The Condor 97:141–153
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WATERBIRD PREDATION ON FISH IN WESTERN LAKE ERIE: A BIOENERGETICS MODEL APPLICATION[1]

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Abstract. To better understand the role of piscivorous waterbirds in the food web of western Lake Erie, we applied a bioenergetics model to determine their total fish consumption. The important nesting species included the Herring Gull (*Larus argentatus*), Ring-billed Gull (*L. delawarensis*), Double-crested Cormorant (*Phalacrocorax auritus*), Great Blue Heron (*Ardea herodias*), Black-crowned Night-Heron (*Nycticorax nycticorax*), and Great Egret (*Casmerodius albus*). The impact of migrant waterbirds, including the Red-breasted Merganser (*Mergus serrator*), on western Lake Erie fish biomass was also considered in the analysis. According to the modeling results, during the early 1990s, piscivorous waterbirds consumed 13,368 tonnes of fish from western Lake Erie each year. This tonnage was equivalent to 15.2% of the prey fish biomass needed to support the walleye (*Stizostedion vitreum*) population in western Lake Erie during a single growing season. The model application was useful in quantifying energy flow between birds and fish in a large lake ecosystem.

Key words: Bioenergetics; ecological impact; fish consumption; Lake Erie; large lakes; modeling; predation; waterbirds.

INTRODUCTION

Large populations of several piscivorous waterbird species, including the Herring Gull (*Larus argentatus*), Ring-billed Gull (*L. delawarensis*), Double-crested Cormorant (*Phalacrocorax auritus*), Great Blue Heron (*Ardea herodias*), Black-crowned Night-Heron (*Nycticorax nycticorax*), and Great Egret (*Casmerodius albus*), reside along the shores of western Lake Erie from spring through autumn (Blokpoel and Tessier 1991, Peterjohn and Rice 1991, Scharf and Trapp 1994). In addition, some piscivorous waterbird species, such as the Red-breasted Merganser (*Mergus serratus*), use the western basin of Lake Erie as a staging area during their spring and fall migrations (Southern 1974, Peterjohn and Rice 1991). The walleye (*Stizostedion vitreum*) is the predominant piscivorous fish in western Lake Erie (Knight et al. 1984, Hartman and Margraf 1992, Knight and Vondracek 1993). Although the walleye is assumed to be the dominant piscivore in this ecosystem (Knight and Vondracek 1993), a rigorous comparison of fish consumption by birds with that by walleyes has not been attempted.

There appears to be substantial overlap in the diets of walleye and piscivorous waterbirds in western Lake Erie. The most important prey fish for western Lake Erie walleye included the gizzard shad (*Dorosoma cepedianum*), alewife (*Alosa pseudoharengus*), white perch (*Morone americana*), emerald shiner (*Notropis atherinoides*), and spottail shiner (*Notropis hudsonius*) (Hartman and Margraf 1992). Other prey fish included the rainbow smelt (*Osmerus mordax*), freshwater drum (*Aplodinotus grunniens*), and yellow perch (*Perca flavescens*) (Hartman and Margraf 1992). Belant et al. (1993) and Hoffman (1977) have shown that gizzard shad, shiners, and alewives were important diet constituents of the Herring Gull, Great Egret, Great Blue Heron, and Black-crowned Night-Heron from western Lake Erie. Peterjohn and Rice (1991) reported large flocks of Red-breasted Mergansers feeding on gizzard shad in Lake Erie during autumn. The diet of Double-crested Cormorants from western Lake Erie has not been examined (J. Ludwig, pers. comm.), however the diet of Lake Ontario Double-crested Cormorants included alewife, yellow perch, white perch, and rainbow smelt (Weseloh and Casselman 1992). In summary, there is potential for feeding competition between pisciv-

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[1] Received 20 June 1994. Accepted 24 August 1994.

orous waterbirds and walleyes in western Lake Erie.

If prey fish populations are sufficiently reduced, walleye growth and recruitment would be reduced. When prey fish are unavailable, walleyes resort to a diet of invertebrates, and growth is substantially slower on an invertebrate diet than on a fish diet (Forney 1966, Priegel 1970). Furthermore, recruitment of juvenile walleyes into the adult population may be greatly reduced if juvenile walleye diet is chiefly comprised of invertebrates rather than fish (Madenjian and Carpenter 1991).

Bioenergetics models can be used to estimate the amount of food consumption by a particular animal population. Hartman and Margraf (1992) fitted a bioenergetics model to the walleye population (approximately 50 million age-one year or older fish) of western Lake Erie, and calculated that walleyes consumed, on average, 88,200 tonnes of prey fish during each growing season (May through November) from 1986 through 1988. Bioenergetic simulation models have been applied to seabird populations on the Oregon coast (Wiens and Scott 1975) and in the Gulf of St. Lawrence (Cairns et al. 1991) to estimate fish consumption. For freshwater systems, Weseloh and Casselman (1992) used a simple bioenergetics model to estimate fish consumption by the Double-crested Cormorant population of Lake Ontario.

Our objectives were to: (1) apply a bioenergetics model to the waterbird populations of western Lake Erie to estimate annual fish consumption by birds, and then (2) compare fish consumption by birds with that by walleyes in western Lake Erie.

Results of our modeling exercise should be of interest to applied and basic ecologists alike. The walleye population in western Lake Erie supports valuable commercial and recreational fisheries (Knight and Vondracek 1993). Due to a decrease in environmental contaminant levels, the Double-crested Cormorant nesting population in western Lake Erie has increased dramatically from the mid-1980s to the present time (Weseloh et al., in press). As has already happened on Lake Ontario (Weseloh and Casselman 1992), anglers and commercial fish harvesters on western Lake Erie may become concerned about the effects of an increasing cormorant population on the fishery. The results of our study can be used to help guide decisions made by fishery managers. From a basic ecology standpoint, waterbird predation on fish is one link in the western Lake Erie food web. Quantification of that link represents one step toward building an overall ecosystem model for the western basin of Lake Erie. Such a model could be used to identify the important energy pathways within the ecosystem.

MODEL

MODEL STRUCTURE FOR NESTING BIRD POPULATIONS

We estimated fish consumption by waterbird populations nesting within the perimeter of the western basin of Lake Erie. For purposes of comparison with the Hartman and Margraf (1992) study, we defined the western basin of Lake Erie as that portion of the lake west of Point Pelee on the Canadian side and west of the mouth of the Huron River (in Ohio) on the U.S. side. Nesting populations of the following species were modeled: Herring Gull, Ring-billed Gull, Double-crested Cormorant, Great Blue Heron, Black-crowned Night-Heron, and Great Egret. See Data for Nesting Populations section for information on the bird nest surveys. Species with fewer than 100 nests, such as the Common Tern (*Sterna hirundo*), were not included in the modeling analyses. Only nesting colonies within the western basin perimeter were included in this analysis.

For the nesting populations, we used a bioenergetics approach similar to the one used by Cairns et al. (1991). This approach, based on the work of Furness (1978) and Wiens (1984), incorporated the allometric relationship between field metabolism and body mass developed by Birt-Friesen et al. (1989). Birt-Friesen et al. (1989) observed a strong correlation between the logarithm of field metabolism, as measured by doubly labeled water and activity timers, and the logarithm of bird body mass. Thus, we modeled daily energy expenditure (DEE) as a function of bird body mass. We assumed an assimilation efficiency of 0.80 for all species considered in the analysis (Cairns et al. 1991). DEE divided by assimilation efficiency equalled the total daily energy consumption by an adult. Total daily energy consumption divided by the average energy density of the diet yielded the daily food mass per adult. The product of daily food mass per adult bird and the proportion of fish in the diet represented the daily fish consumption per adult bird. Refer to Appendix 1 for more details on adult bird bioenergetics.

Concerning the bioenergetics of egg production and the food intake needs of chicks, we proceeded as outlined in Kendeigh et al. (1977). Refer to Appendix 1 for more information on the bioenergetics modeling of hatching-year birds.

Each nesting population was grouped into three life stages: hatching-year, non-breeder, and breeder. Within each life stage, the number of individuals was assumed to decline exponentially with time (Perrins and Birkhead 1983). See Appendix 1 for references on estimating instantaneous mortality rates.

DATA FOR NESTING BIRD POPULATIONS

Number of nests were obtained from surveys conducted by the Canadian Wildlife Service (Blokpoel and Tessier 1991) for gull nests on the Canadian side of Lake Erie and by the U.S. Fish and Wildlife Service (Scharf et al. 1994, Scharf and Trapp 1994) for nests of all waterbird species on the U.S. side of Lake Erie during 1989 through 1991. We assumed that the number of breeding birds was equal to double the number of nests. This assumption was supported by gull colony studies, which showed that polygyny rates were extremely low (<0.5% occurrence) (Shugart 1980, Lagrenade and Mousseau 1983). Polygyny rates for the other four nesting bird species apparently are unknown, but these species are reported as being monogamous (Bent 1922, 1926; Butler 1992).

The nesting population of Double-crested Cormorants has increased dramatically from 1990 to the present time. We therefore used the 1993 estimate of the nesting population (M. Shieldcastle, pers. comm.; D. Weseloh, pers. comm.). Nesting numbers of the herons and egrets have not been compiled from the 1989–1991 Canadian survey. Because the composite population of egrets and herons on the U.S. side of the western basin has remained relatively constant in size from 1975 to the present time (Scharf et al. 1978, Scharf and Trapp 1994), we used nest numbers from the 1976 survey (Blokpoel and McKeating 1978) to represent heron and egret species on the Canadian side of the basin.

The number of non-breeding birds that are associated with the breeding population is difficult to estimate, and typically is not determined. Non-breeding birds are defined as second-year or older birds that do not participate in any breeding activities during a particular year. We assumed that the ratio of non-breeders to the number of nests was 0.609 (Cairns et al. 1991). Clutch size, hatching success, fledging success, hatch-year mortality, non-breeder mortality, breeder mortality, and diet composition were derived from values reported in the literature and from personal observations from researchers conducting studies in the western Lake Erie vicinity. Refer to Table 1 and Figure 1 for more details on the life history characteristics of the nesting bird populations employed in the computer simulations. Because the bulk of the non-breeding population was believed to be comprised of immature birds, we assumed that the non-breeding bird mortality was equal to the subadult mortality reported in the literature. Energy content of the diet items was taken from the literature (Cummins and Wuycheck 1971, Stein and Murphy 1976, Stewart et al. 1983, Hewett and Johnson 1992).

The undocumented values (i.e., those without footnotes) in Table 1 represent values of life history characteristics that were unavailable from the literature for the particular species of interest, and therefore the value from a related species was used. For example, hatch-year mortality refers to the percent reduction in the population size of hatching year birds from the completion of the fledgling period to the time of departure from Lake Erie during fall migration. Hatch-year mortality was unavailable for the Great Egret, but was available for the Great Blue Heron (Table 1). We therefore assumed the same mortality rate for the Great Egret as for the Great Blue Heron. This same pattern was true for the non-breeder and breeder mortality rates (Table 1). Finally, because the Great Egret diet was not as well quantified as that for the Great Blue Heron, we assumed identical diets between these two species because they appear to have similar feeding behaviors.

MODEL FOR MIGRANT BIRD POPULATIONS

Western Lake Erie serves as an important staging area for migrating waterbirds, particularly during autumn months. Mergansers, gulls, and cormorants are the predominant waterbird migrants in western Lake Erie (Southern 1974, Peterjohn and Rice 1991). We therefore included the Red-breasted Merganser, Common Merganser (*Mergus merganser*), Bonaparte's Gull (*Larus phila-*

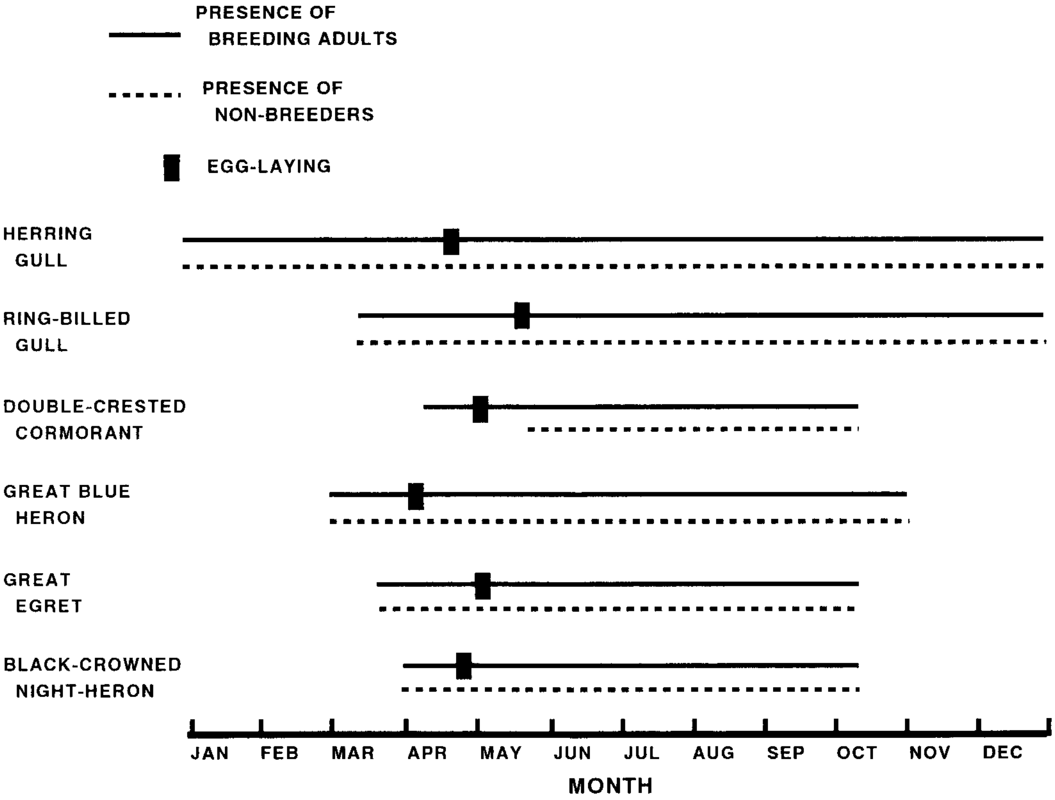

FIGURE 1. Typical arrival, egg-laying, and departure dates for gulls, cormorants, herons, and egrets, nesting on western Lake Erie. The nesting population of Herring Gulls was present during the entire calendar year. Data were taken from Vermeer (1970), Nol and Blokpoel (1983), Peterjohn and Rice (1991), Weseloh and Casselman (1992), and Gabrey (unpubl. data), or provided by B. Buckingham (Ohio Department of Natural Resources, Vickery, Ohio, pers. comm.), M. Shieldcastle (pers. comm.), and D. Weseloh (pers. comm.). All female breeders of a given species were assumed to lay their eggs on one day.

delphia), Ring-billed Gull, Herring Gull, and the Double-crested Cormorant in the migrant bird analysis.

We employed a simple algorithm to estimate fish predation by migratory bird populations during autumn. The duration of the fall migration was assumed to be eight weeks (Peterjohn and Rice 1991). The estimated sizes of migrating populations were 210,000 Red-breasted Mergansers (Peterjohn and Rice 1991), 25,000 Common Mergansers (adjusted average from Christmas bird counts 1983–1992), 20,000 Bonaparte's Gulls (extrapolation from fall surveys from 1986 to 1993 by R. Dolbeer, unpubl. data), 200,000 Ring-billed Gulls (based on fall surveys by R. Dolbeer), 10,000 Herring Gulls (based on fall surveys by R. Dolbeer), and 6,500 Double-crested Cormorants (M. Shieldcastle, pers. comm.). For each migratory population, the 56 days was multiplied by the estimated population size to yield the number of bird-days. The product of bird-days and daily fish consumption per adult bird yielded the total fish consumption during the autumn migration. Daily fish consumption per adult bird was determined as described in the Model Structure for Nesting Bird Populations section. Merganser and Bonaparte's Gull diets were assumed to be 100% fish. Adult weights of mergansers and Bonaparte's Gulls were taken from Dunning (1993).

Estimates of the sizes of the migratory bird populations were taken from a variety of sources. Red-breasted Merganser and Double-crested Cormorant numbers were based on aerial observations. The Common Merganser migratory population size was estimated by adjusting the Christmas bird counts. The Common Merganser population size was expected to peak at Christ-

TABLE 1. Life history characteristics of six fish-eating bird species used in a model of fish consumption by birds in western Lake Erie.

Characteristic	Species					
	Herring Gull	Ring-billed Gull	Double-crested Cormorant	Great Blue Heron	Great Egret	Black-crowned Night-Heron
Number of nests	10,274[1,2]	6,676[1,2]	3,600[1,2,3]	2,627[4,5]	1,446[4,5]	2,788[4,5]
Modal clutch size	3[6]	3[6]	4[7,8]	4[9]	3[10]	4[11]
Calories per egg	128.1[12]	90.1[12,13]	75.4[8,12]	63.9[12,14]	56.3[12,14]	34.9[12,14]
Incubation (days)	28[9]	25[14,15]	27[16]	30[9]	24[16]	24[11]
Hatch rate (% of eggs laid)	80[17]	86[18]	62[19]	86[20]	60[20]	53[11]
Fledging (days)	42[17]	35[21]	53[19]	53[22]	52[10]	35[23]
Fledge rate (% of chicks hatched)	50[17]	40[18]	76[19]	87[22]	61[20]	58[11]
Hatch-year mortality (%/year)	42[24]	42	42	51[25]	51	40[26]
Non-breeder mortality (%/year)	25[24]	25	25	22[25]	22	23[26]
Breeder mortality (%/year)	13	13[27]	20[28]	22[25]	22	23[26]
Mass at hatch (g)	67.0[29]	34.5[13]	37.2[8]	42.0[22]	45.0[10]	24.2[14]
Adult mass (kg)	1.14[30]	0.52[30]	1.89[8]	2.39[30]	0.87[30]	0.88[30]
Diet:						
% Fish	50[28,31]	35[28]	99[28]	72[32]	72	52[32]
% Crustaceans/insects	5[28,31]	25[28,33]	1[28]	17[32]	17	38[32]
% Garbage	35[28,31]	25[28]				
% Earthworms	10[28,31]	15[28]				2[32]
% Rodents/amphibians/reptiles				9[32]	9	9[32]
% Other				3[32]	3	

[1] Scharf et al. 1994; [2] Blokpoel and Tessier 1991; [3] M. Shieldcastle, pers. comm.; [4] Scharf and Trapp 1994; [5] Blokpoel and McKeating 1978; [6] Bent 1921; [7] Bent 1922; [8] Lewis 1929; [9] B. Buckingham, pers. comm.; [10] Gladstone 1979; [11] Tremblay and Ellison 1980; [12] Kendeigh et al. 1977; [13] Meathrel and Ryder 1987; [14] Carey et al. 1980; [15] Nol and Blokpoel 1983; [16] Harrison 1975; [17] Kadlec et al. 1969; [18] Vermeer 1970; [19] Blomme 1981; [20] Pratt 1972; [21] Fetterolf 1983; [22] Quinney 1982; [23] Bent 1926; [24] Paynter 1947; [25] Owen 1959; [26] Henny 1972; [27] Blokpoel and Tessier 1986; [28] Cairns et al. 1991; [29] Pierotti 1982; [30] Dunning 1993; [31] Belant et al. 1993; [32] Palmer 1962; [33] Haymes and Blokpoel 1978.

mas time (Peterjohn and Rice 1991); but because of incomplete coverage of the entire western basin by Christmas bird counts, the average Christmas bird count between 1983 and 1993 was increased by 50%. Fall surveys of gulls along the southern shore of western Lake Erie have been conducted by the personnel at the Ohio Field Station of the Denver Wildlife Research Center from 1986 to the present time (R. Dolbeer, unpubl. data). This survey covered roughly one-sixth of the western basin shoreline, and therefore the average count over years 1986 through 1993 was multiplied by 6 to arrive at the population size estimate. For Herring Gulls and Ring-billed Gulls, this estimate was adjusted by subtracting the estimated size of the nesting population.

Spring migration of waterbirds across western Lake Erie is not nearly as spectacular as the fall migration. Spring flock sizes were roughly an order of magnitude less than those observed in the fall (Peterjohn and Rice 1991), and the duration of spring migration was typically only six weeks rather than eight weeks (Trautman 1940). We therefore multiplied the fish consumption during the fall migration by 1.075 to arrive at the total annual fish consumption by each migrant bird population during spring and fall combined.

SENSITIVITY ANALYSIS

A sensitivity analysis was performed to identify the most important model inputs affecting the model output of annual fish consumption by the nesting waterbird community in western Lake Erie. The individual parameter perturbation method was used (Bartell et al. 1986). Fifteen model inputs were examined. A total of 30 simulation trials was conducted for each of the six nesting waterbird species. In any simulation trial, only one model input was changed from its nominal value; all the other model inputs were retained at their nominal value. A simulation was performed with a particular model input increased 10% from its nominal value; and then another simulation was performed with that same model input decreased 10% from its nominal value. For each input perturbation, the annual fish consumption by the composite nesting population of waterbirds was calculated; the composite nesting population of waterbirds included nesting populations of all six species considered in the modeling analysis. Then, the percent change in total annual fish consumption resulting from the input perturbation was determined.

RESULTS

Gull nests comprised the bulk of the 27,411 surveyed nests, with 10,274 Herring Gull nests (37% of the total nest number) and 6,676 Ring-billed Gull nests (24%) (Table 1). The Great Egret population was the smallest, with 1,446 nests (5%). The largest adult bird masses were for the Great Blue Heron (2.4 kg) and the Double-crested Cormorant (1.9 kg), whereas the lowest adult bird mass of the nesting birds was for the Ring-billed Gull (0.5 kg). Of the nesting birds, fish comprised the highest proportion in the Double-crested Cormorant diet (99% fish), while fish was least important in the diet of the Ring-billed Gull (35% fish) (Table 1).

According to the modeling results, waterbirds consumed a total of 13,368 tonnes of fish from western Lake Erie each year (Table 2). The nesting bird populations, including breeders, non-breeders, and hatching-year birds, consumed a total of 5,999 tonnes of fish, whereas the migrant bird populations consumed an estimated 7,369 tonnes. Of all of the individual categories of waterbirds that were considered in the analyses, the migrant Red-breasted Mergansers were responsible for the greatest amount of fish consumption at 4,914 tonnes (Table 2), or about 67% of the fish consumption by migrant birds. Migrant Ring-billed Gulls accounted for an additional 16% of the fish consumption by migrant birds.

Of the nesting bird populations, the Herring Gull population was the leading consumer of fish (Table 2). The Double-crested Cormorant and Great Blue Heron nesting populations were intermediate consumers of fish, while the nesting populations of the Ring-billed Gull, Black-crowned Night-Heron, and Great Egret were relatively minor fish predators.

Examining the nesting bird populations by life history stage, the breeding birds (all species combined) were the major fish predators, consuming a total of 3,518 tonnes (Table 2). The hatching-year group accounted for a total of 1,509 tonnes, and the non-breeders consumed a total of 972 tonnes.

The sensitivity analysis revealed that number of nests, daily energy expenditure of post-fledged birds, proportion of fish in diet, and assimilation

TABLE 2. Estimated fish consumption (tonnes/year) by gulls, cormorants, herons, and mergansers residing on or migrating through western Lake Erie.

Species	Hatching-year birds	Non-breeding birds	Breeding birds	Migrant birds	Total
Herring Gull	447	429	1,515	130	2,521
Ring-billed Gull	100	101	356	1,178	1,735
Double-crested Cormorant	365	159	720	236	1,480
Great Blue Heron	489	182	597		1,268
Great Egret	35	40	130		205
Black-crowned Night-Heron	73	61	200		334
Red-breasted Merganser				4,914	4,914
Common Merganser				762	762
Bonaparte's Gull				149	149
Total	1,509	972	3,518	7,369	13,368

efficiency were the most important model inputs affecting the estimate of total annual fish consumption by the composite waterbird population nesting on western Lake Erie (Table 3). Total annual fish consumption behaved linearly in response to changes in the number of nests. Fish energy density was of intermediate importance in determining total fish consumption. Non-breeder to nest ratio, the various mortality rates, joules per egg, duration of incubation, time between hatching and fledging, and mass at time of hatching had relatively minor impact on the estimate of total fish consumption (Table 3). Overall, the model output was robust to uncertainty in most of the model inputs.

DISCUSSION

We estimated that waterbirds annually consumed 13,368 tons of fish from western Lake Erie, based on nest counts made from 1989 through 1993. Hartman and Margraf (1992) calculated that the walleye population in western Lake Erie consumed, on the average, 88,200 tonnes of fish between May and November each year during the late 1980s. Thus, the amount of fish biomass removed by waterbirds is relatively small (15.2% of walleye ingestion) compared with fish consumption by walleyes in western Lake Erie during a single growing season. According to a bioenergetics model application to Lake Erie yellow perch (Kitchell et al. 1977), approximately 75% of the annual food consumption by yellow perch in Lake Erie occurred during the growing season (May through November). If a similar pattern in annual consumption was assumed for walleye, then an estimate of annual fish consumption by the walleye population in western Lake Erie would be 117,600 tonnes. Therefore, on an annual basis, piscivorous waterbirds would take 11.4% of the quantity of fish eaten by the walleye population in western Lake Erie.

To fully evaluate the impact of fish consumption by birds on the western Lake Erie ecosystem,

TABLE 3. Sensitivity of the estimate of fish consumption, by the composite population of nesting piscivorous waterbirds in western Lake Erie, to perturbations of various inputs to the bioenergetics model. Each input was separately perturbed +10% and then −10% from its nominal value. Sensitivity was measured as the percent change in total fish consumption resulting from the perturbation to the model input (see Sensitivity Analysis section for more details on the procedures). A sensitivity value of magnitude less than 0.05 was reported as zero.

Model input	Input perturbation error	
	+10%	−10%
Number of nests	+10.0	−10.0
Non-breeder to nest ratio	+1.6	−1.6
Hatch rate	+2.5	−2.5
Fledge rate	+1.1	−1.1
Hatch-year mortality	−0.8	+0.8
Non-breeder mortality	−0.3	+0.3
Breeder mortality	−0.6	+0.6
Daily energy expenditure (for post-fledged birds)	+9.5	−9.5
Proportion of fish in diet	+8.1	−9.4
Caloric density (of fish)	−6.1	+7.1
Calories per egg	0.0	0.0
Assimilation efficiency	−9.1	+11.1
Incubation	−0.5	+0.5
Fledging	−0.3	+0.3
Mass at hatch	0.0	0.0

the biomass of fish consumed by birds should be compared with the standing stock of prey fish. Unfortunately, there are no reliable estimates of total prey fish biomass in western Lake Erie currently available. Bottom trawls used by several natural resource agencies to survey prey fish populations do not sample the entire water column, and therefore may lead to underestimation of fish biomass. An effort to estimate prey fish biomass via acoustical apparatus combined with bottom trawls has been initiated for western Lake Erie (D. Stewart, pers. comm.).

For nesting waterbirds, the model output (i.e., fish consumption) was most sensitive to the following model inputs: number of nests, daily energy expenditure (DEE) of post-fledged birds, proportion of fish in the diet, and assimilation efficiency. Number of nests was taken from extensive surveys of the western Lake Erie basin, and relatively little error was expected in these nest surveys (H. Blokpoel, pers. comm.; W. Scharf, pers. comm.; D. Weseloh, pers. comm.). DEE was estimated from an allometric relationship developed by Birt-Friesen et al. (1989); this relationship was based on field measurements of bird metabolism using the doubly labeled water technique, which allows for accurate estimation of population energy requirements (Birt-Friesen et al. 1989). Data used to build the allometric relationship were from observations on cold water seabirds, such as the Northern Gannet (*Sula bassanus*), but the relationship should be applicable to other waterbirds with flapping flight from cool water regions (Birt-Friesen et al. 1989). Doubly labeled water measurements of the field metabolic rate of waterbirds in western Lake Erie would be a valuable research endeavor, because such an exercise would help verify or refine the above-mentioned allometric relationship. The proportion of fish in diet used in our modeling exercise represented an average (temporally and spatially for a particular species) diet proportion based on North American studies. There was no reason to believe that the proportion of fish in the diets of western Lake Erie waterbirds would substantially deviate from these average numbers. Nevertheless, more detailed diet information specifically for western Lake Erie waterbirds would improve the accuracy of the model. The assimilation efficiency value of 0.8 used in our modeling study was considered an accurate average estimate of assimilation efficiency for most waterbirds (Cairns et al. 1991). The non-breeder to nest ratio is difficult to estimate (D. Weseloh, pers. comm.), and there were no available estimates of this ratio for the western Lake Erie waterbirds. Fortunately, the estimate of total fish consumption was relatively insensitive to this model input. Furthermore, the total fish consumption estimate was very robust to uncertainties in the various mortality estimates.

According to the modeling results, the Double-crested Cormorant nesting population in western Lake Erie annually consumed 1,244 tonnes of fish, which was 9.3% of the total fish predation by birds in the western basin. The cormorant population has expanded rapidly since the 1970s, when less than 60 cormorant nests were recorded throughout all of Lake Erie (Weseloh et al., in press). In 1990 a total of 1,954 nests was observed, and a total of 3,600 nests was estimated for 1993. Presently, there may be some concern that if the cormorant population were to continue to increase, the prey fish base for walleye in western Lake Erie would be in jeopardy. Yet, if the nesting cormorant population doubled in size while populations of the other waterbirds remained constant, total fish consumption by piscivorous waterbirds from western Lake Erie would only show a modest increase from 13,368 to 14,612 or just 9.3%.

Blokpoel and Tessier (1991) reported a total of 34,021 Ring-billed Gull nests on Fighting Island in the Detroit River during 1990. Using the bioenergetics model, we estimated that the Fighting Island nesting population would annually consume 2,838 tonnes of fish. However, this nesting population was not included in our analysis for the following reasons. The Detroit River, rather than Lake Erie or Lake St. Clair, should be the source of the vast majority of the fish consumed by these birds during the breeding and fledging periods, because the Ring-billed Gull typically forages for fish within 24 km of its nest at this time (W. Southern, pers. comm.). Fighting Island is approximately 24 km from the mouth of the Detroit River in western Lake Erie, and about 30 km from Lake St. Clair. After the fledging period, adult and juvenile Ring-billed Gulls may disperse from the nesting site (W. Southern, pers. comm.). The autumn feeding of the Fighting Island gulls on fish in the western basin would be taken into account by our migrant bird analysis. We have estimated that a large migrant population (200,000 birds) of Ring-billed Gulls use western Lake Erie as a staging area for their fall migration, and we have included these birds in arriving at our total fish consumption estimate. Overall, it appears that our estimate of total consumption of fish in western Lake Erie by waterbirds needs little adjustment to account for the Fighting Island gull population.

From an ecological perspective, our modeling exercise quantifies a link (i.e., the consumption of fish by piscivorous waterbirds) in the western Lake Erie food web. The zebra mussel (*Dreissena polymorpha*), a filter feeder on phytoplankton, invaded the western basin during the late 1980s. Water clarity has increased (Leach 1993), however researchers have not yet fully evaluated the impact of the mussels on primary production, on the walleye population, and on recycling of microcontaminants. To understand the flow of energy and microcontaminants within this interesting ecosystem, a Lake Erie ecosystem modeling project has been proposed by the International Joint Commission (V. Cairns, pers. comm.). Our bioenergetics modeling work would contribute to proposed effort by supplying information on the trophic link between piscivorous waterbirds and prey fish.

The bioenergetics approach that we have used to determine fish consumption employed simplifying assumptions concerning bird metabolism and diet. For example, seasonal changes in the daily energy expenditure and diet were ignored. However, diets of some birds (especially gulls) may change over time, particularly at the end of the breeding period (Vermeer 1970, Haymes and Blokpoel 1978, Fox et al. 1990, Belant et al. 1993). Additionally, digestibility may vary from one diet item to another (Brugger 1993). For lack of detailed information on diet throughout the year in western Lake Erie, we used "average" proportions of fish and other diet items across all seasons, based on literature values, in our simulations. Furthermore, energy expenditure may be affected by a bird's behavior, proximity to a food source, or foraging strategy. The metabolic rate of an individual bird varies depending on its activity (Birt-Friesen et al. 1989), with flying the most energetically-demanding activity. Hunt (1972) found that Herring Gulls nesting nearer to a food source (a landfill) spent more time on territory, and therefore less time flying, than those nesting further from the food source. Also, males and females within a population may exhibit different foraging strategies (Fox et al. 1990) and different behaviors (Pierotti 1981, Burger 1986). Thus, reliable data on the seasonal changes in bird metabolism and diet, as well as determination of activity budgets and subsequent incorporation of behavior- and sex-specific energy expenditures, could increase the accuracy of the model.

SUMMARY

This bioenergetics model application not only estimated the magnitude of overall predation on fish by waterbirds in western Lake Erie, but also identified the major consumers of fish within the western Lake Erie waterbird community. The model application has indicated that, indeed, walleye is the dominant piscivore in the western Lake Erie ecosystem. Furthermore, the model allowed for prediction of total fish consumption by waterbirds with varying cormorant populations. The total fish consumption estimate by nesting waterbirds was strongly dependent on the number of nests, and there was a high degree of confidence in nest number estimates. The model application to the western Lake Erie ecosystem revealed gaps in knowledge, particularly with regard to seasonal changes in bird metabolism and diet and to further refinement and verification of the allometric relationship for estimation of daily energy expenditure. The model may be improved as more data become available.

ACKNOWLEDGMENTS

W. Scharf, J. Trapp, M. Shieldcastle, J. Ludwig, and D. Best provided us with nest counts from the U.S. side of Lake Erie, and H. Blokpoel and D. Weseloh furnished us with the complementary data from the Canadian side of the lake. We are grateful to B. Buckingham for sharing his personal observations on the life history characteristics of the breeding populations of waterbirds in western Lake Erie. K. Brugger advised us on modeling waterbird bioenergetics. We thank H. Blokpoel, R. Dolbeer, M. Hansen, K. Muth, D. Weseloh, and an anonymous reviewer for reviewing this manuscript. T. Girard supplied a critical review of the project throughout its development. Thanks to M. Bur, B. Ickes, and R. Dolbeer for suggesting this research project. This article is contribution 884 of the National Biological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, Michigan.

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APPENDIX 1. Bioenergetics model used to calculate the annual consumption of fish by the nesting population of piscivorous waterbirds in western Lake Erie circa 1990. Resident species included the Herring Gull, Ring-billed Gull, Double-crested Cormorant, Great Blue Heron, Black-crowned Night-Heron, and Great Egret. Each species was modeled separately, and then fish consumption for all six populations was summed to arrive at total fish consumption by the nesting bird populations.

The daily energy expenditure (DEE) of a post-fledged bird was calculated using the allometric equation presented by Birt-Friesen et al. (1989):

$$\mathrm{DEE} = 1737.8W^{0.727}$$

where DEE = the daily energy expenditure, in kilojoules, of a post-fledged bird, and W = mass, in kilograms, of the post-fledged bird. This allometric equation was based on measurements of the metabolic rates of free-living seabirds, and therefore this equation was particularly appropriate for estimating fish consumption by birds in natural ecosystems. Cairns et al. (1991) used this allometric equation to estimate the DEE of post-fledged Herring Gulls, Ring-billed Gulls, and Double-crested Cormorants in the Gulf of St. Lawrence.

DEE was converted to kilocalorie units using the following equation:

$$1 \text{ kilojoule} = 0.23892 \text{ kilocalories.}$$

Daily energy intake (DEI) was calculated by dividing DEE by the assimilation efficiency. We assumed an assimilation efficiency of 0.80 for all birds (Furness 1978). Daily food intake (DFI) was calculated by dividing DEI by the average caloric density of the bird diet. The average caloric density (ACD) of the bird diet was calculated using the following equation:

$$\mathrm{ACD} = \sum_{i=1}^{n} (\mathrm{CD}_i)\cdot(\mathrm{PROP}_i)$$

where ACD = average caloric density, in kilocalories per kilogram, of the bird diet, CD_i = caloric density, in kilocalories per kilogram, of diet category i, PROP_i = the proportion of the bird diet, by mass, comprised of diet category i, and n = the total number of diet categories. Thus, the daily fish consumption (DFC) was:

$$\mathrm{DFC} = \mathrm{DFI}\cdot\mathrm{PROP}_{\mathrm{fish}}$$

where DFC = daily fish consumption, in kilograms, DFI = daily food intake, in kilograms, and $\mathrm{PROP}_{\mathrm{fish}}$ = the proportion of the bird diet comprised of fish.

The daily energy expenditure of a pre-fledged bird (DEEN) was estimated using the allometric equation presented in Kendeigh et al. (1977):

$$\mathrm{DEEN} = 1.230W^{0.7749}$$

where DEEN = daily energy expenditure, in kilocalories, of a pre-fledged bird, and W = pre-fledged bird mass, in grams. Nestlings may show spurts in growth (Kendeigh et al. 1977). Gull chick growth has been modeled using a Gompertz equation (Jehl et al. 1990), or has been described as linear (Spaans 1971). In most cases, nestling growth can be closely approximated by a linear fit (Spaans 1971), and we assumed growth to be linear from time of hatching to the completion of fledging. Birds were assumed to reach adult mass at fledging. This was a reasonable assumption because mass at end of the fledging period is typically within 5 to 10% of adult mass (Kadlec et al. 1969, Jehl et al. 1990). The daily food intake by a pre-fledged bird was equal to the sum of the food needed to match the DEEN and the food needed to increase pre-fledged bird mass by the daily growth increment, DG. Thus, the daily fish consumption by a pre-fledged bird was:

$$\mathrm{DFCN} = \frac{\mathrm{DEEN}\cdot\mathrm{PROP}_{\mathrm{fish}}}{0.80\cdot\mathrm{ACD}} + \frac{\mathrm{DG}\cdot\mathrm{PROP}_{\mathrm{fish}}}{0.80}$$

where DFCN = daily fish consumption, in kilograms, by a pre-fledged bird, DEEN = daily energy expenditure, in kilocalories, by a pre-fledged bird, DG = daily growth increment, in kilograms, by a pre-fledged bird, and $\mathrm{PROP}_{\mathrm{fish}}$ and ACD are defined as above. The assimilation efficiency for pre-fledged birds was assigned a value of 0.80 (Cairns et al. 1991).

The time step for all of the simulations was one day. The initial day of the simulated time period was the arrival date, and the departure date marked the final day of the simulation run (see Fig. 1 for arrival and departure dates). At the end of each day, fish consumption for an individual in each of the three life stage categories (i.e., hatch-year, non-breeder, and breeder) was calculated. Individual fish consumption for a particular life stage category was then multiplied by the population size for that life stage category to yield the daily fish consumption by that life stage population. Summing daily fish consumption over all of the simulated days yielded the annual fish consumption for a particular life stage. Within each life stage, simulated bird populations were assumed to decline exponentially, as described in Perrins and Birkhead (1983). Furthermore, number of eggs and number of pre-fledged birds were assumed to decline exponentially. See Ricker (1975) or Hewett and Johnson (1992) for details on converting a survival rate to an instantaneous mortality rate.

APPENDIX 1. Continued.

On the designated egg-laying day (as illustrated in Fig. 1) in the simulation, the energy represented in the eggs was included in the total daily energy expenditure of the breeder population. The energy represented in the eggs was then converted to fish consumption, using the above-detailed algorithm.

This computer simulation program for fish consumption by a nesting bird population was written in TURBO PASCAL version 6.0. A copy is available upon request.