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Autumn waterbird migration over Lake Superior: Numbers, species, and timing



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abstract

The Great Lakes are used as a migratory corridor and for feeding by tens of thousands of waterbirds each spring and fall, yet little species-specific information is available regarding numbers, seasonal timing, and connectivity along the route. The objective of this study was to use land-based surveys to quantify fall migration at two important landmarks in Lake Superior for an assemblage of waterbirds from three orders (Anseriformes, Gaviiformes, and Podicipediformes). Both the Keweenaw Peninsula (KP) and Whitefish Point (WP) showed a temporal pattern of high numbers (peaking at 9000 and 16,000, respectively) in the first 3 h after dawn and a decline (dropping to 1000 and 5000, respectively) over the following 5 h, although the decline was far more abrupt at KP than at WP. Fall totals for WP were nearly 85,000 individual waterbirds, and for KP about 34,500. Species abundance rankings were generally similar for both locations, with the most common species being long-tailed duck (*Clangula hyemalis*), red-necked grebe (*Podiceps grisegena*), greater scaup (*Aythya marila*), and red-breasted merganser (*Mergus serrator*). Most species were far more numerous at WP than at KP, with long-tailed ducks being 65 times more numerous. A notable exception was redhead (*Aythya americana*), which was 33% more numerous at KP than at WP. We suggest that during the fall, Lake Superior acts as a geographic funnel concentrating waterbirds from northwest to southeast and that details of the composition, timing and amplitude of this phenomenon are important considerations for any nearshore Great Lakes development.

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Introduction

Hundreds of thousands of waterbirds (Anseriformes, Gaviiformes, and Podicipediformes) migrate through eastern North America, including the Great Lakes, each spring and fall. Because these lakes lie between a vast breeding range in Canada and Alaska and their non-breeding range in the southeastern United States, many waterbirds use the Great Lakes as a corridor for migration (Perkins, 1964, 1965; Stout, 1995). Despite the knowledge that Lake Superior is an important migratory corridor, little is known about species composition, total numbers, timing, or connectivity across Lake Superior. One reason for this is the difficulty observing and identifying birds traveling day and night over vast areas of water at high speeds. Although radar data can be used to show that migratory birds do cross the Great Lakes in large numbers, radar cannot usually distinguish species (Diehl et al., 2003). While there is evidence that some species of waterbirds do not rely on aquatic landscape features such as rivers during migration (O'Neal et al., 2015), many ducks and other waterbirds do concentrate at points in response to projecting

landmasses in large water bodies, including the Great Lakes (Bergman and Donner, 1964; Johnsgard, 1987; Smith et al., 2015; Svardson, 1953). Such flight concentrations provide the opportunity to use projecting shorelines as survey locations for counts of migrating waterbirds and to begin to understand the details of these mass movements. Here we use key points along the southern shore of Lake Superior to quantify mass fall movement of waterbirds across the Great Lakes, as they move from their breeding to wintering grounds.

In Lake Superior, waterbird surveys have been carried out for decades at Whitefish Point Bird Observatory (WP), Michigan, although very few of these data have been published (although see Devereaux and Mason, 1985; Ewert, 1982). WP data, coupled here with 2014 survey data from the Keweenaw Peninsula (KP), the approximate east-west midpoint in the lake, allow us to estimate the number of each species that pass key points in eastern Lake Superior as well as to begin to address the following questions about waterbird use of this important fall flyway: 1) what is the species-specific timing of these migration movements? 2) to what degree are flight paths species-specific? and 3) to what degree does eastern Lake Superior act as a “funnel,” aggregating waterbirds from northwest to southeast and concentrating them near the outflow of the lake near Whitefish Point? An improved

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understanding of these phenomena can be used to inform the protection, management and development of Lake Superior waters and nearshore areas, including assessing risks from climate change (Mortsch, 1998; Price and Root, 2000), oil pipelines (Matheny, 2014), and wind farm design and siting (Desholm and Kahlert, 2005; Langston, 2013), all of which could impact seasonally concentrated populations of waterbirds. Waterbirds are relatively long-lived in comparison to passerines, and their populations are therefore more sensitive to anthropogenic mortality than birds with higher fecundity (Sæther and Bakke, 2000).

Methods

Study areas

We surveyed migrating waterbirds at two sites (Fig. 1). Hebard Park is located on the north shore of the Keweenaw Peninsula (KP) 5 km west of Copper Harbor (47° 28' 43.08" N, 87° 57' 06.96" W). Whitefish Point Bird Observatory (WP) (46° 46' 13.56" N, 84° 57' 19.92" W) is at the northern tip of the eastern edge of the Upper Peninsula of Michigan. The shoreline at the KP count site runs almost due east-west and is approximately 3 m above lake level, while the observation site at WP is at the tip of a projecting sand spit approximately 1.5 m above lake level. These sites were chosen because they offer projecting points of land into Lake Superior and/or have a history of waterbird counts (Binford, 2006).

Surveys

Surveys were conducted from 15 August 2014 through 15 November 2014. Fall migrating birds at KP and WP are generally flying east or southeast, respectively, following the shoreline 0.4 km to 2.5 km offshore. Identical survey methods were used at both sites, allowing us to directly compare numbers of individuals and daily peaks. Surveys began at sunrise and lasted for 8 h, 7 days per week. Sunrise occurs somewhat earlier to the more eastern WP compared to KP with a 13 minute difference on 15 Oct. 2015. A single observer at each site scanned the horizon from east to west with 10 × 42 binoculars for flocks or individual birds, and then used a 20–60× spotting scope to count and identify the birds when necessary. Counts were not done in foggy weather or when a steady rain was falling. The majority of migrating waterbirds fly between 1 and 30 m above the water but we counted all flying waterbirds

visible above the surface of the water. At both WP and KP, only a tiny percentage (i.e., $\leq 0.5\%$) of observed birds land on the water, and these birds were noted but not included in count numbers. The observers (KP: L. Dombroski, J. Youngman; WP: E. Ripma) all have years of experience identifying waterbirds in flight at migration concentration points along the Great Lakes. Data recorded included species, number of individuals, general flight direction, and date; data were tallied by hour past sunrise.

Results

Overall numbers of birds and species composition

In fall 2014, the total count of east/southeast bound loons, grebes and ducks was 84,959 at WP while the total count at KP was about 40% of that or 34,431 (Table 1). We detected 29 species of waterbirds at WP and 28 at KP. At WP, the five most common species in order of abundance were long-tailed duck (*Clangula hyemalis*), red-necked grebe (*Podiceps grisegena*), greater scaup (*Aythya marila*), red-breasted merganser (*Mergus serrator*) and bufflehead (*Bucephala albeola*); these five accounted for 76% of all birds passing WP. At KP, the five most common species in order of abundance were red-necked grebe, red-breasted merganser, redhead (*Aythya americana*), common loon (*Gavia immer*) and greater scaup and these five accounted for 52% of all birds passing KP. Extremely rare species (≤ 10 individuals) recorded at WP and/or KP included canvasback (*Aythya valisineria*), harlequin duck (*Histrionicus histrionicus*) and Pacific loon (*Gavia pacifica*).

Of the five possible *Aythya* species observed and positively identified at KP (i.e., redhead, greater scaup, canvasback, ring-necked duck (*Aythya collaris*), and lesser scaup (*Aythya affinis*)), all but greater scaup and redhead were extremely scarce at KP, accounting for less than a thousandth of the total seasonal count. Therefore, it is likely that the 1243 ducks assigned to scaup species were actually nearly all greater scaup, and the 3402 *Aythya* sp. were either greater scaup or redheads. Consequently, the KP counts for greater scaup and redhead were very likely higher than shown in Table 1.

Nearly every species that was abundant at both locations was far more abundant at WP compared to KP, consistent with our fall funneling hypothesis that proposes that birds accumulate from northern and northwestern to southeastern Lake Superior. However, even when only considering positively identified individuals, the pattern of abundance



Fig. 1. Map of Lake Superior and survey sites at Keweenaw Peninsula and Whitefish Point, Michigan.

Table 1
Total numbers of each species of waterbirds counted over the 2014 season (15 August–15 November) at Whitefish Point (WP) and Keweenaw Peninsula (KP), and the percentage of each species counted at KP compared to WP. The table is in order of total summed abundance at both sites.

Common name	Scientific name	Total for both sites	Whitefish Point Bird Observatory			Keweenaw Peninsula			KP as % of WP
			Total	Mean # birds per day	Max # birds per day	Total	Mean # birds per day	Max # birds per day	
Long-tailed Duck	<i>Clangula hyemalis</i>	27,814	27,396	20.0	8354	418	4.5	66	2
Red-necked Grebe	<i>Podiceps grisegena</i>	24,562	17,379	186.9	2587	7183			41
Red-breasted Merganser	<i>Mergus serrator</i>	11,783	6097	65.6	613	5686	61.1	2525	93
Greater Scaup	<i>Aythya marila</i>	11,213	9937	107.0	1675	1276	13.7	355	13
Duck sp.		7712	524	5.6	137	7188	77.3	1616	1372
Aythya sp.		4745	1343	14.4	661	3402	36.6	1236	253
Common Loon	<i>Gavia immer</i>	3787	2207	23.7	155	1580	17	329	72
Redhead	<i>Aythya americana</i>	3756	1612	17.3	473	2144	23.1	1080	133
Bufflehead	<i>Bucephala albeola</i>	3482	3350	36	993	132	1.4	87	4
White-winged Scoter	<i>Melanitta fusca</i>	3266	2294	24.7	278	972	10	344	42
American Wigeon	<i>Anas americana</i>	2947	2557	27.5	587	390	4.2	167	15
Common Goldeneye	<i>Bucephala clangula</i>	2353	1863	20	451	490	5.3	212	26
Scaup sp.		1882	639	6.9	152	1243	13.4	443	195
Blue-winged Teal	<i>Anas discors</i>	1855	1474	15.8	287	381	4.1	217	26
Mallard	<i>Anas platyrhynchos</i>	1411	992	10.7	165	419	4.5	29	42
Surf Scoter	<i>Melanitta perspicillata</i>	983	818	8.8	246	165	1.8	70	20
Horned Grebe	<i>Podiceps auritus</i>	956	561	6.0	94	395	4.3	74	70
Red-throated Loon	<i>Gavia stellata</i>	661	561	6.0	76	100	1.1	18	18
Green-winged Teal	<i>Anas crecca</i>	639	587	6.3	71	52	0.6	22	9
Lesser Scaup	<i>Aythya affinis</i>	537	509	5.5	91	28	0.3	10	6
Northern Pintail	<i>Anas acuta</i>	459	410	4.4	50	49	0.5	23	12
Black Scoter	<i>Melanitta nigra</i>	419	379	4.1	95	40	0.4	11	11
Teal sp.		393	269	2.9	63	124	1.3	50	46
Common Merganser	<i>Mergus merganser</i>	343	318	3.4	49	25	0.3	8	8
Surf/Black Scoter		279	138	1.5	65	141	1.5	39	102
Dabbling sp.		252	82	0.9	21	170	1.8	125	207
Gadwall	<i>Anas strepera</i>	238	190	2	48	48	0.5	29	25
Northern Shoveler	<i>Anas clypeata</i>	220	197	2.1	38	23	0.2	15	12
Ring-necked Duck	<i>Aythya collaris</i>	129	99	1.1	19	30	0.3	14	30
American Black Duck	<i>Anas rubripes</i>	104	86	0.9	19	18	0.2	5	21
Merganser sp.		72	0	0	0	72	0.8	24	0
Canvasback	<i>Aythya valisineria</i>	48	45	0.5	22	3	0	2	7
Loon sp.		38	5	0.1	2	33	0.4	6	0
Hooded Merganser	<i>Lophodytes cucullatus</i>	30	21	0.2	10	9	0.1	2	43
Wood Duck	<i>Aix sponsa</i>	15	15	0.2	5	0	0	0	0
Harlequin Duck	<i>Histrionicus histrionicus</i>	3	1	0	1	2	0	1	200
Scoter sp.		2	2	0	2	0	0	0	0
Pacific Loon	<i>Gavia pacifica</i>	2	2	0	1	0	0	0	0
Total		119,390	84,959	956	8984	34,431	394.5	6020	40.5

between KP and WP for redheads is exceptional, with this species being much more common at KP than WP.

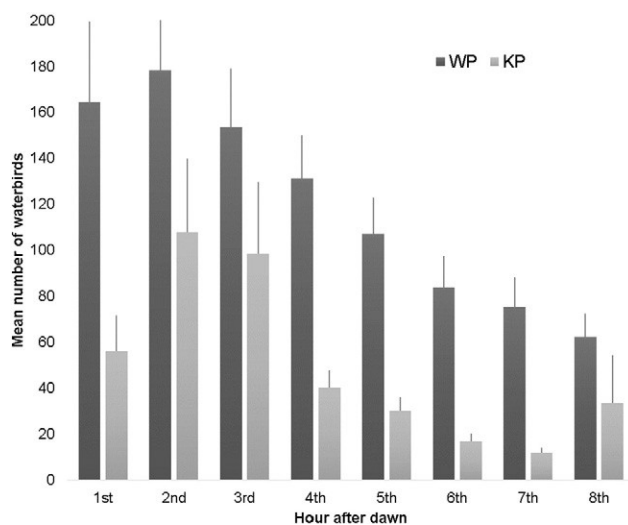


Fig. 2. Mean waterbirds counted per hour at Whitefish Point (WP) and Keweenaw Peninsula (KP) over the 2014 season (August–November). Error bars are ± 1 standard error of the mean.

Daily and seasonal timing

Peak numbers of waterbirds passed both count stations in the first 3 h after dawn and steadily declined over the following 5 h, with a steeper decline at KP compared to WP (Fig. 2). For all waterbird species pooled, peak seasonal migration occurred during October 2014, with 3–5 distinct pulses where large numbers of birds moved during one or two days (Fig. 3A). For all species pooled, staggered peaks of large daily movements started with KP and followed 1–2 days later by a similar peak at WP (Fig. 3A), suggesting sequential movement (connectivity). For the most abundant species, the degree of temporal concentration during the fall was quite variable with some species such as the greater scaup not showing a pattern of abundance between KP and WP that suggests sequential movement (Fig. 3B). Red-necked grebes were among the earliest species to migrate south (Fig. 3D).

Discussion

Approximately 120,000 waterbirds were counted at the two sites, with similar species abundance rankings; the most common species being long-tailed duck (*Clangula hyemalis*), red-necked grebe (*Podiceps grisegena*), greater scaup (*Aythya marila*), and red-breasted merganser (*Mergus serrator*). As expected, most species were far more numerous at WP than at KP, with long-tailed ducks being 65 times more numerous.

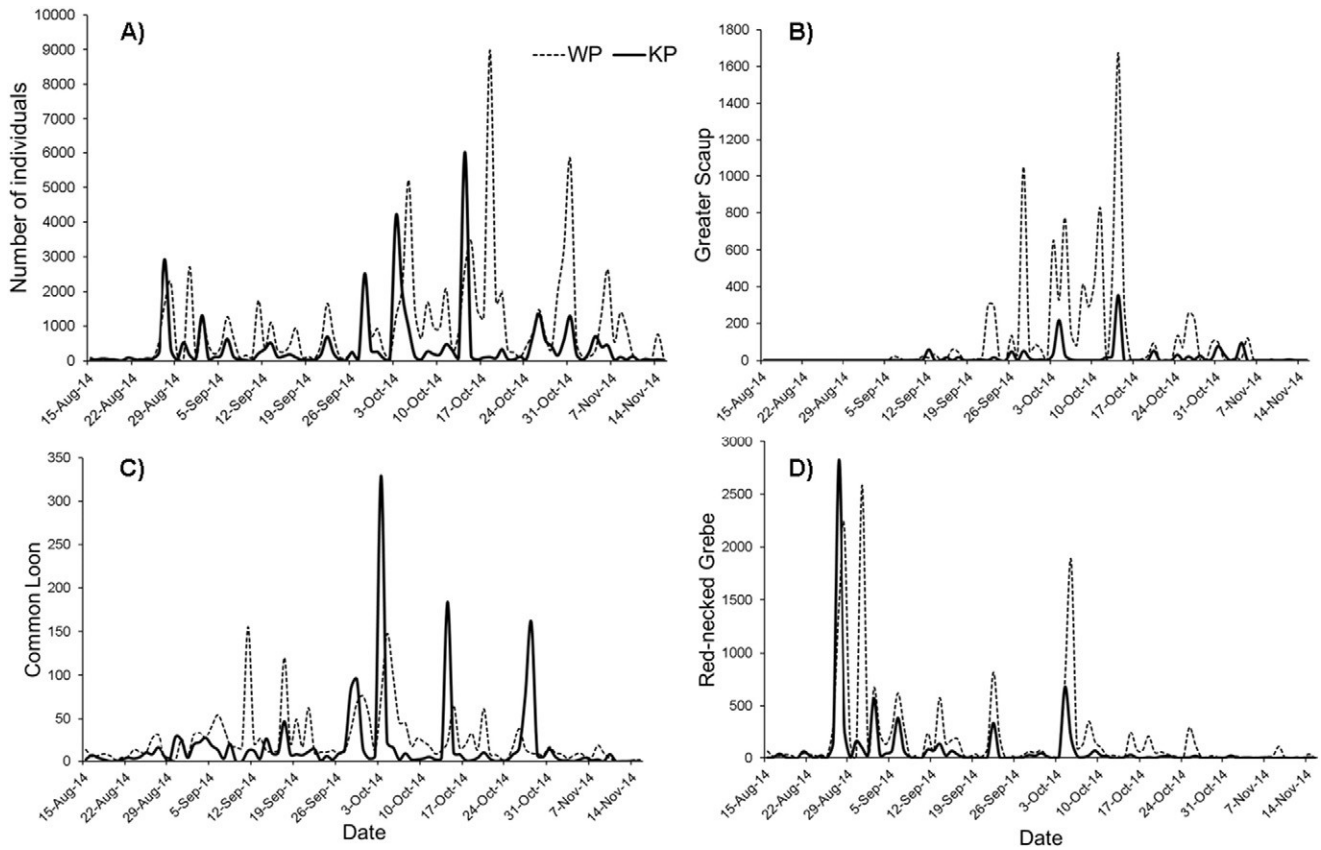


Fig. 3. A) Total number of waterbirds, B) total number of Greater Scaup, C) total number of Common Loon, and D) total number of Red-necked Grebe counted by date over the 2014 season (August–November) at Whitefish Point (WP) and Keweenaw Peninsula (KP).

In general, although the WP counts were much greater, there were a few striking differences in the occurrence of certain species at the two sites. Among the five more abundant species detected at WP, two species (long-tailed duck and bufflehead) were rarely detected on the KP count, suggesting that they follow a different and possibly more eastern path through Lake Superior compared to most other waterbirds. Redheads were detected far more frequently at KP compared to WP, suggesting that, unlike nearly every other waterbird, this species follows a different route after passing KP, with some individuals possibly flying over a narrowing (75 km) of the Upper Peninsula to northern Lake Michigan during the night. Anecdotal observations of large rafts of redheads near Munising, MI (between KP and WP along the south shore of Lake Superior) that had departed by the next morning (Hickman, unpubl. data) and rafts on Little Bay de Noc along the northern shore of Lake Michigan in Michigan's Upper Peninsula (Rutherford, unpubl. data), suggest this distinctly different fall migration route for some redheads. Data from other waterbird counts of shorter duration indicate substantial fall waterbird migration movements southeastward from the NE tip of Isle Royale (Youngman and Flaspohler, 2015) and from Nipigon Bay (Youngman, unpubl. data) and Caribou Island (Wormington et al., 1986). Birds following these routes would likely pass and be counted at WP, but are unlikely to be detected at KP. These observations could explain both the higher numbers of individuals at WP and some of the proportional species differences for long-tailed duck and bufflehead. Such species-specific movement patterns shed new light on the natural history of waterfowl and enable wildlife managers to better understand how important game species utilize the land-water interface in the Great Lakes.

Our observed pattern of greater numbers of individual waterbirds passing in the 3–4 h following sunrise is consistent with other land-based surveys on the Atlantic Ocean (Bond et al., 2007; Cameron, 2014; Smith et al., 2015), and suggests that where monitoring resources are

scarce, surveys could be designed to produce an index of population numbers using surveys approximately half the duration of our 8-hour surveys. However, many waterbirds migrate at night as well (e.g., O'Neal et al., 2015); and, although we were unable to include them in our study, the addition of nocturnal waterbird surveys over Lake Superior is needed. Data on daily and seasonal timing and species composition should be valuable in guiding the siting and seasonal operation of offshore wind energy arrays, monitoring wildlife disease outbreaks such as botulism (Brand et al., 1988) and other anthropogenic activities that could impact migratory waterbirds.

Our observed seasonal species-specific timing of waterbird migration corresponds to previous information on early, mid- and late fall migratory species (Bellrose, 1976). Consistent with the idea that there is strong connectivity between northwest and southeastern sites in eastern Lake Superior, the species lists from the KP and WP were virtually identical. Sequential passage was also suggested by the staggered peaks of large daily movements for all species pooled and red-necked grebes specifically, starting with KP and followed 1–2 days later by a similar peak at WP. Peak movement days for some species appeared to occur on the same date, which is not surprising given the relatively short straight-line distance (240 km) between the two count sites. Using this distance and the average waterbird flying speed of 60 km/h, a continuously flying bird passing KP should reach WP in approximately 4 h and 10 min. However, the degree to which birds make this a continuous flight versus stopping to rest and/or feed remains unknown. Given that Lake Superior is approximately 170 km across at KP, and our survey could only detect birds passing within about 1–2 km of land depending on the species and atmospheric conditions, it is somewhat remarkable that we identified any level of connectivity at all between KP and WP.

Interestingly however, there were disparities in the total seasonal counts for each species between the two sites. This was true even if

unidentified ducks were apportioned into likely species. Thus, although our data suggest many of the birds passing the Keweenaw Peninsula continue on to Whitefish Point, many clearly do not, either passing out of sight of counters or taking alternative routes to the southern Great Lakes.

Migratory birds present unique conservation challenges as a result of their dependence on different breeding, non-breeding and migratory habitats, and the vast majority of migratory birds are not well protected (Runge et al., 2015). By quantifying the seasonal timing and species composition of migratory waterbirds passing two important concentration points in eastern Lake Superior, we provide new information on how birds use nearshore areas. Although land-based waterbird surveys have been conducted in Lake Superior, most of these data remain unpublished, and to our knowledge, this is one of the first papers to estimate numbers and timing for this phenomenon.

Conclusions

In North America, monitoring of migratory waterbird (here, waterfowl, grebes and loons) populations relies largely on aerial surveys and has traditionally been focused on saltwater habitats (Kingsford and Porter, 2009; Silverman et al., 2013; Zipkin et al., 2010), although waterfowl are relatively well monitored inland. To reach marine portions of their migratory route on the Atlantic Ocean and Gulf of Mexico, hundreds of thousands of waterbirds must pass over thousands of kilometers of land with a few key resting and feeding sites. We suggest that the long history of counting concentrated waterbirds at WP and our data from KP support the opinion that Lake Superior can provide important new insights into the use of nearshore habitats by this group of birds and can also serve as a population index for long term monitoring. Similar data have been used to identify changes in the migratory timing of raptors consistent with climate change in the last 40 years (Rosenfield et al., 2011; Sullivan et al., 2015; Van Buskirk, 2012). This work from one season provides new insights into waterbird movement. Repetition of such surveys would provide an improved understanding of annual variation and, with the addition of nocturnal surveys, this information can be used in conservation planning to develop harvest goals (for game species), assess the relative risk of wind array siting, and, with increased understanding of continental scale spatial connectivity, to monitor populations across a vast area of northern Canada that is otherwise currently extremely difficult to survey.

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References

- Bellrose, F.C., 1976. *Ducks, Geese and Swans of North America*. Stackpole Books, Harrisburg, Pennsylvania.
- Bergman, G., Donner, K.O., 1964. An analysis of the spring migration of the Common Scoter and the Long-tailed Duck in southern Finland. *Acta Zool. Fenn.* 105, 1–59.
- Binford, L.C., 2006. *Birds of the Keweenaw Peninsula, Michigan*. Museum of Zoology, University of Michigan, Ann Arbor, Michigan.
- Bond, A.L., Hicklin, P.W., Evans, M., 2007. Daytime spring migrations of scoters (*Melanitta spp.*) in the Bay of Fundy. *Waterbirds* 30, 566–572.
- Brand, C.J., Schmitt, S.M., Duncan, R.M., Cooley, T.M., 1988. An outbreak of type E botulism among common loons (*Gavia immer*) in Michigan's Upper Peninsula. *J. Wildl. Dis.* 24, 471–476.
- Cameron, I.R., 2014. An Analysis of Spring Migration Rates of Scoter Species and Common Eider Recorded at Point Lepreau Bird Observatory on the Bay of Fundy of the Period 2000 to 2012. 41. *New Brunswick Naturalist*, pp. 94–99.
- Desholm, M., Kahlert, J., 2005. Avian collision risk at offshore wind farm. *Biol. Lett.* 1, 296–298.
- Devereaux, J., Mason, L., 1985. Spring Migration of White-winged Scoters, Common Mergansers, and Red-breasted Mergansers Past Whitefish Point, Michigan: A Preliminary Study. 63. *Jack-Pine Warbler*, pp. 42–51.
- Diehl, R.H., Larkin, R.P., Black, J.E. 2003. Radar observations of bird migration over the Great Lakes. *Auk* 120, 278–290.
- Ewert, D., 1982. Spring Migration of Common Loons at Whitefish Point, Michigan. 60. *Jack-Pine Warbler*, pp. 134–143.
- Johnsgard, P.A., 1987. *Diving Birds of North America*. University of Nebraska Press, Lincoln, Nebraska.
- Kingsford, R.T., Porter, J.L., 2009. Monitoring waterbird populations with aerial surveys — what have we learnt? *Wildl. Res.* 36, 29–40.
- Langston, R.H.W., 2013. Birds and wind projects across the pond: a UK perspective. *Wildl. Soc. Bull.* 37, 5–18.
- Matheny, K., 2014. Great Lakes face oil-spill peril, Coast Guard warns. *USA Today* (September 10).
- Mortsch, L.D., 1998. Assessing the impact of climate change on the Great Lakes shoreline wetlands. *Climate Change* 40, 391–416.
- O'Neal, B.J., Stafford, J.D., Larkin, R.P., 2015. Migrating ducks in inland North America ignore major rivers as leading lines. *Ibis* 157, 154–161.
- Perkins, J.P., 1964. 17 flyways over the Great Lakes part I. *Audubon Mag.* 66, 42–45 (September–October).
- Perkins, J.P., 1965. 17 flyways over the Great Lakes part II. *Audubon Mag.* 67, 294–298 (January–February).
- Price, J.T., Root, T.L., 2000. Effects of climate change on bird distributions and migration patterns. In: Sousounis, P.J., Bisanz, J.M. (Eds.), *Preparing for a Changing Climate: The Potential Consequences of Climate Variability and Change*. University of Michigan Atmospheric, Oceanic, and Space Sciences Department, Ann Arbor, Michigan, pp. 65–68.
- Rosenfield, R.N., Lamers, D., Evans, D.L., Evans, M., Cava, J.A., 2011. Shift to later timing by autumnal migrating sharp-shinned hawks. *Wilson J. Ornithol.* 123, 154–158.
- Runge, C.A., Watson, J.E.M., Butchart, S.H.M., Hanson, J.O., Possingham, H.P., Fuller, R.A., 2015. Protected areas and global conservation of migratory birds. *Science* 350 (6265), 1255–1258.
- Saether, B.E., Bakke, Ø., 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81, 642–653.
- Silverman, E.D., Saalfeld, D.T., Leirness, J.B., Koneff, M.D., 2013. Wintering sea duck distribution along the Atlantic coast of the United States. *J. Fish Wildl. Manag.* 4, 178–198.
- Smith, A.D., McWilliams, S.R., Winarski, K.J., Trocki, C.L., Harris, B., Osenkowski, J.E., Paton, P.W.C., 2015. Using land-based surveys to assess sea duck abundance and behavior in nearshore waters of southern New England, USA. *Waterbirds* 38, 252–259.
- Stout, B.E., 1995. *Fall migration of red-necked grebes in the Great Lakes region*. M.S. Thesis. North Dakota State University, Fargo.
- Sullivan, A., Flaspohler, D.J., Froese, R., Ford, D., 2015. Climate variability and the timing of spring raptor migration in Eastern North America. *J. Avian Biol.* 47, 208–218.
- Svardson, G., 1953. Visible migration within Fenno-scandia. *Ibis* 95, 181–211.
- Van Buskirk, J., 2012. Changes in the annual cycle of North American raptors associated with recent shifts in migration timing. *Auk* 129, 691–698.
- Wormington, A., Nisbet, J.R., Finlayson, R., 1986. Some Aspects of Bird Migration at Caribou Island (Lake Superior), Ontario. *Ontario Birds*. 4 pp. 85–97.
- Youngman, J., Flaspohler, D.J., 2015. Unpublished report for Isle Royale National Park.
- Zipkin, E.F., Gardner, B., Gilbert, A.T., O'Connell Jr., A.F., Royle, J.A., Silverman, E.D., 2010. Distribution patterns of wintering sea ducks in relation to the North Atlantic Oscillation and local environmental characteristics. *Oecologia* 163, 893–902.