

## Do Increasing Cormorant Populations Threaten Sportfishes in the Great Lakes? A Case Study in Lake Huron

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**ABSTRACT.** After near extirpation earlier this century in the Great Lakes, double-crested cormorant (*Phalacrocorax auritus*) populations reached all-time highs, raising concerns among sport anglers and fisheries managers, who see cormorants as a significant source of mortality for yellow perch (*Perca flavescens*), whose populations are perceived to have declined in concert with cormorant increases. We partitioned age-specific perch mortality for 1995 into that caused by (1) cormorant predation, (2) angler harvest, and (3) other sources. Cormorant consumption of perch was calculated by simultaneously estimating diet composition (using stomach analysis and number of foraging cormorants from aerial and ground surveys), and daily consumption (using energetic values from the literature). Consumption of perch by cormorants was heaviest during April and May (48% of the diet by weight) when perch spawn, but yellow perch was not an important prey species overall (11%). Primary prey groups were alewife (47%) and sticklebacks (15%). Cormorants consumed 11,400 kg of perch, mostly young fish (ages 1–3), but mortality caused by cormorant predation was estimated at  $\leq 6.3\%$  of mortality for all ages of perch. Neither cormorants nor anglers contributed more than one-fourth of the total annual mortality of any age class of perch. Although cormorants were highly visible predators of perch in Les Cheneaux Islands area, they did not represent a major source of mortality in 1995. Impact of cormorants on perch may vary from year to year, and may relate to fluctuations in timing of the birds' migration relative to perch spawning. However, we conclude that overall impact is not significant, and control measures to limit their populations were not warranted at the time of this study.

**INDEX WORDS:** Predator control, predation, prey dynamics, mortality, sportfishing, population growth.

### INTRODUCTION

Since the late 1970s, the previously threatened double-crested cormorant (*Phalacrocorax auritus*; henceforth referred to as cormorants) has made an impressive comeback in the Great Lakes (Scharf and Shugart 1981, Ludwig 1984, Weseloh *et al.* 1995) and now numbers as many as 115,000 pairs (Weseloh *et al.* 2000). During the 1940s through the 1960s, cormorants were almost extirpated from the Great Lakes due to DDT-related eggshell thinning and hatching deformities (Weseloh *et al.* 1983, Ludwig 1984). The recent explosive growth of the cormorant population has been attributed to a combination of factors, including reductions in the concentrations of DDT and its metabolites and increased nesting and foraging habitat on human-

made reservoirs and aquaculture ponds (Campo *et al.* 1993, Simmonds *et al.* 1995, Belant *et al.* 2000). Furthermore, cormorants in the Great Lakes have had a ready food supply in the form of introduced alewife (*Alosa pseudoharengus*) (Price and Weseloh 1986, Ludwig *et al.* 1989), which may explain their ability to reach population levels that far exceed historic numbers, when alewife were not available. In fact, cormorant diet studies in the Great Lakes since 1980 show that alewife are frequently the dominant prey for cormorants (Craven and Lev 1987, Ludwig *et al.* 1989, Neuman *et al.* 1997, Johnson *et al.* 2002).

Cormorants, whose diet consists almost entirely of fish, appear to be generalist feeders that consume prey species on the basis of energetic profitability, as evidenced by frequent diet switching and consumption of locally abundant fish species (Pilon *et al.* 1983, Craven and Lev 1987, Campo *et al.* 1993,

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Modde *et al.* 1996, Neuman *et al.* 1997). Cormorants are often found to consume commercially or recreationally important species such as stocked trout or salmon (Ludwig *et al.* 1989, Modde *et al.* 1996, Derby and Lovvorn 1997a), which, along with recent increases in cormorant population levels, has given rise to concern about cormorants' impact on fisheries in the Great Lakes (Burnett *et al.* 2002, Lantry *et al.* 2002). The potential threat posed by cormorant species to fisheries has been investigated in numerous areas (Draulans 1988, Linn and Campbell 1992, Davies and Feltham 1996); most studies either concluded that cormorants did not significantly impact fisheries, or failed to provide evidence to the contrary. These studies were typically limited by inability to compare fish population numbers to cormorant consumption rates. To date, little conclusive evidence exists to suggest that any local waterbird population consumes more fish than do piscivorous fish (Weseloh and Casselman 1992, Madenjian and Gabrey 1995). This suggests that although waterbirds are highly visible predators of fish, they may not be important sources of fish mortality. This hypothesis awaits rigorous evaluation.

Changes in cormorant and yellow perch (*Perca flavescens*) populations in Les Cheneaux Islands area of northern Lake Huron have raised specific questions about the possibility that cormorants affect the recreational fishery and compete with anglers for fish. Sport anglers and managers perceive that the yellow perch fishery in the region, which has for decades been the economic backbone of the area (Diana *et al.* 1987), has declined since the late 1970s (Lucchesi 1988, Schneeberger and Scott 1997).

Yellow perch populations have been declining throughout the Great Lakes for several decades, possibly as a result of repeated recruitment failures, among other factors (Lucchesi 1988, Haas and Schaeffer 1992, Robillard *et al.* 1995). In Les Cheneaux Islands, a Michigan Department of Natural Resources (MDNR) study in the mid-1980s revealed that growth overfishing was partially responsible for perch declines (Lucchesi 1988). However, the resulting 175 mm minimum size limit, instituted in 1987 in an effort to reduce mortality for smaller fish, has not helped the fishery (Diana *et al.* 1997). During this time, cormorants have become increasingly populous in the area. Cormorants became reestablished at St. Martins Shoal, just west of Les Cheneaux Islands, in 1980 (after many years of absence). In 1995 cormorants occupied three nesting

colonies, and numbered approximately 4,000 breeding pairs plus an estimated 2,000-3,000 juvenile birds (Ludwig and Summer 1997).

To determine the predatory impact a cormorant population exerts on a fishery, fish mortality from cormorant predation must be compared with total annual fish mortality and other sources of mortality, including angling or commercial fishing (VanDeValk *et al.* 2002). This requires estimating cormorant diet composition and population size, fish population size and mortality, and sport/commercial catch. Since the cormorant population explosion began 15 years ago, no studies on the Great Lakes have endeavored to examine all these pieces simultaneously. Without this information cormorant impacts on fisheries cannot be fully addressed. Lantry *et al.* (2002) estimated cormorant consumption and smallmouth bass (*Micropterus dolomieu*) abundance, and related increasing cormorant populations to declines in smallmouth bass numbers. Burnett *et al.* (2002) compared cormorant consumption to assumed yellow perch abundance (from data published on other populations); they believed that cormorants were capable of consuming enough yellow perch to cause significant declines. Other studies have only examined cormorant diet composition or numbers of fish consumed (Craven and Lev 1987, Ludwig *et al.* 1989, Neuman *et al.* 1997, Johnson *et al.* 2002), without relating these estimates to fish population sizes.

Active cormorant management, and possible control strategies, have been considered in response to growing concern over cormorant consumption of sport or aquaculture fish. Double-crested cormorants have been residents of the Great Lakes for less than a hundred years. They moved eastward naturally from central Canada and colonized Lake Superior in the late 1800s and early 1900s. Questions about cormorants' role in Great Lakes ecosystems and their impact on fisheries are logical and worth pursuit, especially given that the Great Lakes have recently experienced large-scale changes in aquatic community composition, and problems with invasive species such as sea lamprey (*Petromyzon marinus*), zebra mussels (*Dreissena polymorpha*), and alewife. Cormorant control strategies include oiling eggs, destroying nests, killing adults, and harassing birds on nesting islands. There is increasing interest in controlling cormorant populations because of their dramatic growth and perceived effect on fish populations.

The purpose of this study was to determine the relative impacts of cormorant predation and sport

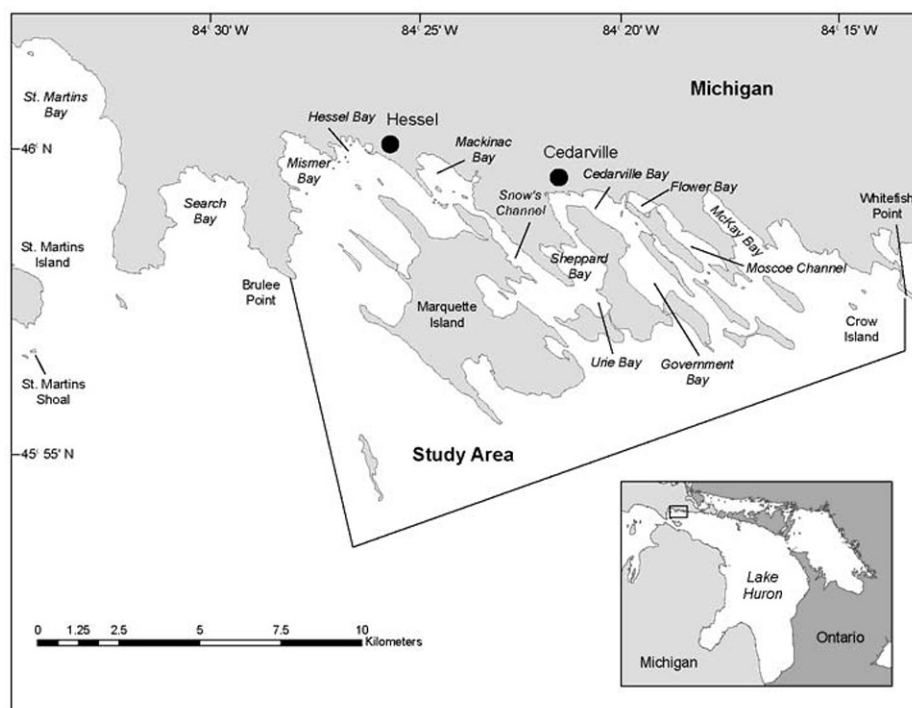


FIG. 1. Les Cheneaux Islands study area.

fishing on the yellow perch population in Les Cheneaux Islands in 1995. The overall project was multifaceted, including aerial surveys of cormorant distributions and abundances, tag and recapture studies on cormorants and yellow perch, creel census of the fishery in Les Cheneaux Islands, and field studies of diet for birds shot on the feeding grounds (Diana *et al.* 1997). We focus here on cormorant consumption; our results are part of a larger study of cormorants and yellow perch (Diana *et al.* 1997). In this paper, we estimate both cormorant consumption of yellow perch, and yellow perch size- and age-specific mortality rates. We used these data to partition mortality into three sources: cormorant predation, sport harvest, and other causes. We then used these estimates to evaluate the effect of cormorants on perch and to predict the likely outcome of management to control cormorant numbers.

## METHODS

Understanding the impact of cormorants on yellow perch requires estimating the portion of age-specific perch mortality actually attributable to cormorant predation. To determine this, we first es-

timated the total biomass of perch consumed by cormorants, which involved separate estimates of cormorant diet composition, abundance of foraging cormorants in the study area, and daily food consumption by individual cormorants. We then converted total biomass into numbers of consumed perch from each size and age class. This information was combined with Schneeberger and Scott's (1997) findings in order to partition total annual mortality of perch.

## Study Area

Les Cheneaux Islands are located on the north shore of Lake Huron near Cedarville, Michigan (Fig. 1). There are approximately 23 islands, surrounded by glaciated channels and bays that interconnect to form a physiographically diverse, shallow, largely oligotrophic aquatic ecosystem. The study area (Fig. 1) encompasses 11,900 hectares (29,300 acres) of water. Lucchesi (1988) found that all recaptured perch originally tagged in Cedarville, Macinac, Sheppard, and Flower bays were found inside the study area. Cormorant colonies are located on Goose and Crow islands within the study area, and on St. Martins Shoal west

of the study area. Only a portion of these cormorants foraged in the study area on any given day.

### Cormorant Diet Composition

Cormorant diet composition has been examined for several locations within the Great Lakes using chick regurgitations and/or adult pellets (Craven and Lev 1987, Christie *et al.* 1987, Ludwig *et al.* 1989, Neuman *et al.* 1997, Johnson *et al.* 2002). Although these techniques are easier, faster, less expensive, and less destructive than sampling live birds, the information that can be drawn from them is limited (Johnson and Ross 1996, Derby and Lovvorn 1997b). Regurgitations are available only for the time that chicks are in the nest and immobile, so that diet composition during other times remains unknown. Even with both regurgitations and pellets, neither the spatial sources nor the size distributions of prey can be reliably estimated. Also, estimates of diet composition from pellet data are biased: some important prey items may be under-represented because bones are either too small or too soft to be retained in the stomach (Johnstone *et al.* 1990, Johnson and Ross 1996). Therefore, to obtain an unbiased estimate for diet composition throughout 1995, we sampled birds for stomach analysis.

A total of 373 cormorants were collected by the MDNR in 1995. From 17 April through 6 October, birds were randomly shot within the study area, their stomachs removed, and the stomach contents identified. Bird collections were mainly done in early morning, but occasionally continued into late morning, depending on success rate. Weight, breeding status, and (where possible) sex were determined in the field. First, plumage characteristics were evaluated; if a bird had breeding plumage (Hatch and Weseloh 1999) dissection was done to determine presence of testes or ovaries. Birds without breeding plumage were not identified to sex, sex of some breeding birds could not be determined, and difficult birds were brought to museum ornithologists for help in determination. To minimize the number of empty stomachs obtained, birds were sampled either after they had been observed foraging, or as they were flying back to nesting colonies from the study area (presumably after feeding). Identification of prey items, using meristic characters for intact fish and bones for digested fish, was made to species with the exception of sculpin, shiner, and crayfish (common and scientific names for all cormorant diet items are listed in

Table 1). Lengths of all intact fish were measured, except for stickleback and sculpin, for which subsets of 100 fish per taxon were measured. Weights for intact fish were estimated using published length-weight regressions (Schneider *et al.* 1991) for all taxa except yellow perch. Weights for digested fish were estimated from average weights of intact fish of each prey type found in cormorant stomachs. To provide more detailed information for yellow perch consumed, we estimated lengths for many digested perch using cleithrum or preoperculum lengths and regressions for total length to bone length. Perch weight was estimated using length-weight regressions developed from Les Cheneaux perch population. Cormorant diet composition was then determined by calculating the proportion by weight of each taxon in the diet.

To characterize temporal variability of the cormorant diet, the year 1995 was divided into dietary periods, each qualitatively different and often distinguishable from adjacent periods by pronounced shifts in foraging behavior. First, cutoff date ranges were determined from observations of foraging birds and preliminary results from the diet analysis. A computer program was developed to select dates from these ranges such that differences in diet composition between periods were maximized; specifically, the program minimized the probability that distributions of prey items consumed across periods were equal. This was achieved by maximizing a Chi-square statistic using independent variables period and prey group. For simplicity, only the seven most abundant prey types (plus "other") were used. In order to estimate the proportion of perch in the diet on a finer temporal scale, the six periods were further divided into subperiods of 9–12 days.

Interdependences between sex, season, and yellow perch consumption were examined with a three-way loglinear analysis, using the likelihood ratio statistic (G). Each of 194 reliably sexed adults with non-empty stomachs were classified by sex, season sampled, and presence or absence of yellow perch in their stomachs. The best statistical model was selected, using a combination of partitioning and stepwise procedures (Fienberg 1981). Strengths of relevant associations were measured using Pearson's coefficient of mean squares contingency (C).

### Abundance of Foraging Cormorants

Aerial counts of foraging and roosting cormorants in the study area were conducted throughout 1995, approximately three times per week.

**TABLE 1.** *Prey items found in double-crested cormorant stomachs.*

Family	Common name	Scientific name
Astacidae	crayfish	family Astacidae
Catostomidae	longnose sucker	<i>Catostomus catostomus</i>
	white sucker	<i>C. commersoni</i>
Centrarchidae	pumpkinseed	<i>Lepomis gibbosus</i>
	rock bass	<i>Ambloplites rupestris</i>
	smallmouth bass	<i>Micropterus dolomieu</i>
Clupeidae	alewife	<i>Alosa pseudoharengis</i>
	gizzard shad	<i>Dorosoma cepedianum</i>
Cottidae	mottled sculpin	<i>Cottus bairdi</i>
	slimy sculpin	<i>C. cognatus</i>
	spoonhead sculpin	<i>C. ricei</i>
Cyprinidae	bluntnose minnow	<i>Pimephales notatus</i>
	creek chub	<i>Semotilus atromaculatus</i>
	longnose dace	<i>Rhinichthys cataractae</i>
	shiner	<i>Notropis</i> spp.
Esocidae	northern pike	<i>Esox lucius</i>
Gasterosteidae	brook stickleback	<i>Culaea inconstans</i>
	ninespine stickleback	<i>Pungitius pungitius</i>
	threespine stickleback	<i>Gasterosteus aculeatus</i>
Ictaluridae	brown bullhead	<i>Ameiurus nebulosus</i>
Lotidae	burbot	<i>Lota lota</i>
Osmeridae	rainbow smelt	<i>Osmerus mordax</i>
Percidae	johnny darter	<i>Etheostoma nigrum</i>
	yellow perch	<i>Perca flavescens</i>
Percopsidae	trout-perch	<i>Percopsis omiscomaycus</i>
Petromyzontidae	lamprey	family Petromyzontidae
Salmonidae	bloater	<i>Coregonus hoyi</i>
	lake whitefish	<i>Coregonus clupeaformis</i>
	round whitefish	<i>Prosopium cylindraceum</i>
	splake	<i>Salvelinus namaycush</i> × <i>S. fontinalis</i>

Surveys were done in the morning, with a standard flight pattern of 163 km always flown in the same direction. It took approximately 1.2 hours for each survey. We were interested in the bird counts for the nearshore Les Cheneaux area only, so most of the survey involved a transect along the shoreline and bays, and a second along offshore island perimeters. Separate counts were made of birds on the three nesting colonies (Ludwig and Summer 1997). Because birds counted on colonies might feed in locations outside the study area, we estimated the proportion of birds from each colony that foraged in the study area. For this estimate, we observed, from the ground, bird movements to and from each colony during May and June 1995. Movements (arrivals or departures) were classified as “study area” or “other.” Study area usage was the mean proportion of movements to or from the study area, weighted by the length of the observation period. Because no ground observations were made after 1

July, we assumed that study area usages remained constant through the year. The colony counts and foraging locations were only used to estimate prey consumption by nestlings; adult numbers and consumption were estimated from aerial counts.

For each day  $k$  that an aerial count was made, we calculated cormorant equivalents ( $CE_k$ ), the equivalent number of cormorants feeding in Les Cheneaux Islands study area:

$$CE_k = B_k + \sum_i (U_i)(C_i)_k \quad (1)$$

where  $B_k$  is the number of birds foraging in the bays on day  $k$ ,  $U_i$  is the study area usage for colony  $i$ , and  $(C_i)_k$  is the number of active bird nests counted on colony  $i$  for day  $k$ . Finally, weekly means for  $CE$  were calculated for the entire period of occupation in 1995. Since these calculations were a combination of many variables measured di-

rectly but with uncertain variance, 95% confidence limits could not be calculated.

### Daily Consumption by Cormorants

Because no empirical methods were feasible for this study, cormorant daily caloric intake was estimated from published information on consumption, or from seabird metabolic rates. Daily caloric intake for nestlings was taken directly from Dunn (1975), who determined consumption by observing nestlings directly. For this study, nestling intake was estimated per adult breeder, and a brood size range of 3-3.5 was used (Ludwig and Summer 1997). We incorporated breeding asynchrony into the calculation of total intake by assuming cohorts of breeders incubating eggs at 10-day intervals starting the first week of May, corresponding roughly to observations made at colonies.

For mature birds, and immature birds older than 1 year, field metabolic rate (FMR) was estimated from Hennemann (1983), who determined basal metabolism (BM) for cormorants by holding them in closed containers and measuring oxygen depletion. Using Hennemann's equation, we estimated BM from body weight and then multiplied by 2.7 (Nagy 1987) to obtain FMR. Daily caloric intake was calculated from FMR by (1) assuming that birds were not gaining or losing mass, and (2) dividing FMR by assimilation efficiency (AE), taken to be 0.85 (Dunn 1975, Nagy 1987). Daily caloric intake was estimated separately for mature and immature birds (identified by plumage), where differences in caloric intake for each type were based only on body weight. Mean body weights for mature and immature birds, proportions of these groups foraging in Les Cheneaux Islands, and change in proportions over time were taken from sampled birds. For simplicity, we assumed that metabolic rates did not vary through the year. Finally, daily consumption was calculated by dividing daily caloric intake by the caloric density of fish,

which for simplicity was assumed to be constant among fish species and equal to 5.0 kJoules/g wet weight (Dunn 1975, Haas and Schaeffer 1992).

### Yellow Perch Mortality from Cormorant Predation

In general, the biomass of perch consumed by cormorants was calculated as:

$$\text{biomass} = (P_{YP} \cdot CE) \left[ (C_B)(DC_B + (C_Y \cdot DC_Y)) + (C_{NB} \cdot DC_{NB}) \right] \quad (2)$$

where  $P_{YP}$ : proportion by mass of yellow perch in cormorant diet  
 $CE$ : cormorant equivalents  
 $C_B$ : proportion breeders in total population  
 $C_{NB}$ : proportion nonbreeders in total population  
 $C_Y$ : average number of young per breeder  
 $DC_B$ : daily consumption for breeders  
 $DC_{NB}$ : daily consumption for nonbreeders  
 $DC_Y$ : daily consumption for young

Total perch biomass consumed was estimated by allowing all parameters to vary with time independently, calculating biomass consumed on a daily basis, and summing over the entire period. Since we could not calculate confidence limits on this equation, we used low and high estimates for each parameter to calculate a range of biomass consumed. Biomass consumed was calculated separately, using proportions of perch included in the diet for the perch spawning season (period 1, day 1-30) and for the rest of the year (periods 2-6, day 31-173), due to differences in proportions and size distribution of perch in the cormorant diet and in the perch population at these times.

Daily changes in consumption estimates were calculated using data from Table 2 for proportional prey consumption in each time period, a 7-day average curve of cormorant equivalents over the study

**TABLE 2.** Dates and qualitative descriptions of the six dietary periods for cormorants in Les Cheneaux Islands area, Lake Huron, 1995.

Period	Dates	# Days	# Samples	Description
1	17/4-16/5	30	85	Perch spawning; pike and sunfish also important
2	17/5-3/7	48	97	Stickleback and larger (age > 1 yr.) alewife
3	4/7-1/8	29	67	Alewife spawning; many yearling alewife in diet
4	2/8-19/8	18	44	Diet highly diverse; alewife, sculpin, other prey
5	20/8-13/9	25	53	Young-of-year alewife, bullhead, and sunfish
6	14/9-6/10	23	27	Young-of-year alewife, yellow perch

period, average mass for breeders and nonbreeders in each dietary period, and the proportion of breeders and nonbreeders in the population. The latter parameters were based on ratios and sizes of birds shot for diet data. High and low estimates were done using the highest and lowest value of each parameter estimated during each dietary period as inputs, rather than means.

Biomass of perch consumed was then converted to numbers of perch of different sizes. The average weight of perch for each size class and the size frequency of perch in the diet produced a unique relationship between biomass and number of perch consumed, allowing determination of one from the other. Size-specific numbers of perch measured from cormorant stomachs were converted to age-specific numbers consumed using a key developed from age-at-size data for yellow perch in bays de Noc, Lake Michigan (Schneeberger and Scott 1997), an area similar to Les Cheneaux Islands in latitude and climate. Growth rates of yellow perch were statistically similar between these two populations, but collections from Les Cheneaux Islands included few small fish, resulting in the need to use bays de Noc data for age-at-size data on perch less than 175 mm in length.

Size- and age-specific mortality rates were estimated by dividing numbers consumed by estimated population size (Schneeberger and Scott 1997). Perch population size was estimated using a mark-recapture experiment. A modified Petersen formula was applied to data from 8,402 fish marked and 199 recaptured, resulting in a final estimate of 2,762,360 ( $\pm 747,597$ ; 95% CL) (Schneeberger and Scott 1997). Size-specific mortality from cormorant predation was determined separately for the perch spawning season (period 1) and the rest of the year (periods 2-6), which required the application of two separate length-at-age keys. Population estimates for periods 2-6 did not reflect mortality that had occurred during period 1. Size-specific mortality from cormorant predation for periods 2-6 was compared with mortality from angling over the same time period (Schneeberger and Scott 1997). Sport harvest estimates were based on a contact creel survey conducted in the area. Total harvest from May to October was estimated at 66,469 yellow perch, with 99% taken from July to October. Since there was no angler harvest prior to the conclusion of perch spawning, we assumed mortality from angling was negligible during period 1. Age-specific mortality rates from cormorant predation were also calculated and compared to age-specific rates from angling.

Mortality from cormorant predation and angling were compared with total annual mortality of yellow perch. Total mortality was estimated from catch curves constructed from experimental gillnet catches and were estimated annually from 1991 to 1995 (Schneeberger and Scott 1997). Mortality was also calculated from tag-return data using ESTIMATE (Brownie *et al.* 1985).

This was a 1-year study, but the timing of cormorant migrations (arrival in May) and perch spawning (that occurs at ice out, which varies out from April to May) could affect the magnitude of predation of perch by cormorants. To determine possible impacts of increased predation rates or altered size selectivity during perch spawning, we conducted a sensitivity analysis, using the best 1995 estimates for all input variables. First we changed only the proportion of perch in the cormorant diet during spawning, from observed levels up to 90%. Then we also altered the size distribution to include more large fish in the diet. For both of these changes, we estimated the number of perch consumed per age class and the mortality rate. These simulations were done to better understand the range of consumption that might occur in years when the perch spawning season overlaps totally with presence of cormorants in the area.

## RESULTS

Cormorants were much more likely to consume perch during the spawning period than other times ( $n = 194$  cormorants,  $G = 6.13$ ,  $df = 3$ ,  $p = 0.106$ ). However, a model using interactions between sex of cormorant and consumption of perch did not explain the frequencies observed, suggesting that consumption of perch did not vary by sex. A model including interactions among sex, season, and consumption were also significant ( $G = 5.19$ ,  $df = 1$ ,  $p = 0.023$ ). The significance of this model was based on a slightly higher consumption of perch by male cormorants in the second season, when overall consumption of perch was very low (~1% of the diet). Therefore, we assumed perch consumption varied by season but not by sex (accepting model 1), and we also assumed consumption of other species did not differ by sex. For further calculations, we pooled sexes.

The cormorant diet comprised 30 taxonomic groups, encompassing 14 fish families and one invertebrate family (Table 1). Rather abrupt shifts in diet composition, lasting 3-5 days, occurred between periods 1 and 2, while other dietary shifts occurred

**TABLE 3.** Diet composition of cormorants collected from Les Cheneaux Islands area in 1995. Values are percents by number (N) and biomass (B) of prey items from each prey category for each dietary period. A dash (-) represents less than 0.1 percent.

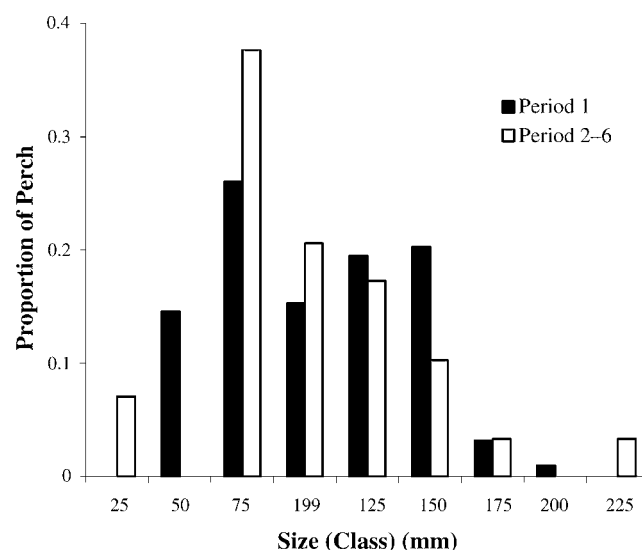
Prey Group	Period 1		Period 2		Period 3		Period 4		Period 5		Period 6		Total	
	N	B	N	B	N	B	N	B	N	B	N	B	N	B
alewife	—	—	6.2	40.0	61.1	88.9	25.1	28.5	35.1	29.8	91.8	65.1	29.2	46.8
stickleback	13.5	0.8	91.4	46.0	33.8	5.4	21.3	3.3	38.4	8.4	0.7	0.2	57.9	15.1
yellow perch	42.1	47.7	0.2	1.2	0.4	0.9	1.6	7.0	—	—	0.4	13.9	2.1	10.5
Centrarchidae	9.4	14.7	0.2	2.7	0.1	0.2	1.1	11.9	1.7	15.1	0.6	3.8	0.8	6.3
sculpin	0.3	—	0.6	1.0	1.4	0.6	41.7	23.6	15.3	11.8	—	—	5.0	4.0
northern pike	2.8	18.1	—	2.5	0.2	—	0.3	0.3	—	—	—	—	0.2	3.9
minnow	24.0	4.1	—	—	0.3	0.2	1.6	1.1	3.7	2.3	4.7	9.2	2.1	1.6
white sucker	1.7	11.7	—	—	0.1	1.9	0.8	12.0	0.2	8.5	—	—	0.2	4.8
brown bullhead	0.8	2.4	—	—	—	—	0.8	9.7	1.0	19.4	—	—	0.2	3.4
smelt	0.8	—	0.5	0.4	1.8	0.4	—	—	0.5	—	0.1	—	0.7	0.2
Salmonidae	—	—	0.1	1.3	0.2	1.4	—	—	0.2	0.7	—	—	0.1	0.9
crayfish	3.3	0.2	0.4	0.2	0.2	—	4.4	0.8	1.7	0.4	—	—	0.9	0.2
unidentified	0.6	—	—	0.1	0.2	—	0.8	0.4	0.5	0.3	0.1	0.1	0.2	0.1
other	0.8	0.1	0.1	4.5	—	—	0.2	1.5	1.6	3.2	1.5	7.5	0.4	2.1

much more gradually (Table 2). Alewife was by far the most important diet component, and it was the main diet item in biomass during periods 3 through 6 (4 July–6 October; Table 3). During periods 2–4, most alewife consumed were spawning adults or yearling fish; however, during periods 5–6, approximately 80% of alewife captured were young-of-the-year (YOY). Cormorant consumption appeared to be opportunistic, often changing to forage on species that were spawning. While we had no estimates of abundance of prey in nature (except for perch), most likely changes in prey consumed by cormorants reflected changes in prey availability and behavior.

Consumption of perch was highly variable with time. Yellow perch comprised 48% of the biomass of cormorant diet during period 1, dropped substantially during periods 2–5, then rose again to 14% during period 6. Within period 1, perch steadily decreased as a diet component, comprising on average 66% of the diet during days 1–10, 50% during days 11–20, and 34% during days 21–30. Many of the primary species in the diet were spawning when they were consumed: yellow perch, northern pike, rock bass, and pumpkinseed in period 1; stickleback and alewife in period 2; and alewife in period 3. The majority of cormorant stomachs contained only one species of prey, except in early spring and late summer when diversity of prey in an individual's stomach was higher.

The mean length of perch consumed, for all dietary periods combined, was 116 mm (N = 1,385). Interestingly, most of the perch consumed during

period 1 were too small to be spawning fish, with 76% smaller than 150 mm, the minimum size of a mature female. Size distribution of perch in the cormorant diet during period 1 was not statistically different from natural perch size distribution during periods 2–6 (Fig. 2,  $\chi^2 = 0.72$ , df = 2,  $p = 0.70$ ).



**FIG. 2.** Size frequencies of perch in the cormorant diet in 1995. Size classes are designated as the minimum size in the range, i.e., 25 mm = 25–49 mm. The two distributions were not statistically different; however, young-of-year perch were consumed only in periods 2–6 (the 25 mm size class).



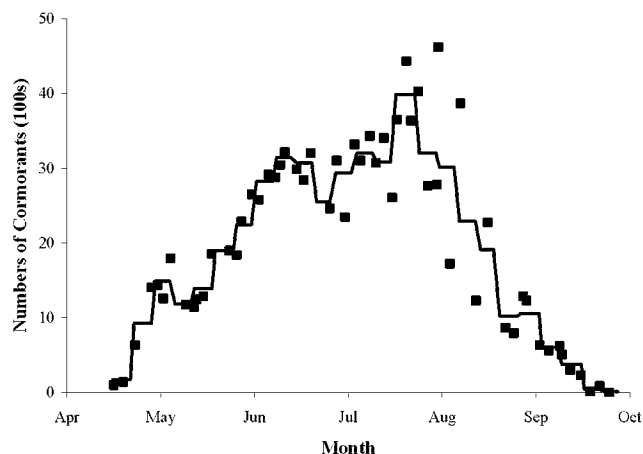
**TABLE 4.** Study area usages for the three colonies of cormorants in Les Cheneaux Islands area, 1995. Number of nests are to the nearest hundred, taken from Ludwig and Summer (1997). Location is relative to the bounded study area (Fig. 1).

Colony	Number of nests	Location	Study area usage
St. Martins Shoal	2,000	~ 5 km W	0.26
Goose Island	1,800	within	0.57
Crow Island	300	within	0.67

YOY yellow perch were found in the stomachs later in the year, while no YOY could be consumed during spawning. Therefore, size frequency distributions were kept separate for all analyses.

Estimates of study area usages (Table 4) suggested that cormorants from the three colonies contributed differently to the pool of foraging birds within Les Cheneaux Islands. St. Martins Shoal, the largest colony, is farthest from the study area, and had the lowest usage (26%); Goose and Crow islands, both within the study area, had higher usages (57% and 67%, respectively). When study area usages were added to raw aerial counts of cormorants (Diana *et al.* 1997), the resulting estimates for cormorant equivalents (from Equation 1) revealed an increase in numbers through mid-June, followed by relative stability through late July, followed again by drastic fluctuations overlaying a downward trend in local population size through the first week of October, when essentially no cormorants remained in the area (Fig. 3). Some portion of the early and later fluctuations most likely resulted from migrating birds stopping briefly in Les Cheneaux Islands before traveling farther north or south. Later fluctuations were probably also related to the 1995 year class fledging and leaving the area, perhaps in large groups.

Estimates of daily consumption by nestlings increased through age 40 days, followed by a slight decrease. Our estimates of consumption by breeding and nonbreeding cormorants ranged from 510 to 540 grams/day; this represents about 25% of body weight per day. Very few nonbreeders (~1% of birds sampled) were present in the area early in the year, but by August, nearly half of birds sampled were nonbreeders. Most breeding terminated by beginning of September, and so no distinction between breeders and nonbreeders was made after mid September.



**FIG. 3.** Cormorant equivalents (CE) for birds foraging in Les Cheneaux Islands area in 1995. See Equation 1 for the definition of CE.

Having independently estimated the proportion of perch in the cormorant diet, cormorant equivalents, cormorant daily consumption, and the proportion of breeders and nonbreeders in the population, we then incorporated these estimates into the calculation for biomass of perch consumed by cormorants, using Equation 2. We estimate that 7,100 kg of yellow perch were consumed during perch spawning (period 1), and 4,300 kg during the remainder of 1995, for a total of 11,400 kg. By substituting ranges encompassing reasonable levels of uncertainty for all parameters in Equation 2, a consumption range of 6,600 to 17,500 kg was estimated. Given the size frequencies of perch in the diet and mean weights for each size class, these biomass estimates correspond to a range of 270,000 to 720,000 individual perch consumed, with a best estimate of 470,000. Only 5% of these perch, or 24,000 (range of 14,000 to 37,000) were of legal size (length > 175 mm) when consumed. An estimated 7,000 to 17,000 YOY perch were consumed during periods 2–6. No estimates of YOY abundance were made during 1995, so the precise effect of cormorant predation on recruitment is unknown. Given a prediction of 4.4 million perch at age 1 (Schneeberger and Scott 1997), the removal of up to 17,000 YOY should have no substantial effect on recruitment.

Mortality from cormorant predation on perch older than YOY was heaviest at smaller sizes: 75–175 mm in early spring and 75–100 mm during the rest of the year. In contrast, angling mortality was greatest at 175–200 mm (Table 5). That cor-

**TABLE 5.** The number, in thousands, and percent by size of yellow perch age 1 and older consumed by cormorants (under low, best, and high estimates of cormorant consumption) and caught by anglers during 1995 for period 1, the period of perch spawning (a), and periods 2-6, the remainder of the year (b). Population estimates are in thousands.

Size (mm)	Population estimate	Consumed by cormorants						Caught by anglers	
		Low		Best		High		#	%
		#	%	#	%	#	%		
(a) Period 1 (17 April –16 May 1995)									
25–50	8	—	—	—	—	—	—		
50–75	2,232	25.1	1.1	43.6	2.0	68.7	3.1		
75–100	2,234	44.8	2.0	77.7	3.5	122.3	5.5		
100–125	847	26.7	3.2	46.3	5.5	72.9	8.6		
125–150	1,717	33.6	2.0	58.2	3.4	91.8	5.3		
150–175	1,134	35.0	3.1	60.6	5.3	95.5	8.4		
175–200	640	5.7	0.9	9.9	1.5	15.5	2.4		
200–225	459	1.4	0.3	2.4	0.5	3.8	0.8		
225–375	529	—	—	—	—	—	—		
Total	9,800	172.3		298.7		470.5			
(b) Periods 2–6 (17 May–16 October 1995)									
50–75	39	—	—	—	—	—	—	—	—
75–100	1,097	38.3	3.5	64.6	5.9	95.1	8.7	—	—
100–125	3,210	20.9	0.7	35.3	1.1	51.9	1.6	—	—
125–150	1,337	17.4	1.3	29.3	2.2	43.2	3.2	—	—
150–175	1,760	10.4	0.6	17.6	1.0	25.8	1.5	0.2	—
175–200	874	3.5	0.4	6.0	0.7	8.8	1.0	46.4	5.3
200–225	623	—	—	—	—	—	—	11.8	1.9
225–250	401	3.5	0.9	6.0	1.5	8.8	2.2	5.4	1.3
250–275	181	—	—	—	—	—	—	1.8	1.0
275–300	104	—	—	—	—	—	—	0.4	0.4
300–325	101	—	—	—	—	—	—	0.4	0.4
325–350	53	—	—	—	—	—	—	0.1	0.2
350–375	20	—	—	—	—	—	—	—	—
Total	9,800	94.0		158.8		233.6		67	

morants and anglers affected different sizes of perch is not surprising, because anglers were restricted to larger fish by the 175 mm size limit, and cormorants consume smaller fish even when larger fish are available (Campo *et al.* 1993).

Neither cormorant predation nor angling constituted a significant source of mortality at any size or time of year, when compared with total annual mortality of 45% (Schneeberger and Scott 1997). Examination of perch mortality by age (Table 6, Fig. 4) reveals that even the highest estimate for cormorant consumption of perch yielded mortality rates from predation less than 10% for all ages, which accounted for about one-fifth or less of the total annual mortality (45%). Mortality from sum-

mer angling was less than 3% for all age classes, which was less than one-fifteenth of total annual mortality. Because cormorants and anglers consumed different sizes of perch, they affected different ages as well (Fig. 4), although the overlap was greater for ages than sizes. Cormorant predation generally accounted for a greater proportion of mortality at younger ages (1–3), in contrast to anglers who removed principally ages 3 and older.

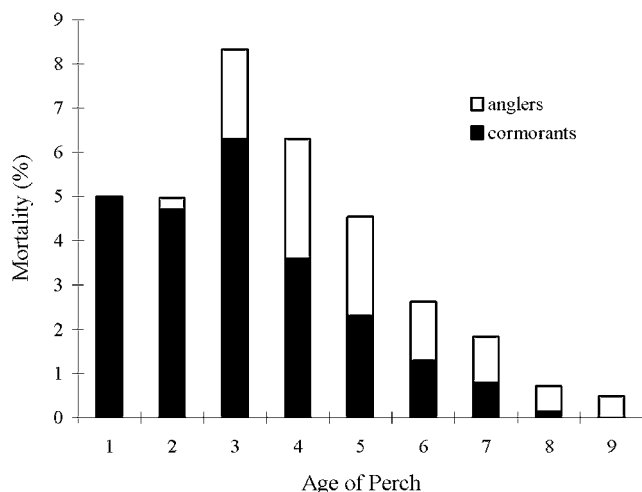
Altering the size or fraction of yellow perch in cormorant diets during season 1 would cause higher consumption rates for perch, but would not dramatically increase the mortality due to cormorant predation. Allowing perch to comprise 90% of the diet during the first 30 days, the estimated number of

**TABLE 6.** Number, in thousands, and percent of the perch population age 1 and older eaten by cormorants (low, best, and high estimates) and taken by anglers in 1995. Size ranges are for April, prior to period of fastest growth. Totals for cormorant consumption do not include young-of-year perch. Population estimates are in thousands. For perch population and angling data see Schneeberger and Scott (1997).

Age class	Approx. size range (mm)	Population estimate	Consumed by cormorants						Caught by anglers	
			Low		Best		High			
			#	%	#	%	#	%	#	%
1	25–150	4,416	127.6	2.9	218.9	5.0	335.1	7.6	—	—
2	50–200	2,429	66.9	2.8	115.0	4.7	177.5	7.3	6.4	0.3
3	75–225	1,336	48.7	3.6	83.9	6.3	130.1	9.7	26.8	2.0
4	100–275	735	15.3	2.1	26.4	3.6	41.1	5.6	19.6	2.7
5	125–350	404	5.4	1.3	9.3	2.3	14.2	3.5	9.0	2.2
6	150–350	222	1.7	0.8	3.0	1.4	4.5	2.0	2.9	1.3
7	150–350	122	0.6	0.5	1.0	0.8	1.5	1.2	1.3	1.1
8	175–350	67	—	—	0.1	0.1	0.1	0.1	0.4	0.6
9	225–350	37	—	—	—	—	—	—	0.2	0.5
10	300–350	20	—	—	—	—	—	—	—	—
11	300–375	11	—	—	—	—	—	—	—	—
Total			266.2		457.6		704.1		67	

perch consumed was increased by 66% (780,000 perch consumed, compared with 470,000). The biomass consumed was 18,800 kg (compared with 11,400 kg). However, the highest mortality rate was 11.3% (age 3), about one-fourth of total annual mortality. Allowing the proportion of perch 150 mm and larger to increase from 0.24 (as in 1995) to

0.5 for perch consumed during spawning, the estimated total number consumed fell back to 580,000. Under this scenario, cormorants eat fewer but larger fish. The cormorant-caused mortality rates declined for ages 1–3 and increased for ages 4 and older compared with mortality rates from the first simulation. The highest rate for all ages still occurred at age 3, and was 10.7%.



**FIG. 4.** Mortality of different age classes of yellow perch in Les Cheneaux Islands area in 1995 caused by cormorant predation and by angling. Total annual mortality for perch was estimated at 45% (Schneeberger and Scott 1997).

## DISCUSSION

Although the cormorant diet contained approximately 48% yellow perch by mass during the perch spawning period, this study suggests that cormorant predation on perch in 1995 was not substantial, compared to other mortality sources. Angling was not a significant source of perch mortality in 1995 either, suggesting that perhaps predation by piscivorous fish is substantial. Little information exists regarding the consumption of perch by other fish in Les Cheneaux Islands. However, burbot, northern pike, and splake are all common large fishes in the area that feed on yellow perch (Scott and Crossman 1973) and could consume moderate- to large-sized perch. Furthermore, medium-sized fish in the area, such as smallmouth bass, rock bass, brown bullhead, and pumpkinseed, may prey on juvenile perch. Commercial gillnetting is another possible source of mortality. However, most gillnetting effort occurs south of the main islands in deeper

water, where perch are likely to be scarce. There were no reports of tagged perch from Native American fisheries (Schneeberger and Scott 1997), suggesting that mortality from gillnetting is minimal.

Our results, using conservative calculations, suggest that cormorants probably do not consume enough commercial or sport fish to affect these populations greatly in this area. This inference is consistent with other studies of cormorant foraging in the Great Lakes. Weseloh and Casselman (1992) estimated that the Lake Ontario cormorant population consumed 0.5% of the available fish biomass, in contrast to predatory fish, which consume upwards of 10% of the available biomass (20 times the amount cormorants eat). Madenjian and Gabrey (1995) used a bioenergetics model to estimate that the entire waterbird population (including gulls, cormorants, and herons) of western Lake Erie consumed the equivalent of 15% of the prey fish biomass consumed by predatory walleye alone. Convincing evidence exists that cormorants can have significant impact on aquaculture facilities (Schramm *et al.* 1987, Stickely 1991), and on populations of planted fingerlings in reservoirs (Modde *et al.* 1996). However, these examples represent artificially high prey concentrations, and are far from representative. Simmonds *et al.* (1995), using modeling techniques, concluded that cormorant predation on most of the Oklahoma reservoirs studied was not enough to reduce fish yields for anglers detectably; those findings are consistent with results here.

Other studies on yellow perch/cormorant interactions also support the general finding that cormorants do not greatly affect yellow perch populations. In one study on Lake Ontario, cormorant consumption (estimated from pellets) may have affected yellow perch abundance (population numbers assumed from other studies), reducing age-3 perch by 29–54% (Burnett *et al.* 2002). The authors hypothesized that cormorant predation had the potential to limit the perch stock and that perch populations remained low in the 1990s after cormorant invasion. Most studies found no significant impact by cormorant predation on perch populations. The most comprehensive study, on Oneida Lake, compared measured cormorant consumption (from pellet analyses) to measured perch abundance, and concluded that cormorants and anglers caused similar mortality on yellow perch, although anglers removed older fish than cormorants (VanDeValk *et al.* 2002). They also found that total mortality of perch had not increased since cor-

morant colonization. Mortality caused by cormorants and anglers in that study (40%) was much higher than in this study, but conclusions were similar. The bulk of findings concur with our results: cormorants take small perch, in age-size categories that have high mortality from other sources, and typically do not comprise sufficient mortality to affect yellow perch population dynamics.

In 1995, northern Michigan experienced a warm spring that resulted in perch spawning earlier than usual. Many larger spawning perch may not have been susceptible to cormorant predation, because they had spawned and dispersed before cormorants arrived in the area. In contrast, spawning was late in 1996; it peaked after many cormorants had migrated into the study area. Perch may have comprised a greater proportion of the cormorant diet or may have been represented by a different size distribution in the cormorant diet in 1996 compared to 1995. However, reasonable year-to-year variation in cormorant predation on perch during spawning would not drastically alter age-specific mortality rates, provided perch and cormorant population sizes are comparable to 1995 estimates. While Ludwig and Summer (1997) predicted that the cormorant population in Les Cheneaux Islands would continue to expand until at least 2000, recent evidence shows the population stabilizing. Weseloh *et al.* (2002) determined that the rapid population growth of cormorants in the study area in the early 1990s (from 614 nests in 1991 to 4,031 nests in 1995) reached equilibrium; current populations appear stabilized (4,223 nests in 2000).

The relative contributions of different sources of mortality on perch, as well as total annual mortality, may also vary annually. Lucchesi (1988) and Schneeberger and Scott (1997) used comparable techniques to estimate total annual mortality in 1986 and 1995, respectively. In 1986 total mortality was 55% and in 1995 it was 45%, and these estimates were not significantly different (Schneeberger and Scott 1997). The composition of these mortality rates appears to have changed substantially over that time period; Lucchesi (1988) estimated 1986 fishing mortality for adult perch to be as high as 40%, whereas Schneeberger and Scott (1997) estimated 1995 fishing mortality to be no greater than 5%. Cormorant predation was not shown to cause high perch mortality in 1995, while in 1986 the cormorant population in Les Cheneaux was two orders of magnitude smaller and would have accounted for an even smaller fraction of perch mortality. The larger, more important, ques-

tion underlying these issues concerns the additivity of mortality sources on perch. Does mortality from cormorant predation (or angling) occur in addition to other sources of mortality (additive), or does it replace other sources (compensatory)? The comparison of only 2 years of mortality data is not sufficient to answer this question.

We know little about the indirect effects of cormorants on target populations (such as perch), or on other aspects of these aquatic systems. For example, cormorants prey on burbot and northern pike (18% of the diet by biomass in period 1), known predators of yellow perch, thereby introducing indirect positive effects on perch. During period 2, cormorants preyed heavily on stickleback, a common forage fish for many species (possibly including larger perch). Also, cormorant predation on alewives, which are widely abundant throughout Lake Huron, may alleviate alewife competition with yellow perch, as well as predation by alewife on small perch. We estimate that in 1995, cormorants consumed about 123,000 kg of alewife in Les Cheneaux Islands. Because no population or biomass estimates were made for alewife in this area, the impact of this cormorant predation cannot be known precisely. However, cormorants may be indirectly benefiting yellow perch by preying heavily upon the invasive alewife.

Alewife is the primary prey of cormorants nearly everywhere the two species are found together (Christie *et al.* 1987, Ludwig *et al.* 1989, Neuman *et al.* 1997, Johnson *et al.* 2002, this study), and are possibly intimately linked to cormorant population dynamics. Ludwig *et al.* (1989) regressed percent alewife in the cormorant diet against an alewife abundance index for the upper Great Lakes and found that the cormorant diet responded sensitively to changes in alewife abundance. Cormorant reproductive success may depend on alewife populations and fluctuations. Weseloh and Ewins (1994) found a significant positive relationship between alewife abundance index and percent increase in breeding cormorants three years later, when fledglings mature. This finding suggests that (1) abundant alewife may have contributed to widespread cormorant population growth, and (2) if food limitation is to occur for cormorants, it will probably be controlled by alewife abundance. In the Apostle Islands of Lake Superior, where alewife are scarce or absent, rates of cormorant population increase began to decline in the mid 1980s (Craven and Lev 1987), earlier than any colony in the Great Lakes where alewife are abundant.

The results of this study indicate that control of cormorants in Les Cheneaux Islands would not significantly reduce perch mortality, and therefore would probably be a waste of time, money, and effort. In addition, substantial intercolony movement of cormorants, demonstrated for Les Cheneaux Islands area (Belyea 1997), suggests that colonies comprise metapopulations, which would render local cormorant control less feasible. In New York, egg oiling has been used as a control measure on Little Galloo Island since 1992, reducing the number of nests by about 11% per year and stabilizing the population of cormorants (Johnson *et al.* 2002, Weseloh *et al.* 2002). Similar egg destruction programs on Gull, Bass, and Calf islands eliminated nesting on those islands by the year 2000. The overall results of all these control methods have not decreased cormorant populations in Lake Ontario (Weseloh *et al.* 2002). The metapopulation status of cormorants, and the lack of results implicating cormorants in large reductions of sport fish populations indicate that local cormorant control does not appear warranted as part of a fisheries management strategy in the Great Lakes. However, population control methods may reduce cormorant impacts near the sites of control programs (Johnson *et al.* 2002).

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