect their subsequent recruitment to the adult stock.

Estimating the impact of cormorant predation on angler harvest rates requires extrapolation of our 1997 rates to subsequent years. Assuming that angling success is directly proportional to population size (Isbell and Rawson 1989; Beard et al. 1997), cormorant consumption of percids in a given year will have little effect on harvest rates during that year. However, cormorant consumption may affect future harvest through reductions in numbers of fish recruiting to older age-classes. If, by applying the 1997 age-specific harvest rates by anglers and cormorants (Table 4), we forecast the fate of a single year-class (starting at age 2) of walleyes and yellow perch over an 8-year period, 16% of the walleye year-class and 58% of the yellow perch year-class would be consumed by cor-

morants by age 10. Similar projections for anglers would result in removal of 54% of the walleyes and 34% of the yellow perch. Because most of the total annual mortality of age-2 and older percids was probably caused by fishing in the precormorant years (Forney 1980), these calculations suggest a large effect of cormorants on potential angler harvest of yellow perch and a lesser effect on walleyes.

Potential biases make our estimates of angler harvest, fish abundance, and cormorant consumption uncertain but are unlikely to change the major conclusions. Variances associated with estimates of angler harvest were low (CV = 8% for walleye, 10% for yellow perch). The population estimate for age-4 and older walleyes exhibited high precision (CV = 10%). The age-2 and older yellow perch population estimate was based on only 14 recaptures, producing low precision (CV = 25%), but was consistent with an independent index of age-2 and older abundance calculated from gill-net catches (2.1 million; VanDeValk et al. 1998). Our estimate of age-1 yellow perch abundance on May 1 rests on the assumption that the catch per hectare swept by trawls was an accurate measure of density. Estimates of age-0 yellow perch density from the area swept agreed with independent estimates of abundance calculated from numbers consumed by adult walleyes and yellow perch in late summer (Forney 1977). Because body size of young in the fall and yearlings in the spring was not different, we expect that trawl efficiency remained high over winter.

Our estimate of subadult walleye abundance may be too high. We assumed gear selectivity for age-1–3 walleyes to be the same as for age-4 and older. It is more likely that gear efficiency decreases with increasing walleye size. Therefore, our estimated mortality rates of subadults from cormorants are probably conservative.

We considered cormorant consumption estimates from pellets adequate for our analyses. Recent studies on the Great Lakes used pellets to describe cormorant diets (Ross and Johnson 1995; Neuman et al. 1997), and otoliths can be used to identify and assign ages to prey (Schreiber and Clapp 1987). Our spring and summer estimates of daily rations calculated from the pellet method (18% of adult body weight) basically agreed with bioenergetic requirements reported in the literature (20–30%; reviewed by Dunn 1975); however, the fall estimate (14%) probably was low. Pellets may underestimate cormorant consumption for three reasons. First, the method does not account for

otoliths that disappear (Duffy and Laurenson 1983; Johnstone et al. 1990), which is especially problematic when cormorants consume smaller fish—typically in the fall when age-0 fish reach vulnerable size. However, this has little effect on estimates of age-1 and older percids because these larger otoliths are probably retained. Second, otolith wear may underestimate size of fish consumed (Veldkamp 1995; Suter and Morel 1996), reducing estimates of total consumption by weight. Third, consumption is underestimated if cormorants produce more than 1 pellet/d (Carss 1997). Our estimates of numbers of age-1 and older fish consumed from the bioenergetic method would be high if small fish were not accounted for because it would increase the number of larger individuals needed to meet demands. Thus, the correct consumption of age-1 and older percids is probably between our pellet and bioenergetic estimates.

Cormorant foraging range also can introduce error in assessing local effects of consumption. Double-crested cormorants have operative ranges up to 40 km from colonies but most forage within 20 km (Custer and Bunck 1992; Johnsgard 1993; Hatch and Weseloh 1999). Potential overestimation of fish removed from Oneida Lake by cormorants could occur if cormorants left Oneida Lake to feed elsewhere. The only other water body within 20 km of Oneida Lake is Onondaga Lake, which is much smaller (12.0 km², Effler and Harnett 1996) and predominated by nonpercid species (Ringler et al. 1996). Because the species composition in cormorant diets mirrored the Oneida Lake fish community, biases associated with cormorant foraging on other water bodies is probably minimal.

Our study indicates that anglers and cormorants using Oneida Lake both exploit adult yellow perch and that cormorants influence future angler harvest of yellow perch and, to a lesser degree, walleye. These conclusions are based on quantitative comparisons of cormorant consumption, angler harvest, and fish population size and are specific to Oneida Lake. Cormorants are opportunistic feeders and generally consume species in proportion to their abundance (Craven and Lev 1987; Suter 1995). In systems predominated by species of little or no sport or commercial value (e.g., alewives in the Great Lakes; O’Gorman and Stewart 1999), important sport or commercial species often account for a minor portion of the fish consumed by cormorants (Neuman et al. 1997). In Oneida Lake, the most abundant species are also important sport fish, which is typical of many reservoirs where

reductions in sport fish populations have been conjectured to be due to cormorant consumption (Otenbacher et al. 1994). The challenge to scientists is to identify when and where cormorant feeding affects fish populations and to quantify the impact. The challenge for society and fisheries managers is to decide how to allocate the fish resource and balance the needs of cormorants and the interests of anglers.

Acknowledgments

This work was supported by New York Federal Aid Project FA-5R to the Cornell Warmwater Fisheries Unit. We thank Randy Jackson, Kenneth Stromberg, Martin Stapanian, and Robert Ross for critical and constructive reviews of the manuscript. We also thank our pilot, Niel Ringler, for his skill and dedication to the creel survey and the staff at the Oneida Fish Cultural Station for their cooperation in mark-recapture studies. Finally, we thank Milo Richmond, Jeremy Coleman, and the U.S. Geological Survey-Biological Resources Division for their continued support of cormorant research on Oneida Lake. This is contribution 204 from the Cornell Biological Field Station.

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