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Spatial and temporal comparisons of double-crested cormorant diets following the establishment of alewife in Lake Champlain, USA

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ABSTRACT

Increasing numbers of double-crested cormorants (*Phalacrocorax auritus*) on Lake Champlain have caused concerns related to potential impacts on the yellow perch (*Perca flavescens*) population. However, with the establishment of alewife (*Alosa pseudoharengus*) in 2003, cormorant foraging may have changed. We examined cormorant diets from four areas of Lake Champlain to assess past, current, and potential future impacts of cormorants on the changing fish community. During the breeding seasons of 2001–2002 and 2008–2009, we observed spatial and temporal differences in cormorant diets. Yellow perch dominated diet composition during 2001–2002 at Young Island (73% and 90% yearly weight totals) during all reproductive periods. Four Brothers Islands diet composition in 2002 varied according to reproductive period. In 2008 and 2009, alewife were predominant in diets at Four Brothers Islands (56% and 71%) and the South site (65% and 62%), with yellow perch comprising a high proportion of diets at Young Island (44% and 56%). Results from a MANOVA confirmed differences among sites, reproductive period, and the interaction of these factors ($P<0.0001$) when describing diet compositions for the post-alewife years. PCA results denoted a general shift in cormorant diets from 2001–2002 to 2008–2009. Our study demonstrated that the diet of piscivorous birds may shift with a new forage species and may vary significantly within a single large water body. Accordingly, efforts to manage piscivorous birds with the intent to decrease mortality of specific fish species should be site specific when possible.

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Introduction

Double-crested cormorants (*Phalacrocorax auritus*; hereafter cormorants) are piscivorous, opportunistic predators that feed on a variety of fish species near their roosting areas and other nearby water bodies (Custer and Bunck, 1992; Hatch and Weseloh, 1999; Coleman et al., 2005; Seefelt and Gillingham, 2006). On many lakes where cormorants have established nesting colonies, declines in resident sportfish populations, such as yellow perch (*Perca flavescens*) (Burnett et al., 2002; Rudstam et al., 2004; Fielder, 2008, 2010), walleye (*Sander vitreus*) (Rudstam et al., 2004), and smallmouth bass (*Micropterus dolomieu*) (Lantry et al., 2002), have been observed. There are also concerns about cormorants feeding on newly stocked walleye and salmonids (Ross and Johnson, 1999; Blackwell et al., 1997; Jensen, 2001). As public pressure for cormorant management increases, a detailed assessment of cormorant feeding patterns is needed to guide effective management.

Like many other large lakes in the Midwest and Northeast, Lake Champlain has experienced increasing numbers of cormorants since the 1970s (Hatch, 1995; Weseloh et al., 1995; Weseloh et al., 2002). Lake Champlain is located between the states of New York and Vermont, USA, and Quebec, Canada, and drains into the Richelieu River and eventually into the St. Lawrence River (Fig. 1). Cormorants on Lake Champlain have been managed by federal and state agencies

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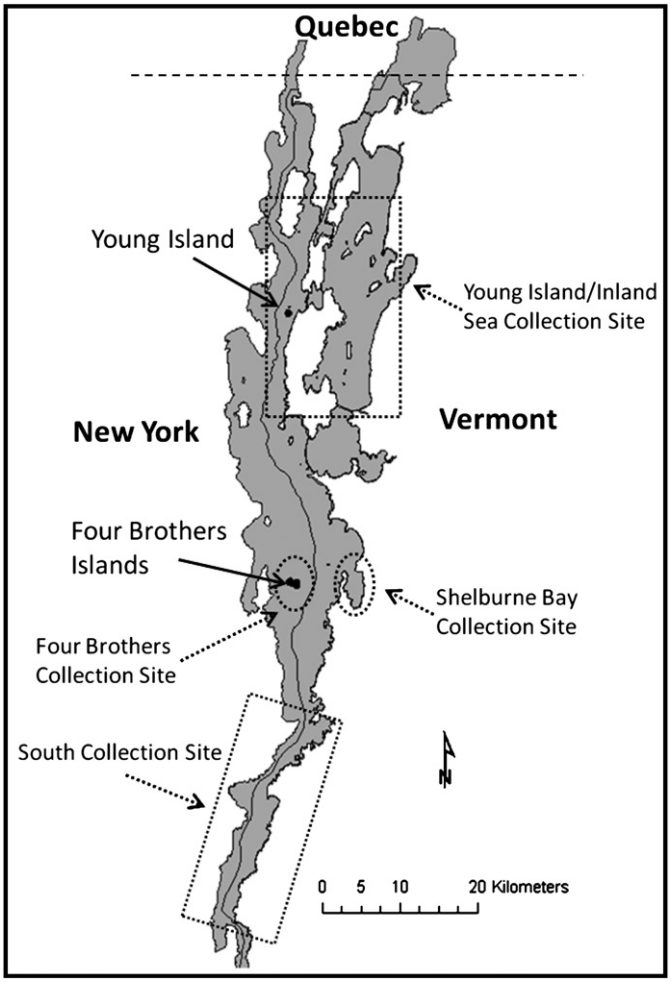

Fig. 1. Map of Lake Champlain with the major cormorant colonies (Young and Four Brothers Islands) and collection sites (Four Brothers, Shelburne Bay, South, and Young Island/Inland Sea) labeled.

to minimize the destruction of vegetation and concomitant effects on co-nesting species. In 1999, an egg-oiling program was initiated on the Young Island colony (Grand Isle, VT) to reduce reproductive success and control population levels of nesting cormorants. Management later included a culling program to more rapidly reduce cormorant numbers as a means of restoring native vegetation to the colony island. In the past decade, anglers have also expressed concerns about cormorant foraging on local sportfish populations, particularly yellow perch (John Gobeille, Vermont Fish and Wildlife Department, personal communication).

Cormorant impacts can vary across systems, and potential angler–cormorant conflicts should be addressed with system-specific information. Although cormorant impacts on sportfish populations have been documented in some systems (Rudstam et al., 2004; Fielder, 2010; Dorr et al., 2010), studies on cormorant foraging habits in other locations have found that cormorants feed on fish and invertebrates not targeted by commercial fishermen or recreational anglers (Craven and Lev, 1987; Ludwig et al., 1989; Seefelt and Gillingham, 2006; Diana et al., 2006; Johnson et al., 2010). Neuman et al. (1997) compared cormorant diets from multiple sites in the Great Lakes region and found large variations spatially and temporally, suggesting that using diet data from one site to infer the impact of cormorants at another site is inappropriate. The contrasting results from studies assessing cormorant impacts on sportfish populations stress the need to base management on local conditions.

Changes in prey fish availability can result in changes in cormorant diets and potential impacts on fish communities. Smallmouth bass and yellow perch populations in eastern Lake Ontario were negatively affected by cormorants in the 1990s (Burnett et al., 2002; Lantry et al., 2002). However, since then, round goby (*Neogobius melanostomus*) has become established in eastern Lake Ontario and currently constitutes up to 93% of the diet (by number) of cormorants nesting on Little Galloo, Snake, and Pigeon Islands (Johnson et al., 2006, 2010). Therefore, the presence of round goby in cormorant diets should reduce cormorant foraging on previously impacted sportfish. Similar diet switches may occur in other areas where a new invasive fish becomes established, and therefore, the potential impacts of cormorants.

Alewife (*Alosa pseudoharengus*) were first observed in Lake Champlain in 2003 and by 2007 had spread throughout the lake and are now reproducing naturally (Marsden and Hauser, 2009). With the introduction of alewife to Lake Champlain, cormorants were presented with a new prey item as observed in the Great Lakes (Neuman et al., 1997; Seefelt and Gillingham, 2006; Diana et al., 2006). This potential change in cormorant foraging pattern highlights the need for updated diet information in Lake Champlain.

Data regarding the diet composition of cormorants on Lake Champlain have been collected, but none after the establishment of alewife. Fowle (1997) collected undigested remains of fish regurgitated by cormorant chicks on Young Island in 1995 and 1996 and found that yellow perch represented more than 78% of the total regurgitate biomass collected each year; however, it was concluded that cormorants probably were not significantly affecting yellow perch populations. Because of increasing concerns about impacts of cormorants on fish populations in Lake Champlain and recent changes in the fish community, a comparison of the diet composition of cormorants before and after alewife establishment is important. Accordingly, the objectives of the present study were to (1) determine cormorant diet composition prior to and since alewife establishment by comparing diets in 2008–2009 to those from 2001–2002; and (2) investigate temporal and geographical differences in diet composition within a breeding season.

Methods

Field collection

Lake Champlain is located on the border between New York and Vermont, USA, and extends into Quebec, Canada (Fig. 1). In 2001 and 2002, cormorants were followed from breeding colonies (Young Island and Four Brothers Islands) to foraging locations and collected with shotguns as they returned to the colony during four reproductive

Table 1
Number of cormorant stomach samples collected from sampling locations during each reproductive period on Lake Champlain containing identifiable stomach contents during the pre-alewife (2001–2002) and post-alewife (2008–2009) periods.

		Reproductive period				
Year	Collection site	Incubation	Nestling	Fledgling	Post-fledgling	Total
2001	Young Island	5	35	16	12	68
2002	Four Brothers	10	12	3	2	27
	Young Island	7	14	8	7	36
2008	Four Brothers	20	19	17	17	73
	Shelburne Bay	2	15	2	18	37
	South	17	20	13	17	67
	Young Island	19	18	20	21	78
2009	Four Brothers	20	19	20	18	77
	Shelburne Bay	3	6	16	16	41
	South	20	17	20	20	77
	Young Island	15	17	20	16	68

stages (incubation, nestling, fledgling, and post-breeding). During 2008 and 2009, cormorants were collected after foraging within the sampling locations or when returning to colonies from a sampling location. The birds were collected with a shotgun during control operations conducted by Vermont Wildlife Services from four locations on Lake Champlain. These locations included the 'inland sea' and Young Island vicinity (YI); Shelburne Bay, east of Four Brothers Islands (SB); waters near Four Brothers Islands (FB); and the southern portion of the lake, south of Sloop Island (South). Collection sites varied such that SB and YI are generally shallower (<43 m) with yellow perch and other warm-water fishes present; whereas FB and South areas are generally deeper (>43 m) with alewife, emerald shiner (*Notropis atherinoides*), and rainbow smelt (*Osmerus mordax*) present. Collections were distributed over time such that approximately 20 birds were collected from each location during each of the four reproductive stages. Attention was given to collect birds which had likely already foraged; however, cormorants were not followed from the colonies and observed foraging before collection as they were in 2001 and 2002. In all years, cormorants, or their removed stomachs, were frozen and stored for later processing.

Diet evaluation

Cormorants, or cormorant stomachs, were thawed and the stomach contents extracted. Diet items were identified to the lowest possible taxon. Total, standard, or backbone length and/or scales were taken from diet items when possible to aid in assigning weights to prey items. Weights of diet items were determined using standard length–weight regressions (Schneider et al., 2000) except for yellow perch and rainbow smelt. Lake specific length–weight relationships were developed from yellow perch collected in 2001 and 2002 (M. Eisenhower and D. L. Parrish, unpublished data) and whole rainbow

Table 2
Cormorant diet composition (% by number) from each sampling location during each of the four reproductive periods on Lake Champlain during pre-alewife (2001–2002) and post-alewife (2008–2009) time periods. Site = sampling location; period = reproductive period; n = total number of items in diet.

Year	Site	Period	n	Alewife	Cyprinid[a]	*Lepomis* spp.[b]	Rainbow smelt	Rock bass	White perch	Yellow perch	Other[c]	Unidentified
2001	Young Island	Incubation	66	–	1.5	7.6	0.0	0.0	0.0	84.8	1.5	4.5
		Nestling	558	–	2.5	2.0	32.1	0.0	0.5	54.1	3.9	4.8
		Fledgling	175	–	6.9	5.1	0.6	0.6	0.6	71.4	6.9	8.0
		Post-fledgling	749	–	11.6	0.3	74.6	0.0	0.0	12.4	0.3	0.8
2002	Four Brothers	Incubation	386	–	5.4	0.8	61.9	0.0	0.0	23.6	2.1	6.2
		Nestling	600	–	4.8	0.2	82.7	0.0	0.0	8.3	0.5	3.5
		Fledgling	24	–	0.0	0.0	66.7	0.0	0.0	25.0	4.2	4.2
		Post-fledgling	86	–	8.1	1.2	72.1	0.0	4.7	4.7	4.7	4.7
	Young Island	Incubation	169	–	0.0	0.0	53.8	0.0	0.0	42.0	0.6	3.6
		Nestling	214	–	1.4	2.8	1.9	0.0	0.0	91.6	0.9	1.4
		Fledgling	120	–	3.3	3.3	0.8	0.0	0.0	81.7	5.0	5.8
		Post-fledgling	102	–	2.0	2.0	0.0	0.0	26.5	54.9	1.0	13.7
2008	Four Brothers	Incubation	159	87.4	0.6	1.9	3.1	0.0	0.6	3.1	2.5	0.6
		Nestling	136	59.6	10.3	2.2	0.7	0.0	9.6	16.2	0.0	1.5
		Fledgling	384	0.5	0.0	0.0	98.4	0.0	0.0	0.8	0.0	0.3
		Post-fledgling	446	54.7	1.3	0.0	25.8	0.9	0.0	16.1	0.4	0.7
	Shelburne Bay	Incubation	13	0.0	0.0	0.0	0.0	0.0	0.0	53.8	46.2	0.0
		Nestling	106	23.6	0.9	1.9	32.1	3.8	3.8	12.3	20.8	0.9
		Fledgling	7	0.0	0.0	0.0	71.4	0.0	0.0	0.0	0.0	28.6
		Post-fledgling	209	32.5	2.9	0.5	56.9	2.9	0.5	2.4	1.4	0.0
	South	Incubation	165	95.8	0.6	0.0	1.8	0.0	0.0	0.6	1.2	0.0
		Nestling	170	75.9	10.0	1.8	0.0	0.0	2.4	8.8	1.2	0.0
		Fledgling	69	68.1	0.0	1.4	0.0	0.0	1.4	26.1	1.4	1.4
		Post-fledgling	504	42.7	3.4	2.2	24.6	0.2	0.2	25.4	1.4	0.0
	Young Island	Incubation	103	4.9	5.8	5.8	34.0	0.0	1.9	39.8	2.9	4.9
		Nestling	40	2.5	2.5	2.5	0.0	0.0	42.5	42.5	0.0	7.5
		Fledgling	54	11.1	0.0	1.9	0.0	20.4	29.6	29.6	7.4	0.0
		Post-fledgling	325	90.8	0.9	0.0	0.3	0.3	0.3	6.2	0.9	0.3
2009	Four Brothers	Incubation	331	93.1	0.0	0.3	2.1	0.0	0.6	3.9	0.0	0.0
		Nestling	281	79.4	0.0	1.1	2.8	0.0	0.4	16.4	0.0	0.0
		Fledgling	184	21.2	38.6	0.0	0.0	0.0	1.6	26.6	12.0	0.0
		Post-fledgling	251	12.4	6.0	0.8	0.0	0.0	0.0	75.7	4.8	0.4
	Shelburne Bay	Incubation	9	0.0	0.0	11.1	0.0	0.0	11.1	77.8	0.0	0.0
		Nestling	56	0.0	0.0	0.0	1.8	0.0	0.0	75.0	23.2	0.0
		Fledgling	312	6.4	53.2	0.0	13.5	0.0	0.6	10.9	15.4	0.0
		Post-fledgling	194	29.4	1.5	1.0	17.5	0.5	0.0	48.5	1.5	0.0
	South	Incubation	407	98.5	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0
		Nestling	229	53.3	0.0	0.9	35.4	0.0	0.0	8.7	1.7	0.0
		Fledgling	191	47.1	28.8	0.0	15.2	0.0	0.5	5.2	3.1	0.0
		Post-fledgling	113	2.7	16.8	4.4	0.0	3.5	1.8	65.5	4.4	0.9
	Young Island	Incubation	29	3.4	0.0	27.6	0.0	0.0	20.7	37.9	6.9	3.4
		Nestling	83	30.1	8.4	4.8	0.0	0.0	7.2	45.8	2.4	1.2
		Fledgling	76	5.3	1.3	2.6	0.0	0.0	6.6	78.9	2.6	2.6
		Post-fledgling	118	1.7	0.0	0.8	1.7	1.7	0.0	89.8	4.2	0.0

[a] Includes bluntnose minnow (*Pimephales notatus*), emerald shiner (*Notropis atherinoides*), golden shiner (*Notemigonus crysoleucas*), spottail shiner (*Notropis hudsonius*), and unidentified minnow/shiner.

[b] Includes bluegill (*Lepomis macrochirus*) and pumpkinseed (*Lepomis gibbosus*).

[c] Includes banded killifish (*Fundulus diaphanus*), black crappie (*Pomoxis nigromaculatus*), bowfin (*Amia calva*), bullhead (*Ameiurus* spp.), darter (*Etheostoma* spp.), fantail darter (*Etheostoma flabellare*), lake herring (*Coregonus artedi*), crayfish, *Esox* spp., largemouth bass (*Micropterus salmoides*), logperch (*Percina caprodes*), longnose dace (*Rhinichthys cataractae*), mottled sculpin (*Cottus bairdii*), sculpin (*Cottus* spp.), smallmouth bass (*Micropterus dolomieu*), tessellated darter (*Etheostoma olmstedi*), troutperch (*Percopsis omiscomaycus*), walleye (*Sander vitreus*), and white sucker (*Catostomus commersoni*).

smelt removed from cormorant stomachs. For prey items that were too digested to obtain a length, lengths were assigned from either (1) the same species mean length from the same cormorant stomach (preferred method), (2) the same species and age based on scales (or young-of-year assigned age) collected from the same site and/or reproductive period, or (3) the mean length for that species from the same site and/or reproductive period.

To determine if cormorant diets varied over time and space, diet compositions (proportion by weight) were tested among the collection sites and reproductive periods by year using a multivariate analysis of variance (MANOVA). We also included the interaction of collection site and reproductive period. The eight most frequently encountered diet items were retained as responses in the MANOVA (alewife, cyprinids, *Lepomis*, rainbow smelt, rock bass (*Ambloplites rupestris*), white perch (*Morone americana*), yellow perch, and others; see Table 2 for further details of species categories). There was some violation of independence between samples due to assigning mean length and weight to digested prey items; however, biases in results from this are likely minimal because assigned lengths were based on the same species and age from the same cormorant stomach when possible, and in most cases mean length was derived from the same site and period. Principal components analysis (PCA) was employed to visualize any shifts in cormorant diets before and after alewife established in Lake Champlain and what accounted for such shifts. The number of principal components retained in the analysis was determined according to latent root criterion. All components with Eigenvalues>1 were retained and remaining components underwent varimax rotation. Any violation of independence in the data as a result of using mean length and weight assigned to individual fish (from different cormorant stomachs) would not affect our ability to use PCA for the descriptive purposes of this study (McGarigal et al., 2000).

Results

We collected 131 cormorants for diet analysis during the 2001–2002 seasons (Table 1). Diets included 3119 identifiable prey items (3249 total prey items) representing 21 species. The most common prey items identified during the pre-alewife period were yellow perch and rainbow smelt. Unidentified items accounted for 0.8–13.7% of prey items by number in a single location and reproductive period (Table 2). Yellow perch accounted for 62–95% of consumption by weight for cormorants at Young Island during 2001 and 2002 during all reproductive periods (Fig. 2). At Four Brothers Islands in 2002, rainbow smelt and other fish (e.g. cyprinids, *Lepomis*, and white perch) were the major contributors to cormorant diets, except during the incubation period, when yellow perch dominated the diet.

Five hundred eighteen cormorants were collected with stomach contents during the post-alewife period, 2008–2009 (Table 1). There were 5728 identified prey items (5754 total prey items) encompassing 26 species of fish (Table 2). Unidentified items accounted for 0–28.6% of prey items by numbers in a single location and reproductive period. Alewife constituted large proportions of cormorant diets at Four Brothers and South locations during incubation and nestling reproductive periods in 2008 and also during the fledgling period in 2009 (Fig. 3). Rainbow smelt was the main diet item at Four Brothers and Shelburne Bay during the fledgling period and remained common in the diet at these locations during the post-fledgling period in 2008. Young Island cormorants consistently consumed yellow perch in high proportions, except during the nestling and fledgling periods in 2008 and the incubation period in 2009 when white perch was the most common diet item by weight. Shelburne Bay and Young Island displayed the highest variety of diet items consumed during 2008, with rock bass accounting for up to 25% of diet by weight.

When comparing pre- and post-alewife cormorant diets, alewife became a major component of cormorant diets at Four Brothers Islands. Alewife were the most common fish species in diets, comprising up to 98% (overall proportion 48%) of the prey items by number consumed at a single location and reproductive period (Table 2). Yellow perch, which were overall 14% of the identified prey items during the pre-alewife period, increased to 18% of the overall identified prey items at Four Brothers during the post-alewife period. Overall rainbow smelt frequency decreased from 74% during pre-alewife to 24% during the post-alewife period.

Young Island cormorants continued to consume large numbers of yellow perch (overall pre-alewife 46% and post-alewife 38% of identified prey); however, there was an increase in the number of species consumed during the various reproductive stages between the pre- and post-alewife cormorant diets (Table 2). White perch were numerically important during the post-alewife period (6% of all diet items compared to 1% during the pre-alewife period). Rainbow smelt

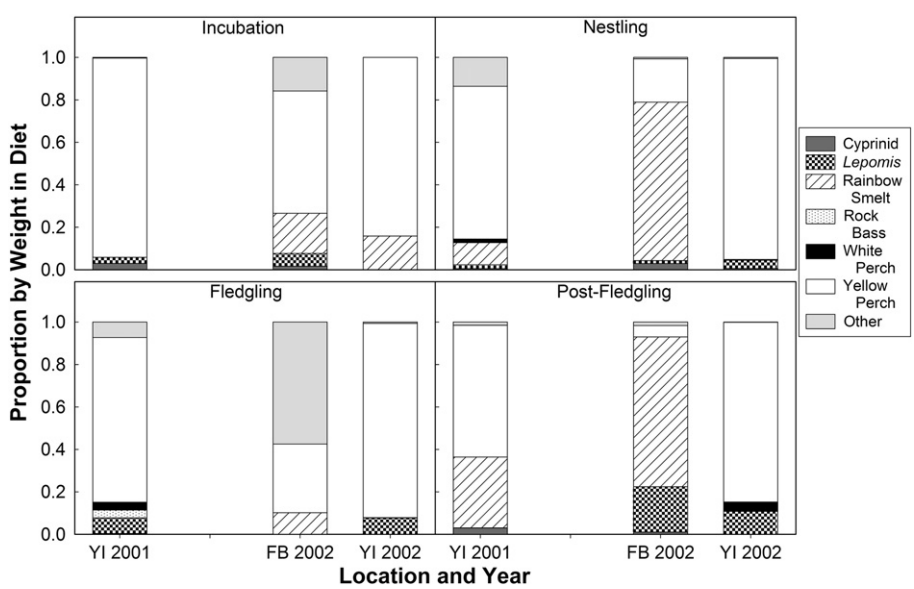

Fig. 2. Cormorant diet composition by weight for identifiable items from Four Brothers Islands (FB) and Young Island (YI) during the 2001 and 2002 reproductive seasons on Lake Champlain. See Table 2 for a description of individual species included in cyprinid, *Lepomis*, and other categories. Note: 57% of total weight at Four Brothers during fledgling in 2002 was due to a single lake herring consumed.

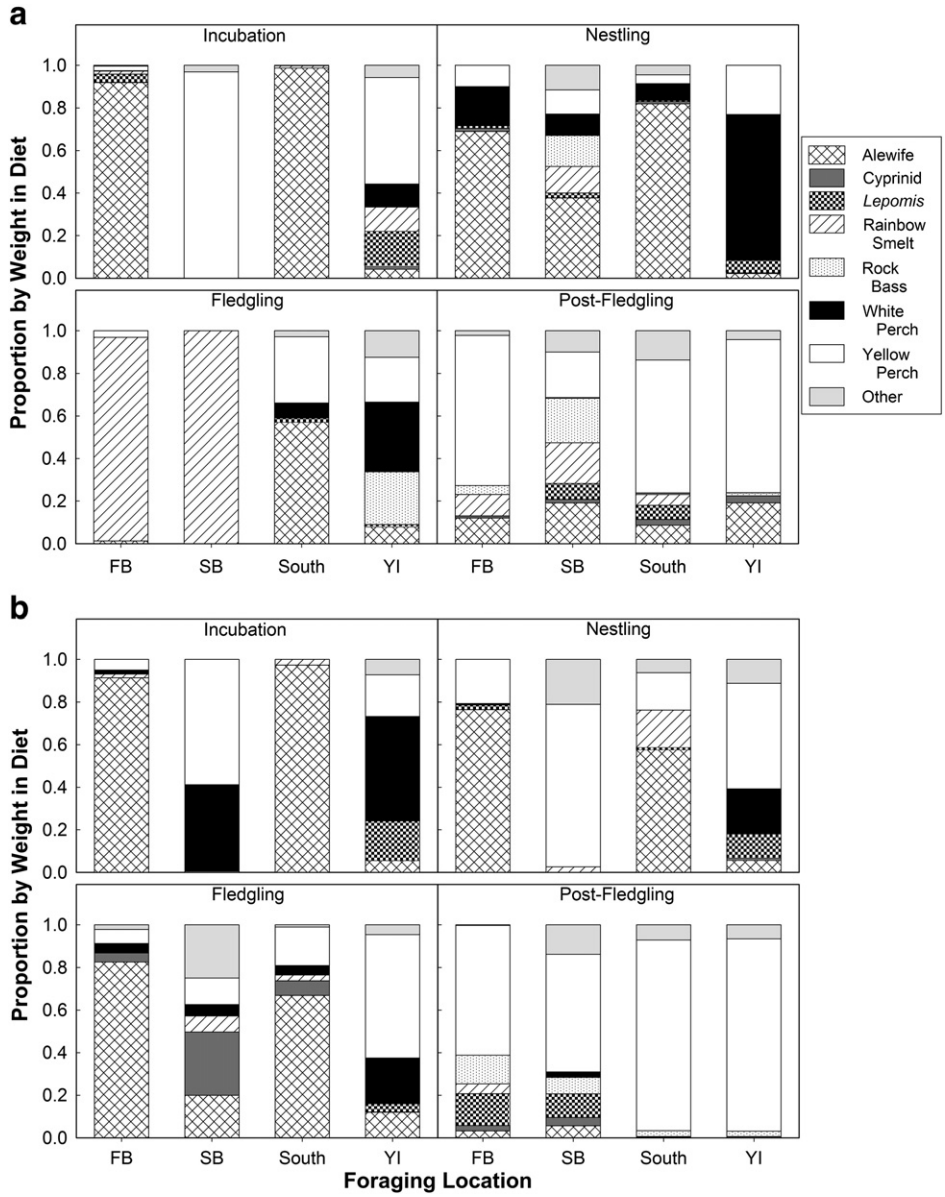

Fig. 3. Cormorant diet composition by weight for identifiable items during the 2008 (a) and 2009 (b) reproductive seasons from Four Brothers (FB), Shelburne Bay (SB), South, and Young Island (YI) on Lake Champlain. See Table 2 for a description of individual species included in cyprinid, *Lepomis*, and other categories.

frequency decreased from pre- to post-alewife periods (39% to 5%), as did the numbers of unidentified prey items (8% to 2%). Alewife represented a high percentage of cormorant diets after their establishment (overall frequency 41%).

MANOVA results for pre-alewife years indicated no diet composition difference between reproductive periods at Young Island during 2001 ($P=0.1$; $\alpha=0.05$; Table 3). In 2002, statistical significance was found in the full model ($P=0.04$) and between diets from Four Brothers and Young Island (site $P=0.0037$). During the post-alewife period, site, reproductive period, and site*reproductive period interaction were significant effects when examining diet compositions for 2008 and 2009 (all $P<0.0001$; Table 3). The full 2008 model accounted for 90% of the variation in the diet compositions and the full 2009 model accounted for 81% of the total variation in cormorant diet compositions (Table 3). Closer examination of species-specific trends at the four locations over time revealed alewife consumption generally decreased as the reproductive periods progressed at Four Brothers and South sites during 2008 and 2009 and remained low during all reproductive periods at Shelburne Bay and Young Island during 2008 and 2009, with the exception of the post-fledgling period at Young Island in 2008 (Fig. 4). Cormorant consumption of rainbow smelt increased at Four Brothers and Shelburne Bay during the fledgling and post-fledgling periods in 2008; however, no increase in rainbow smelt contribution over time was evident during 2009 at any location. In 2008 and 2009, white perch were consumed in low proportions at all locations except Young Island, where their contribution varied among periods. Yellow perch consumption was consistently higher at Young Island and Shelburne Bay than Four Brothers and South sites during 2008 and 2009 during most reproductive periods. Consumption of yellow perch at Four Brothers and South locations generally increased as the reproductive season progressed in 2008 and 2009. Consumption of other fish species was generally low, but variable, at all locations during both years over time.

Six components were retained in the PCA analysis based on latent root criterion, and accounted for 88% of the total variation (Table 4). The first two axes explained only 20% and 15% of the variation in this diet compositional data. The remaining axes explained approximately

Table 3
Results from the MANOVA for 2001–2002 and 2008–2009 testing for differences among the four reproductive periods (incubation, nestling, fledgling, and post-fledgling) and collection sites (Four Brothers, Shelburne Bay, South, and Young Island). The MANOVA independent variables were the eight major species in diet as percent composition by weight. Note: 2001 included only Young Island and 2002 included only Young Island and Four Brothers. See Fig. 4 for species categories and individual trends for species in cormorant diets in 2008 and 2009.

Year	Factor	Wilks' λ	df (num, dem)	F	P
2001	Full model[a]	0.5827	24, 165.92	1.41	0.11
	Intercept		8, 57	146.39[b]	<0.0001
2002	Full model	0.2522	56, 269.18	1.40	0.04
	Intercept		8, 49	223.36[b]	<0.0001
	Site	0.5499[c]	8, 49	3.37[b]	0.0037
	Period	0.6494	24, 142.72	0.95	0.53
	Site*period	0.6572	24, 142.72	0.93	0.57
2008	Full model	0.0968	120, 1664	5.38	<0.0001
	Intercept		8, 232	504.60[b]	<0.0001
	Site	0.4553	24, 673.47	8.74	<0.0001
	Period	0.5677	24, 673.47	6.05	<0.0001
	Site*period	0.2766	72, 1418.8	4.63	<0.0001
2009	Full model	0.1917	120, 1720.9	3.74	<0.0001
	Intercept		8, 240	579.70[b]	<0.0001
	Site	0.4415	24, 696.67	9.45	<0.0001
	Period	0.7220	24, 696.67	3.45	<0.0001
	Site*period	0.5501	72, 1467.4	2.10	<0.0001

[a] 2001 full model only includes the factor period.
[b] Exact F.
[c] F-test value.

13%–14% of the variation. The first principal component was strongly influenced by yellow perch (principal component loading 0.89) and alewife (−0.88). The second principal component was heavily influenced by rainbow smelt (0.99); as well as yellow perch (−0.31) and alewife (−0.30). Despite relatively even distribution of variance among the six components, diet compositions are distinguishable between pre- and post-alewife periods based on the first two principal components (Fig. 5).

Discussion

It is clear from this study that alewife have become a dominant food item for double-crested cormorants feeding in Lake Champlain. Cormorant diets were comprised of up to >98% alewife, especially when foraging near Four Brothers Islands and in the southern portion of the lake. Although no single principal component accounted for >20% of the variation when explaining these diet data, a shift in the cormorant diet composition after alewife became established was still evident, in particular at the Four Brothers location. The incorporation of alewife into cormorant diets from four large and distinct areas on Lake Champlain confirms that alewife are an important food item, and with continued availability, may remain important in the diets. However, cormorants continued to rely on yellow perch, especially near Young Island. Rainbow smelt also remained seasonally important in the diets of cormorants foraging around Four Brothers Islands and Shelburne Bay. Lack of difference in diet composition between reproductive stages during the pre-alewife period may be due to limited sample sizes. It may also be partially due to the diet samples being summarized by colony location, instead of foraging location; cormorants from Four Brothers colony forage throughout Lake Champlain (Duerr et al., 2012). By sampling according to foraging location, potential localized effects of cormorants on fish species can be better determined.

When round goby became established in eastern Lake Ontario, cormorant diets reflected this change almost immediately and round goby became dominant in the diet (Johnson et al., 2006; Johnson et al., 2010). Although this study did not monitor cormorant diets simultaneously with the establishment of alewife, within five years of the alewife introduction this species became a dominant diet item

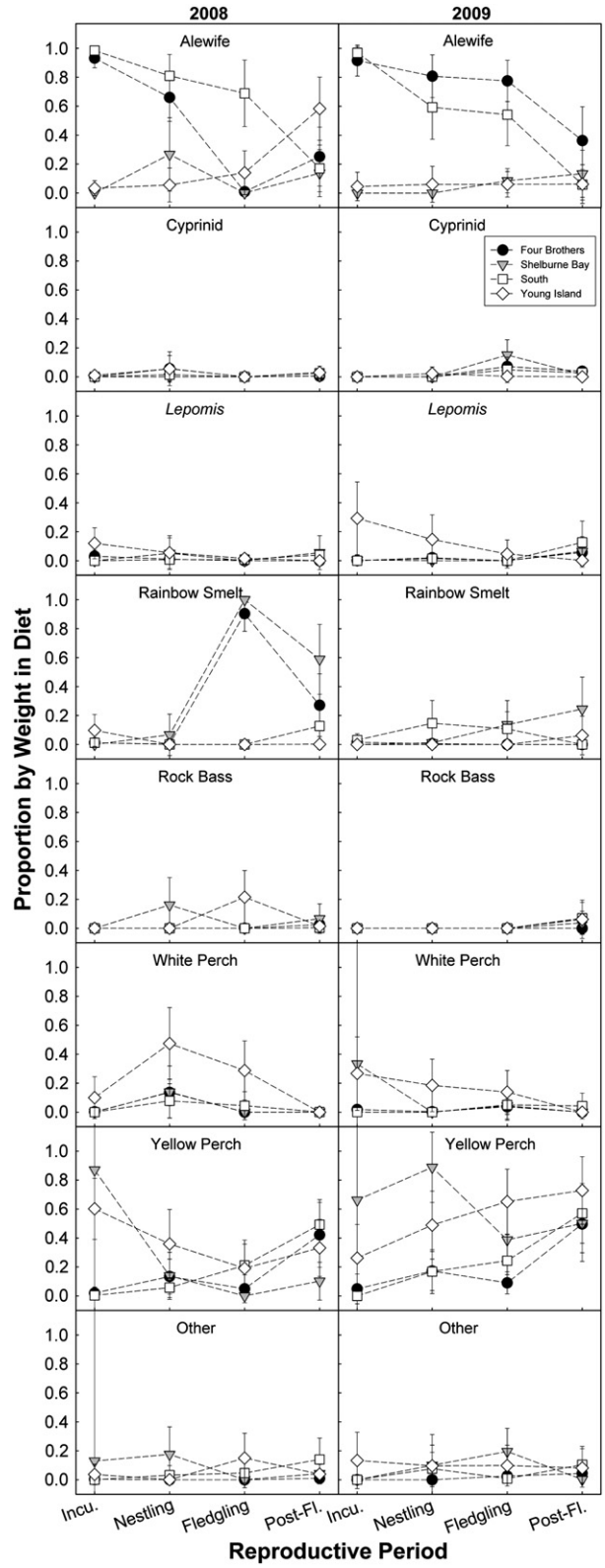

Fig. 4. Mean proportion by weight for identified species in cormorant diets in 2008 and 2009 during each reproductive period (incubation [Incu.], nestling, fledgling, post-fledgling [Post-Fl.]) from Four Brothers, Shelburne Bay, South, and Young Island collection sites in Lake Champlain with 95% confidence intervals around means. See Table 2 for a description of individual species included in cyprinid, *Lepomis*, and other categories.

Table 4
Principal component loadings for the cormorant diet composition (% by weight) input data when retaining six principal components based on latent root criterion. Loadings > |0.3| are in bold font. See Table 2 for species contained in cyprinid, *Lepomis*, and other categories.

Variable	PC1	PC2	PC3	PC4	PC5	PC6
Alewife	**−0.88**	**−0.30**	−0.22	−0.20	−0.15	−0.16
Cyprinid	0.01	−0.03	**0.73**	−0.01	**−0.34**	0.09
Lepomis	0.02	−0.04	−0.02	−0.03	0.02	**0.99**
Rainbow smelt	−0.01	**0.99**	−0.07	−0.06	−0.04	−0.04
Rock bass	0.00	−0.03	−0.01	−0.01	**0.88**	0.04
White perch	−0.01	−0.05	−0.05	**1.00**	−0.02	−0.03
Yellow perch	**0.89**	**−0.31**	−0.17	−0.22	−0.15	−0.13
Other	0.02	−0.04	**0.72**	−0.05	**0.36**	−0.11
% of variance	19.5	14.8	14.1	13.6	13.3	13.1
Cumulative %	19.5	34.3	48.4	62.0	75.3	88.4

for cormorants on Lake Champlain in at least two foraging locations, Four Brothers Islands and in the southern section of the lake. This suggests that some cormorants in Lake Champlain have switched their mode of feeding from demersal on yellow perch to pelagic foraging on alewife. This switch in foraging mode also has a geographic component. Cormorants still forage on yellow perch near Young Island; however, cormorants from the Four Brothers colony, currently the largest nesting colony on the lake and the only one where a substantial number of young are produced, may be able to capitalize on the regular food resources in nearby pelagic zones of the lake. From 2002 to 2003, cormorants from Four Brothers shifted away from pelagic foraging locations close to the breeding site, where they predominately consumed rainbow smelt in 2002, to more distant littoral locations in 2003 (Duerr et al., 2012). An associated increase in energy demand accompanied this shift in foraging distribution (Duerr et al., 2012). Thus, reduced energetic demands associated with alewife as a regular food supply near the Four Brothers Islands may have potential to increase cormorant reproductive output at the Four Brothers colony.

Even though alewife have become an important and sometimes dominant component of cormorant diets on Lake Champlain, effects of cormorant predation on yellow perch are still unknown. Significant negative effects on smallmouth bass populations were found in eastern Lake Ontario when smallmouth bass only comprised 0.8%–7.2% of the diet of cormorants (Johnson et al., 2002; Lantry et al., 2002). On Oneida Lake, in central New York, cormorant diets consisted of 1.6%–16.5% subadult walleye and 33.3%–64.7% subadult yellow perch and this consumption level was large enough to reduce walleye and yellow perch populations significantly (Rudstam et al., 2004). In contrast to the negative impact cormorants had on yellow perch in Oneida Lake (Rudstam et al., 2004), a previous study conducted on Lake Champlain, based on gillnet catches of yellow perch through the cormorant reproductive season, indicated that cormorants were likely not negatively affecting the yellow perch population around Young Island (Eisenhower and Parrish 2009). Assuming that the cormorant population on Lake Champlain remains stable, the presence of alewife could lessen any negative effects cormorants exert on the yellow perch population. However, without information on the yellow perch population, such as population estimates, growth and/or mortality trends, we still are unable to ascertain the actual impact cormorants have on yellow perch.

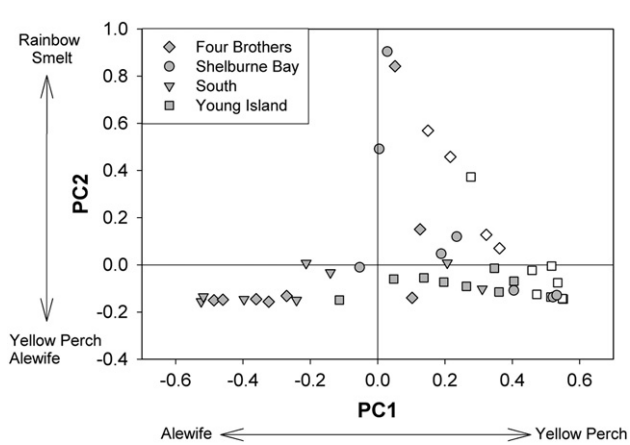

Fig. 5. Biplot ordination of the first two principal components explained by cormorant diet composition (% by weight) on Lake Champlain. Open symbols represent specific site-reproductive period values during pre-alewife years (2001–2002) and shaded symbols represent post-alewife years (2008–2009). Percent yellow perch (principal component loading 0.89) and alewife (−0.88) in the diets influenced the first axis. Percent rainbow smelt (0.99) in the diets strongly influence the second axis. See Table 4 for a complete list of principal component loadings.

Researchers in other areas have suggested that alewife might reduce cormorant predation on yellow perch by acting as a buffer (O'Gorman and Burnett, 2001; Diana et al., 2006). Observed differences in diets of cormorants during the post-fledgling period between 2008 and 2009 could provide additional corroboration. In 2008, young-of-year alewife and rainbow smelt numerically dominated diets at all locations (combined 67%–91% of fish species consumed) during the post-fledgling period. In 2009, young-of-year alewife and rainbow smelt were not predominant in the diet and even absent in some locations in the post-fledgling period. Instead, 2009 post-fledgling diets were predominately yellow perch (48%–90% of fish species consumed). One reason for this shift in the post-fledgling period would be the availability of young-of-year rainbow smelt and alewife. In 2008, the average catch of young-of-year rainbow smelt and alewife in index trawls was 1003 and 523 individual fish; however, the catches dropped dramatically in 2009 to 264 and 106 individuals at the same standard sites (Staats and Pientka, 2010). The ability of cormorants to forage effectively when alewife and rainbow smelt are scarce illustrates their capacity for adapting to changing prey populations. Adaptive foraging by cormorants, spatially and within and between years, also indicated that spatially and temporally limited diet studies may miss important information for evaluating potential impacts of cormorants.

Continued management of cormorants on Lake Champlain should reflect the current understanding of their effects on the ecosystem and established conservation and management goals. Currently no cormorant reproduction is permitted on Young Island and nesting is restricted on Four Brothers Islands with the goal of reducing negative impacts on native vegetation and co-nesting species. Results from this study support the view that management of cormorants should be site specific, potentially even within a single water body, if the rationale for management actions includes reducing predation pressure by cormorants on fish species such as yellow perch in Lake Champlain. We found cormorant diets to vary significantly across geographic locations and reproductive stages and have changed composition in response to alewife and rainbow smelt availability. There also should be efforts undertaken to assess population parameters of the fish species in question, such as population and mortality levels, which when implementing cormorant control should be monitored and assessed for changes. Without proper baseline data and continued monitoring, management efforts cannot be implemented most effectively to achieve the desired results.

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