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RESTORING PISCIVOROUS FISH POPULATIONS IN THE LAURENTIAN GREAT LAKES CAUSES SEABIRD DIETARY CHANGE

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Abstract. Ecosystem change often affects the structure of aquatic communities thereby regulating how much and by what pathways energy and critical nutrients flow through food webs. The availability of energy and essential nutrients to top predators such as seabirds that rely on resources near the water's surface will be affected by changes in pelagic prey abundance. Here, we present results from analysis of a 25-year data set documenting dietary change in a predatory seabird from the Laurentian Great Lakes. We reveal significant declines in trophic position and alterations in energy and nutrient flow over time. Temporal changes in seabird diet tracked decreases in pelagic prey fish abundance. As pelagic prey abundance declined, birds consumed less aquatic prey and more terrestrial food. This pattern was consistent across all five large lake ecosystems. Declines in prey fish abundance may have primarily been the result of predation by stocked piscivorous fishes, but other lake-specific factors were likely also important. Natural resource management activities can have unintended consequences for nontarget ecosystem components. Reductions in pelagic prey abundance have reduced the capacity of the Great Lakes to support the energetic requirements of surface-feeding seabirds. In an environment characterized by increasingly limited pelagic fish resources, they are being offered a Hobsonian choice: switch to less nutritious terrestrial prey or go hungry.

Key words: *aquatic food web; ecosystem change; fatty acids; food availability; Herring Gull; Larus argentatus; Laurentian Great Lakes; prey fish; seabird; stable isotopes.*

INTRODUCTION

Large-scale aquatic ecosystem change is often associated with alterations in the structure of biological communities (Pauly et al. 1998, Rahel 2000, Eby et al. 2006). This in turn, affects how much and by what pathways energy and critical nutrients flow through food webs. Removal and/or redirection of energy among ecosystem compartments occurs as a result of processes such as stocking of piscivorous fish, exotic species introductions, and fishing (Pauly and Christensen 1995, Rahel 2000, Crawford 2001, Eby et al. 2006).

Top predators track changes in resource availability through their selection of prey and, in so doing, integrate food web processes over time (Cairns 1992). Temporal changes in food web interactions can thus be characterized through retrospective measurement of biochemical indicators of organism trophic position and energy/nutrient flow in archived tissue samples of high trophic level predators (Hebert et al. 2006). Examples of such "ecological tracers" are nitrogen and carbon stable isotopes and fatty acids. Stable nitrogen isotopes are useful in defining an organism's trophic position as the heavier isotope, ¹⁵N, is progressively enriched through the food web leading to greater $\delta^{15}\text{N}$ values in organisms occupying higher trophic positions (DeNiro and Epstein 1981). Carbon isotopes provide information regarding the flow of carbon to consumers in that they can be used to differentiate between aquatic

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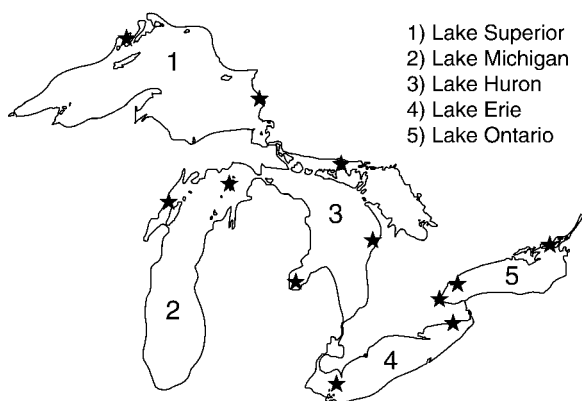


FIG. 1. Location of 12 Laurentian Great Lakes Herring Gull study colonies (stars).

and terrestrial food sources (Rau 1980, France 1995). Pelagic primary producers, i.e., phytoplankton, are depleted in the heavier ^{13}C isotope compared to terrestrial primary producers, leading to more negative $\delta^{13}\text{C}$ values in lake carbon sources (Rau 1980, France 1995). Fatty acids (FA) are the main constituents of many types of lipids and are required for normal growth and development. Some of these FA, originally synthesized by primary producers, are termed essential because they cannot be synthesized with high efficiency by consumers (Arts et al. 2001). In pelagic systems these FA pass from lower to higher trophic levels where they are highly conserved (Kainz et al. 2004). Their utility as tracers of food web pathways stems from the fact that during trophic transfer, prey FA patterns are largely retained in higher trophic level species, allowing inferences to be made regarding predator diet composition (Napolitano 1998, Iverson et al. 2004). Furthermore, the FA compositions of various prey types differ and these differences can provide insights into pathways of energy and nutrient transfer (Napolitano 1998, Iverson et al. 2004). Thus, retrospective ecological tracer analysis provides an historical perspective on food web trophodynamics allowing an evaluation of the extent and significance of food web change over time.

Herring Gulls (*Larus argentatus*; see Plate 1) have been used as monitors of environmental conditions on the Laurentian Great Lakes since the early 1970s (Hebert et al. 1999a). Eggs have been collected annually from two to three colonies on each of the five Great Lakes (Fig. 1) and stored in a frozen archive. In Herring Gulls, resources used for egg formation are primarily exogenous (Hobson et al. 1997); therefore, the chemical constituents of eggs will reflect dietary integration over the several-week period of egg formation. Changes in ecological tracer profiles in gull eggs can provide insights into how Great Lakes food webs may be changing. Here, we examine long-term (25-year) temporal trends in egg isotope and FA signatures and investigate the broadscale factors contributing to these changes.

METHODS

Egg collection and storage protocols, stable isotope, and FA analyses have been reported previously (Hebert et al. 1999b, 2006). Estimation of gull trophic position using egg $\delta^{15}\text{N}$ is described elsewhere (Hebert et al. 1999b).

Annual estimates of prey fish abundance were obtained for each Great Lake (Superior, Michigan, and Ontario 1978–2005; Huron 1992–2005; Erie 1988–2005) according to previously described methods (Argyle 1982, Owens et al. 2003, Ontario Ministry of Natural Resources 2005, Bunnell et al. 2006, Gorman 2007). To estimate prey fish availability to gulls, annual indices of rainbow smelt (*Osmerus mordax*) abundance were used for Lakes Superior, Michigan, and Huron. Smelt was the most abundant prey fish in Lake Superior and a major prey species in Lakes Michigan and Huron (Madenjian et al. 2002, Dobiesz et al. 2005, Gorman 2007). It is available to gulls during spring spawning (Gorman 2007). For Lake Erie, an index of prey fish abundance was calculated by summing annual catch-per-trawl hour statistics for small, pelagic/nearshore species (Ontario Ministry of Natural Resources 2005). This index included data from the lake's western basin incorporating: young-of-the-year white perch (*Morone americana*), white bass (*Morone chrysops*), walleye (*Sander vitreus*), and smallmouth bass (*Micropterus dolomieu*) and all life-stages of gizzard shad (*Dorosoma cepedianum*), emerald shiner (*Notropis atherinoides*), alewife (*Alosa pseudoharengus*), rainbow smelt, and spottail shiner (*Notropis hudsonius*). In Lake Ontario, estimates of the most abundant prey fish species, the alewife, were used to evaluate prey fish availability (Owens et al. 2003). For all the Great Lakes, annual indices of prey fish abundance were calculated by standardizing each year to the year of greatest abundance; therefore, prey fish abundance values ranged between 0 and 1.

Correlation analysis was used to examine relationships between time, gull trophic position, egg $\delta^{13}\text{C}$ values, and egg FA index. Principal components analysis (PCA; StatSoft, Inc., Tulsa, Oklahoma, USA), 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. A second PCA utilizing trophic position, egg $\delta^{13}\text{C}$, and egg FA index was used to calculate an overall Herring Gull diet index (see Results). Lake-specific relationships between prey fish abundance and gull diet index were assessed using correlation analysis of untransformed (Lakes Huron and Ontario) or \log_e fish abundance data (Lakes Superior, Michigan, and Erie). In all tests, $P < 0.05$ was deemed statistically significant.

RESULTS

Stable nitrogen isotope analysis of archived egg samples indicated that Herring Gull trophic position

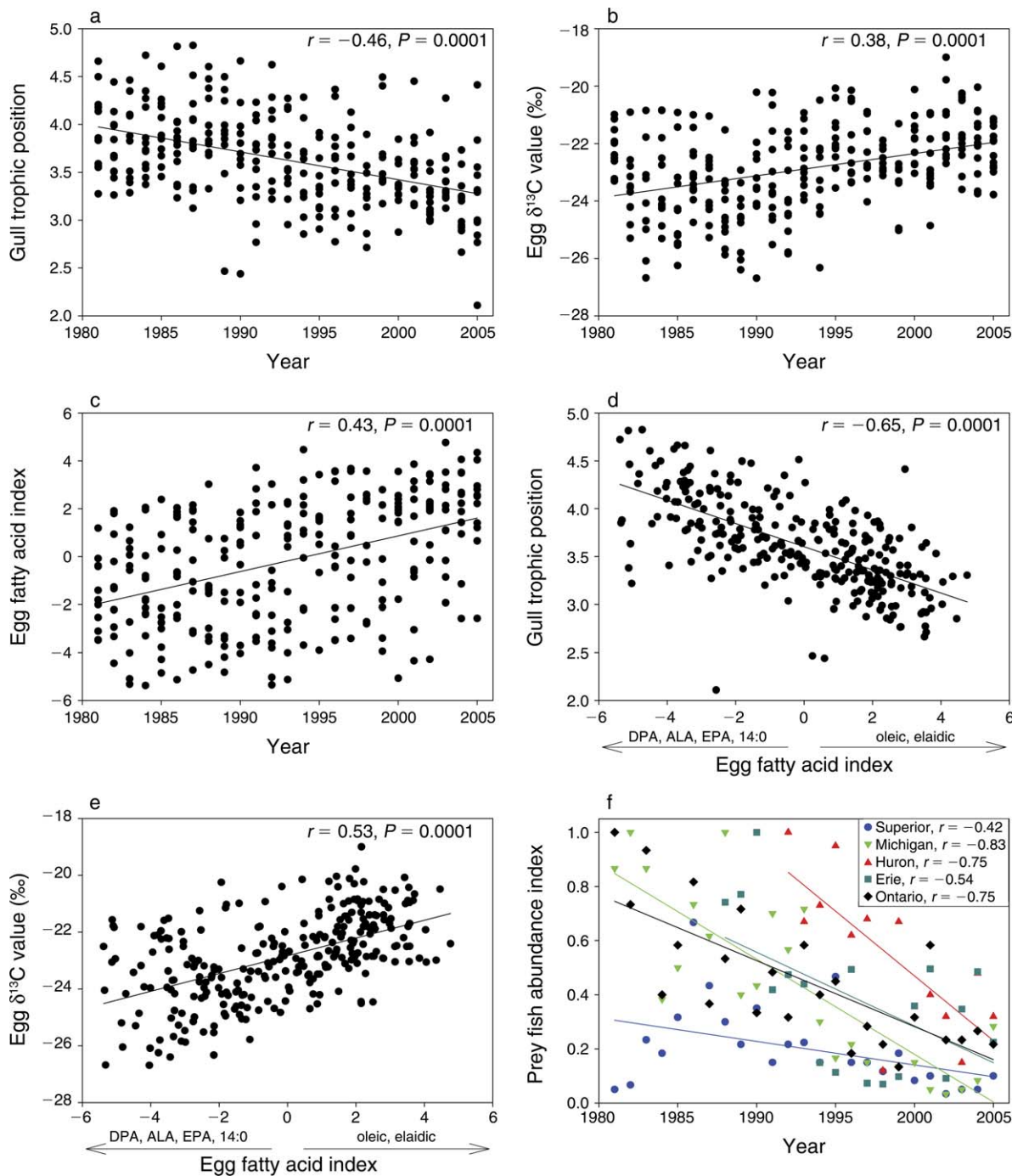


FIG. 2. Trends in Herring Gull diet indicators and prey fish abundance from across all five Great Lakes: (a) temporal trends in gull trophic position, (b) temporal trends in gull egg $\delta^{13}\text{C}$ value, (c) temporal trends in gull egg fatty acid index (which separates samples based on the proportions of omega-3 fatty acids and 14:0 [lower index values] vs. oleic acid and elaidic acid [higher index values], as shown by the arrows below panels d and e), (d) correlation between egg fatty acid index and gull trophic position, (e) correlation between egg fatty acid index and egg $\delta^{13}\text{C}$ value, and (f) temporal trends in prey fish abundance for each Great Lake.

(inferred from egg $\delta^{15}\text{N}$ values) declined over the past 25 years (Fig. 2a). During the same period, carbon isotope values in gull eggs increased (Fig. 2b). A significant negative correlation was found between gull trophic

position and egg $\delta^{13}\text{C}$ values ($r = -0.43$, $P = 0.0001$). Principal component 1 (PC1) from the PCA of the FA data accounted for 46% of the variation in egg FA. PC1 sample scores were subsequently used as an index of egg

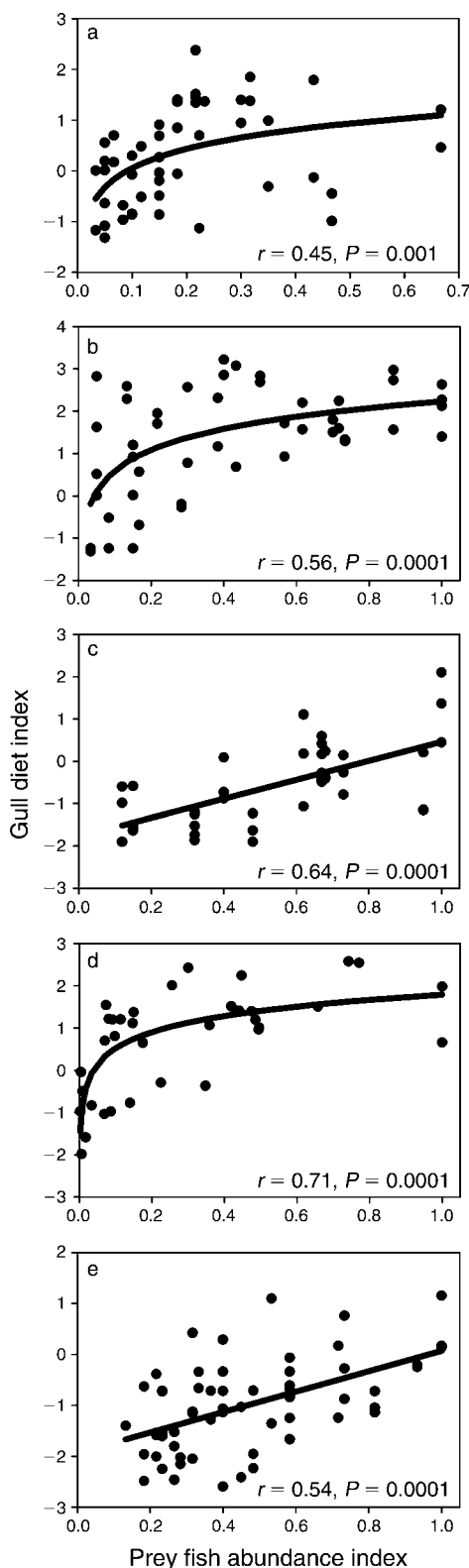


FIG. 3. Correlation between annual indices of gull diet and prey fish abundance for (a) Lake Superior, (b) Lake Michigan, (c) Lake Huron, (d) Lake Erie, and (e) Lake Ontario. Note the different x-axis scale for panel a.

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) vs. proportions of oleic acid (18:1n-9c) and elaidic acid (18:1n-9t). The egg FA index data changed through time, with egg signatures shifting, in more recent years, toward increasing importance of oleic and elaidic acids (Fig. 2c). The index was well correlated with gull trophic position and egg $\delta^{13}\text{C}$ values (Fig. 2d, e). As the contribution of oleic and elaidic acids to total FA levels increased, gull trophic position decreased (Fig. 2d) and egg $\delta^{13}\text{C}$ values increased (Fig. 2e). In each of the five Great Lakes, statistically significant temporal declines in annual indices of prey fish abundance were observed during the same 25-year period (Fig. 2f).

To examine relationships between indices of prey fish abundance and gull diet, gull dietary indicators (i.e., gull trophic position, egg $\delta^{13}\text{C}$ values, and PC1 scores from the analysis of FA percent composition data) were summarized using a second PCA. PC1 (71% of variance explained) scores from this PCA constituted a gull diet index. Greater diet index values reflected increasing trophic position, decreasing egg $\delta^{13}\text{C}$ values, and increased proportions of omega 3/myristic acid and decreased proportions of oleic and elaidic acids to total FA levels. For each of the Great Lakes, the gull diet index and annual estimates of prey fish abundance were significantly correlated (Fig. 3a-e).

DISCUSSION

The temporal decline in gull trophic position indicated that gulls were feeding on lower trophic level prey in recent years. 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, b). With a reduction in the proportion of fish in the gull diet, egg $\delta^{15}\text{N}$ values would be expected to decline (Hebert and Sprules 2002). Temporal increases in egg carbon isotope values suggested that the decline in gull trophic position was concomitant with a shift to a more terrestrial diet. The negative correlation between gull trophic position and egg $\delta^{13}\text{C}$ values was consistent with the hypothesis that birds were shifting from aquatic foods, namely prey fish, to terrestrial food sources. This hypothesis was corroborated by temporal changes in egg FA composition.

Temporal changes in diet composition were expected to result in altered egg FA profiles because bird egg FA composition reflects diet FA composition (Farrell 1998). Long carbon-chain omega-3 FA and short carbon-chain FA are found at disproportionately high concentrations in phytoplankton-based food webs compared to terrestrial systems (Napolitano 1998). Therefore, eggs containing greater proportions of these FA would have been



PLATE 1. Herring gulls (*Larus argentatus*) breeding on the Laurentian Great Lakes. Photo credit: Bruce Szczechowski.

formed from gull diets richer in aquatic foods. Eggs containing greater proportions of elaidic and/or oleic acids were indicative of gulls that had been consuming more food of terrestrial origin, likely in part, human refuse. Elaidic acid is a trans fat that is only found to a very limited extent in the natural world; its primary source is anthropogenic foodstuffs. The positive correlation between the egg fatty acid index and gull trophic position and the negative correlation with egg $\delta^{13}\text{C}$ values provided further evidence of an aquatic to terrestrial shift in gull diet composition through time.

These shifts in dietary tracers indicated that aquatic food consumption by gulls declined through time. We suggest that such a change was the result of reductions in pelagic prey fish abundance. In each of the five Great Lakes, statistically significant temporal declines in annual indices of prey fish abundance were observed during the same 25-year period. 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. When prey fish abundance was lower, the gull diet index reflected the consumption of more terrestrial food.

Since 1980, multiple factors have likely acted together to reduce prey fish abundance in the Great Lakes (Johannsson et al. 2000, Madenjian et al. 2002, Mills et al. 2003, O’Gorman et al. 2004, Dobiesz et al. 2005, Gorman 2007). Examples of the factors that could have decreased prey fish abundance are (1) predation by piscivorous fishes, (2) reductions in nutrient loading, and, more recently, (3) establishment of exotic invertebrates, and (4) increases in populations of other predatory seabirds. Predation by piscivorous fish appears to have been the one factor that was universally important across all five lakes because of massive stocking of mainly exotic salmon and trout. During the period 1966–1998, approximately 745 million salmonines were stocked into the Great Lakes (Crawford 2001). These stocking activities were conducted as part of fisheries management programs designed to reduce populations of exotic prey fish, to create recreational fisheries, and to restore populations of native fishes. Stocked exotic salmonids, in particular, consume a significant proportion of prey fish biomass and are important in regulating prey fish abundance (Madenjian et al. 2002, Mills et al. 2003, O’Gorman et al. 2004, Dobiesz et al. 2005, Gorman 2007). Other

factors that may have contributed to prey fish declines in specific lakes were reductions in phosphorus loadings and the invasion of dreissenid mussels (*Dreissena polymorpha*, *D. bugensis*) (Johannsson et al. 2000, O'Gorman et al. 2004). For example, in Lake Erie, dreissenids have redirected pathways of energy flow from pelagic to benthic lake compartments (Johannsson et al. 2000). This redirection of pelagic production to the benthos likely reduced the capacity of this system to support components of the pelagic food web, including some prey fishes. Another factor that may have contributed to declines in prey fish abundance was increased Double-crested Cormorant (*Phalacrocorax auritus*) populations. Although numbers have increased greatly, prey fish consumption by cormorants is not likely to have had a significant lake-wide impact on prey fish populations. In the early 1990s, estimated fish consumption by all waterbird species in western Lake Erie was only 15% of that attributed to the primary piscivorous fish species, the walleye (Madenjian and Gabrey 1995). More recent estimates for Lake Ontario based upon increased cormorant numbers indicate that cormorants could be taking up to 18% of prey fish biomass (Casselman and Weseloh 2007). This more recent estimate is substantial but may represent a "worst-case" scenario for the impact of cormorants on prey fish populations. That possibility stems from the fact that the density of breeding cormorants on Lake Ontario (1.24 birds/km² in 2005) exceeds that observed on the other Great Lakes (2005 data: Erie, 0.68 birds/km²; Michigan, 0.60 birds/km²; Huron, 0.51 birds/km²; and Superior, 0.05 birds/km²; population data from D.V.C. Weseloh, unpublished data; lake surface area data from Government of Canada and U.S. EPA [1995]). Certainly on sparsely colonized Lake Superior, declines in prey fish populations cannot be attributed to cormorant predation. The degree to which mussels, cormorants, and other factors exacerbated reductions in prey fish abundance brought about by piscivorous fish predation would have varied from lake to lake. Despite some uncertainties in the mechanisms contributing to prey fish declines, the declines themselves are clear, as are constraints on the availability of aquatic foods, i.e., prey fish, to surface-feeding seabirds.

From a nutritional perspective, fish may be the preferred prey of many seabirds (Hebert et al. 2002). However, the nutritional benefits of fish consumption will be balanced by the energetic costs of obtaining them. With declining prey fish abundance, surface-feeding seabirds (i.e., gulls and terns) must either spend more time and energy foraging for fewer prey fish or switch to terrestrial resources that are more readily obtainable. In the Great Lakes, Herring Gulls have opted for the latter but this apparent choice may be an illusion; a "Hobson's choice." Hobson's choice is really no choice at all; it is a "take-it-or-leave-it" scenario (Fisher 1660). Faced with dwindling aquatic prey availability, gulls have been forced into dietary change.

Because of their high degree of foraging plasticity, Herring Gulls can buffer the energetic impact of aquatic food web change by altering their feeding strategies. Nutritional implications of such dietary changes are uncertain; however, at colonies where Herring Gulls feed to a greater degree on terrestrial food, body condition of adult birds is poorer, egg volume is reduced, and productivity is lower (Hebert et al. 2002). At Great Lakes colonies where Herring Gulls have ready access to both garbage and fish, they preferentially consume fish (Belant et al. 1998). These results suggest that shifts to terrestrial foods, namely garbage, have negative fitness consequences for birds. Great Lakes Herring Gull populations have declined over the last two decades although a number of factors are likely responsible (Morris et al. 2003). For other species that are more closely tied to the use of pelagic aquatic resources, e.g., terns, effects on individual fitness and population size may be more severe.

The results that we document here indicate large-scale ecosystem-level declines in pelagic prey availability. The consequences of these changes both to seabirds and other components of the Great Lakes ecosystem require further study; however, it is clear that resource management activities can have unintended consequences for non-target species within the ecosystem (see Eby et al. 2006). Long-term, integrative ecological monitoring programs offer the means to detect such impacts and elucidate their cause.

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