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Foraging Ecology, Bioenergetics and Predatory Impact of
Breeding Double-crested Cormorants (*Phalacrocorax auritus*)
in the Beaver Archipelago, Northern Lake Michigan

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Nancy E. Seefelt

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FORAGING ECOLOGY, BIOENERGETICS AND PREDATORY IMPACT OF BREEDING DOUBLE-CRESTED CORMORANTS (*PHALACROCORAX AURITUS*) IN THE BEAVER ARCHIPELAGO, NORTHERN LAKE MICHIGAN

By

Nancy E. Seefelt

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ABSTRACT

FORAGING ECOLOGY, BIOENERGETICS AND PREDATORY IMPACT OF DOUBLE-CRESTED CORMORANTS (*PHALACROCORAX AURITUS*) IN THE BEAVER ARCHIPELAGO, NORTHERN LAKE MICHIGAN

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As Double-crested Cormorant (*Phalacrocorax auritus*) populations have increased throughout the Great Lakes, many sport and commercial fish populations have declined. A high density of birds combined with their fish eating habits has led to their implication in these declines. From 1999 through 2002, a Smallmouth Bass (*Micropterus dolomieui*) population study was rekindled after a twenty plus year hiatus in the Beaver Archipelago. This work documents an intensive study on the population dynamics and foraging ecology of breeding cormorants of the same area between 2000 and 2004. The population size of breeding birds, well as their reproductive output, was estimated and the diet of birds was determined using regurgitates and the stomachs of harvested birds. Pellets were not used in analysis because they did not provide reliable quantitative data regarding bird diet. Breeding population size, as well as reproductive output, appears to vary substantially from year to year, and may be linked to the availability of alewife (*Alosa pseudoharengus*). Breeding bird diet consists primarily of species of little commercial or sport value; the importance of individual prey species in bird diet varies temporally and spatially.

To determine important foraging areas, VHF radio telemetry was used to track the foraging activities of ten cormorants. Using triangulation, birds were monitored from both land and water daily, weather permitting, throughout the breeding season. In addition, rafting locations of cormorants were documented by boat survey throughout the breeding season. Radiotelemetery indicated that cormorants typically foraged 2.5 km for away from the colony, at the northeastern end of Beaver Island. This area overlaps with the area determined by rafting locations, however the latter were centered further south. Neither area overlaps with known bass habitat.

Colonial waterbirds are an important component of Great Lakes ecosystems. One important aspect is the role of these birds as top predators in aquatic food webs. In order to investigate this role, bioenergetics models, using allometric equations, were applied to breeding cormorants and their offspring in the study area. The models estimated the total prey biomass consumed as 1444.11 tonnes of prey in 2000, and 1586.17 tonnes of prey in 2001. Each year the majority of the prey biomass was aewife, with these fish comprising a greater percentage of prey biomass in 2001.

In addition, two types of simulation models, Rebuild and Forecast, to investigate a possible connection between the declining bass populations and the avian predators. Rebuild models indicate that is was unlikely that cormorants alone caused the observed bass decline; birds may have contributed to the decline in synergism with low recruitment, angling mortality or other factors. Forecast models suggest that direct cormorant predation on bass is not currently the leading factor limiting the bass population size in the region, even if bass are experiencing relatively low recruitment. Combined with the data collected on bird diet, foraging locations and bioenergetics, these models enhance our understanding of the relationships between cormorants and fish populations in the study area and may benefit fisheries managers in other systems.

DEDICATION

This work is dedicated to my family and friends...
and the natural beauty that abounds in wild places.

ACKNOWLEDGEMENTS

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CHAPTER 1

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The Double-crested Cormorant in Lake Michigan: A review of population trends, ecology and current management

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Key Words: *Phalacrocorax auritus*, Beaver Archipelago, colonial waterbirds

Introduction

The Double-crested Cormorant (*Phalacrocorax auritus*), or DCCO, is the most widely distributed cormorant of the six North American cormorant species (Hatch and Weseloh, 1999). The breeding range extends from the Pacific Coast (Alaska to Mexico) to the Atlantic Coast (Newfoundland to the Caribbean). The DCCO is the only species of cormorant to breed in large numbers in the interior of the U.S. and Canada (Hatch and Weseloh, 1999). These breeding interior populations are strongly migratory and mostly winter along the south-eastern Atlantic Coast and Gulf Coast (Root, 1988). In addition, large numbers also winter at inland lakes, rivers and impoundments in the south-eastern U.S., and have become more numerous at catfish and other aquaculture facilities (Stickley et al., 1992; Mott et al., 1998). The DCCO is the cormorant species most frequently cited as conflicting with sport and commercial fisheries in North America (Hatch and Weseloh, 1999).

There are six allopatric breeding populations of DCCOs, including the West Coast, Alaska, Bahamas, Florida, Atlantic, and Interior Populations (Hatch, 1995). Of these, the Interior Population, which includes the Great Lakes Basin, is the largest, with more breeding pairs than all other populations combined. Although this population is centered in the northern prairies, in the Great Lakes, cormorants

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are widely distributed and colonies can be found throughout the lakes and the St. Lawrence River. Large colonies can be found in eastern and western Lake Ontario, western Lake Erie, and across the Upper Lakes (Hatch, 1995; Weseloh et al., 2002). In Lake Michigan, the three major breeding areas are southern and northern Green Bay, and the Beaver Archipelago (Ludwig et al., 1989; Scharf and Shugart, 1998).

This work is an attempt to review and consolidate what is currently known about DCCOs in Lake Michigan. This includes an overview of the occurrence of DCCOs in the Great Lakes basin, as well as a discussion of both population trends and ecology of these birds in Lake Michigan. Finally, this work describes the recent changes in management legislation concerning DCCOs in the United States.

History of occurrence and population trends

DCCO populations have fluctuated greatly over much of their range throughout the past centuries. Early reports state that these birds were abundant across their range in the 1800s (Lewis, 1929), including in the Great Lakes Basin by the end of this century (Wires et al., 2001). However, by 1900, cormorants were not found breeding in the Lake Michigan Basin (Barrows, 1912; Ludwig et al., 1989). Yet, during the early 1900s, cormorant populations expanded again in the upper Great Lakes, with the first official breeding record in 1913, in western Lake Superior (Baillie, 1947). By the 1930s, several breeding colonies were active in northern Green Bay, Lake Michigan (Baillie, 1947; Ludwig, 1984). Due to persecution, commercial fishing practices and the general use of organochlorine chemicals, cormorant populations declined again from the 1940s through the early 1970s (Baillie, 1947; Ludwig, 1984; Craven and Lev, 1987; Ludwig et al., 1989). According to Ludwig (1984), waterbird surveys from 1959 through 1969, yielded no cormorant nests in Lake Michigan and the U.S. waters of Lake Huron, and by sometime between 1960 and 1962, DCCOs were completely extirpated as a breeding bird from Michigan.

After 1973, DCCOs began their most recent resurgence in the upper Great Lakes (Scharf, 1978; Ludwig et al., 1989; Scharf and Shugart, 1998), with at least a few pairs nesting on two islands and shoreline areas of southern Green Bay (Ludwig, 1984). This recovery has been attributed to the inclusion of DCCOs on the list of protected species under the 1918 Migratory Bird Treaty Act in 1972 (DEIS, 2001). Thus, a decline in human depredation, combined with a decline in both commercial fishing and chemical residue contamination levels (Ludwig, 1984), as well as changes in the fish communities (Hatch, 1995) may have provided new opportunities for cormorant recovery across the Great Lakes. The population expansion of non-native fish commonly found in their diet, including Alewife

(*Alosa pseudoharengus*), has also been linked to the cormorant population recoveries (Weseloh and Ewins, 1994). Overall, the number of breeding pairs in the Great Lakes has increased from 89 nests in 1970 to 38,000 by 1991 (Weseloh et al., 1995).

Formal nest count data for DCCOs in U.S. waters of the Great Lakes are available from 1977 (Scharf, 1978) and additional surveys were conducted in 1984 (Ludwig et al,. 1984), 1989-1990 (Scharf and Shugart, 1998), and 1997 (Cuthbert et al., 1997) (Table 1). The number of breeding DCCO colonies in the U.S. Great Lakes region has grown from four in 1977 to sixty-nine in 1997; in Lake Michigan this is paralleled by an increase from three in 1977 to twenty-seven active colonies in 1997 (Cuthbert et al., 1997). DCCOs have shown an overall population increase in the U.S. Great Lakes region, from 171 pairs in 1977 to 48,931 pairs in 1997. This same trend is true for Lake Michigan alone, where the number of breeding pairs increased from 75 pairs in 1977 to 28,158 pairs in 1997. Interestingly, in 1977 and 1989-1990, Lake Michigan cormorants comprised around 43% of the overall population nesting in U.S. waters of the Great Lakes. However, by 1997, the Lake Michigan DCCO population comprised over 57% of breeding pairs in the U.S. Great Lakes (Cuthbert et al., 1997).

The revival of cormorant populations has been no less pronounced in the Beaver Archipelago where, as of 1997, they were estimated to comprise almost 39% of the nesting DCCO pairs within Michigan waters of the Great Lakes (Cuthbert et al., 1997; Ludwig and Summer, 1997) and over 41% of the Lake Michigan breeding population (Cuthbert et al., 1997) (Table 2). Historically and more recently, there have been six active breeding DCCO colonies in the Beaver Archipelago, including Grape and Timm's spits (portions of Hog Island) and Pismire, Hat, Whiskey and Gull Islands. Overall, through 1997, the Beaver Archipelago breeding DCCO population has followed the general increasing trend seen lake wide. However, between 1997 and 2000, the population declined by 13.5%. In addition, between 2000 and 2001, the population size decreased by another 4.1% (Table 2). Colonies on Timm's Spit and Whiskey Island have disappeared, while both Pismire and Gull Islands experienced growth. The overall decline in the Beaver Archipelago may be indicative of a stabilizing population or changes in suitable nesting habitat due to lower lake levels. Lower lake levels may have allowed greater access to some colonies for mammalian predators, and has also increased the size of some small, more remote islands in the archipelago. Similarly, in Green Bay, DCCO populations also appear to be stabilizing, since there are few remaining unoccupied sites and existing colonies are probably approaching upper size limits (K. Stromborg, U.S. Fish and Wildlife Service, New Franklin, WI, U.S.A., pers. comm..).

Table 1. Lake Michigan and Great Lakes breeding Double-crested Cormorant population estimates beginning in 1977 and ending 1997. Both the number of breeding pairs and active colonies have increased substantially over this twenty year period. In 1997, the Lake Michigan colonies comprised 57.55% of the breeding cormorants in the U.S. waters of the Great Lakes.

	Lake Michigan Breeding Pairs	Lake Michigan Colonies	Great Lakes Breeding Pairs	Great Lakes Colonies
1977[a]	75	3	171	4
1984[b]	684	9	NA	NA
1989-90[c]	4743	18	11099	36
1997[d]	28158	27	48931	69

[a] Nest count data from Scharf, 1978.

[b] Nest count data from Ludwig, 1984.

[c] Nest count data from Scharf and Shugart, 1998.

[d] Nest count data from Cuthbert et al., 1997.

Table 2. Numbers of Double-crested Cormorant pairs breeding at colonies in the Beaver Archipelago, northern Lake Michigan beginning in 1984 and ending in 2001. Note that the number of breeding pairs increases until 1997, where after there is an overall population decline. Some colonies, such as Pismire and Gull, have continued to show an increase as the regional population declines, while Timm's and Whiskey colonies have dissolved.

	Pismire	Grape	Timm's	Hat	Whiskey	Gull	Total
1984[a]	57	0	0	54	0	139	250
1989[b]	35	291	0	294	0	260	880
1997[c]	383	3509	753	4617	560	1887	11709
2000	987	2431	277	4917	0	1532	10125
2001	1035	2146	0	4511	0	2013	9705

[a] Nest count data from Ludwig, 1984.

[b] Nest count data from Scharf and Shugart, 1998.

[c] Nest count data from Cuthbert et al., 1997.

Ecology

DCCOs are seasonal inhabitants of Lake Michigan, typically arriving in April in northern regions. In the Beaver Archipelago, egg laying and incubation begins in May or early June, chicks are hatched in mid to late June, and young birds fledge by late July or early August. Most birds leave the area by September; however it is not uncommon to see some DCCOs in October in the archipelago. There are also migrant birds that pass through the region in spring and autumn, and immature (non-breeding) birds that summer in the archipelago. Since the resurgence of the

DCCO population in the Beaver Archipelago, there has been a growing concern how this seasonal residency and the migration influx may influence local prey species.

DCCOs are opportunistic fish predators that often feed in shallow waters (Lewis, 1929; Birt et al., 1987). Information on prey taken by these birds has been widely gathered, but generally only in context of perceived fishery conflicts (Hatch and Weseloh, 1999). Seasonal variation in cormorant diet is evident in most studies, but simple lists and percentages do not reveal the ecological factors contributing to this predation pattern and the impact on fisheries. Since the local impacts on prey populations and ecosystem dynamics have remained unclear, it has been recommended that research efforts focus more closely on foraging behaviour and predator-prey interactions (Hatch and Weseloh, 1999). Currently, some areas in Lake Michigan, including the Beaver Archipelago, are being investigated to further understand cormorant-fish relationships.

Prey species and prey size are factors that may help determine the impact DCCOs have on fisheries (Ainley et al., 1981; Fowle, 1997). Because of the loss of large, native, piscivorous fish in the 1940s and an increase in salmonid stocking programs, prey fish populations have fluctuated across the region (Christie et al., 1987). In addition, introduced Alewife became abundant in all lakes, except Lake Superior, by the 1950s (Hatch and Weseloh, 1999). Other non-native forage fish, such as Rainbow Smelt (*Osmerus mordax*), have also become established.

Breeding cormorants remain relatively close to breeding colonies when foraging (Custer and Bunck, 1992). Although cormorants may have only small and localized effects on fish populations during migration (Kirsch, 1995), it has been demonstrated that these birds may deplete fish prey around breeding colonies in some areas (Birt et al., 1987). In Lake Ontario, for example, cormorants had a significant effect on specific age classes of Smallmouth Bass (*Micropterus dolomieui*) (Adams et al., 1999; Johnson et al., 1999; Schneider and Adams, 1999). However, most studies reflect that cormorant diets tend to include species that are of little commercial or sport value. Yet these species may be important in community trophic dynamics (Craven and Lev, 1987). Therefore, cormorants may have a secondary effect on sport fisheries by competing with desired species for forage fish and other prey such as crayfish. Although the effects on forage fish numbers may be limited and may only occur in localized areas (Madenjian and Gabrey, 1995), this combined with direct sport and commercial fish depredation may have some impact on some sport and commercial fish populations.

Historically, there have been several studies documenting the diet of cormorants in the upper Great Lakes, including Lakes Huron, Michigan and Superior (Craven and Lev, 1987; Ludwig et al., 1989; Ludwig and Summer, 1997; Maruca, 1997; Neuman et al., 1997). Ludwig et al. (1989) documented food items (n=8512) in the regurgitates of adults and chicks at several locations in Lakes Huron, Michigan and Superior from 1986 to 1989. By number, Alewife and Nine-spine Stickleback (*Pungitius pungitius*) accounted for 41% of the diet. By biomass, the important species included Alewife (57%), Yellow Perch (*Perca flavescens*) (13%), Rainbow Smelt (8%), and White Sucker (*Catostomous commersoni*) (7%). Diet varied seasonally, and by August, the diet of cormorants in each study area surveyed contained 100% Alewife (Ludwig et al., 1989). In addition, Ludwig and Summer (1997) documented food items (n=6293) in the regurgitates of adults and chicks at nesting colonies in the Les Cheneaux Islands of northern Lake Huron in 1995. By weight, Alewife constituted 72% of the nestling diet. As part of the same study, Maruca (1997), using 373 stomachs, documented that adult cormorant diet contained approximately 48% Yellow Perch during the perch spawning season. In July, however, adults fed primarily on Alewife. Weseloh and Ewins (1994) have suggested that cormorant reproductive success may be intimately linked to Alewife population dynamics.

The Beaver Archipelago, and particularly the habitat around Garden and Hog Islands, has long been known for its excellent Smallmouth Bass fishing, and this evaluation has been published in the national media a number of times (Robinson, 1995). Recently, however, there have been numerous reports of a decline in the sport fishery by local anglers (Hooker, 1999a, 1999b, 1999c). In partial response to these reports, Central Michigan University (CMU) and the Michigan Department of Natural Resources (MDNR) initiated an intense population sampling in May of 1999. Compared to similar data gathered using trap nets by researchers at CMU nearly 20 years ago, not only is the Smallmouth Bass population down by an astounding 75-80%, but other fish species, including Brown Bullhead (*Ictalurus nebulosus*) and Rock Bass (*Ambloplites rupestris*) have declined by as much as 98% (D. Peterson, University of Georgia, Athens, GA, U.S.A., pers. comm.). It is therefore quite clear that there has been a recent and very rapid decline in the Beaver Archipelago fishery. The factors that have caused these declines have remained unclear. Present research is investigating whether the local DCCO breeding population could have played a role in the decline of local fish populations.

Most recent regurgitate and stomach content data suggest that DCCOs in the Beaver Archipelago feed primarily on Alewife during the breeding season. During 2000 and 2001, a total of 1128 regurgitate samples (10,600 individual prey items) were collected. When regurgitated food items are compared by mass, Alewife comprised 72.00% of the diet (57,073 g of 79,230 g) (Figure 1). Of the 150 stomachs (3363 individual prey items) analyzed in 2000 and 2001, Alewife mass comprised 72.83% of the diet (18,603 g of 25,550 g) (Figure 1). Other prey commonly found in the diet of Beaver Archipelago DCCOs are crayfish (*Orconectes sp.*), sculpin (*Cottus sp.*), Nine-Spine Stickleback, and White Sucker. Other miscellaneous prey include Spottail Shiner (*Notropis hudsonius*), Johnny

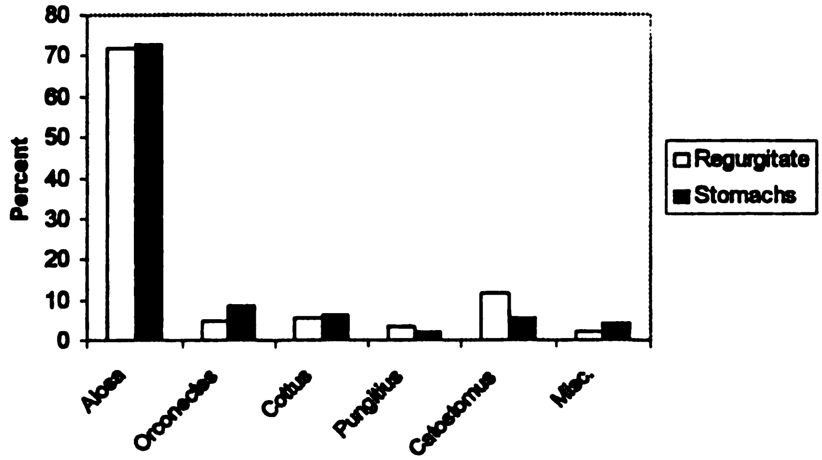

Figure 1. Diet of Double-crested Cormorants in the Beaver Archipelago, 2000 and 2001 combined, shown as percent mass for both regurgitate (n = 1128) and stomachs (n = 150). Alewife (*Alosa*) provide the most biomass in cormorant diets. For regurgitate samples, Alewife comprise 57,073 g of 79,230, while for stomach samples, Alewife comprise 18,603 g or 25,550 g. However crayfish (*Orconectes*), sculpin (*Cottus*), stickleback (*Pungitius*) and sucker (*Catostomous*) are also frequently taken.

Darter (*Etheostoma nigrum*), Trout-perch (*Percopsis omiscomaycus*) and Brook Stickleback (*Culaea inconstans*). Only one Smallmouth Bass was found in this investigation. No sample has yet yielded evidence of Rockbass or Brown Bullhead in the diet of archipelago DCCOs. As in previous studies in the Upper Great Lakes (Ludwig et al., 1989; Ludwig and Summer, 1997), Alewife became increasingly more important in the diet of Beaver Archipelago DCCOs as the breeding season progressed.

Current management

Cormorant-human conflicts are not a new phenomenon. Because of their perceived negative effect on aquatic communities, several studies have been conducted investigating cormorant influences on fisheries both in Europe (Suter, 1995; Warke and Day, 1995) and in the Great Lakes (Madenjian and Gabrey, 1995; Maruca, 1997; Neuman et al., 1997; Schiavone, 2001). Research suggests that waterbirds actually play central roles in marine food webs (Cairns, 1992), and this probably holds true in Great Lakes community dynamics. In order to get a realistic picture of the impact bird predators have on fish populations in Lake Michigan, it is necessary to incorporate quantitative data on the diets, population size and energy requirements of the cormorant population. In addition, reliable data on the size of the fish populations, with the appropriate spatial and temporal scales, are necessary (Draulans, 1988). Currently, in the Beaver Archipelago, data of this sort are being collected in order to facilitate the reconstruction of fish communities and to determine the extent of the role the cormorant resurgence may have had in recent fishery declines in the region. Similar approaches have been successfully used in Lake Erie to assess the impact DCCOs have on fish populations (Madenjian and Gabrey, 1995; Hebert and Morrison, 2003).

Currently, there is no long-term management plan for DCCO populations in Lake Michigan. In the Wisconsin waters of Green Bay, a landowner has successfully deterred cormorants from nesting on his small island using devices designed to scare the birds. In addition, there has also been an isolated incidence of vandalism at a colony on a northern island in Green Bay (K. Stromborg, U.S. Fish and Wildlife Service, New Franklin, WI, U.S.A., pers. comm.). Yet, overall in Lake Michigan, there have not been actions to manage cormorant populations. Since the resurgence of DCCO populations, research has focused mainly on monitoring breeding colony size, diet and toxicology within this basin. However, there has been an aggressive DCCO management program in the Lake Ontario Basin. In 1992, the New York State Department of Environmental Conservation (NYSDEC) began focused research to determine the actual impacts DCCOs have on fisheries and other aspects of both the Lake Oneida and eastern Lake Ontario ecosystems (Farquhar et al., 2003). This research, although still ongoing, has led to the implementation of a five-year management plan for U.S. waters of the eastern basin of Lake Ontario beginning in 1999. Management practices have focused on using egg-oiling, nest removal, harassment and habitat modification to control DCCO numbers, without the implementation of lethal control of adults and chicks (Farquhar et al., 2003). Egg-oiling has proved successful at reducing reproductive success of DCCOs in U.S. waters of Lake Ontario. Within five years, the number of breeding pairs should be reduced to target numbers with continued annual oiling activities (Schiavone, 2003).

Resolving human-cormorant conflicts has become a focus of the U.S. Fish and Wildlife Service. In 1998, a Depredation Order (50 CFR 21.47) was enacted which authorized "commercial aquaculture producers in 13 states...to take DCCOs, without a federal permit, when found committing or about to commit depredations to aquaculture stocks" (DEIS, 2001). Since this original action did not allow for Federal management or population control of DCCOs, and did not take into account more recent concerns, it has been considered ineffectual.

In the fall of 2001, the U.S. Department of the Interior Fish and Wildlife Service in conjunction with the U.S. Department of Agriculture APHIS Wildlife Services released a Draft Environmental Impact Statement (DEIS) for DCCOs. The purpose of that document was to describe and evaluate alternatives which focused on reducing conflicts between DCCOs and people (commercial, recreational and other issues) and to ensure the long-term health of cormorant populations (DEIS, 2001). Apparently, although most Americans were ambivalent with regard to DCCOs, there were many individuals concerned about the conservation and management of these birds. The DEIS categorized these concerned parties as follows: 1) animal protectionists that support non-lethal management; 2) individuals, including resource professionals, that favour conserving DCCOs and not scapegoating the birds; 3) others, including resource professionals, that emphasize conservative DCCO management; and 4) citizens who are directly affected by DCCOs, including aquaculturists, and favour more aggressive management. These differing viewpoints have added much emotion to the debate and the resolution of cormorant-human conflicts.

In order to facilitate both dialog and action, the DEIS proposed six alternatives ranging from no action (allowing current management plans to stand) to a cormorant hunting season. Each alternative outlined in the DEIS was analyzed as to how each would impact cormorant populations, fish, other birds, vegetation, federally listed Threatened and Endangered species, water quality, human health, economic issues and others (DEIS, 2001). The new "Proposed Action" favoured by the Services establishes "a new Depredation Order to address public resource conflicts." The new action would authorize "State, Tribal and Federal land management agencies to implement a DCCO management program, while maintaining Federal Oversight of DCCO populations via reporting and monitoring requirements" (DEIS, 2001). Participation of State agencies is strictly voluntary and these management plans will allow for local DCCO control with federal oversight. This new Public Resource Depredation Order will allow for some taking of cormorants at breeding and roosting sites, as well as egg oiling and destruction (DEIS, 2001).

In March 2003, the Department of the Interior, Fish and Wildlife Service released the proposed rule for DCCO management (50 CFR Part 21, 68 FR 12653). Then, in August 2003, the Final Environmental Impact Statement (FEIS) was released. According to the FEIS (2003), the Public Resource Depredation Order "will cause the estimated take of <160,000 DCCOs, which is not predicted to have a significant negative impact on...DCCO populations." In addition, it will minimize the local impact on other birds, reduce both fishery and vegetation impacts on a local scale and reduce depredation on both aquaculture and hatchery facilities. However, this new order "is not likely to significantly benefit recreational fishing economies or commercial fishing" (FIES, 2003). The final rule (50 CFR Part 21.48, 68 FR 25396) released on 08 October 2003, allows for local cormorant control in twenty-four states. It established not only a Public Resource Depredation Order, but also revised the original Aquaculture Depredation Order. In addition, the new rule also requires the monitoring of cormorant numbers and careful record keeping to insure that populations remain sustainable. This final rule took effect 07 November 2003. Currently, it is difficult to comment on how this action will influence Lake Michigan populations of DCCOs.

Conclusion

The DCCO, an indigenous species, has shown a remarkable population recovery over the past three decades in Lake Michigan and other Great Lakes. Often perceived as depredating fish stocks, thus far, in northern Lake Michigan, these birds do not seem to have negatively impacted either sport or commercial fisheries. However, cormorant-fish relationships are still being investigated and soon more information may be available, especially with respect to the northern Lake Michigan ecosystem including the Beaver Archipelago. It will be interesting to see how this new information in combination with the new management rule will influence DCCO populations of Lake Michigan.

Summary

The Double-crested Cormorant (*Phalacrocorax auritus*), a colonial waterbird native to North America, has experienced a substantial population increase throughout the Great Lakes, including Lake Michigan, over the past thirty years. This resurgence in combination with a simultaneous decline in some sport and commercial fisheries has led to their implication in fishery depredations. Research in Lake Michigan has largely focused on monitoring breeding population numbers and investigating prey species in the diet. Currently in northern Lake Michigan, specifically the Beaver Archipelago, the most important prey item in the cormorant diet appears to be Alewife (*Alosa pseudoharengus*). However, research is still being conducted to investigate what impact these birds may have on this species and other fisheries in northern Lake Michigan. In addition, the U.S. Department of Interior's Fish and Wildlife Service, in conjunction with the U.S. Department of Agriculture's APHIS Wildlife Services, has released a rule change that will allow for more aggressive management of cormorants when they are in conflict with economic and ecological interests. How this new rule will influence the Lake Michigan cormorant population remains uncertain.

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CHAPTER 2

A COMPARISON OF THREE METHODS TO INVESTIGATE THE DIET OF BREEDING DOUBLE-CRESTED CORMORANTS (*PHALACROCORAX AURITUS*) IN THE BEAVER ARCHIPELAGO, NORTHERN LAKE MICHIGAN

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Abstract

In order to understand the role of waterbirds in aquatic food webs it is important to first get an accurate depiction of their diet. Three methods of dietary assessment (pellets, regurgitate and stomach contents) are compared here for breeding Double-crested Cormorants (*Phalacrocorax auritus*) of the Beaver Archipelago, northern Lake Michigan. By numerical frequency (percent number), each method yielded different depictions of the diet. However, in terms of presence and absence (percent frequency) of possible prey types, stomach content data did agree with both pellets and regurgitate data. However, differences were noted between regurgitate and pellets. In terms of biomass measured (percent biomass) in regurgitate and stomachs, data gathered agreed. In essence, pellets underestimate the importance of alewife (*Alosa pseudoharengus*) and overestimate the importance of crayfish (*Orconectes* sp.) in the diet when compared to both regurgitate and stomach analysis. The non-lethal method of regurgitate collection and analysis appears most practical in assessing cormorant diet in this system. In combination with information on avian foraging ecology and prey populations, these data may be used to investigate the relationships among cormorants and their prey, and lead to a better understanding of Great Lake food web dynamics.

Introduction

Research suggests that waterbirds play central roles in marine food webs (Cairns 1992), and this probably holds true in North American Great Lakes community dynamics. Several studies have been conducted investigating the influence of piscivorous birds on fisheries in Europe (Suter 1995, Warke and Day 1995) and the Great Lakes (Maruca 1997, Neuman *et al.* 1997, Schiavone 2001). Interactions between piscivores and their prey can lead to cascading direct and indirect effects at many trophic levels within lake communities (Kerfoot 1987). To gain insight into the impact avian predators have on fish populations, it is necessary to integrate quantitative data collected on many aspects of the biology and behavioral ecology of the avian populations in question, as well as an accurate account of the prey populations they may influence. In the Beaver Archipelago, data of this sort are being collected in order to facilitate the reconstruction of fish communities and to determine the extent of the role the Double-crested Cormorant (*Phalacrocorax auritus*), or DCCO, resurgence may have had in recent fishery declines in the region. Similar approaches have been successfully used in Lake Erie to assess the impact DCCOs have on fish populations (Madenjian and Gabrey 1995, Hebert and Morrison 2003). Central to gaining an understanding of the role of piscivorous birds in aquatic systems is the acquisition of accurate dietary data.

The DCCO is an opportunistic fish predator that often feeds in shallow waters (Lewis 1929, Birt *et al.* 1987). Over the past several decades, the population of cormorants inhabiting the interior of North America has increased and expanded (Hatch and Weseloh 1999). High densities of birds combined with their observed fish-eating behaviors have led some natural resource biologists as well as the general public to implicate cormorants in declines of both commercial (Ludwig *et al.* 1989, Neuman *et al.* 1997) and recreational fisheries throughout the Great Lakes region (Lantry *et al.* 1999, Neuman *et al.* 1997). Although cormorants may have only small and localized effects on fish populations during migration (Kirsh 1995), Birt *et al.* (1987) documented that this species may deplete fish prey around their breeding colonies in a marine environment. Cormorant diets often include species that are of little commercial value but may be important to community trophic dynamics (Craven and Lev 1987). Therefore, cormorants may have a secondary effect on sport fisheries by competing with desired species for forage fish. Although the effects on forage fish numbers may be limited and only occur in localized areas (Madenjian and Gabrey 1995), combined with direct sport fish depredation, cormorants may impact sport fish distributions and/or numbers.

Studies assessing DCCO diet have used several methods including the analysis of pellets, regurgitate, and stomach contents of harvested birds. Pellets, indigestible material such as bones and scales encased in mucous that are typically regurgitated on a daily basis, may easily be collected in large numbers at breeding colonies. In addition, pellet analysis is relatively inexpensive and fairly easy to complete (Carss *et al.* 1997). However, pellets have been shown less effective at determining cormorant diet in some studies (Duffy and Laurenson 1983, Johnstone *et al.* 1990, Blackwell and Sinclair 1995, Trauttmansdorff and Wassermann 1995, Zijlstra and van Eerden 1995, Carss *et al.* 1997) and these limitations are discussed below.

Analysis of stomach contents and regurgitated food items (boli) can be useful tools to investigate cormorant diet because both methods allow for study of relatively fresh material (Carss *et al.* 1997). Bones and scales of partially digested fish can be used to determine fish age classes, as well as estimate lengths and widths by utilizing fish reference collections (Blackwell *et al.* 1995, Ross and Johnson 1995). There are drawbacks to stomach analysis, including the necessity of killing birds, potential small samples that may not be representative of breeding population diet, and presence of highly eroded biomass (Wires *et al.* 2003). However, stomach content analysis is useful because such dietary data are accompanied by age, sex and other information for each bird (Carss *et al.* 1997). Regurgitate samples, like pellets, are easily collected from breeding colonies because both nestling and adult birds will regurgitate stomach contents when disturbed (Lewis 1929). However, these regurgitate samples may not be complete and also show varying levels of digestion (Waneless *et al.* 1993, Carss *et al.* 1997). Because good sample sizes are easily collected, regurgitated food items are considered a rigorous method for estimating of nestling diet, but not necessarily adult diet (Wires *et al.* 2003).

This study analyzes the use of each method (pellets, regurgitate and stomach contents) to assess the diet of DCCOs at breeding colonies in the Beaver Archipelago in northern Lake Michigan. The goal of this study is to ascertain which method(s) yields the most accurate portrayal of DCCO diet in northern Lake Michigan. This work is part of a larger study investigating cormorant foraging ecology and fish population dynamics in the Beaver Archipelago. These data have guided efforts in estimating DCCO diet in the study area.

Materials and Methods

Study Area

The Beaver Archipelago is located in Michigan waters of colder, northern basin of Lake Michigan. The islands and surrounding mainland areas are primarily forested, sparsely populated, and considered the Northern Lacustrine-Influenced Ecoregion (Fuller *et al.* 1995). Inshore areas consist of sand, cobble, rock and occasional small wetlands (EPA 2000). Open water areas around the islands include areas that exceed 80 m (262 ft) in depth (EPA 2000). Fish communities, although changed and degraded compared to pre-settlement conditions, are still developed within this aquatic ecosystem. Nearshore areas provide habitats for warm water fish, including Centrarchids, and pelagic prey fish, including alewife (*Alosa pseudoharengus*), dominate open water areas (EPA 2000). Overall, the northern basin of Lake Michigan is characterized as a "typical phosphorus-limited lake ecosystem" (Chen *et al.* 2002).

The Beaver Archipelago consists of about ten islands. Three of the larger islands (Gull, Hog and Hat Islands) and one small island (Pismire Island) contained nesting colonies of DCCOs that ranged in size from 277 to 4918 nests in 2000. The Hog Island colonies were located on two peninsulas known as Grape Spit and Timms Spit. For this work the diet of cormorants on Pismire Island (987 nests) and Grape Spit (2431 nests), because of their close proximity to each other (approximately 2 km or 1.25 miles), were examined together.

Pellets and Regurgitates

Pellets and regurgitate samples were collected by hand from the ground adjacent to individual nests in the Pismire Island and Grape Spit colonies on 24 June 2000. In addition, regurgitates were collected from areas away from nests. Adults were observed regurgitating as they left the colony while young chicks remained in their nests. Therefore, adults likely produced samples collected within the colony but not immediately adjacent to nests. Each sample was placed in a plastic Whirl-pak® bag (510 g) and returned to the lab within 1-3 hours of collection in a cooler. Pellets were subsequently dried at 43°C in an oven for 24 hours and then stored in plastic bags inside a plastic container. Pellets were kept at room temperature. Regurgitate samples were frozen immediately.

Sixty pellets (30 from each colony) were rehydrated using warm water. Rehydration allowed for manual removal of the mucous using rinse water and forceps. Pellet contents were further rinsed with cold water and sorted using a No.16 Standard Sieve (1.19 mm opening) and a No. 35 Standard Sieve (0.5 mm opening). All otoliths and some bones, including jaws, pharyngeal bones, operculae, cleithra and vertebrae, were removed and placed in vials containing 70% ethanol to retard any bacterial or fungal growth. Later, using a reference collection (University of Michigan Museum and personal collection), the number and prey species (or genera) were recorded for each pellet. Because most bones and otoliths were eroded, no attempts were made to calculate original length and fresh mass of prey. These methods are similar to those outlined in Carss *et al.* (1997).

A total of 44 regurgitate samples, 31 from Pismire Island and 13 from Grape Spit, were thawed and analyzed. Each prey item was identified to species when possible and recorded. In addition, all identified prey items, including partially digested prey, were individually weighed. Complete fish were measured to the nearest 0.5 mm. Regurgitate samples were then preserved in 70% ethanol.

Stomach Contents

Twenty-five birds used for the stomach analysis were collected using shotguns on 23 June and 06, 15, 23 July 2000 (USFWS Permit No. MB022886). These birds were harvested as they returned to their breeding colonies. After birds were collected, they were placed in plastic bags and frozen. Later, the birds were thawed and examined as outlined in Carss *et al.* (1997). The esophagus, crop and complete stomachs (proventriculus and pylorus) were removed from each bird and total mass of these organs and their contents were recorded. These organs were then dissected and all prey items were removed and identified to species when possible. All prey items, including partially digested prey, were individually weighed. Complete fish were measured to the nearest 0.5 mm. Stomach contents were then preserved in 70% ethanol. In addition, each bird was sexed by examining reproductive organs.

Analysis

Numerical frequencies of prey items in the samples were calculated for each method and were converted to percentages (also referred to as percent numbers). Wires *et al.* (2001) defines percent number as the number of specimens of a taxon as a percent of all specimens in a sample. Raw data from each method for both alewife and crayfish (*Orconectes* sp.) were analyzed using contingency tables for 3x2 and 2x2 comparisons and Chi-Square Goodness of Fit Tests (Sokal & Rohlf, 1995). Data were also examined by comparing the number of samples that contained a particular prey item for each method. These data, converted to percentages, are referred to as percent frequencies by Wires *et al.* (2001). The values for both Alewife and crayfish were compared for each method using 3x2 and 2x2 contingency tables and Chi-Square Goodness of Fit Tests (Sokal and Rohlf 1995). All other prey items were found rather infrequently within the samples and were not further analyzed.

Biomasses of prey items for both regurgitate and stomach content data were converted to percents. Percent biomass is defined as the biomass of a taxon as a percent of total biomass (Wires *et al.* 2002). Because there was a large range of sample masses (2.0 g to 136.7 g for regurgitates and 1.4 g to 413.7 g for stomach contents), these data were converted to proportions; an arcsine transformation was performed to normalize data (Sokal and Rohlf 1995). Transformed data for Alewife and crayfish were then analyzed using a Mann-Whitney Test (Minitab 13 for Windows).

Results

Analysis of pellets, regurgitate and stomachs shows that in late June-July 2000 the diet of DCCOs in the Beaver Archipelago included alewife (*Alosa pseudoharengus*), crayfish (*Orconectes* sp.), sculpin (*Cottus* sp.), nine-spine stickleback (*Pungitius pungitius*), sucker (*Catostomus* sp.), johnny darter (*Etheostoma nigrum*), Trout-perch

(*Percopsis omiscomaycus*), and spottail shiner (*Notropis hudsonius*). Birds harvested for stomach contents included nine males and sixteen females.

Percent number data indicated that pellets produced by Beaver Archipelago cormorants are comprised of 82.29% crayfish and only 2.54% alewife (Figure 1). Regurgitate samples indicate, by percent number, crayfish constitute 39.54% of the samples, while alewife comprise 28.60% (Figure 2). Stomach content data, by percent number, indicated that crayfish comprised 31.96% of the stomach contents and alewife made up 46.80% (Figure 3).

The 3x2 contingency table (Table 1) and Chi-Square Goodness of Fit Tests for the raw numerical frequency data indicate that values differ from expected and therefore, each method differed from each other in estimating the diet of DCCOs for both alewife ($\chi^2 = 387.06$, critical value = 5.99 at $\alpha = 0.05$, df = 2) and crayfish ($\chi^2 = 119.02$, critical value = 5.99 at $\alpha = 0.05$, df = 2). The 2x2 contingency tables (not shown) also indicate that each method differed from the other two in describing the DCCO diet.

Table 2 shows the number of samples that contained a particular prey item for each method of dietary assessment. The 3x2 contingency table (Table 3) indicated that these data differed from expected and therefore, each method differed from each other in estimating the diet of DCCOs for both alewife ($\chi^2 = 9.53$, critical value = 5.99 at $\alpha = 0.05$, df = 2) and crayfish ($\chi^2 = 6.46$, critical value = 5.99 at $\alpha = 0.05$, df = 2). However, pairwise comparisons using 2x2 contingency tables (not shown) indicate that pellets and stomach content data for both alewife ($\chi^2 = 3.35$, critical value = 3.84 at $\alpha = 0.05$, df = 1) and crayfish ($\chi^2 = 1.50$, critical value = 3.84 at $\alpha = 0.05$, df = 1) were statistically similar. The type of method had no effect. In addition, regurgitate and stomach content data, when analyzed using 2x2 contingency table (not shown), were also statistically similar for both alewife ($\chi^2 = 0.61$, critical value = 3.84 at $\alpha = 0.05$, df = 1) and crayfish ($\chi^2 = 0.74$, critical value = 3.84 at $\alpha = 0.05$, df = 1).

Regurgitate samples indicate that, by percent biomass, crayfish constituted 15.83% of the DCCO diet, while alewife comprise 68.82% of their diet (Figure 4). Stomach content data, by percent biomass, indicate that crayfish comprise 19.74% of the diet and alewife made up 69.24% of the diet (Figure 5). The Mann-Whitney Test (Figure 6) indicates that biomass of alewife (confidence intervals = 0.01 to 36.21, W = 1652.0, p = 0.1207, adjusted for ties) and crayfish (confidence intervals = -36.20 to –0.01, W = 1428.0, p = 0.1207, adjusted for ties) estimated by each method are not statistically significant from each other at $\alpha = 0.05$. Both dietary assessment methods appear to be equal predictors of the Alewife and crayfish biomass in the DCCO diet.

Discussion

Different methods of investigating the diet of DCCOs can lead to different estimations of prey abundance and occurrence in the diet. By numerical frequency, each method yielded different results. However, in terms of presence and absence of possible prey types, each method agreed, with some exceptions. Spottail shiner appeared in both pellets and stomachs, but not regurgitate samples. Likewise, pellets did not show any evidence of trout-perch in the diet of DCCOs, while the other two methods showed they are captured in small numbers. In addition, stomach content data did agree with both pellets and regurgitate data in terms of number of samples in which alewife and crayfish occur. Regurgitate and pellets, however, differ from one another. Finally, in terms of biomass measured in regurgitate and stomachs, values for alewife and crayfish were not statistically significant from each other.

Historically there have been several studies documenting diet of cormorants in the upper Great Lakes, including Lakes Huron, Michigan and Superior (Craven and Lev 1987, Ludwig *et al.* 1989, Ludwig and Summer 1997, Maruca 1997, Neuman *et al.* 1997). Ludwig *et al.* (1989) documented food items (n=8512) in regurgitates of adults and chicks at several locations in Lakes Huron, Michigan and Superior from 1986 to 1989. By number, alewife and nine-spine stickleback accounted for 41% of the diet. By biomass, the important species included alewife (57%), yellow perch (*Perca flavescens*) (13%), rainbow smelt (8%), and white sucker (*Catostomous commersoni*) (7%). Diet varied seasonally, and by August, the diet of cormorants in each study area surveyed contained 100% alewife (Ludwig *et al.* 1989). In addition, Ludwig and Summer (1997) documented food items (n=6293) in the regurgitates of adults and chicks at nesting colonies in the Les Cheneaux Islands of northern Lake Huron in 1995. By weight, alewife constituted 72% of the diet. As part of the same study, Maruca (1997), examined 373 stomachs and documented that adult cormorant diet contained approximately 48% yellow perch during the perch spawning season. In July, however, adults fed primarily on alewife. With the exception of Lake Superior, throughout the Great Lakes region, open water fish species, including alewife, are important in DCCO diet (Wires *et al.* 2001). Weseloh and Ewins (1994) have suggested that cormorant reproductive success may be intimately linked to alewife population dynamics. In this study, it appears that in late June and July alewife is an important prey item in Beaver Archipelago DCCOs when analyzing both regurgitate and stomach samples. However, pellet analysis does not support this finding.

The limitations of pellet analysis have been demonstrated in other works, including studies with captive birds (Johnstone *et al.* 1990, Trauttmansdorff and Wassermann 1995, Zijlstra and van Eerden 1995) and in the field (Duffy and Laurenson 1983, Blackwell and Sinclair 1995). However, several studies (Ross and Johnson 1995, 1999, Warke and Day 1995, Johnson *et al.* 1999, 2001a, 2001b, 2003) have relied on pellets as indicators of the diet. In the Beaver Archipelago, evidence of some prey types was not apparent in pellets. This has been documented in other systems, as well (Brown and Ewins 1996).

Pellets have been shown less effective at determining cormorant diet in some studies because of species-related differential recovery of prey types (Johnstone *et al.* 1990). In essence, small prey and soft-bodied species may be under represented (Brugger 1993). Also, ototliths and bones may be eroded in pellets (da Silva and Neilson 1985, Jobling and Breiby 1986), thus the estimation of prey length and fresh mass are often in error (Carss *et al.* 1997). Prey found in pellets may also represent secondary consumption by cormorants (Blackwell and Sinclair 1995). The assumption that pellets reflect the remains of prey taken during the previous 24-hour period has been shown to be invalid in some species. Thus, pellets are less useful in estimating daily food intake and energy requirements (Russel *et al.* 1995). Additionally, DCCO nestlings digest bones, possibly due to minerals needed for rapid growth (Dunn 1975), and do not produce pellets until about seven weeks of age (Trauttmansdorff and Wassermann 1995, Zijlstra and van Eerden 1995). Therefore, pellet analysis does not reflect nestling diet.

However, pellets have proved more useful in describing cormorant diets than feces (Johnson and Ross 1996).

In northern Lake Michigan (Ludwig *et al.* 1989) and in similar systems such as northern Lake Huron (Ludwig and Summer 1997, Maruca 1997), alewife have been shown to be important prey. Because alewife remains are only detected at low levels in the samples, pellet analysis does not appear to accurately depict the importance of these fish in the diet of Beaver Archipelago cormorants. This could indicate different digestion of prey types. However, in eastern Lake Ontario, Johnson *et al.* (1999, 2001a, 2001b, 2003) have used pellets to detect the presence and the importance of alewife in the diet of DCCOs. Yet, Derby and Lovvorn (1997), when comparing pellets and stomach contents, found that each sampling technique did lead to different estimates of fish and crayfish in the diet of DCCOs in an area with known changes in prey availability.

Regurgitate and stomach contents analyzed in this study more accurately depict the importance of alewife in the diet of DCCOs in the Beaver Archipelago, especially in comparison to the work by Ludwig *et al.* (1989). However, both methods have weaknesses and limitations, including the probability of under- and over- estimating daily food intake (Carss *et al.* 1997). Therefore, caution should be used when using either method to estimate daily food intake, because some digestion has inevitably occurred prior to sample collection (Wanless *et al.* 1993). However, with addition of other information (e.g., feeding observations, foraging patch location), use of both regurgitate and stomach content data can be applied to bioenergetics models, and contribute to the understanding of relationships among waterbirds and their prey.

Other concerns include the accuracy of both regurgitates and stomach samples in describing the diet of both adults and chicks. However, Lewis (1929) noted by observation at breeding colonies that both male and female birds feed nestlings and adults appear to feed older chicks the same prey types consumed by adults. Therefore, regurgitate samples may provide a more complete assessment of cormorant diet during the breeding season. In addition, collection of regurgitates when nestlings are young may allow examination of seasonal and age-related diet differences, especially because young birds do not produce pellets. Such data are valuable in assessing important prey in the diet, the relative abundance of these prey, how these prey populations may be influenced by cormorants, and if these predator-prey relationships may vary as the breeding season progresses.

Choice of dietary assessment method used when investigating the diet of DCCOs may lead to different inferences in prey abundance and importance. According to Derby and Lovvorn (1997), daily changes in bird foraging behavior and time of data collection may account for some of these discrepancies. Such discrepancies may be reflected in this study, for birds were harvested for stomach contents over a month long time period, while both pellets and regurgitates were collected in one day. However, regurgitate and stomach content data do suggest that DCCOs in the Beaver Archipelago feed on alewife during the breeding season. During 2000 and 2001, a total of 1128 regurgitate samples (10,600 individual prey items) were collected. Each year, samples were collected on three dates during the breeding season in an attempt to determine seasonal changes in the diet. When regurgitated food items are compared by mass, alewife comprised 72.00% of the samples (57,073 g of 79,230 g) (unpublished data). Of the 150 stomachs (3363 individual prey items) collected during the breeding seasons of 2000 and 2001, Alewife mass comprised 72.83% of the samples (18,603 g of 25,550 g) (unpublished data). This supports the findings of previous studies in the Upper Great Lakes (Ludwig *et al.* 1989, Ludwig and Summer 1997, Maruca 1997), where alewife become increasingly more important in the diet of DCCOs as the breeding season progresses.

Under the current Lake Management Plan, Lake Michigan is to be managed by an ecosystem approach (EPA 2000). Seabirds, such as DCCOs, that occupy high trophic levels are an integral part of aquatic food webs because they are very mobile and can integrate ecosystem processes over wide spatial and temporal scales (Hebert and Sprules 2002). Avian piscivores may be valuable environmental indicators in lake systems (Hebert and Sprules 2002) and, therefore, accurately estimating seabird diet may prove imperative in monitoring ecosystem health and processes.

Conclusions

Regardless of limitations, pellets can be useful in qualitatively documenting what prey types occur in the diet of DCCOs and other waterbird species. Both regurgitate and stomach analyses appear to be more useful in both qualitative descriptions and quantitative analysis of prey importance in the diet of breeding Beaver Archipelago DCCOs. Because it is a non-lethal method, regurgitate collection and analysis is the most practical way to assess cormorant diets in this system. Regurgitates can be collected in good numbers, can be analyzed quickly, and provide information on prey type, length and mass. Information on size and age class of fish taken by birds, as well as total biomass, is important in determining the influence cormorants may have on a fishery (Wires *et al.*

2001). In a lake ecosystem, predation on fish can have complex effects on other trophic levels and help determine community structure (Vanni 1987). The ability to estimate cormorant diet more accurately will strengthen attempts to understand the importance of these birds as predators in this study area. Diet studies alone cannot answer complex questions as to the relationships among DCCOs and their prey. However, it is an important step, in combination with more detail information on avian foraging ecology and prey population dynamics, in investigating community level interactions.

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Table 1. 3X2 contingency table showing the actual (and expected) values of the numerical frequency data for Alewife (*Alosa pseudoharengus*) and crayfish (*Orconectes*) in pellets, regurgitates and stomachs. Chi-Square Tests indicate that values differ from expected for both Alewife ($\chi^2 = 387.06$, critical value = 5.99 at $\alpha = 0.05$, df = 2) and crayfish ($\chi^2 = 119.02$, critical value = 5.99 at $\alpha = 0.05$, df = 2).

Sampling Method	*Alosa*	*Orconectes*	Totals
Pellets	26 (204)	841 (663)	867
Regurgitate	123 (68.9)	170 (224.1)	293
Stomachs	205 (81.1)	140 (263.9)	345
Totals	354	1151	1505

Table 2. Number of analyzed samples where individual prey items were found in pellets, regurgitates and stomachs (n = 60 for pellets, n = 44 for regurgitates, and n = 25 for stomachs). The percent frequencies of each prey item are shown in parenthesis.

Sampling Method	*Alosa*	*Orconectes*	*Cottus*	*Pungitius*	*Catostomus*	*Etheostoma*	*Percopsis*	*Notropis*
Pellets	18(30)	55(92)	25(42)	20(33)	7(12)	9(15)	0	11(18)
Regurgitate	29(66)	19(43)	9(20)	8(18)	1(2)	6(4)	2(5)	0
Stomachs	14(56)	16(64)	7(28)	5(20)	1(4)	4(16)	4(16)	1(4)

Table 3. 3X2 contingency table showing the actual (and expected) values of the number of samples that contained Alewife (*Alosa pseudoharengus*) and crayfish (*Orconectes*) in pellets, regurgitates and stomachs. Chi-Square Tests for 3x2 comparison indicate that values differ from expected for both Alewife ($\chi^2 = 9.53$, critical value = 5.99 at $\alpha = 0.05$, df = 2) and crayfish ($\chi^2 = 6.46$, critical value = 5.99 at $\alpha = 0.05$, df = 2). Comparisons using 2x2 contingency tables show that pellets and stomach contents data for both Alewife ($\chi^2 = 3.35$, critical value = 3.84 at $\alpha = 0.05$, df = 1) and crayfish ($\chi^2 = 1.50$, critical value = 3.84 at $\alpha = 0.05$, df = 1) were statistically similar. Also, regurgitate and stomach contents data were statistically similar for both Alewife ($\chi^2 = 0.61$, critical value = 3.84 at $\alpha = 0.05$, df = 1) and crayfish ($\chi^2 = 0.74$, critical value = 3.84 at $\alpha = 0.05$, df = 1).

Sampling Method	*Alosa*	*Orconectes*	Totals
Pellets	18 (29.5)	55 (43.5)	867
Regurgitate	29 (19.4)	19 (28.6)	293
Stomachs	14 (12.1)	16 (17.9)	345
Totals	61	90	1505

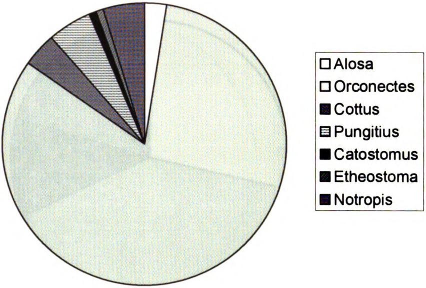

Figure 1. Pellet numerical frequency data showing the diet of Beaver Archipelago cormorants as percentages.

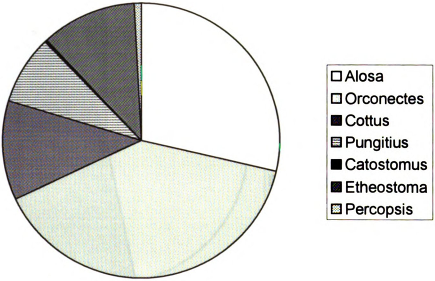

Figure 2. Regurgitate numerical frequency data showing the diet of Beaver Archipelago cormorants as percentages.

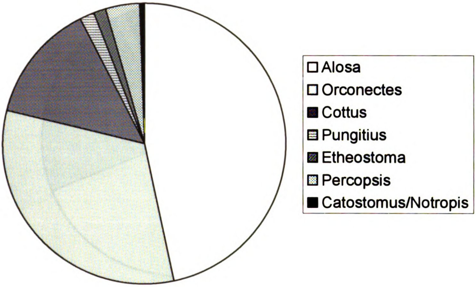

Figure 3. Stomach contents numerical frequency data showing the diet of Beaver Archipelago cormorants as percentages. Percent values for *Catostomus* and *Notropis* are small (both 0.23%) were combined for clarity.

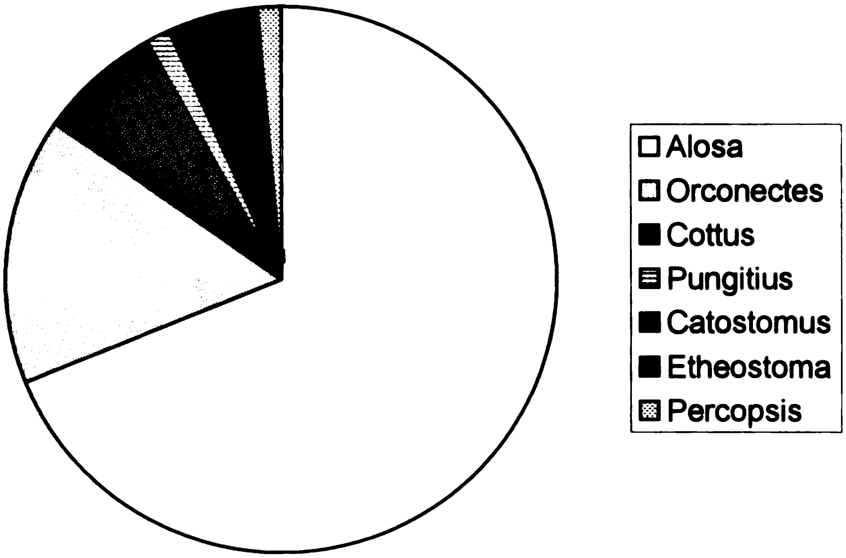

Figure 4. Regurgitate biomass data showing the diet of Beaver Archipelago cormorants as percentages.

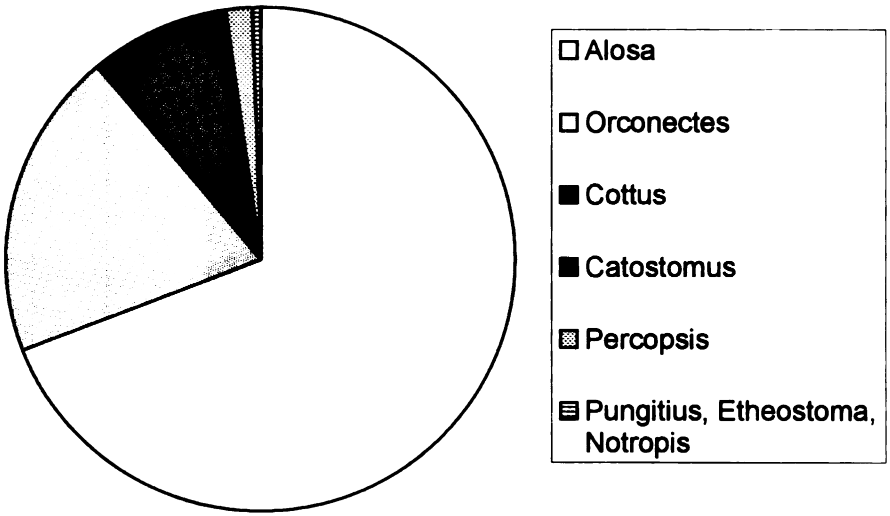

Figure 5. Stomach contents biomass data showing the diet of Beaver Archipelago cormorants as percentages. Percent values for *Pungitius*, *Etheostoma* and *Notropis* are small (1.48%, 1.43% and 1.48%, respectively) were combined for clarity.

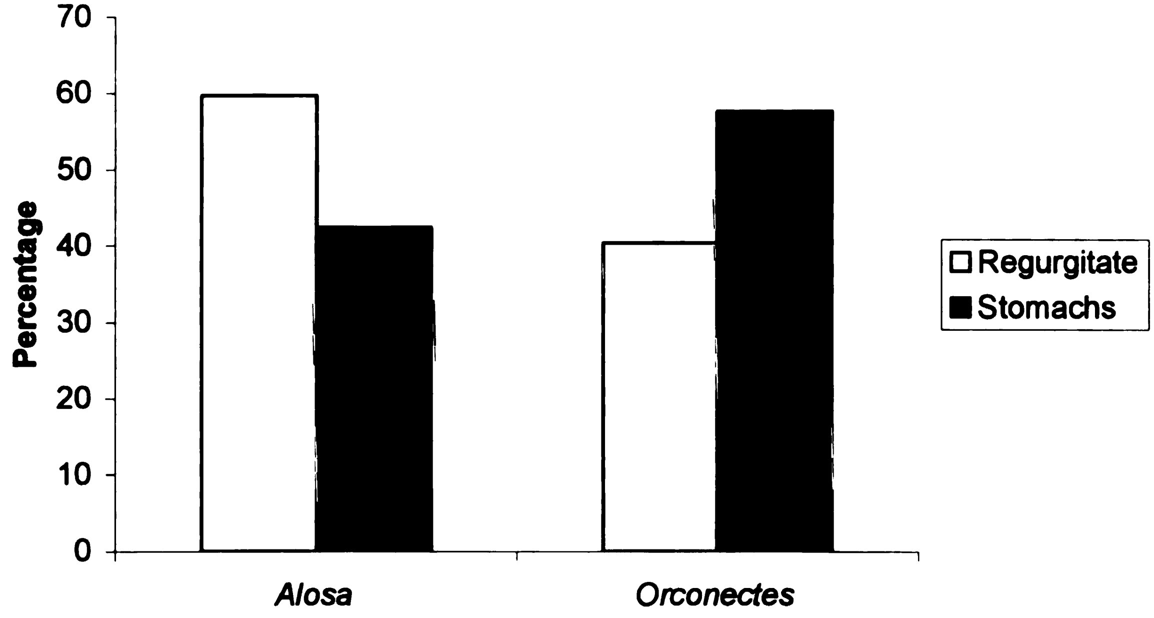

Figure 6. Means of arcsine transformed biomass data. The Mann-Whitney Τεστ ινδιχατεδ τηατ βιομασσ οφ Αλεωιφε (χονφιδενχε ιντερϖαλσ = 0.01 το 36.21, Ω = 1652,0, π = 0.1207, αδφυστεδ φορ τιεσ) ανδ χραψφιση (χονφιδενχε ιντερϖαλσ = –36.20 το –0.01, Ω = 1428.0, π = 0.1207, αδφυστεδ φορ τιεσ) εστιματεδ βψ εαχη μ ετηοδ ωερε νοτ στατιστιχαλλψ σιγνιφιχαντ φρομ εαχη οτηερ ατ α = 0.05.

CHAPTER 3

POPULATION ESTIMATE AND DIETARY EVALUATION OF DOUBLE-CRESTED CORMORANTS (*PHALACROCORAX AURITUS*) BREEDING IN THE BEAVER ARCHIPELAGO, NORTHERN LAKE MICHIGAN

Abstract

The Double-crested Cormorant (*Phalacrocorax auritus*) has shown resurgence in population levels within the Great Lakes Basin, including Lake Michigan, over the past several decades. Since the abatement of the general use of organochlorine pesticides, these birds have made a remarkable comeback, and have been implicated in the decline of both commercial and recreational fisheries. In most regions, the role of cormorants in these declines has remained uncertain. The population size of breeding birds, well as their reproductive output, was estimated over several years in the Beaver Archipelago, northern Lake Michigan. In addition, the diet of birds was determined using regurgitates and the stomachs of harvested birds. The population size of breeding birds has declined since 1997, in the region. However, breeding population size, as well as reproductive output, appears to vary substantially from year to year, and may be linked to the availability of alewife (*Alosa pseudoharengus*). Breeding bird diet consists primarily of species of little commercial or sport value; the importance of individual prey species in bird diet varies temporally and spatially, in the Beaver Archipelago. Population and diet studies alone cannot answer complex questions as to the relationships among cormorants and their prey, but are important steps, in combination with more detailed information on avian foraging ecology and prey population dynamics, in investigating community level interactions.

Introduction

The Double-crested Cormorant (*Phalacrocorax auritus*), or DCCO, is the most widely distributed cormorant of the six North American cormorant species (Hatch and Weseloh 1999). The breeding range extends from the Pacific Coast (Alaska to Mexico) to the Atlantic Coast (Newfoundland to the Caribbean) and is the only species of cormorant to breed in large numbers in the interior of the U.S. and Canada (Hatch and Weseloh 1999). The DCCO has shown resurgence in population levels within the Great Lakes Basin over the several decades (Ludwig 1984, Ludwig and Summer 1997). Although probably inhabiting the Great Lakes Basin since about the turn of the century, and with a slow and steady population increase since its Great Lakes colonization, this species suffered a sharp decline in the 1950s and 60s because of dieldrin-mediated egg-shell thinning (Ludwig *et al.* 1995). Since the abatement of the general use of organochlorine pesticides, these birds have made a remarkable comeback, to the point of being implicated in the decline of both commercial (Ludwig *et al.* 1989, Neuman *et al.* 1997) as well as recreational fisheries throughout the Great Lakes Region (Lantry *et al.* 1999, Neuman et al. 1997).

Formal nest count data for DCCOs in Lake Michigan are available from 1977 (Scharf 1978) and additional surveys were conducted in 1984 (Ludwig 1984), 1989-1990 (Scharf and Shugart 1998), and 1997 (Cuthbert *et al.* 1997). The number of DCCO colonies in the U.S. Great Lakes region has grown from four in 1977 to sixty-nine in 1997; in Lake Michigan this is paralleled by an increase from three in 1977 to twenty-seven active colonies in 1997 (Cuthbert *et al.* 1997). DCCOs have shown an overall population increase in the U.S. Great Lakes region, increasing from 171 pairs in 1977 to

48,931 pairs in 1997. This same trend is true for Lake Michigan, where the number of breeding pairs increased from 75 pairs in 1977 to 28,158 pairs in 1997 (Cuthbert *et al.* 1997). Interestingly, in 1977 and 1989-1990, Lake Michigan cormorants comprised around 43% (4743 pairs) of the overall population nesting in U.S. waters of the Great Lakes, and by 1997, the Lake Michigan DCCO population comprised over 57% (28,158 pairs) of the breeding population (Cuthbert *et al.* 1997). The revival of cormorant populations has been no less pronounced in the Beaver Archipelago where, as of 1997, they were estimated to comprise almost 39% of the nesting DCCO pairs within Michigan waters of the Great Lakes (Cuthbert *et al.* 1997, Ludwig and Summer 1997) and over 41% of the Lake Michigan breeding population (Cuthbert *et al.* 1997).

Several studies have documented the diet in breeding populations of Double-crested Cormorants in the Great Lakes, including Lake Ontario (Johnson *et al.* 1999, Schiavone 2001, Schiavone 2003), Lake Huron (Ludwig *et al.* 1989, Ludwig and Summer 1997, Maruca 1997, Neuman *et al.* 1997) and Lake Superior (Craven and Lev 1987, Ludwig et al. 1989). In these studies, non-game forage fish, such as alewife (*Alosa pseudoharengus*), typically comprise most of the annual diet. Ludwig *et al.* (1989) documented food items (n=8512) in regurgitates of adults and chicks at several locations in Lakes Huron, Michigan and Superior from 1986 to 1989. By number, alewife and nine-spine stickleback (*Pungitius pungitius*) accounted for 41% of the diet. By biomass, the important species included alewife (57%), yellow perch (*Perca flavescens*) (13%), rainbow smelt (*Osmerus mordax*) (8%), and white sucker (*Catostomous commensoni*) (7%). As in other studies, diet varied seasonally, but by biomass, the most important species was alewife. In fact, by August, the diet of cormorants in each study area surveyed contained 100% alewife (Ludwig *et al.* 1989).

Ascertaining the number of potential predators in an ecosystem is necessary to better understand the influence these predators. In addition, in a lake ecosystem, predation on fish can have complex effects on other trophic levels and help determine community structure (Vanni, 1987). This study investigates DCCO breeding colonies, within the Beaver Archipelago, northern Lake Michigan from 2000 to 2004, in order to 1) estimate breeding population numbers, as well as changes in colony size and location, 2) estimate reproductive success and output, and 3) estimate the diet of breeding cormorants and their young. This work will be used to further investigate cormorant foraging ecology and bioenergetics, as well as how DCCOs may impact fish population dynamics in the Beaver Archipelago.

Methods

Study Area

The Beaver Archipelago, located in Michigan waters of the colder, northern basin of Lake Michigan, consists of about ten main islands and numerous small islands (Figure 1). The number of smaller islands depends on fluctuating lake levels. Four of the larger islands (Gull, Hog, Hat and Whiskey Islands) and two small islands (Pismire and SE Garden Island) provided sites for nesting DCCOs at some time between 2000 and 2004. The Hog Island colonies were located on two peninsulas known as Grape Spit and Timm's Spit. Throughout this work, in reference to dietary data, Pismire, Grape, Hat, and Timm's are collectively referred to as the Main Archipelago. (By their location, both

Whiskey and SE Garden can be considered in the Main Archipelago, however, no dietary samples were collected at these sites.) Colonies, excluding Whiskey, of the Main Archipelago group are within an area of 78 square kilometers (approximately 21 square miles), to the north and east of Beaver Island. Gull Island consists of two colonies, North and South, on one island and is separated from the main island group by almost 18 km (11 miles) of open water to the west of Beaver Island. From aerial surveys, it was concluded that the cormorants breeding at Gull Island remain close to these colonies and do not regularly travel to the Main Archipelago.

Population Estimates

In order to estimate the breeding population of DCCOs and to minimize disturbance to the nesting colonies, three boat surveys were conducted during 2000, and again in 2001, within the Beaver Archipelago. Each year, these surveys were made on islands shown to support nesting colonies of cormorants following spring aerial surveys, including Pismire, Grape, Hat and Gull Islands. Timm's Island was included in 2000, but did not support breeding birds in 2001. In 2000, count dates were 05-12 June, 24 June – 07 July, and 18-20 July. In 2001, count dates were 25-30 May, 20 – 22 June and 18 –25 July. Since islands supporting cormorant colonies were accessed by watercraft, weather conditions were largely responsible for the range of count date duration for each sample period. Year to year variations in the onset of nesting are responsible for different first count dates each year. Dates for each year roughly correspond to time periods when reproductive attempts are at their seasonal high, with egg-laying and incubation being the predominant activities (late May and early June), when most pairs are actively brooding and rearing young (mid June through mid July) and when chicks are beginning to fledge and nests that remain are those that are successful (late July). Nests were considered successful if they were well maintained and were occupied by large chicks (or large chicks were close proximity to the nests) in July. The methods of these surveys followed that of Cuthbert *et al.* (1997), where nest, eggs and chicks were hand tallied for each colony. Numbers of nests counted during the first count of each season were used to estimate the number of breeding pairs of cormorants in the Beaver Archipelago. By counting eggs and chicks, as well as the number of active nests as the breeding season progressed, population reproductive success was also estimated (see analysis below).

In 2002, breeding birds were again estimated using boat surveys, following aerial surveys. On Pismire Island, three surveys were completed as the season progressed in the same manner described above; count dates were 27 May, 17 June and 13 July in 2002. Other colonies, including Grape, Gull and Hat Islands were counted only once by ground survey during the breeding season on 13 July, 15 July and 24 July, respectively. In addition, a new colony location, SE Garden was established and nests were documented in mid July.

In 2003, nest counts were repeated on Pismire Island on 04 June, 09 July and 29 July, in the same manner followed in previous years. In addition, the SE Garden colony was counted on 05 June and again on 29 July. Hat Island colony was counted on 20 June. Gull Island colonies were not counted in 2003. No other colonies were active in 2003.

In 2004, the Pismire Island colony was counted on 01 June and 29 July by ground survey. The SE Garden Colony was counted on 15 June and again on 18 June by ground survey. Whiskey Island was visited on 28 June to count a re-established colony and re-visited on 26 July to observe if any DCCOs were successful. Gull and Hat Island colonies breeding bird estimates were obtained from aerial photo taken on 09 June. To verify the validity of the counts from these digital photos, ground counts of Pismire Island were compared to counts obtained from an aerial photo of the Pismire colony.

Diet Estimates

To assess the diet of cormorants inhabiting the Beaver Archipelago and to maintain consistency with techniques used in previous studies, regurgitate samples and stomach contents of harvested bird were used to estimate diet composition. A third method, pellet analysis, was determined to be less reliable for DCCO diet quantification in the study area (see Chapter 2).

Adult and young cormorants readily regurgitate both fresh and partially digested food items when disturbed. Regurgitate samples (boli) were collected by hand from the ground adjacent to individual nests during colony visits in 2000 and 2001. Regurgitates were also collected from areas away from nests. Adults were observed regurgitating as they left the colony while young chicks remained in their nests. Therefore, adults likely produced samples collected within the colony but not immediately adjacent to nests. Each sample was placed in a plastic Whirl-pak® bag (510 g) and returned to the lab within 1-3 hours of collection in a cooler. Upon return to the lab, regurgitate samples were frozen immediately.

In the lab, regurgitates were thawed and analyzed. Each prey item was identified to species (or genera) and recorded. All of these prey items, including partially digested (mostly intact prey), were individually weighed. Complete fish were measured to the nearest 0.5 mm. In some cases, otoliths and some bones, including jaws, pharyngeal bones, operculae, cleithra and vertebrae, were used to identify more digested prey. Using a reference collection (University of Michigan Museum and personal collection), these prey were identified to species (or genera) and counted. Because most bones and otoliths were eroded, no attempts were made to calculate original length and fresh mass of prey from these mostly digested samples. These methods are similar to those outlined in Carss *et al.* (1997). Regurgitate samples were then preserved in 70% ethanol.

Birds used for the stomach analysis were collected using shotguns between 23 June and 08 August 2000, and between 31 May and 10 August 2001 (USFWS Permit No. MB022886). These birds were typically harvested along a flight path as they returned to their breeding colonies. (Most birds were collected near Pismire and Grape Colonies.) A total of 53 birds were harvested in 2000, and 97 birds were harvested in 2001. After birds were collected, they were placed in plastic bags and frozen. Later, the birds were thawed and examined as outlined in Carss *et al.* (1997). The esophagus, crop and complete stomachs (proventriculus and pylorus) were removed from each bird and total mass of these organs and their contents were recorded. These organs were then dissected and all prey items were removed and identified to species when possible. All prey items, including partially digested prey, were individually weighed. Complete fish were measured to the nearest 0.5 mm. Stomach contents were then preserved in 70% ethanol. In addition, each bird was sexed by examining reproductive organs.

Analysis

Breeding DCCO population estimates for 2000 and 2001 were first tallied to describe the changes in the number of breeding DCCOs at each of the colonies as the breeding season progressed. By comparing early nest and egg counts with mid season nest, egg and chick counts at each colony, mean clutch size for the early season birds and mean clutch size for mid season birds were calculated. These mean clutch sizes were used to calculate mean clutch size for all colonies combined for each season (early and mid) for each of the years (2000 and 2001). Both within and between year differences in mean clutch size were detected. The South Gull Island colony was not used to determine mean clutch size for either season or year. Many nests at this location are in trees and, although an accurate nest count was possible, it was difficult to determine the number of eggs and/or chicks in these nests. The mean clutch size data were then analyzed using a Single Factor Anova (Microsoft Excel). Because differences were detected, pair-wise t-tests were then performed to compare early and mid season clutch sizes for each year. In addition, between year comparisons for early season mean clutch sizes and mid season mean clutch sizes were also analyzed using t-tests (Microsoft Excel). A Bonferroni Correction was used to re-set appropriate significance levels for these t-tests ($\alpha = 0.008$).

The proportion of successful nests were determined by comparing the number of active nests at the beginning of the breeding season with the number of active nest remaining at the end of each breeding season for each of the colonies each year. These proportions were then analyzed using a t-test. In addition, the total reproductive output for breeding DCCOs in 2000 and 2001 were estimated by multiplying the mean clutch size with the number of active nests remaining at each of breeding season. Reproductive output varied from colony to colony in each year. These values calculated by overall means were higher then individual colonies combined and may over represent the number of chicks fledged.

Dietary data from each year (2000 and 2001) were analyzed separately. The regurgitate and stomach content samples were combined into one data set (see Chapter 2). In 2000, 248 samples were collected, which included 3493 food items (22,040.5 g). In 2001, a total of 880 samples were collected, which included 10,512 food items (81,496 g). Initially, numerical frequencies of prey items in the samples were calculated for each year and were converted to percentages (also referred to as percent numbers). Wires *et al.* (2001) defines percent number as the number of specimens of a taxon as a percent of all specimens in a sample.

All colonies were combined for each year to determine the biomasses of prey items in both regurgitate and stomach content samples and these were converted to percents. Percent biomass is defined as the biomass of a taxon as a percent of total biomass (Wires *et al.* 2002). Biomass is considered a more appropriate method in determining potential impacts DCCOs may have on their prey (Cairns 1992). The biomass data set was then divided into two categories, the Main Archipelago (Pismire, Hog, Hat Islands) and Gull Island colonies. For the Main Archipelago data set, regurgitates and stomach contents samples were combined because all birds were collected near Pismire and Grape colonies. Main Archipelago and Gull Island data sets for each year were analyzed separately.

In addition, the biomass data sets from the Main Archipelago for both 2000 and 2001 were examined to determine whether DCCO diet changes as the breeding season progresses. Each data set was broken in to three phases: Pre-nesting and Incubation (20 April – 14 June), Nestling to Fledging (15 June to 31 July), and Post-Nesting (01 August – 10 September).

Results

The number of breeding DCCOs in the Beaver Archipelago has fluctuated over the past twenty years (Table 1). From 1984 to 1997, the breeding population increased from 250 to 11709 breeding pairs, over a 46 fold increase. However, between 1997 and 2000, the population declined by 13.5%, from 11709 to 10125 pairs. Between 2000 and 2001, the population size decreased by another 4.1%, from 10125 to 9705 pairs. In addition, between 2001 and 2002, the number of DCCO pair attempting to breed declined by another 31.4%, from 9705 to 6657 pairs. However the actual number of successful breeders in 2002 was much lower (see below). The number of breeding pairs increased between 2002 and 2003, from 6657 to 9119+ pairs. Because the nests were not counted on Gull Island in 2003, the magnitude of this increase remains uncertain. However, in 2004, the number breeding pairs again declined to 6407 (Table 1).

The number of active breeding pairs tends to decline as the season progresses in the Beaver Archipelago (Figure 2). In 2000, the largest number of nests were counted at the onset of the breeding season during the early count season at each of the colonies, including Pismire, Grape, Hat and Gull (North and South, collectively). However, in 2001, this was the case at Gull Island colonies only. At Pismire and Grape, there were modest increases in breeding bird at the mid season count (28 and 34 nests, respectively). At Hat Island, this increase was more pronounced (340 nests) (Figure 2). Regardless, by the late count date each year, the number of active breeders declined at all colonies. In 2000, the final number of active nests was 6652, a decrease of 34.3% from the early nest count. In 2001, the final number of active nests was 7642, a decrease of 21.3% from the early nest count.

The Pismire colony accentuates the year-to-year variability in the proportion on nests that survive to the late count dates (Figure 3). In 2000, the late count date shows a decline of 54.9% (from 967 to 436 nests). Comparably, in 2001, this decline is only 25.0% (from 1035 to 776 nests). During the 2002 breeding season, no nests survived to fledging on Pismire Island. (Similarly, only two nests of 1339 survived to fledging at the Grape Spit colony.) In 2003, the number of nests declined 30.8 % from early to late nest count dates (from 1167 to 807 nests). In 2004, the late count date shows a decline of 50.1% (from 725 to 362 nests) (Figure 3).

Mean clutch size also varied from early to mid breeding season and from year to year in the Beaver Archipelago in 2000 and 2001 (Figure 4a). Single Factor Anova analysis indicated a significant difference among the mean clutch sizes as compared within each year and between years ($F = 11.18755$, $df = 3$, $p = 0.000861$). Pair-wise t-tests indicated that only the late season clutch size between year comparisons was significant ($df = 3$, $p = 0.00279$).

Again, Pismire Colony illustrates the variability in mean clutch size from year to year (Figure 4b). In 2000, the mean clutch size of 1.86 was calculated. In 2001, mean clutch sized increased to 2.45 young per pair. Mean clutch size was not calculated in 2002 (few eggs and no chicks were produced). In 2003, mean clutch size was 2.13 and, in 2004, mean clutch size decreased to 0.557 (Figure 4b).

The mean number of successful breeders increased from 2000 to 2001 (Figure 5a). This increase, as examined by a t-test, was not significant (df = 3, p = 0.056781). Year to year variability in the number of successful breeders is apparent at Pismire colony (Figure 5b). Only an estimated 45% of the initial breeders at Pismire were successful in 2000. This estimate increased in 2001 to 75%. No breeders were successful in 2002. In 2003, however, an estimated 69% of the pairs were successful. Yet, in 2004, this declined to only 50% (Figure 5b).

The estimated number of chicks produced in the Beaver Archipelago increase between 2000 and 2001, from 9659 chicks to 16786 chicks, respectively (Figure 6a). This is an increase in chick production of 174%. Year to year variability in chick production is illustrated by Pismire colony (Figure 6b). In 2000, an estimated 811 chicks were produced. This increased to 1901 chicks in 2001. No chicks were produced in 2002. An estimated 1720 chicks were produced in 2003. This declined to 209 chicks in 2004 (Figure 6b).

Figure 7 shows the percent of each prey type, by numerical frequency, when all colonies and all collection days are combined for each year separately (2000 and 2001). In all of the diet figures, the miscellaneous category may include small numbers or masses of species present as categories on other figures. Other species that were found include several rainbow smelt (*Osmerus mordax*), one burbot (*Lota lota*), one smallmouth bass (*Micropterus dolomieui*) and one salmonid. In 2000, alewife and crayfish comprised 33.2% and 31.8% of the prey in the samples. Other prey included sculpin (*Cottus* spp.) (12.3%), nine-spine stickleback (*Pungitius pungitius*) (10.3%), spottail shiner (3.5%), johnny darter (*Etheostoma nigrum*) (3.1%), and brook stickleback

(*Culaea inconstans*) (3.1%), with some prey, including sucker (*Catostomus* spp.) and trout perch (*Percopsis omiscomaycus*), each comprised 1% or less of the samples (Figure 7a). In 2001, alewife comprised 58.1% of the samples, while nine-spine stickleback, sculpin and crayfish comprised 20.2%, 12.6% and 4.1%, respectively. Brook stickleback were present (2.0%) as were sucker, spottail shiner, trout perch and johnny darter (all at 1% or less) (Figure 7b).

When all colonies and all collection days are combined in 2000, alewife comprised 55.8 % by biomass (Figure 8a). Crayfish, sucker and sculpin comprised 18.8%, 11.9% and 5.5% of prey biomass, respectively. All other prey items combined comprised a total of 10.3% (Figure 8a). Several trends are apparent when this data set was divided into Main Archipelago and Gull Island data sets. The Main Archipelago data set varies only slightly from the combined data set (Figure 8b). However, the Gull Island samples show an increase in the amount of alewife in the diet (77.6%) (Figure 8c). In addition, Gull Island samples have proportionally more sucker present (15.0%). The other prey in the diet of Gull Island DCCOs included nine-spine stickleback (4.1%) and sculpin (2.3%). No crayfish were present in Gull Island samples (Figure 8c).

When all colonies and all collection days are combined in 2001, alewife became an increasingly important prey item by biomass at 77.1% (Figure 9a). Sucker and sculpin comprised 9.8% and 6.1% of prey biomass, respectively. All other prey items combined, including nine-spine stickleback and crayfish, comprised a total of 7.5% (Figure 9a). Again, when this data set was divided into Main Archipelago and Gull Island data sets, the Main Archipelago data set varies only slightly from the combined data set (Figure 9b). However, the Gull Island samples again show an increase in the amount of alewife in the diet (87.3%)(Figure 9c). In the Gull Island samples, sucker, sculpin and nine-spine stickleback have a combined 12.7% biomass. Again, crayfish were not present in Gull Island samples (Figure 9c).

When the Main Archipelago biomass data set for 2000 was examined by collection date, several seasonal changes in the diet were apparent (Figure 10). During Pre-nesting/Incubation, alewife (49.0%) and spottail shiner (29.0%) comprised the majority of the samples. Other prey present included Johnny Darter (11.0%), sucker (7.0%), sculpin (3.0%) and nine-spine stickleback (3.0%)(Figure 10a). As the breeding season progressed to the Nestling/Fledgling stage, Alewife (54.0%) and crayfish (24.0%) dominated the diet. Sucker (11.0%) and sculpin (6.0%) comprised most of the remaining prey biomass (Figure 10b). However, during Post-nesting, crayfish biomass became more prevalent (36.0%). Alewife (22.0%), sucker (19.0%) and sculpin (8.0%) comprised much of the remaining biomass. The large miscellaneous category (11.0%) was comprised mostly of unidentifiable flesh. Much was suspected to be either alewife or sucker (Figure 10c).

When the Main Archipelago biomass data set for 2001 was examined by collection date, again, several seasonal changes in the diet were apparent (Figure 11). During Pre-nesting/Incubation, nine-spine stickleback (38.0%), sculpin (30.0%) and alewife (22.0%) comprised the majority of the samples. All other prey combined comprised 10% of the biomass (Figure 11a). As the breeding season progressed to the Nestling/Fledgling stage, alewife (81.0%) dominated the diet; sucker comprised 10.0% of prey biomass (Figure 11b). During Post-nesting, alewife biomass declined to 70% and sucker biomass increased to 16.0% (Figure 11c). In 2001, crayfish were not as important in DCCO diet as described by biomass.

Discussion

DCCO populations have monitored periodically over the last several decades and it has been recommended in recent management plans that population monitoring on the breeding grounds be continued at regular intervals (FEIS 2003). In the past, waterbird censuses have been conducted in the U.S. waters of the Great Lakes every eight to twelve years (Scharf 1978, Scharf and Shugart 1993, Cuthbert *et al.* 1997). In the Beaver Archipelago, an additional survey was conducted in 1984 (Ludwig *et al.* 1984). In this work, where breeding DCCOs were counted each reproductive season beginning in 2000 and ending in 2004, year-to-year variability in breeding population size is quite apparent. Although the earlier, more periodic population counts are invaluable in documenting the recovery of these birds across the Great Lakes, the current DCCO breeding populations seem to be stabilizing in northern Lake Michigan (Seefelt and Gillingham 2004a). In addition, the within season trends emphasize the importance in timing DCCO censuses when estimating breeding population size, as described by Ewins *et al.* (1995).

As a reflection of a change in population size, the number of breeding birds at specific colony sites has fluctuated in the Beaver Archipelago from year-to-year. In other areas, such colony dynamics have been attributed to changes in suitable habitat, often due to species interactions, predation and/or human disturbance (Kury and Gochfeld 1975, Ellison and Cleary 1978, Verbeek 1982, Gotmark 1992, Cairns *et al.* 1998, Skagen *et al.* 2001, Seefelt and Gillingham, 2004b). In addition, changes in water level have had an impact on the breeding habitats of a wide variety of birds, including Piping Plovers (*Charadrius melodus*) (North 1986) and pelicans (Pyrovesti 1997). Lowering of lake level has been the trend in the Lake Michigan-Huron basin over the past several years, with the highest rate in lake level reduction occurring between 1998 and 2000, and the lowest water levels documented in 2003 (NOAA 2003). Such changes in lake level affect the shape and size of shoreline habitat. The number of available nest sites may, in part, regulate seabird populations (Croxall 1987). Although DCCOs in the Great Lakes may not be limited by the number available nest sites (Hatch and Weseloh 1999), trends in colony location and size in the Beaver Archipelago are partially due to changes in availability of desirable nesting locations, which have been influenced by changing water levels (Seefelt and Gillingham 2004b).

Not only has the breeding population fluctuated over the past several years in the study area, the reproductive success of these birds has also been variable. In 2002, a decline in reproductive success at the Grape Spit colony can be attributed, in part, to mammalian predators (Seefelt and Gillingham 2004b). However, the major trends across the study area are probably due to year-to-year climatic differences and changes in prey availability; such changes in prey availability could be due to colder water (and air) temperatures, as well as unrelated fluctuations prey population sizes. It was noted that during the 2002 field season, both air and water temperatures remained unseasonably low through early July (personal observation). In response, DCCOs at Pismire, SE Garden, and Gull North colonies, as well as the depredated Grape Spit colony, abandoned nesting attempts. Ring-billed Gulls (*Larus delawarensis*), Herring Gulls (*Larus argentatus*) and Caspian Terns (*Sterna caspia*) showed similar trends (Seefelt and Gillingham 2004b). In

2004, both water and air temperatures were lower than average and a reduced reproductive output was documented at Pismire. Although many factors could be influencing the variability in nesting success and fledged chick numbers, it is apparent that weather patterns and lake water temperatures do impact DCCO colonies in the study area.

Croxall (1987) suggested that another factor that can regulate seabird populations is food shortages. Hatch and Weseloh (1999) remark that the local densities of birds may be affected by the temporal and spatial distribution of prey. A decline in suitable prey could have attributed to reproductive failure at some colonies and a decline in the number of successful breeding birds in 2002 and 2004. Due to lower water temperatures (personal observation), large numbers of adult alewife may not have returned to shallow waters during the prime DCCO breeding season during these years. Although alewife biomass in Lake Michigan has remained relatively stable between the early 1980s and 2003, (Madenjian *et al.* 2002, Madenjian *et al.* 2004), local availability of these fishes may have fluctuated. In addition, warm spring temperatures in 1998 led to moderately high levels of age-3 alewives in 2001; in fact, this year class dominated survey catches in 2001 (Madenjian *et al.* 2004). Age-3 alewife, due to their size, are an attractive prey size to DCCOs. The large number of alewife in the diet of DCCOs in 2001 as compared to 2000, could be in response to this increased availability of alewife of a preferred size.

Although there is no evidence that during 2000 or 2001 DCCOs in the Beaver Archipelago were influenced by a food shortage, it does appear that birds shifted their diet based on food availability within the study area. Actual relative availability of prey in the Beaver Archipelago is not known, however, cormorants are opportunistic predators feeding on a variety of prey species (Lewis 1929, Birt *et al.* 1987). It is likely that these birds shift their diet in response to prey availability, especially when schooling species of an appropriate size are present in large numbers in shallow waters. Ludwig *et al.* (1989) documented by comparing alewife trawling estimates with DCCO diet data that bird diet does shift based on the availability of alewife when years were compared. Further, the current study supports suggestions that cormorant reproductive success may be linked to alewife availability (Weseloh and Ewins 1994). Although the breeding population declined in 2001 as compared to 2000, mean clutch size and estimates of chicks produced increased

Ludwig *et al.* (1989) found the regional differences diet were apparent when cormorants from several areas of the Upper Great Lakes were compared. For the most part, alewife were important prey in all regions, but other prey, such as yellow perch, lake whitefish and centrarchids, occurred in the diet in some regions while these prey were uncommon or absent in other regions. These differences were assumed to exist because of differences in prey availability and habitat types. In the current study, such differences are apparent yet again, but on an even finer scale. In the Main Archipelago, open water schooling species such as alewife are prevalent in the diet of DCCOs; however, other species, more prevalent in more inshore habitats, including crayfish, are also quite common. In comparison, crayfish are completely absent in the diet of Gull Island DCCOs and alewife constitute a higher percentage of prey documented in the diet of these birds. Further, the local differences observed in bird diet supports that Main Archipelago and Gull Island birds to not mix during the breeding season.

This work supports other work in the Upper Great Lakes region the documented seasonal shifts in the diet of cormorants (Ludwig *et al.* 1989, Ludwig and Summer 1997, Hatch and Weseloh 1999). These shifts in the diet may indicate changes in prey availability, but could also reflect prey choice based on other factors including handling time (Stickley *et al.* 1992). In the Beaver Archipelago, the overall trend was that alewife became increasingly more important in the diet of DCCOs as the breeding season progressed. This trend is slightly different in 2000, when alewife biomass declined during the Post-nesting phase. Although this could reflect changes in alewife availability, this trend could also be explained by the fact that many birds harvested during this time period in 2000 were young, less experienced birds. These birds were collected near the colony site, where crayfish are an abundant prey.

Seabirds are an important aspect of the Great Lakes ecosystem (Hebert and Sprules 2002). Several studies have been conducted investigating the influence of fish-eating birds on fisheries both in Europe (Suter 1995, Warke and Day 1995) and in the Great Lakes (Madenjian and Gabrey 1995, Maruca 1997, Neuman *et* al. 1997, Schiavone 2001). Research suggests that waterbirds play central roles in marine food webs (Cairns 1992), and this probably holds true in Great Lakes community dynamics. The ability to estimate cormorant numbers and diet accurately will strengthen attempts to understand the importance of these birds as predators in this study area. These data can be used to develop bioenergetic models that can assess of the importance of avian predators in energy transfer and nutrient cycling in aquatic systems (Wiens and Scott 1975). The primary parameters incorporated into most bioenergetic models include calculated daily energy demands, food type and daily consumption, and population estimates (Fowle

1997) and such models have been useful in estimating total fish consumption by avian populations. Although population and diet studies alone cannot answer complex questions as to the relationships among DCCOs and their prey, these are important steps, in combination with more detail information on avian foraging ecology and prey population dynamics, in investigating community level interactions.

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Table 1. Population estimates of breeding Double-crested Cormorants in the Beaver Archipelago, northern Lake Michigan from 1984 to 2004.

	Pismire	**Grape**	**Timm's**	**Hat**	**Whiskey**	**Gull**	**SE Garden**	**Total**
1984[a]	57	0	0	54	0	139	0	250
1989[b]	35	291	0	294	0	260	0	880
1997[c]	383	3509	753	4617	560	1887	0	11709
2000	987	2431	277	4917	0	1532	0	10125
2001	1035	2146	0	4511	0	2013	0	9705
2002	615	1339	0	3659	0	957	87	6657
2003	1164	0	0	7341	0	(?)	614	9119
2004	725	0	0	3515	95	1274	798	6407

[a] Nest count data from Ludwig, 1984.

[b] Nest count data from Scharf and Shugart, 1993.

[c] Nest count data from Cuthbert et al., 1997.

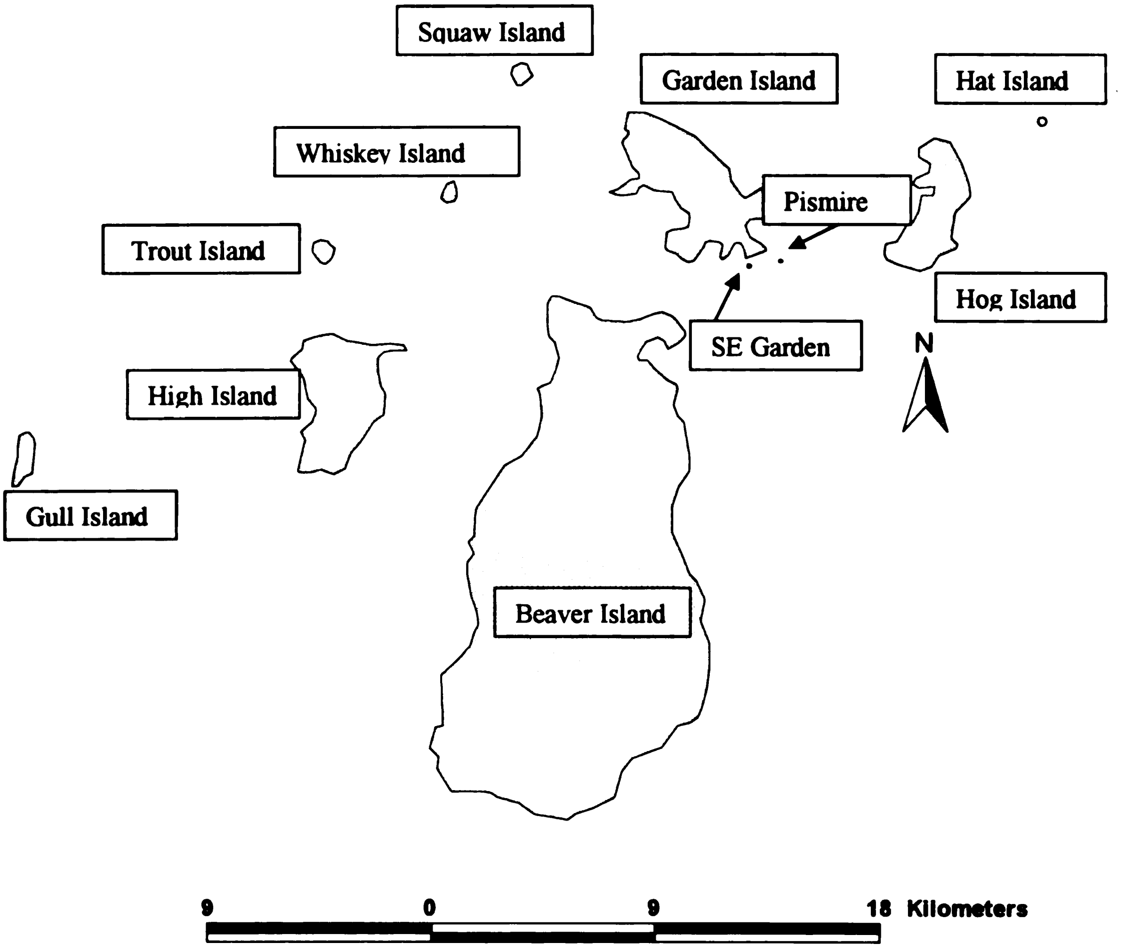

Figure 1: The Beaver Archipelago of northern Lake Michigan.

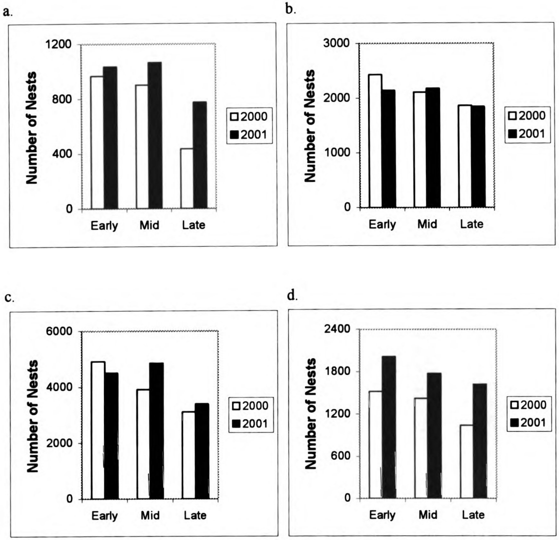

Figure 2. Number of active cormorant nests counted during the early, mid and late breeding season in 2000 and 2001, for a) Pismire, b) Grape, c) Hat, and d) Gull Island colonies.

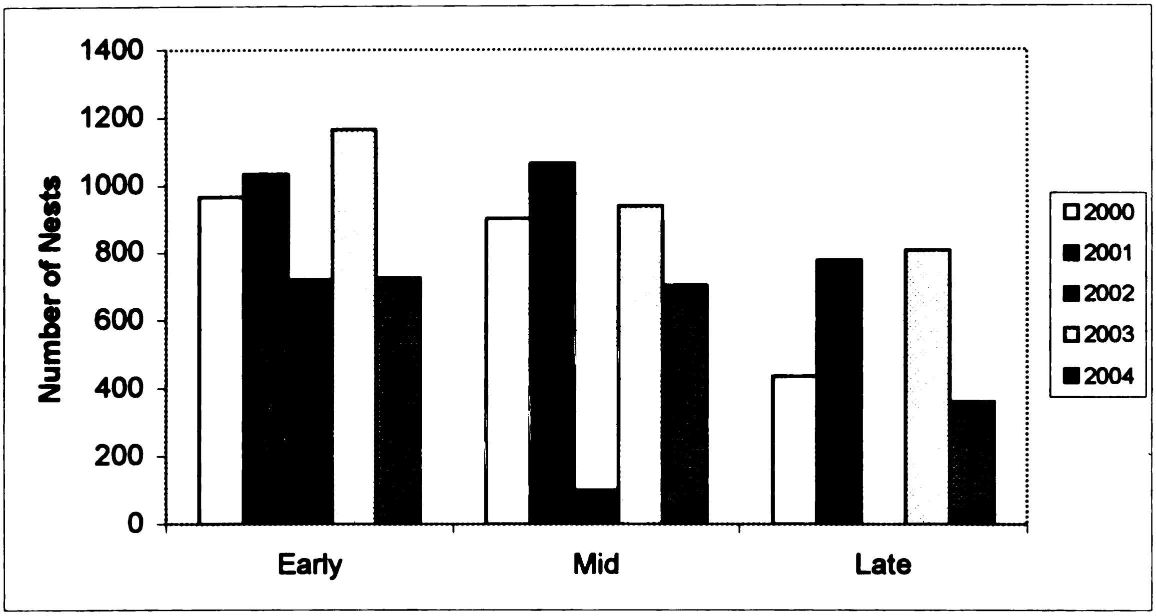

Figure 3. Number of active cormorant nests counted during the early, mid and late breeding season from 2000 through 2004 at Pismire Island. Note that no nests remained at the end of the 2002 breeding season.

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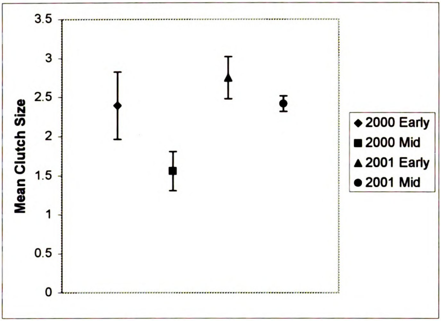


b.

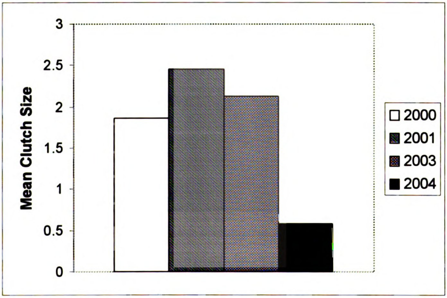
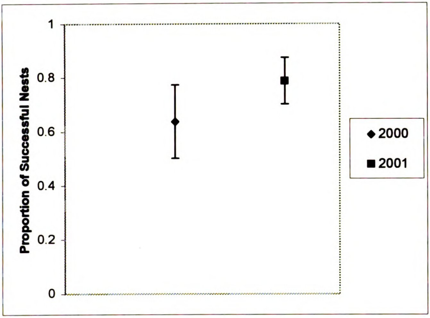


Figure 4. a) Mean clutch size (with standard error) for all colonies during the early and mid breeding season in 2000 and 2001. Late clutch sizes in mid 2000 and 2001 are significantly different from each other. b) Mean clutch size in the mid breeding season for Pismire Island in 2000, 2001, 2003 and 2004.

a.



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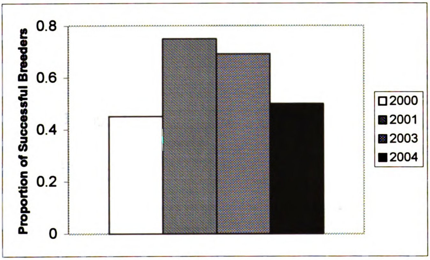

Figure 5. a) Mean number of successful breeding pairs (with standard errors) for all colonies during the 2000 and 2001 breeding seasons. b) Mean number of successful breeding pairs for Pismire Island in 2000, 2001, 2003 and 2004.

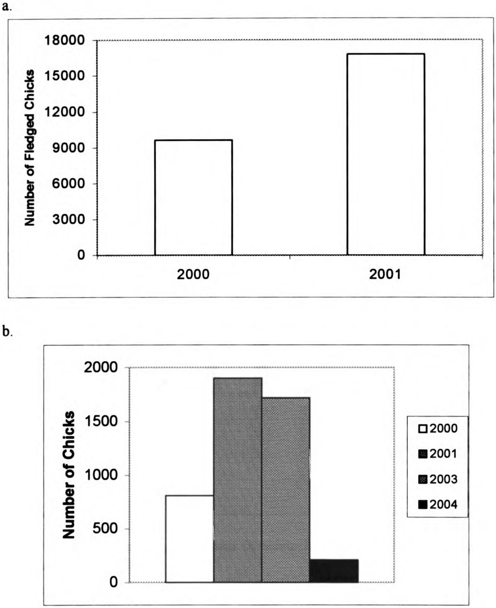

Figure 6. a) Estimates for the number of chicks produced for pairs breeding at all colonies during the 2000 and 2001 breeding seasons. b) Estimates for the number of chicks produced for breeding pairs on Pismire Island in 2000, 2001, 2003 and 2004.

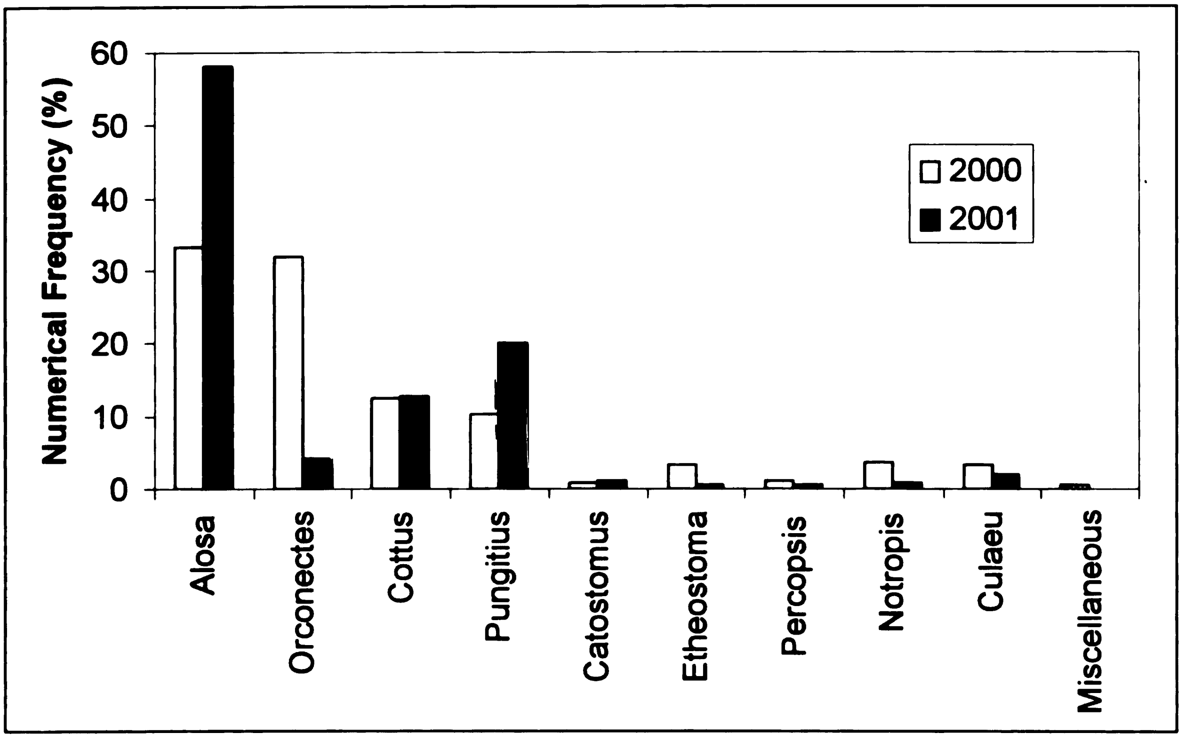

Figure 7. Numerical frequency data showing the diet of Beaver Archipelago cormorants as percentages for 2000 and 2001.

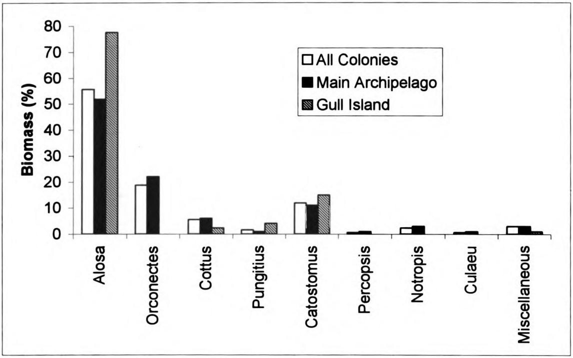

Figure 8. Biomass data showing the diet of Beaver Archipelago cormorants as percentages, 2000, for all colonies, Main Archipelago colonies, and Gull Island colonies.

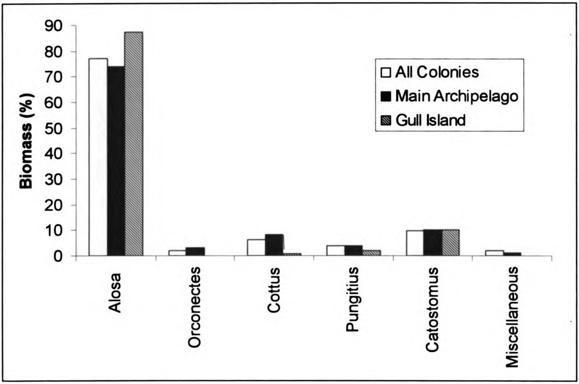

Figure 9. Biomass data showing the diet of Beaver Archipelago cormorants as percentages, 2001, for all colonies, Main Archipelago colonies, and Gull Island colonies.

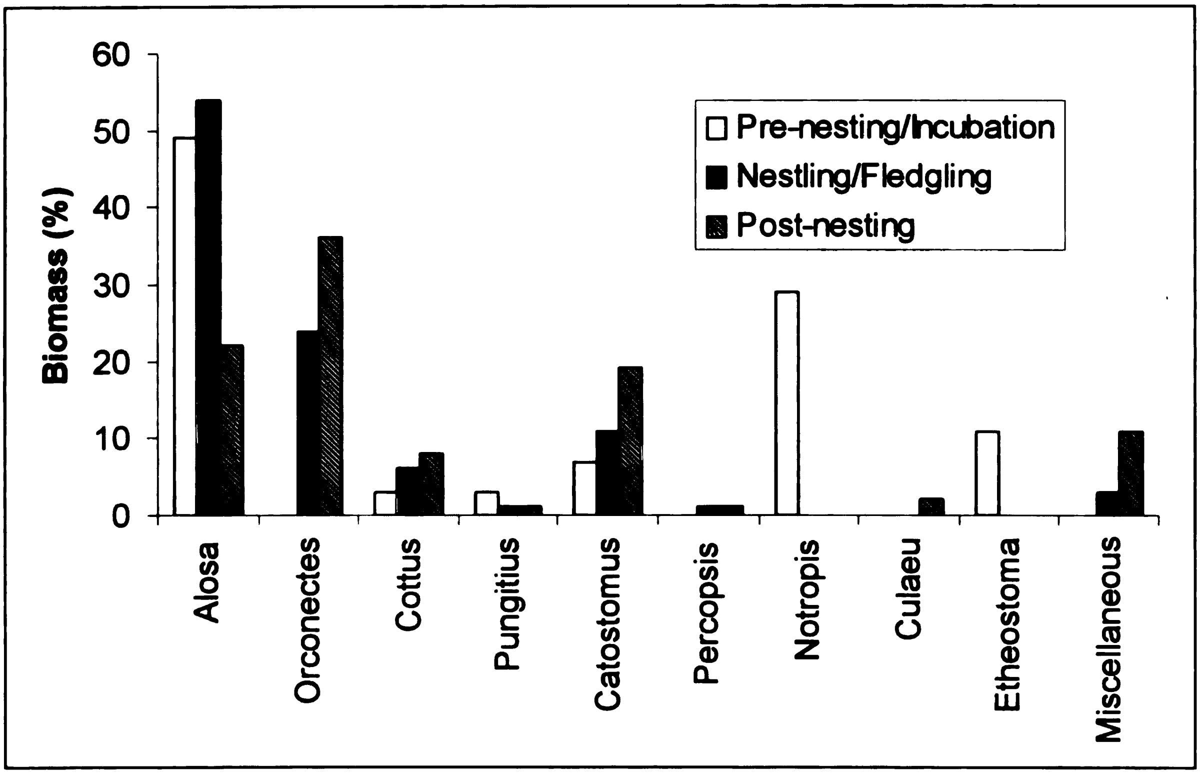

Figure 10. Biomass data showing the diet of Main Archipelago cormorants as percentages, 2000, for Pre-nesting and Incubation, Nestling and Fledgling, and Post-nesting periods

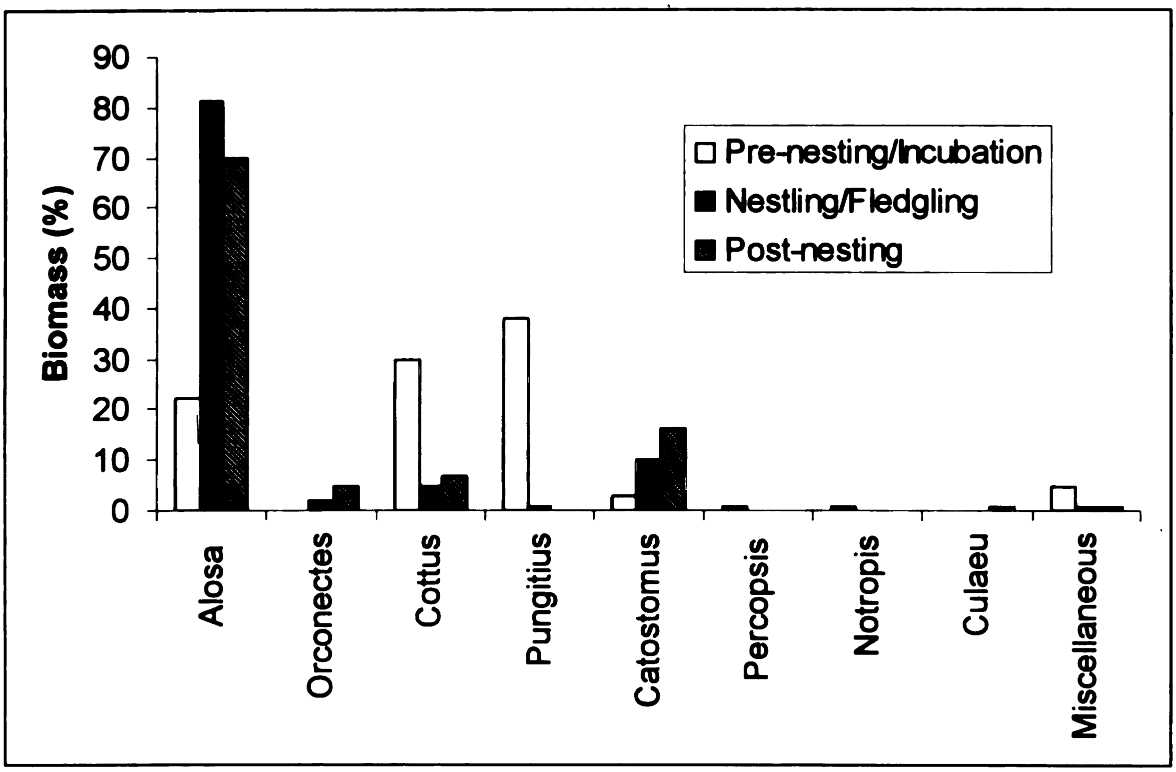

Figure 11. Biomass data showing the diet of Main Archipelago cormorants as percentages, 2001, for Pre-nesting and Incubation, Nestling and Fledgling, and Post-nesting periods

CHAPTER 4

USING RADIOTELEMETRY AND RAFTING LOCATIONS TO DETERMINE FORAGING LOCATIONS OF DOUBLE-CRESTED CORMORANTS (*PHALACROCORAX AURITUS*) IN THE BEAVER ARCHIPELAGO, NORTHERN LAKE MICHIGAN

Abstract

During summer 2003, VHF radio telemetry was used to track the foraging activities of ten Double-crested Cormorants (*Phalocrocorax auritus*) nesting on Pismire Island or at the Southeast Garden Colony in the Beaver Archipelago, northern Lake Michigan. Leg hold traps were used to capture birds and backpack radio-transmitters were harnessed to the birds. Using triangulation, birds were monitored from both land and water on a daily basis, weather permitting, throughout the breeding season. In addition, rafting locations of cormorants were documented by boat throughout the breeding season. Radiotelemetery indicated that cormorants typically foraged 2.5 km away from the colony, at the northeastern end of Beaver Island. This area overlaps with the area determined by rafting locations, however the latter were centered further south. These data allow for better estimation on foraging patch use by cormorants and indicate the birds are not typically concentrating their foraging in areas where the Smallmouth Bass fishery has recently declined. Not only has this led to better understanding of cormorant foraging patterns, but these data also provide information concerning the activity budgets of archipelago birds. Together, these data can be used to estimate cormorant bioenergtics and, in combination with data on prey population dynamics, will help unravel the complex relationships between cormorants and their prey in the study area.

Introduction

Over the past several decades, the population of Double-crested Cormorants (*Phalacrocorax auritus*), or DCCOs, has increased substantially in size throughout the Great Lakes Basin (Ludwig 1984, Cuthbert *et al.* 1997, Ludwig and Summer 1997, Wires *et al.* 2001), including the Beaver Archipelago of northern Lake Michigan (Seefelt and Gillingham, 2004a). The high density of birds combined with their observed fish eating behaviors have led to their implication in declines of both commercial (Ludwig *et al.*, 1989; Neuman *et al.* 1997) and recreational fisheries throughout the Great Lakes region (Neuman *et al.* 1997, Lantry *et al.* 1999). Cormorants are opportunistic fish predators that often feed in shallow waters (Lewis 1929, Birt *et al.* 1987) and breeding birds remain relatively close to breeding colonies when foraging (Custer and Bunck 1992). Although cormorants may have only small and localized effects on fish populations during migration (Kirsh 1995), it has been demonstrated that these birds deplete some species of prey fish around breeding colonies in marine systems (Birt et al. 1987).

The Beaver Archipelago, and particularly the habitat around Garden and Hog Islands, has been considered in the past to have excellent smallmouth bass (*Micropterus dolomieu*) fishing, and this evaluation has been published in the national media a number of times (Robinson 1995). Cormorants have been documented to feed on smallmouth bass (Blackwell *et al.* 1997, Neuman *et al.* 1997, Schiavone 2001, 2003) with records of bass predation in the Beaver Islands (Ludwig *et al.* 1989). Seider (2003) attempted to estimate the population size of bass in the Beaver Archipelago (Seider 2003), although this species has not been documented as an important prey item in cormorant diet (see Chapter 3). However, compared to similar data gathered by researchers nearly 20 years ag

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ago (Lennon unpublished data, Seider 2003), the bass population has declined by 75-80%. It is therefore quite clear that there has been a recent and rapid decline in the Beaver Archipelago bass fishery. However, the role of cormorants in this decline has remained uncertain.

Cormorant diet often includes primarily species that are of little commercial value but important in community trophic dynamics (Craven and Lev 1987). Therefore, cormorants may have a secondary effect on sport fisheries by competing with desired species for forage fish and other prey such as crayfish. Although the effects on forage fish numbers may be limited and may only occur in localized areas (Madenjian and Gabrey 1995), this combined with direct sport fish depredation may have some impact on sport fish populations.

There are studies in which feeding flights were followed by airplane to learn foraging distances birds travel from the breeding colonies and potential home ranges of these birds (Ainley and Boekelheide 1990, Custer and Bunck 1992). However, in Lake Michigan, there is little information on the localization of foraging sites within such large potential areas. With these data lacking, it is not easy to ascertain the ecological impacts that large numbers of foraging birds may have aquatic communities, including fish populations which may often be localized within particular habitats (ie. littoral zone and open water). Waneless *et al.* (1995), Gremillet (1997) and Gremillet *et al.* (1998, 1999) have successfully used radiotelemetry to monitor shags and cormorants. These studies have allowed for better estimation on foraging patch use and seasonal variation, which, in turn, has lead to better understanding of behavior patterns.

The objective of this study was to determine the important foraging areas for breeding DCCOs in the Beaver Archipelago of northern Lake Michigan in 2003, by utilizing VHF radiotelemetry and by observing rafting areas throughout the breeding season. By doing so, this work will shed light on whether cormorants are concentrating their foraging in important bass habitats or in other habitat types. This work, in combination with other work on the foraging ecology and bioenergetics of DCCOs in the study area, will enable researchers to ascertain the impact of these birds on the fishery in the present, as well as possible future scenarios.

Methods

Study Site

The study was conducted under permit (U.S. Department of the Interior Permit No. 20852-03-89) in the Beaver Archipelago of northern Lake Michigan. This archipelago consists of about ten main islands and numerous small islands (Figure 1). The number of smaller islands depends on fluctuating lake levels. Two of the larger islands (Gull and Hat) and two small islands (Pismire and Southeast Garden) provided sites for nesting DCCOs in 2003. Pismire Colony (lat 45° 45.8'N, long 85° 26.6'W) and the Southeast (SE) Garden Colony (lat 45° 45.8'N, long 85° 27.0'W) are relatively close together (approximately 1.5 km or 0.92 miles apart) and are the focal colonies of this work. These colonies were chosen due to their central location within the archipelago and their close proximity to important habitat areas for smallmouth bass. In 2003, 1164 breeding pairs were established at Pismire Colony and 615 pairs were documented at SE

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Garden Colony during June. By late July, the number of nests had declined to 807 and 355, respectively (Seefelt and Gillingham, 2004b).

Telemetry

VHF transmitters (Model RI-2C Backpack, Holohil Systems Ltd., 112 Cavanagh Road, Carp, Ontario, Canada, K0A 1LO; 6.4 g with whip antennae; frequency range 150.026-150.204 MHz) were used. Harnesses were constructed and attached to radiotransmitters in the lab prior to trapping birds using standard methods outlined in Dunston (1972). Harnesses were composed primarily of Teflon Tubing. At junctions, seams were fastened by stitches (needle and thread), fast-setting marine adhesive and Teflon-coated fiberglass tape. One connection was left free to allow for quick attachment to the birds in the field. The mass of the transmitter and harness was 20g, which is between 1-2% of the body weight of adult birds.

On 04 June 2003, eight birds were trapped using soft-catch leg hold traps (model SN3 5798, Forestry Suppliers, P.O. Box 8397, Jackson, Mississippi, USA, 39284) on Pismire Island. To insure the capture of experienced adult birds, these traps were placed at a well-established, central location in the colony. Once birds were captured, they were promptly removed from the traps and placed in wet pillowcases. Birds were then carried to another area on Pismire Island away from cormorant nests and out of site of nesting birds to be processed. Each bird was weighed and then the harness (with radiotransmitter) was attached. Seam construction followed the same method used in the laboratory. As soon as the harness was attached, birds were released. Handling was kept at a minimum. To minimize colony disturbance at Pismire Island, on 05 June 2003, two birds, for a total of ten, were trapped and harnessed using the same methods as at the SE Garden Colony.

Birds were monitored via radiotelemetry from a boat on a daily basis, weather permitting, throughout the breeding season (04 June – 31 July) and during post-breeding (01 August – 13 September) using a receiver (model LA 12-Q, AVM Instrument Co. Ltd, 1213 S. Auburn, P.O. Box 1898, Colfax. California, U.S.A., 95713; frequency coverage 150.000 – 151.999 MHz) and 8-element yagi aerial. It was difficult to sight birds, so triangulation was used to document bird locations, as follows. Once a bird's signal was heard, the GPS location of the boat was taken (using a Garmin Handheld GPS Unit) and a compass bearing (Brunton® Outback Electronic Compass) based on the strongest signal strength was taken. This process was repeated two more times at two different locations within 10 minutes. In addition, date and time (beginning and ending) were noted. In some cases, signals were detected coming from the colonies. If this was the case, birds were assumed to be at or near the colonies. To avoid disturbing birds, a more accurate location was not attempted. On several occasions, birds were actually sighted foraging in open water.

When weather did not permit boat travel, birds were monitored from land on the northeast portion of Beaver Island, referred to as Sucker Point or Gull Harbor (lat 45° 44.9' N long 85° 29.9' W). From this station, it was noted whether birds were on colony (or near colony) or whether they were away, presumably foraging. In addition, birds were also monitored from the southeastern portion of Garden Island (lat 45° 46.5' N long 85° 27' W) to the same end. In addition, from these data the general daily activity periods at the colony were determined.

Rafting Locations

Beginning 18 May 2003 and ending 13 September 2003, cormorant rafting locations were marked by boat survey. In general, daily surveys of rafts were conducted on the northern and eastern waters around Beaver Island, weather permitting. Also, in-shore areas of Garden Island that are considered to be primary smallmouth bass habitat, including Garden Island Harbor, Northcut Bay and Sturgeon Bay, were also surveyed (Figure 2). Garden Island Harbor is 2.25 km (1.4 miles) from Pismire Island, Northcut Bay is 1 km (0.62 miles) from Pismire Island, and Sturgeon Bay is 0.5 km (0.3 miles) from Pismire Island. In addition, the Paradise Bay-St. James Harbor area of Beaver Island (3 km or 1.86 miles from Pismire Island) was also surveyed, as were the waters between Garden and Hog Island (north of Pismire Island, south of Grape Spit). These areas are also considered to be good habitat for smallmouth bass. In addition, on several occasions, surveys were conducted around the entire periphery of Beaver Island.

Groups of rafting birds ranging from three to approximately 300 birds were located on these surveys. In some cases when rafts were large (exceeding 50 birds) it was necessary to estimate bird numbers as opposed to actually counting individuals. Each rafting site was marked using a Garmin hand-held GPS unit and an approximated water depth was noted (as read on a Humminbird Fish-finder Depth sensor). The date and time were also recorded.

Analysis

Locations for each bird were determined using triangulation with Locate II (Nams, 2001. These data were then imported into ArcView GIS 3.3 and locations for all birds were plotted together. Then, Kernel Estimator: Extension Animal Movement (Hooge and Eichenlaub 1997) was used to determine primary foraging areas, based on the density of locations as determined by telemetry. This estimator provided 20% density contours based on the number of actual locations and determined the area where birds were most likely found when away from the colony; these areas were then compared to known smallmouth bass habitat, as documented by Lennon (unpublished data) and Seider (2003). Furthermore, the area within each density contour was then compared to water depth contours (nautical soundings map of Lake Michigan – Waugashance Point to Seul Choix Point, NOAA 1989). In addition, locations were divided into two data sets based on date: 09 June – 31 July (breeding) and 01 August – 07 September (post-breeding). Plots were compared to determine any seasonal differences.

Rafting locations, as well as the number of birds per raft and date, were imported into ArcView GIS 3.3. These were plotted and then 20% density contours were determined, which weighted each raft location by the number of birds observed per raft. These areas were then compared to known smb habitats, and the area within each density contour was then compared to water depth contours (NOAA 1989). In addition, rafting locations were divided into three data sets based on date: 18 May –13 June (pre-nesting and incubation), 14 June – 31 July (nestling to fledgling) and 01 August – 10 September (post-breeding). Plots were compared to determine any seasonal differences.

Results

A total of 131 foraging locations were plotted for the ten birds with radio transmitters from 09 June 2003 through to 07 September 2003 (Figure 2). All birds remained in the Beaver Archipelago until at least 31 August 2003, with eight birds remaining in the area through 13 September 2003. A total of 223 on (or near) colony locations were documented by boat and an additional 185 were documented from Beaver Island. The Garden Island observations indicated the birds typically began leaving their colonies at 05:00 EST and all birds return to roost by 19:00 EST during the breeding season.

Figure 3 shows the 20% density contour for all foraging locations marked using radiotelemetry. The harnessed birds tended to concentrate their foraging efforts in an area at the northeastern end of Beaver Island. This area is centered at about 2.5 km (1.55 miles) from the colony and is close to Luney Point and the Paradise Bay – St. James Harbor mouth. It is also an area with dramatic depth contours, with areas of only 1-3 meters dropping rather abruptly to areas greater than 18 meters. In addition, there are several shoals (NOAA 1989) and a channel used by ferry service to Beaver Island. Overall, birds did not show any seasonal changes in overall foraging locations, except for one bird that foraged very close to Pismire Island during June and part of July. These points are not shown in Figure 3, because it was difficult to discern when this bird was on colony or foraging in the water near the colony. However, this bird did forage in the area shown in Figure 4 during the post-breeding time period.

A total of 271 observed rafting locations, with an average of 33 birds per raft, are shown in Figure 4. Figure 5 shows the 20% density contours weighted by the number of birds per raft. Interestingly, this area overlaps the foraging areas for birds with radiotransmitters. However, the highest density of weighted rafting locations is further south and is centered near Conn's Point and the north end of Sand Bay, Beaver Island.

Like the area defined by telemetry, the major rafting areas also have rather dramatic depth contours, with areas of 1- 3 meters dropping off to areas of 18 meters or more. The areas highlighted to the southeast and west of Beaver Island are due to a few large rafts (200+ birds) observed at these sites in July. Very few rafts were documented in in-shore areas of Garden Island, St. James Harbor – Paradise Bay, and between Garden and Hog Islands.

Discussion

Both VHF radiotelemetry and the observation of rafting sites produced a similar pattern in mapped foraging locations. The primary foraging areas for many of the DCCOs in the Beaver Archipelago is centered near the northeastern portion of Beaver Island, especially near dramatic depth contours. Cormorants nesting on Pismire and SE Garden Islands do appear to remain close to the colonies when foraging, but both methods indicate that important habitat areas for smallmouth bass are probably not used extensively by DCCOs in the study area; this includes areas relatively close to the colonies. Cormorants, therefore, are probably not directly competing with bass for local prey items. In addition, other studies indicate that birds do tend to forage in areas within a few kilometers of their colonies, as shown in DCCOs breeding in the Wisconsin waters of Green Bay, Lake Michigan (Custer and Bunck 1992), and in Great Cormorants (*Phalacrocorax carbo carbo*) breeding at the Chausey Islands, France (Gremillet 1997).

Cormorant foraging locations in the Beaver Archipelago seem to correspond with areas that are frequented by alewife (*Alosa pseudoharengus*). Alewife are presently a major planktivorous species in the lake community and an important energy link to upper consumer levels. In addition, alewife are an important link between inshore and deep lake communities (Eck et al. 1987, Madenjian et al. 2004). During early summer, alewife begin to move inshore for spawning, only to then return to deepwater in fall. This cycle is repeated each year. Because of this life history and abundance, alewife are considered to be a key species in Lake Michigan and their population trends appear to be a driving force in fish community dynamics (Eck *et al.* 1987, Madenjian *et al.* 2002, 2004). Interestingly, in the study area, alewife are documented to be an important prey for cormorants and typically comprise an estimated 72% of the prey biomass consumed by breeding DCCOs and their chicks each year (Seefelt and Gillingham 2004a).

Cormorants nesting at Hat and Gull Islands were not studied in this work. These colonies typically support more nesting pairs than either Pismire or SE Garden Colonies, with Hat Island consistently being the largest colony (Seefelt and Gillingham 2004a). Hat Island is relatively near some areas of the smallmouth bass habitat around Hog Island, as described by Seider (2003). However, open-water areas, specifically areas of depth dramatic depth contours are much closer to this colony. Furthermore, there has been little evidence of bass in the diet of these birds (see Chapter 3). The Gull Island Colonies are separated from the main island group by a stretch of open water to the west of Beaver Island. From aerial surveys (unpublished data), it was concluded that the cormorants breeding at Gull Island remain close to these colonies and do not regularly travel to the Main Archipelago. In addition, DCCO dietary data from Gull Island documents that these birds are dependent on alewife (see Chapter 3).

The primary foraging locations documented using birds harnessed with radiotransmitters and rafting locations of DCCOs are concentrated in areas removed from smallmouth bass habitat, as sampled by Seider (2003). DCCO foraging areas, as determined by telemetry and rafting sites, do support bird dietary data gathered in the study which shows birds primarily feed on alewife and other species unimportant to sport and commerial fisheries. The data presented in this work will be used further to develop, in part, a time-budget analysis bioenergetics model. These data can then be used, in combination with data on prey population dynamics, to investigate the complex relationships between cormorants and their prey in the study area.

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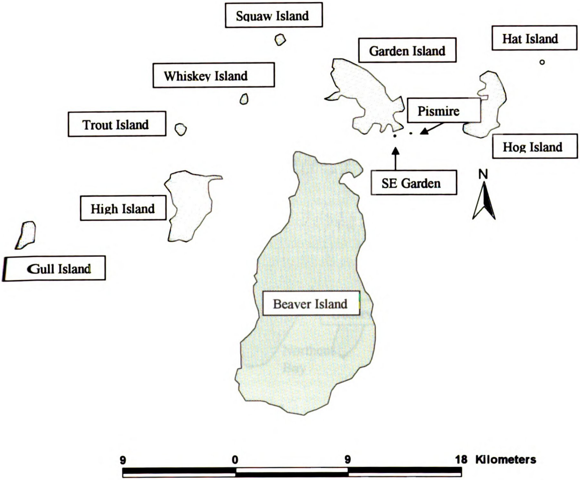

Figure 1. The Beaver Archipelago of northern Lake Michigan.

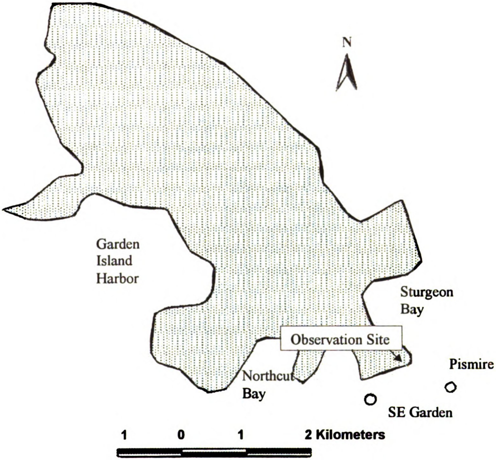

Figure 2. The bays of Garden Island and their proximity to Pismire and SE Garden **Colonies**.

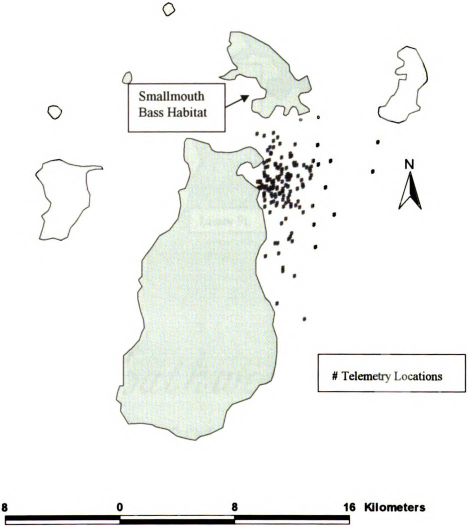

Figure 3. Bird locations determined by radiotelemetry and triangulation.

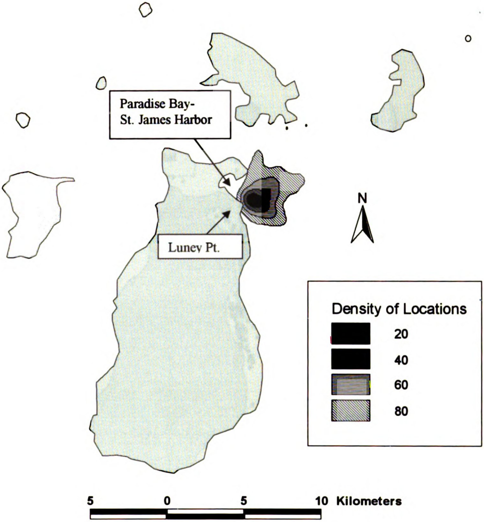

Figure 4. Weighted density contours for foraging areas as determined by radiotelemetry.

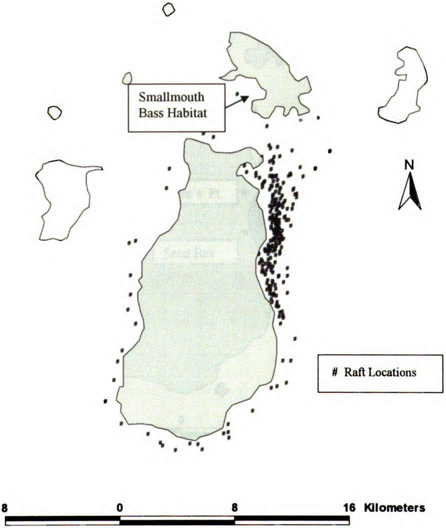

Figure 5. Locations of cormorant rafting sites as determined by boat surveys.

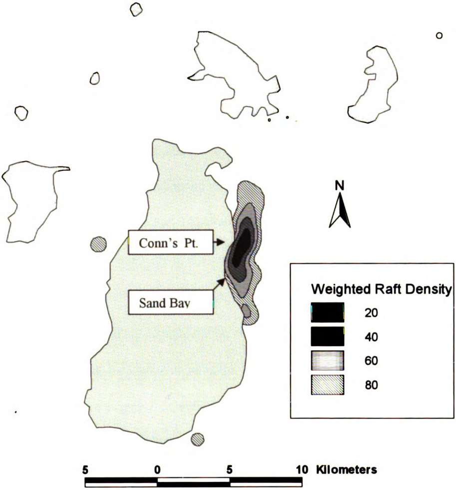

Figure 6. Weighted density contours for foraging areas as determined by boat survey.

CHAPTER 5

BIOENERGETICS AND PREY CONSUMPTION OF BREEDING DOUBLE-CRESTED CORMORANTS (*PHALACROCORAX AURITUS*) IN THE BEAVER ARCHIPELAGO, NORTHERN LAKE MICHIGAN

Abstract

Colonial waterbirds are important component of Great Lakes ecosystems. One important aspect is the role of these birds as top predators in aquatic food webs. In order to investigate this role, bioenergetics models, using allometric equations, were applied to breeding Double-crested Cormorants (*Phalacrocorax auritus*) and their offspring in the Beaver Archipelago, northern Lake Michigan. These models were parameterized using detailed information collected during the breeding seasons between 2000 and 2001, as well as literature values. The breeding season was divided into stages in the models to reflect changes in cormorant diet documented in the study area. The models estimated the total prey biomass consumed as 1444.11 tonnes of prey in 2000, and 1586.17 tonnes of prey in 2001. Each year the majority of the prey biomass was alewife (*Alosa pseudoharengus*), with alewife comprising a greater percentage of prey biomass in 2001. An increase in cormorant reproductive success in 2001 may be linked to this increase in alewife biomass; the breeding bird population size, however, declined in 2001 as compared to 2000. The other prey items, which are not considered to be species of commercial or sport value, were also important contributors to bird diet and did tend to vary from year-to-year. Overall, the application of bioenergetics models allow for greater understanding of the role of cormorants as predators and as energy links in the system.

Introduction

Over the last several decades, the Double-crested Cormorant (*Phalacrocorax auritus*), or DCCO, has substantially increased in numbers throughout the Great Lakes Basin (Ludwig 1984, Cuthbert *et al.* 1997, Ludwig and Summer 1997, Wires *et al.* 2001), including the Beaver Archipelago of northern Lake Michigan (Seefelt and Gillingham, 2004). The high density of birds combined with their observed fish eating behaviors have led to their implication in declines of both commercial (Ludwig *et al.* 1989, Neuman *et al.* 1997) and recreational fisheries throughout the Great Lakes region (Neuman *et al.* 1997, Lantry *et al.* 1999). Cormorants are opportunistic predators (Lewis 1929, Birt *et al.* 1987) that feed primarily on species of little commercial or sport value, but still important in community trophic dynamics (Craven and Lev 1987). Although the effects on non-game forage fish populations may be limited and may only occur in localized areas (Madenjian and Gabrey 1995), cormorant predation on these fish may have some impact on overall aquatic community structure.

Waterbird bioenergetics can assess of the importance of avian predators in energy transfer and nutrient cycling in aquatic systems (Wiens and Scott 1975). Models are used to calculate the food requirements necessary for a bird's daily energy expenditure and thus, can estimate total prey consumption (Cairns *et al.* 1991). By this quantification, the demands avian predators place on aquatic communities can be determined (Madenjian and Gabrey 1995). Since cormorants are wide-ranging generalists, it is difficult to measure energy demands directly. However, many indirect modeling approaches have been developed which estimate energetics of metabolism and adjust for other factors that may influence energy requirements (Wiens 1984).

The primary parameters incorporated into bioenergetic models include calculated daily energy demands, food type and daily consumption, and population estimates (Fowle 1997). Direct measurements of wild bird metabolism have been be used to develop allometric equations that predict avian metabolic rates (Kendeigh *et al.* 1977). In addition, techniques such as doubly-labeled water and time-budget methods can be used to directly measure metabolism of free ranging birds (Nagy 1989, Birt-Friesen *et al.* 1989). Many indirect modeling approaches have been developed to extrapolate individual metabolic estimates to whole populations (Wiens 1984, Cairns *et al.* 1991, Glahn and Brugger 1995, Madenjian and Gabrey 1995, Fowle 1997). In all models, energy consumption was based on metabolism. Furthermore, these models have applied specific caloric requirements to daily energy expenditure to estimate food consumption, and have been useful in estimating total fish consumption by avian populations.

Several studies have been conducted investigating the influence of fish-eating birds on fisheries both in Europe (Suter 1995, Warke and Day 1995) and in the Great Lakes (Madenjian and Gabrey 1995, Maruca 1997, Neuman *et al.* 1997, Schiavone 2001, 2003). Research suggests that waterbirds play central roles in marine food webs (Cairns 1992), and this probably holds true in Great Lakes community dynamics. In order to get a realistic picture of the impact bird predators have on fish populations, it is necessary to incorporate quantitative data on the diets, population size and energy requirements of the cormorant population. In addition, reliable data on the size of the fish populations, with the appropriate spatial and temporal scales, is necessary (Draulans 1988). Yet even with the latter lacking, bioenergetics approaches can still aid in uncovering the energy demands placed on aquatic systems by avian predators. This can then allow for further investigation to explore possible impacts these predators may have on their prey and to compare the prey consumption by birds to other sources of mortality.

In this work, a bioenergetics approach based on allometric equations was used to investigate the energy demands and estimate annual prey consumption of breeding DCCOs and their chicks in the Beaver Archipelago, northern Lake Michigan during the 2000 and 2001 breeding seasons. The biomass of individual prey species consumed by birds were estimated each year and compared. Waterbird predation on fish and other species is an important link in the northern Lake Michigan web and should allow a further understanding other ecology of this system. In addition, this work can be directly compared to work in other systems, such as western Lake Erie (Madenjian and Gabrey 1995, Hebert and Morrison 2003), in an effort to understand the role of cormorants in Great Lake ecology.

Methods

Study Area

The Beaver Archipelago of northern Lake Michigan consists of about ten islands. Three of the larger islands (Gull, Hog and Hat Islands) and one small island (Pismire Island) contained nesting colonies of DCCOs in 2000 and 2001 (Figure 1). The Hog Island colonies were located on two peninsulas known as Grape Spit, on the west side of the island, and Timm's Spit, on the east side of the island. Population and dietary data collected in the Main Archipelago in 2000 and 2001 were used in the construction of the bioenergetics models. The Main Archipelago colonies include only Pismire, Grape, Timm's and Hat. Gull Island consists of two colonies, North and South, on one island

and is separated from the main island group by almost 18 km (11 miles) of open water to the west of Beaver Island. From aerial surveys (unpublished data), it was concluded that the cormorants breeding at Gull Island remain close to these colonies and do not regularly travel to the Main Archipelago. The purpose of these models was to determine total prey consumption by breeding DCCOs and their young in the Main Archipelago in 2000 and 2001, and compare these years. The models were limited to the Main Archipelago because this was the area of concern in respect to fish populations.

Model Construction

The major model parameters include (1) seasonal arrival/departure dates, (2) population estimates of adult and chicks, (3) diet data, and (4) estimates of daily energy expenditure (DEE). Population estimates and diet data were collected in the study area by the author (See Chapter 3) and, whenever possible, model inputs were measured in the field each year. Some model inputs, however, were taken from the literature. A complete list of model parameters for each year is shown in Table 1.

To provide better accuracy in the model, the breeding season was divided into three categories: pre-nesting/incubation stage (20 April – 12 June), nestling stage (13 June – 31 July), and post-nesting stage (01 August –10 September). Diet data were categorized by date to reflect the changes in DCCO diet as the breeding season progresses, and were used to determine the biomass of individual prey species consumed by cormorants over the breeding season (Table 2). Models were applied to each year's data separately.

The bioenergetic models follow a procedure outlined by Madenjian and Gabrey (1995) and then modified to include individual prey species by Hebert and Morrison (2003); however, in this work, models were developed using a spreadsheet (Microsoft Office Excel®). The models are dependent on allometric equations that use body mass in order to determine DEE (daily energy expenditure) for breeding adult DCCOs and their chicks. These equations have been successfully used in the past (Birt-Friesan *et al.* 1989, Cairns *et al.* 1991, Madnejian and Gabrey 1995, Hebert and Morrison 2003). The equation for adults is as follows (Birt-Friesen *et al.* 1989):

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

A body mass (W) for adult cormorants was determined by averaging the 150 birds harvested for the dietary study during 2000 and 2001. The daily energy intake (DEI) is determined by dividing DEE by the assimilation efficiency (given as 0.80 by Furness 1978). In addition, the bioenergetics of egg production was included in the model following the work of Kendeigh *et al.* (1977). The greatest number of nests counted each year was used to best estimate the maximum energy input needed for egg production. Daily food consumption (DFC) is found by dividing DEI by the average caloric density (ACD) of bird diet. This is calculated using the following equation:

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

where CD_i = caloric density (kcal/kg) of diet category I , PROP_i = the proportion of the bird diet (by mass) comprised of prey type i, and n = total number of diet categories. Daily food consumption (DFC) is found by dividing DEI by the average caloric density

(ACD) of bird diet for each stage of the breeding season. In addition, the total DEI for all adult birds was summed throughout each segment of the breeding season. The DEI of individual prey types was then determined by multiplying total cormorant DEI by the proportion of occurrence a particular prey species appears in the diet by mass during each stage of the breeding season. Then prey DEI was multiplied by energy content conversion factors for each prey type (Table 3, Cummins and Wuycheck 1971, Bryan *et al.* 1996) to determine the biomass of each prey type consumed. These values were calculated for each time period of the breeding season (pre-nest/incubation, nestling and post-breeding stages) and then combined to determine the total biomass (tonnes) of prey consumed for each year by adult birds.

The time period for cormorant chick models were divided into two segments, pre-fledging and post-fledging, which corresponded to the nestling and post-breeding time segments, respectively, for adult birds. To simplify the model, all eggs hatched simultaneously and all young fledged on the same date. An allometric equation (from Kendeigh *et al.* 1977) is used to determine the daily energy expenditure of a pre-fledged bird (DEEN):

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

Again, an assimilation efficiency, given as 0.80 by Furness 1978, was used. Daily food consumption by a pre-fledged bird (DFCN) is determined by the following equation:

$$\mathrm{DFCN} = \frac{\mathrm{DEEN} * \mathrm{PROP}_i}{0.80 * \mathrm{ACD}} + \frac{\mathrm{DG} * \mathrm{PROP}_i}{0.80}$$

Since pre-fledged birds are growing throughout the season, this equation includes a daily growth increment (DG), which is equal to the food needed to increase the mass of the bird. Growth rate per day is considered to be a linear relationship and modeled as described in Madenjian and Gabrey (1995). Since young birds continue to grow and gain mass after fledging, this same equation was used to determine post-fledged birds' DFC, however growth was modeled at a slower rate. The total consumption of prey biomass by chicks was determined using the same method used in adult populations. These biomass values were added to adult values to determine total biomass of each prey type consumed for each time period of the breeding season and also yearly totals. In addition, the total biomass of prey consumed by a single chick that survived the entire simulation for each year was calculated by summing the ACD for one chick during both the pre-fledging and post-fledging time periods.

Sensitivity Analysis

Sensitivity analysis was performed to determine which model parameters were most influential in calculating total DEI and, therefore prey consumption, by breeding cormorants and their chicks. An individual parameter perturbation method was used (Bartell *et al.* 1986, Madenjian and Gabrey 1995). Thirteen model inputs were examined for a total of 26 simulations. For each sensitivity analysis simulation, only one model input was changed while all other parameters were left at their original values. A simulation was conducted for an individual model input by raising it from its original value by 10%; a second simulation was performed for that same model input by lowering its value 10% from its original value. The outputs from these simulations were compared to the original model's output to determine percent change.

Results

The models calculated the DFC (daily food consumption) per adult breeding bird in 2000 based on the ACD (average caloric density) of the diet to be 0.55 kg during the pre-nesting/incubation period, 0.55 kg during the nestling period, and 0.65 kg during the post-breeding period (Table 4). The DFC values per adult bird for 2001 were 0.55 kg, 0.48 kg and 0.51 kg, respectively (Table 3). For chicks in 2000, the DFC per chick based on ACD of the diet ranged from 15.0 g to 320.8 g from hatching to the end of the pre-fledging period (Figure 2a) for a total of 9.0 kg of food consumed/chick (Table 5). For the post-fledging period, DFC per chick in 2000 ranged from 0.60 kg at fledging to 0.65 kg, when chicks attained adult size (Figure 2b), for a total of 26.0 kg of food consumed/chick (Table 4). In 2001, the DFC per chick ranged from 13.2 g to 281.4g from hatching to the end of the pre-fledging period (Figure 2a) for a total of 7.9 kg of food consumed/chick (Table 5). For the post-fledging period, DFC per chick in 2001 ranged from 0.47 kg at fledging to 0.51 kg, when chicks attained adult size (Figure 2b), for a total of 20.4 kg of food consumed/chick (Table 5).

According to modeling results, breeding DCCOs and their young consumed a total of 1444.11 tonnes of prey in 2000. Of this, 426.73 tonnes were alewife (*Alosa pseudoharengus*), 354.11 tonnes were crayfish (*Orconectes* spp.), 59.75 tonnes were sculpin (*Cottus* spp.), 13.19 tonnes were nine-spine stickleback (*Pungitius pungitius*), 300.97 tonnes were sucker (*Catostomus* spp.), 167.50 tonnes were spottail shiner (*Notropis hudusonius*), and 121.87 tonnes of other prey (Figure 3). In 2001, adult and young birds consumed a combined 1586.17 tonnes of prey. Alewife comprised 695.78 tonnes, crayfish 55.29 tonnes, sculpin 369.37 tonnes, nine-spine stickleback 171.96

tonnes, sucker 271.23 tonnes, spottail shiner 5.48 tonnes, and 17.06 tonnes of other prey (Figure 3). For both years, the other category contains primarily johnny darter (*Etheostoma nigrum*), trout-perch (*Percopsis osmiscomaycus*), and brook stickleback (*Culaea inconstans*). Some prey items, such as spottail shiner, were common in the pre-nesting/incubation diet samples but uncommon during the other stages. Because of their rarity, when spottail shiner were found in the nestling or post-breeding diet, they were included in the other category.

Sensitivity analysis revealed that adult and young assimilation efficiency, the number of nests, and adult mass were most influential in determining model output (Table 5). The other model inputs had relatively low impacts on model results, with changes two parameters, calories per egg and mass at hatching, showing virtually no influence on model output. Overall, the models were fairly robust in regard to any uncertainty in model inputs.

Discussion

According to the bioenergetics models, breeding DCCOs and their young consumed an estimated 1444.11 tonnes and 1586.17 tonnes of prey during 2000 and 2001, respectively. During both years, alewife contributed the greatest biomass to these totals, relative to other prey species. Using an average mass of 14 g for alewife, as determined by dietary analysis (see Chapter 3), in 2000, it is estimated that cormorants in the Main Archipelago consumed over 30.4 million of these fish. In 2001, it is estimated that over 49.6 million alewives were consumed. In addition, in 2001, alewife comprised over one and a half times the biomass to the birds' diet as compared to 2000. Alewife biomass in Lake Michigan has remained relatively stable between the early 1980s and 2003 (Madenjian *et al.* 2002, Madenjian *et al.* 2004), however local availability of these fishes may have fluctuated between 2000 and 2001. In addition, according to Madenjian et al. (2004), warm spring temperatures in 1998 led to moderately high numbers of age-3 alewives in 2001 in Lake Michigan; these fish are an attractive prey size for DCCOs. In addition, alewives, as compared to other available prey, have a higher energy density (kcal/kg) (Cummins and Wuycheck 1971, Bryan et al. 1996). This, as well as their size and schooling habits, may make these fish quite a desirable prey to cormorants and explain why birds rely on alewife as a major energy source.

In addition to changes in alewife biomass consumed, several other prey species showed year-to-year variability in terms to their importance to cormorant diet. Crayfish and spottail shiner were both prominent in terms of biomass consumed in 2000. However, in 2001, the biomass each species contributed to the diet sharply declined. Interestingly, the other category, which includes only fish, also showed a sharp decline in 2001. This emphasizes the importance of each prominent prey type in 2001, and, likewise, highlights the importance of alternative prey in 2000 in contributing to the overall energy demands of the breeding DCCO population and their offspring. In comparison, both nine-spine stickleback and sculpin biomass increased in importance as contributors to DCCO diet in 2001 as compared to 2000. Only one prey type, sucker, remained relatively constant in terms of biomass when both years are compared. Interestingly, the energy density of fish, with the exception of suckers, is higher then crayfish (Cummins and Wuycheck 1971, Bryan et al. 1996).

The number of breeders declined from 2000 to 2001, however the biomass of prey consumed increased according to the model. This increase in prey biomass consumed is due to higher reproductive success (more chicks) in 2001, as compared to 2000. Hatch and Weseloh (1999) remark that the local densities of DCCOs may be affected by the temporal and spatial distribution of prey. Number of young produced by each pair each year (reproductive success) could also be influenced by yearly prey availability patterns; Wesoloh and Ewins (1994) suggest that cormorant reproductive success may be intimately linked to Alewife populations.

Interestingly, the DFC for both adult birds and chicks was higher in 2000 than in 2001, and therefore, so was the biomass of prey necessary to raise a chick to fledging. In addition, DFC was shown to change as the breeding season progressed during both years in proportion to ACD of the diet. Yearly variations are due to the overall greater energy density of the diet in 2001, as compared to 2000. In essence, less prey were consumed per individual in 2001, but more chicks were successfully raised to fledging. This is reflected in the relatively modest increase of total prey biomass consumed in 2001, even with more chicks produced. From the model, it appears that comparing energy density of prey types consumed, and also prey availability, may be better parameters in forecasting of the number of chicks successfully fledged per year, as opposed to strictly relying on the number of nests.

In earlier works (Madenjian and Gabrey 1995, Hebert and Morrison 2003), there was an attempt to model the importance of non-breeding cormorants in the system, as well as the migratory seasons. This is not the case in this work. In the Beaver Archipelago, it was difficult to ascertain the population of non-breeders during the breeding season. When plumage patterns and gonad development (harvested birds only) were used to determine maturity, overall very few non-adults were documented in flocks and harvested birds (unpublished data). An exception to this was the post-breeding season, when some birds collected were fledglings. Better estimation of the number of non-breeding birds during the breeding season and the inclusion of migration would enhance this work. Further work is necessary to fully estimate the biomass of prey consumed by all DCCOs in the system.

As with the work of Madenjian and Gabrey (1995), better estimates of prey fish populations is necessary to fully understand the impact the breeding DCCOs and their young may have on these prey populations in the study area. Recently, an attempt has been made to estimate the population size of smallmouth bass (*Micropterus dolomieui*) in the study area (Seider 2003), although this species has not been documented as a prey item in cormorant diet (with the exception of one fish in 2000). However, there is little information regarding the availability of other species, which appear to be far more important in the DCCO diet, on a local level. This work was an attempt to better quantify the role of cormorants as predators on a local scale and how their impact may vary from year-to year; however, without better estimates of prey availability, understanding whether cormorants are exhibiting prey selectivity, as well as their ecological role, remains unclear.

In 2003, alewife was the most abundant prey fish in Lake Michigan with an estimated lake-wide biomass of 42.876 kilotonnes (kt) (kt = 1000 metric tones) (Madenjian *et al.* 2004). Given that alewife populations have remained relatively stable in recent years (Madenjian *et al.* 2004), Beaver Archipelago breeding DCCOs consumed approximately 1% of the available lake-wide alewife biomass in 2000, and approximately 1.6% in 2001, based on alewife consumption figures estimated by this work. In the last lake-wide waterbird survey in 1997, Beaver Archipelago cormorants comprised approximately 41% of the breeding DCCOs in Lake Michigan (Cuthbert *et* al. 1997). If this trend holds true presently, and all Lake Michigan breeding DCCOs have a similar diet, cormorants consumed an estimated 2.4% of the available lake-wide alewife biomass in 2000, and approximately 4% in 2001. None-the-less, it is possible that cormorants are functioning as important predators of alewife and other prey fish on a local scale within the Beaver Archipelago. However, it is also likely that predatory fish populations are consuming far more alewife and other prey biomass on an annual basis, both lake-wide and on a local basis (Madenjian and Gabrey 1995). Therefore, predatory fish may be far more important in influencing prey populations in Lake Michigan. In fact, long-term trends in alewife biomass suggest that salmonids were effective in reducing lake-wide alewife biomass from historical highs, and have also been effective in maintaining relatively low lake-wide alewife biomass over the last several decades (Madenjian *et al.* 2002). The Double-crested Cormorant is just one predator that, in synergism with other predators, as well as other ecological factors, contributes to overall Lake Michigan ecosystem functioning.

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Table1. Life history characteristics of Double-crested Cormorants used to model prey consumption by breeding adult and young birds in the Beaver Archipelago, 2000 and 2001.

Characteristic	**2000**	**2001**
Number of Nests (seasonal high)	8316	8096
Calories per egg [a]	75.4	75.4
Clutch Size – Early Season	2.60	2.89
Clutch Size – Mid Season	1.50	2.38
Number of Incubation Days [b]	28	28
Hatch Rate (% of eggs laid) [c]	62	62
Fledge (days) [b]	50	50
Fledged Rate (% of chicks hatched)	29	49
Hatch-year Mortality (% year) [d]	42	42
Breeder Mortality (% year) [e]	20	20
Mass at Hatch (g) [b]	34	34
Adult Mass (kg)	2.0	2.0

[a] Kendeigh et al. 1977

[b] Hatch and Weseloh 1999

[c] Blomme 1981

[d] Madenjian and Gabrey 1995

[e] Cairns et al. 1991

All other inputs were measured in the field by the authors

Table 2. Proportions of the biomass of individual prey items consumed by breeding adult and young cormorants for the pre-breeding/incubation, nestling and post-breeding time periods for 2000 and 2001.

	2000			2001		
Prey Item	Pre-nesting/ Incubation	Nestling	Post-breeding	Pre-nesting/ Incubation	Nestling	Post-breeding
Alewife (*Alosa pseudoharengus*)	0.49	0.54	0.22	0.22	0.81	0.70
Crayfish (*Orconectes* spp.)	0	0.24	0.36	0	0.02	0.05
Sculpin (*Cottus* spp.)	0	0.06	0.08	0.30	0.05	0.07
Nine-spine Stickleback (*Pungitius pungitius*)	0.01	0.01	0.01	0.38	0.01	0
Sucker (*Catostomus* spp.)	0.11	0.11	0.19	0.03	0.10	0.16
Spottail Shiner (*Notropis hudsonius*)	0.29	0	0	0.01	0	0
Other*	0.01	0.04	0.14	0.06	0.01	0.02

* This category may contain species that have proportions listed as "0" during that same time period.

Table 3. Average caloric density (kcal/kg) for prey species.

Prey Species	**Caloric Density (kcal/kg)**
Alewife (*Alosa pseudoharengus*) [a]	1.977
Crayfish (*Orconectes* spp.) [a]	1.077
Sculpin (*Cottus* spp.) [a]	1.493
Nine-spine Stickeback (*Pungitius pungitius*) [a]	1.493
Sucker (*Catostomus* spp.) [b]	0.884
Spot-tail Shiner (*Notropis hudsonius*) [b]	1.193

[a] From Cummins and Wuycheck (1971)
[b] From Bryan *et al.* (1996)

Table 4. Total DFC (daily food consumption) in kilograms for adults during each period of the breeding season for 2000 and 2001.

	2000	**2001**
Pre-nesting/Incubation Stage	0.55	0.55
Nestling Stage	0.55	0.48
Post-breeding Stage	0.65	0.51

Table 5. Total seasonal food consumption (kg) per pre-fledged and post-fledged chicks for 2000 and 2001.

	2000	**2001**
Pre-fledged Chick	9.0	7.9
Post-fledged Chick	26.0	20.4
Season Totals	35.0	28.3

Table 6. Sensitivity analysis results.

Model Input	**Input Perturbation Error** **+10%**	 **-10%**
Number of Nests	+10.0	-10.0
Adult Mass	+7.2	-7.4
Hatch Rate	+2.5	-2.5
Fledge Rate	+1.1	-1.1
Hatch-year Mortality	-0.8	+0.8
Breeder Mortality	-0.6	+0.6
Calories per Egg	0.0	0.0
Adult Assimilation Efficiency	-9.1	+11.1
Young Assimilation Efficiency	-9.1	+11.1
Energy Density of Prey (kcal/kg)	-0.1	+0.1
Mass at Hatching	0.0	0.0
Incubation Length (days)	-0.5	+0.5
Fledging Length (days)	-0.3	+0.3

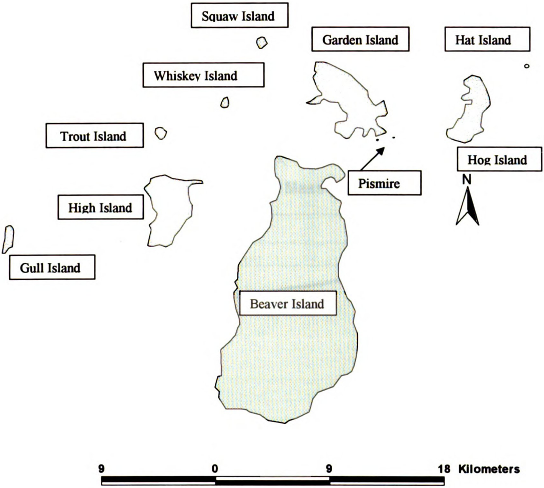

Figure 1. The Beaver Archipelago of northern Lake Michigan.

a.

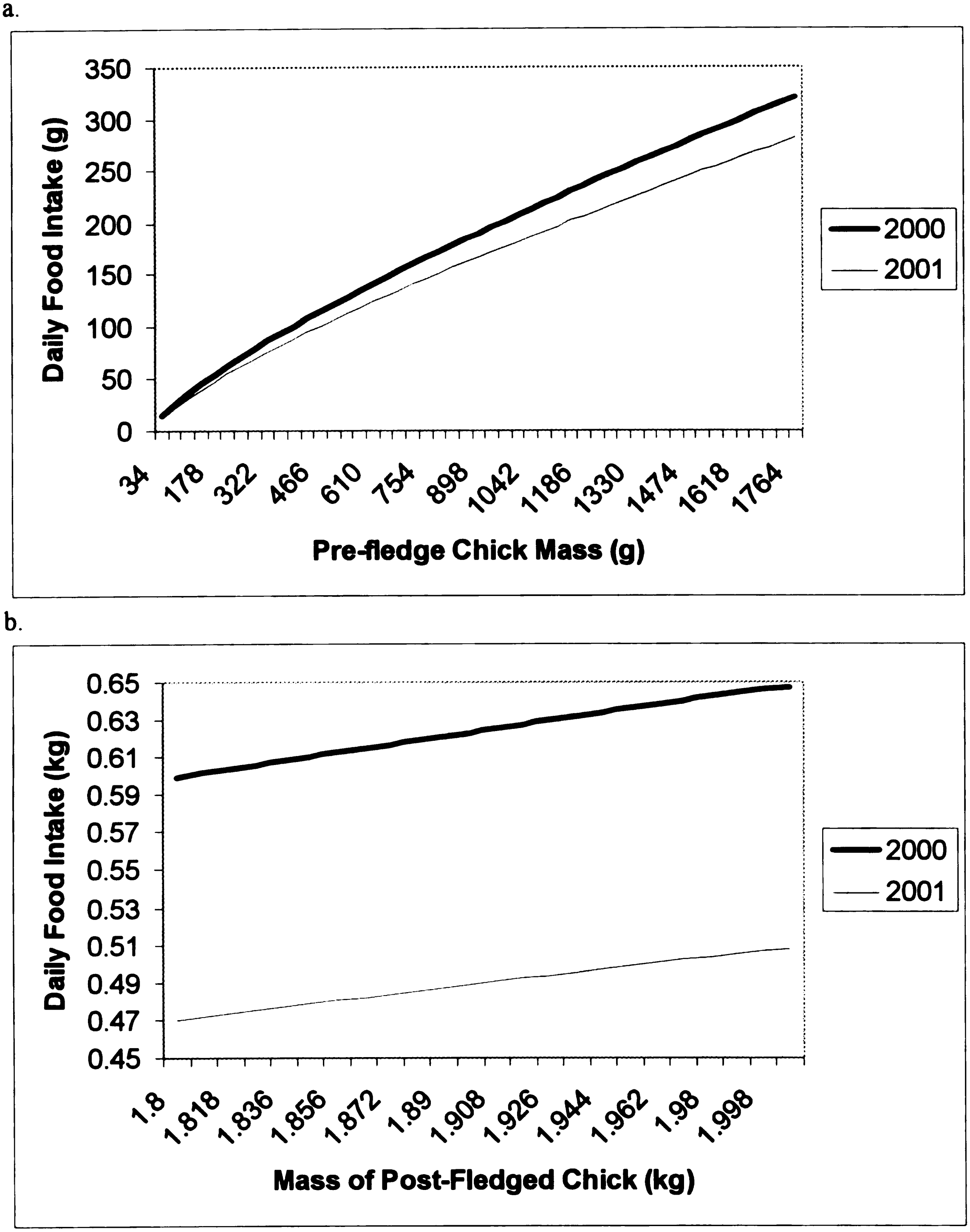

Figure 2. a) Daily food consumption (g) for pre-fledged chicks in 2000 and 2001, and b) daily food consumption (kg) of post-fledged chicks up to the time they attain adult mass in 2000 and 2001.

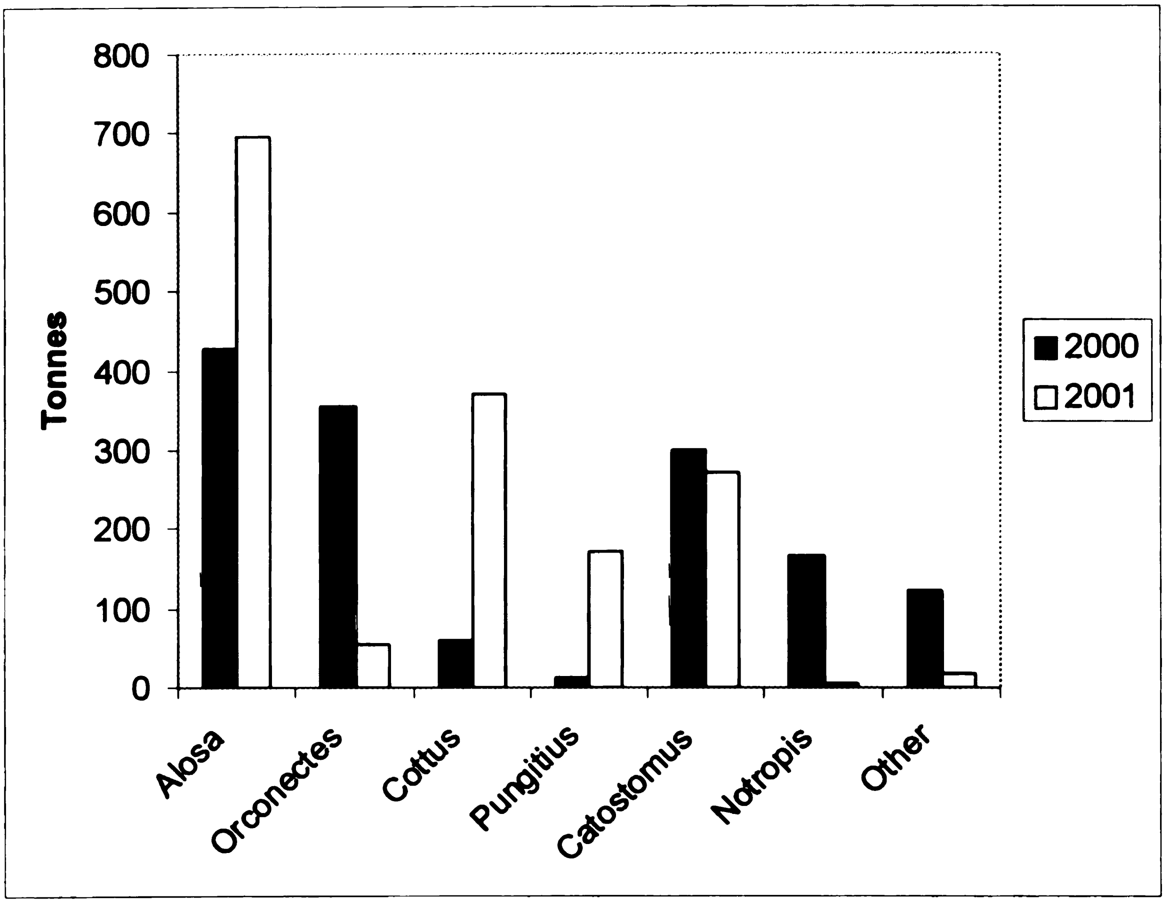

Figure 3. Biomass of prey consumed (tonnes) by breeding cormorants and their young in the Beaver Archipelago in 2000 and 2001.

CHAPTER 6

SIMULATION MODELS TO INVESTIGATE THE POTENTIAL IMPACT OF DOUBLE-CRESTED CORMORNANTS ON A SMALLMOUTH BASS POPULATION IN THE BEAVER ARCHIPELAGO, NORTHERN LAKE MICHIGAN

Abstract

As Double-crested Cormorant (*Phalacrocorax auritus*) populations have increased throughout the Great Lakes, many sport and commercial fish populations have declined. A high density of birds combined with their fish eating habits has led to their implication in these declines. From 1999 through 2002, a smallmouth bass (*Micropterus dolomieui*) population study was rekindled after a twenty plus year hiatus in the Beaver Archipelago. Then, from 2000 through 2004, there was an intensive study on the population dynamics and foraging ecology of breeding cormorants of the same area. These data, as well as literature values, were used to develop two types of simulation models, Rebuild and Forecast, to investigate a possible connection between the declining bass populations and the avian predators. Current data suggest that cormorants in the region feed primarily on forage fish and crayfish. However, the Rebuild models were designed to investigate what levels of cormorant predation were necessary to cause a bass decline. Forecast models were constructed to determine whether low levels of predation by cormorants could impact present bass populations and what the future may hold for this fishery. Rebuild models indicate that is was unlikely that cormorants alone caused the observed bass decline; birds may have contributed to the decline in synergism with low recruitment, angling mortality or other factors. Forecast models suggest that direct cormorant predation on bass is not currently the leading factor limiting the bass population size in the region, even if bass are experiencing relatively low recruitment. Together, these models enhance our understanding of the relationships between cormorants and fish populations in the study area and may benefit fisheries managers in other systems.

Introduction

Over the past several decades, the population of Double-crested Cormorants (*Phalacrocorax auritus*), or DCCO, in the Great Lakes Basin has increased (Ludwig 1984, Cuthbert *et al.* 1997, Ludwig and Summer 1997, Wires *et al.* 2001). The revival of cormorant populations has been no less pronounced in the Beaver Archipelago where, as of 1997, they were estimated at 11,709 breeding pairs, or almost 39% of the nesting DCCO pairs within Michigan waters of the Great Lakes (Cuthbert *et al.* 1997, Ludwig and Summer, 1997) and over 41% of the Lake Michigan breeding population (Cuthbert *et al.* 1997). Although populations and reproductive success has varied over the past several years, the Beaver Archipelago has continued to support an abundant breeding population of cormorants (Seefelt and Gillingham 2004a).

Cormorants are opportunistic fish predators that often feed in shallow waters (Lewis 1929, Birt *et al.* 1987) and breeding birds remain relatively close to breeding colonies when foraging (Custer and Bunck 1992). The high density of birds combined with their observed fish eating behaviors have led to their implication in declines of both commercial (Ludwig *et al.* 1989, Neuman *et al.* 1997) and recreational fisheries throughout the Great Lakes region (Lantry *et al.* 1999; Neuman *et al.* 1997). Although cormorants may have only small and localized effects on fish populations during migration (Kirsch 1995), it has been demonstrated that these birds may deplete fish prey around breeding colonies in marine systems (Birt *et al.* 1987). Because many of the fish populations of concern around cormorant colonies in the Great Lakes have already experienced significant declines before they were studied, scientists find it difficult if not impossible to identify the actual mechanism(s) (predation vs. recruitment failure) behind fish population declines (Draulans 1988, Cairns 1992, Hatch and Weseloh 1999).

The Beaver Archipelago, and particularly the habitat around Garden and Hog Islands, has been considered in the past to have excellent smallmouth bass (*Micropterus dolomieu*), or smb, fishing, and this evaluation has been published in the national media a number of times (Robinson 1995). Cormorants have been documented to feed on smb in the Great Lakes (Blackwell *et al.* 1997, Neuman *et al.* 1997, Johnson *et* al. 1999, Schiavone 2001, 2003), with a few records of bass found in DCCO diet in the Beaver Islands (Ludwig *et al.* 1989). However, smb has not been documented as an important prey item in cormorant diet in the past (Ludwig *et al.* 1989) or more recently (See Chapter 3). Yet, recent smb population estimates in the Beaver Archipelago indicate that bass have declined (Seider 2003). Compared to similar data gathered by researchers in the study area in the late 1980s, the smb population has declined by 75-80% (Seider 2003). Although it is quite clear that there has been a decline in the Beaver Archipelago bass fishery, the role of cormorants may have played in this decline has remained uncertain.

Overall, it has been shown that cormorants have only small effects on open water fish species (Weseloh and Casselman 1992, Madenjian and Gabrey 1995, Hatch and Weseloh 1999). However, exactly how this impact has been documented is an area of controversy. In terms of direct impact, dietary studies have concluded that cormorants, at least in most systems, eat too few fish of commercial and/or sporting value to impact these species. Cormorant diets, instead, usually include species that are of little commercial value, but these same species may be important to community trophic dynamics (Craven and Lev 1987). This has led some to hypothesize that the increase of cormorants in some systems, feeding primarily on forage fish, may be a consequence of diminished predatory fish stocks as opposed to the factor leading to the decline of these stocks (Hatch and Weseloh 1999). In addition, it has been hypothesized that cormorants may have a secondary effect on sport fisheries by competing with desired species for forage fish. Although the effects on forage fish numbers may be limited and only occur in localized areas (Madenjian and Gabrey 1995), this combined with direct sport fish depredation may impact sport fish distributions and/or numbers.

Several studies in the Great Lakes have attempted to determine if cormorants do have a secondary impact on predaceous fish. In Lake Ontario, cormorants were estimated to consume <1% of the available forage fish, as compared to 13.3% taken by salmonids in the early 1990s (Madenjian and Gabrey 1995). Similarly, in the early 1990s in Lake Erie, cormorants were estimated to take <2% of the biomass of forage fish consumed by walleye (*Stizostedian vitreum*). Other predators (including mergansers and gulls) ate more fish than cormorants (Weseloh and Casselman 1992). This evidence implying a very minor impact of cormorants may be misleading because of scale. Both of these studies are lake-wide estimates, as opposed to local. Some may argue that the impact cormorants may have on local forage fish is much greater and these local changes do influence local populations of sport/commercial species. To date, there are few data available regarding the relationship between fisheries and cormorants in Lake Michigan.

Several studies have been conducted investigating the influence of fish-eating birds on fisheries both in Europe (Suter 1995, Warke and Day 1995) and in the Great Lakes (Maruca 1997, Neuman *et al.* 1997, Schiavone 2001, 2003). Research suggests that waterbirds play central roles in marine food webs (Cairns 1992), and this probably holds true in Great Lakes community dynamics. In order to get a realistic picture of the impact bird predators have on fish populations, it is necessary to incorporate quantitative data collected on diets, population size, and energy requirements of cormorant populations. In addition, reliable data on the population size, appropriate spatial and temporal dynamics of the fish populations are also necessary (Draulans 1988).

Breeding DCCOs may have some impact on local smb populations in the Beaver Archipelago, even if predation rates are relatively small. Interspecific competition may also occur between cormorants and bass in the study area, but it is beyond the scope of this study to explore the possible importance of competition. The predation models developed here build on previous and ongoing investigations to address the dynamics of cormorants and smb populations in the Beaver Archipelago. Since it is currently impossible to directly quantify the role of cormorant predation in the documented decline of the smb population, models were developed that permit the quantitative analysis of existing data on fish and cormorant populations in the study area. The first of these models determines what level of DCCO predation was necessary to simulate the documented decline in smb in the Beaver Archipelago, and whether the implied resulting contribution to cormorant diet is consistent with what was documented historically regarding bird diet. The second model simulates future population dynamics of the smb population based on what has been currently known about the diet of breeding archipelago birds. This opportunity for gaming and data exploration through modeling may enhance our understanding of the relationships between smb and cormorant populations in the Beaver Archipelago of northern Lake Michigan.

General Methods

Study Area

The Beaver Archipelago of northern Lake Michigan consists of about ten islands. Four of the larger islands (Gull, Hog, Whiskey and Hat Islands) and two small islands (Pismire Island and SE Garden Island) contained nesting colonies of DCCOs at some time between in 2000 and 2004 (Figure 1). These same sites, with the exception of SE Garden, have shown some activity over the past several decades (Cuthbert *et al.* 1997). The Hog Island colonies were located on two peninsulas known as Grape Spit, on the west side of the island, and Timm's Spit, on the east side of the island. In any given year between 2000 and 2004, there were typically four or five sites active simultaneously, however the number of birds per site fluctuated greatly (Seefelt and Gillingham 2004b). The primary bass habitat in the region is centered in near-shore waters of Garden and Hog Islands, as well as Paradise Bay -St. James Harbor, Beaver Island (Seider 2003). Because of this, only cormorants nesting in the Main Archipelago, which is defined as all breeding sites except those at Gull Island, are considered in this work.

Basic Model Description

Age-structured models were created to simulate the smb population dynamics, as conceptualized in Figure 2. In each model, the bass population was divided into six age classes: age-0 (young of the year or YOY), age-1, age-2, age-3, age-4 and adult. In general, fish in each age class could proceed to the next age class, terminating as adults, or could die, each year. Fish could remain in the adult age class for several years; adult bass in the area have been documented to reach greater than ten years of age (Seider

2003). According to Latta (1963), who studied smb in northern Lake Michigan including a portion of the Beaver Archipelago, male bass mature at age four or five, while females mature at age five or six, in this region. This same trend is seen in northern Lake Huron (Fry and Watt 1957, Watt 1959). Immature fish, ages zero through three, were vulnerable to cormorant predation in all simulations; age-4 fish were vulnerable to predation in most simulations. Adult fish, defined as fish five years old and greater, are typically at least 29.58 cm (11.65 inches) (Seider, unpublished data) and of greater length than the typical prey of cormorants in the area. Alewife (*Alosa pseudoharengus*), an important prey item for cormorants in the area, average between 12 to 13 cm (4.7 to 5.1 in), as determined by dietary analysis (unpublished data).

These age-structured models were constructed using STELLA 7.0.3 (High Performance Systems, Inc.). Models operated with monthly time steps. At the start of June adults produced eggs and these recruited as age-0 at the start of July according to:

$$N_{0,y,7} = \alpha ERN_{5,y,6}$$

Here $N_{a,y,m}$ represents numbers of smb of age a (5 is used for adults) in year y at the start of a month m (1=January, 2=February, ...). α is a spawning constant representing the proportion of eggs that survive to age-0 at the start of July, when they are potentially vulnerable to DCCO predation. E is the eggs produced per clutch and R represents the proportion of adult fish that are females that successfully produce a clutch of eggs.

Fish of all ages (excluding eggs) that survived to the start of June were advanced to the next age at that time. The proportion of fish dying of an age category in a given month and year is $\gamma_{a,y,m}$. Thus, the numbers of fish at the start of a month for ages 0 through 4, other than for age-0 in July (recruitment) is given by:

$$N_{a,y,m} = N_{a,y,m-1}\,(1 - \gamma_{a,y,m-1}) \qquad m \neq 1,7$$

$$N_{a,y,1} = N_{a,y-1,11}\,(1 - \gamma_{a,y-1,11})$$

$$N_{a,y,7} = N_{a-1,y,6}\,(1 - \gamma_{a-1,y,6})$$

and the number of adults is given by:

$$N_{5,y,m} = N_{5,y,m-1}\,(1 - \gamma_{5,y,m-1}) \qquad m \neq 1,7$$

$$N_{5,y,1} = N_{5,y-1,11}\,(1 - \gamma_{5,y-1,11})$$

$$N_{5,y,7} = N_{5,y,6}\,(1 - \gamma_{5,y,6}) + N_{4,y,6}\,(1 - \gamma_{4,y,6})$$

Mortality was set to zero for all ages for January through April, and for September through November. For age-0 through age-4 the only source of mortality during May through August was from DCCOs. Although, adults did not suffer DCCO mortality in any of the models, in some model runs they suffered mortality due to sport fishing from June through August (younger fish were not vulnerable). All ages suffered "background" natural mortality in December. Because background natural mortality occurred at the end of the year when other mortality sources were not operating, and because sport fishing and DCCO predation impact different age categories, a given age category suffered mortality from only a single source during a given month.

These models, as implemented in STELLA 7.0.3, facilitated calculations that allowed for random variation in mortality rates. For models where mortality rates did not vary randomly, mortality due to sport fishing or DCCOs took the same value in all months for which it was non-zero. For scenarios where these rates varied randomly they were drawn from the same uniform distribution (defined by lower and upper bounds) for each month within a year for months they took non-zero values. Mortality rates (or the bounds for their uniform distributions) varied among ages in different ways in different simulation scenarios, and in some cases rates (or bounds for the uniform distributions) varied among years. Although models calculate population estimates for all age classes, output results are focused on adult bass populations; these fish are the fishable population and of the greatest interest to the public and resource managers.

Models are based on site-specific data collected in the Beaver Archipelago, as well as literature values. The bass population estimates used in the models are from Lennon (unpublished data) and Seider (2003). Mark and recapture data from the field were used to determine smb population estimates using the Schnabel method. Unfortunately, the gear used in the field was only accurate in capturing age three fish and older. The number of age-0, age-1 and age-2 fish, were determined using back calculations based on natural annual mortality rates, as well as from population estimations from other studies in similar Lake Michigan habitats (Latta 1963) and Lake Huron habitats (Fry and Watt 1957, Watt 1959). In addition, due to a lack of good estimates in some locations in the Main Archipelago, the bass population estimates of Garden Island Harbor (GIH), which is the largest population, were used in modeling efforts. This harbor is also considered to have some of the best bass habitat in the archipelago (Robinson 1995). Using GIH population estimates under-represents the total number of smb in the Main Archipelago; in actuality, if all sites are considered, there are more bass present in the archipelago then depicted in these models. Still, the Schnabel method requires closed populations; therefore, each field site was considered separate in the fisheries data set obtained for these modeling exercises and no immigration or emigration occurs. Figure 3 shows the smb population estimates in GIH beginning in 1972 and ending in 2002. Cormorant population data used in these models were obtained from actual nest counts of breeding birds (Ludwig 1984, Cuthbert *et al.* 1997, Scharf and Shugart 1998, see Chapter 3) (Figure 4).

Models required annual natural mortality rates in the absence of cormorant predation. An instantaneous natural mortality rate of 0.47, based on thirteen populations of smb populations in Michigan (Beamsederfer and North 1995) was converted to an annual natural mortality rate (0.3746). In some variations of the models, annual natural mortality rates were allowed to vary randomly within a specified uniform distribution, in order to simulate more natural conditions. The bounds of the uniform distribution were 0.3297 and 0.4288, based on instantaneous mortality rates from twenty-seven smb populations from Ontario and thirty-one smb populations from Wisconsin, respectively (Beamsederfer and North 1995).

Another important input into these models was recruitment. Three parameters were used to determine recruitment in these models: spawning constant, the spawning population and the number of eggs per clutch. Only spawning constant (the proportion of eggs spawned in June that are recruited into the YOY population in July when these fish are first vulnerable to cormorant predation) was allowed to vary in any of the simulations. Both the spawning population (the proportion of the total adult population that are spawning females in a given year) and the number of eggs per clutch (number of eggs produced by each spawning female each year) are constant in all models. The values used for these two parameters were consistent with spawning information found in the literature (Latta 1963, Raffetto *et al.* 1990).

Rebuild Model

Baseline Model Description

The first simulation model, Rebuild, reconstructed the bass population at the beginning of 1988 (as determined from estimated values at the end of 1987) and simulates the decline in the smb population by 1999. In this deterministic model, all parameter values were set as constants (Table 1).

All immature age classes (age-0 through age-4) were subject to the same DCCO predation rate of 0.145 in this model. This means that each vulnerable age class suffered equal DCCO predation pressure, as determined by a proportion of each age class available to birds each month (henceforth referred to as "equal predation"). Cormorant predation was modeled to occur only in May, June, July and August, which represented the breeding season for these birds in the study area.

The smb literature provided a range of possible values for many of the model parameters. For the Baseline Rebuild Model, parameter values that would most limit the smb population size and cause the population to be most sensitive to cormorant predation were selected. This was done to construct a more sensitive model that produced "worst case" scenarios for a smb population under the influence of DCCO predation. One parameter, spawning constant was given a low value (0.10). This value represents low recruitment levels that could be caused by Lake Michigan ecological factors (water temperature, habitat reduction, etc.), intraspecific or interspecific competition, and/or a catch and release fishery during the spawning season. Catch-and-release angling can physically stress smb (Schreer *et al.* 2001), which can lead to nest abandonment (Kiefer *et al.* 1995, Ridgway and Shuter 1997), and therefore, negatively impact nesting success of smb (Philipp *et al.* 1997). Loss of the male from the nest site could potentially lead to the loss of eggs and fry.

In the Baseline Rebuild model, the adult population was not subject to angling mortality. According to recent creel surveys, few adult fish are harvested from the study area (Seider 2003), although catch-and-release fishing does occur. In addition, although angling has occurred historically in the study area (Robinson 1995), there is no information regarding the number of adults harvested in the past.

Baseline Model Analysis

Model output from STELLA 7.0.3 was imported into Microsoft Excel for analysis. Initially, an adult population graph was constructed that simulated the smb decline in the study area. In addition, model output for the number fish of each age class removed by cormorants was converted to biomass, based on age-length estimates of smb in the study area (Seider 2003), and mass-length relationships for smb given by the following equation (Schneider *et al.* 2000):

$$\log W = -4.91466 + 3.02635(\log L)$$

Where W is mass in grams and L is total length in millimeters. The total biomass of bass removed each year could then be calculated, based on the number of bass in each age class, each month, removed by cormorants each year.

Using cormorant bioenergetics data (see Chapter 5), the proportion of cormorant diet by biomass composed of smb could be determined. Initially, these data were examined using the entire Main Archipelago DCCO population. The total daily energy intake (DEI) (kcal) provided by smb in the cormorant diet over the entire season was found by multiplying the mass (g) of bass consumed each year by a conversion factor (1.493 kcal/kg) (Cummins and Wuycheck 1971). This resulting value was then divided by cormorant total DEI, to yield the proportion of the diet, by biomass, composed of smb. Baseline cormorant population level DEI from 2000, was used to determine cormorant DEI for each year (see Chapter 5). These are proportions based on the number of birds each year as compared to the number of birds in 2000. The bioenergetics data from 2000 were used because this year appears to represent a typical year in terms of cormorant energy demands and reproductive output (see Chapter 3 and Chapter 5).

In addition, percent biomass smb provide to the DCCO diet was examined using Pismire and Grape Colony birds only. These birds reside relatively close to prime smb habitat, especially GIH, as compared to Hat Island birds, and have a greater potential to impact GIH bass. It has been documented that DCCOs remain close (typically within 2 – 4 km) to their breeding colonies when foraging (Custer and Bunck 1992, see Chapter 4). Percent biomass was calculated using the same method described above, however the total DEI for each year was determined based on the proportion of birds nesting at Pismire and Grape as compared the remainder of the Main Archipelago. These proportions are based on site-specific estimates, when possible, or extrapolated from the total Main Archipelago estimates using average proportions when necessary.

Baseline Model Results

The Baseline Rebuild Model resulted in an adult population that initially increased and then showed a steady decline to the estimated population size measure in the field (Figure 5a). The percent biomass of bird diet composed of smb for all Main

Archipelago DCCOs and for Pismire and Grape colony birds only is shown in Figure 5b. The percent biomass smb comprise in cormorant diet show high initial values, when bird numbers are beginning to increase, but then decrease and stabilize, as the bass population declines and DCCO population grows.

The Baseline Rebuild model does simulate the population decline of smb that was observed and estimated by fisheries biologists. According to this simulation, the population decline could have resulted from cormorant predation if other population parameters such as annual natural mortality were similar to other Michigan populations and if the spawning constant (a measure of how many eggs spawned in June are recruited as YOY in July), and therefore recruitment, is low throughout the length of the simulation. However, the implied contribution smb make to DCCO diet is larger then expected as compared to historical data (Ludwig *et al.* 1989) if the Pismire and Grape birds, who reside closest to the GIH bass population, are examined alone.

Forecast Model

Baseline Model Description

The second simulation model, Forecast, attempted to determine the future adult bass population size based on present conditions by running ten-year simulations beginning in 2002 and ending in January of 2012. Population sizes for each age class of bass were changed to reflect the estimated smb population size as determined by fisheries biologists in 2002 (Seider 2003). In this deterministic model, all parameter values were set as constants (Table 1), and most were set at the same values as used in the Baseline Rebuild model. Cormorant predation rate, however, was set as equal predation at 0.05

for all immature age classes for the duration of the DCCO breeding season. Although substantially lower than the value used in the Baseline Rebuild model, this predation level is actually higher then what is likely to have occurred in the field between 2000 and 2004, as based on cormorant dietary data (see Chapter 3). This value was used to simulate if low, but measurable, predation rates could influence the population size of immature bass.

Baseline Model Analysis

Model output from STELLA 7.0.3 was imported into Microsoft Excel for analysis. Initially, a graph was constructed that simulated the future trends of the adult smb population in the study area. Using model output for the number fish of each age class removed, the biomass of fish removed by cormorants was calculated using the same methods as described above.

Baseline Model Results

If cormorant predation pressure remains low, the Forecast Baseline Model predicts a recovery in the adult population size by end of the simulation, although some oscillation does occur (Figure 6a). This is in the absence of adult harvest by anglers, but does simulate what can occur in a catch-and-release fishery (limited recruitment due to spawning constant set at 0.10). In addition, as the number of adult bass increase, the biomass (kg) of immature smb consumed by cormorants also increases linearly over the simulation period (Figure 6b).

Sensitivity Analysis

Sensitivity analysis was performed to determine which model parameters were most influential in calculating the final population size of adult bass. Each Baseline model (Rebuld and Forecast) was analyzed individually. An individual parameter perturbation method was used (Bartell *et al.* 1986, Madenjian and Gabrey 1995). Twenty-one model inputs were examined for each model for a total of 42 simulations per model. For each sensitivity analysis simulation, only one model input was changed while all other parameters were left at their original values. A simulation was conducted for an individual model input by raising it from its original value by 10%; a second simulation was performed for that same model input by lowering its value 10% from its original value. The outputs from these simulations were compared to the original model's output to determine percent change.

Sensitivity analysis for the Baseline Rebuild revealed that YOY natural mortality, adult natural mortality, and changes in equal predation rates across all immature age classes combined, were most influential in determining final adult population size (Table 2). The other model inputs had relatively low impacts on model results, with changes in the initial population size of each age class showing the lowest impacts on final adult population size. Overall, the models were fairly robust in regard to some uncertainty in model inputs.

Sensitivity analysis for the Baseline Forecast revealed that YOY natural mortality was most influential in determining final adult population size (Table 3). Adult natural mortality had the second highest impact on final adult population size. Changes in equal predation rates across all immature age classes combined, spawning constant, number of eggs produced by each spawning adult, and the number of spawning adults, had similar impacts on model output. The other model inputs had relatively low impacts on model results, with changes in the initial population size of each age class and YOY predation by cormorants showing the lowest impacts on final adult population size. Overall, the models were fairly robust in regard to some uncertainty in model inputs.

Tests for Model Robustness

Rebuild Model – Simulation Experiments

The Baseline Rebuild model indicated that cormorant predation in combination with low recruitment may have resulted in the observed decline in the adult smb population. However, the proportion of DCCO diet composed of smb, by biomass, implied by the model in respect to cormorants of Pismire and Grape colonies, was higher than historical values (Ludwig *et al.* 1989). Here, alternative explanations for the smb decline are explored using variations of the Rebuild model. This includes a further investigation of recruitment levels, but also an examination of how angling mortality and changes in natural mortality could influence adult smb population size. In addition, these exercises further investigate the robustness of the Rebuild model.

First, several individual parameters were allowed to vary randomly within set upper and lower limits found in the literature. These parameters included annual natural mortality for bass age-1 to adult (varying between 0.3297 and 0.4288) (Beamsederfer and North 1995) and spawning constant (varying between 0.10 and 0.25). These spawning constant values are consistent with low recruitment levels in the literature (Latta 1963). During each of these simulations, only one variable was tested at a time. Changes in model output, in reference to the adult smb population, were minimal when compared to the Baseline Rebuild model.

The Baseline Rebuild Model was then modified to produce several variants. The first variation held all variables constant (Table 1) but excluded age-4 bass from predation mortality. It was necessary to increase the equal predation pressure by cormorants on the younger age classes in order to produce a similar decline in the adult smb population. Age-4 bass are rather large, averaging about 25 cm (9.8 in) (Seider, unpublished data). This prey size, as determined from actual dietary data obtained from regurgitates and harvested birds, is much larger than most prey taken by DCCOs in the region (Seefelt, unpublished data).

The second variation was an attempt to calculate what predation level by cormorants was necessary to drive the population down when all variables remained the same except spawning constant. A new value of 0.40 for the spawning constant was used to better represent an average natural recruitment of eggs into the YOY population, as measured in northern Lake Michigan by Latta (1963). This model was run twice; the first time included equal predation of all immature age classes and the second excluded age-4 fish from predation mortality while the other immature age classes suffered equal predation mortality.

The Baseline Rebuild Model was then modified to allow for varying cormorant predation rates across age classes. Initially, for each scenario described below, a control model was constructed, which allowed for varying conditions but were "seeded" with starting value in each varying parameter to produce consistent results. These control models were used to "tune" the Rebuild models to produce the documented decline in the smb population. For each of the following variants, thirty experimental simulations were run. In all scenarios, variable annual natural mortality rates for age-1 through adult fish were used to better replicate natural conditions (Table 4). In Scenarios 1 and 2, the spawning constant was also allowed to vary randomly within low levels. Main differences between these two models can be seen in the handling of cormorant predation pressure on the different age classes (Table 4). Scenario 3 allowed for greater variability in the spawning constant, thus allowing for stronger and weaker year classes. Predation pressure was modeled to be greater on younger age classes, which is more consistent with field data (Table 4). Scenario 4 examined what level of cormorant predation pressure would be necessary if smb showed average YOY recruitment levels more typical of those measure by Latta (1963). Again, younger age classes suffer greater mortality due to cormorant predation. In addition, age-4 bass in this scenario were not vulnerable to cormorant predation (Table 4).

The Baseline Rebuild model was modified to allow for angling mortality to influence adult population size. Angling mortality was allowed to occur on adult bass during June, July and August. The nominal value used was 10%, meaning that this percentage of the adult population present was removed each month during the angling period each year. Cormorant predation was modeled to occur on the immature age classes simultaneously with angling mortality on adult bass to produce the final adult population measured in the field. Angling mortality was raised to 20%, 30% and 40% and the consequential cormorant predation rate was determined for each simulation.

Finally, the influence cormorant predation was removed from the Baseline Rebuild model. Several parameters were examined individually to determine what other conditions may have resulted in a similar smb population decline. These parameters included increasing annual natural mortality rates of YOY fish, increasing the background annual natural mortality rates for ages-1 through adult fish, and increasing overall mortality of adult fish only. Each parameter was examined individually while all other variables remained constant.

Forecast Model – Simulation Experiments

First, annual natural mortality for bass age-1 to adult and spawning constant were allowed to vary randomly within set upper and lower limits in the Baseline Forecast model, following the same procedure used in testing the Baseline Rebuild model. In addition, the influence of randomly varying spawning constant (within set upper and lower limits) was also tested. Changes in model output, in reference to the adult smb population, were minimal in both variants when compared to the Baseline Rebuild model.

The Baseline Forecast model was modified to produce several different scenarios in order to investigate potential impacts cormorant predation may have on the future size of the adult smb population. In the first variation, the influence of cormorant predation rate on the size of the adult population at the end of the simulation was investigated. Simulations were run with the equal predation mortality, set at 0.075, 0.10, 0.15, 0.20 and 0.25 per month when birds are present, for each immature age class over the length of the simulation. All other variables remained unchanged. A second variation repeated these simulations, but set the spawning constant at 0.20, to simulate increased but still low recruitment rates, as compared to average literature values (Latta 1963). Currently, smb recruitment levels are unknown in the study area. In addition, a low spawning constant can also reflect the influence of a catch-and-release fishery, which has been shown to lower hatching rates in recruitment levels in smb (Philip *et al.* 1997).

The Baseline Forecast model was modified to investigate the impact of allowing the levels of cormorant predation to vary randomly between set limits for the duration of the simulation. Two different scenarios (referred to as Forecast Constant Predation Pressure Scenarios) were examined. Each also allowed for variable annual natural mortality rates and variable spawning constants, within set limits (Table 5). For each variant, a control model was first constructed to "tune" the model. Thirty simulations were run for each experimental model. Scenario 1 held cormorant predation mortality equal across all immature age classes (YOY through age four). Scenario 2 allowed for different cormorant predation rates for different age classes, with higher mortality rates for the younger age classes and no cormorant predation on age-4 fish (Table 5).

The Forecast Constant Predation Pressure Scenario 1 (described above) was then modified to examine how cormorant predation could influence the adult population size if birds increased their predation pressure on smb as the immature fish became more abundant in the system. In these variations, all simulations allowed for a bass population recovery beginning in 2002 and ending in 2007, but then modeled an increase in cormorant predation mortality beginning in 2008 through and ending in January of 2012 for immature age classes. Five simulations were run with progressively higher cormorant predation mortality rates beginning in 2008 (Table 6).

To further investigate the potential impact of increased cormorant predation mortality beginning in 2008, two stochastic models were developed, referred to as Forecast Increased Predation Pressure Scenarios (Table 7). As with those above, both scenarios allowed for the bass to recover through 2007 and then subjected the immature smb population to increased predation pressure beginning in 2008. As with earlier models, both were constructed with the same constraints on annual natural mortality and spawning constant (Table 7). In Scenario 1, the increase in cormorant predation mortality was held equal across all immature age classes (YOY through age-4). In addition, this model was constructed to produce a final adult population size that was roughly equal to the initial adult population size. Scenario 2 allowed for varying cormorant predation rates across age classes, with higher mortality for the younger age classes (Table 7). Scenario 2 was constructed to produce a final adult population size that was greater than the initial population size.

Experimental Simulation Analysis

All model output from STELLA 7.0.3 was imported into Microsoft Excel for analysis. Initially, for each Rebuild variant, adult population graphs were constructed for each model type using calculated means and standard deviations from experimental simulations. In addition, the percent of cormorant diet by biomass composed of smb was calculated using the method described for the Baseline Rebuild model. These proportions were calculated for all Main Archipelago breeding birds, as well as birds nesting on Pismire and Grape colonies only.

For Rebuild Models that simulated the influence of angling, the total number of adult fish removed by anglers was examined. In addition, the biomass (kg) of fish removed by cormorants was also calculated using the same methods as described above.

For each Forecast variant, adult population graphs were using calculated means and standard deviation from experimental simulations. In addition, the biomass (kg) of fish removed by cormorants was also calculated using the same methods as described above.

Experimental Simulation Results

When the Baseline Rebuild model was modified so that age-4 bass were invulnerable to cormorant predation, the adult population exhibits a higher peak population size before declining as compared to the original model (Figure 7a). It was necessary to increase cormorant predation mortality from 0.145 to 0.185 in this simulation in order to drive the adult bass population down. In this variant, the percent biomass smb comprise in cormorant diet show a high initial value, when bird numbers are beginning to increase, but then decreases and stabilizes, as the bass population declines and when the DCCO population reaches a larger size (Figure 7b). Removing age-4 bass from the diet of cormorants causes only a slight increase on the values of percent biomass of bird diet (Figure 7b).

Figure 8 shows the adult population trends of the modified Baseline Rebuild model where the spawning constant was reset to 0.40, both when age-4 bass are vulnerable to cormorant predation and when these fish are not vulnerable to cormorant predation, while all other variables remained same. Cormorant predation mortality was increased to 0.2175 and 0.27, respectively, in these simulations in order to drive the adult population down to estimated levels. Figure 9a shows the trends in percent biomass consumed by Main Archipelago birds when all immature fish are vulnerable to cormorant predation and when all immature bass except age-4 are vulnerable to cormorant predation. Figure 9b shows the same trends, but includes only Pismire and Grape DCCO colonies in the analysis. Here, the percent biomass consumed increases initially before declining. Removing age-4 bass from the diet of cormorants causes a slight increase the percent biomass consumed.

The population size of adult bass simulated in Rebuild Scenarios 1 and 2 followed the same general trend exhibited in the Baseline Rebuild model (Figure 10). As in earlier models, the percent biomass for both scenarios peaks initially and then declines (Figure 11). The percent biomass consumed by cormorants, when examining both Main Archipelago birds and Pismire and Grape birds alone, is similar but is initially slightly greater in Rebuild Scenarios 1 and 2, as compared to the Baseline Rebuild model.

The population size of adult bass simulated in Rebuild Scenarios 3 and 4 mirrors the general trend exhibited in the Baseline Rebuild model. The recovery in the mid 1990s of the adult population is not as pronounced in Scenario 4 as in Scenario 3 (Figure 12). As in earlier models, the percent biomass peaks initially and then declines, yet the percent biomass consumed by cormorants exhibits greater oscillations in Scenario 3 (Figure 13). The biomass consumed in Scenario 3 is initially greater when compared to the Baseline Rebuild model (Figure 13). In addition, the initial biomass consumed by birds in the Main Archipelago in Rebuild Scenario 4 is over three times greater than in the Baseline Rebuild model. When Pismire and Grape Colonies are considered alone, the biomass values obtained more than double in Rebuild Scenario 4 (Figure 13).

Angling has an impact on the cormorant predation pressure necessary to drive the adult smb population size down to observed estimated levels (Figure 14). When a 10%

angling rate is introduced in the model, the cormorant predation rate decreases to 0.1138 (from a baseline value of 0.145). As angling is increased to 20%, the cormorant predation pressure declines to 0.0957. At 30% angling, cormorant predation pressure required is 0.083, and at 40% angling, cormorant predation declines further to 0.735. The number of adult bass harvested over the duration of simulation varies from 988 bass at 10% angling rate to 2587 bass at 40% angling rate (Figure 15a). The corresponding biomass consumed by cormorants over the duration of the simulation period declines from 2507 kg, when angling is set at 10%, to 1859 kg when angling is set at 40% (Figure 15b).

In the absence of cormorant predation, a 0.99 mortality rate for YOY fish can drive the adult smb population size down to estimated levels when all other parameters remain unchanged (Figure 16). In addition, if natural mortality for age-1 through adult fish is increased to 0.535, the final resulting adult population is similar to estimated levels when all other parameters are unchanged (Figure 16). Finally, if adult mortality is increased to 0.885, the adult population shows a similar final population size when all other parameters remain unchanged (Figure 16).

The Forecast Baseline model predicts a recovery in the adult population size by end of the simulation. This is in the absence of adult harvest by anglers, but does simulate what can occur in a catch-and-release fishery (spawning constant set at 0.10). As cormorant predation increases, the resulting final adult bass population size decreases (Figure 17a). Simultaneously, the biomass (kg) consumed by cormorants shows a slight increase or stable trend at low levels of cormorant predation (0.05 and 0.075, respectively) (Figure 17b). As cormorant predation increases (0.10 to 0.25), the resulting biomass consumed declined by the end of the simulation because the smb population decline more than makes up for the higher per capita mortality rates (Figure 17b).

When the Forecast Baseline model is modified with a 0.20 spawning constant, the adult bass population shows a greater recovery as compared to the original model, but still shows the similar oscillation (Figure 18a). As cormorant predation increases, the resulting final adult bass population size decreases (Figure 18a). However, the bass population can withstand greater cormorant predation pressure before declining as compared to the original Forecast Baseline model. The trends in biomass (kg) consumed by cormorants are similar to the original model. However, biomass consumed increases over time at 0.05, 0.075 and 0.10 cormorant predation levels) (Figure 18b). As cormorant predation increases (0.15 to 0.25), the resulting biomass trend shows a decline (Figure 18b).

In the Forecast Constant Predation Pressure Scenario 1, experimental simulations show the same adult population trends when compared to the Baseline Forecast model (Figure 19a). However, the final adult population size is smaller in this variant. Overall, the biomass (kg) of immature bass consumed increases as the simulation progresses (Figure 19b). Bass biomass consumed in this scenario is greater than the Baseline Forecast model.

Forecast Constant Predation Pressure Scenario 2, in the experimental simulations shows similar adult population trends when compared to the Baseline Forecast model (Figure 20a). However, the final adult population size is smaller in this variant and the population appears to plateau in the latter portion of the experimental simulations. Overall, the biomass (kg) of immature bass consumed increases as the simulation progresses, but shows greater oscillation as compared to earlier Forecast models (Figure 20b). Bass biomass consumed in this scenario is greater than the Baseline Forecast Model.

When the Forecast Constant Predation Pressure Scenario 1 was modified to allow for increased predation pressure by cormorants as immature bass became more abundant, the resulting adult population varied relative to this predation pressure (Figure 21a). Predation levels were increased to vary from 0.05 to 0.10 or to vary from 0.10 to 0.15, the final adult population size was greater than the initial size. Levels of predation pressure that varied between 0.15 and 0.25, the final adult population size was roughly equal to the initial population size. Higher predation pressure by cormorants on immature smb caused an overall decline in final adult population size (Figure 21a). As predation pressure increased, the biomass (kg) of immature bass consumed by DCCOs increased. However, biomass consumption peaked and stabilized at predation pressures that varied between 0.20 to 0.30 and 0.30 to 0.40 (Figure 21b).

The Forecast Increased Predation Pressure Scenario 1 simulated an adult population that oscillated and then produced a final adult population size that roughly equaled the initial population size (Figure 22a). Biomass (kg) consumed by cormorants peaked when birds were first allowed to consume a greater percentage of immature bass. Biomass consumption then declined, but remained at greater values as compared to consumption values during the first six simulation years (Figure 22b).

The Forecast Increased Predation Pressure Scenario 2 simulated an adult population that oscillated, and then produced a final adult population size that was greater than initial population size (Figure 23a). Biomass (kg) consumed by cormorants increase when birds were first allowed to consume a greater percentage of immature bass. Biomass consumption then declined slightly, but then increased by the end of the simulation to the peak level observed (Figure 23b).

Discussion

The Rebuild models simulated the population decline of smb in the Beaver Archipelago of northern Lake Michigan that was observed and estimated by fisheries biologists. The variants developed from the original model indicated that several sets of conditions could lead to this decline. According to these simulations, the population decline could have resulted from cormorant predation if other population parameters such as annual natural mortality were similar to other Michigan populations and if the spawning constant (a measure of how many eggs spawned in June are recruited as YOY in July) was low. If the spawning constant was increased, a greater level of predation by cormorants was necessary to drive the adult population down. In addition, other factors such as angling harvest, increased natural mortality of YOY (low recruitment), or increased natural mortality of other age classes, could also cause this decline, combined with DCCO predation mortality. Furthermore, the smb decline could have resulted from substantial sport fishing or a period of relatively poor recruitment, without the influence of cormorant mortality. However, an increase in the annual natural mortality rates of age-1 and older fish alone are unlikely to explain the observed smb decline pattern, because the necessary increases would be very atypical.

Rebuild simulation models required that the relatively few birds present at the beginning of the simulations remove a relatively large number of bass (proportional to the entire bird diet) in order to cause the bass decline. As the cormorant population grows, the birds must continue to consume the same proportion of the immature smb population present even when the bass population is declining. In natural systems, this scenario is probably unlikely; cormorants are more like to feed on schooling species that are more abundant in the system (Hatch and Weseloh 1999).

The Forecast Models predict that, given current low predation pressure on immature smb by DCCOs, the adult bass population should increase over a ten-year period, even at low spawning constants, if annual natural mortality rates are similar to other regional populations. In these models, angling harvest was not simulated because currently few adult fish are thought to be harvested from the area (based on recent creel surveys). If birds respond to an increased availability of immature bass as the smb population grows by consuming a larger proportion of these fish, several different results are possible. With a relatively low spawning constant, simulations result in smb adult population growth at lower cormorant predation pressure, a return to initial adult population size at moderate cormorant predation pressure, or a decline in adult smb at higher cormorant predation pressure. However, if the spawning constant increases to levels documented historically in other regional smb populations, the adult population should show growth, even at higher cormorant predation mortality on bass ages YOY through two, and low to moderate predation mortality on age-3 bass. However, these models did not take into account whether a recovering bass population will renew interest in the fishery and attract more anglers. How this could influence the overall bass productivity remains somewhat uncertain. The models do suggest that increased angling would slow smb population growth; at moderate to high angling mortality, the smb population would remain small or even decline.

One purpose of the Rebuild Models was to explore the role cormorants might have played in the decline of the smb population in the Beaver Archipelago. Unfortunately, there are large gaps in the data sets, which adds uncertainty to these gaming exercises. However, model results regarding percent biomass can be compared to one study that included at least part of the study area. From 1986 through 1989, Ludwig *et al.* (1989) documented the food habits of DCCOs in the upper Great Lakes, including the Beaver Archipelago. Although the area considered the Beaver Islands in this historical work also includes an area outside the Main Archipelago, the Ludwig *et al*, (1989) work does document a few smb in DCCO diet. The methods involved only counting food items regurgitated during the handling of birds and estimating prey mass; few prey were actually collected and/or measured in this historical work. Sample sizes are comparably small, but this data set indicates that smb typically represent less than 1% of the biomass of prey items collected each year. In parts of northern Lake Michigan, it was estimated that smb could possibly represent up to 3% of the biomass of prey items collected in 1989; however, again, this is based on very few bass collected in a small sample (total number of food items equaled 286) and includes a larger area of northern Lake Michigan containing areas known for higher bass densities. Regardless, by estimated biomass, alewife, sucker (*Catostomos* spp.), and common shiner (*Notropis hudsonius*) are all more prominent in the samples collected (Ludwig *et al.* 1989). Because the exact study area is unclear, it is difficult to directly compare Rebuild Models to this historical work. However, it appears likely, based on percent biomass estimates from the models, that other factors (such as low recruitment, angling, etc.) may need to work in concert with cormorant predation to produce the observed decline. This is especially the case when Pismire and Grape birds, which are most likely to frequent known smb habitats, are considered.

A study from Green Bay and Lake Michigan waters surrounding the Door Peninsula and Washington Island, Wisconsin, documented spawning populations of smb (Kroeff 1996, 1997). Fish in these systems show similar life history traits to Beaver Archipelago smb, including age at first spawning (males as young as age 4) and longevity (reaching greater than ten years of age). According to Kroeff (1996, 1997), the spawning population appeared stable during the study period, however there were strong year classes (1987, 1989, 1991) and weak year classes (1990, 1992, 1997) present in the population. Weak year classes may have been a result of low nesting success (Kroeff 1996) or due to poor survival past the nest stage (Kroeff 1997). In addition, these smb populations did support a sport fishery at the same time. Interestingly, these smb populations resided in areas close to DCCO breeding colonies. In 1989-1990, there were at least five colonies in Green Bay, supporting 410 nesting pairs (Scharf and Shugart 1998). By 1997, there were fifteen active colonies in Green Bay with an estimated 7000 to over 9000 nesting pairs. The relationship between the smb populations and breeding cormorant populations is currently unknown. However, the bass population did appear to be relatively stable even as the cormorant population grew in the area.

Overall, models developed in this work support other studies that indicate that cormorants alone have a limited impact on fish populations in large systems (Weseloh and Casselman 1992, Madenjian and Gabrey 1995, Hatch and Weseloh 1999). However, other research suggests that cormorants may be impacting the smb population in the eastern basin of Lake Ontario based on bird diet analysis and fish population dynamics (Schneider *et al.* 1999, Johnson *et al.* 2001, Ross *et al.* 2003). In fact, beginning in 1992, the New York State Department of Environmental Conservation (NYSDEC) began focused research to determine the actual impacts DCCOs have on fisheries and other aspects of the eastern Lake Ontario ecosystems (Farquhar *et al.* 2003). This research, although still ongoing, has led to the implementation of a five-year management plan for U.S. waters of the eastern basin of Lake Ontario beginning in 1999. Management practices have focused on reducing the number of breeding pairs, and thus the predatory impact cormorants have on fishes, particularly species of commercial and sport value (Schiavone, 2003).

In Oneida Lake, New York, declining yellow perch (*Perca flavescens*) and walleye populations have been linked to cormorant predation (Rudstam *et al.* 2004). In this work, a long-term and very complete data series regarding fish populations in conjunction with records of cormorant expansion into the lake were used to investigate observed fish population declines. The authors admit that several other system-wide changes have also occurred in Oneida Lake, including the introduction of zebra mussels (*Dreissena polymorpha*) and a decline in gizzard shad (*Dorosoma cepedianum*). However, the analysis suggests that cormorant predation on yellow perch and juvenile walleye is a leading factor in the decline of the fisheries (Rudstam *et al.* 2004). Oneida Lake is a closed system where percids are the dominant fishes and there are few alternative prey for DCCOs. It is likely that in such a system, where the dominant fish providing an important sport fishery are also the most common species, that cormorants could influence the fishery. Rudstam *et al.* (2004) agree that the effects DCCOs have on fish populations in smaller inland lakes are probably greater than those in coastal and Great Lakes systems. In addition, in areas like northern Lake Michigan, the possible prey species available to cormorants are much more diverse and tend to include species of little direct sport or commercial value, especially alewives (See Chapter 3).

Currently, there is little evidence of cormorants having direct predatory impact on smb in the Beaver Archipelgao. Of 10,600 prey items documented in the bird diet in 2000 and 2001, only one smb was found (see Chapter 3); therefore, it is quite clear that currently cormorant predation is not a major contributing factor to the small population size of smb in the study area. Besides diet, other information recently gathered on cormorants in the Beaver Archipelago support that breeding birds probably have a limited impact on smb. According to both radiotelemetry work and the documentation of rafting locations, cormorants do not appear to be concentrating their foraging efforts in smb habitat during the breeding season, even though some of these areas are close to the colonies (see Chapter 4). Therefore, it is also unlikely that birds and bass are competing for the same food base as bass in the region. In addition, Seider (2003) cites that the growth rates and condition of bass in the archipelago have not declined in recent times as compared to the historical work.

Major habitat changes have also occurred in the study area over the past decade. Lake Michigan, as well as both lakes Huron and Superior, have been experiencing low water levels that rival record low lake levels recorded in 1926 and 1964 (NOAA 2003). This trend in lake level has occurred in the Lake Michigan-Huron basin over the past several years, with the highest rate in lake level reduction occurring between 1998 and

2000 (NOAA 2003). Such changes in lake level affect the shape and size of shoreline habitat, and have made some historical smb spawning habitat unavailable. Also, structure in these littoral zone habitats has also declined (personal observation). Finally, the introduction of many exotic species into the Great Lakes basin, in particular the zebra mussel, has also altered the Lake Michigan ecosystem, especially in reference to water clarity and changes in community trophic structure. Such changes in the ecology of the Beaver Archipelago may have impacted recruitment and/or other smb population variables.

The models developed here have several constraints. Although each was structured using real data in conjunction with literature values, these models cannot currently be verified or tested for validity. In addition, these models do not have density dependent processes built into their structure. Density dependent processes could theoretically have some impact on certain parameters, including the number of recruits per spawner and per capita mortality rates. Instead, in the models developed here, these parameters are generally constant or drawn randomly from the same distribution in different years, and not explicitly dependent upon smb density. In the study area, smb populations are small, especially when compared to historic data (Lennon, unpublished data, Seider 2003) and similar Great Lakes habitats (Fry and Watt 1957, Watt 1959, Latta 1963). Therefore, density dependent processes were not considered in model construction.

The biggest constraint on these models, however, is the lack of complete fisheries data. Data sets such as those used in Oneida Lake (Rudstam *et al.* 2004) are rare, especially in larger systems, such as the Great Lakes. In addition, it is entirely possible that an increase in the removal of bass by cormorants from the system did not occur until DCCO population size increased in the mid-1990s, as opposed to in the late 1980s when the cormorant population was smaller. But research in other Great Lakes systems indicate that the recent population growth of breeding cormorants across the region was probably linked to alewife availability (Hatch and Weseloh 1995), even though alewife lake-wide biomass estimates have declined from historical highs in the 1950s and 1960s (Madenjian *et al.* 2002). In 2003, alewives constituted an estimated 43% of the total prey biomass in Lake Michigan (Madenjian *et al.* 2004). In addition, it seems unlikely that increasing the number of bass consumed by birds would support such a growing cormorant population. Although cormorants are opportunistic, these birds appear to focus their foraging efforts on species that school in large numbers (Hatch and Weseloh 1995). Diet estimates in the region also indicated that Beaver Archipelago birds also focus on slow moving and/or bottom dwelling species such as crayfish (*Orconectes* spp.) and sculpin (*Cottus* spp.), but not smb (see Chapter 3).

The incorporation of additional, and perhaps more complete, smb population data from the Beaver Archipelago could have provided different modeling results. For example, from mark and recapture studies in the region, as well as information gathered from anglers regarding tagged fish, adult bass populations show immigration and emigration patterns between the archipelago and the northwest coast of Michigan's lower peninsula (Latta 1963, MDNR and Seider, unpubl. data). Besides predation, another factor that can influence northern smb populations is water temperature. Low water temperatures can impact spawning success (Latta 1963), winter survival of YOY (Toneys and Coble 1979), as well as the productivity and survival of older age classes (Fry and

Watt 1957, Beamesderfer and North 1995). Further investigation of other possible causes in the smb population decline such as habitat variables, poor recruitment, emigration – immigration rates, and/or other predators in the system are warranted in the study area. For example, although is has been documented that the smb population provided an important sport fishery during the period of population decline (Robinson 1995), there is little data available on the actual angling mortality. Even when the smb population was larger in the past, it was still relatively small compared to other regional populations and it is unlikely that the adult population could have supported high levels of angling pressure. In addition, how these factors have influenced bass recruitment in Great Lakes systems remains unknown. Regardless, it is possible that cormorant predation on bass in the Beaver Archipelago may have worked synergistically with other factors the produce apparent bass decline. However, it is most likely that direct predation on bass by birds is not currently limiting the smb recovery.

As stated, cormorants in the Beaver Archipelago do feed primarily on other prey species, specifically, alewife, which comprise much of the diet (see Chapter 3). Since alewife numbers can vary from year to year, it is important to further explore the relationship between cormorants and this prey species. Predation pressure on resident bass could change depending on the availability of alternate prey sources. Field data indicate that not only can the cormorant diet vary yearly, but also on a seasonal basis. However, other primary prey for DCCOs in the region appears to be crayfish, sticklebacks (*Pungitius pungitius* and *Culaea inconstans*), sculpin, sucker and johnny darter (*Etheostoma nigrum*). From diet data, it appears that these species are taken more frequently when alewife availability is lower (earlier in the bird breeding season) due to water temperature, or if the number of alewife available should vary year-to-year (See Chapter 3).

Currently, there is no long-term management plan for DCCOs populations in the Beaver Archipelago of northern Lake Michigan. The population of breeding birds in the region has declined and may have stabilized at lower levels as compared to 1997. It is also apparent from dietary data and other observations that, over the past five years, smb have not been an important prey item in breeding bird diet. Concurrently, there has been an effort to better manage the remaining smb population. Beginning in 2002, the opening day for the smb sport fishery was rescheduled in the archipelago to begin on 01 July each year in an effort protect the remaining spawning stock. The impact that this has had on the fishery remains unknown and warrants investigation. In other systems, such management schemes have had limited success in promoting reproduction due to illegal angling activity (Philipp *et al.* 1997).

Conclusions

Overall, the modeling reported here indicates that for cormorants to have a substantial influence on bass populations in the study area, they would need to consume greater numbers of smb then is consistent with limited diet information. Yet, DCCOs could have played a contributing role along with factors, such as low recruitment, angling, and higher natural mortality, in the smb decline. With such a large population of breeding cormorants in the system, it is unrealistic to assume that there is no predation on smb. However, over the duration of the recent cormorant diet study, bass were not found to be an important prey item in the diet of DCCOs.

The relationship between cormorant populations and fisheries will continue to be an important issue in the Great Lakes Basin and other systems around the world. This work helps to build an understanding of these dynamics, but in no way completely unravels the complexity seen in natural systems. Continued population monitoring of both smb and DCCOs in the area is necessary, as is continued collection of cormorant dietary data, in order to better understand the relationships in this predator-prey system. The diet of migratory and nomadic non-breeding birds that spend time in the Beaver Archipelago, and their subsequent impact on local prey populations, also warrants investigation. In addition, it is necessary to explore other potential factors such as low recruitment, past angling history, immigration and emigration rates, and ecological changes that may have impacted the smb population in the study area. With further development and the incorporation of accurate system specific field data, it may be possible to uncover the community dynamics that currently are not well understood. Understanding the influence breeding cormorant populations may have on local fish populations, including but not limited to the smb fishery, in the Beaver Archipelago could have applications in other systems.

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Table 1. Model Parameters for Baseline Rebuild and Forecast Models

Model Parameter	**Rebuild**	**Forecast**
Population Size:		
YOY [a, b]	8767	6867
Age One [a, b]	1285	1030
Age Two [a, b]	935	766
Age Three [c, d]	680	557
Age Four [c, d]	454	257
Adult [c, d]	226	270
Annual Natural Mortality Rate		
YOY [a]	.85	.85
Age One through Adult [e]	.3746	.3746
Spawning Population (proportion of the total adult population that are spawning females) [a, f]	0.125	0.125
Number of Eggs per Clutch [a]	5200	5200
Spawning Constant (proportion of eggs that are recruited to YOY population) [a, f]	0.10	0.10
Cormorant Predation (proportion of each age class removed each month of the breeding season)	0.145	0.05

[a] Latta (1963)
[b] Watt (1957)
[c] Lennon (unpublished data)
[d] Seider (2003)
[e] Beamesderfer and North (1995)
[f] Raffetto *et al.* (1990)

Table 2. Sensitivity analysis results for the Baseline Rebuild model showing the influence of each model parameter on the final adult smallmouth bass population size.

Model Input	**Input Perturbation Error**	
	+10%	**-10%**
Spawning Constant	+9.9	-9.7
Number of Eggs per Spawning Female	+9.9	-9.7
Number of Spawning Females	+9.9	-9.7
YOY Mortality	-51.6	+59.2
Age One Mortality	-6.7	+6.8
Age Two Mortality	-7.1	+7.2
Age Three Mortality	-7.6	+7.8
Age Four Mortality	-8.4	+8.7
Adult Mortality	-25.7	+35.0
All Cormorant Predation	-27.2	+39.2
YOY Cormorant Predation	-3.3	+3.3
Age One Cormorant Predation	-6.2	+6.7
Age Two Cormorant Predation	-6.6	+7.1
Age Three Cormorant Predation	-7.2	+7.8
Age Four Cormorant Predation	-8.0	+8.7
Population Size YOY	+2.2	-2.2
Population Size Age One	+0.7	-0.7
Population Size Age Two	+1.1	-1.1
Population Size Age Three	+1.6	-1.6
Population Size Age Four	+2.9	-2.9
Population Size Adult	+1.5	-1.5

Table 3. Sensitivity analysis results for the Baseline Forecast model showing the influence of each model parameter on the final smallmouth bass adult population size.

Model Input	**Input Perturbation Error**	
	+10%	**-10%**
Spawning Constant	+9.4	-9.4
Number of Eggs per Spawning Female	+9.4	-9.4
Number of Spawning Females	+9.4	-9.4
YOY Mortality	-53.1	+53.1
Age One Mortality	-7.8	+7.9
Age Two Mortality	-8.3	+8.6
Age Three Mortality	-9.0	+9.4
Age Four Mortality	-9.8	+10.3
Adult Mortality	-17.1	+20.8
All Cormorant Predation	-10.8	+12.2
YOY Cormorant Predation	-1.0	+1.0
Age One Cormorant Predation	-2.3	+2.3
Age Two Cormorant Predation	-2.5	+2.5
Age Three Cormorant Predation	-2.7	+2.8
Age Four Cormorant Predation	-3.0	+3.1
Population Size YOY	+3.9	-3.9
Population Size Age One	+1.1	-1.1
Population Size Age Two	+1.4	-1.4
Population Size Age Three	+1.5	-1.5
Population Size Age Four	+1.0	-1.0
Population Size Adult	+1.1	-1.1

Table 4. The parameters for the four different scenarios created from the Rebuild model that allow for varying cormorant predation rates across immature bass age classes. (Cormorant Predation Rate is the proportion of fish in each age class removed per month of the breeding season by birds.)

Scenario	Model Parameter	Lower Limit	Upper Limit
All	Annual Natural Mortality Rate		
	YOY	0.85	0.85
	Age 1 through Adult	0.3297	0.4288
1	Cormorant Predation Rate		
	YOY, Age 1, Age 2, Age 3	0.15	0.25
	Age 4	0.025	0.075
	Spawning Constant	0.10	0.25
2	Cormorant Predation Rate		
	YOY, Age 1, Age 2	0.15	0.35
	Age 3	0.05	0.12
	Age 4	0.05	0.10
	Spawning Constant	0.10	0.25
3	Cormorant Predation Rate		
	YOY	0.15	0.40
	Age One, Age 2	0.15	0.35
	Age 3	0.10	0.15
	Age 4	0.05	0.10
	Spawning Constant	0.10	0.40
4	Cormorant Predation Rate		
	YOY	0.30	0.50
	Age One, Age 2	0.27	0.40
	Age 3	0.05	0.05
	Age 4	0	0
	Spawning Constant	0.36	0.44

Table 5. The parameters used to construct the two Forecast Constant Predation Pressure Scenario models, where cormorant predation rates remain constant throughout the simulation. (Cormorant Predation Rate is the proportion of fish in each age class r removed per month of the breeding season by birds.)

Scenario	**Model Parameter**	**Lower Limit**	**Upper Limit**
Both	Annual Natural Mortality Rate		
	YOY	0.85	0.85
	Age 1 through Adult	0.3297	0.4288
Both	Spawning Constant	0.10	0.20
1	Equal Cormorant Predation Rate		
	YOY through Age 4	0.05	0.10
2	Cormorant Predation Rate		
	YOY, Age One, Age 2	0.10	0.20
	Age 3	0.05	0.10
	Age 4	0	0

Table 6. The cormorant predation mortality rates used in the modified Forecast Constant Predation Pressure Scenario models to examine how increased cormorant predation on immature bass due to greater bass availability could influence adult population size. (Cormorant Predation Rate is the proportion of fish in each age class removed per month of the breeding season by birds.)

Simulation	**Model Parameter**	**Lower Limit**	**Upper Limit**
All	Annual Natural Mortality Rate		
	YOY	0.85	0.85
	Age 1 through Adult	0.3297	0.4288
All	Spawning Constant	0.10	0.20
All	2002- 2007		
	Equal Cormorant Predation Rate		
	YOY through Age 4	0.05	0.10
1	2008 –2012 Predation Rate	0.10	0.20
2	2008 –2012 Predation Rate	0.15	0.25
3	2008 –2012 Predation Rate	0.20	0.30
4	2008 –2012 Predation Rate	0.25	0.35
5	2008 –2012 Predation Rate	0.30	0.40

Table 7. The parameters used for the construction of the Forecast Increased Predation Pressure Scenarios. (Cormorant Predation Rate is the proportion of fish in each age class removed per month of the breeding season by birds.)

Scenario	Model Parameter	Lower Limit	Upper Limit
Both	Annual Natural Mortality Rate		
	YOY	0.85	0.85
	Age 1 through Adult	0.3297	0.4288
Both	Spawning Constant	0.10	0.20
Both	2002-2007 Equal Cormorant Predation Rate		
	YOY through Age 4	0.05	0.10
1	2008-2012 Equal Cormorant Predation Rate		
	YOY through Age 4	0.15	0.25
2	2008-2012 Cormorant Predation Rate		
	YOY, Age One, Age 2	0.15	0.20
	Age 3	0.10	0.15
	Age 4	0.075	0.125

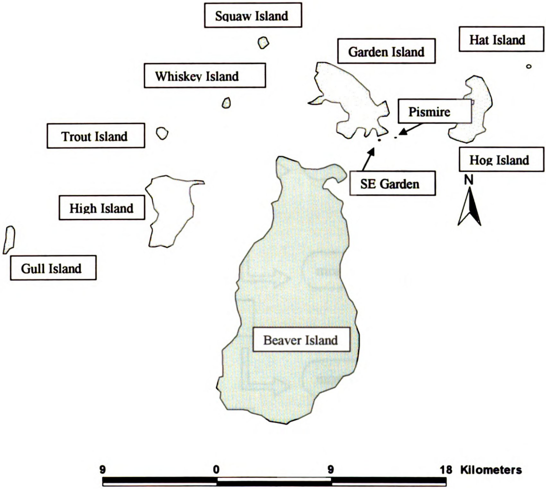


Figure 1: The Beaver Archipelago of northern Lake Michigan.

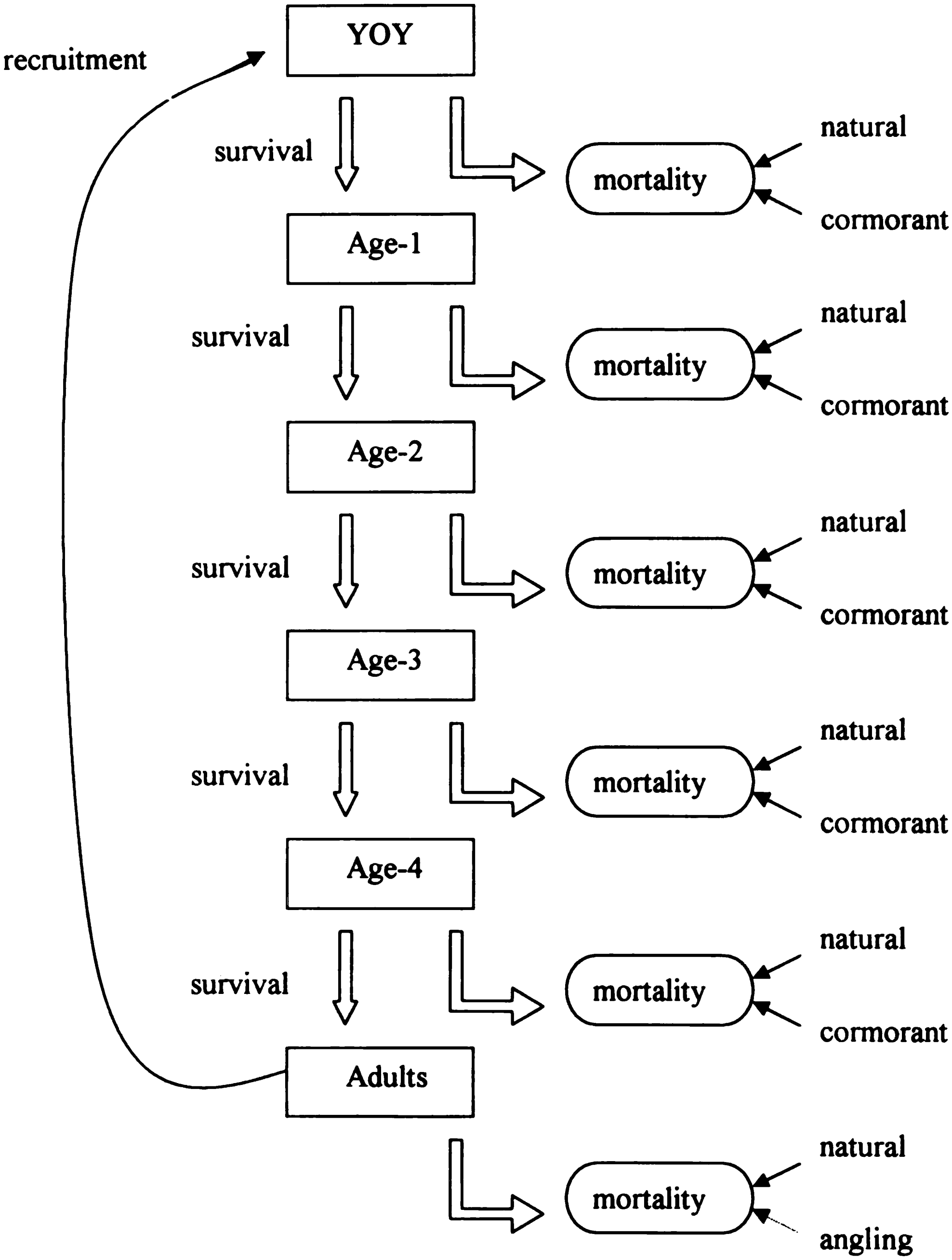


Figure 2: Conceptual model depicting the smallmouth bass population.

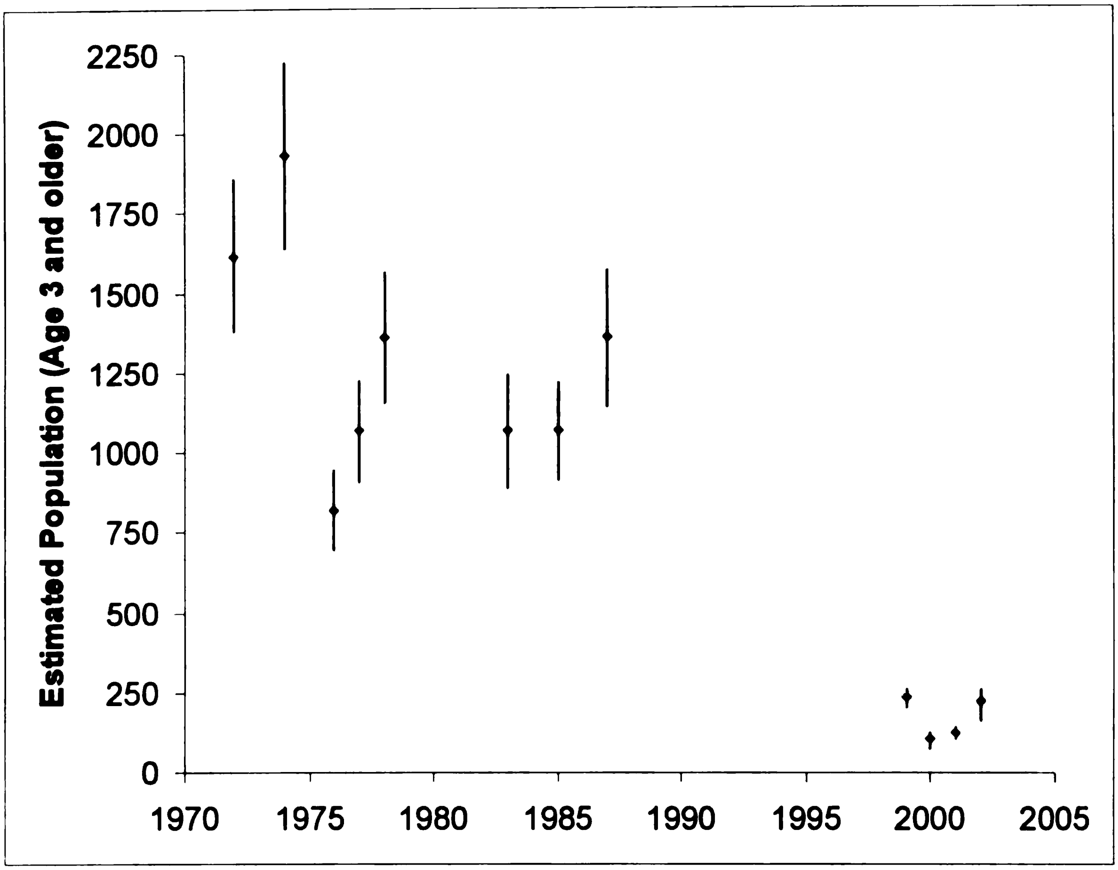


Figure 3. The population size of age three and older smallmouth bass in Garden Island Harbor as determined by the Schnabel method (with standard deviations). Estimates for 1970s and 1980s from Lennon (unpublished data) and later estimates from from Seider (2003).

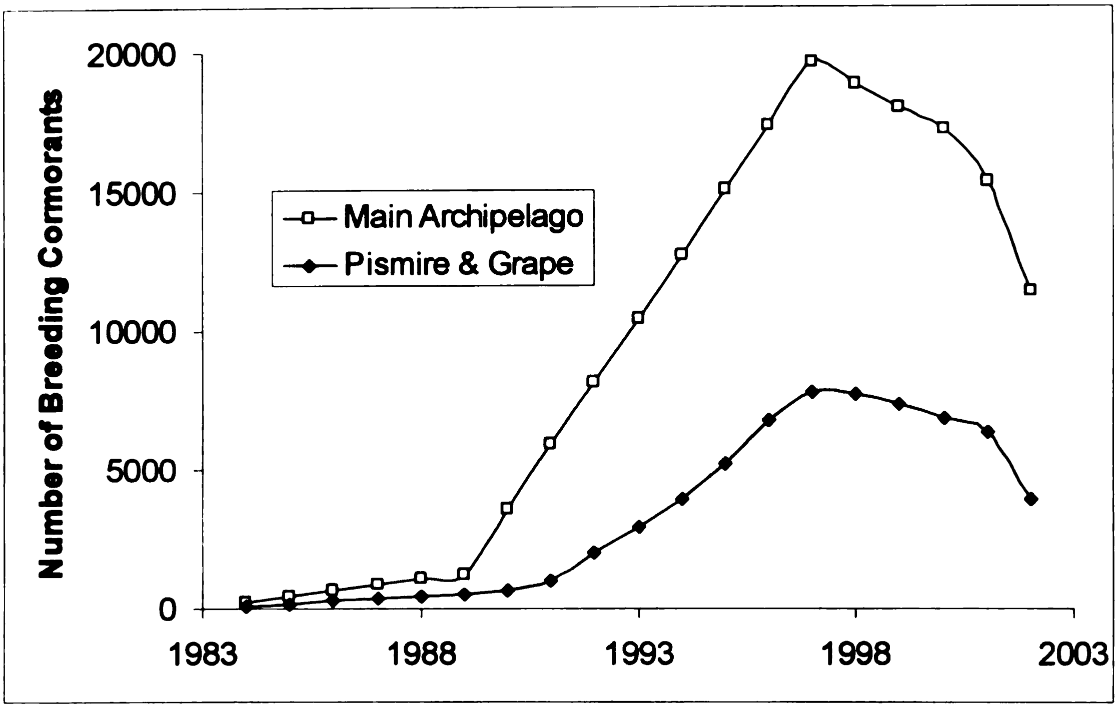
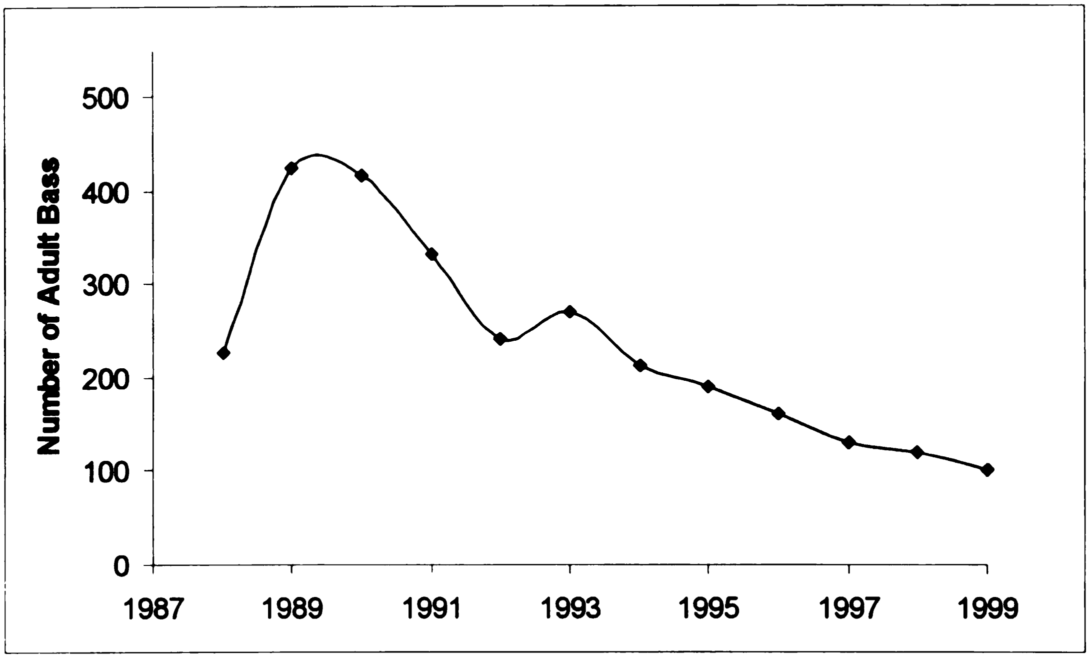


Figure 4. The overall trends in the population size of Double-crested Cormorants nesting in the Main Archipelago and when just Pismire and Grape colonies are combined. Curves are based on actual nest counts in 1984 (Ludwig 1984), 1989 (Scharf and Shugart 1993), 1997 (Cuthbert et al. 1997) and the current study (2000-2002).

a.



b.

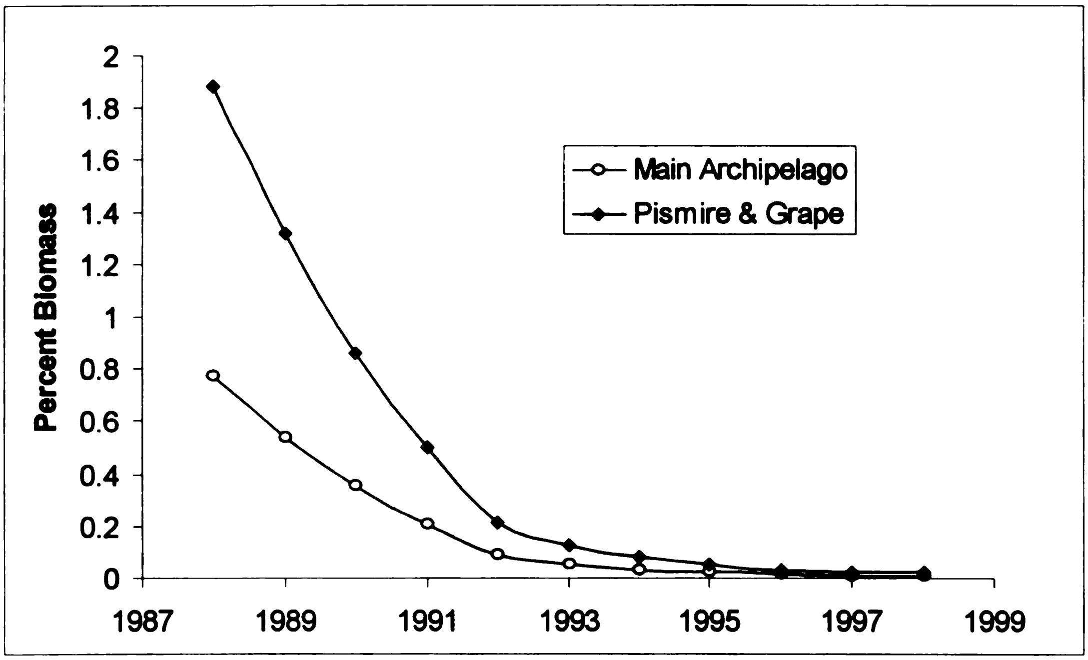
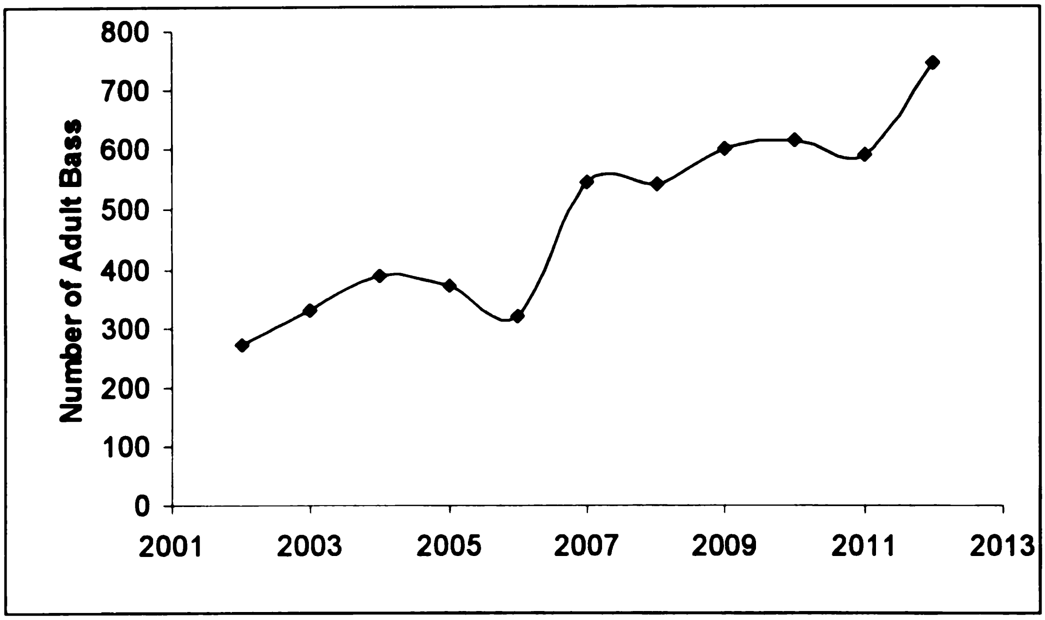


Figure 5. Results of the Baseline Rebuild model simulation showing a) the trends in the adult smallmouth bass population size and b) the percent biomass of bird diet composed of smallmouth bass for the entire Main Archipelago cormorant population and the Pismire and Grape colonies cormorant population alone.

a.



b.

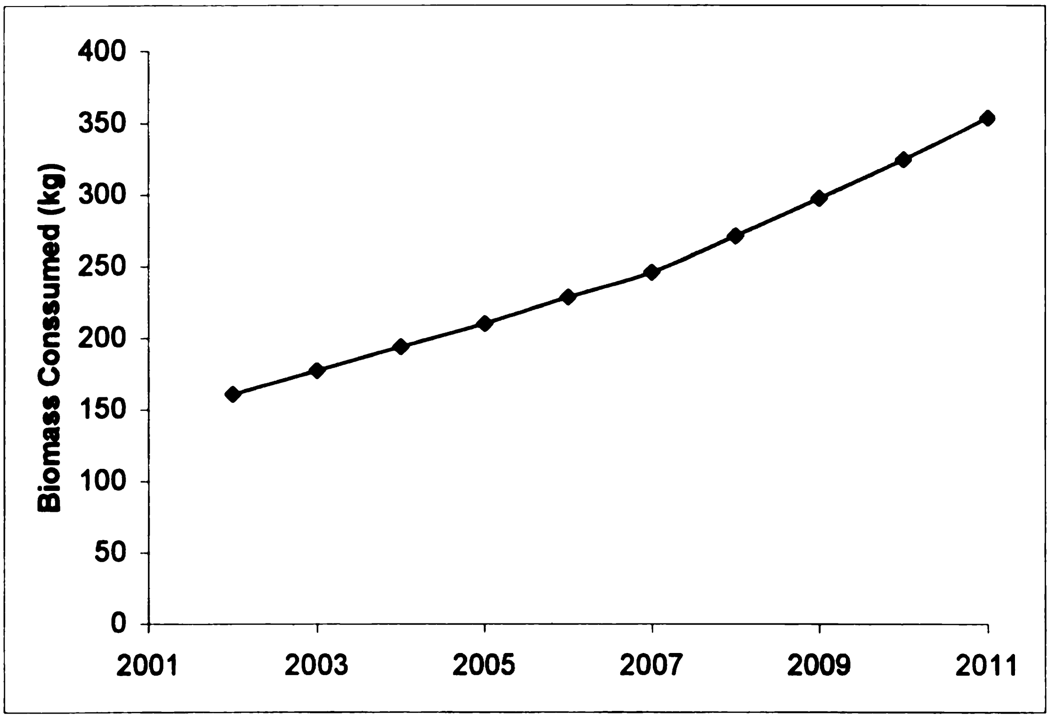


Figure 6. Results of the Baseline Forecast model simulation showing a) the trends in the adult smallmouth bass population size and b) the biomass of smb (kg) consumed by the cormorant population.

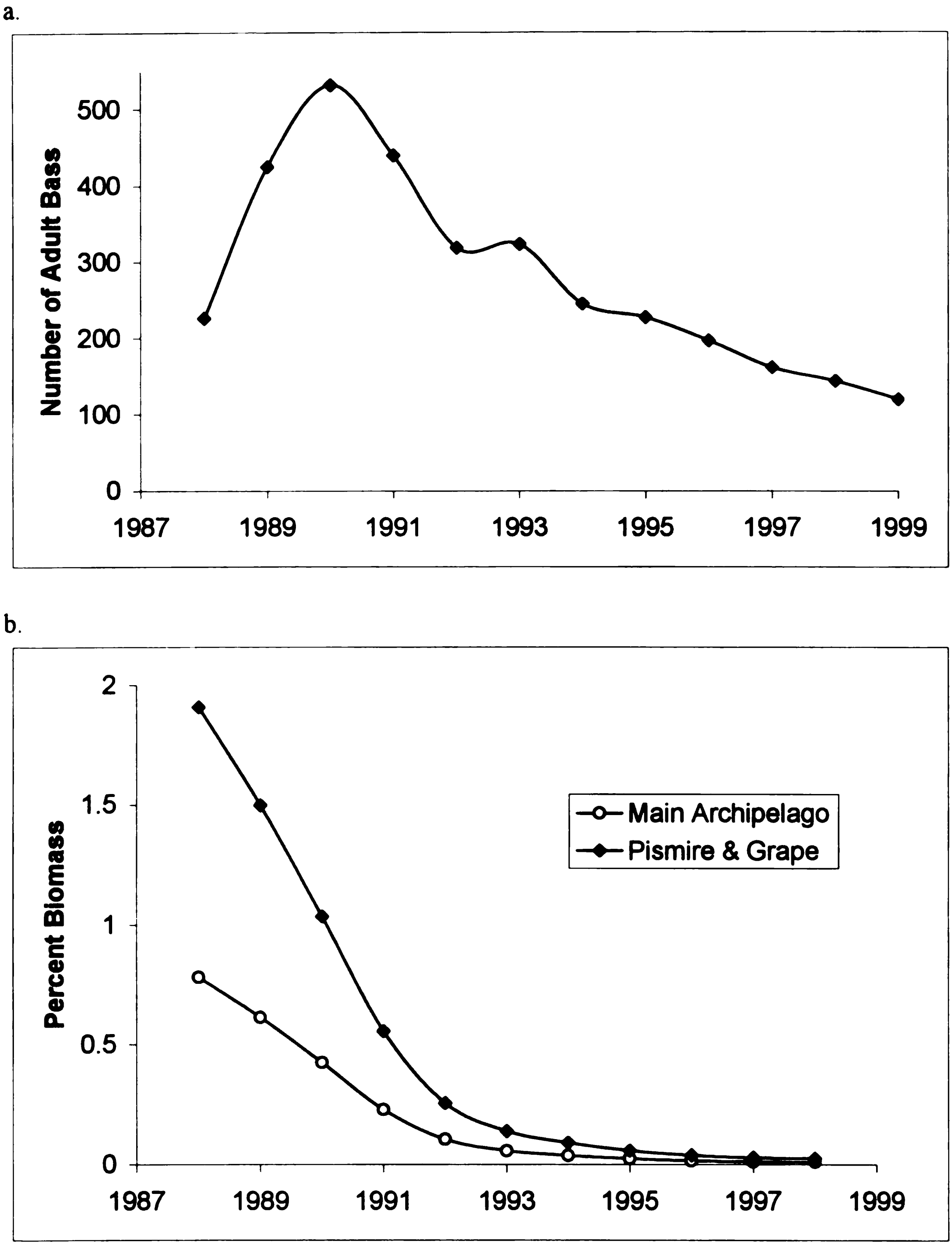


Figure 7. Results of the modified Baseline Rebuild model with no age four predation simulation showing a) the trends in the adult smallmouth bass population size and b) the percent biomass of bird diet composed of smallmouth bass for the entire Main Archipelago cormorant population and the Pismire and Grape colonies cormorant population alone.

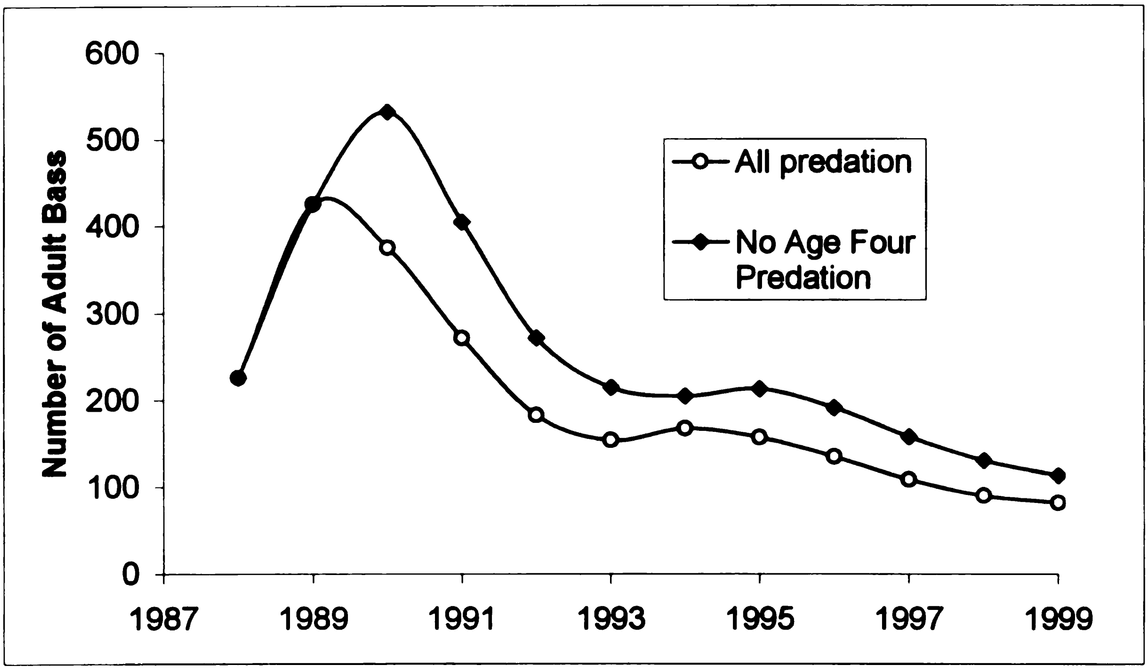


Figure 8. Results of the modified Baseline Rebuild model with spawning constant set at 0.40 showing the simulated trends in the adult smallmouth bass population size when all immature age classes are subject to cormorant predation and when age four bass are invulnerable to cormorant predation.

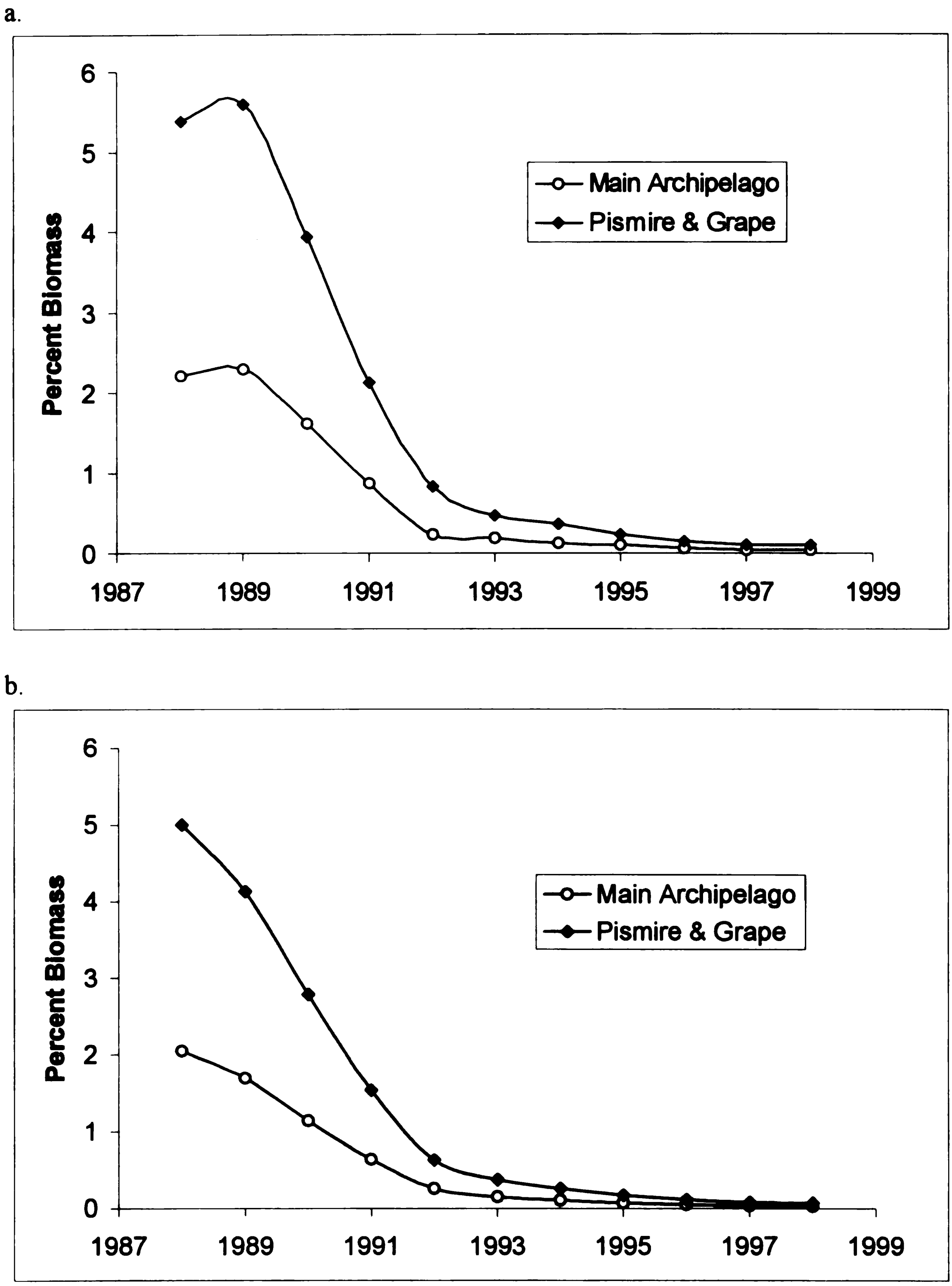
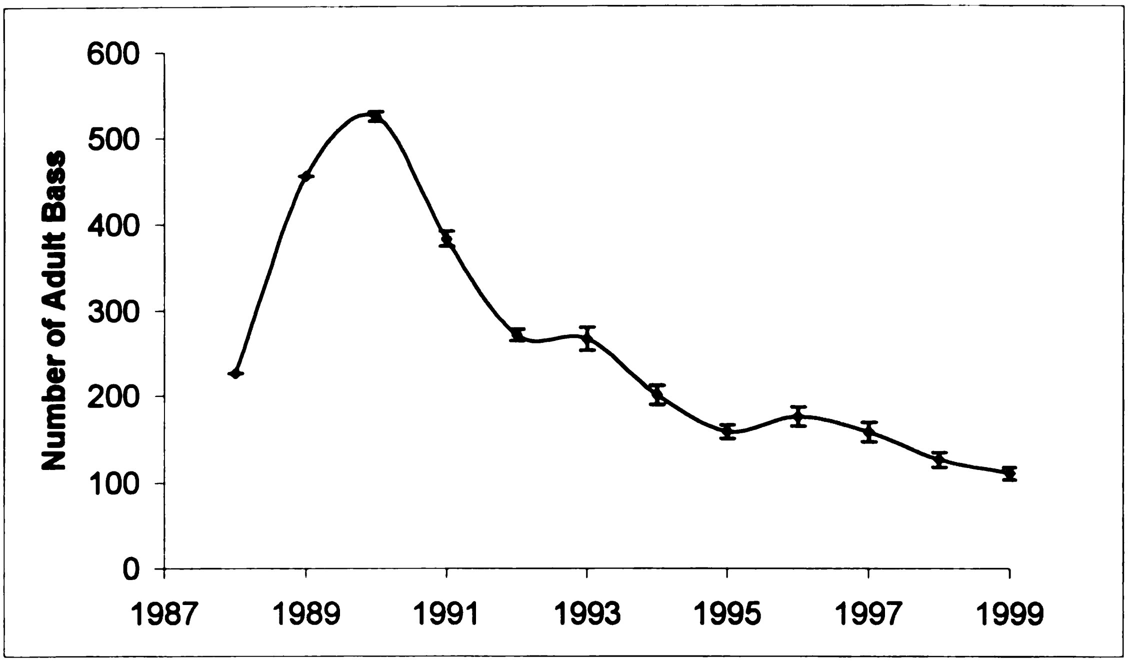


Figure 9. Results of the modified Baseline Rebuild model with spawning constant set at 0.40 showing the simulated trends percent biomass consumed by Main Archipelago birds, and Pismire and Grape colonies birds when a) all immature age classes are vulnerable to predation and b) when age four bass are invulnerable to predation.

a.



b.

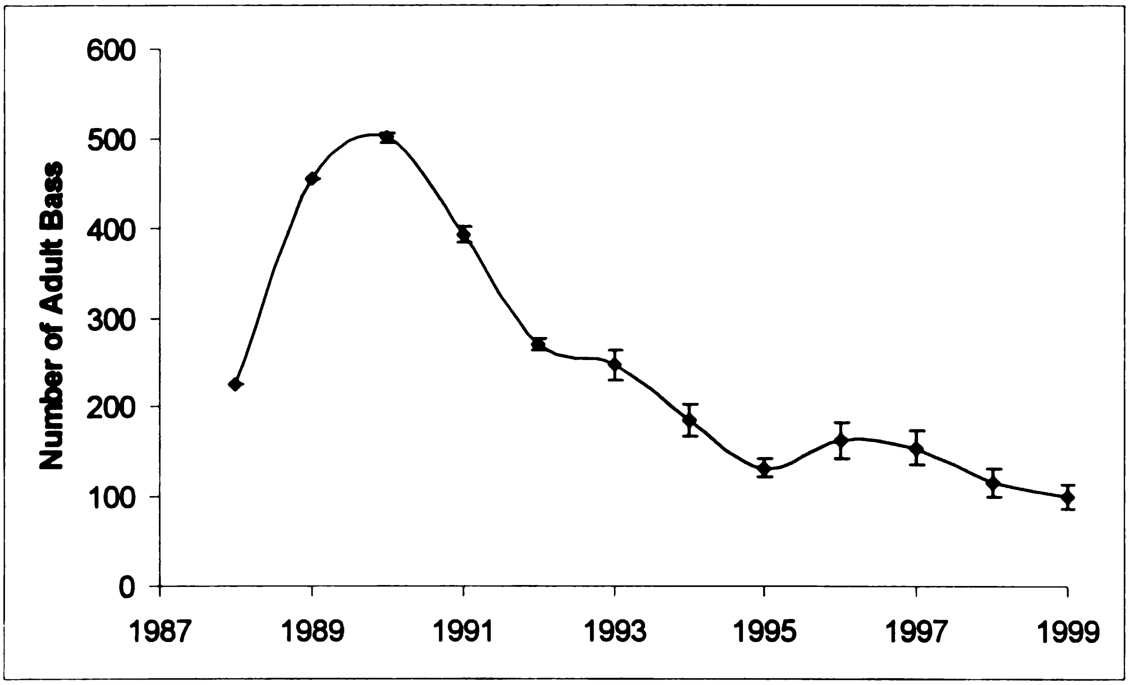
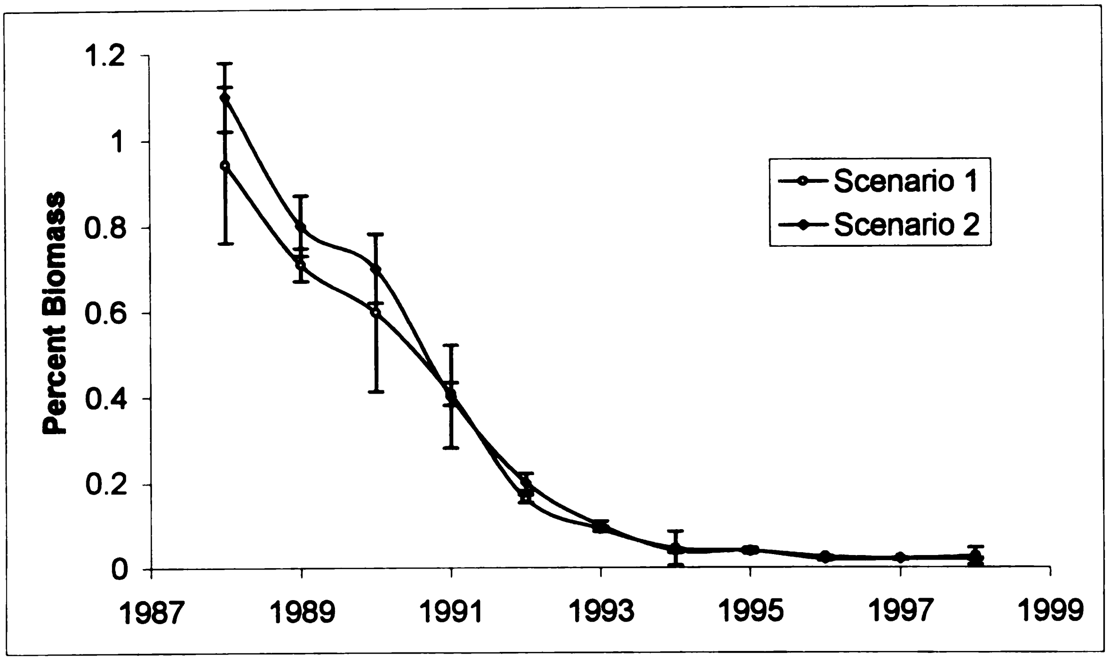


Figure 10. Simulated adult population size (means and standard deviations) for a) Rebuild Model Scenario 1 and b) Rebuild Model Scenario 2.

a.



b.

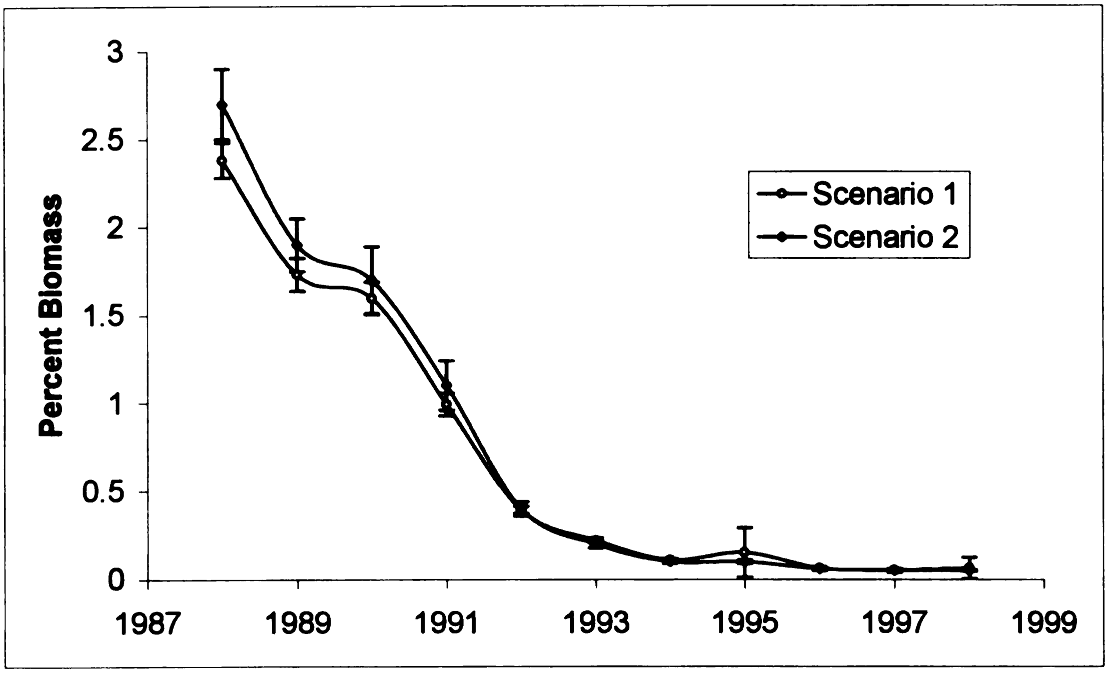
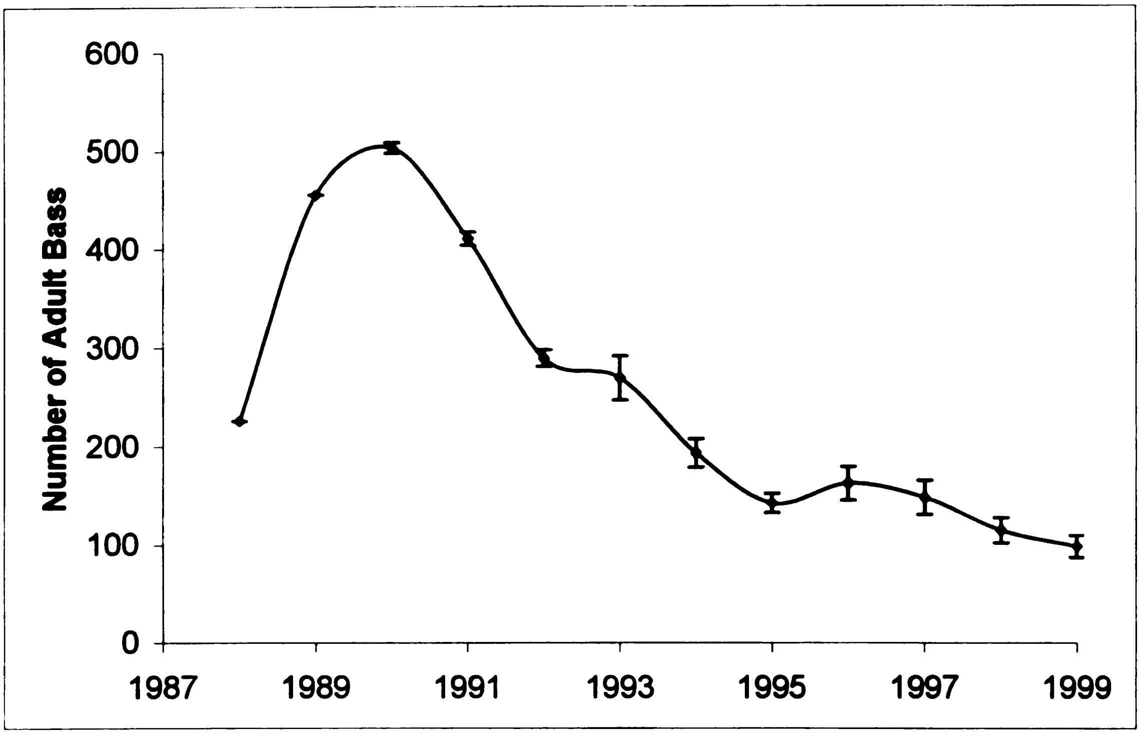


Figure11. Experimental (means and standard deviations) percent biomass of bird diet composed of smallmouth bass as simulated in Rebuild Scenarios 1 and 2 for a) all Main Archipelago birds, and b) only birds nesting on Pismire and Grape Islands.

a.



b.

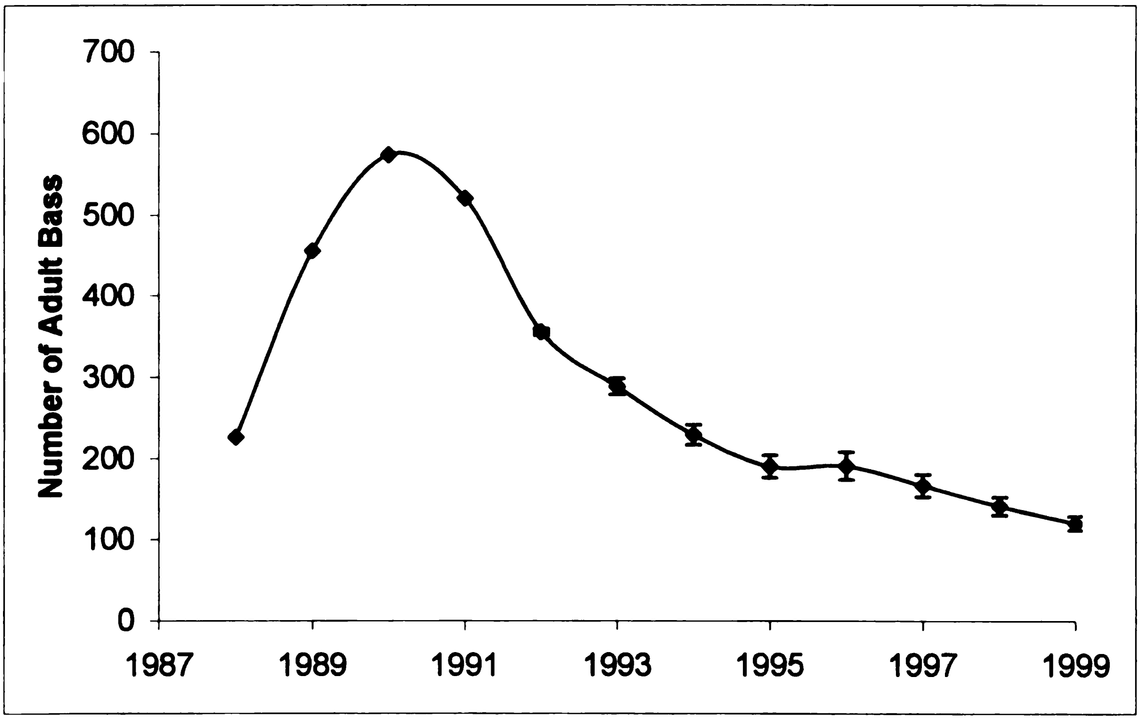
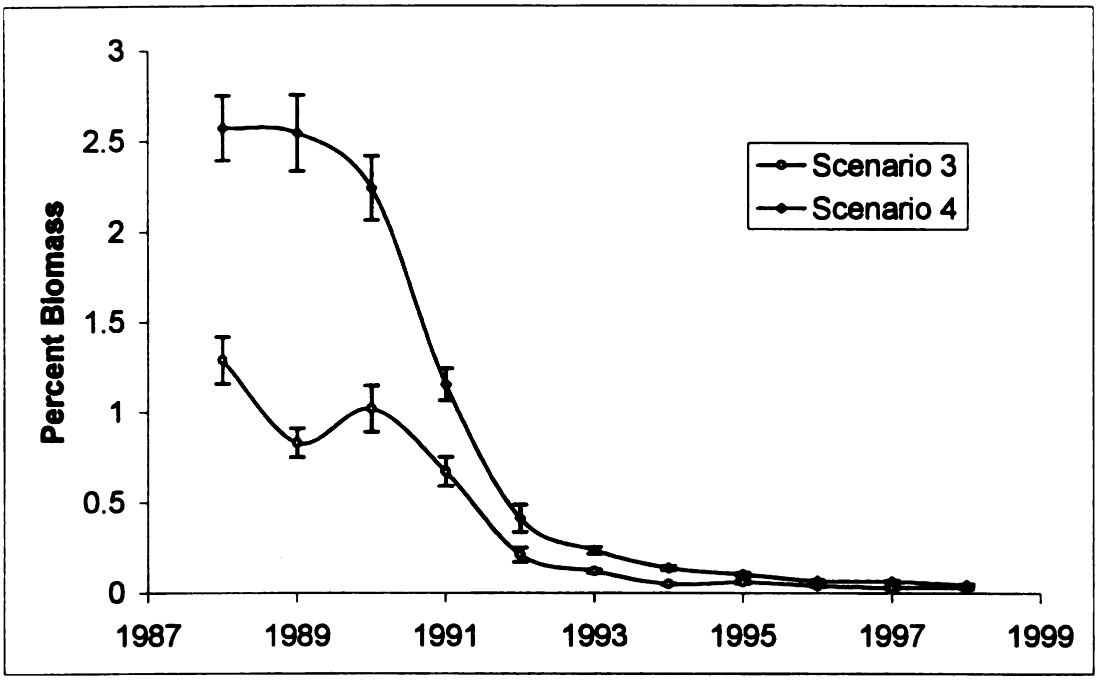


Figure 12. Simulated adult population size (means and standard deviations) for a) Rebuild Model Scenario 3 and b) Rebuild Model Scenario 4.

a.



b .

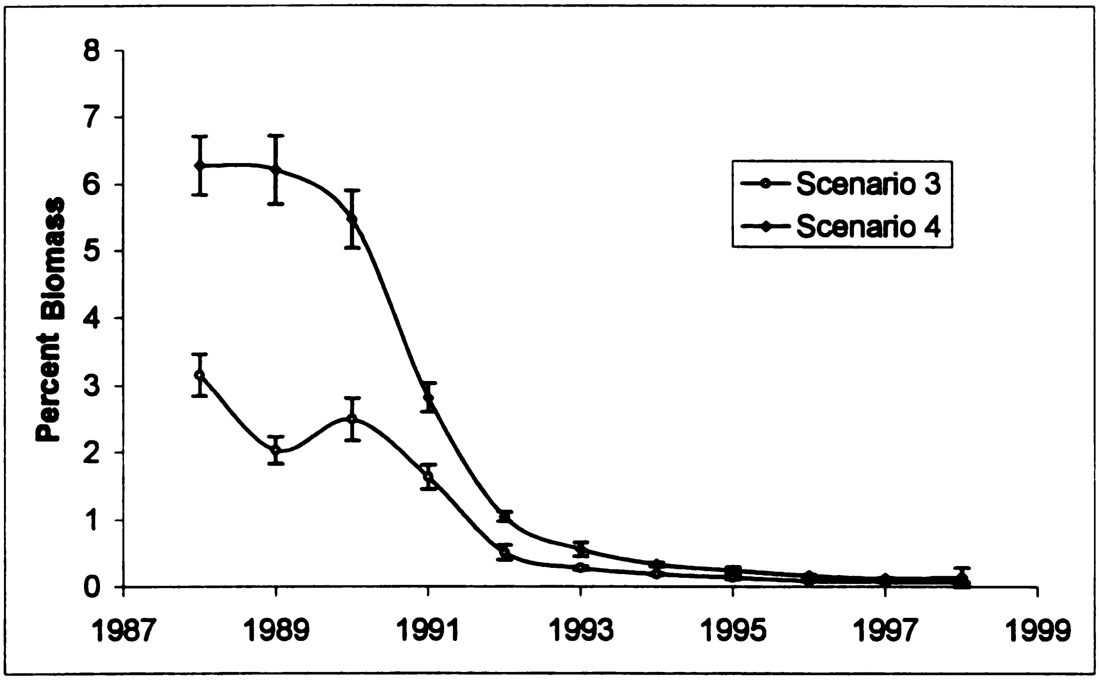
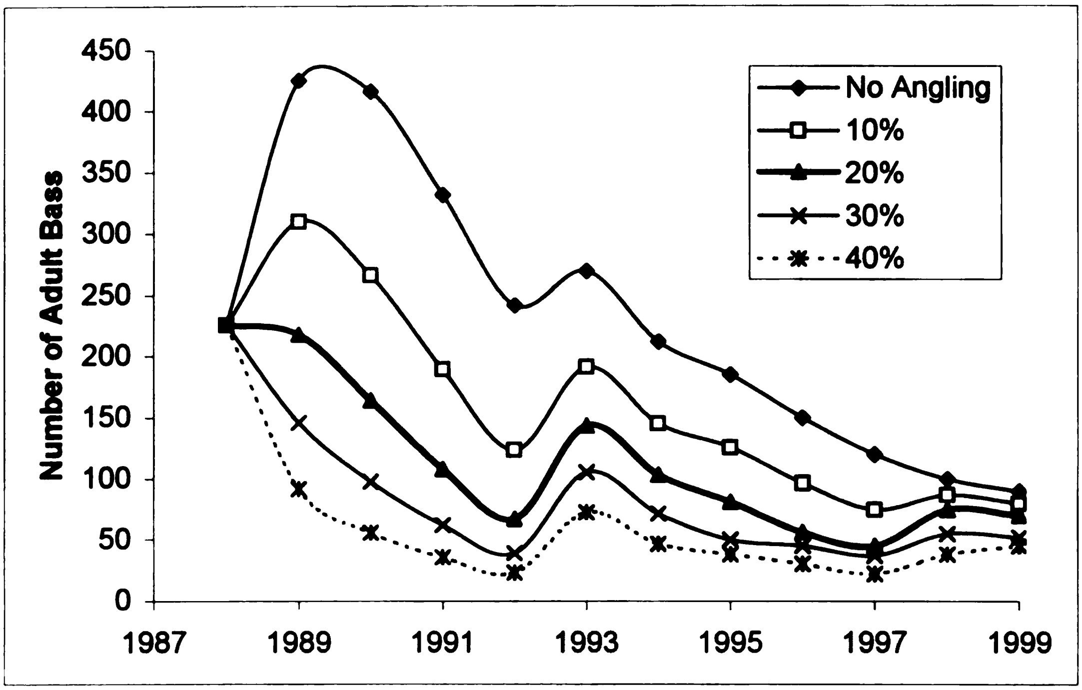


Figure 13. Experimental (means and standard deviations) percent biomass of bird diet composed of smallmouth bass as simulated in Rebuild Scenarios 3 and 4 for a) all Main Archipelago birds, and b) only birds nesting on Pismire and Grape Islands.

a.



b.

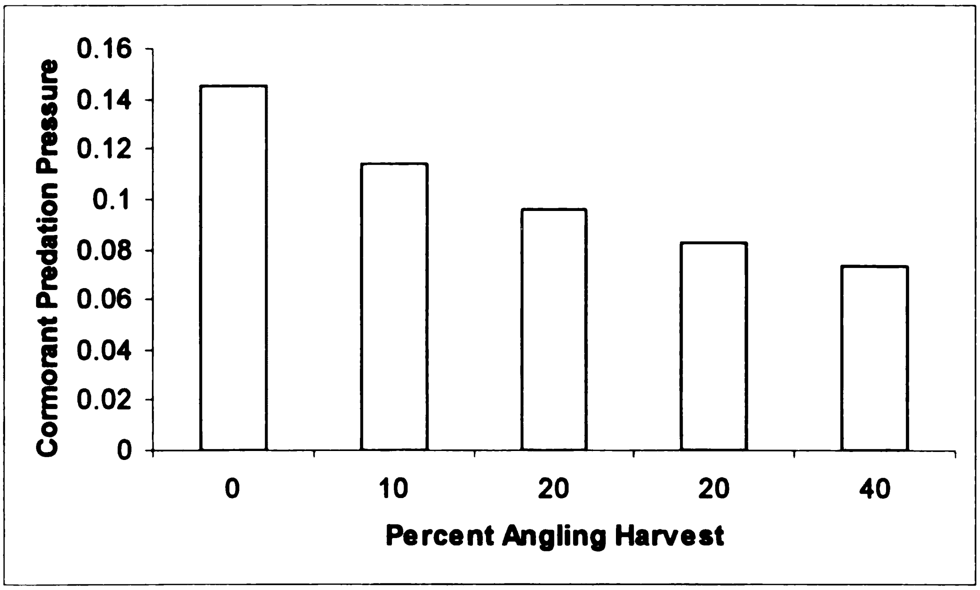


Figure 14. a) Simulated adult bass population sizes when adult populations are subject to varying levels of angling harvest. b) The cormorant predation pressure necessary to work in synergism with angling harvest to drive the adult population to observed levels.

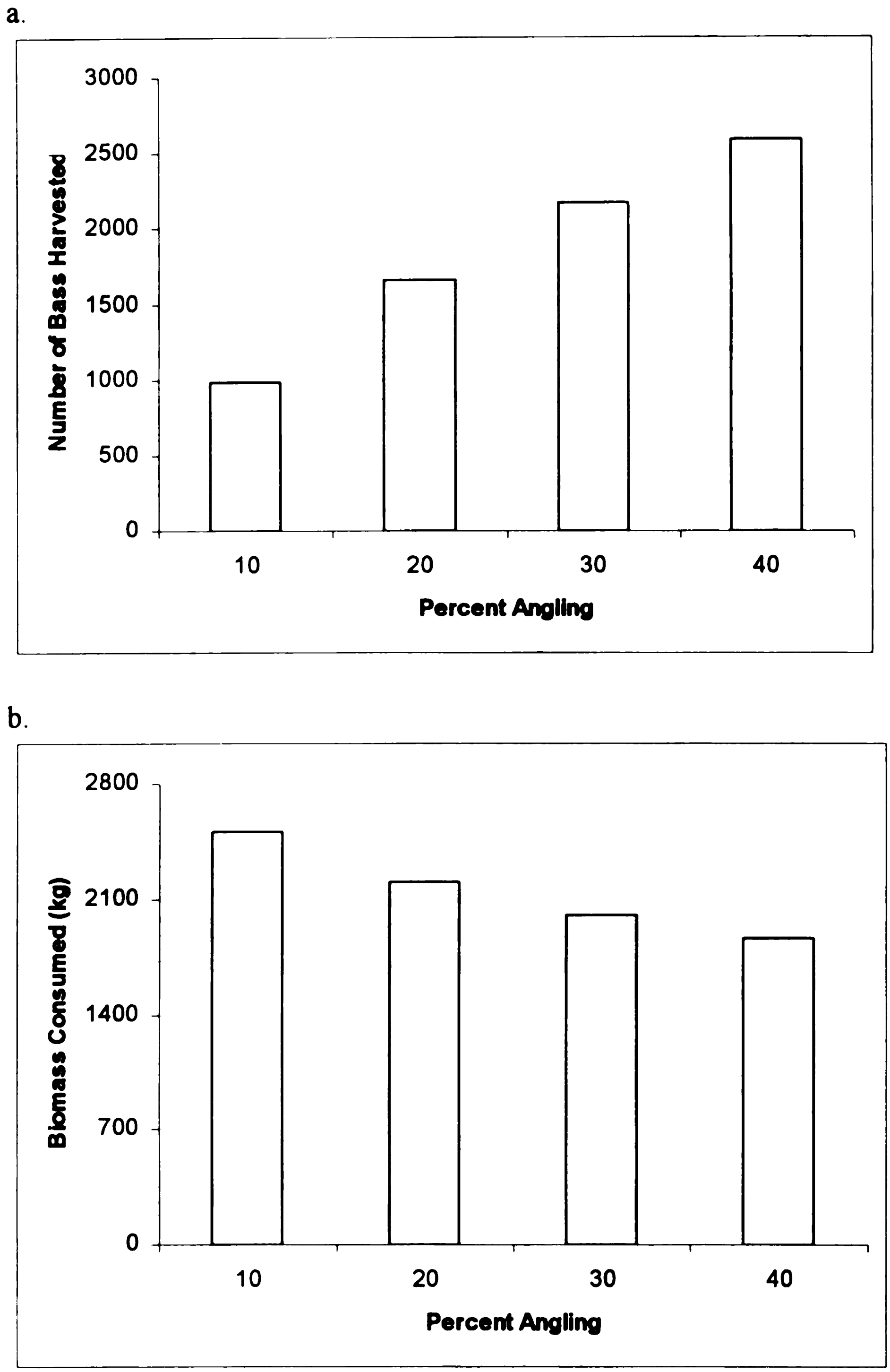


Figure 15. a) Simulated number of adult bass removed by anglers at varying harvest levels beginning in 1988 and ending in 1999. b) The biomass (kg) of immature bass needed to be removed by cormorants over the same simulation period when angling pressure varies.

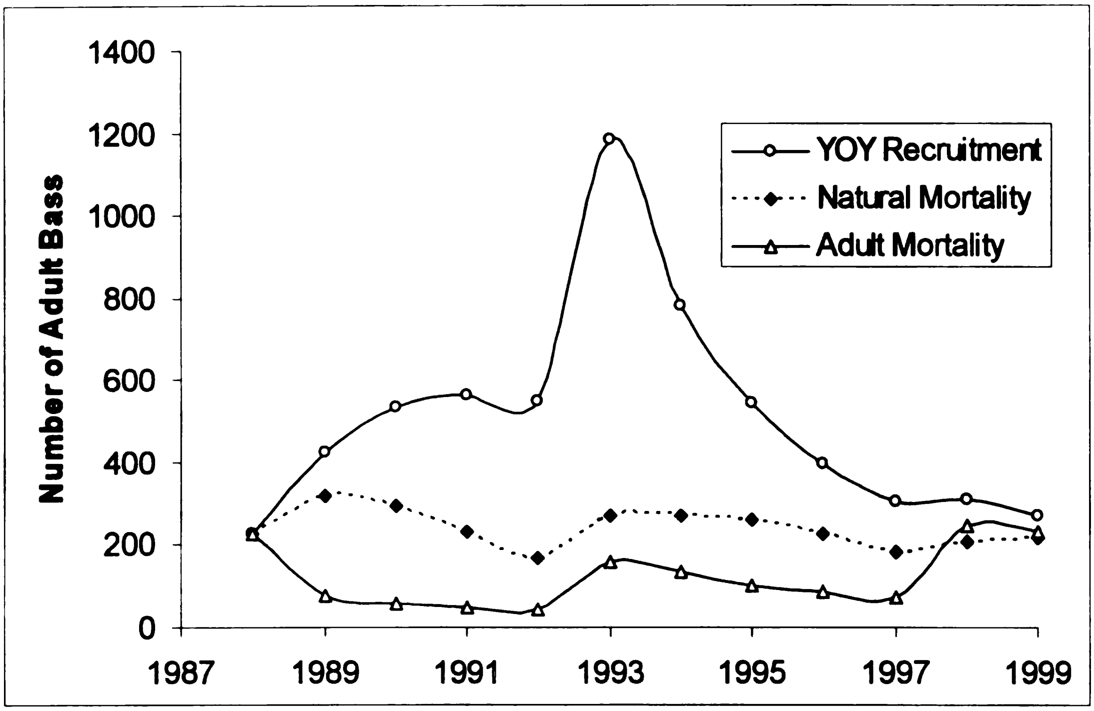
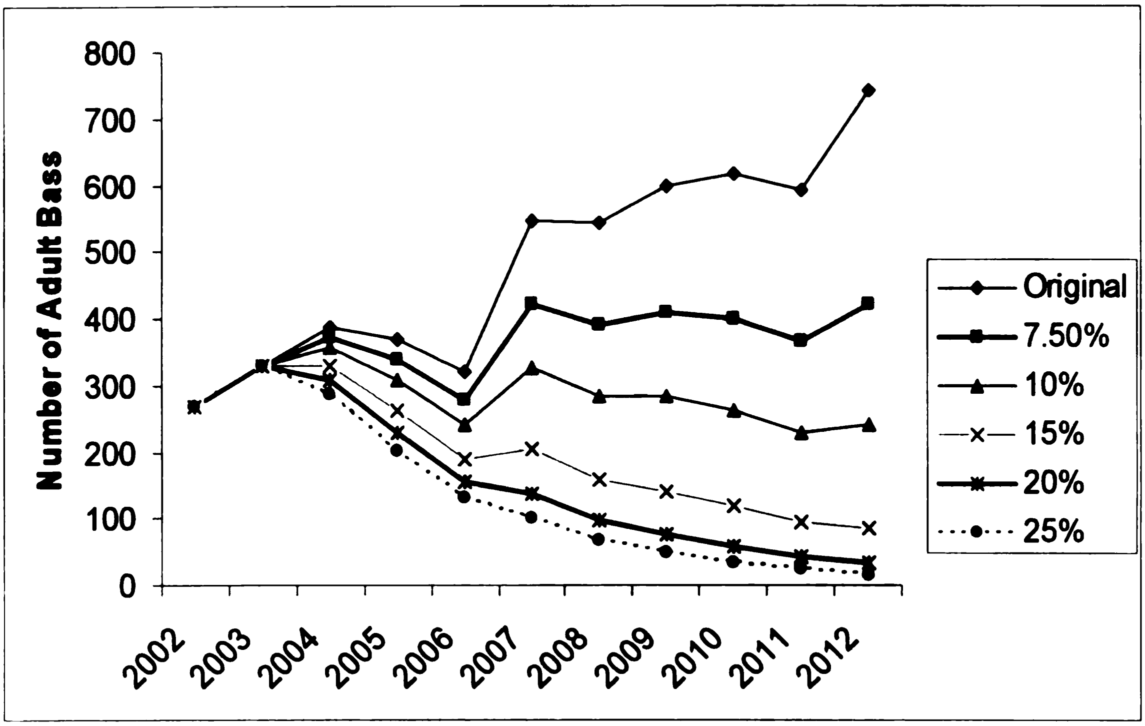


Figure 16. Simulated impacts that increased YOY mortality (0.99), increased annual natural mortality for age 1 through adult fish (0.535), and increase adult mortality (0.885), in the absence of cormorant predation. Each variable was tested separately while all other variables remained unchanged.

a.



b.

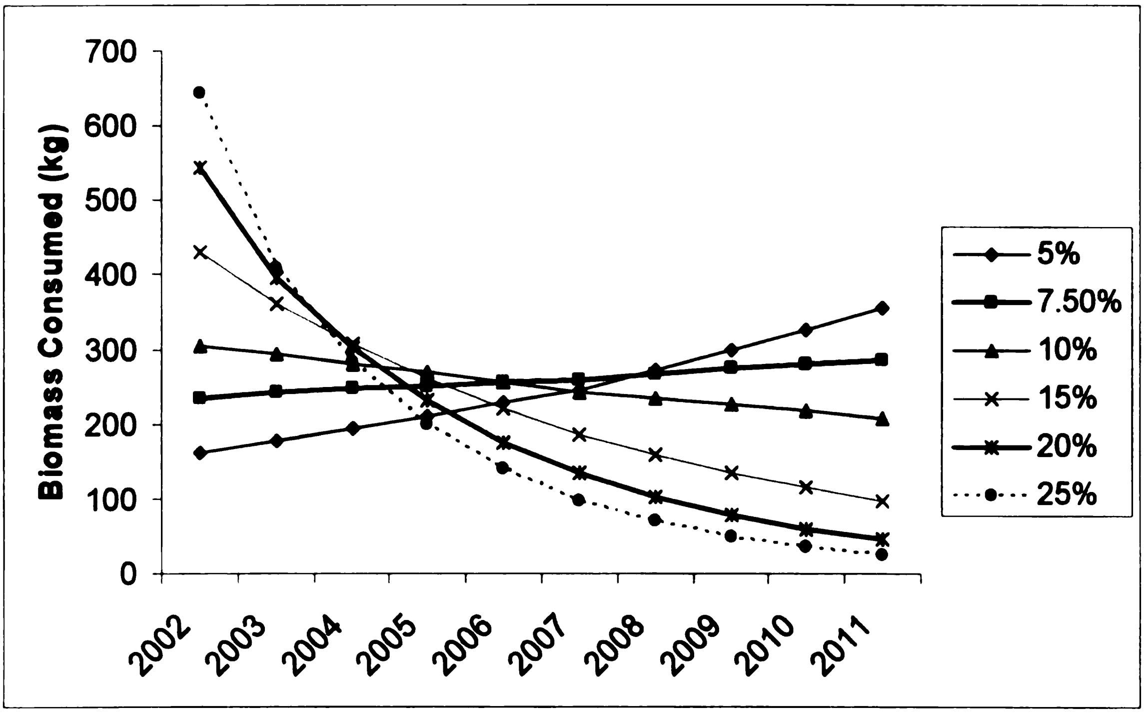
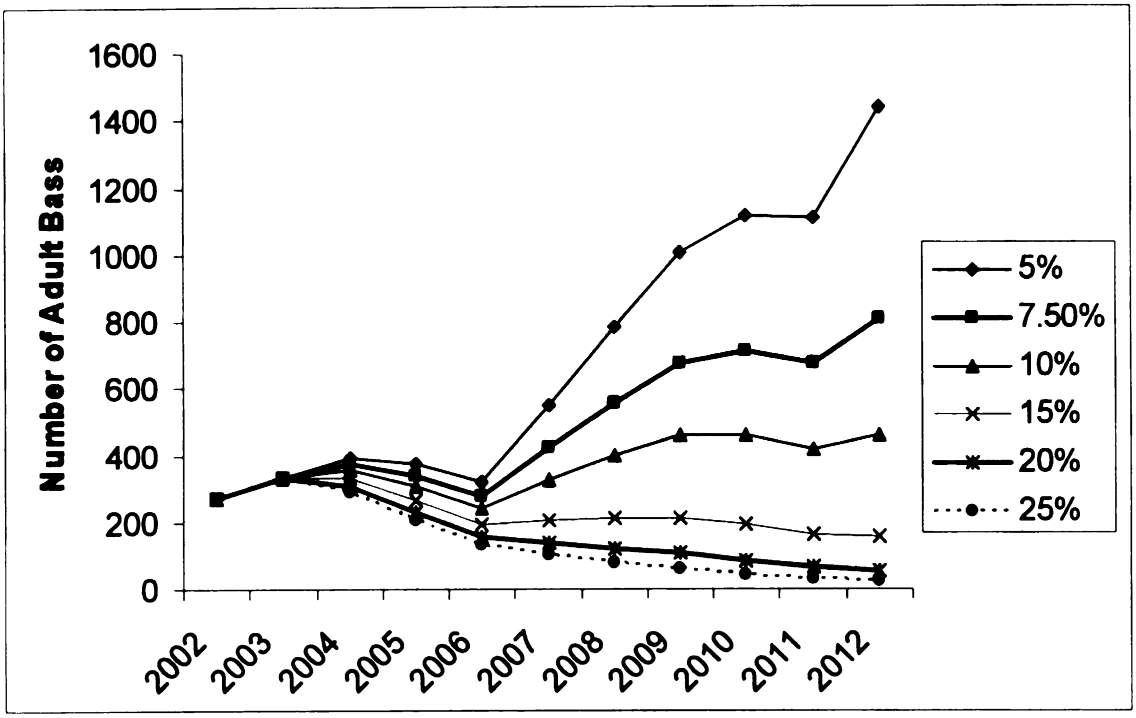


Figure 17. The simulated results for the Baseline Forecast Model with spawning constant set a 0.10 showing a) the resulting adult population size when cormorant predation is increased and b) the biomass (kg) of bass consumed by cormorants in each simulation.

a.



b.

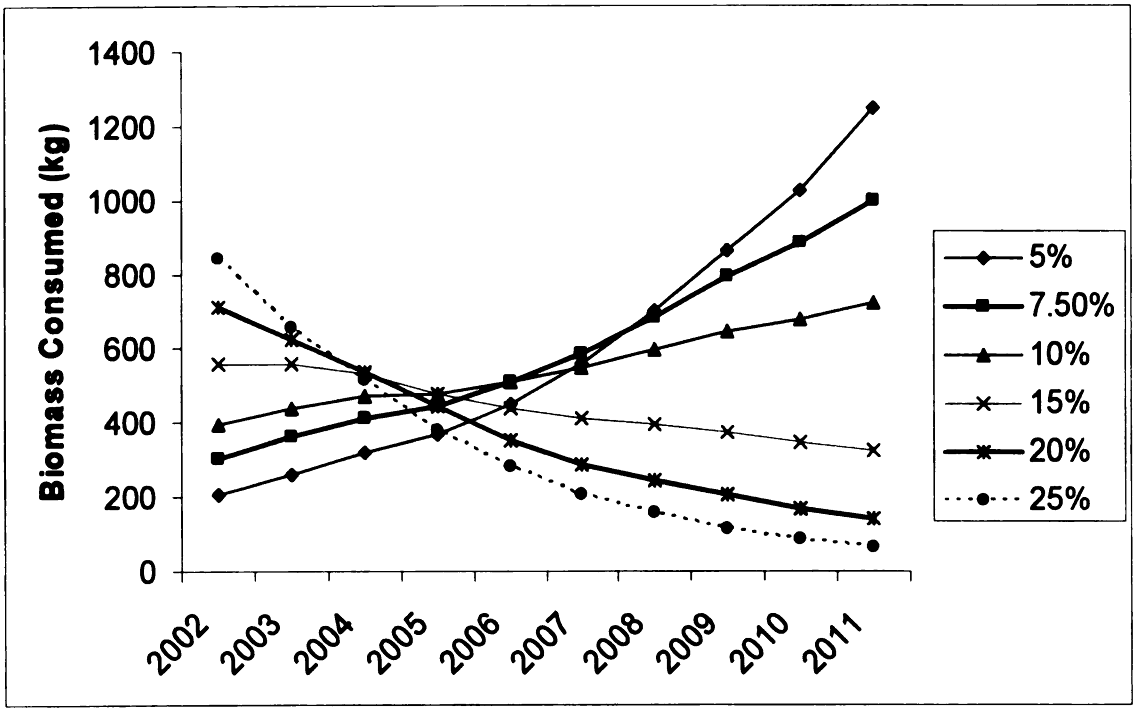
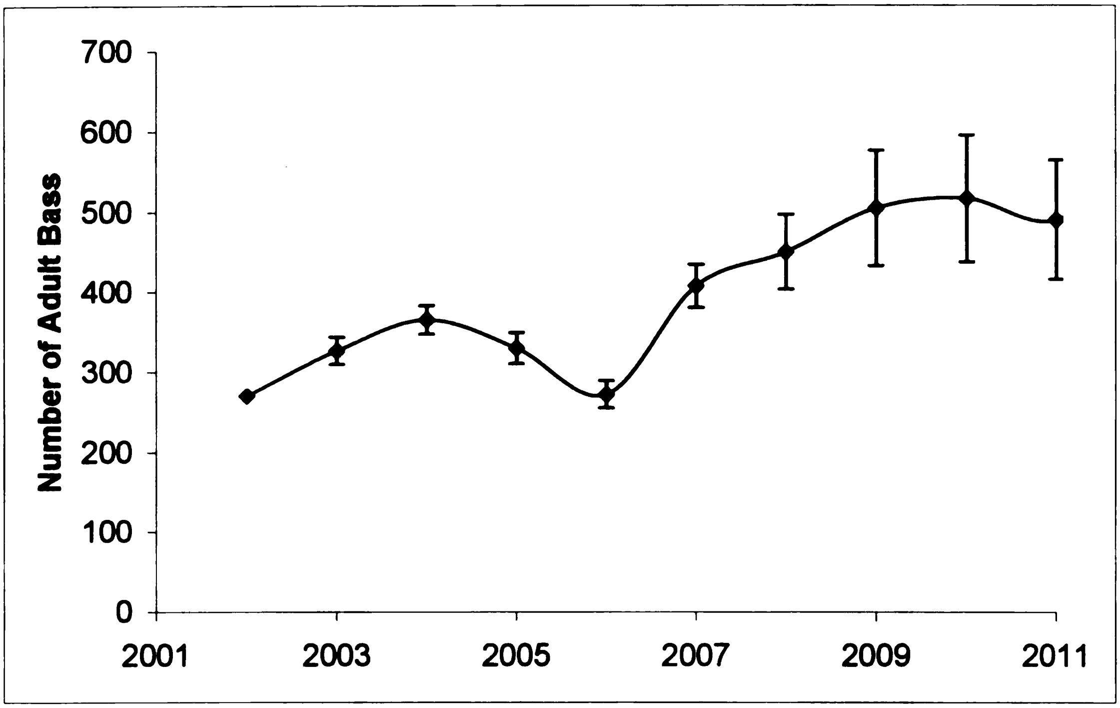


Figure 18. The simulated results for the Baseline Forecast Model with spawning constant set a 0.20 showing a) the resulting adult population size when cormorant predation is increased and b) the biomass (kg) of bass consumed by cormorants in each simulation.

a.



b.

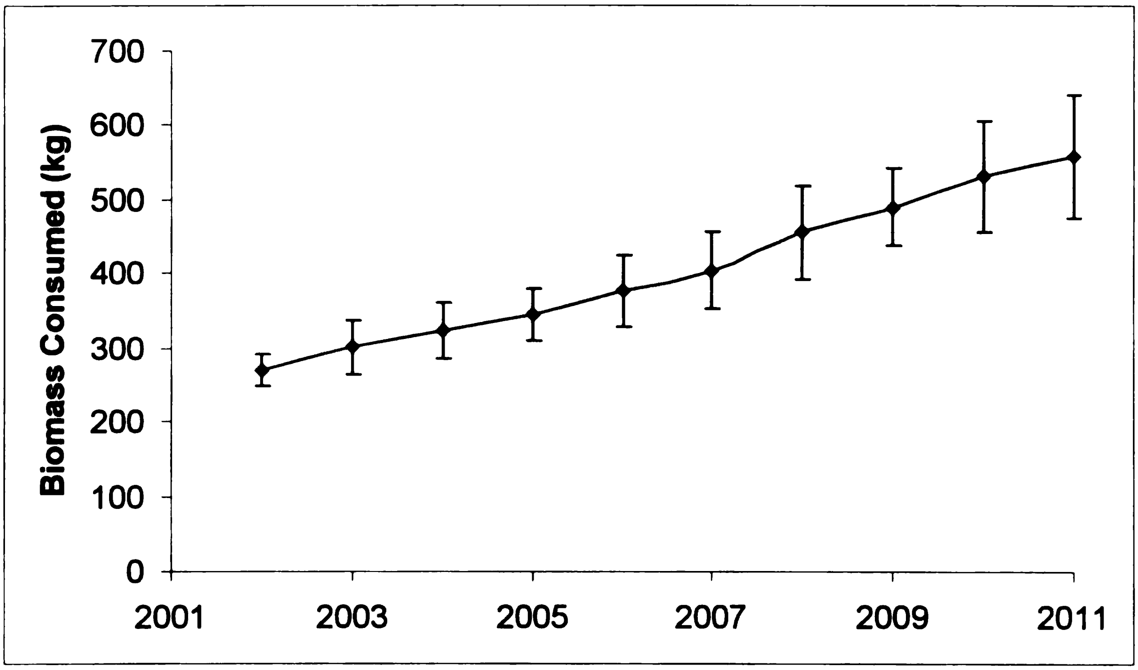
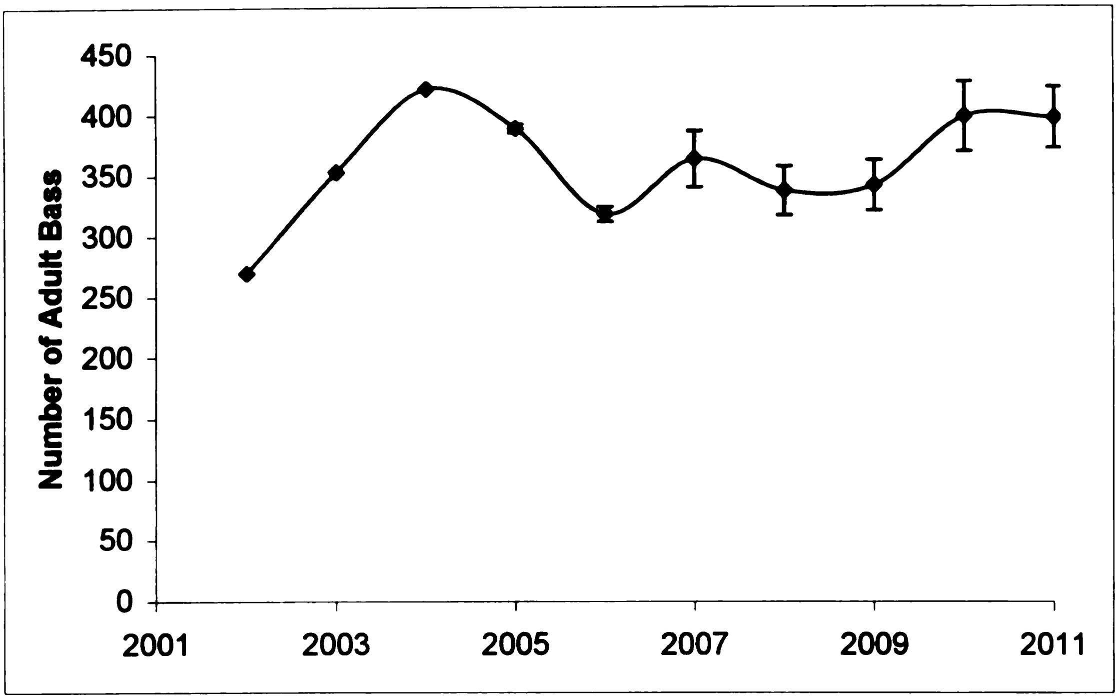


Figure 19. Forecast Constant Predation Pressure Scenario 1 output showing a) the resulting adult bass population for experimental (means and standard deviations) simulations and b) the biomass (kg) of immature bass consumed by cormorants in experimental simulations (means and standard deviations).

a.



b.

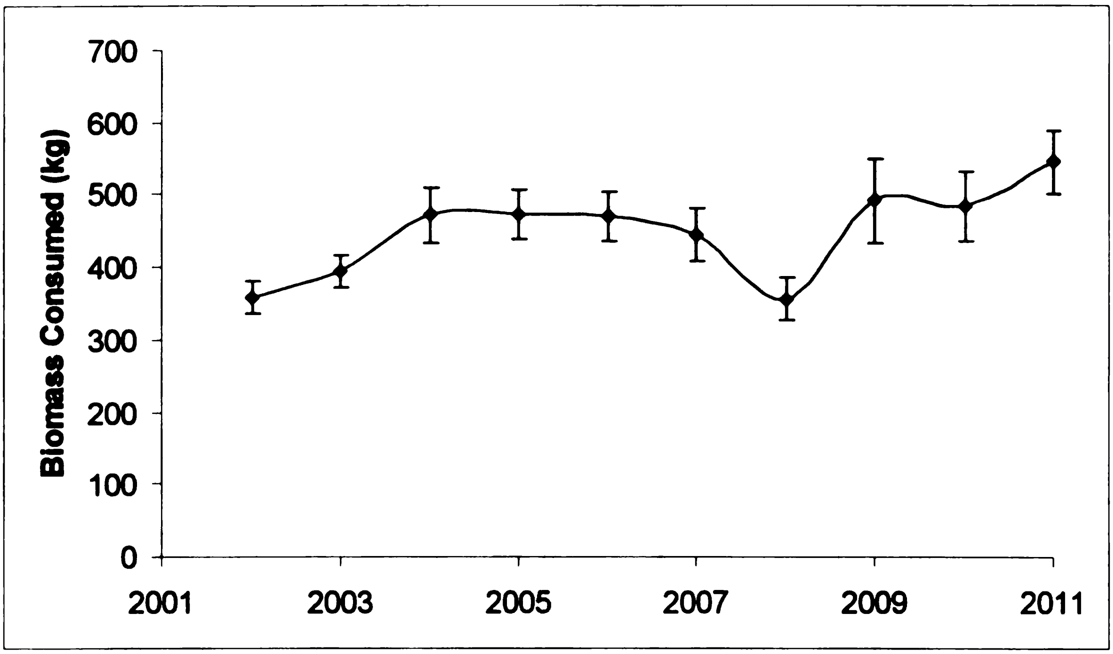
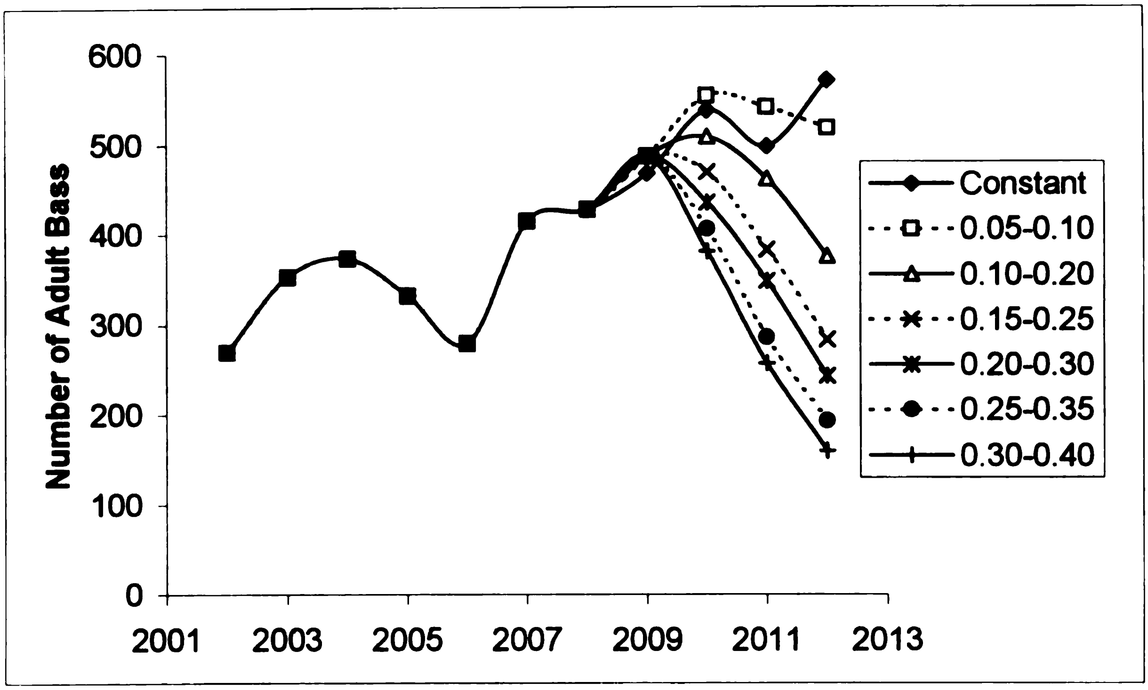


Figure 20. Forecast Constant Predation Pressure Scenario 2 output showing a) the resulting adult bass population for experimental (means and standard deviations) simulations and b) the biomass (kg) of immature bass consumed by cormorants in experimental simulations (means and standard deviations).

a.



b.

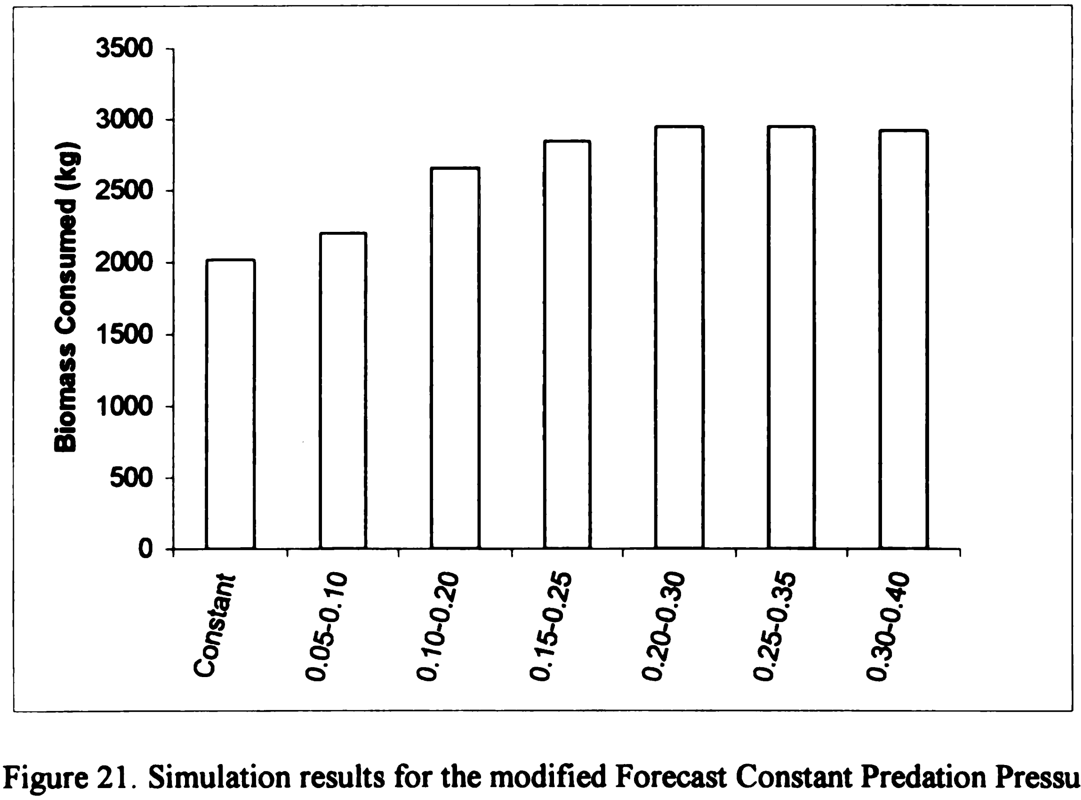


Figure 21. Simulation results for the modified Forecast Constant Predation Pressure Scenario 1 (Predator Response) exploring the influence of increasing cormorant pressure as bass numbers recover as compared to constant predation pressure showing a) adult population size and b) the biomass (kg) of immature bass consumed over the entire simulation period.

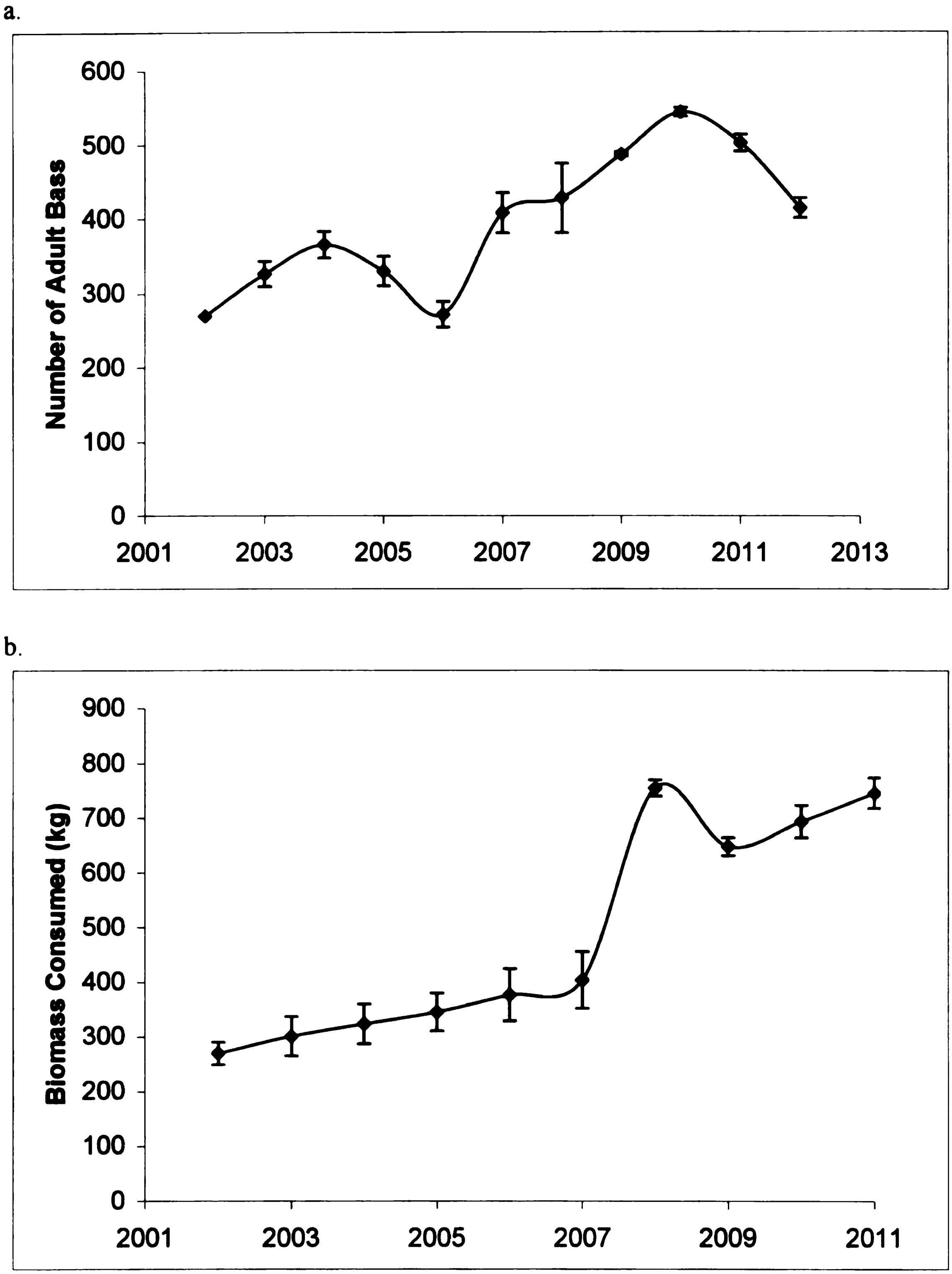
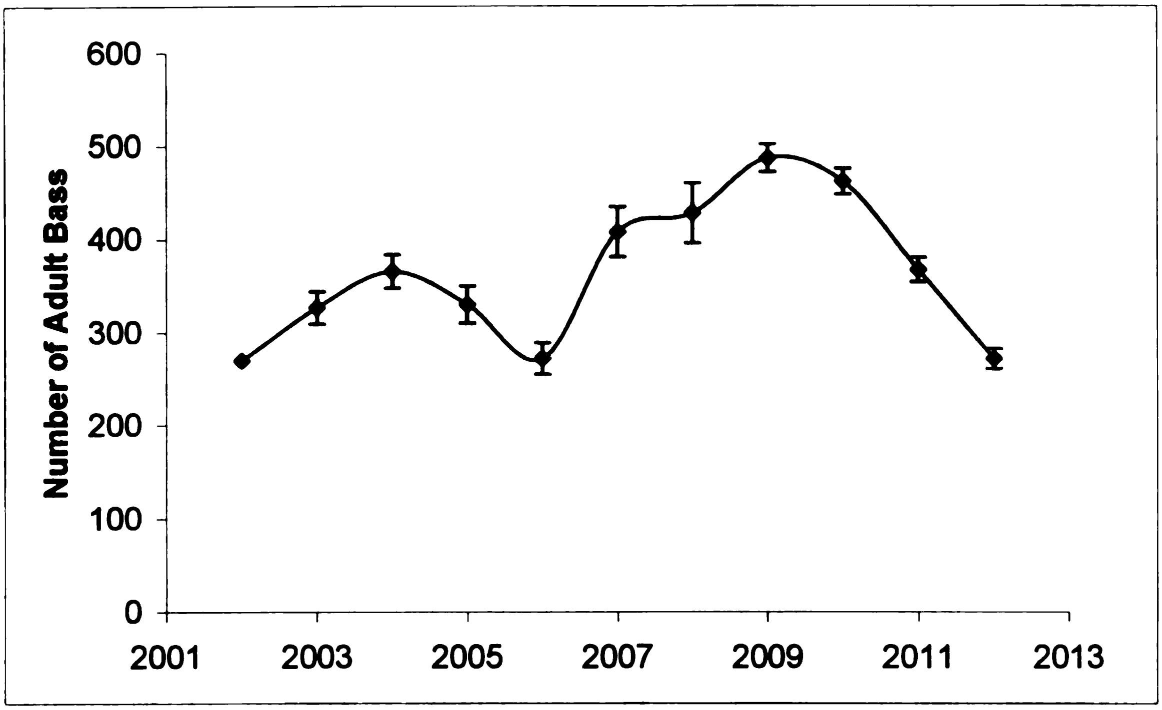


Figure 22. Experimental (means and standard deviations) output for Forecast Predator Response Scenario 1 showing a) simulated adult bass population and b) the biomass (kg) of immature bass consumed.

a.



b.

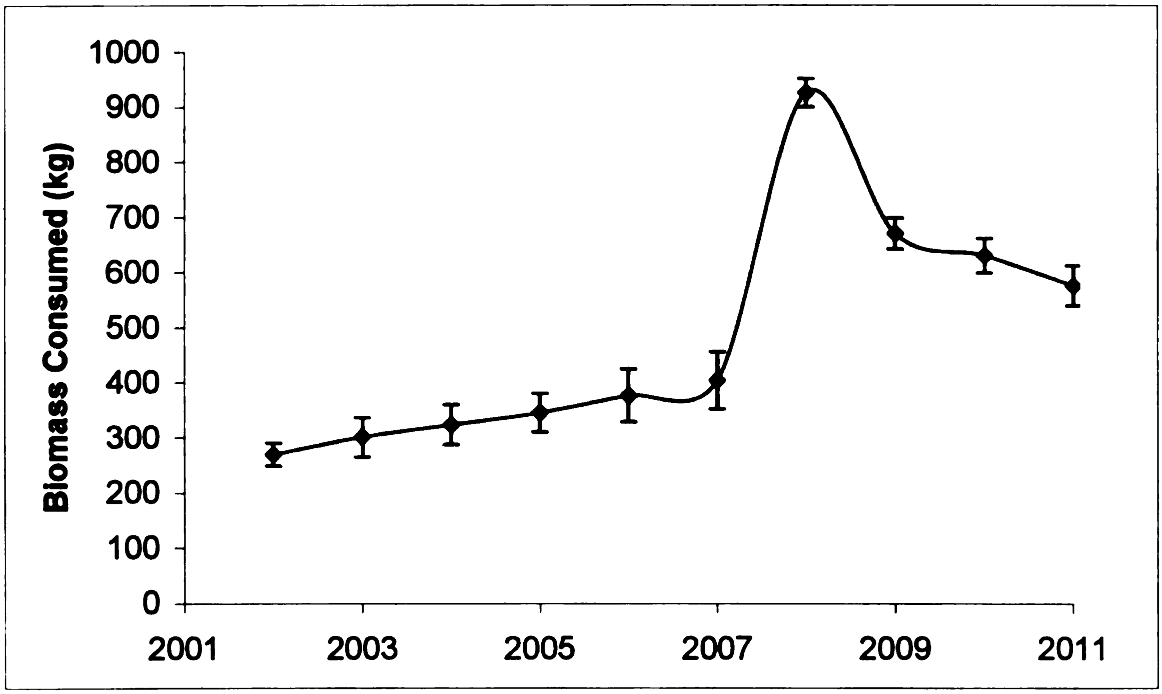


Figure 23. Experimental (means and standard deviations) output for Forecast Predator Response Scenario 1 showing a) simulated adult bass population and b) the biomass (kg) of immature bass consumed.

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