Diet shift of double-crested cormorants in eastern Lake Ontario associated with the expansion of the invasive round goby

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ABSTRACT

The proliferation of the invasive round goby (*Apollonia melanostoma*) in the Great Lakes has caused shifts in the trophic ecology in some areas. We examined the diet of double-crested cormorants (*Phalacrocorax auritas*) prior to, and immediately after, round goby population expansion at two colonies, Pigeon and Snake Islands, in eastern Lake Ontario from 1999 to 2007. Cormorant diet was determined from the examination of 10,167 pellets collected over the nine-year period. By the second year round gobies were found in the diet (2002 at Snake Island and 2003 at Pigeon Island) they were the main species consumed by cormorants at each colony. The dominance of round goby in cormorant diets had a significant effect on both daily fish consumption and seasonal trends in fish consumption compared to the pre-goby years. Seasonal differences that were observed during the pre-goby years were lost once gobies became the main diet component of cormorants. The rapid switch to a benthic prey such as round goby, from a largely limnetic fish diet demonstrates the adaptive foraging ability of cormorants. Round goby may act as a buffer for yellow perch and smallmouth bass, two sport fish impacted by cormorant predation in eastern Lake Ontario.

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Introduction

In recent decades populations of double-crested cormorants (*Phalacrocorax auritus*) have increased at a rate of 29% per year in the Great Lakes region (Weseloh et al., 1995) with population growth characteristics examined on some individual lakes (Blackwell et al., 2002). This increase has created concern regarding cormorant impacts on fish populations (Des Granges and Reed 1981; Bur et al., 1999; Johnson et al., 2002). Evidence has been presented that suggests no impacts (Craven and Lev, 1987; Neuman et al., 1997; Belyea et al., 1999) whereas other studies have documented localized impacts on sport fish populations (Burnett et al., 2002; Lantry et al., 2002; Rudstam et al., 2004; Fielder, 2008). Further complicating the ability to assess possible cormorant impacts on fish populations is the recent establishment and proliferation of the round goby (*Apollonia melanostoma*) in the Great Lakes (Walsh et al., 2007), a species that is now common in cormorant diets (Somers et al., 2003; Johnson et al., 2009) and has also been reported in the diets of cormorants in Europe (Bzoma, 1998).

Proliferation of invasive species in new habitats often results in an expansion of predator populations to make use of a new or increased food source (Strayer et al., 2006). Two recent invasive species in the Great Lakes, zebra mussels (*Dreissena polymorpha*) and quagga mussels (*D. bugensis*), are consumed by waterfowl and mussel availability has been shown to increase waterfowl usage in areas where dreissenids are abundant (Petrie and Knapton, 1999). In the Great Lakes round goby are thought to have altered energy pathways (Johnson et al., 2005; Dietrich et al., 2006), influence the growth rate of smallmouth bass (*Micropterus dolemieu*) (Steinhart et al., 2004), and adversely impact mottled sculpin (*Cottus bairdi*) populations (Janssen and Jude 2001). To what extent the presence of round goby in the Great Lakes may influence the feeding ecology of piscivorous waterbirds is unknown.

The eastern basin of Lake Ontario has been a frontier for examining cormorant-fish interactions with cormorant diet studies beginning there in 1992 (Neuman et al., 1997). Little Galloo Island, in New York waters supports the largest cormorant colony in the basin with annual assessments of cormorant diet being made since 1992 (Johnson et al., 2002; Johnson et al., 2009). The second and third largest cormorant colonies, Pigeon and Snake Islands, are located in Ontario Provincial waters. Although Neuman et al. (1997) examined cormorant diets at Pigeon and Snake Islands in 1992, this study had low sample size (197 adult cormorant pellets and 164 chick boli) and was limited temporally (only April–June). Consequently, a more intensive investigation on the diet of double-crested cormorants at Pigeon and Snake Islands was initiated in 1999 and continued through 2007. Since this period encompassed both pre-goby and post-goby periods it offered the

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potential to provide unique insight into the adaptive foraging behavior of the double-crested cormorant. The diet of cormorants in Lake Ontario has been shown to vary seasonally and be dominated by pelagic (i.e. alewife, three-spine stickleback) and bentho-pelagic (i.e. yellow perch) prey species with limited consumption of native benthic species such as slimy sculpin (*C. cognatus*) and darters (*Etheostoma spp.*) (Neuman et al., 1997; Johnson et al., 2002). Although consumption of round goby was anticipated it was unknown if cormorants would substantially alter their foraging behavior to fully exploit this new abundant benthic prey resource. Furthermore, if round goby were to become a major diet component of cormorants would it influence seasonal diet variation that was well documented in eastern Lake Ontario? The objectives of this research were (1) to determine annual diet and fish consumption, (2) assess seasonal and annual changes in diet composition, (3) assess changes in the diet of cormorants due to the presence of round goby, and (4) determine the contribution of smallmouth bass and yellow perch (*Perca flavescens*) in the diet.

Methods

Double-crested cormorant pellets, which provide the most cost-effective, representative, and non-intrusive means of assessing the diet of adult cormorants (Neuman et al., 1997; Johnson et al., 2006), were collected at both Pigeon (1 ha; 44° 04'N, 76° 33'W) and Snake (0.5 ha; 44° 11'N, 76° 32'W) Islands from late April and to early October, 1999–2007. This period was divided into three separate feeding phases, pre-chick (prior to chick hatch, generally through early June), chick (chicks present and being fed by adults, generally from early June to late July), and post-chick (no adult feeding of chicks generally after late July). These feeding phases were selected based on previous work on cormorant diets at Little Galloo Island (Johnson et al., 2002) due to differences in diet composition and daily fish consumption (i.e., number of fish per pellet). Pellets were collected on 1–3 times during each feeding phase and frozen until examination in the laboratory. A target sample size of 150 pellets per date was established using power analysis based on sample variability at Little Galloo Island (Ross and Johnson, 1999). In 2007 sample size was reduced to 85 pellets per date based on power analysis due to less variability in cormorant diets (i.e., predominately round goby). Target pellet sample size was not met at Pigeon Island in 2002 and 2003 when raccoons (*Procyon lotor*) gained access to the island which greatly reduced the number of cormorants nesting as well as nesting success.

In the laboratory, pellets were thawed and diagnostic materials (bones, otoliths, scales) were removed from each pellet and placed in vials of alcohol. Eye lenses were also removed and were used to determine the number of fish consumed in instances where the number of lens (divided by 2) exceeded the fish count from diagnostic material in some pellets. Diagnostic material and eye lenses were later examined under a dissecting microscope to determine diet composition and the number of fish per pellet. Diagnostic bones, otoliths and scales were compared to a reference collection of similar material from known specimens to aid in species identification. When empty pellets were encountered they were recorded as zero prey and included in the fish consumption analysis.

We followed the same procedure as Johnson et al. (2002) to estimate the annual fish consumption at Pigeon and Snake Islands. This method incorporates the use of a model developed by Weseloh and Casselman (1992) that estimates the number of cormorant feeding days for each feeding phase based on population size, age structure, and residence time. The population size (nest counts × 2) and fledgling productivity for each colony was provided by the Canadian Wildlife Service. Fledgling productivity at Pigeon Island averaged 1.1 fledglings per nest (range 0 [raccoons] to 1.8) and 1.6 (range 1.2 to 1.8) at Snake Island over the nine-year period. Although the number of pellets produced by cormorants in a 24-h period varies (Carss et al., 1997), many investigators consider the average to be a single pellet (Craven and Lev, 1987; Orta,

1992; Derby and Lovvorn, 1997). For this study we assumed that cormorants at Pigeon and Snake Islands produced a single pellet each day and each pellet (combined with a fecal correction factor) represented daily fish consumption for one cormorant. The fecal correction factor (1.042) was multiplied by the number of fish found in each pellet and represented diagnostic material that exits the cormorant in the feces (Johnson and Ross, 1996). Fish consumption and diet composition information were generated for each feeding phase so that the number of each species consumed during each phase could be estimated. Total diet composition was based on weighted means of the three feeding phases.

We estimated the biomass consumed by cormorants of four prey species (yellow perch, smallmouth bass, rock bass [*Ambloplites rupestris*], pumpkinseed [*Lepomis gibbosus*] by multiplying the average mass of each by the number consumed. Prey fish size was determined by measuring approximately 100 intact otoliths for each species from each feeding period. Otolith-length fish length relationships for smallmouth bass (Adams et al., 1999), yellow perch (Burnett et al., 2002), and rock bass and pumpkinseed (Ross et al., 2005) were used to estimate length and mass of each of these species consumed by cormorants at Pigeon and Snake Islands. Temporal variation in diet composition at the Pigeon and Snake Island colonies was estimated using the equation of Horn (1966).

$$C_\lambda = \frac{2 \sum\limits_{i=1}^{s} X_i Y_i}{\sum\limits_{i=1}^{s} X_i^2 + \sum\limits_{i=1}^{s} Y_i^2}$$

where:

C_λ	overlap value
s	total items in both categories
X_i	proportion of total diet of fish species X contributed by food taxon i.
Y_i	proportion of total diet of fish species Y contributed by food taxon i.

Overlap values can range from 0, when samples contain no food in common, to 1, when there is identical representation of food between samples. When using this formula, overlap values (C_λ) ≥ 0.60 are considered biologically significant (Zaret and Rand, 1971). A 2 × 3 factorial analysis of variance was performed to test for differences in the number of fish per pellet and seasonal trends in the number of fish per pellet between pre- and post-goby periods.

Results

From 1999 to 2007, annual counts of cormorant nests at Pigeon Island ranged from 325 to 2228 and at Snake Island from 411 to 1344. We examined a total of 10,167 pellets including 4472 from Pigeon Island and 5695 from Snake Island (Table 1). At both colonies the number of fish per pellet increased ($F_{1,46} = 25.47$, $P < 0.0001$) during the post-goby years (Table 1). Furthermore, there was a shift ($F_{2,46} = 13.05$, $P < 0.0001$) in the seasonal trend in the number of fish per pellet pre versus post-goby (Table 1). Prior to round goby being a major diet component at both colonies the number of fish per pellet decreased over the season from 22.4 (pre-chick feeding period) to 10.2 (post-chick feeding period) at Pigeon Island and 18.3 to 12.1 at Snake Island (Table 1). During post-goby years the number of fish per pellet was greatest during the post-chick feeding period at both colonies.

Round goby first appeared in the diet of cormorants at Snake Island in 2002 (1.6% of diet) and at Pigeon Island in 2003 (0.7% of diet) and by the second year gobies were the major fish consumed at each colony (Pigeon Island 36.0%, Snake Island 29.2%) (Tables 2a, 2b and 3). By the second year they were observed in the diet at both the Snake

Table 1
Number of pellets examined and mean number of fish per pellet by feeding period at Pigeon (PI) and Snake (SI) Islands during pre-goby years (1999–2003 PI, 1999–2002 SI) and post-goby years (2004–2007 PI, 2003–2007 SI).

Feeding period		Island	No. pellets	Fish/pellet
Pre-chick	Pre-goby	Pigeon	1089	22.4
		Snake	897	18.3
	Post-goby	Pigeon	516	15.9
		Snake	1049	22.5
Chick	Pre-goby	Pigeon	1039	13.1
		Snake	883	13.8
	Post-goby	Pigeon	535	13.8
		Snake	739	27.7
Post-chick	Pre-goby	Pigeon	893	10.2
		Snake	1109	12.1
	Post-goby	Pigeon	400	29.8
		Snake	1018	32.4

(29.2% in 2003) and Pigeon (36.0% in 2004) Island colonies round goby were numerically the primary prey consumed by cormorants. From 1999 to 2003 (pre-goby) threespine stickleback (*Gasterosteus aculeatus*) (28.9%), alewife (*Alosa pseudoharengus*) (22.6%) and yellow perch (19.9%) were numerically the primary prey of cormorants at Pigeon Island (Table 2a). Cyprinids (9.0%), rock bass (7.3%), slimy sculpin (*Cottus cognatus*) (6.1%), pumpkinseed (2.4%) and smallmouth bass (2.1%) all contributed at least 2% of the diet. From 2003 to 2007 (post-goby) round goby (79.4%) dominated the diet of cormorants at Pigeon Island (Table 2b). The three prey species that contributed most heavily to the diet pre-goby (i.e. threespine stickleback, alewife, yellow perch) declined to 0.8%, 8.3%, and 7.3%, respectively, from 2004 to 2007.

Temporal differences in diet composition were evident at the Pigeon Island colony from 1999 to 2003. Generally threespine stickleback (51.1%) were most abundant in the diet during the pre-chick feeding period, alewife (59.7%) during the chick feeding period, and yellow perch (39.3%) during the post-chick feeding period (Table 2a). The contribution of cyprinids, rock bass, and smallmouth bass in the diet was highest late in the feeding season whereas the contribution of slimy sculpin declined after the pre-chick feeding period (Table 2a). Except for alewife substantially increasing (30.1%) in the diet of cormorants during the chick feeding period, most seasonal differences in diet composition observed from 1999 to 2003 were not evident during post-goby years.

At the Snake Island colony, yellow perch was the major prey fish consumed (39.4%) from 1999 to 2002 (pre-goby) (Table 3b). Threespine stickleback (15.0%), cyprinids (14.1%), alewife (10.9%), rock bass (6.7%), pumpkinseed (6.2%) and slimy sculpin (4.3%) all contributed at least 2% of the diet at this time. From 2003 to 2007, round goby was the major prey (74.7%) of cormorants at Snake Island with yellow perch declining to 11.1% of the diet (Table 3b). Cyprinids (4.1%), alewife (2.9%), and rock bass (2.0%) were the next most abundant prey in cormorant diets from Snake Island post-round goby.

Table 2b
Annual percent diet composition of double-crested cormorants (*Phalacrocorax auritas*) from Pigeon Island by feeding period, eastern Lake Ontario post-goby years (2004–2007).

	Pre-chick	Chick	Post-chick	Total
Round goby	81.1	53.1	86.4	79.4
Alewife	5.5	30.1	1.1	8.3
Yellow perch	5.5	7.9	8.2	7.3
Cyprinid	1.4	2.1	1.4	1.7
Rock bass	1.0	2.3	1.8	1.7
3 spine stickleback	1.3	2.7	0.6	0.8
Slimy sculpin	3.3	0.5	–	0.3
Smallmouth bass	0.4	1.1	0.2	0.3
Pumpkinseed	0.1	0.1	0.2	0.1
Other	0.4	0.1	0.1	0.1

The seasonal variation in diet composition during pre-goby years observed at Snake Island was not as evident as at Pigeon Island. Yellow perch were the main fish consumed by cormorants at Snake Island during each feeding period during pre-goby years with the highest contribution occurring in the diet during the post-chick feeding period (52.0%) (Table 3a). Similar to Pigeon Island, threespine stickleback contributed most heavily to the diet during the pre-chick feeding period (27.9%) and alewife increased substantially in the diet during the chick feeding period (25.2%) (Table 3a). Also during the pre-goby years at Snake Island the contribution of rock bass in the diet increased over the season while the contribution of slimy sculpin decreased. At Snake Island during post-goby years the contribution of threespine stickleback in the diet was again highest during the pre-chick feeding period (6.7%) as was the contribution of alewife during the chick feeding period (8.2%); however, these values were much lower than during the pre-goby period (Table 3b). As at Pigeon Island, the contribution of round goby in the diet at Snake Island was highest during the post-chick feeding period.

Mean diet overlap among feeding periods during pre-goby years at Pigeon Island was low ($\bar{x} = 0.41$, range 0.35 to 0.50) but increased substantially post-goby ($\bar{x} = 0.83$, range 0.81 to 0.84). At Snake Island, mean diet overlap among feeding periods was 0.80 (range 0.79 to 0.82) during pre-goby and 0.98 (range 0.98 to 0.99) during post-goby years.

From 1999 to 2007, we estimate that cormorants from Pigeon Island consumed 87.6 million fish. The dominant fish consumed were round goby (38.8 million), alewife (12.6 million), threespine stickleback (11.4 million), and yellow perch (11.1 million) (Fig. 1a). Cormorants from this colony also ate 4.6 million rock bass, 3.9 million cyprinids, 2.6 million slimy sculpin, 1.0 million smallmouth bass, and 1.0 million pumpkinseed. From 1999 to 2007 cormorants from the Snake Island colony consumed an estimated 75.9 million fish including 35.1 million round goby, 16.6 million yellow perch, 6.0 million cyprinids, 5.2 million threespine stickleback, 4.5 million alewife, 2.9 million rock bass, 2.4 million pumpkinseed, and 1.7 million slimy sculpin (Fig. 1b). Annual consumption of yellow perch and smallmouth bass decreased by 58%

Table 2a
Annual percent diet composition of double-crested cormorants (*Phalacrocorax auritas*) from Pigeon Island by feeding period, eastern Lake Ontario pre-goby years (1999–2003).

	Pre-chick	Chick	Post-chick	Total
3 spine stickleback	51.1	15.1	0.2	28.9
Alewife	4.5	59.7	17.5	22.6
Yellow perch	18.3	9.2	39.3	19.9
Cyprinid	6.9	4.0	18.2	9.0
Rock bass	4.3	6.0	13.0	7.3
Pumpkinseed	2.8	0.3	2.4	2.4
Smallmouth bass	0.4	2.6	4.4	2.1
Other	1.7	0.3	1.9	1.6
Round goby	0.2	0.1	–	0.1

Table 3a
Annual percent diet composition of double-crested cormorants (*Phalacrocorax auritas*) by feeding period from Snake Island eastern Lake Ontario pre-goby years (1999–2002).

	Pre-chick	Chick	Post-chick	Total
Yellow perch	34.9	31.4	52.0	39.4
3 spine stickleback	27.9	15.6	1.2	15.0
Cyprinid	11.5	11.0	19.7	14.1
Alewife	1.9	25.2	6.1	10.9
Rock bass	3.5	7.9	9.3	6.7
Pumpkinseed	9.2	3.1	4.7	6.2
Slimy sculpin	8.2	3.4	1.6	4.3
Other	2.8	1.4	2.3	2.2
Smallmouth bass	0.1	1.0	1.5	0.9
Round goby	–	–	1.6	0.3

Table 3b
Annual percent diet composition of double-crested cormorants (*Phalacrocorax auritas*) by feeding period from Snake Island eastern Lake Ontario post-goby years (2003–2007).

	Pre-chick	Chick	Post-chick	Total
Round goby	66.3	68.1	78.4	74.7
Yellow perch	10.4	14.6	9.9	11.1
Cyprinid	4.6	3.6	4.5	4.1
Alewife	1.4	8.2	1.2	2.9
Rock bass	1.7	2.5	2.6	2.0
3 spine stickleback	6.7	1.4	0.7	1.8
Pumpkinseed	3.5	0.3	1.0	1.3
Slimy sculpin	4.4	0.2	0.3	1.1
Smallmouth bass	0.3	0.7	0.5	0.5
Other	0.7	0.4	0.9	0.5

(4.60 million/year to 1.95 million/year) and 68% (0.23 million/year to 0.07 million/year) respectively, during the post-goby period (Fig. 2).

By examining the otoliths recovered in the pellets we estimated the average size of yellow perch, smallmouth bass, rock bass, and pumpkinseed consumed by cormorants from these colonies to be 130 mm (24 g), 160 mm (50 g), 110 mm (26 g), and 110 mm (26 g), respectively. Multiplying the average mass of each species by the estimated total number consumed yielded an estimate of 665,000 kg (73,900 kg/year) of yellow perch, 194,000 kg (21,500 kg/year) of rock bass, 87,000 kg (9,700 kg/year) of pumpkinseed and 50,000 kg (5,600 kg/year) of smallmouth bass consumed by cormorants from Pigeon and Snake Islands from 1999 to 2007. Mean annual biomass of yellow perch and smallmouth bass consumed decreased by 58% (69,300 kg/year to 29,200 kg/year) and 79% (13,200 kg/year to 2,800 kg/year) respectively, during the post-goby period (Fig. 2).

Discussion

Double-crested cormorants are opportunistic predators (Lewis, 1929; Seefelt and Gillingham, 2006) that consume prey based on energetic profitability (Belyea et al., 1999). Their opportunistic foraging behavior likely resulted in the differences observed during pre- and post-goby years at Pigeon and Snake Islands in regard to the estimated
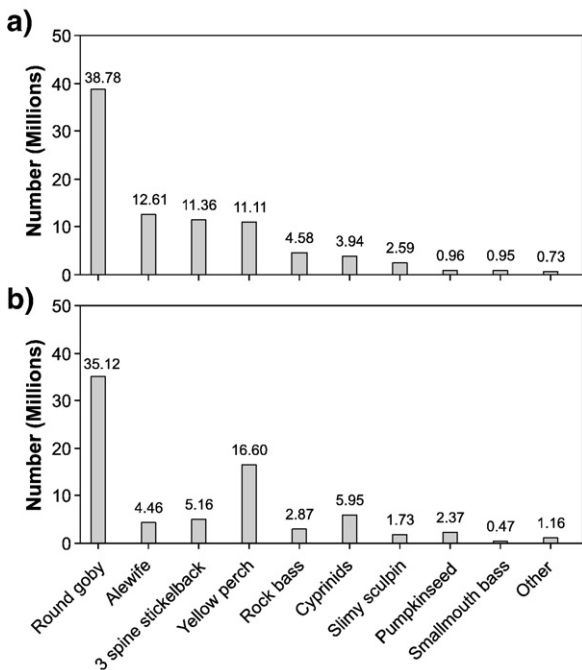
Fig. 1. Estimated number of fish consumed by double-crested cormorants from the a) Pigeon and b) Snake Island colonies in eastern Lake Ontario, 1999–2007.
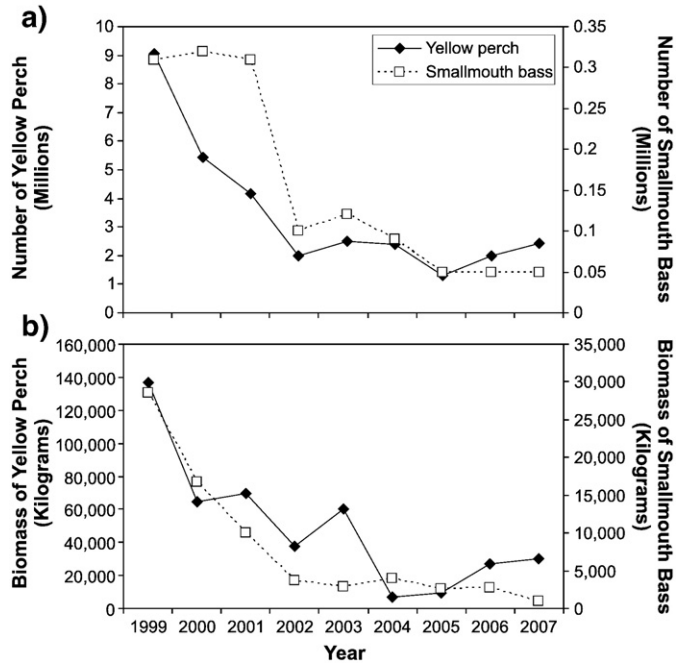
Fig. 2. Estimated a) number and b) biomass of yellow perch and smallmouth bass consumed annually by double-crested cormorants at Pigeon and Snake Islands, Lake Ontario 1999–2007.

number of fish consumed daily as well as seasonal trends in the number of fish consumed per day. Pre-goby, daily fish consumption (fish/pellet) declined over the season. From an energetic standpoint cormorants likely require more energy per day during the pre-chick feeding and chick feeding period than during the post-chick feeding period. Although daily fish consumption declined at both colonies during the chick feeding period during pre-goby years, alewives became a major component of the diet during this period. Adult alewives which were moving inshore to spawn at this time, and thus became seasonally available to cormorants, have high caloric value compared to most other species that are common in cormorant diets (Rottiers and Tucker, 1982). However, the caloric value of alewife has been shown to fluctuate seasonally with their energy density being lowest from May through August (Rand et al., 1994), an interval that encompasses portions of all three cormorant feeding periods.

The significant increase in daily fish consumption post-goby suggests that round goby, which made up 79% of the diet of cormorants at Pigeon Island and 75% at Snake Island, may be of lower caloric value than the prey fish that dominated cormorant diets during pre-goby years. Unlike pre-goby years when daily fish consumption decreased over the season, daily fish consumption generally increased (except during the chick feeding period at Pigeon Island) over the season post-goby with the highest consumption occurring during the post-chick feeding period. This seems counter intuitive when considering the energetic needs of cormorants associated with reproduction and feeding chicks and may be related to changes in the energy content of the prey. At both colonies the contribution of round goby in the diet was highest during the post-chick feeding period. Since the energy density of round goby during the cormorant nesting period in eastern Lake Ontario is similar to that of alewives (B. Lantry, USGS, pers. comm.) the lower caloric value is likely due to smaller fish being consumed during the post-goby period, or, perhaps, increased energy demands associated with the switch to a benthic prey species.

During pre-goby years, diet composition at both Pigeon and Snake Islands was similar to what has been reported for cormorants throughout the Great Lakes (Belyea et al., 1999; Neuman et al., 1997; Johnson et al., 2002; Hebert and Morrison, 2003). Similar to our findings, most of these studies found seasonal variation in cormorant diets with yellow

perch and alewife being major components of the diets. Previous studies at Pigeon and Snake Islands carried out in 1992 by Neuman et al. (1997) found that centrarchids were the major component of the diet of cormorants during the pre-chick feeding period. This was not observed in this study as centrarchids made up only 7.5% and 12.8% of the diet of cormorants at Pigeon (1999–2003) and Snake (1999–2002) Islands, respectively. Neuman et al. (1997) did find that alewives dominated fish found in chick boli at Pigeon and Snake Islands. This is the same time period (i.e. chick feeding period) when we found alewives to be major components of the diet at Pigeon (59.7%) and Snake (25.2%) Islands.

The dominance of round goby in the diet of cormorants at Pigeon and Snake Islands during the post-goby years greatly reduced the seasonal variation in diet composition compared to pre-goby years. This was especially true at Pigeon Island where threespine sticklebacks (pre-chick period), alewife (chick period), and yellow perch (post-chick period) each dominated the diet at specific times during the pre-goby period. Once round goby were established in the diet of cormorants they were the main prey fish consumed during each feeding period at both colonies. Only at Pigeon Island, which is more of an off-shore colony compared to Snake Island, did any prey species (alewife) exhibit a similar seasonal trend in consumption post-goby.

The rapid switch to round goby in the diet of cormorants at these two colonies further illustrates both the opportunistic and adaptive abilities of this predator. Not only did cormorants switch to a newly abundant prey species, but in doing so completely changed their foraging behavior. Cormorants from these two colonies switched their foraging behavior from primarily a limnetic (alewife and threespine stickleback) and demersal (yellow perch) strategy to a benthic foraging strategy to take advantage of abundant prey that were located near the substrate.

From 1999 to 2007 (9 years) we estimate that cormorants from Pigeon and Snake Islands consumed about 164 million fish, an average of 18.2 million fish per year. At nearby Little Galloo Island in eastern Lake Ontario Johnson et al. (2002) estimated that over the nine-year period from 1992 to 2000 cormorants from that colony consumed an average of 32.8 million fish per year. However, management actions initiated in 1999 to limit reproductive success of cormorants at Little Galloo Island have reduced fish consumption at that colony to 16.2 million per year (Johnson et al., 2009). Consequently, from 1999 to 2007 cormorants from these three colonies consumed about 34.4 million fish annually.

During pre-goby years, yellow perch was a large component of the diet at Pigeon Island (19.9%) and the major prey of cormorants at Snake Island (39.4%). Yellow perch have also been found to be a major component of the diet of cormorants in several other studies (Belyea et al., 1999; Johnson et al., 2002; Van DeValk et al., 2002; Hebert and Morrison, 2003) and some studies have reported negative impacts on perch populations (Burnett et al., 2002; Rudstam et al., 2004; Fielder 2008). During post-goby years, the contribution of yellow perch in the diet declined to 7.3% at Pigeon Island and 11.1% at Snake Island. Estimated average annual consumption of yellow perch pre-goby was 1.89 million at Pigeon Island and 2.85 million at Snake Island. Post-goby these consumption estimates decreased to 0.89 million at Pigeon Island and 1.04 million at Snake Island. Consequently, we estimate that about 13 million fewer yellow perch were consumed from 2003 to 2007 when cormorants from these two colonies switched their diet to primarily round goby. Similarly, about 600,000 fewer smallmouth bass were consumed at these colonies post-goby.

Invasive species often exhibit exponential population growth when colonizing new habitats (Sakai et al., 2001). This period is usually followed by a decline in abundance ultimately attaining a population size lower than the initial maxima. It is likely that during this study round goby had reached peak levels of abundance in eastern Lake Ontario (1999–2007) and had not yet begun to decline. Consequently, this study may describe peak consumption of round goby by cormorants in eastern Lake Ontario. If round goby remain the major diet component of cormorants in eastern Lake Ontario, it could influence the residency

time of birds on the lake. Historically, the seasonal availability of alewife (present in near-shore waters only when spawning in June and July) has had a major effect on cormorant diet composition. A permanent shift to round goby, which remain abundant in near-shore waters throughout the year, as their major prey could allow cormorants to return earlier and remain later at eastern Lake Ontario colonies.

This study, which encompassed the rapid colonization of round gobies in Lake Ontario, demonstrates both the importance of this invasive benthic species in the trophic ecology of the lake ecosystem as well as the adaptive foraging behavior of double-crested cormorants to switch from largely pelagic prey to a benthic prey species. Unlike the pre-goby years when the consumption of seasonally available fish species led to temporal variation in diet composition, there is now little temporal variation in diet composition as round goby dominate the diet throughout the season. The significant increase in daily fish consumption during post-goby years suggests that gobies have less energy value than the species they replaced in the diet of cormorants. The dominance of round gobies in the diet of cormorants at the Pigeon and Snake Island colonies and concurrent reductions in the consumption of yellow perch and smallmouth bass suggests that gobies may be buffering predation on these species that have been previously shown to be impacted by cormorant predation in the eastern basin of Lake Ontario.

Acknowledgments

References

Adams, C.M., Schneider, C.P., Johnson, J.H., 1999. Predicting the size and age of smallmouth bass consumed by double-crested cormorants in eastern Lake Ontario, 1993–94. 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. New York State Dep. of Envir. Conserv. Albany, NY, pp. 6-1–6-8.

Belyea, G.Y., Maruca, S.L., Diana, J.S., Scneeberger, P.J., Scott, S.J., Clark Jr., R.D., Ludwig, J. P., Summer, C.L., 1999. Impact of double-crested cormorant predation on the yellow perch population in the Les Cheneaux Islands of Michigan. In: Tobin, M.E. (Ed.), Symposium on double-crested cormorants: population, status and management issues in the Midwest; 9 December 1997; Milwaukee, WI. Tech. Bull. 1879. U. S. Department of Agriculture, Animal and Plant Health Inspection Service, pp. 47–60. M.E. Tobin, Tech. Coord.

Blackwell, B.F., Stapanian, M.A., Weseloh, D.V.C., 2002. Dynamics of the double-crested cormorant population on Lake Ontario. Wildlife Soc. Bull. 30, 345–353.

Bur, M.T., Tinnirello, S.L., Lovell, C.D., Tyson, J.T., 1999. Diet of the double-crested cormorant in western Lake Erie. In: Tobin, M.E. (Ed.), Symposium on double-crested cormorants: population, status and management issues in the Midwest; 9 December 1997; Milwaukee, WI. Tech. Bull. 1879. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, pp. 73–85. M.E. Tobin, Tech. Coord.

Burnett, J.A., Ringler, N.H., Lantry, B.F., Johnson, J.H., 2002. Double-crested cormorant predation on yellow perch in the eastern Basin of Lake Ontario. J. Great Lakes Res. 28, 202–211.

Bzoma, S., 1998. The contribution of round goby (Neogobius melanostomus Pallas, 1811) to the food supply of cormorants (Phalacrocorax carbo Linnaeus, 1758) feeding in the Puck Bay. Bull. Sea Fish Institute 2, 39–47.

Carss, D.N., et al., 1997. Techniques for assessing cormorant diet and food intake: towards a consensus view. In: Baccetti, N., Cherubini, G. (Eds.), European Conference on Cormorants: Supplement alle. Ricerche di Bilogia della Selvaggina, vol. 26, pp. 197–230.

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

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

Des Granges, J.L., Reed, A., 1981. Disturbance and control of selected colonies of double-crested cormorants in Quebec. Colon. Waterbirds 4, 12–19.

Dietrich, J.P., Morrison, B.J., Hoyle, J.A., 2006. Alternative ecological pathways in the eastern Lake Ontario food web-round goby in the diet of lake trout. J. Great Lakes Res. 32, 395–400.

Fielder, D.G., 2008. Examination of factors contributing to the decline of yellow perch population and fishery in Les Cheneaux Islands. Lake Huron with emphasis on the role of double-crested cormorants. J. Great Lakes Res. 34, 506–523.

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

Horn, H.S., 1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100, 419–424.

Janssen, J., Jude, D.J., 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calument Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. J. Great Lakes Res. 27, 319–328.

Johnson, J.H., Ross, R.M., McCullough, R.D., 2002. Little Galoo Island. Lake Ontario: a review of nine years of double-crested cormorant diet and fish consumption information. J. Great Lakes Res. 28, 182–192.

Johnson, J.H., Ross, R.M., 1996. Pellets versus feces: their relative importance in describing the food habits of double-crested cormorants. J. Great Lakes Res. 22, 795–798.

Johnson, J.H., McCullough, R.D., Ferquhar, J.F., 2009. Double-crested cormorant studies at Little Galloo Island, Lake Ontario 2008: diet composition, fish consumption, and the efficacy of management activities in reducing fish predation. Annual Report New York State Department of Environmental Conservation Bureau of Fisheries Lake Ontario Unit and St. Lawrence River Unit to Great Lakes Fishery Commission's Lake Ontario Committee. Section 14.

Johnson, J.H., Ross, R.M., McKenna, J.E., Lewis, G.E., 2006. Estimating the size of fish consumed by double-crested cormorants: considerations for better understanding cormorant–fish interactions. J. Great Lakes Res. 32, 91–101.

Johnson, T.B., Bunnell, D.B., Knight, C.T., 2005. A potential new energy pathway in central Lake Erie: the round goby connection. J. Great Lakes Res. 31 (Suppl. 2), 238–251.

Lantry, B.F., Eckert, T.H., Schneider, C.P., Chrisman, J.R., 2002. The relationship between the abundance of smallmouth bass and double-crested cormorants in the eastern basin of Lake Ontario. J. Great Lakes Res. 28, 193–201.

Lewis, H.F., 1929. The natural history of the double-crested cormorant (*Phalacrocorax auritus auritus* L). Ru-Mi-Lou Books, Ottawa, Ont.

Neuman, J., Pearl, D.L., Ewins, P.J., Black, R., Weseloh, D.V., Pike, M., Karwowski, K., 1997. Spatial and temporal variation in the diet of double-crested cormorants (*Phalacrocorax auritus*) breeding on the lower Great Lakes in the early 1900 s. Can. J. Fish. Aquat. Sci. 54, 1569–1584.

Orta, J., 1992. Family Phalacrocoracidae (cormorants). In: Del Hoyo, J., Elliot, A., Sargatal, J. (Eds.), Handbook of the birds of the world: Lynx Edicions, Barcelona, vol. 1, pp. 326–353.

Petrie, S.A., Knapton, R.W., 1999. Rapid increase and subsequent decline of zebra and quagga muscles in Long Point Bay. Lake Erie: possible influence of waterfowl predation. J. Great Lakes Res. 25, 772–782.

Rand, P.S., Lantry, B.F., O'Gorman, R., Owens, R.W., Stewart, D.J., 1994. Energy density and size of prey fishes in Lake Ontario, 1978–1990: implications for salmonine energetics. Trans. Am. Fish. Soc. 123, 519–534.

Ross, R.M., Johnson, J.H., 1999. Fish losses to double-crested cormorants in eastern Lake Ontario, 1992–1997. In: Tobin, M.E. (Ed.), Symposium on double-crested cormorants: population, status and management issues in the Midwest; 9 December 1997; Milwaukee, WI. Tech. Bull. 1879. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, pp. 61–70. M.E. Tobin Tech Coord.

Ross, R.M., Johnson, J.H., Adams, C., 2005. Use of fish otolith-length regressions to infer size of double-crested cormorant prey fish from recovered otoliths in Lake Ontario. Northeastern Nat. 12, 133–140.

Rottiers, D.V., Tucker, R.M., 1982. Proximate composition and caloric content of 8 Lake Michigan fishes. U.S. Fish and Wildlife Service Tech. Paper, p. 108.

Rudstam, L.G., Van DeValk, A.J., Adams, C.M., Coleman, J.T.H., Forney, J.L., Richmond, M. E., 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake, New York. Ecol. Appl. 14, 149–163.

Sakai, A.K., et al., 2001. The population biology of invasive species. Annu. Rev. Ecol. Syst. 32, 305–332.

Seefelt, N.E., Gillingham, J.C., 2006. A comparison of three methods to investigate the diet of breeding double-crested cormorants (*Phalacrocorax auritus*) in the Beaver Archipelago, northern Lake Michigan. Hydrobiologia 567, 57–67.

Steinhart, G.B., Stein, R.A., Marschall, E.A., 2004. High growth rate of young-of-the-year smallmouth bass in Lake Erie: a result of the round goby invasion? J. Great Lakes Res. 30, 381–389.

Strayer, D.L., Eviner, V.T., Jeschke, J.M., Pace, M.L., 2006. Understanding the long-term effects of species invasions. Trends Ecol. Evol. 21, 645–651.

Somers, C.M., Lozer, M.N., Kjoss, V.A., Quinn, J.S., 2003. The invasive round goby (*Neogobius melanostomus*) in the diet of nesting double-crested cormorants (*Phalacrocorax auritus*) in Hamilton Harbor, Lake Ontario. J. Great lakes Res. 29, 392–399.

Van DeValk, A.J., Adams, C.M., Rudstam, L.G., Forney, J.L., Brooking, T.E., Gerken, M., Young, B., Hooper, J., 2002. Comparison of angler and cormorant harvest of walleye and yellow perch in Oneida Lake, New York. Trans. Am. Fish. Soc. 131, 392–399.

Walsh, M.G., Dittman, D.E., O'Gorman, R.O., 2007. Occurrence and food habits of the round goby in the profundal zone of southwestern Lake Ontario. J. Great Lakes Res. 33, 83–92.

Weseloh, D.V., Casselman, J., 1992. Calculated fish consumption by double-crested cormorants in eastern Lake Ontario. Col. Waterbird Soc. Bull. 16, 63–64.

Weseloh, D.V., Ewins, P.J., Struger, J., Mineau, P., Bishop, C.A., Postupalsky, S., Ludwig, J. P., 1995. Double-crested cormorants of the Great Lakes: changes in population size, breeding distribution, and reproductive output between 1913 and 1991. Colonial Waterbirds **18**(Spec. Publ. 1), pp. 48–59.

Zaret, T.M., Rand, A.S., 1971. Competition in tropical stream fishes support for the competitive exclusion principle. Ecology 52, 336–342.