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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 & 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* (Lesson)], 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 & Gabrey, 1995; Hebert

& 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 & 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 (Neuman et al., 1997; Lantry et al., 1999). Although cormorants may have only small and localized effects on fish populations during migration (Kirsch, 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 & 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 & 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 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 & Laurenson, 1983; Johnstone et al., 1990; Blackwell & Sinclair, 1995; Trauttmansdorff & Wassermann, 1995; Ziljstra & van Eerden, 1995; Carss et al., 1997) and these limitations are discussed below.

Analysis of stomach contents and regurgitated food items 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 & 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 (Wanless 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.

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* (Wilson)], 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 10 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.

Methods

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 h of collection in a cooler. Pellets were subsequently dried at 43 °C in an oven for 24 h 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. (Hagen)] were analyzed using contingency tables for 3×2 and 2×2 comparisons and χ^2 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 3×2 and 2×2 contingency tables and χ^2 goodness-of-fit tests (Sokal & 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., 2001). Because there was a large range of sample masses (2.0 g to 136.7 g for regurgitates and 1.4–413.7 g for stomach contents), these data were converted to proportions; an arcsine transformation was performed to normalize data (Sokal & 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. (L.)], nine-spine stickleback [*Pungitius pungitius* (Cuvier)], sucker [*Catostomus* sp. (Luseure)], johnny darter [*Etheostoma nigrum* (Rafinesque)], trout-perch [*Percopsis omiscomaycus* (Walbaum)], and spottail shiner [*Notropis hudsonius* (Clinton)]. Birds harvested for stomach contents included nine males and sixteen females.

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

The 3×2 contingency table (Table 1) and χ^2 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 2×2 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 3×2 contingency table (Table 3) indicated that these data differed from expected and therefore, each method differed from

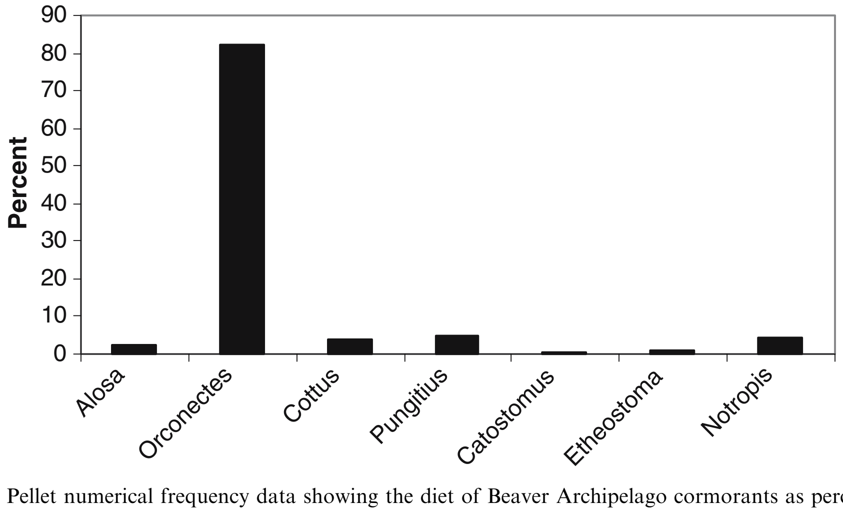

Figure 1. Pellet numerical frequency data showing the diet of Beaver Archipelago cormorants as percentages.

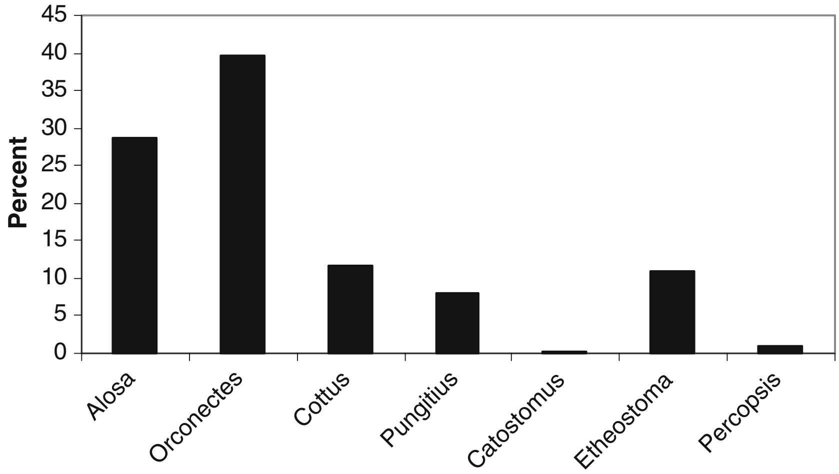

Figure 2. Regurgitate numerical frequency data showing the diet of Beaver Archipelago cormorants as percentages.

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 2×2 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 2×2 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 comprised 68.82% of their diet (Fig. 4). Stomach content data, by percent biomass, indicate that crayfish comprised 19.74% of the diet and alewife made up 69.24% of the diet (Fig. 5). The Mann–Whitney test (Fig. 6) indicates that biomass of alewife (confidence intervals = 0.01 to 36.21, $W = 1652.0$,

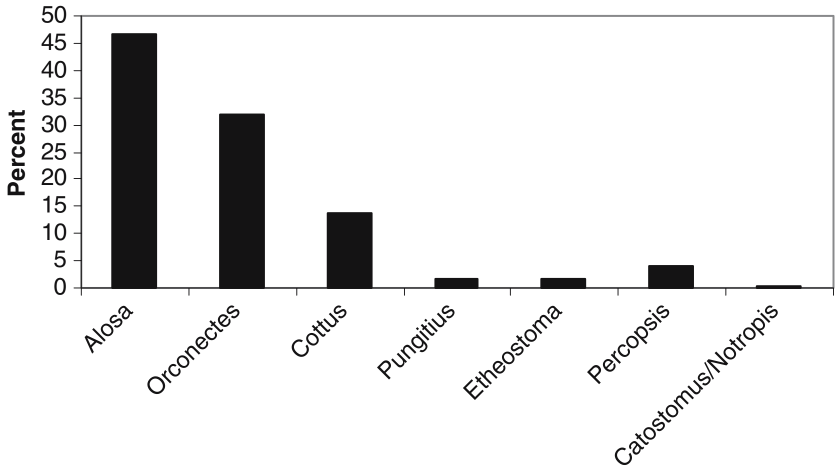

Figure 3. Stomach contents numerical frequency data showing the diet of Beaver Archipelago cormorants as percentages. Percent values for *Catostomus* and *Notropis* are small (both 0.23%) and were combined for clarity.

Table 1. 3×2 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

Sampling method	*Alosa*	*Orconectes*	Total
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

Chi-square tests indicate that values differ from expected for both alewife (χ^2 = 387.06, critical value = 5.99 at α = 0.05, df = 2) and crayfish (χ^2 = 119.02, critical value = 5.99 at α = 0.05, df = 2).

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 significantly different from each other at α = 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 are not significantly different 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 & Lev, 1987; Ludwig et al., 1989; Ludwig & 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* (Mitchill)] (13%), rainbow smelt [*Osmerus mordax*

Table 3. 3×2 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

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

Chi-square tests for 3×2 comparison indicate that values differ from expected for both alewife (χ^2 = 9.53, critical value = 5.99 at α = 0.05, df = 2) and crayfish (χ^2 = 6.46, critical value = 5.99 at α = 0.05, df = 2). Comparisons using 2×2 contingency tables show that pellets and stomach contents data for both alewife (χ^2 = 3.35, critical value = 3.84 at α = 0.05, df = 1) and crayfish (χ^2 = 1.50, critical value = 3.84 at α = 0.05, df = 1) were statistically similar. Also, regurgitate and stomach contents data were statistically similar for both alewife (χ^2 = 0.61, critical value = 3.84 at α = 0.05, df = 1) and crayfish (χ^2 = 0.74, critical value = 3.84 at α = 0.05, df = 1).

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)

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)

The percent frequencies of each prey item are shown in parenthesis.

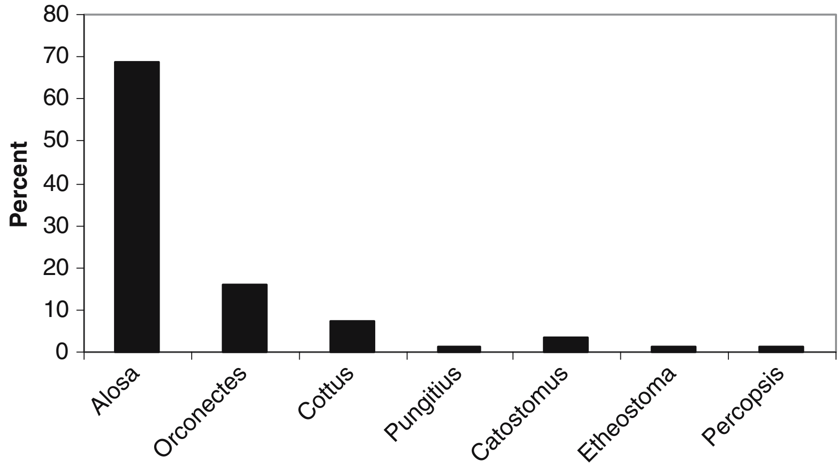

Figure 4. Regurgitate biomass data showing the diet of Beaver Archipelago cormorants as percentages.

(Mitchill)] (8%), and white sucker [*Catostomus commersoni* (Lacepède)] (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 & 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 & 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.

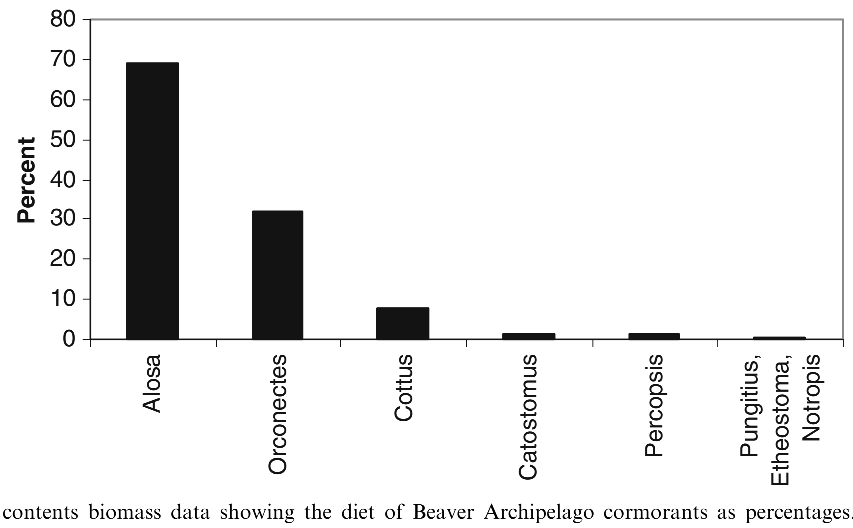

Figure 5. Stomach contents biomass data showing the diet of Beaver Archipelago cormorants as percentages. Percent values for *Pungitius*, *Etheostoma* and *Notropis* are small (1.48, 1.43 and 1.48%, respectively) and were combined for clarity.

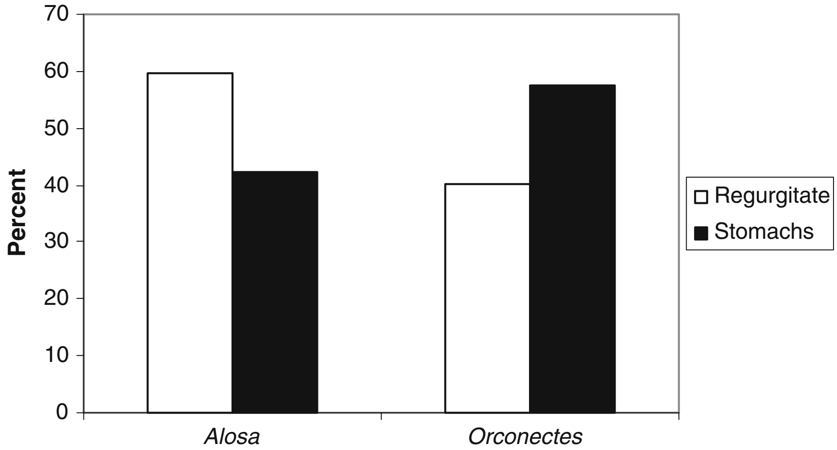

Figure 6. Means of arcsine transformed biomass data. The Mann–Whitney test indicated that biomass of alewife (confidence intervals = 0.01 to 36.21, W = 1652,0, p = 0.1207, adjusted for ties) and crayfish (confidence intervals = −36.20 to −0.01, W = 1428.0, p = 0.1207, adjusted for ties) estimated by each method are not significantly different from each other at a = 0.05.

The limitations of pellet analysis have been demonstrated in other works, including studies with captive birds (Johnstone et al., 1990; Trauttmansdorff & Wassermann, 1995; Ziljstra & van Eerden, 1995) and in the field (Duffy & Laurenson, 1983; Blackwell & Sinclair, 1995). However, several studies (Ross & Johnson, 1995, 1999; Warke & Day, 1995; Johnson et al., 1999, 2001a, b, 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 & 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 & Neilson, 1985; Jobling & 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 & Sinclair, 1995). The assumption that pellets reflect the remains of prey taken during the previous 24-h 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 & Wassermann, 1995; Ziljstra & van Eerden, 1995). Therefore, pellet analysis does not reflect nestling diet. However, pellets have proved more useful in describing cormorant diets than feces (Johnson & Ross, 1996).

In northern Lake Michigan (Ludwig et al., 1989) and in similar systems such as northern Lake Huron (Ludwig & 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, b, 2003) have used pellets to detect the presence and the importance of alewife in the diet of DCCOs. Yet, Derby & 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 & 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) (Seefelt & Gillingham, unpublished data). This supports the findings of previous studies in the Upper Great Lakes (Ludwig et al., 1989; Ludwig & 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 & Sprules, 2002). Avian piscivores may be valuable environmental indicators in lake systems (Hebert & 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 analyses 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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References

Birt, V. L., T. P. Birt, D. Goulet, D. K. Cairns & W. A. Montevecchi, 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. Marine Ecology Progress Series 40: 205–208.

Blackwell, B. F., W. B. Krohn & R. B. Allen, 1995. Foods of nestling Double-crested Cormorants in Penobscot Bay, Maine, USA: temporal and spatial comparisons. Colonial Waterbirds 18(Special Publication 1): 199–208.

Blackwell, B. F. & J. A. Sinclair, 1995. Evidence for secondary consumption of fish by Double-crested Cormorants Marine Ecology (Progress Series) 123: 1–4.

Brown, K. M. & P. J. Ewins, 1996. Technique-dependent biases in determination of diet composition: an example with Ring-billed Gulls. Condor 98: 34–41.

Brugger, K. E., 1993. Digestibility of three fish species by Double-crested Cormorants. Condor 95: 25–32.

Cairns, D. K., 1992. Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. Condor 94: 811–824.

Carss, D. N. & The Diet Assessment and Food Intake Working Group, 1997. Techniques for assessing cormorant diet and food intake: towards a consensus view. Supplemento alle Ricerche di Biologia della Selvaggina 26: 197–230.

Chen, C., R. Ji, D. J. Schwab, D. Beletsky, G. L. Fahnenstiel, M. Jiang, T. H. Johengen, H. Vnaderploeg, B. Eadie, J. W. Budd, M. H. Bundy, W. Gardner, J. Cortner & P. J. Lavrentyev, 2002. A model study of coupled biological and physical dynamics in Lake Michigan. Ecological Modelling 152: 145–168.

Craven, S. R. & E. Lev, 1987. Double-crested Cormorants in the Apostle Islands, Wisconsin, USA: population trends, foods habits and fishery depredations. Colonial Waterbirds 10: 64–71.

da Silva, J. & J. D. Neilson, 1985. Limitations of using otoliths recovered in scats to estimate prey consumption in seals. Canadian Journal of Fish and Aquatic Sciences 42: 1439–1442.

Derby, C. E. & J. R. Lovvorn, 1997. Comparison of pellets versus collected birds for sampling diets of Double-crested Cormorants. Condor 99: 549–553.

Duffy, D. C. & L. J. E. Laurenson, 1983. Pellets of Cape Cormorants as indicators of diet. Condor 85: 305–307.

Dunn, E. H., 1975. Caloric intake of nestling Double-crested Cormorants. Auk 92: 553–565.

Environmental Protection Agency (EPA), 2000. Lake Michigan Lake Management Plan.

Fuller, K., H. Shear & J. Wittig (eds), 1995. The Great Lakes Atlas. Enviornment Canada and the U.S. Environmental Protection Agency.

Hatch, J. J. & D. V. C. Weseloh, 1999. Double-crested Cormorant (Phalacrocorax auritus). In Poole, A. & F. Gill (eds), The Birds of North America. Inc., Philidelphia, Pennsylvania, No. 441.

Hebert, C. E. & H. A. Morrison, 2003. Consumption of fish and other prey items by Lake Erie waterbirds. Journal of Great Lakes Research 29: 213–227.

Hebert, C. E. & W. G. Sprules, 2002. The relevance of seabird ecology to Great Lakes Management. Journal of Great Lakes Research 28: 91–103.

Jobling, M. & A. Breiby, 1986. The use and abuse of fish otoliths in the studies of feeding habits of marine piscivores. Sarsia 71: 265–274.

Johnson, J. H. & R. M. Ross, 1996. Pellets versus feces: their relative importance in describing the food habits of Double-crested Cormorants. Journal of Great Lakes Research 22: 795–798.

Johnson, J. H., R. M. Ross & C. M. Adams, 1999. Diet composition of Double-crested Cormorants in Eastern Lake Ontario, 1998. In Final Report: To Assess the Impact of Double-crested Cormorant Predation on the Smallmouth Bass and Other Fishes of the Eastern Basin of Lake Ontario. Joint Report of NYSDEEC Bureau of Fishes and the US Geological Survey Biology Resource Division.

Johnson, J. H., R. M. Ross, R. D. McCullough & B. Edmonds, 2001a. Diet composition and fish consumption of Double-crested Cormorants from the Pigeon and Snake Island colonies of eastern Lake Ontario in 2000. NYSDEC Special Report, Section 5: 1–9.

Johnson, J. H., R. M. Ross, R. D. McCullough & B. Edmonds, 2001b. Diet composition and fish consumption of Double-crested Cormorants from the Little Galloo Island colony of eastern Lake Ontario in 2000. NYSDEC Special Report, Section 3: 1–7.

Johnson, J. H., R. M. Ross, R. D. McCullough & B. Edmonds, 2003. Diet composition and fish consumption of Double-crested Cormorants from the Little Galloo Island colony of eastern Lake Ontario in 2002. NYSDEC Special Report, Section 3: 1–8.

Johnstone, I. G., M. P. Harris, S. Waneless & J. A. Graves, 1990. The usefulness of pellets for assessing the diet of adult Shags *Phalacrocorax aristotelis*. Bird Study 37: 5–11.

Kerfoot, W. C., 1987. Cascading effects and indirect pathways. In Kerfoot, W. C. & A. Sih (eds), Predation: Direct and Indirect Impacts on Aquatic Communities. University of New England Press, Hanover, New Hampshire, 57–70.

Kirsch, E. M., 1995. Double-crested Cormorants along the upper Mississippi River. Colonial Waterbirds 18(Special Publication 1): 131–136.

Lantry, B. F., T. H. Eckert & C. P. Schneider, 1999. The relationship between the abundance of Smallmouth Bass and Double-crested Cormorants in the Eastern Basin of Lake Ontario. In Final Report: To Assess the Impact of Double-crested Cormorants Predation on the Smallmouth Bass and Other Fishers of the Eastern Basin of Lake Ontario. NYSDEC Special Report, February 1999, Section 12: 1–10.

Lewis, H. G., 1929. The Natural History of the Double-crested Cormorant. Ru-Mi-Loo Books, Ottawa, Ontario.

Ludwig, J. P. & C. L. Summer, 1997. Population status and diet of cormorants in Les Cheneaux Islands area. In Diana, J. S., G. Y. Belyea & R. D. Clark Jr. (eds), History, Status, and Trends in Populations of Yellow Perch and Double-crested Cormorants in Les Cheneaux Islands, Michigan. State of Michigan Department of Natural Resources, No. 17: 5–25.

Ludwig, J. P., C. N. Hull, M. E. Ludwig & H. J. Auman, 1989. Food habits and feeding ecology of nesting Double-crested Cormorants in the upper Great Lakes, 1986–1989. The Jack-Pine Warbler 67: 115–126.

Madenjian, C. P. & S. W. Gabrey, 1995. Waterbird predation of fish in western Lake Erie: a bioenergenics model application. Condor 97: 141–153.

Maruca, S. L., 1997. The impact of cormorant predation on yellow perch in Les Cheneaux Islands, Lake Huron. In Diana, J. S., G. Y. Belyea & R. D. Clark Jr. (eds), History, Status, and Trends in Populations of Yellow Perch and Double-crested Cormorants in Les Cheneaux Islands, Michigan. State of Michigan Department of Natural Resources, No. 17: 47–70.

Neuman, J., D. L. Pearl, P. J. Ewins, R. Black, D. V. Weseloh, M. Pike & K. Karwowski, 1997. Spatial and temporal variation in the diet of Double-crested Cormorants (*Phalacrocorax auritus*) breeding in the lower Great Lakes in the early 1990s. Canadian Journal of Fisheries and Aquatic Sciences 54: 1569–1584.

Ross, R. M. & J. H. Johnson, 1995. Seasonal and annual changes on the diet of Double-crested Cormorants: implications for Lake Ontario's fishery. Great Lakes Resource Review 2: 1–9.

Ross, R. M. & J. H. Johnson, 1999. Effect of altered salmonid stocking methods on cormorant predation in eastern Lake Ontario. In Final Report: To Assess the Impact of Double-crested Cormorants Predation on the Smallmouth Bass and Other Fishers of the Eastern Basin of Lake Ontario. NYSDEC Special Report, February 1999, Section 11: 1–10.

Russel, A. F., S. Wanless & M. P. Harris, 1995. Factors affecting the production of pellets by Shags *Phalacrocorax aristotelis*. Seabird 17: 44–49.

Schiavone, A., 2001. Double-crested Cormorant predation on Smallmouth Bass and other fishes of the eastern basin of Lake Ontario: summary of 2000 studies. NYSDEC Special Report: Section 1: 1–5.

Sokal, R. R. & F. J. Rohlf, 1995. Biometry (3rd edn.). W.H. Freeman and Company, New York, 887 pp.

Suter, W., 1995. The effect of predation by wintering cormorants *Phalacrocorax carbon* grayling *Thymallus thymallus* and trout (Salmonidae) populations: two case studies from Swiss rivers. Journal of Applied Ecology 32: 29–46.

Trauttmansdorff, J. & G. Wassermann, 1995. Number of pellets produced by immature cormorants *Phalacrocorax carbo sinensis*. Ardea 83: 133–134.

Vanni, M. J., 1987. Indirect effect of predators on age-structured prey populations: planktivorous fish and zooplankton. In Kerfoot, W. C. & A. Sih (eds), Predation: Direct and Indirect Impacts on Aquatic Communities. University of New England Press, Hanover, New Hampshire, 149–160.

Wanless, S., M. P. Harris & A. F. Russel, 1993. Factors influencing food-load sizes brought in by Shags *Phalacrocorax aristotelis* during chick rearing. Ibis 135: 19–24.

Warke, G. M. A. & K. R. Day, 1995. Changes in the abundance of cyprinid and percid prey affect the rate of predation by cormorants *Phalacrocorax carbo carbo* on salmon *Salmo salar* smolt in northern Ireland. Ardea 83: 157–166.

Weseloh, D. V. C. & P. J. Ewins, 1994. Characteristics of a rapidly increasing colony of Double-crested Cormorants (*Phalacrocorax auritus*) in Lake Ontario: population size reproductive parameters and band recoveries. Journal of Great Lakes Research 20: 443–456.

Wires, L. R., D. N. Carss, F. J. Cuthbert & J. J. Hatch, 2003. Transcontinental connections in relation to cormorant-fishery conflicts: perceptions and realities of a ''bete noire'' (black beast) on both sides of the Atlantic. Vogelwelt 124: 389–400.

Wires, L. R., F. J. Cuthbert, D. R. Trexel & A. R. Joshi, 2001. Status of the Double-crested Cormorant (*Phalacrocorax auritus*) in North America. Final Report to USFWS.

Ziljstra, M. & M. R. van Eerden, 1995. Pellet production and the use of otoliths in determining the diet of Cormorants *Phalacrocorax carbo sinensis*: trials with captive birds. Ardea 83: 123–131.