Diets of aquatic birds reflect changes in the Lake Huron ecosystem

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Human activities have affected the Lake Huron ecosystem, in part, through alterations in the structure and function of its food webs. Insights into the nature of food web change and its ecological ramifications can be obtained through the monitoring of high trophic level predators such as aquatic birds. Often, food web change involves alterations in the relative abundance of constituent species and/or the introduction of new species (exotic invaders). Diet composition of aquatic birds is influenced, in part, by relative prey availability and therefore is a sensitive measure of food web structure. Using bird diet data to make inferences regarding food web change requires consistent measures of diet composition through time. This can be accomplished by measuring stable chemical and/or biochemical "ecological tracers" in archived avian samples. Such tracers provide insights into pathways of energy and nutrient transfer.

*In this study, we examine the utility of two groups of naturally-occurring intrinsic tracers (stable isotopes and fatty acids) to provide such information in a predatory seabird, the herring gull (*Larus argentatus*). Retrospective stable nitrogen and carbon isotope analysis of archived herring gull eggs identified declines in gull trophic position and shifts in food sources in Lake Huron over the last 25 years and changes in gull diet composition were inferred from egg fatty acid patterns. These independent groups of ecological tracers provided corroborating evidence of dietary change in this high trophic level predator. Gull dietary shifts were related to declines in prey fish abundance which suggests large-scale alterations to the Lake Huron ecosystem. Dietary shifts in herring gulls may be contributing to reductions in resources available for egg formation. Further research is required to evaluate how changes in resource availability may affect population sustainability in herring gulls and other waterbird species. Long-term biological monitoring programs are required to identify ecosystem change and evaluate its ecological significance.*

Keywords: herring gull, *Larus argentatus*, waterbirds, ecosystem change, stable isotopes, fatty acids

Introduction

Lake Huron provides important habitat for breeding birds (Prince and Flegel, 1995). The most re-

cent census (1997–2001) of colonial waterbirds in Canadian waters of Lake Huron found approximately 146,000 birds (D.V.C. Weseloh, Environment Canada, Canadian Wildlife Service, Downsview, ON unpublished data). This total comprised nine species (in order of abundance):

ring-billed gull (*Larus delawarensis*), herring gull, double-crested cormorant (*Phalacrocorax auritus*), common tern (*Sterna hirundo*), Caspian tern (*Hydroprogne caspia*), black-crowned night-heron (*Nycticorax nycticorax*), great blue heron (*Ardea herodias*), great egret (*Casmerodius albus*), and great black-backed gull (*Larus marinus*). Many of these species are top predators that track changes in resource availability through their selection of prey and, in so doing, integrate food web processes over time (Cairns, 1992; Piatt et al., 2007). This integrative feature, when combined with new techniques to conduct retrospective measurement of chemical and/or biochemical indicators of organism trophic and energy/nutrient flow in archived tissue samples of high trophic level predators, can provide insights into temporal changes in food webs (Hebert et al., 1999a, 2006, 2008).

Since 1974, Environment Canada's Great Lakes Herring Gull Monitoring Program has collected egg samples to evaluate trends in levels of environmental contaminants (Mineau et al., 1984; Hebert et al., 1999b). More recently, these eggs have also been used to assess temporal changes in gull diets. These dietary assessments are possible because all samples collected as part of the Herring Gull Program have been maintained in a frozen archive allowing retrospective analysis of tracers of food web interactions. In herring gulls, exogenous resources are primarily used for egg formation (Hobson et al., 1997); therefore, the chemical composition of eggs will reflect dietary integration over the several-week period of egg formation.

The dietary tracers that have been utilized to date include stable isotopes of nitrogen and carbon and fatty acids. Stable nitrogen isotopes have been used to determine gull trophic position as the heavier isotope, ^{15}N, is progressively enriched from trophic level to trophic level resulting in greater $\delta^{15}N$ values in biota occupying higher trophic positions (DeNiro and Epstein, 1981). Carbon isotopes have also been used to determine pathways of carbon flow to gulls; in particular to differentiate between aquatic and terrestrial prey (Rau, 1980; France, 1995). $\delta^{13}C$ values in pelagic primary producers, i.e. phytoplankton, are more negative than those of terrestrial primary producers because they are depleted in the heavier ^{13}C isotope. This leads to more negative $\delta^{13}C$ values in lake carbon sources (Rau, 1980; France, 1995). Food sources of anthropogenic origin, i.e. garbage, often are enriched in ^{13}C because of the importance of corn (C4 photosynthetic pathway)-based

foodstuffs in North American diets (Pollan, 2006). Fatty acids (FA) are becoming an increasingly important tool in tracing food web interactions. They are the primary components of many lipid types and are required for normal growth and development. Some FA are termed essential because they cannot be synthesized with high efficiency by consumers and must originate in primary producers where they are synthesized (Arts et al., 2001). These FA are highly conserved as they are transferred from lower to higher trophic level biota (Kainz et al., 2004). Because prey FA patterns are largely retained in higher trophic level species, inferences can be made regarding the diet of the predator (Napolitano, 1998; Iverson et al., 2004; Hebert et al., 2008). Furthermore, the FA compositions of various food types differ and these differences can provide insights into pathways of energy and nutrient transfer (Napolitano, 1998; Iverson et al., 2004, 2007). Through the measurement of ecological tracers in archived herring gull eggs we investigate whether there is evidence of food web change in Lake Huron, the factors that have likely contributed to the observed changes, and the implications of those changes to an important reproductive endpoint, i.e. egg size, in herring gulls.

Methods

Annual collections (under Canadian Wildlife Service research permits) of 10-13 eggs were made at three colonies on Lake Huron: Double Island in the North Channel, Chantry Island in the main body of the lake, and Channel/Shelter Island in Saginaw Bay (Figure 1). Each egg was collected from a different, completed three egg clutch. Eggs from Double and Chantry Islands were first collected in 1974. Channel/Shelter Island samples were first obtained in 1980. Eggs were transferred to Environment Canada's National Wildlife Research Centre in Ottawa where measurements, including length and breath, were recorded. This allowed the calculation of egg volume according to the equation:

$$\text{Volume (cm}^3) = 0.489(\text{length} \times \text{breadth}^2)/1000$$

$$(\text{Ryder 1975})$$

After measurement, the eggs were opened and the contents homogenized. For each colony and year, 10–13 eggs were pooled into one sample. Egg pools were stored in solvent-rinsed glassware in frozen archives (-40 to $-80°C$). These pools
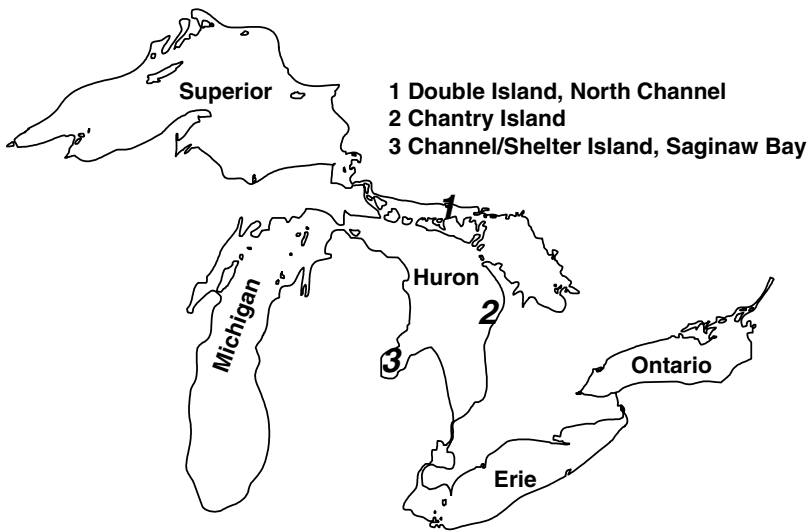
Figure 1. Location of the Lake Huron herring gull colonies monitored annually as part of the Canadian Wildlife Service's Great Lakes Herring Gull Monitoring Program.

(1981–2005) were used for stable isotope and fatty acid analyses. Protocols for these analyses have been reported previously (Hebert et al., 1999b, 2006, 2008). Estimation of gull trophic position using egg δ^{15}N is described elsewhere (Hebert et al., 1999b). Trophic position estimates account for possible inter-colony differences in baseline δ^{15}N values (see Hebert et al., 1999b). Using trophic position instead of δ^{15}N allows data from different colonies to be analyzed together.

Annual estimates of prey fish abundance were obtained for Lake Huron (1992–2005) according to previously described methods (Argyle, 1982; Roseman et al., 2007). Briefly, autumn trawl sampling was performed annually at five ports in U.S. waters: Detour, Hammond Bay, Alpena, Au Sable Point, and Harbor Beach. At each location, 10-minute on-contour tows using a 21 m wing trawl were made on approximate 9 m depth intervals at fixed transects from 9 to 110 m in depth (see Roseman et al., 2007 for details). To estimate prey fish availability to gulls, annual indices of rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*) abundance were used. Alewife have historically been the most abundant prey fish species in the lake (Dobiesz et al., 2005; Riley et al., 2008) but smelt may be an important prey species for gulls during spring spawning (see Gorman, 2007 for an example from Lake Superior). An annual index of prey fish abundance was calculated by standardizing each year to the year of greatest abundance; therefore, prey fish

abundance values for both species ranged between 0 and 1.

Relationships between time, gull trophic position, egg δ^{13}C values, and egg FA index were examined using correlation analysis. Principal components analysis (PCA) (StatSoft, 2005), using correlation matrices, was used to calculate the egg FA index. For this analysis, percent composition data for 13 individual FA, each of which constituted $\geq 0.5\%$ of total egg fatty acid levels, were used. An overall herring gull diet index was calculated from the results of a second PCA utilizing trophic position, egg δ^{13}C, and egg FA index (see Results below). In these analyses, data from all three Lake Huron colonies were utilized. Relationships between alewife and smelt abundance and gull diet index were also assessed using correlation analysis. $P < 0.05$ was deemed statistically significant.

Results

There were statistically significant temporal changes in egg stable isotope values and egg fatty acid patterns. Egg stable nitrogen isotope values declined through time indicating that herring gull trophic position was lower in more recent years (Fig. 2a). Egg carbon isotope values increased through time (Fig. 2b). Gull trophic position (δ^{15}N) was negatively correlated with egg δ^{13}C values (r = 0.59, p = 0.0001). Principal component 1 (PC1) from the PCA of the percent composition data
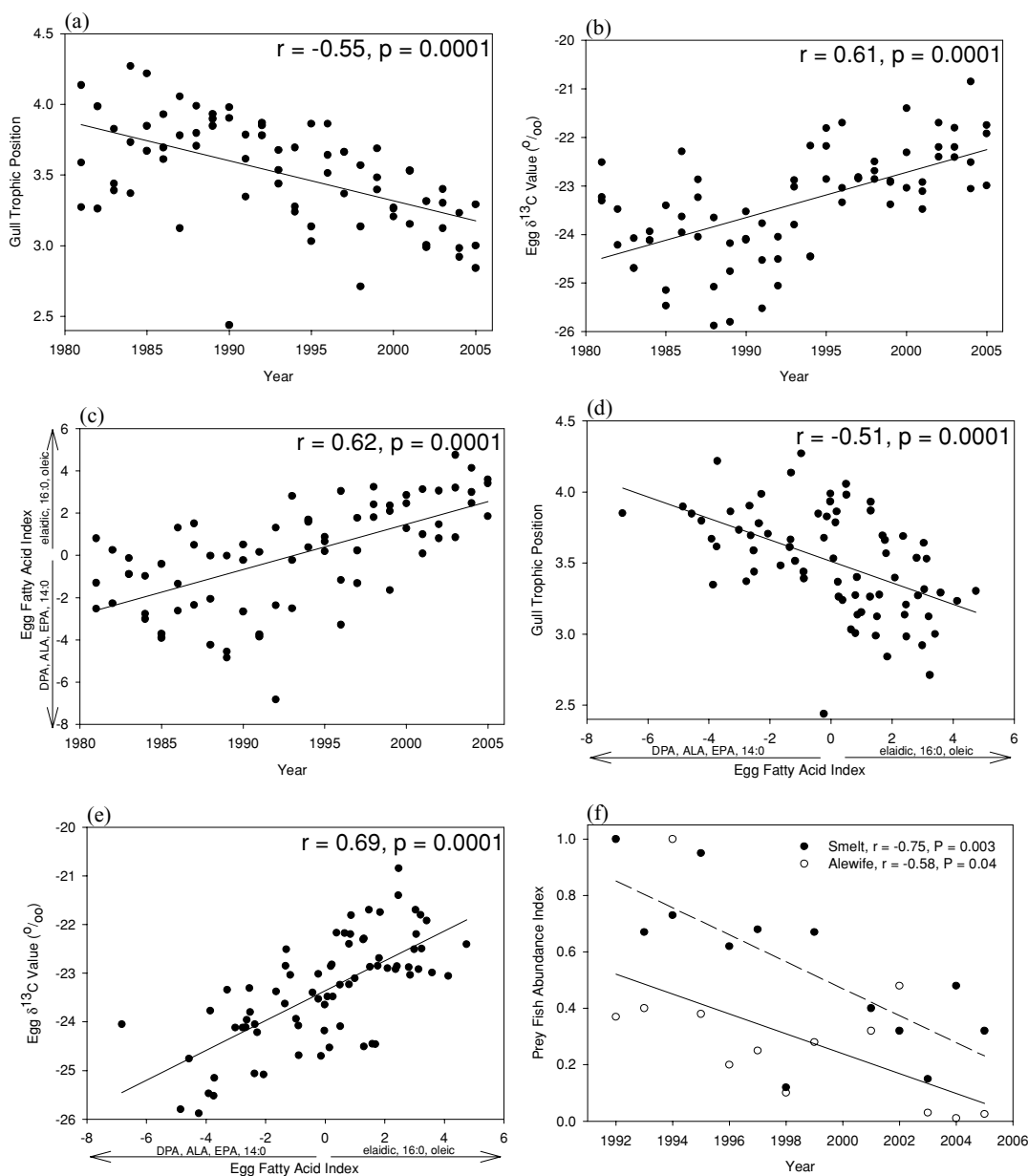
Figure 2. Lake Huron trends in gull diet indicators and prey fish abundance, (a) temporal trends in gull trophic position, (b) temporal trends in gull egg δ^{13}C value, (c) temporal trends in gull egg fatty acid index, (d) correlation between egg fatty acid index and gull trophic position, (e) correlation between egg fatty acid index and egg δ^{13}C value, (f) temporal trends in alewife and smelt abundance.

accounted for 47% of the variation in the FA data. PC1 sample scores were subsequently used as an index of egg FA composition. This index separated samples based upon differences in the proportions of omega-3 FA (in order of variable loadings on PC1: docosapentaenoic acid (DPA, 22:5n-3c), α-linolenic acid (ALA, 18:3n-3), eicosapentaenoic acid (EPA;

20:5n-3)), as well as short carbon-chain myristic acid (14:0) versus proportions of elaidic acid (18:1n-9t), palmitic acid (C16:0), and oleic acid (18:1n-9c). The egg FA index data changed through time. In more recent years, omega-3 FA contributed less to total FA levels (Fig. 2c). Egg FA index correlated with gull trophic position and egg δ^{13}C values
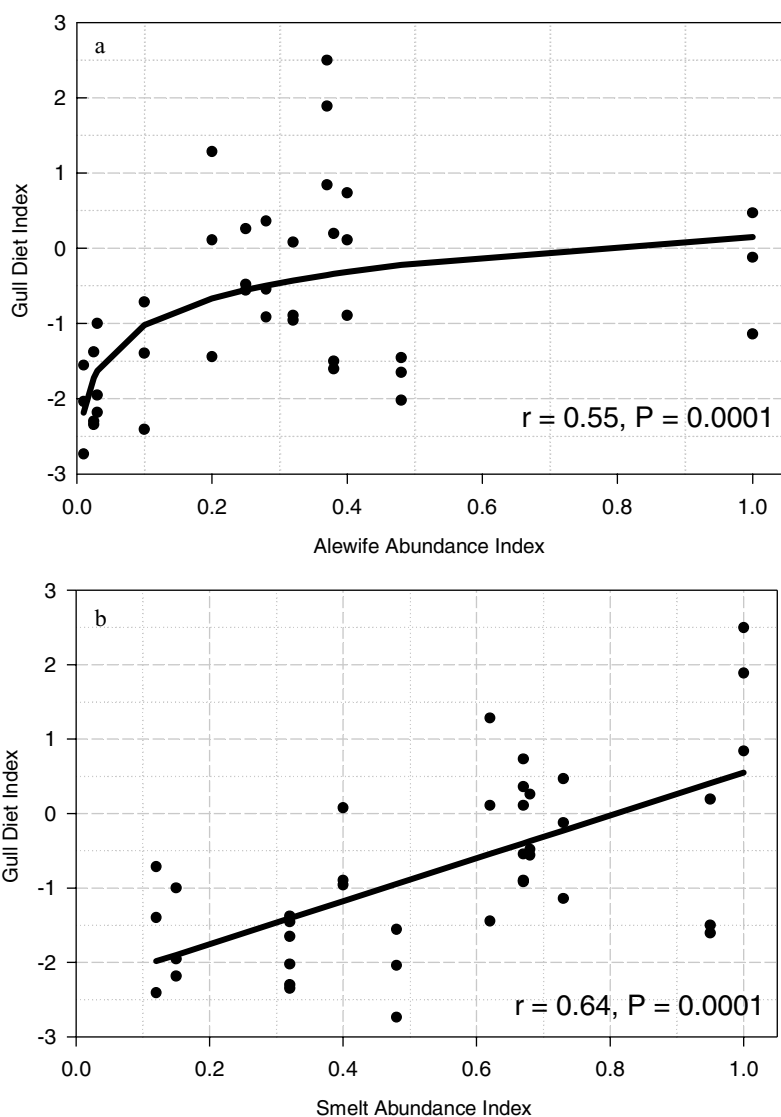
Figure 3. Correlation between annual (1992–2005) indices of gull diet and prey fish abundance (a) alewife, (b) smelt.

(Fig. 2d, 2e). As the contribution of elaidic, palmitic, and oleic acids to total FA levels increased, gull trophic position decreased (Fig. 2d) and egg $\delta^{13}C$ values increased (Fig. 2e). Statistically significant temporal declines in annual indices of alewife and rainbow smelt abundance were also observed during 1992–2005 (Fig. 2f).

To examine relationships between indices of prey fish abundance and gull diet, gull dietary indicators (i.e. gull trophic position, egg $\delta^{13}C$ values, and PC1 scores from the analysis of FA percent composition data) were summarized using a second PCA. PC1 (72% of variance explained) scores from this PCA

constituted a gull diet index. Greater diet index values reflected increasing trophic position, decreasing egg $\delta^{13}C$ values, and increased proportions of omega 3/myristic acid and decreased proportions of elaidic, palmitic, and oleic acids to total FA levels. The gull diet index was significantly correlated with annual abundance estimates of both alewife and rainbow smelt (Fig. 3a-b).

Egg size i.e. mean annual egg volume calculated for each colony, declined significantly through time (Fig. 4a) and correlated with the gull diet index (Fig. 4b). Larger eggs corresponded to a gull diet characterized by consumption of higher trophic level prey,
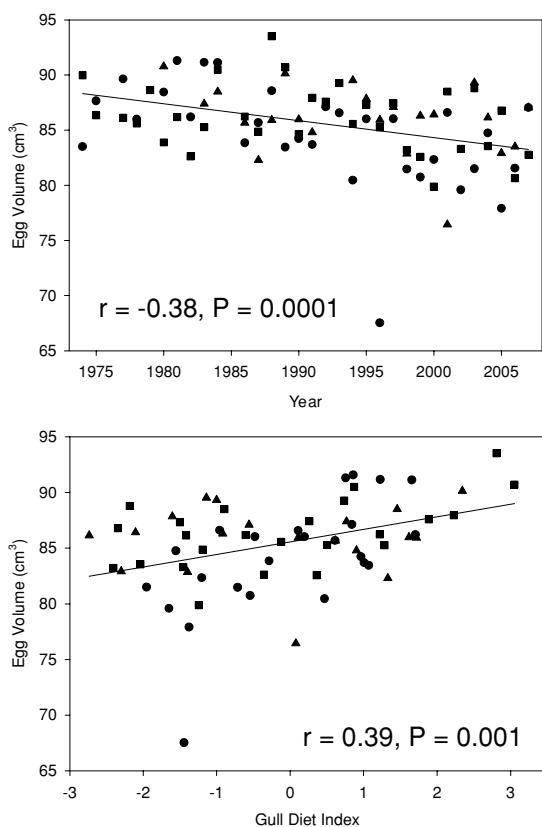
Figure 4. (a) Temporal trends in Lake Huron herring gull egg size and (b) relationship between egg size and gull diet index. Symbols represent different colonies: Double Island (circles), Chantry Island (squares), Channel/Shelter Island (triangles).

with more negative $\delta^{13}C$ values, and egg FA levels composed of greater proportions of omega-3 FA and myristic acid.

Discussion

Retrospective analysis of archived eggs indicated that significant temporal changes occurred in the diets of Lake Huron herring gulls from 1981-2005. Temporal declines in gull trophic position revealed that gulls fed on lower trophic level prey in more recent years. Concomitant with this change was an increase in egg $\delta^{13}C$ values indicating a shift in food source. Both of these changes could have been the result of a decrease in the proportion of fish in the gull diet. Prey fish occupy higher trophic levels than other foods that gulls consume, particularly those that are associated with terrestrial ecosystems, e.g. garbage, small mammals, invertebrates (Hebert et al., 1999a, 1999b). Egg $\delta^{15}N$ values (and trophic

position) would be expected to decline with a reduction in the proportion of fish in the gull diet (Hebert and Sprules, 2002). Increases in egg $\delta^{13}C$ values were consistent with such a change, given the fact that prey associated with terrestrial food webs would be expected to have more positive $\delta^{13}C$ values than aquatic prey. Shifts in the relative proportions of aquatic versus terrestrial food in the gull diet would be expected to alter egg fatty acid patterns. The temporal changes we observed in egg FA patterns, e.g. less omega 3 FA in eggs from more recent years, were consistent with a decline in the proportion of aquatic foods in the gull diet. Therefore, the results from these independent groups of ecological tracers, i.e. stable isotopes and fatty acids, provide corroborating evidence of such a dietary shift.

Egg FA patterns are strongly influenced by the composition of the avian diet (Farrell, 1998). Therefore, temporal changes in diet composition were expected to result in altered egg FA profiles through time. Compared to terrestrial systems, phytoplankton-based food webs have disproportionately high concentrations of long carbon-chain omega-3 FA and short carbon-chain FA (Napolitano, 1998). Therefore, eggs containing greater proportions of these FA would have been formed from gull diets richer in aquatic foods. Eggs containing greater proportions of elaidic and/or oleic acids likely reflected greater consumption by laying females of foods of terrestrial origin; partly human refuse. Trans fats, such as elaidic acid, are found to a very limited extent in the natural world. Their primary sources are in foods of anthropogenic origin. The positive correlation between the egg fatty acid index and gull trophic position and the negative correlation with egg $\delta^{13}C$ values provided further evidence of a temporal shift in the gull diet with an increasing reliance on terrestrial foods through time. It is likely that this trend resulted from declines in pelagic prey fish abundance. In Lake Huron, statistically significant declines in annual indices of alewife and smelt were observed over time. When prey fish abundance was greater, the gull diet index reflected consumption of higher trophic level prey, i.e. prey fish, with carbon isotope and FA signatures indicative of the consumption of aquatic resources. During the early 1980s, herring gull diets on Lake Huron were assessed using conventional methods involving the analysis of chick regurgitates. At that time, fish were the predominant dietary item (Fox et al., 1990) and this is consistent with the gull diet index data presented here. However, more recent trends

in this index suggest that as prey fish abundance declined through time gulls incorporated more terrestrial foods into their diets.

Multiple factors likely acted together to reduce prey fish abundance across the Great Lakes. These factors included: 1) predation by piscivorous fish, 2) reductions in lake productivity brought about by reductions in nutrient loading, 3) establishment of dreissenid mussels, 4) increases in populations of double-crested cormorants (Hebert et al., 2008). Severe winters may have also contributed to the decline of Lake Huron alewife in the early part of this decade. Regardless of the mechanisms regulating prey fish abundance, there has been a shift in the diets of Lake Huron herring gulls. The degree to which these dietary shifts contributed to documented declines in Lake Huron herring gull populations (see Morris et al., 2003) is uncertain. However, reductions in egg size of herring gulls breeding on Lake Huron point to the possibility that resources available for egg production have become more constrained in recent years. Egg size can be an important factor regulating early chick survival (Parsons 1970, 1976; Williams, 1994 for review) which ultimately could influence the recruitment of new individuals into the Lake Huron herring gull population. Continued declines in egg size and/or quality would be cause for concern with respect to the long-term viability of herring gull populations. Furthermore, dietary studies completed on Lake Superior herring gulls indicated that at colonies where birds were feeding to a lesser degree on fish, body condition of breeding adults was poorer and egg size and reproductive success were reduced (Hebert et al., 2002). Diet may have been an important factor leading to the disappearance of herring gull colonies in some parts of that lake, e.g. Jackfish Bay. The importance of diet composition in regulating physiological and reproductive parameters in breeding herring gulls has also been documented elsewhere (Pierotti 1982, 1987; Graves, 1984; van Klinken, 1992).

Conclusions

Here we have documented long-term alterations in the diets of Lake Huron herring gulls and linked these changes to reductions in prey fish abundance. Clearly, continued monitoring of Great Lakes waterbirds is required not only for evaluating the state of their populations, but also for gaining insights into larger ecosystem-scale change. To that end, long-term monitoring programs, such as the Great Lakes Herring Gull Monitoring Program, can assist in placing current ecosystem conditions into a historical perspective. However, we should strive for better integration of monitoring efforts across taxa. Declines in prey fish populations have important implications for all high trophic level predators that rely on them as food. These include predatory fish, birds, and possibly mammalian piscivores. Integration of information from these various groups would provide a more holistic picture of the scope and causes of ecosystem change and the ramifications of such change on the health of individuals and the sustainability of populations and communities.

Acknowledgments

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