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Trends in herring gull egg quality over four decades reflect ecosystem state

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ABSTRACT

Egg quality (size, energy density) is important in determining early survival of birds. Here, we examine temporal (1981–2019) trends in herring gull (*Larus argentatus*) egg volume and energy density at breeding colonies on all five Laurentian Great Lakes. Temporal declines in egg volume were observed at 4/6 colonies on the upper Great Lakes (Lakes Superior, Michigan, Huron). On the lower Great Lakes (Lakes Erie, Ontario, and connecting channels) egg volume declined at 3/8 colonies and increased at one site. Egg energy density (kJ/g of egg contents) declined at 4/6 upper Great Lakes colonies and at 2/8 lower Great Lakes colonies. All of the upper Great Lakes colonies showed declines in either egg volume or energy density, or both, and these declines were related to dietary markers in eggs (fatty acids, stable nitrogen and carbon isotopes). On the lower Great Lakes and connecting channels, declines in egg volume or energy density were related to dietary endpoints in 3/5 instances. An information-theoretic approach indicated that trends in egg volume were best explained at the colony level while egg energy density trends were best explained by lake of origin. Diet-related declines in herring gull egg quality are likely a reflection of broad-scale ecosystem changes limiting aquatic food availability for gulls, particularly on the upper Great Lakes. These changes may be contributing to population declines in herring gulls and other surface-feeding aquatic birds. This study highlights the value of long-term monitoring of wildlife for identifying ecosystem change.

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Introduction

Aquatic birds are useful indicators of environmental change in both freshwater and marine environments (Furness and Camphuysen, 1997; Hebert et al., 1999a). On the Laurentian Great Lakes, herring gulls (*Larus argentatus*) have been used in this capacity for decades. Studies have focused on the assessment of spatial and temporal trends in contaminant levels (Gilman et al., 1979; Weseloh et al., 2006, 2011), detection of emerging contaminants (Gebbinck et al., 2011; Chen et al., 2012a,b; Gauthier et al., 2019), and identification of ecosystem change through modification of

food web structure (Hebert et al., 2008, 2009; Laurich et al., 2019). With respect to the last topic, herring gulls are opportunistic generalists that make use of food resources as they become available. When foraging aquatically, they feed at the water's surface and so are constrained to feed on prey that inhabit surface and/or shallow, near-shore waters. On the Great Lakes, small prey fish are an important food source for herring gulls (Fox et al., 1990; Ewins et al., 1994; Hebert et al., 1999b). Fish are a high quality food that is rich in energy and nutrients (Hebert et al., 2002); but if fish are not available, herring gulls will utilize other food resources (Fox et al., 1990; Laurich et al., 2019).

Diet, through its effects on various components that contribute to reproductive success including egg quality (size/volume, energy content, biochemical composition), timing of breeding, adult

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attentiveness during incubation and chick rearing, and/or rates of chick provisioning, plays a role in regulating the fitness of birds (Martin, 1987). Here, we focus on aspects affecting egg quality: egg volume and energy content, in gulls. Egg volume may be an important determinant of egg quality as it reflects the quantity of lipid and protein reserves provisioned by the female during egg formation and available to the chick during embryonic development and at hatch. For birds in general, chicks hatching from larger eggs exhibit higher hatching success, larger size, enhanced immune function, more rapid growth, and higher nestling survival (Martin, 1987; Krist, 2011). For example, Bolton et al. (1992) found that in lesser black-backed gulls (*Larus fuscus*), larger eggs produced chicks that were skeletally larger and also heavier for their size; both factors could contribute to increased chick survival. In herring gulls, egg size/volume has been found to be important in determining chick survival and growth early in chick-rearing and subsequent survival to fledging (Parsons, 1970; Davis, 1975). Egg energy content is also an important factor regulating recruitment of chicks into gull populations through the provision of resources for early chick growth. Egg energy content increases with yolk content because yolk contains higher levels of lipids and proteins than albumen (Martin, 1987). Because egg quality can affect hatching success and survival of young, it should only be reduced in environments where food resources are constrained. Here, we examine patterns in herring gull egg volume and egg energy density on each of the five Laurentian Great Lakes over a 39-year period (1981–2019). We also investigate possible dietary and environmental factors (temperature) that may be contributing to these patterns.

Methods

Herring gull eggs were collected annually from 14 colonies on the Laurentian Great Lakes (Fig. 1). Median clutch size for herring gulls is three eggs (Nisbet et al., 2017). Each year at each site, one egg was collected from 10 to 13 3-egg clutches in late April–early May. For some year/colony combinations, eggs were not collected or measurements were not available, but for the most part, data were available from most years during the 1981 to 2019 study period. Exceptions to this were: the St. Lawrence River colony where collections were first made in 1986, the Detroit River where nesting effectively ceased in 2009, and the Niagara River where data were available from Weseloh Rocks up to 2015. After collection, eggs were transported to the National Wildlife Research Centre (NWRC) in Ottawa, Ontario, Canada. Maximum length and breadth of each egg were recorded prior to the egg being opened. Egg volume (cm^3) was calculated according to Ryder (1975):

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

Eggs were processed individually and egg contents (albumen and yolk), were homogenized together. For each location and in each year, one egg pool was created that consisted of the individual eggs combined on an equal-weight basis. Subsamples of these pools were stored frozen prior to analysis (-40°C for stable isotope analysis, -80°C for fatty acid analysis). As part of ongoing chemical contaminant biomonitoring studies, egg lipid and moisture content (% wet weight) were quantified for each pool using a gravimetric method. Egg energy densities were estimated using the mass balance approach described in Paterson et al. (2009, 2014). Carbohydrate content of avian eggs is typically <1% and was thus considered to contribute negligibly to egg energy densities. Caloric contents of 9.50 and 5.65 kcal g^{-1} were used for egg lipid and protein, respectively. A conversion factor of 4187 J kcal^{-1} was used to estimate energy densities (see Paterson et al., 2009, 2014 for details).

Details regarding stable isotope analyses have been described previously (Hebert et al., 1999b; Hebert and Popp, 2018). Stable isotope values were reported in delta notation as parts per thousand deviation from a standard (N, atmospheric air; C, Vienna Pee-Dee belemnite). Stable isotope data were normalized to internal reference materials. Quality control was maintained through sample duplicates, and analytical precision was $\pm 0.2\text{‰}$. Egg pools were also used for fatty acid analysis. Analytical methods are described in Hebert et al. (2006) and McMeans et al. (2012). A 37-component fatty acid methyl ester standard (Supelco; no. 47885-U) was used to identify and quantify fatty acid methyl esters in eggs by comparing their retention times to those of the fatty acid methyl ester standard. Results were reported as micrograms of fatty acid methyl ester per milligram dry weight tissue. Here we focus on the omega-3 and omega-6 fatty acids. Total omega-3 fatty acid values were the sum of five fatty acids: alpha-linolenic acid (ALA, 18:3n-3), eicosatrienoic acid (ETA, 20:3n-3), eicosapentaenoic acid (EPA, 20:5n-3), docosapentaenoic acid (DPA, 22:5n-3), and docosahexaenoic acid (DHA, 22:6n-3). Total omega-6 fatty acid values were the sum of five fatty acids: linoleic acid (LNA, 18:2n-6), γ -linolenic acid (GLA, 18:3n-6), 11,14-eicosadienoic acid (20:2n-6), dihomo- γ -linolenic acid (20:3n-6), and arachidonic acid (ARA, 20:4n-6). Other omega-3 and omega-6 fatty acids were not detected in gull eggs.

Egg fatty acid profiles reflect the fatty acid composition of the laying females' diet (Farrell, 1998; Surai et al., 2001; Surai and Speake, 2008). Long carbon-chain omega-3 (n-3) fatty acids are found at disproportionately high concentrations in phytoplankton-based food webs compared to terrestrial systems (Hixson et al., 2015). Therefore, eggs containing greater proportions of these fatty acids would have been formed from diets containing more aquatic foods. Higher levels of n-3 fatty acids in the tissues of consumers have been associated with increased fish consumption (Huang et al., 1990; Dewailly et al., 2003) while omega-6 (n-6) fatty acids are abundant in terrestrial foods (Olsen, 1998). Here, we use the ratio of n-3 to n-6 fatty acids as an index of the relative amount of aquatic food in the gull diet (Hebert et al., 2008).

Temporal trends in egg volume (1981–2019) and egg energy density (1981–2018) were evaluated for each colony using non-parametric statistics (Spearman correlation coefficients, r_s). Temporal trends were visualized using locally weighted scatterplot smoothing (LOWESS) (Cleveland, 1979). For statistical analysis of the egg volume data, an annual mean value was generated for each colony based upon the eggs measured at each colony in each year. For egg energy density and dietary endpoints (fatty acids, stable isotopes) one annual colony-specific value was generated for each parameter based upon the analysis of the pooled egg sample from each colony in each year.

Information regarding seasonal temperature departures from a long-term reference for the Great Lakes region were obtained from Environment and Climate Change Canada (ECCC, 2019). Gridded historical temperature anomalies are interpolated from adjusted and homogenized climate station data at a 50 km resolution across Canada. Seasonal temperature anomalies are the difference between the annual temperature for a particular season and a baseline value defined as the average over the 1961–1990 reference period. That reference period was chosen because it is recognized by the World Meteorological Organization as a standard reference period for long-term climate change assessments (ECCC, 2019). Seasonal, i.e., winter (December of preceding year, January, February), spring (March, April, May), temperature anomalies from 1981 to 2019 specific to the Laurentian Great Lakes were included in this analysis. Seasonal temperature anomaly data were used to assess the degree to which temperatures immediately preceding the herring gull egg-laying period (April–May) could result in temperature-mediated phenological changes that could

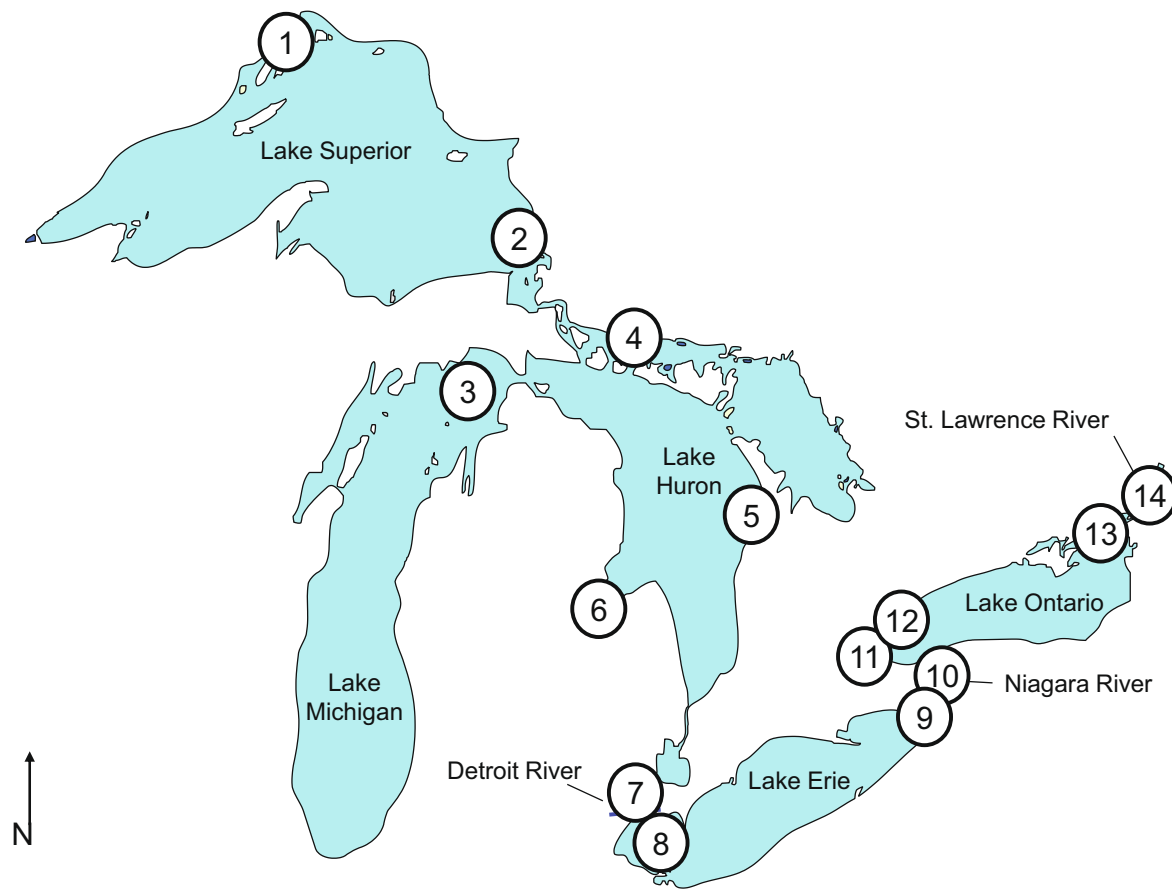


Fig. 1. Sites of collection for egg data. (1) Granite Island, (2) Agawa Rocks, (3) Gull Island, (4) Double Island, (5) Chantry Island, (6) Channel Shelter Island, (7) Fighting Island, (8) Middle Island, (9) Port Colborne, (10) Weseloh Rocks, (11) Hamilton Harbour, (12) Toronto Harbour, (13) Snake Island, (14) Strachan Island.

disrupt food web connections between gulls and their prey. No specific examples of such phenological effects impacting Great Lakes waterbirds have yet been identified but they could occur through a variety of mechanisms. For example, increased air temperatures could result in water temperatures reaching optimal spawning temperatures for prey fish, such as rainbow smelt (*Osmerus mordax*), earlier in the spring. Such mechanisms could result in temporal “disconnects” between gulls and availability of their prey.

An information-theoretic approach (Burnham and Anderson, 2002) was used to assess how well candidate models explained trends in egg volume and egg energy density. Predictor variables included in the models were: collection site (colony), collection lake (Detroit River site categorized with Lake Erie sites; Niagara River and St. Lawrence River sites categorized with sites on Lake Ontario), regional collection location (upper or lower Great Lakes), year of collection, aquatic versus terrestrial food in the gull diet ($n-3/n-6$ fatty acid ratio), food source ($\delta^{13}\text{C}$), bird trophic position ($\delta^{15}\text{N}$), and winter and spring annual average temperature departures from the 1961–1990 reference value for the Great Lakes region (ECCC, 2019). Models were evaluated using Akaike’s Information Criterion (AIC_c). The most parsimonious model exhibiting the smallest difference in AIC_c values across models (ΔAIC_c) (model threshold = $\Delta\text{AIC}_c < 2$) was deemed best at explaining trends in egg volume and energy density. Statistical significance was evaluated at $\alpha = 0.05$, and all statistics were done using Statistica (ver. 12, StatSoft Inc., Tulsa, Oklahoma, USA).

Results

Temporal declines in egg volume were observed at colonies on Lakes Superior (Granite Island $r_s = -0.39$, $p < 0.02$; Agawa Rocks $r_s = -0.41$, $p < 0.02$), Michigan (Gull Island $r_s = -0.45$, $p < 0.01$), Huron (Double Island $r_s = -0.60$, $p < 0.001$), and at colonies on the Detroit River (Fighting Island $r_s = -0.66$, $p < 0.001$), Niagara River (Weseloh Rocks $r_s = -0.80$, $p < 0.001$), and Lake Ontario (Toronto Harbour $r_s = -0.58$, $p < 0.001$) (Table 1, Fig. 2). Increases in egg volume were only observed at Strachan Island on the St. Lawrence River ($r_s = 0.47$, $p < 0.01$) (Table 1, Fig. 2). Declines in egg volume were more consistently observed at colonies on the upper Great Lakes (4/6 colonies) than on the lower lakes (3/8 colonies). Comparing egg volume between the earliest and most recent year available, Double Island on Lake Huron showed the largest change (1981 versus 2019, 14.8% decline) followed by Weseloh Rocks on the Niagara River (1981 versus 2015, 11.4% decline).

Temporal declines in egg energy density were observed at colonies on Lakes Michigan (Gull Island $r_s = -0.60$, $p < 0.001$), Huron (Double Island $r_s = -0.39$, $p < 0.02$; Chantry Island $r_s = -0.56$, $p < 0.001$), Erie (Port Colborne $r_s = -0.58$, $p < 0.001$), and Ontario (Snake Island $r_s = -0.42$, $p < 0.02$) (Table 1, Fig. 3). Declines in egg energy density were more consistently observed at colonies on the upper Great Lakes (4/6 colonies) than on the lower lakes (2/8 colonies).

All colonies on the upper lakes showed declines in egg volume, egg energy density, or both; and these declines were accompanied by

Table 1

Relationships between egg volume or egg energy density, time, dietary markers, and annual average temperature departures from 1961 to 1990 reference values for the Great Lakes region. Shaded cells (arrows within cells show direction of trend/relationship) denote statistically significant Spearman correlations indicating: temporal decrease in egg volume (except Strachan Island*) or egg energy density; egg volume/energy density increase with increasing n-3/n-6, increasing $\delta^{15}\text{N}$, decreasing $\delta^{13}\text{C}$ (more negative $\delta^{13}\text{C}$ values), decreasing temperature departures (colder years). Sites 1–6 upper Great Lakes (Superior, Michigan, Huron), sites 7–14 lower Great Lakes (Erie, Ontario, connecting channels) (see Fig. 1).

Site #	Waterbody	Correlations with egg volume						Correlations with egg energy density					
		Time	n-3/n-6	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Winter	Spring	Time	n-3/n-6	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Winter	Spring
1	Superior	↓	↑										
2	Superior	↓		↑							↓		
3	Michigan	↓	↑	↑	↓			↓	↑	↑	↓		
4	Huron	↓	↑	↑	↓			↓	↑	↑			
5	Huron						↓	↓	↑	↑			
6	Huron						↓	↓	↑	↑			
7	Detroit R	↓		↑	↓				↑				
8	Erie												
9	Erie		↑					↓		↑		↓	
10	Niagara R	↓		↑	↓								
11	Ontario		↑	↑									
12	Ontario	↓											
13	Ontario							↓					
14	St. Lawrence R	↑	↑	↑									

p>0.05 no correlation
p<0.05
p<0.01
p<0.001

decreases in egg n-3/n-6 ratios (decreased aquatic food), egg $\delta^{15}\text{N}$ values (decreased trophic position), and increases in egg $\delta^{13}\text{C}$ values (possibly increased terrestrial food) (Table 1). On the lower lakes and connecting channels, temporal declines in egg volume or egg energy density were related to dietary endpoints in 3/5 instances (Table 1). At the one colony (Strachan Island) exhibiting an increase in egg volume through time, egg volume increased with egg n-3/n-6 ratios and egg $\delta^{15}\text{N}$ values (Table 1). Spring temperature departures were negatively correlated with egg volume at two Lake Huron colonies (Channel Shelter Island $r_s = -0.40$, $p < 0.03$ and Chantry Island $r_s = -0.40$, $p < 0.02$) while egg energy density was negatively correlated with winter temperature departures at one colony on Lake Erie (Port Colborne $r_s = -0.39$, $p < 0.03$). Hence, for these sites, warmer temperatures were associated with reductions in egg volume or energy density.

An information-theoretic approach indicated that trends in egg volume and egg energy density were influenced by dietary endpoints (Tables 2 and 3). Trends in egg volume were best explained at the colony level (i.e., there was significant variability in the degree to which colonies within the same lake exhibited temporal changes in egg volume; Table 2) while temporal trends in egg energy density were generally consistent among colonies located on the same lake (Table 3).

Discussion

In birds, egg quality (size and composition) reflects food abundance and female energy reserves during the period of egg production (Martin, 1987). Although species have evolved average strategies for regulating egg quality, there is scope for individual variation in egg size and composition as a function of feeding conditions. Under conditions of constrained dietary resources, e.g., lipid and protein, adverse impacts on egg quality have been demonstrated (Martin, 1987). Experimentally increasing protein content (Leeson and Summers, 1997) or essential amino acid availability (Waldroup and Hellwig, 1995) in the diet of chickens results in an increase in egg size. In gulls, egg formation requires adequate stores of lipid, protein, and micronutrients and imposes significant

costs to breeding females (Monaghan and Nager, 1997). Deficiencies in lipid and/or protein can affect egg formation (Hiom et al., 1991; Bolton et al., 1992). These studies highlight the important role that diet plays in regulating the availability of resources necessary for egg formation which are reflected in endpoints such as egg volume and egg energy density (Hebert et al., 2009; Paterson et al., 2014). In this study, declines in egg volume and energy density were particularly evident at gull colonies located on the upper Great Lakes (Lakes Superior, Michigan, and Huron).

The Laurentian Great Lakes have undergone profound ecological change over the past half century (Johannsson et al., 2000; Madenjian et al., 2002; Mills et al., 2003; Dobiesz et al., 2005; Gorman, 2007; Bunnell et al., 2014; Paterson et al., 2014; Dai et al., 2019). Bunnell et al. (2014) provide a review of changes in fish and lower trophic levels for all five Great Lakes and document significant changes in the abundance or biomass of aquatic invertebrates, prey fish, and predatory fish from about 1978 to 2010. The upper Great Lakes have shown declines in productivity as they have become more oligotrophic in recent decades (Bunnell et al., 2014). In lakes Michigan and Huron, this largely resulted from reductions in phosphorus loadings (Bunnell et al., 2014). Exacerbating declines in productivity have been intentional and accidental introductions of exotic species that have altered the structure of biological communities. Intentional introductions of exotic Pacific salmonids (pink, coho and chinook salmon, *Oncorhynchus gorbuscha*, *O. kisutch* and *O. tshawytscha*, respectively) have significantly affected prey fish populations in the lakes (Crawford, 2001). Accidental introductions of exotic species, particularly those that act as ecosystem engineers (sensu Jones et al., 1994, 1997), have also had significant impacts. Zebra (*Dreissena polymorpha*) and quagga (*D. bugensis*) mussels arrived via ballast water from ships and have altered pathways of energy and nutrient transfer (Hecky et al., 2004). Abundant dreissenid mussel populations exist in all of the lakes, with the exception of Lake Superior, and they have shifted energy production from the open pelagic waters of the lakes to benthic regions. This process has been described as ecosystem benthification (Mayer et al., 2013). Oligotrophication and benthification have acted together to reduce biomass in pelagic waters.

Bottom-up processes may be combining with top-down food web processes (predation by stocked piscivorous fish) to reduce the abundance of prey fish, particularly in the upper Great Lakes (Bunnell et al., 2014). Quality of prey fish may also be decreasing (Paterson et al., 2014). For example, Dai et al. (2019) reported that energy density in Lake Huron rainbow smelt was up to 31% lower in 2017 compared to earlier years. Lake Huron smelt also had lower energy densities than those from Lake Erie, reflecting differences in primary productivity between the two lakes. For surface-feeding birds, such as herring gulls, reductions in the availability of pelagic prey fish may have constrained their ability to obtain aquatic food (Hebert et al., 2008, Laurich et al., 2019). Fish may be the preferred

prey of gulls because of their high nutritional quality (Hebert et al., 2002), but the nutritional benefits of fish consumption must be balanced by the energetic costs of obtaining them. As prey fish abundance and quality decline, surface-feeding birds such as gulls, must spend more energy foraging or alter their diets to utilize alternative food resources such as terrestrial food (Hebert et al., 2008).

Reductions in aquatic food availability may be limiting the resources available to herring gulls for egg formation (Hebert et al., 2009). Such changes parallel those observed in other regions of North America. For example, Blight (2011) hypothesized that declines in breeding populations of glaucous-winged gulls

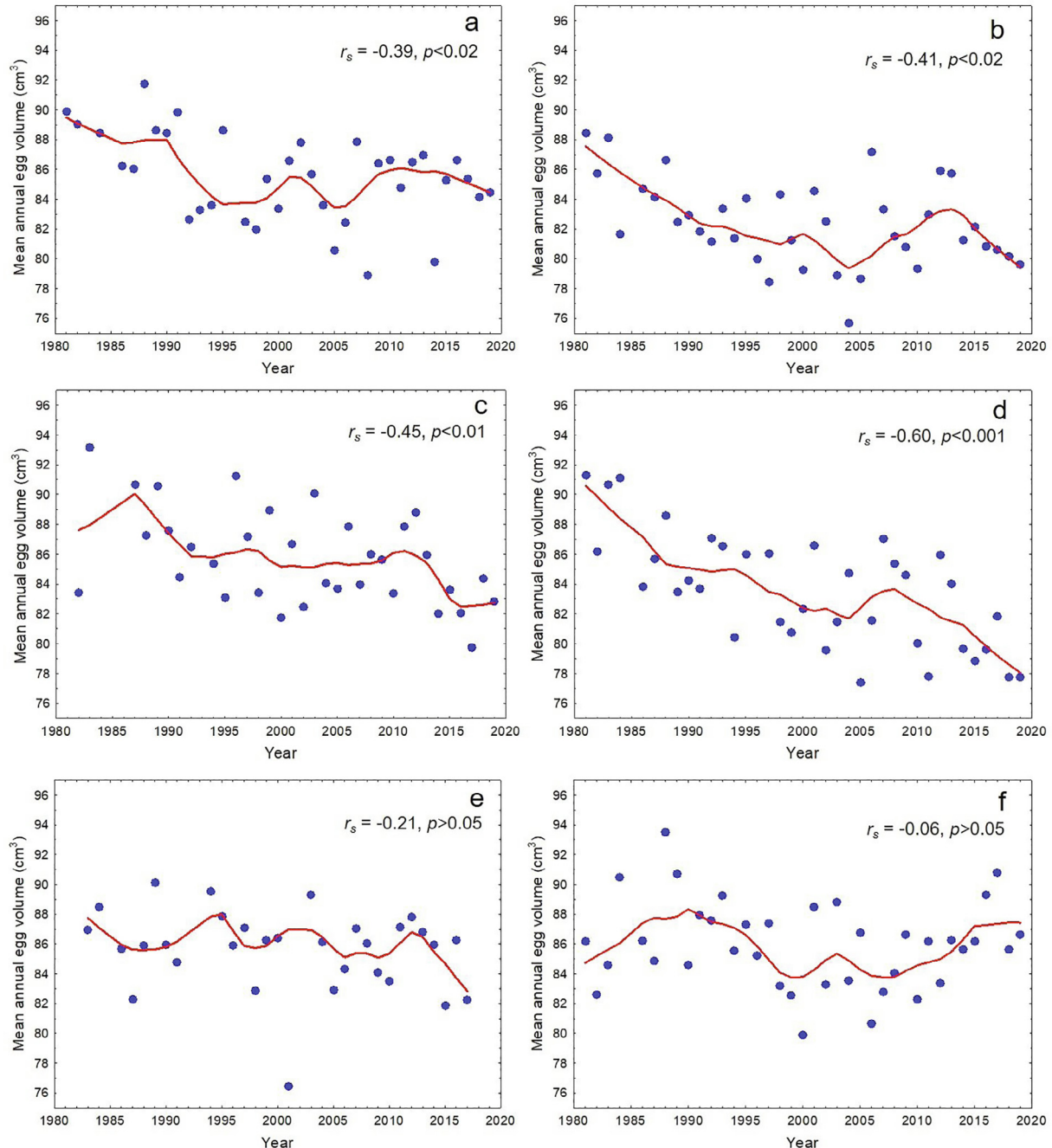


Fig. 2. Temporal trends in annual herring gull egg volume (cm³). Trend lines were generated using locally weighted scatterplot smoothing (LOWESS). Upper Great Lakes panels a–f: (a) Granite Island, Lake Superior (b) Agawa Rocks, Lake Superior (c) Gull Island, Lake Michigan (d) Double Island, Lake Huron (e) Channel Shelter Island, Lake Huron (f) Chantry Island, Lake Huron. Lower Great Lakes panels g–n: (g) Fighting Island, Detroit River (h) Middle Island, Lake Erie, (i) Port Colborne, Lake Erie (j) Weseloh Rocks, Niagara River (k) Hamilton Harbour, Lake Ontario (l) Toronto Harbour, Lake Ontario (m) Snake Island, Lake Ontario (n) Strachan Island, St. Lawrence River.

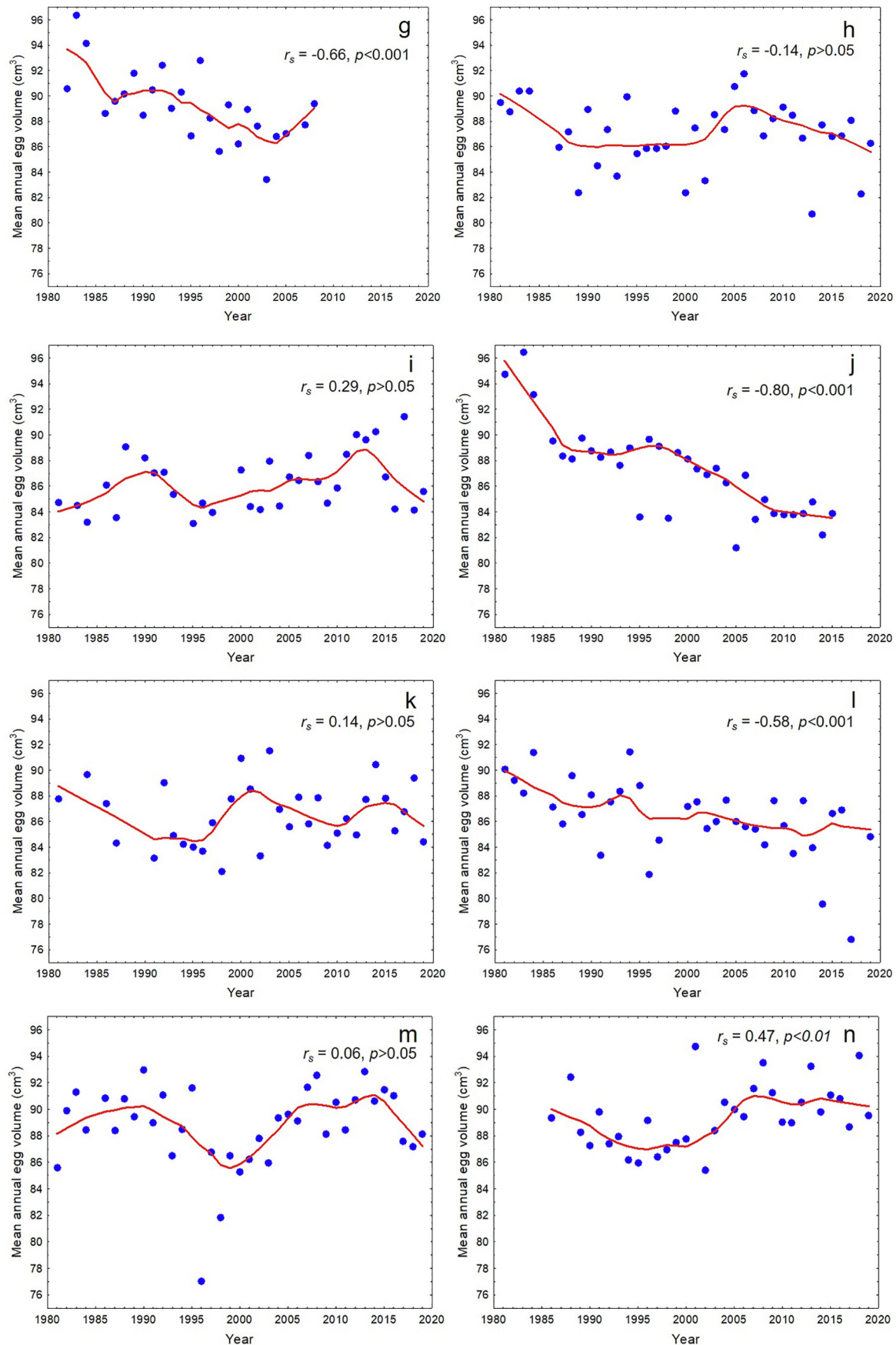


Fig. 2 (continued)

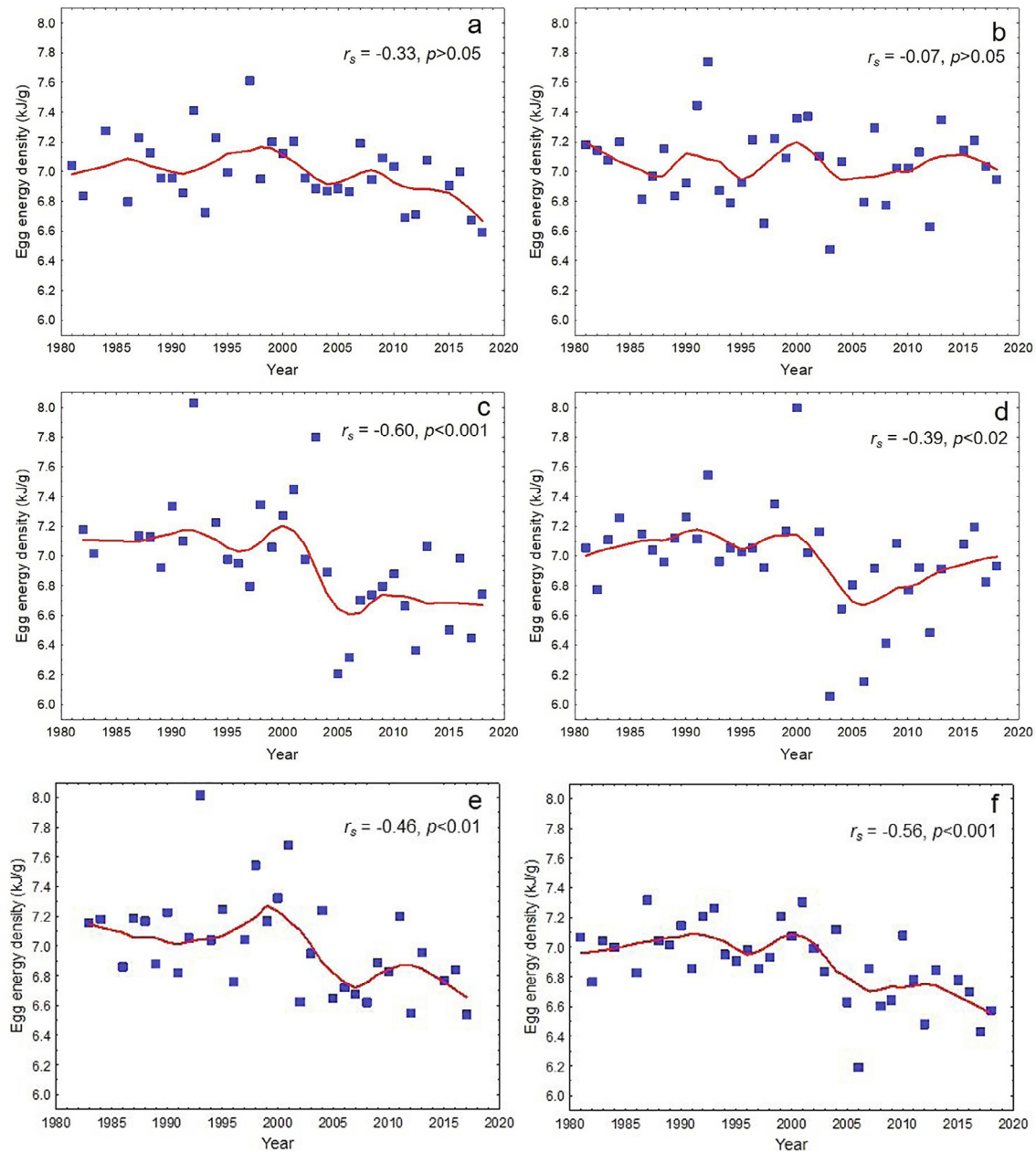


Fig. 3. Temporal trends in annual herring gull egg energy density (kJ/g). Trend lines were generated using locally weighted scatterplot smoothing (LOWESS). Upper Great Lakes panels a–f: (a) Granite Island, Lake Superior (b) Agawa Rocks, Lake Superior (c) Gull Island, Lake Michigan (d) Double Island, Lake Huron (e) Channel Shelter Island, Lake Huron (f) Chantry Island, Lake Huron. Lower Great Lakes panels g–n: (g) Fighting Island, Detroit River (h) Middle Island, Lake Erie, (i) Port Colborne, Lake Erie (j) Weseloh Rocks, Niagara River (k) Hamilton Harbour, Lake Ontario (l) Toronto Harbour, Lake Ontario (m) Snake Island, Lake Ontario (n) Strachan Island, St. Lawrence River.

(*L. glaucescens*) off the coast of British Columbia, Canada, may have been the result of decreased prey fish availability. During the period of that study (1902–2010), gull eggs showed a 5% decline in mean egg volume and a decrease in mean clutch size over a 48-year period (1962–2009) from 2.82 to 2.25 eggs per clutch. Because of the early timing of egg collections completed as part of the Great Lakes Herring Gull Monitoring Program clutch size data for Great Lakes herring gulls are not available. However, we expect that food constraints on egg production would first affect egg size rather than clutch size because change in the latter represents a stepwise decrease in reproductive potential (Martin, 1987). In our study, declines in egg size observed in the upper Great Lakes are comparable to those observed by Blight (2011) but over a much shorter period. Furthermore, the declines observed in herring gull egg vol-

ume at colonies such as Double Island (–14.8%) and Weseloh Rocks (–11.4%) in the Niagara River were substantially greater. Genetic factors (Martin, 1987) and physiological constraints on egg viability may limit the maximal degree to which egg size can be decreased to adjust for poor feeding conditions. In very poor situations, we would expect reductions in clutch size as well.

Declines in egg energy density provided further evidence of food stress in gulls. The fact that energy density trends across gull colonies within individual lakes were more consistent than for egg volume may have reflected the fact that trends in energy density represent a system-wide, fundamental ecosystem attribute. Organisms such as fish and birds will respond to changes in prey availability in different ways, but tissue energy density may provide the means to integrate those differences into a common, compara-

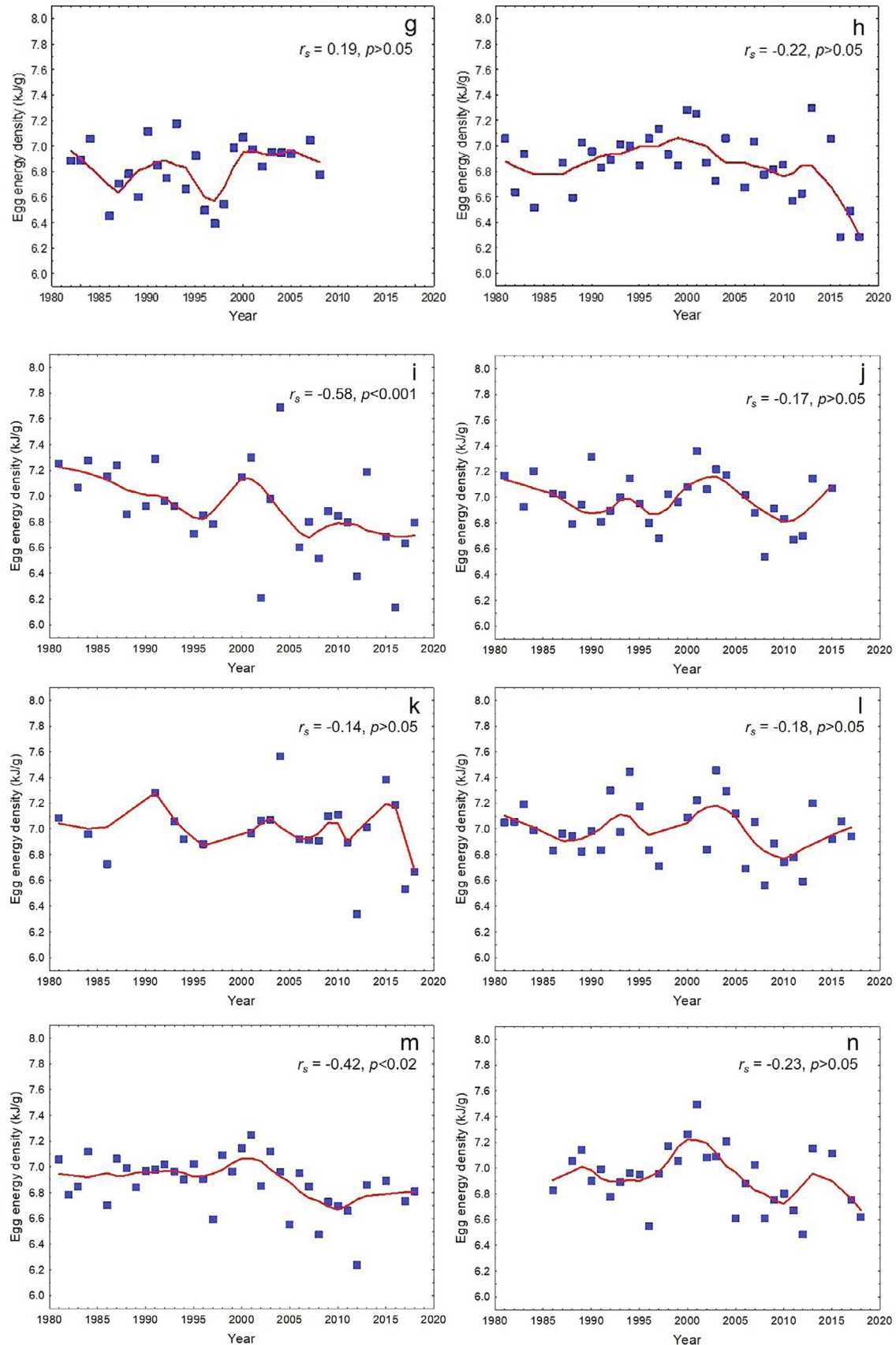


Fig. 3 (continued)

Table 2

Model results from AIC analysis examining factors influencing herring gull egg volume. Year = Year of egg collection, Colony = Collection site, Lake = Collection lake, Region = Collection region (upper or lower Great Lakes), n-3/n-6 = egg omega 3 fatty acid/omega 6 fatty acid ratio, $\delta^{15}\text{N}$ = egg nitrogen isotope value, $\delta^{13}\text{C}$ = egg carbon isotope value, Winter temp = Dec–Feb annual temperature departure from 1961 to 1990 winter average, Spring temp = March–May annual temperature departure from 1961 to 1990 spring average.

Var.1	Var.2	Var.3	Var.4	Var.5	Var.6	Var.7	Var.8	AIC	AICc	ΔAICc	AICc Weight
Year	n-3/n-6	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Colony				2288.900	2289.122	0.000	0.119
Year	n-3/n-6	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Region	Colony			2288.900	2289.186	0.064	0.115
Year	n-3/n-6	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Lake	Colony			2288.900	2289.186	0.064	0.115
Year	n-3/n-6	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Region	Lake	Colony		2288.900	2289.258	0.136	0.111
Year	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Colony					2289.935	2290.101	0.980	0.073
Year	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Region	Colony				2289.935	2290.157	1.035	0.071
Year	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Lake	Colony				2289.935	2290.157	1.035	0.071
Year	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Region	Lake	Colony			2289.935	2290.221	1.099	0.069
Year	Spring temp	n-3/n-6	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Colony			2290.361	2290.647	1.526	0.055
Year	Spring temp	n-3/n-6	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Lake	Colony		2290.361	2290.720	1.598	0.053
Year	Spring temp	n-3/n-6	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Region	Colony		2290.361	2290.720	1.598	0.053
Year	Spring temp	n-3/n-6	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Region	Lake	Colony	2290.361	2290.800	1.678	0.051
Year	n-3/n-6	$\delta^{13}\text{C}$	Colony					2290.951	2291.117	1.995	0.044

Table 3

Model results from AIC analysis examining factors influencing herring gull egg energy density. Year = Year of egg collection, Colony = Collection site, Lake = Collection lake, Region = Collection region (upper or lower Great Lakes), n-3/n-6 = egg omega 3 fatty acid/omega 6 fatty acid ratio, $\delta^{15}\text{N}$ = egg nitrogen isotope value, $\delta^{13}\text{C}$ = egg carbon isotope value, Winter temp = Dec–Feb annual temperature departure from 1961 to 1990 winter average, Spring temp = March–May annual temperature departure from 1961 to 1990 spring average.

Var.1	Var.2	Var.3	Var.4	Var.5	AIC	AICc	ΔAICc	AICc Weight
Year	$\delta^{15}\text{N}$	Lake			179.572	179.691	0.000	0.226
Year	$\delta^{15}\text{N}$	Region	Lake		179.572	179.738	0.048	0.221
Year	Spring temp	$\delta^{15}\text{N}$	Lake		180.467	180.633	0.942	0.141
Year	Spring temp	$\delta^{15}\text{N}$	Region	Lake	180.467	180.689	0.998	0.137
Year	Winter temp	$\delta^{15}\text{N}$	Lake		181.221	181.388	1.697	0.097
Year	Winter temp	$\delta^{15}\text{N}$	Region	Lake	181.221	181.444	1.753	0.094
Year	n-3/n-6	$\delta^{15}\text{N}$	Lake		181.509	181.675	1.985	0.084

ble metric. For example, Paterson et al. (2014) reported similar long-term temporal declines in energy density in prey fish, lake trout, and herring gulls from Lake Huron, likely reflecting system-wide constraints on food availability to all of these taxa. Previous research has indicated, that on gull colonies where fish availability is limited, body condition of adult birds is poorer, egg volume is reduced, and productivity is lower (Hebert et al., 2002, 2009). Faced with reduced aquatic prey availability, gulls have been forced into a Hobsonian choice (sensu Hebert et al., 2008), switch to less nutritious food or go hungry. Because of their high degree of foraging plasticity, herring gulls can, at least partly, buffer the energetic impact of aquatic food web change by altering their feeding strategies. However, shifts away from high quality aquatic prey, namely fish, may be having negative fitness consequences for Great Lakes herring gulls. For example, limited availability of long-chain n-3 fatty acids has been shown to have adverse effects on other bird species (Twining et al., 2016). The dietary changes documented here are likely contributing to declines in herring gull breeding populations at some locations. It is likely that other surface-feeding aquatic bird species such as common terns (*Sterna hirundo*) and Caspian terns (*Hydroprogne caspia*) are also being detrimentally affected by reductions in aquatic prey.

Gull populations have declined at many locations across the Great Lakes, particularly in the upper lakes. For example, at Pukaskwa National Park on Lake Superior (75 km northwest of Agawa Rocks), herring gull nest numbers are used as an indicator of park ecological integrity (Drake et al., 2017). Nest numbers declined by 70% from 1977 to 2017, and evidence points to dietary change playing an important role in this decline (Laurich et al., 2019). On Lake Huron, the precipitous decline in prey fish, namely alewife (*Alosa pseudoharengus*), has likely played an important role in regulating dietary change in breeding herring gulls (Hebert et al., 2009). The herring gull population breeding on Weseloh Rocks on

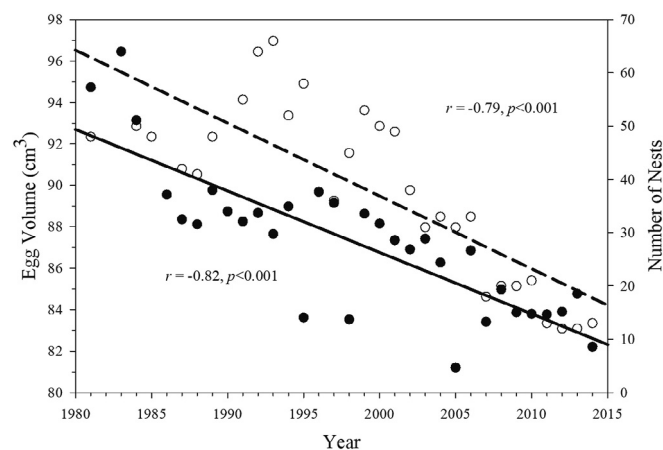


Fig. 4. Temporal declines in annual egg volume (cm^3) (solid symbols/solid line) and number of herring gull nests (open symbols/dashed line) at Weseloh Rocks on the Niagara River. Egg volume was correlated with nest numbers (Pearson $r = 0.57$, $p < 0.01$).

the Niagara River has experienced a very substantial decline through time (Fig. 4). This decrease coincided with declines in resources available for egg formation as reflected in trends in egg volume (Fig. 4) and egg volume was correlated with nest numbers (Pearson $r = 0.57$, $p < 0.01$). While this, by no means, proves that dietary constraints are the primary factor contributing to population decline, it does point to the possibility that food availability for gulls has become constrained at this site and could be contributing to the decline in the breeding gull population. At other locations, food availability has likely acted in concert with other factors in reducing gull reproductive success and population size.

For example, on the Detroit River, vegetation encroachment on previously bare nesting grounds eliminated breeding habitat for herring gulls. This factor, in conjunction with changes in food availability, may have played a key role in eliminating breeding herring gulls from that site after 2008.

Climate change is an overarching factor that could affect food availability for aquatic birds, but in our study there was only a limited indication that increased temperatures in spring and winter negatively affected egg size/energy density. However, more effort should be devoted to understanding how climate change is affecting temperate latitude wildlife. For example, rising temperatures associated with climate change could be contributing to phenological mismatches between herring gulls and their prey. Having said that, assessing climate change-related impacts on wildlife inhabiting temperate areas, is complicated by the many other stressors that may affect wildlife in such human-dominated landscapes. This may make it difficult to disentangle climate change-related factors from the effects of other stressors. Although not examined here, it is unlikely that legacy chemical contaminants, e.g. PCBs, are responsible for the declines in egg quality observed here as their levels decreased greatly throughout the duration of this study (de Solla et al., 2016).

Identifying and quantifying ecosystem change is difficult because of the complex nature of ecosystems. One way to assess such change is to study species which act as integrators of ecological processes. Here, we highlight the integrative capacity of an aquatic bird to provide insights into ecosystem change in the Laurentian Great Lakes. Alterations in gull eggs and diets documented here likely stem from reduced pelagic prey fish availability associated with high predator fish demand as well as oligotrophication and benthification of the Great Lakes, particularly Lakes Superior, Michigan and Huron (see Hebert et al., 2008; Bunnell et al., 2014). Insights into the state of other ecosystems are being gained through aquatic bird monitoring programs in other parts of Canada: Arctic Canada (Braune and Letcher, 2013), Atlantic Canada (Burgess et al., 2013), Pacific Canada (Elliott and Elliott, 2016), inland Canada (Hebert, 2019). However, regular, comprehensive integration of avian monitoring data with information from other taxa such as fish (see Paterson et al., 2014) would improve our ability to detect large-scale ecosystem change and understand the mechanisms underlying such change.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

- Blight, L.K., 2011. Egg production in a coastal seabird, the Glaucous-Winged Gull (*Larus glaucescens*), declines during the last century. *PLoS One* 6, <https://doi.org/10.1371/journal.pone.0022027> e22027.
- Bolton, M., Houston, D., Monaghan, P., 1992. Nutritional constraints on egg formation in the Lesser Black-backed Gull: an experimental study. *J. Anim. Ecol.* 61, 521–532.
- Braune, B.M., Letcher, R.L., 2013. Perfluorinated sulfonate and carboxylate compounds in eggs of seabirds breeding in the Canadian Arctic: temporal trends (1975–2011) and inter-species comparison. *Environ. Sci. Technol.* 47, 616–624.
- Bunnell, D.B., Barbiero, R.P., Ludsins, S.A., Madenjian, C.P., Warren, G.J., Dolan, D.M., Brenden, T.O., Briland, R., Gorman, O.T., He, J.X., Johengen, T.H., Lantry, B.F., Lesht, B.M., Nalepa, T.F., Riley, S.C., Riseng, C.M., Treska, T.J., Tsehaye, I., Walsh, M.G., Warner, D.M., Weidel, B.C., 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: Bottom-up and top-down regulation. *BioScience* 64, 26–39.
- Burgess, N.M., Bond, A.L., Hebert, C.E., Neugebauer, E., Champoux, L., 2013. Mercury trends in herring gull (*Larus argentatus*) eggs from eastern Canada, 1972–2008: temporal change, or dietary shift? *Environ. Pollut.* 172, 216–222.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, p. 488.
- Chen, D., Letcher, R.J., Gauthier, L.T., Chu, S.G., McCrindle, R., 2012a. Newly discovered methoxylated polybrominated diphenylbenzenes have been contaminants in the eggs of herring gulls from the North American Great Lakes for thirty years. *Environ. Sci. Technol.* 46, 9456–9463.
- Chen, D., Letcher, R.J., Burgess, N.M., Champoux, L., Elliott, J.E., Hebert, C.E., Martin, P., Wayland, M., Weseloh, D.V.C., Wilson, L., 2012b. Flame retardants in eggs of four gull species (Laridae) from breeding sites spanning Atlantic to Pacific Canada. *Environ. Pollut.* 168, 1–9.
- Cleveland, W.S., 1979. Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.* 74, 829–836.
- Crawford, S.S., 2001. Salmonine introductions to the Laurentian Great Lakes: an historical review and evaluation of ecological effects. *Can. Spec. Publ. Fish. Aquat. Sci.* 132, 1–205.
- Dai, Q., Bunnell, D.B., Diana, J.S., Pothoven, S.A., Eaton, L., O'Brien, T.P., Kraus, R.T., 2019. Spatial patterns of rainbow smelt energetic condition in Lakes Huron and Erie in 2017: evidence for Lake Huron resource limitation. *J. Great Lakes Res.* 45, 830–839.
- Davis, J.W.F., 1975. Age, egg size and breeding success of the Herring Gull *Larus argentatus*. *Ibis* 117, 460–472.
- de Solla, S.R., Weseloh, D.V.C., Hughes, K.D., Moore, D.J., 2016. Forty-year decline of organic contaminants in eggs of Herring Gulls (*Larus argentatus*) from the Great Lakes, 1974 to 2013. *Waterbirds* 39 (Special Publication 1), 166–179.
- Dewailly, E., Blanchet, C., Gingras, S., Lemieux, S., Holub, B.J., 2003. Fish consumption and blood lipids in three ethnic groups of Québec (Canada). *Lipids* 38, 359–365.
- Dobiesz, N.E., McLeish, D.A., Eshenroder, R.L., Bence, J.R., Mohr, L.C., Ebener, M.P., Nalepa, T.F., Woldt, A.P., Johnson, J.E., Argyle, R.L., Makarewicz, J., 2005. Ecology of the Lake Huron fish community, 1970–1999. *Can. J. Fish. Aquat. Sci.* 62, 1432–1451.
- Drake, C., Robinson, C., MacLaurin, J., 2017. Annual Report for Resource Conservation in Pukaskwa National Park for 2016–17. Canada Parks Agency, Pukaskwa National Park, Heron Bay, Ontario, Canada, p. 35.
- Elliott, K.H., Elliott, J.E., 2016. Origin of sulfur in diet drives spatial and temporal mercury trends in seabird eggs from Pacific Canada 1968–2015. *Environ. Sci. Technol.* 50, 13380–13386.
- Environment and Climate Change Canada, 2019. Canadian Gridded Temperature Anomalies CANGRD Accessed August 30, 2019. <https://open.canada.ca/data/en/dataset/3d4b68a5-13bc-48bb-ad10-801128aa6604>.
- Ewins, P.J., Weseloh, D.V., Groom, J.H., Dobos, R.Z., Mineau, P., 1994. The diet of herring gulls (*Larus argentatus*) during winter and early spring on the lower Great Lakes. *Hydrobiologia* 279 (280), 39–55.
- Farrell, D.J., 1998. Enrichment of hen eggs with n-3 long-chain fatty acids and evaluation of enriched eggs in humans. *Amer. J. Clinical Nutr.* 68, 538–544.
- Fox, G.A., Allan, L.J., Weseloh, D.V., Mineau, P., 1990. The diet of herring gulls during the nesting period in Canadian waters of the Great Lakes. *Can. J. Zool.* 68, 1075–1085.
- Furness, R.W., Camphuysen, C.J., 1997. Seabirds as monitors of the marine environment. *ICES J. Mar. Sci.* 54, 726–737.
- Gauthier, L.T., Laurich, B., Hebert, C.E., Letcher, R.J., 2019. Tetrabromobisphenol-A-bis(dibromopropyl ether) flame retardant in eggs, regurgitates and feces of Herring Gulls from multiple North American Great Lakes locations. *Environ. Sci. Technol.* 53, 9564–9571.
- Gebbink, W.A., Letcher, R.J., Hebert, C.E., Weseloh, D.V.C., 2011. Twenty years of temporal change in perfluoroalkyl sulfonate and carboxylate contaminants in Herring Gull eggs from the Laurentian Great Lakes. *J. Environ. Monitor.* 13, 3365–3372.
- Gilman, A.P., Peakall, D.B., Hallett, D.J., Fox, G.A., Norstrom, R.J., 1979. Herring Gulls (*Larus argentatus*) as monitors of contamination in the Great Lakes. In: *Animals as Monitors of Environmental Pollutants*. National Academy of Sciences, Washington, D.C., pp. 280–289.

- Gorman, O.T., 2007. Changes in a population of exotic rainbow smelt in Lake Superior: boom to bust, 1974–2005. *J. Great Lakes Res.* 33 (Supplement 1), 75–90.
- Hebert, C.E., Norstrom, R.J., Weseloh, D.V., 1999a. A quarter century of environmental surveillance: the Canadian Wildlife Service's Great Lakes Herring Gull Monitoring Program. *Environ. Rev.* 7, 147–166.
- Hebert, C.E., Shutt, J.L., Hobson, K.A., Weseloh, D.V., 1999b. Spatial and temporal differences in the diet of Great Lakes herring gulls (*Larus argentatus*): evidence from stable isotope analysis. *Can. J. Fish. Aquat. Sci.* 56, 323–338.
- Hebert, C.E., Shutt, J.L., Ball, R.O., 2002. Plasma amino acid concentrations as an indicator of protein availability to breeding herring gulls (*Larus argentatus*). *Auk* 119, 185–200.
- Hebert, C.E., Arts, M.T., Weseloh, D.V., 2006. Ecological tracers can quantify food web structure and change. *Environ. Sci. Technol.* 40, 5618–5623.
- Hebert, C.E., Weseloh, D.V.C., Idrissi, A., Arts, M.T., O'Gorman, R., Gorman, O.T., Locke, B., Madenjian, C.P., Roseman, E.F., 2008. Restoring piscivorous fish populations in the Laurentian Great Lakes causes seabird dietary change. *Ecology* 89, 891–897.
- Hebert, C.E., Weseloh, D.V.C., Idrissi, A., Arts, M.T., Roseman, E.F., 2009. Diets of aquatic birds reflect changes in the Lake Huron ecosystem. *Aquat. Ecosyst. Health Manag.* 12, 37–44.
- Hebert, C.E., Popp, B.N., 2018. Temporal trends in a biomagnifying contaminant: application of amino acid compound specific stable nitrogen isotope analysis to the interpretation of bird mercury levels. *Environ. Toxicol. Chem.* 37, 1458–1465.
- Hebert, C.E., 2019. The river runs through it: the Athabasca River delivers mercury to aquatic birds breeding far downstream. *PLoS ONE* 14, (4). <https://doi.org/10.1371/journal.pone.0206192> e0206192.
- Hecky, R.E., Smith, R.E.H., Barton, D.R., Guildford, S.J., Taylor, W.D., Charlton, M.N., Howell, T., 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 61, 1285–1293.
- Hiom, L., Bolton, M., Monaghan, P., Worrall, D., 1991. Experimental evidence for food limitation of egg production in gulls. *Ornis Scand.* 22, 94–97.
- Hixson, S.M., Sharma, B., Kainz, M.J., Wacker, A., Arts, M.T., 2015. Production, distribution, and abundance of long-chain omega-3 polyunsaturated fatty acids: a fundamental dichotomy between freshwater and terrestrial ecosystems. *Environ. Rev.* 23, 414–424.
- Huang, Z., Leibovitz, H., Lee, C.M., Millar, R., 1990. Effect of dietary fish oil on ω -3 fatty acid levels in chicken eggs and thigh flesh. *J. Agri. Food Chem.* 38, 743–747.
- Johannsson, O.E., Dermott, R., Graham, D.M., Dahl, J.A., Millard, E.S., Myles, D.D., Leblanc, J., 2000. Benthic and pelagic secondary production in Lake Erie after the invasion of *Dreissena* spp. with implications for fish production. *J. Great Lakes Res.* 26, 31–54.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957.
- Krist, M., 2011. Egg size and offspring quality: a meta-analysis in birds. *Biol. Rev.* 86, 692–716.
- Laurich, B., Drake, C., Gorman, O.T., Irvine, C., MacLaurin, J., Chartrand, C., Hebert, C. E., 2019. Ecosystem change and population declines in gulls: shifting baseline considerations for assessing ecological integrity of protected areas. *J. Great Lakes Res.* 45, 1215–1227. <https://doi.org/10.1016/j.jglr.2019.08.009>.
- Leeson, S., Summers, J.D., 1997. Commercial Poultry Nutrition. University Books, Guelph, ON, Canada.
- Madenjian, C.P., Fahnenstiel, G.L., Johengen, T.H., Nalepa, T.F., Vanderploeg, H.A., Fleischer, G.W., Schneeberger, P.J., Benjamin, D.M., Smith, E.B., Bence, J.R., Rutherford, Lavis, D.S., Robertson, D.M., Jude, D.J., Ebener, M.P., 2002. Dynamics of the Lake Michigan food web, 1970–2000. *Can. J. Fish. Aquat. Sci.* 59, 736–753.
- Martin, T.E., 1987. Food as a limit on breeding birds: a life-history perspective. *Ann. Rev. Ecol. Syst.* 18, 453–487.
- Mayer, C.M., Burlakova, L.E., Eklöv, P., Fitzgerald, D., Karatayev, A., Ludsins, S.A., Millard, S., Mills, E.L., Ostapenya, A.P., Rudstam, L.G., Zhu, B., Zhukova, T.V., 2013. The benthification of freshwater lakes: exotic mussels turning ecosystems upside down. In: Nalepa, T.F., Schloesser, D.W. (Eds.), *Quagga and Zebra Mussels: Biology, Impacts, and Control*, Second Edition. Taylor and Francis, New York, NY, pp. 575–586.
- McMeans, B.C., Arts, M.T., Rush, S.A., Fisk, A.T., 2012. Seasonal patterns in fatty acids and stable isotopes of *Calanus hyperboreus* (Copepoda, Calanoida) from Cumberland Sound, Baffin Island. *Mar. Biol.* 159, 1095–1105.
- Mills, E.L., Casselman, J.M., Dermott, R., Fitzsimons, J.D., Gal, G., Holeck, K.T., Hoyle, J. A., Johannsson, O.E., Lantry, B.F., Makarewicz, J.C., Millard, E.S., Munawar, I.F., Munawar, M., O'Gorman, R., Owens, R.W., Rudstam, L.G., Schaner, T., Stewart, T. J., 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970–2000). *Can. J. Fish. Aquat. Sci.* 60, 471–490.
- Monaghan, P., Nager, R.G., 1997. Why don't birds lay more eggs? *Trends Ecol. Evol.* 12, 270–274.
- Nisbet, I.C., Weseloh, D.V., Hebert, C.E., Mallory, M.L., Poole, A.F., Ellis, J.C., Pyle, P., Patten, M.A., 2017. Herring Gull (*Larus argentatus*). In: Rodewald, P.G. (Ed.), *The Birds of North America*. Cornell Lab of Ornithology, Ithaca. Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/hergul>.
- Olsen, Y., 1998. Lipids and essential fatty acids in aquatic food webs: what can freshwater ecologists learn from mariculture? In: Arts, M.T., Wainman, B.C. (Eds.), *Lipids in Freshwater Ecosystems*. Springer-Verlag, New York, NY, pp. 161–202.
- Parsons, J., 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull *Larus argentatus*. *Nature* 228, 1221–1222.
- Paterson, G., Whittle, D.M., Drouillard, K.G., Haffner, G.D., 2009. Declining lake trout (*Salvelinus namaycush*) energy density: Are there too many salmonid predators in the Great Lakes? *Can. J. Fish. Aquat. Sci.* 66, 919–932.
- Paterson, G., Hebert, C.E., Drouillard, K.G., Haffner, G.D., 2014. Congruent energy density trends of fish and birds reflect ecosystem change. *Limnol. Oceanogr.* 59, 1171–1180.
- Ryder, J.P., 1975. Egg-laying, egg-size and success in relation to immature-mature plumage of Ring-billed gulls. *Wilson Bull.* 87, 534–542.
- Surai, P.F., Bortolotti, G.R., Fidgett, A.L., Blount, J.D., Speake, B.K., 2001. Effects of piscivory on the fatty acid profiles and antioxidants of avian yolk: studies on eggs of the gannet, skua, pelican and cormorant. *J. Zool.* 255, 305–312.
- Surai, P.F., Speake, B.K., 2008. The natural fatty acid compositions of eggs of wild birds and the consequences of domestication. In: Meester, F., Watson, R.R. (Eds.), *Wild-type Food in Health Promotion and Disease Prevention: The Columbus Concept*. Humana Press, Totowa, New Jersey, pp. 121–137.
- Twining, C.W., Brenna, J.T., Lawrence, P., Shipley, J.R., Tollefson, T.N., Winkler, D.W., 2016. Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. *PNAS* 113, 10920–10925.
- Waldroup, P.W., Hellwig, H.M., 1995. Methionine and total sulfur amino acid requirements influenced by stage of production. *J. Appl. Poultry Res.* 4, 283–292.
- Weseloh, D.V.C., Pekarik, C., de Solla, S.R., 2006. Spatial patterns and rankings of contaminant concentrations in herring gull eggs from 15 sites in the Great Lakes and connecting channels, 1988–2002. *Environ. Monit. Assess.* 113, 265–284.
- Weseloh, D.V.C., Moore, D.J., Hebert, C.E., de Solla, S.R., Braune, B.M., McGoldrick, D. J., 2011. Current concentrations and spatial and temporal trends in mercury in Great Lakes Herring Gull eggs, 1974–2009. *Ecotoxicology* 20, 1644–1658.