TWO UNPRECEDENTED AUK WRECKS IN THE NORTHWEST ATLANTIC IN WINTER 2012/13

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ABSTRACT

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An unprecedented irruption of thousands of Razorbills *Alca torda* into Florida in winter 2012/13 was followed by a "wreck" of Razorbills and Atlantic Puffins *Fratercula arctica* in outer Cape Cod, Massachusetts, in January–March 2013. We describe these events using citizen-science sources (eBird and beached-bird surveys) and band recoveries, then we discuss them in relation to extreme weather and oceanographic change. We explored effects on likely source populations using census and monitoring data, along with possible contributions from population increases, reduced food supply, and extreme weather. Winter 2012/13 followed a marine heatwave throughout the northwest Atlantic, whose effects included reduced availability of plankton. We attribute the irruption of Razorbills into Florida partly to delayed effects of Hurricane Sandy, which disrupted their coastal habitat sufficiently to cause starving birds to move south on the Labrador Current as far as Florida. Despite the continuation of anomalously warm ocean temperatures in subsequent years and a reduction in plankton communities in the Bay of Fundy and Gulf of Maine that continues to date, no comparable events have been recorded in subsequent winters; this supports our theory that the delayed effects of Hurricane Sandy contributed to these wrecks. We highlight the power of these datasets to detect and to investigate birds' responses to extreme and anomalous conditions, which in turn provides insight into the dynamics of rapidly changing ecological systems.

Key words: Razorbill, Atlantic Puffin, mass mortality, irruption, wreck, ocean heating, Hurricane Sandy

INTRODUCTION

Apparent increases in the number of mass mortality events (MMEs) affecting wild species globally are a cause for concern, especially if they represent real increases in mortality rather than increased awareness and reporting (Fey *et al.* 2015). Large-scale die-offs of marine birds may provide information about changes in the ecosystems on which they depend. Seabird MMEs ("wrecks") are particularly important in the context of global declines of seabird populations (Croxall *et al.* 2012) because most marine bird wrecks occur within typical ranges of the species distributions and are often associated with extreme weather events, such as protracted severe onshore winds (Heubeck *et al.* 2011, Morley *et al.* 2016, Anker-Nilssen *et al.* 2017).

The Razorbill *Alca torda* is a medium-sized member of the family Alcidae (auks) that breeds in boreal and subarctic regions of the North Atlantic. Their winter range, unlike that of more pelagic auks (e.g., Atlantic Puffins *Fratercula arctica* and murres *Uria* spp.), is relatively well known because it is essentially coastal (Huettmann *et al.* 2005) or inshore (Gaston & Jones 1998). Razorbill distribution thus allows for the detection of behavioral changes and especially MMEs. Although most of the North American breeding population likely spends part of winter in the Bay of Fundy and Gulf of Maine

(Huettmann *et al.* 2005, Clarke *et al.* 2010, M. Dodds unpubl. data) along with individuals from Greenland (Linnebjerg 2012), the usual winter range in eastern North America has extended as far south as Cape Hatteras, North Carolina, in recent years (Davis 1994, Brinkley 2013). Numbers observed off Massachusetts, New Jersey, and New York increased substantially from the early 1980s through the early 2000s, suggesting a southward shift in range, a significant increase in the population, or both (Veit & Guris 2008, Veit & Manne 2015).

In December 2012, during a marine heatwave in the northwest Atlantic (Mills *et al.* 2013), an irruption (i.e., a large-scale incursion of birds outside their normal range) of Razorbills extended into Florida and the Gulf Coast, including first records for Louisiana. This was followed by a wreck of beached birds, especially in Florida (Greenlaw *et al.* 2014). Citizen-scientists were the first to call attention to the Florida invasion, especially on eBird (Brinkley 2013, Sullivan *et al.* 2014) and BirdCast (2012). The irruption and associated wreck occurred well to the south of the normal winter range and continued throughout winter 2012/13, with Razorbills seen in larger numbers than usual from Massachusetts to Florida, including records in the Gulf of Mexico. Over this period, dead Razorbills were reported in several east coast states, with estimated casualties in the hundreds. Many Little Auks *Alle alle* and murres were also found dead along the east coast during this same period, but in much smaller numbers than Razorbills.

Following the Florida invasion, the first recorded North American wreck of Razorbills and Atlantic Puffins occurred at Cape Cod, Massachusetts. This was within the known winter range of both species, so it is considered to be a wreck but not an irruption. We treat these MMEs together because they involve the same population of Razorbills over the same winter and because there was some temporal overlap.

Our principal objectives in this paper were: to describe the pattern of the winter 2012/13 irruption and the associated wrecks using all available sources of information; to investigate the most likely causes of the irruption; to explore the extent to which irruptions might foreshadow similar MMEs (by comparing events of subsequent winters); to investigate the likely origins of the birds involved; and to investigate possible impacts on populations of breeding Razorbills.

METHODS

Study area

We examined the east coast of the United States from Florida to Cape Cod (Fig. 1). This region extends from warm sub-tropical waters in the south through progressively cooler waters in the north. It encompasses the South Atlantic Bight (Georgia to North Carolina), the Mid-Atlantic Bight (Virginia to New York), and Southern New England (Connecticut to Massachusetts), ending at Cape Cod (Nisbet *et al.* 2013). Razorbills are frequently seen around Cape Cod in winter and have been increasing steadily over the last 30 years (Veit & Manne 2015). However, the Razorbill is a rare winter species in Florida (Greenlaw *et al.* 2014); until

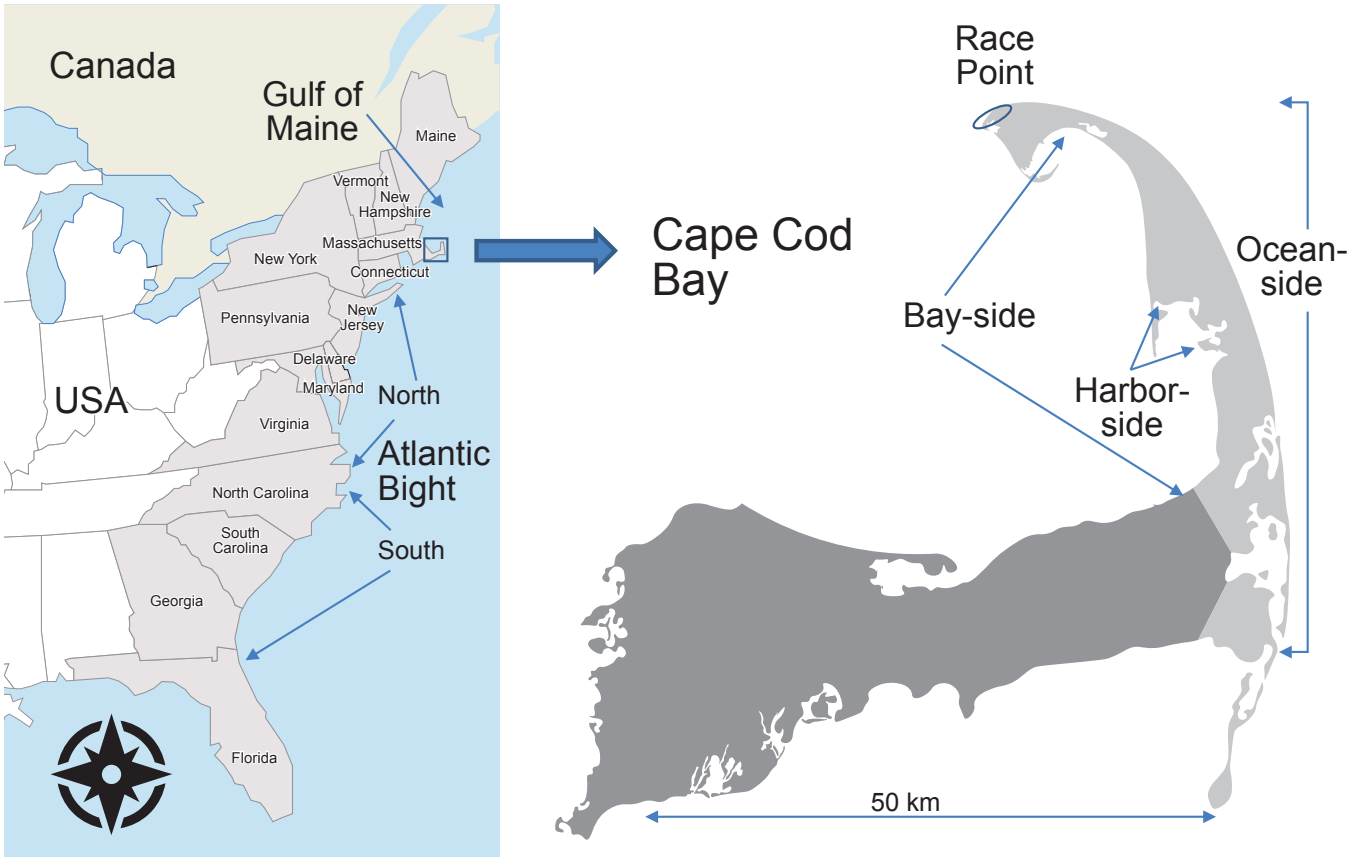

Fig. 1. Map of the study area showing geographic regions referenced in the text. Inset shows a larger-scale map of outer Cape Cod (light grey) and the categorization of beaches by wind exposure ("water location types").

November 2012, there were only 15 records of Razorbills in Florida, not including a banded bird recovered dead in St. Lucie County in 2003 (see *Band recoveries* in Results section, below). Most of these (12 of 16, including the latter bird) were dead or weak birds that were stranded on Atlantic beaches. Cape Cod constitutes the most important faunal break for seabirds along the east coast of the United States between Florida and the Bay of Fundy, particularly in winter, when a variety of species congregate in coastal regions and offshore (Nisbet *et al.* 2013). Prevailing winds during winter are from the west to north, and currents in Cape Cod Bay (1 560 km^2), at the southern end of the Gulf of Maine, move in a counterclockwise direction. This augments persistent current flow from west to east, toward outer Cape Cod, which is accompanied by strong tides and wave action on the eastern side of Cape Cod Bay (Fig. 1, insert). The bay-side shores of outer Cape Cod should be favored to intercept seabird carcasses. In addition, east coast winter storms (ECWS) drive many seabirds into the cul-de-sac of Cape Cod Bay before they attempt to regain the open ocean to the north.

Observations of free-flying birds

The Florida irruption was brought to the attention of the birder community by records submitted to eBird, the online citizen-science database maintained by the Cornell Laboratory of Ornithology. Data from eBird for the entire winter (November–March) were the primary source of quantitative information on the distribution and the numbers of Razorbills involved in the irruption (eBird 2018). These observations were predominantly of live birds; mortality of Razorbills was revealed by opportunistic surveys of beaches (see **Beached birds** in Methods section, below). Records of carcasses were compiled by wildlife agencies, museums, and the public. Generally, moribund birds were taken to wildlife rehabilitation centers; very few survived for subsequent release. Most that died were saved for necropsy and eventual preparation for museum specimens. Birds that were euthanized were submitted for post-mortem examination to appropriate wildlife diagnostic laboratories (see **Age, sex, and condition of affected birds** in Methods section, below).

eBird observations overall

We downloaded eBird data for 01 December–28 February in each year from 2004 to 2018 (Sullivan *et al.* 2014). We included all observations for eastern North America, including pelagic data where available. We excluded any Christmas Bird Count (CBC) data that may have been represented in the eBird database. We also used more spatially constrained datasets in the townships on outer Cape Cod that were covered by the intensive beached-seabird surveys (see *Cape Cod – intensive sampling* under **Beached birds** in Methods section, below). We used the frequency of occurrence from completed checklists to generate the presence or absence of Razorbills. We aggregated these data to create monthly frequencies from the weekly frequency data taken from the eBird site. Additionally, we scaled these data by the annual mean and standard deviation to create a standardized index of monthly frequencies of occurrence, which enhanced the visualization of extremities in the presence or absence of the species over time. We extended this analysis to the most recent winter (2017/18) to check whether the anomalously high sea surface temperatures (SST) of summer 2017 (second only to those of 2012; collection of remotely sensed data started around 1980) resulted in more Razorbills south of their normal range.

eBird on outer Cape Cod

We obtained count data for Razorbill and Atlantic Puffin from eBird (2018) in the same five townships (Orleans to Provincetown) on outer Cape Cod that were included in intensive beached-seabird surveys during five winters, from 2012/13 to 2016/17 (see *Cape Cod – intensive sampling* under **Beached birds** in Methods section, below). Almost all available data were for Razorbills. We excluded any CBC data that may have been represented in the eBird database (see next paragraph).

Christmas Bird Counts

CBCs are systematic counts of birds seen by citizens in pre-determined circles on land on a pre-determined date in December (e.g., Arbib 1981, Link *et al.* 2006, LeBaron 2007). Data from CBCs usually constitute a longer time series than eBird (e.g., some CBCs date to the early 20th century), but these counts are almost always land-based and not designed to assess trends in marine species in general. Further, the limited duration and seasonality of counts makes them less useful for characterizing movements or presence during other periods. However, the coastal habitats used by Razorbills make them more accessible for CBCs than is true for most seabirds, which highlights their value in this particular application (see Veit & Guris 2008, Veit & Manne 2015). Robben *et al.* (2014), addressing this same extension of Razorbill range in 2012/13, examined CBC data from the eastern seaboard during this winter and one either side of it, so we did not pursue this approach further.

At-sea observations

In principle, observations at sea should be more appropriate than land-based observations for assessing changes in seabird distribution. The Eastern Canada Seabirds at Sea (ECSAS) program began in 2005 using ships of opportunity to provide data on seabird abundance and distribution (Gjerdrum *et al.* 2012). Surveys count all birds seen from the bridges of ships moving at least 4 kt (7.4 km/h), looking forward and scanning to a 90° angle on either side, within 300 m of the observer. The spatial and temporal distribution of coverage depends entirely on availability of suitable vessels, which is low during the winter in the Canadian portion of the Razorbill's winter range. Maps from these surveys during winter show little survey effort (i.e., few ships of opportunity) in the Gulf of Maine, including during the 2012/13 winter. Consequently, they could not contribute significantly to addressing the question of a possible change in the Canadian portion of the winter range in 2012/13 and were not included in these analyses.

Data bias

Count data from completed checklists contributed to eBird largely by recreational birders are subject to biases, such as the "weekend" effect (*cf.*, Courter *et al.* 2013) whereby more weekly data per observer are contributed on weekends than on weekdays. eBird (2018) reduces this bias by summarizing data by week; we further minimized bias by extracting data by month.

For Cape Cod, we followed Veit & Manne (2015) in using the highest count in each winter as a measure of annual abundance. We extracted count data for Razorbills and converted counts of large alcids to Razorbills by dividing the percentage of a Razorbill count by the total number of murres and Razorbills, then multiplying

the number of large alcids by this percentage. If murres were not identified, we treated the large alcids as Razorbills; murres occurred in low numbers on outer Cape Cod during these five winters (eBird 2018, DBM pers. obs.), with no incursions (*cf.*, Veit & Guris 2008). Thus, any error introduced by false inclusion of murres into converted large alcid (spp.) counts is negligible. We extracted high counts for each month of the following five winters, which provided more information on seasonal and annual fluctuations in winter abundance. Storms can influence high counts of seabirds (including Razorbills), so we also noted any influence of storms on our monthly tally of high counts. Finally, we also tallied the number of monthly high counts (≥ 100) for each winter and over all five winters in each of the five townships. Land-based count data from outer Cape Cod for the pelagic Atlantic Puffin were so scarce that we simply tallied all eBird counts (after eliminating duplicate counts) for each of the five winters.

Beached birds

Through the Wildlife Health Event Reporter (WHER, www.whmn.org/wher), we compiled data from agencies that record beached birds; this includes wildlife rehabilitation centers, the citizen-science network Seabird Ecological Assessment Network (SEANET), and individuals who collected beached birds during winter 2012/13. The WHER and SEANET websites became non-functional after this event, but SEANET data from recent winters were provided by JDS.

SEANET is a citizen-science program based at Tufts University (Medford, Massachusetts). It brings together interdisciplinary researchers and members of the public in a long-term collaboration to help identify and mitigate threats to marine birds. Each volunteer walks a designated ≥ 1-km segment of a beach in search of carcasses. Volunteers walk their segment(s) at least once per month and submit a survey reporting the presence or absence of beached birds. Data are excluded from analyses if a volunteer fails to walk their segment(s) in at least nine months of the year. A monthly encounter rate is calculated for each beach route by tallying the total number of beached birds (of any species) found during that month and dividing that tally by the total kilometers of beach traveled in that month. Carcasses found and marked on a previous survey are recorded as "resighted birds" and are not included in encounter rate for any subsequent surveys. If beached birds are detected, photos and morphometric data are taken to confirm the species, and the carcass is marked with plastic cable ties to avoid re-counting on subsequent surveys.

Volunteer-monitored beaches are not equally distributed across all states or within states, and some states, such as Florida, have no volunteer coverage (and therefore no baseline data or systematic records of mortality events). Within states, certain regions (e.g., Cape Cod) are monitored more intensively than others: volunteers walk their designated beaches on a pre-determined schedule and do not alter that schedule based on reports of seabird mortality events. SEANET is intended to yield a broad baseline for seabird mortality; it is not designed to be particularly sensitive to small-scale changes in that baseline, such as MMEs. If a die-off is spatially or temporally concentrated, volunteers may not detect it at all. Carcass persistence on beaches is highly variable from beach to beach; at some sites, carcasses may remain and be resighted for months, while at others, carcasses may be deposited and washed away within one tide cycle. On such beaches, focal mortality events may be difficult to detect using these methods.

For this study, beaches were grouped by state. Average monthly encounter rates (carcasses/km) were determined for each state by pooling the number of carcasses found across all monitored beaches and dividing that by the total kilometers walked. Carcasses were identified to species whenever possible, using photos submitted by the volunteers. Some partial carcasses were classified as "large unknown alcids". Based on size and coloration, these were either Common Murres *U. aalge*, Thick-billed Murres *U. lomvia*, or Razorbills, but further classification was not possible. Encounter rates were determined this way for Razorbills specifically, and for all alcids including Razorbills, all murres, Atlantic Puffins, Black Guillemots *Cepphus grylle*, Little Auks, and any unidentified alcids.

Florida

Florida lacks SEANET coverage (see above), so when it became apparent that Razorbills were staging a major incursion into Florida, one of us (AWK) posted messages to online birding listservs and to a listserv sponsored by the Florida Wildlife Rehabilitation Association asking that specimens be saved for the Florida Museum of Natural History (FMNH).

Cape Cod – intensive sampling

One of us (DBM) initiated beached-seabird surveys on outer Cape Cod (five townships: Eastham, Orleans, Provincetown, Truro, Wellfleet) from 27 January to 28 March 2013 (61 days). In subsequent winters (2013/14 through 2016/17), surveys ran from 01 November to 15 April (166–167 days) and were both preceded by the removal of all carcasses from beaches in late October and followed by the continual removal of all carcasses after each survey during all five winters. Surveys were conducted at sites that were categorized into four types based on their exposure to wind ("water location types"): "bay-side" (Cape Cod Bay except Wellfleet Harbor, winds from Cape Cod Bay); "harbor-side" (Wellfleet Harbor, winds from Cape Cod Bay); "ocean-side" (winds from the Atlantic Ocean); and "Race Point" (at Provincetown, winds from both Cape Code Bay and the Atlantic Ocean). We used chi-squared analysis to test for differences in the number and proportion of Razorbill carcasses among the four water location types.

A total of 21–25 beaches on outer Cape Cod were surveyed each winter. Beach segments surveyed were generally 0.4–4.3 km long (rarely, up to 7.7 km). Fourteen segments were usually surveyed twice per month, weather permitting, and 7–11 segments were surveyed opportunistically once per month (Van Pelt & Piatt 1995). During the survey period of winter 2012/13, surveys were more frequent at many beaches. Otherwise, beaches representing the four water location types were surveyed alternately in approximately the same proportions each month over each winter, except for the severe winter of 2014/15 when the formation of a thick ice shelf along the coast prevented most surveys along the bay-side and harbor-side for 50–55 days in late January to late March (see photograph of First Encounter Beach in Courchesne 2015; STAR 2016). During this period, DBM adjusted his surveys to sample Race Point and the ocean-side beaches, where the shoreline remained open, more frequently.

We measured lengths (in km) of individual beaches using Google Earth Pro 2018 (version 7.3.2). DBM walked each beach on and near the wrack line(s) or other areas where carcasses may occur, removing all carcasses to avoid double-counting and returning to the starting point along the same route. Previous studies indicate

that search success for carcasses is high (Newton & Little 2009); observers typically miss a small percentage during the first pass along a route but detect missed carcasses during the second pass (Camphuysen & Heubeck 2001). Thus, incomplete detection of carcasses contribute negligible error (except for buried carcasses, which are impossible to detect). To be consistent with SEANET data as presented in this study, we calculated mean carcass encounter rates for intensive surveys by tallying the number of beached birds and dividing that tally by the total distance traveled for any subset of data. We did this regardless of whether we were comparing encounter rates among winters, water location types, species and species-groups (e.g., all alcids), or storm intervals during the "wreck" winter of 2012/13.

Age, sex, and condition of affected birds

Mortality of Razorbills was revealed by opportunistic surveys of beaches on which carcasses were found. Generally, moribund birds were taken to wildlife rehabilitation centers; very few survived for subsequent release. Most that died were saved for necropsy and eventual preparation as museum specimens. Birds that were euthanized were submitted for post-mortem examination to appropriate wildlife diagnostic laboratories. Records of these birds were used to determine the condition of affected birds.

At the FMNH, suitable remains were prepared as skins or skeletons, and the following were recorded: size of gonads; width and condition of oviduct; presence/absence and size of bursa of Fabricius; molt and wear of remiges and rectrices to determine age (hatch year/second year (HY/SY) or after second year (ASY), adapted from Nevins & Carter (2003)); fat score (emaciated, no fat, trace fat, light fat, moderate fat, heavy fat); stomach contents, if any; and body condition, using the weights of the pectoralis major and supracoracoideus muscles from one side.

At Tufts University, Southeastern Cooperative Wildlife Disease Study, and the National Wildlife Health Center (NWHC), gross necropsies were used to record carcass condition, keel score, fat stores, sex, stomach contents, and, where possible, cause of death. At Cape Cod, DBM used two categories to assign the approximate time since death; carcasses were "fresh" (less than one week old) if the bird was ≥ 75% intact (i.e., ≥ 75% of all feather tracts remaining, with fresh or fairly fresh soft parts present), versus "not fresh" if the carcass was less than 75% intact, with fewer feather tracts and older soft parts (Žydelis *et al.* 2006, Lucas *et al.* 2012). Some of the latter carcasses consisted of "angel-wings," i.e., both wing bones (with primary and secondary feathers) attached to a bare sternum. This was strongly suggestive of at-sea predation or scavenging (Newton & Little 2009). Carcass remnants such as individual small bones and feathers were ignored. DBM's binary and unequal categorization of the approximate carcass age and condition since death is less precise than SEANET's assessment (SEANET 2010) of carcass age and condition, but it allowed quick assessment in the field and direct comparison to most previous studies. We used chi-squared analysis for Razorbills and Fisher's exact test (two-tailed) for Atlantic Puffins to test for differences in the number and proportion of "fresh" and "not fresh" carcasses on Cape Cod. We also assessed the age of Atlantic Puffin carcasses using the number of bill grooves (if the head was present) following Harris (2014), along with wear and molt of flight feathers; adult Atlantic Puffins molt their flight feathers mainly between January and April (Harris & Yule 1977, Pyle 2009, Harris & Elkins 2013, Harris *et al.* 2014), unlike Razorbills, which complete flight feather molt in late summer and fall (Pyle 2009).

Origins of affected birds

We examined all North American records of Razorbills (n = 233) and Atlantic Puffins (n = 490) banded at breeding colonies using encounter data provided by the Bird Banding Office (National Wildlife Research Centre in Ottawa, Canada) and Bird Banding Laboratory (US Geological Survey) on 20 July 2018. Of these, 58 Razorbill and 16 Puffin recoveries were in winter (Nov–Mar).

Possible causes of the wrecks

Winter storms

Most seabird wrecks coincide with unusually intense storms (Underwood & Stowe 1984, Duff *et al.* 2013), so we examined the timing and extent of extreme weather events relative to the timing of Razorbill and Atlantic Puffin mortality. The NOAA Storm Events Database and weather records from the University of North Carolina's Southeast Regional Climate Center were searched for local storm reports in Florida between 01 December 2012 and 31 March 2013. We also considered possible impacts of Hurricane Sandy, which, although it preceded the first record of Razorbills in Florida by over a month, struck the entire shelf portion of the usual Razorbill winter range outside the Gulf of Maine, disrupting both fish habitat (Secor *et al.* 2018) and sediment transport (Miles *et al.* 2015).

ECWSs extend from the Bay of Fundy to northern Florida but are most concentrated in southeastern Massachusetts (Hirsch *et al.* 2001). To qualify as an ECWS, sustained wind speeds must reach a threshold of at least 20 kt (37 km/h) for at least 12 h (Hirsch *et al.* 2001); a "strong ECWS" is defined by a higher wind threshold (at least 45 kt [83 km/h] for at least 12 h), while some storms approach hurricane-force (64 kt [119 km/h]). The possible influence of winter storms on the Cape Cod auk wreck was assessed by examining ECWS records from the Northeast Regional Climate Center. These records were supplemented with examination of the Storm Events Database (NCEI 2018a); local climatological data at the Chatham Municipal Airport (NCEI 2018b) and at Provincetown, Massachusetts (Weather Underground 2018); daily weather maps (Weather Prediction Center 2018); and personal observation of these storms by DBM. We compared differences in mean carcass encounter rates (birds/km) among the five storm intervals for all seabirds, for Razorbills only, and for all other seabirds. The relationship between the timing of ECWS arrival and the pooled carcass encounter rates was calculated over five periods of unequal duration, beginning with the arrival of each storm: before Nemo (12 days: 27 Jan to 07 Feb), during and after Nemo (9 days: 08–16 Feb), and during and after the three ECWSs following Nemo (18 days: 17 Feb to 06 Mar; 14 days: 07–20 Mar; and 8 days: 21–28 Mar).

Oceanographic changes

The 2012/13 winter followed the warmest SSTs on record in the northwest Atlantic (Mills *et al.* 2013, Chen *et al.* 2014) and especially in the Gulf of Maine, where tens of thousands of Razorbills normally winter (Huettmann *et al.* 2005, Clarke *et al.* 2010). The positive SST anomaly (or "marine heatwave") extended throughout the usual Razorbill winter range, from the Scotian

Shelf and Gulf of Maine south to Cape Hatteras (Chen *et al.* 2014). Related SST anomalies in the Gulf of St. Lawrence were implicated in the temporary abandonment of large Northern Gannet *Morus bassanus* colonies in the summer of 2012 (Montevecchi *et al.* 2013). We therefore also examined changes in the ocean environment as a possible cause.

Food shortage

Irruptions are usually associated with disruption of food supplies in the normal winter range, so we looked for evidence of reduced availability of forage fish in the Gulf of Maine in fall and early winter.

Population increase

Robben *et al.* (2014) suggested that a population increase may have contributed to the Florida wreck, so we solicited census data from the Canadian Wildlife Service.

RESULTS

Florida

Observations of live birds

In late November 2012, Florida experienced the beginning of a major irruption. It was described by Pranty (2013) as "massive and unprecedented" with a maximum of 600 individuals on the Dade County CBC (Miami-Dade County; Fig. 2). Razorbills were recorded on 20 counts and in all coastal regions, including as far into the Gulf of Mexico as Pensacola (Escambia County) in extreme northwestern Florida. By mid-February, eBird showed over 2 100 records of Razorbills in Florida, and they had been seen on the Gulf Coast as far west as Louisiana (Brinkley 2013).

In the eBird data for Razorbills in Florida during the winter of 2012/13, the standardized index of the weekly frequency of occurrence shows a frequency of occurrence of five standard deviations above the mean for the 1993–2018 period (Fig. 3a). Since 2008, Razorbills have appeared at a rate of about one per year (Kratter 2018), compared with 14 records between 1967 and 2011 (Greenlaw *et al.* 2014). Such an increase in records, however, is far too low to be reflected in eBird data.

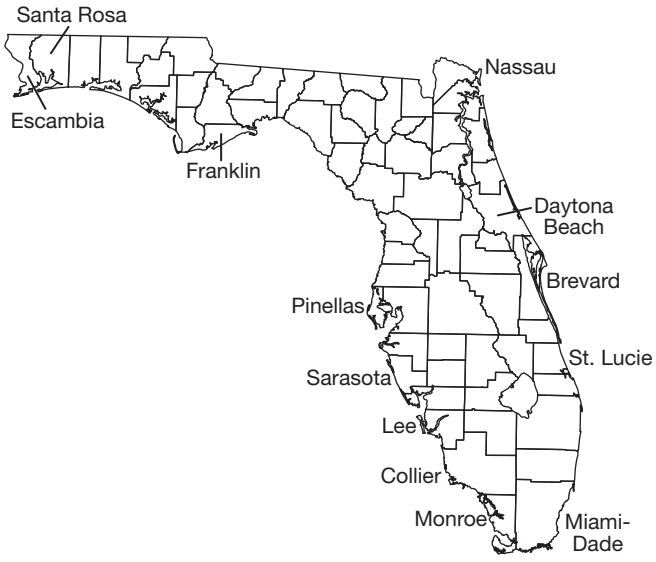

Fig. 2. Map of Florida showing counties named in text.

Beached birds

On 07 December 2012, a live but weak Razorbill was brought to the Marine Science Center, a wildlife rehabilitation clinic in Ponce Inlet, near Daytona Beach. Another was brought to the same clinic on 10 December, and by 11 December, live individuals were being reported from several localities in northeastern Florida. By 14 December, Razorbills were widespread along the Atlantic coast of Florida and had begun to be reported in the Gulf of Mexico (Sarasota County).

The earliest Razorbill specimen submitted to the FMNH was found on 09 December 2012 in Brevard County, and the last was found on 08 May 2013 in Collier County (Gulf Coast). The specimens spanned the Florida coast from the northernmost locale on the Atlantic coast (Ft. Clinch State Park, Nassau County) and westernmost locale on the Panhandle (Ft. Pickens, Gulf Islands National Seashore, Escambia County) south to the Florida Keys (Monroe County) along both the Gulf and Atlantic coasts. At least one Razorbill was found in each of the 13 Atlantic coast counties, as well as five of the 21 Gulf Coast counties (Escambia, Franklin, Sarasota, Lee, and Collier). The only previous records for the Gulf of Mexico were single specimens from northwest Florida (Santa Rosa County) in May 1979 (Stevenson & Anderson 1994) and the mid-coast Gulf Coast in Pinellas County on 13 April 2005 (Kratter & Small 2007). No specimens were recovered from the Gulf Coast between Sarasota and Franklin counties, though live individuals were reported in this region. Much of this area is within the relatively undeveloped Big Bend region, where access roads are few, observers are scarce, and beaches are rare. Of the sixty carcasses collected between December 2012 and March 2013, fifty were collected in December, four in January, four in February, and two in March. Two subsequent carcasses, one each in April and May, were considered part of the same event.

Age, sex, and condition of affected birds

Of the 82 specimens at the FMNH, five (6.1%) were in their second molt cycle or older (i.e., SY or ASY). All others were hatch year/second year birds. The female:male sex ratio (57.6%:42.4%) was not significantly different from 1:1 ($X^2 = 1.373$, $P = 0.24$, $n = 59$ birds). The mass range (341.3 g to 537.0 g, $n = 57$) was less than the mean mass of adults (734.5 g ± 19.2 standard errors (SE), $n = 21$) and one of two HY/SYs (which weighed 630 g and 510 g) in late January in the Bay of Fundy (Huettmann *et al.* 2005). All birds that were prepared were emaciated, with a noticeably protruding keel and reduced breast muscles. The percentage of total body weight contributed by breast muscles did not change significantly with total weight.

Band recoveries

Two recoveries in December 2012/13 were juveniles banded the previous summer, one on Matinicus Rock, Maine and one on Machias Seal Island (MSI), New Brunswick. There were no band recoveries in Florida in the winters following 2012/13. The first band recovery in Florida was in February 2003 from a juvenile banded the previous summer as a chick in the Bay of Fundy; this recovery was overlooked in the Florida checklist (Greenlaw *et al.* 2014).

Winter storms

No storms were recorded in Florida between December 2012 and March 2013. There were no strong onshore winds in coastal eastern Florida in December 2012, so the Florida wreck of Razorbills was not caused by birds being driven ashore by storms. The birds evidently starved offshore, so we question how they came to be so far out of their normal region in conditions with inadequate food supply.

The outstanding weather event on the eastern coast of North America in 2012/13 was Hurricane Sandy, which made landfall in New Jersey on 29 October 2012. It was the largest Atlantic hurricane ever recorded, its winds extending over a diameter of 1 800 km. It did not make landfall in Florida, but it did cause heavy seas and significant erosion along the whole Atlantic coast 28–29 October (NOAA 2013a). Winds of tropical-storm strength extended over 1 600 km of coastline from South Carolina to central Maine (NOAA 2013b),

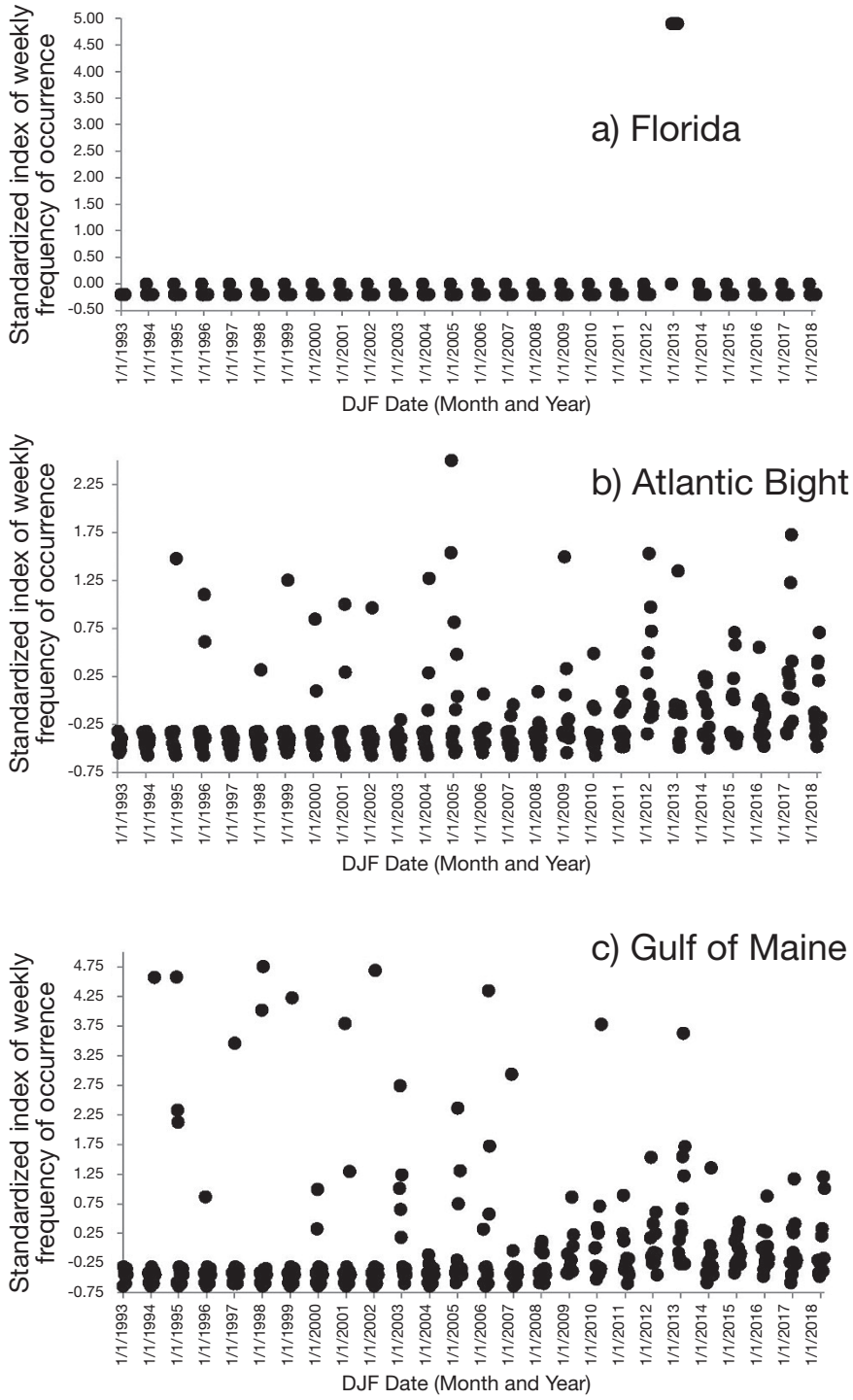

Fig. 3. Standardized index of the weekly frequency of occurrence of Razorbills in three regions of eastern North America for December to February 1993–2018 (eBird 2018). Data points represent the weekly frequency of occurrence data standardized by the mean and standard deviation for the entire period, averaged as weekly occurrences for each month.

which includes much of the normal winter range of Razorbills. This event preceded the Razorbill incursion into Florida by over a month, but it caused widespread disruption of coastal waters from Florida to Massachusetts, including increased turbidity (Miles *et al.* 2015) and disturbance of fish habitat (Secor *et al.* 2018) throughout the southern portion of Razorbills' winter range.

Atlantic Bight and Southern New England

Observations of live birds

States bordering the Atlantic Bight did not show anomalous counts in winter 2012/13; the highest count was in late winter 2004/05 (Fig. 3b). Subsequent winters through 2017/18 showed steadily increasing frequencies of Razorbills after 2006. No peak exceeded twice the standard deviation, although numbers in winter 2016/17 (the second warmest on record and the warmest since 2012/13) were higher than any winter since 2012/13.

TABLE 1
Total lengths (km) of beach surveyed and number of Razorbill carcasses recorded by SEANET volunteers and staff, November 2012 through March 2013, by state

State	No. km surveyed	No. Razorbill carcasses
ME	207.4	0
MA	373.3	43
RI	63.4	3
NJ	80.3	1
NC	358.9	18
SC	66.0	0
GA	36.1	0
FL	24.6	0
Total	**565.8**	**65**

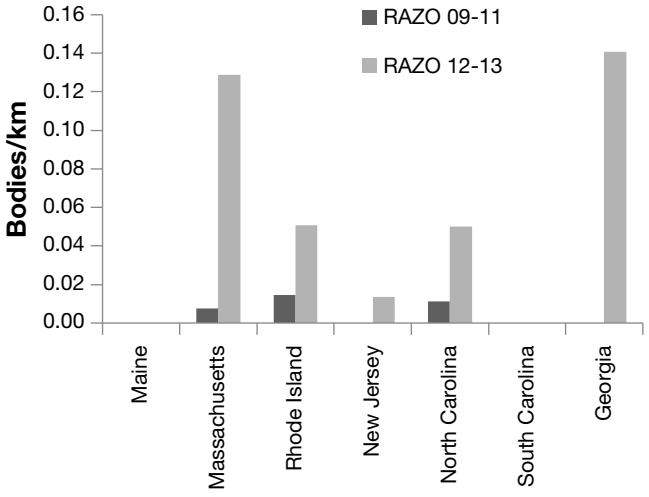

Fig. 4. Number of Razorbill bodies found per km of beached searched in winters 2009/10 and 2010/11 (RAZO 09-11), compared to 2012/13 (RAZO 12-13), as reported to SEANET (n = 65). North Carolina data is for winter 2011/12 only; Georgia data is for winter 2009/10 and 2010/11 only. In 2012/13 Razorbills were found at 7× the rate (bodies/km) of previous winters. One carcass in Georgia from March 2013 is not shown. In winters 2013/14 through 2015/16, one carcass was collected in North Carolina in March 2015 and two in Massachusetts in winter 2015/16 (one each in November and March (J.D. Stanton unpubl. data)).

Beached birds

SEANET data from beached birds were grouped by state (Table 1). Encounter rates were determined this way for Razorbills specifically (Fig. 4) and for all alcids (Fig. 5), including Razorbills, murres, Atlantic Puffins, Black Guillemots, Little Auks, and any unidentifiable alcids. Carcass counts from Massachusetts to North Carolina for Razorbills and for all alcids were much higher in winter 2012/13 than in the two previous and four following winters. In subsequent winters, single Razorbill carcasses were detected in Massachusetts (28 November 2015 and 09 March 2016) and in North Carolina (02 March 2015), while eight dead or moribund alcids (six Little Auks during winter 2012/13, one Thick-billed Murre in December 2015, and one Razorbill in February 2017) were reported, retrieved, or salvaged along South Carolina beaches (Hill *et al.* 2014, 2016; Southern 2017). No moribund alcids or carcasses were found in any winter other than 2012/13 in Georgia; sample sizes in Georgia and South Carolina were much lower than in states further north. Very limited sampling in Florida (25 km walked) detected no alcids at all (J.D. Stanton unpubl. data).

Condition of affected birds

Necropsies of carcasses from New York and North Carolina showed emaciation as the main cause of death in all cases (Table 2), except for two Razorbills that were found at the Virginia/North Carolina border and necropsied by the NWHC. The latter birds were in good body condition with fish in their digestive tracts, which suggests that they died of another cause such as bycatch or even overeating. No toxins were detected during the evaluations by the NWHC.

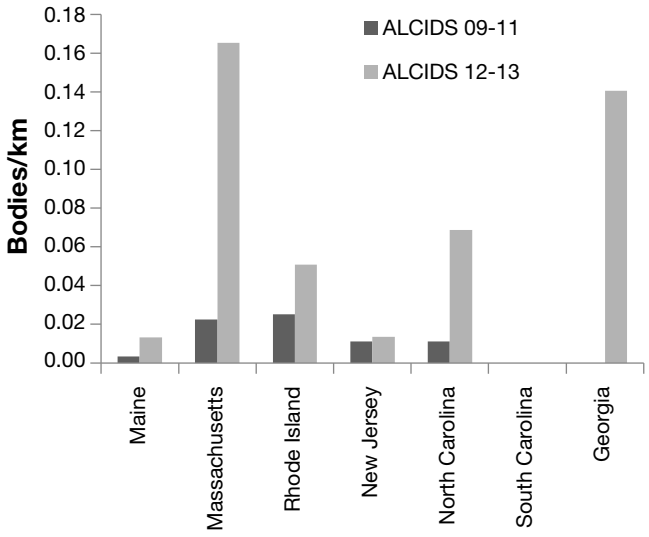

Fig. 5. Number of alcid bodies found per km of beached searched in winters 2009/10 and 2010/11 (ALCIDS 09-11), compared to 2012/13 (ALCIDS 12-13), as reported to SEANET. North Carolina data are for winter 2011/12 only; Georgia data for winter 2009/10 and 2010/11 only. In 2012/13 alcids were found at 4.5× the rate (bodies/km) of previous winters.

Band recoveries

In winter 2012/13, the only band recovery was from one Razorbill in North Carolina in March who was banded in New Brunswick as adult in 2010. As with the Florida recoveries, the first band returns from the Mid-Atlantic Bight were three in March 2003 in North Carolina: two birds banded as adults in New Brunswick in 2001 and one banded in Quebec as an adult (After Third Year or ATY) in 1991 (thus, at least 15 years old). Outside of the winter period, one band was recovered in May 2003 from a bird banded as a chick in Newfoundland in 2001.

Winter storms

The small numbers of beached birds and band recoveries between Florida and Cape Cod did not warrant exploration for possible impacts of winter storms.

TABLE 2
Necropsies of alcids found on beaches during winter 2012/13.
Other alcid species are included only when part of the same beaching event as Razorbills or Atlantic Puffins.

Laboratory	Location	Species	Number	Sex	Findings
Tufts University Cumming School of Veterinary Medicine	Cape Cod, MA	Atlantic Puffin	17	14 F, 2 M, 1 unknown	Emaciation, poor body condition
		Murres (3 Thick-billed, 1 unknown)	4	2 M, 2 F	Emaciation
		Black Guillemot	1	1 F	Ante-mortem fracture
National Wildlife Health Center	Long Island, NY	Razorbill	3	Adult M	Emaciation/starvation
	VA/NC border	Razorbill	3	Unknown	Good body condition, fish in gastrointestinal tracts, unknown cause of death
North Carolina State University	Hubert, NC	Razorbill	1	Unknown	First winter juvenile; poor body condition with localized fungal respiratory infection (Aspergillosis?)

TABLE 3
High counts of Razorbills by month and year, and number of townships with high counts during the five consecutive winters beginning 2012/13 on outer Cape Cod (Orleans to Provincetown). All data from eBird.

Month	2012/13		2013/14		2014/15		2015/16		2016/17		Total	
	High Count[a]	No. of Twshps	High Count	No. of Twshps	High Count	No. of Twshps	High Count	No. of Twshps	High Count	No. of Twshps	High Count	No. of Twshps
Nov	1475	2	110	1	2900	2	1300	5	531	2	6316	12
					(15)						(3431)	
Dec	12260	5	3710	4	1410	4	10900	4	10515	3	38795	20
	(1735)										(28270)	
Jan	709	4	13000	3	5503	5	7296	3	5190	4	31698	19
			(500)		(900)						(14595)	
Feb	1609	4	1540	3	6526	2	12400	3	3260	3	25335	15
	(156)				(3990)		(7494)		(2164)		(15344)	
Mar	1947	3	415	3	4407	2	11599	2	3200	3	21568	13
Apr	2022	4	110	1	115	1	600	2	721	1	3568	9
	(308)								(244)		(1377)	
Total	20072	22[b]	18885	15	20061	16	44095	19	23417	16	127280	88
	(6330)		(6385)		(10837)		(39189)		(21844)		(84585)	

[a] Monthly high counts (underlined) occurred during or within 2 days after passage of an ECWS or a consequential local storm; monthly high counts in parentheses are without storms, in months when monthly high counts with storms occurred.

[b] Total number of townships is composed of five townships summed over all townships and all years for each month and year, and for the total of all months and years.

Cape Cod

Observations of live birds

Data from the Gulf of Maine (Fig. 3c) show that more Razorbills were sighted in each of the nine years preceding the winter of 2012/13 and fewer were sighted in all subsequent years. At Cape Cod, high counts of ≥ 100 Razorbills occurred during every winter month and every year, although numbers were lowest at the beginning (November) and end (April) of winter, when Razorbills generally arrive at and leave outer Cape Cod (Table 3). The number of townships with high counts during each winter was 15–22, with the most high counts occurring during the winter of 2012/13 after strong storms (Table 4). Among the five townships, counts of ≥ 100 birds that included all six months and five winters combined (i.e., maximum potential total of 30 high counts) were highest in Provincetown (28) and Truro (24), lowest in Orleans (8), and intermediate in Wellfleet and Eastham (14 each). That was despite First Encounter Beach (Eastham Township) being the hotspot on the bay-side for counting seabirds during storms. Few high counts (2) were reported from Wellfleet Harbor. The highest counts (and many others), which are first observed in December or January, are often influenced by storms (e.g., the maximum of 13000 Razorbills at Race Point Beach), but several of the highest counts also occurred without storms (e.g., maximum of 11599 Razorbills at Race Point), especially during winter 2015/16. Thus, storms influenced counts, but the total number of Razorbills without storms (66% of the total number with storms; range 32%–93% over each of the five winters: Table 3) would still constitute a designated status as "common" to "locally abundant" in each of the five winters. This includes 2012/13, when Razorbills, though more widely distributed including the bay-side, were no more numerous than in any of the four following winters (Table 3). The prolonged high counts for four consecutive months (December through March) in Provincetown during winter 2015/16, when the influence of storms was minor, remains unexplained. It may have been due to high concentrations of sand lance *Ammodytes* spp., which also attracted many other seabirds and whales (Veit *in litt*.).

The total numbers of Atlantic Puffins seen from land on outer Cape Cod during the five winters starting in 2013/14 were 71, 1, 2, 2, and 26 birds, respectively. During winter 2012/13, the highest counts were 52 (observed from Skaket Beach, Orleans on 10 February, shortly after the passage of superstorm Nemo) and 16 (observed from First Encounter Beach, Eastham on 28 December, also following the passage of a strong ECWS). In winter 2016/17, a high count of 22 birds was recorded on 25 January, again at First Encounter Beach and closely following a strong ECWS.

Christmas Bird Counts

We did not examine CBC data in detail (see Methods section), but the coordinator of the Grand Manan CBC (Durlan Ingersoll, who is also a fisherman) reported *in litt*. that "We only had three razorbills on the Grand Manan count [December 2012] … when fishing I normally would see many, many razorbills flying by, this year I am not seeing this. In other years the numbers would be thousands flying by, and this year I might have seen the occasional flock numbering 20 birds or so."

Beached birds

Twenty-one beaches (9 bay-side, 6 harbor-side, 5 ocean-side, 1 at Race Point) were surveyed between 27 January and 28 March 2013. Over all five winters combined, the distance surveyed for each water location type was: 747.5 km bay-side, 125.6 km harbor-side, 377.5 km ocean-side, and 192.3 km at Race Point.

During mid to late winter 2012/13, when most coastal and some pelagic seabirds that are regularly present were represented, 475 dead beached seabirds of 23 species were encountered (Appendix 1); SEANET/WHER counts were probably duplicated for 18 of these (16 Razorbills, 1 Atlantic Puffin, 1 Common Loon *Gavia immer*). Over half (56%) of the dead seabirds were Razorbills; the second most numerous species was Atlantic Puffin (see below). Four other species of alcid were represented in far smaller numbers (Appendix 1). Relative to the "wreck" winter of 2012/13, the abundance of Razorbills and Atlantic Puffins was an order of magnitude less during each of the following four winters (Appendix 2); in winter 2014/15 dead Razorbills were outnumbered by dead Thick-billed Murres.

The mean encounter rate from all surveys for all carcasses during winter 2012/13 was 2.43 birds/km (range 2.47–3.26) at bay-side and harbor-side beaches and at Race Point, compared to 0.69 birds/km for ocean-side beaches (a 4- to 6-fold difference). The mean encounter rate at most beaches was about 3 birds/km except at all five ocean-side beaches, where the rate was ≤1 bird/km (Fig. 6). Despite different survey efforts among water location types, the

TABLE 4
East Coast Winter Storms (ECWS) recorded by the US Coast Guard Air Station Cape Cod, Jan–Mar 2013. ECWS are storms maintaining wind speed of 20 kt (37 km/h) for more for 12 hours (Hirsch *et al.* 2001).

Dates	Max. wind speed (km/h) per day, respectively	Direction (degrees, bearing)	Name
19–20 Jan	74, 66	225° (SW)	
30–31 Jan	76, 93	180° (S), 270° (W)	
08–09 Feb	113, 116	045° (NE)	Nemo
22–28 Feb	72, 74	045° (NE), 360° (N)	
07–09 Mar	77, 76, 66	022° (NNE)	
19–21 Mar	60, 53, 45	090° (E), 270° (W), 180° (S)	

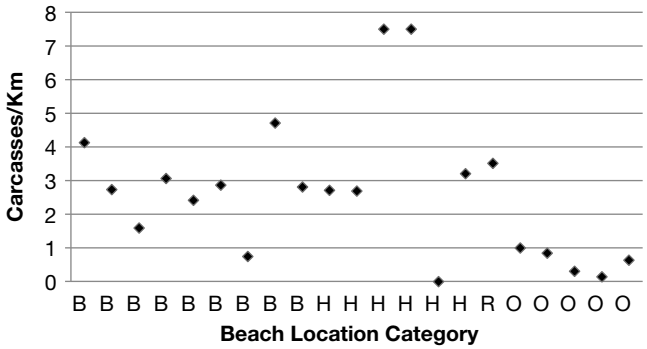

Fig. 6. Mean carcass encounter rate of Razorbills on Cape Cod beaches, by water location type. B = Bay-side, H = Harbor-side, R = Point Race, O = Ocean-side.

mean ocean-side encounter rate was significantly less than the other three types (Fig. 6). More seabirds of all species and a greater proportion of each population were encountered on the bay-side, harbor-side, and at Race Point compared to the ocean-side; this was true also of Razorbills only, and all seabirds except Razorbills (λ^2, $df = 3$, all values > 30, $P < 0.001$). The proportion of birds of each of the 14 most numerous species ($n \geq 4$) located on ocean-side beaches ranged from 0% (7 species) to 15%, except for the Little Auk (45%; 5 of 11 birds on ocean-side beaches).

Observed numbers of dead Razorbills during winter 2012/13 were significantly greater than expected at all four water location types compared to the four following winters (Table 5; $X^2 = 1\,444$, $df = 3$, $P < 0.0001$). Over all five winters, observed numbers of Razorbills were less than expected at ocean-side beaches, in comparison to the other three water location types ($X^2 = 59$, $df = 3$, $P < 0.0001$). Numbers of Atlantic Puffin carcasses during the winter 2012/13 and over all five winters were much greater than expected at Cape Cod beaches of all water location types (Table 5). Over all five winters, numbers of puffin carcasses were greater than expected at bay-side beaches in comparison to the other three water location types.

During the nine-day period following the arrival of superstorm Nemo, the mean carcass encounter rate for all seabirds (4.12 birds/km), for Razorbills only (2.56 birds/km), and for all seabirds except Razorbills (1.56 birds/km) was approximately double that of the subsequent three ECWS periods (Fig. 7). Mean encounter rates were similar across these three latter periods for all seabirds (range: 2.09–2.37), Razorbills only (range: 1.16–1.37), and all seabirds except Razorbills (range: 0.72–1.21). Proportionally ~40% more Razorbills (compared to all other seabirds) were encountered during the nine-day period bracketing superstorm Nemo, in contrast to all three ECWS periods combined following Nemo (Fig. 7). We found no relationship between ECWS during the following four winters and the timing of beached Razorbill carcasses on outer Cape Cod. Even during the 13 days between the Great Blizzard of January 2015 and the next ECWS, DBM detected only four Razorbill carcasses.

Age and condition of affected birds – Razorbills

The Wild Care Center in Eastham, Massachusetts reported 30 alcids among the 63 seabirds admitted during the winter of 2012/13 (01 November–28 February): eleven Little Auks, seven Razorbills,

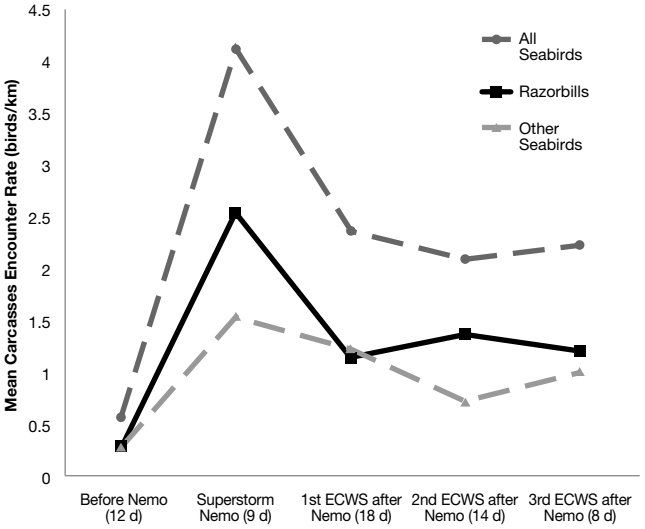

Fig. 7. The mean carcass encounter rate (birds/km) for all beached seabirds, Razorbills only, and other seabirds during five periods of unequal duration before, during, and after superstorm Nemo on outer Cape Cod from 27 January to 28 March 2013 (full explanation in text).

TABLE 5
Observed and expected numbers of Razorbills and Atlantic Puffins from deposited carcasses on beaches of outer Cape Cod during the wreck winter of 2012/13, as compared to the following four winters (2013–2017) combined. Expected numbers have been effort-adjusted.

Razorbill						
Water Location Type	**Wreck Winter (2012/13)**		**Following Four Winters (2013–2017)**		**All Five Winters**	
	Observed	**Expected**	**Observed**	**Expected**	**Observed**	**Expected**
Bay-side	155	24	53	153	208	177
Harbor-side	39	6	1	24	40	30
Race Point	54	6	12	40	66	46
Ocean-side	16	12	12	78	28	89
Total	264		78		342	
Atlantic Puffin						
Water Location Type	**Wreck Winter (2012/13)**		**Following Four Winters (2013–2017)**		**All Five Winters**	
	Observed	**Expected**	**Observed**	**Expected**	**Observed**	**Expected**
Bay-side	34	4	6	24	40	28
Harbor-side	1	1	2	4	3	5
Race Point	1	1	2	6	3	7
Ocean-side	3	2	4	12	7	14
Total	39		14		53	

six Atlantic Puffins, three Common Murres, and three Thick-billed Murres. Twenty-two of the alcid deaths were attributed to storms, 14 specifically to the "major winter storm" Nemo (08–10 February). These 22 alcids were weighed and all were under the average weight recorded for the species (underweight by 6%–31% in seven Razorbills, 11%–53% in six Atlantic Puffins, 27%–35% in two Common Murres, 37%–45% in three Thick-billed Murres, and 23%–36% in two Little Auks). One Atlantic Puffin weighed only 180 g when it was found alive (> 50% below average weight), but it died on arrival.

During the wreck winter, 264 dead Razorbills washed ashore. DBM critically examined the body condition of 40 entire Razorbills, which were all emaciated or severely emaciated; internal organs (heart, liver, etc.) appeared normal, but the pectoral muscle profile was never greater than flat (i.e., never convex) and only a few birds had any fat. Gastrointestinal tracts contained no animal matter, not even a trace of material such as fish bone. The remaining 224 entire Razorbills were subject to external examination only; all had thin keels and were light. Of these 264 dead Razorbills that washed ashore during the wreck winter, 247 (94%) were aged as ASY, 6 as SY, and 11 could not be aged. In contrast, of the 78 washed ashore during the following four winters, 26 (72%) were aged as ASY, 10 as SY, and 42 could not be aged. The proportion of adults during the wreck winter was significantly greater than the following four winters ($\lambda^2 = 138$, $df = 2$, $P < 0.0001$).

Age and condition of affected birds – Atlantic Puffins

Cape Cod also suffered the largest wreck of Atlantic Puffins yet recorded in North America. DBM retrieved 39 carcasses between 29 January and 17 March 2013 (Appendix 3); all were examined by AWD for age (from number of bill grooves, following Harris (2014)) and stage of wing molt (Table 6). Of the 31 specimens that could be aged, nine (29%) were SY, one was ASY, and 21 (68%) were ATY (i.e., with two or more bill grooves and of possible breeding age). Wing condition varied relative to degree of wear and completion of molt; of the 37 specimens for which the condition of the primaries could be assessed, 8 (23%) were freshly molted but 26 (74%) had not yet molted. These later carcasses showed varying degrees of wear, ranging from very worn with some bleached flight feathers ($n = 1$), to worn or only slightly worn ($n = 12$). Only one adult (ATY) bird was in active primary molt, which was asymmetrical. In subsequent winters, none of the collected carcasses were in active molt and half were only slightly worn.

The number and proportion of fresh Atlantic Puffin carcasses deposited on the beaches of outer Cape Cod during the winter of 2012/13 significantly exceeded those of the other four winters combined (Table 5; Fisher's exact test [two-tailed] $P = 0.001$). In the four subsequent winters combined, one-third of the 2012/13 number were found; age ratios suggest higher proportions of SY birds (6 of 10) than in 2012/13 (9 of 30).

TABLE 6
Age and condition of the wings of Atlantic Puffin carcasses on Cape Cod in (A) winter of 2012/13 and (B) subsequent winters. Adults predominated in 2012/13; subadults predominated in subsequent winters.

(A)

	Condition of wings					
Age[a]	**New**[b]	**Worn/ Slightly worn**	**Moderately worn**	**Very worn/ bleached**	**Active molt**	**Totals**
SY	1	2	4	-	-	7
ASY	-	-	1	-	-	1
ATY	2	8	7	3	1	21
Unk	5	2	1	-	-	8
Totals	**8**	**12**	**13**	**3**	**1**	**37**[c]

[a] SY = Second Year; ASY = After Second Year; ATY = After Third Year; Unk = Unknown
[b] No specimen available
[c] Plus two incomplete bodies that could not be categorized

(B)

	Age			Flight feather condition					Total specimens assessed
	SY	**ATY**	**Unknown**	**Slightly worn**	**Moderately worn**	**Very worn**	**Very worn/ bleached**	**Active molt**	
Feb 2014	0	1	0	0	0	0	1	0	1
Feb–Mar 2015	2	3	0	2	2	0	1	0	5
Feb 2017	3	-	4	5	1	0	1	0	7
Totals	**5**	**4**	**4**	**7**	**3**	**0**	**3**	**0**	**13**

The proportion of "fresh" versus "not fresh" carcasses of both Atlantic Puffins and Razorbills was higher in winter 2012/13 than in subsequent winters (Table 7), which reflects greater temporal concentration of mortality in the winter of the wreck.

Necropsies

Gross necropsies (Table 2) were conducted by the Cummings School of Veterinary Medicine at Tufts University on 30 seabirds salvaged in February and March 2013 at Cape Cod. Of these, there were 17 Atlantic Puffins, three Thick-billed Murres, one Black Guillemot, and one murre of unknown species (too scavenged to identify). Carcass condition, keel score, fat stores, sex, and stomach contents were recorded. Of the 22 alcids, 17 (77%) were female, one male (5%), and four were of unknown sex due to scavenging of the gonads. Most birds were emaciated (82%) and some were in poor body condition (9%); two were too scavenged to assess body condition. Only one bird showed evidence of pre-mortem trauma playing a role in mortality. Almost all had empty digestive tracts; two had a small amount of plant matter. Necropsies were also performed on two Thick-billed Murres and a Little Auk found on the coasts of New Hampshire and southern Maine; all were

TABLE 7
Observed and expected numbers of "Fresh" and "Not Fresh" condition Razorbill and Atlantic Puffin carcasses on beaches of outer Cape Cod during the wreck winter of 2012/13 in comparison to the following four winters (2013–2017) combined. See text for definitions of "Fresh" and "Not Fresh". A higher proportion of carcasses were "fresh" in winter 2012/13.

Razorbill						
Carcass Condition	**Wreck Winter (2012/13)**		**Following Four Winters (2013–2017)**		**All Five Winters**	
	Observed	**Expected**	**Observed**	**Observed**	**Expected**	**Observed**
Fresh	233	198	31	66	264	171
Not Fresh	24	59	54	19	78	171
Total	257		85		342	
Atlantic Puffin						
Carcass Condition	**Wreck Winter (2012/13)**		**Following Four Winters (2013–2017)**		**All Five Winters**	
	Observed	**Expected**	**Observed**	**Observed**	**Expected**	**Observed**
Fresh	35	30	4	9	39	26.5
Not Fresh	6	11	8	3	14	26.5
Total	41		12		53	

TABLE 8
Origin and age of banded Razorbills and Atlantic Puffins encountered in winter 2012/13

	Banding				**Encounter**		
Species/ band no.	**Date**	**Location**	**Age**[a]	**Bander**[b]	**Date**	**Location**	**Age (years)**
Razorbill							
0895-14853	30 Jul 2001	Îles Sainte-Marie, QC	AHY	SCF	10 Mar 2013	MA	12+
0895-15153	16 Jul 2007	Île Corossol, QC	Local	SCF	09 Mar 2013	MA	6
0895-17368	24 Jul 2005	Machias Seal Island, NB	AHY	UNB	09 Mar 2013	MN	10+
0895-23853	09 Jul 2012	Matinicus Rock, ME	Local	NAS	17 Dec 2012	FL	<1
0895-24756	03 Jun 2010	Machias Seal Island, NB	ATY	UNB	21 Mar 2013	NC	5+
0895-24942	08 Jul 2012	Machias Seal Island, NB	Local	UNB	24 Dec 2012	FL	<1
Atlantic Puffin							
1055-05323	05 Aug 2006	Eastern Egg Rock, ME	ATY	NAS	19 Feb 2013	Cape Cod	>9
1015-08548	25 Jul 2005	Machias Seal Island, NB	ATY	UNB	08 Feb 2013	Cape Cod	8
0875-78491	04 Aug 1999	Seal Island National Wildlife Refuge, ME	Local	NAS	13 Feb 2013	Cape Cod	14
1905-10415	14 Aug 1996	Machias Seal Island, NB	Local	UNB	02 Feb 2013	Cape Cod	17

[a] AHY = After Hatch Year; Local = chick unable to fly; ATY = After Third Year (adult)

[b] SCF = Service canadien de la faune (Canadian Wildlife Service); UNB = University of New Brunswick; NAS = National Audubon Society

emaciated males. One of the Thick-billed Murres had chronic perforation of the proventriculus and inflammation of the coelom. Emaciation appeared to be the main cause of death in all cases.

Band recoveries – Razorbills

In winter 2012/13, two banded Razorbills were recovered at Cape Cod (adults banded at different Quebec colonies, one as adult and one as chick), and another recovered in Maine had been banded as adult on MSI in New Brunswick (Table 8). The remains of another bird that was banded as a chick in 2002 on MSI were found on a Boston beach in August 2014; pictures of the carcass suggest it may also have been involved in the 2012/13 wreck. In subsequent winters (2013/14 through 2017/18), the only Razorbill band recoveries were two from late February 2018: one bird that was banded in Quebec as an adult in 1995 and found dead in Massachusetts, and one banded in the Gannet Islands (Labrador) as an adult in 2004 and found dead in Maine. None of the Razorbills found by DBM on outer Cape Cod beaches over the five winters from 2012 to 2017 was banded.

Almost half the banded Razorbills encountered in winters before 2012 (1926–2011) were juveniles (25 of 54 = 46%). In winter 2012/13, 33% (2 of 6) were juveniles, so this small sample was not dominated by inexperienced young birds on their first migration.

Band recoveries – Atlantic Puffins

Four banded Atlantic Puffins were reported during the wreck at Cape Cod (Table 8). All were found dead in February 2013 and had been banded at Gulf of Maine colonies: one from each of Eastern Egg Rock and Seal Island National Wildlife Refuge (SINWR) in Maine and two from MSI in New Brunswick. All were encountered as adults. The bird from SINWR had been banded as a chick and was 14 years old when recovered, one bird from MSI was banded as a chick and was 17 years old when recovered, and the other MSI bird was banded as adult and recovered 8 years later. In terms of recoveries that happened in February, these four from 2013 represent the highest total on record for this species in the Bird Banding Laboratory data. The only other February recoveries are single records from 1982, 1997, 2010, 2015, and 2018. In these last three winter recoveries, one was a bird banded on MSI as ASY in 2007 and recovered in New Brunswick in 2010, one was banded as a chick on MSI in 1994 and recovered on Cape Cod in February 2015, and one was banded as a chick on MSI in 1996 and recovered in southwestern Nova Scotia in February 2018. The other recoveries were of birds both banded and recovered in Newfoundland and Labrador.

Winter storms

Of the 15 ECWS and 11 strong storms that occurred in 2012/13 from October to April (NRCC 2018), six dominated coastal Massachusetts from December through March, including superstorm Nemo on 08–09 February 2013 (NCDC 2018; Table 4). For Nemo, two low-pressure systems with hurricane-force wind gusts merged off the New England coast. Significant pressure highs to the north of New England caused cold air to stall over the area. Nemo was the most severe winter storm to hit coastal Massachusetts since the "Great Blizzard" of 05–07 February 1978, the "Storm of the Century" on 12–15 March 1993, another superstorm on 06–08 January 1996, and the blizzard of 11–12 February 2006. Nemo also coincided with a new moon, which caused storm surges of 0.9–1.2 m inshore and waves of more than 9 m in height 24 km offshore. The mean wind direction backed from easterly (070°) on 08 February to the northerly (350°) on 09 February, which drove birds deep into Cape Cod Bay.

The other five ECWSs that dominated coastal Massachusetts between December 2012 and March 2013 occurred on 27 December, 31 January, 17 February, 07–08 March, and 21–22 March. Three of these five storms were categorized as strong ECWSs, although none had the geographical coverage, heavy snowfall, or sustained winds of Nemo. Prevailing winds toward the eastern shore of Cape Cod Bay occurred on approximately 85% of the days from January to March 2013, which aligns with the high number of birds recovered on bay-side rather than ocean-side beaches.

DISCUSSION

Change of Razorbill population

Recent increases in the number of Razorbills off Southern New England in winter have been attributed in part to an increase in population size (Veit & Guris 2008, Veit & Manne 2015). Robben *et al.* (2014) suggested that these changes also contributed to the Florida irruption described here.

A very small proportion (5%–6%) of the North American population of Razorbills breeds in the northeastern US: about 600 pairs in the Gulf of Maine (Nisbet *et al.* 2013) and 2400 pairs in the Bay of Fundy (A.W. Diamond unpubl. data). This contributes very little to the thousands of birds involved in winter sightings from the mid-1990s to the early 2010s off the US east coast (Brinkley 2013) or the Bay of Fundy (Huettmann *et al.* 2005). Most of the North

TABLE 9
Change in breeding populations (pairs) of Razorbills in Canada, showing 66% increase in colonies censused since 2000

Region	Chapdelaine *et al*. 2001	Latest	Year	% Change	Source[a]
Newfoundland	636	1383	2005–2013	+117	CWS unpubl. data (S. Wilhelm)
Labrador	11569	18460	2002–2010	+60	CWS unpubl. data
New Brunswick	895	2825	2016	+215	Ronconi & Wong 2003; A.W. Diamond unpubl. data
Quebec	18046	30052	2004–2013	+66.6	SCF unpubl. data (J.-F. Rail)
Total	**31146**	**52720**		**+69**	

[a] CWS = Canadian Wildlife Service; SCF = Service canadien de la faune

American population breeds in Canada, divided almost equally between the Gulf of St. Lawrence and the coast of Labrador; in the most recent published estimate, Chapdelaine *et al.* (2001) assessed the population at 38 000 breeding pairs of which 80% (31 146 pairs) were in these two areas. Most of the colonies included in Chapdelaine's assessment have since been re-counted by various groups, and here we provide an updated estimate of 52 720 pairs in those colonies (Table 9). This represents a 69% increase in numbers since the Chapdelaine *et al.* (2001) count. Thus, the breeding population has increased substantially during this century, but there is no evidence of a sudden increase in numbers immediately before the irruption into Florida; the 'slow' life-history of Razorbills makes such an abrupt increase unlikely.

Characteristics of the wrecks

The Florida wreck clearly arose from a classic irruption, or an excursion outside of the normal range that is usually caused by a food shortage. The Cape Cod wreck, by contrast, took place within the normal winter range and was evidently caused by protracted very strong onshore winds (Heubeck *et al.* 2011, Harris & Elkins 2013, Morley *et al.* 2016). In this case, the winds were exacerbated by the physical layout of Cape Cod acting as a trap once birds were blown into it Cape Code Bay (Proctor & Lynch 1993). There was no evidence in either wreck of oil contamination or disease, which can also contribute to mass mortality of seabirds.

In both wrecks, most birds were underweight and appear to have starved. Large auks need to eat at least 50% of their body weight in fish each day; if they cannot find this, they lose body weight, and if severe food shortage lasts for three to five days, they die of starvation (Piatt *et al.* 2020). The succession of severe ECWS that battered Cape Cod in late winter, particularly Nemo, would have disrupted feeding conditions for seabirds for days at a time. Stellwagen Bank, which is immediately north of Cape Cod Bay, is a rich feeding area for seabirds and other marine predators, and Razorbill numbers there peak in January (Pittman & Huettman 2006), perhaps associated with the abundance of sand lance or Atlantic herring *Clupea harengus* (Richardson *et al.* 2014). The succession of storms would likely have driven many birds from the Bank into Cape Cod Bay. The Florida wreck, on the other hand, did not have an obvious proximate cause of severe onshore winds, yet the immediate cause of mass mortalities was apparently exhaustion brought on by starvation; the question then becomes, what caused the starvation?

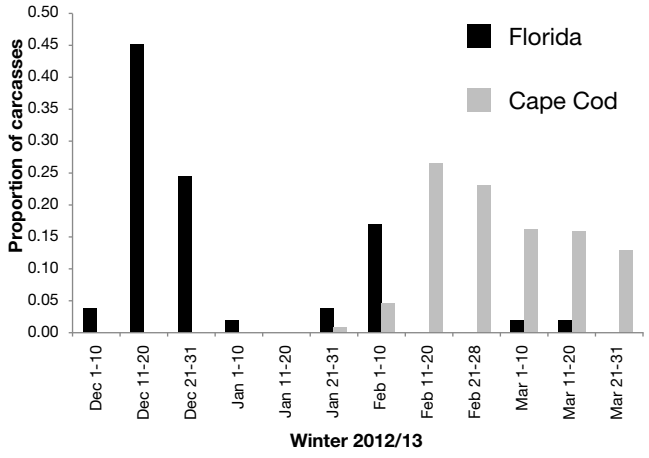

Fig. 8. Timing of Razorbill wrecks in Florida (n = 53) and Cape Cod (n = 264), by proportion of carcasses found per ~10-day period.

Causes of the wrecks

Both events followed a heat wave in the northwest Atlantic that has been described as "the largest, most intense warm event in the northwest Atlantic in the last 30 years" (Mills *et al.* 2013). It extended as far northeast as Iceland, deep into the northern Labrador Sea, and south to Cape Hatteras; throughout this area, SSTs were 1–3°C above normal. In the Gulf of Maine, this was equivalent to 3.5 standard deviations above the mean SST from 1982 to 2011. The cause of the heatwave has been attributed to an anomalous northward shift of the jet stream in winter 2012 (Chen *et al.* 2014). Effects ranged from increased melting of Greenland glaciers (Nghiem *et al.* 2012) to possibly affecting the trajectory of Hurricane Sandy (Greene *et al.* 2013). The area of ocean with abnormally high SST extended throughout the normal winter range of Razorbills (Gulf of Maine to Cape Hatteras: Fig. 1 in Chen *et al.* 2014). Anomalously high temperatures were particularly prominent in the Gulf of Maine and the Bay of Fundy, where Razorbills usually concentrate in winter (Huettmann *et al.* 2005, Clarke *et al.* 2010), and extended throughout the water column (Koopman *et al.* 2014).

Another possible factor in the Florida invasion was the presence of cooler water close to shore during winter 2012/13. A path for invading Razorbills could follow cooler water after an initial displacement further north by anomalously warm waters with low food availability. The patterns of cooler water close to shore and related SST anomalies may be connected to Gulf Stream separation, which is when warm-water eddies detach from the Gulf Stream and reduce the strength and connectivity of this powerful current (Andres 2016, Schoonover *et al.* 2017).

Extreme SST anomalies lead to seabird wrecks through their effects on ocean productivity (Jones *et al.* 2018) and responses of forage fish to temperature (Piatt *et al.* 2020). Such wrecks can occur in the absence of storms driving birds ashore, as for example in the massive mortality of Common Murres on the US west coast in 2014–2016 (Piatt *et al.* 2020), and operate through three fundamental processes: (i) reduced productivity of the phytoplankton at the base of the marine food-web; (ii) physiological effects on fish prey, which are ectotherms and are subject to increased metabolic demands because higher water temperatures increase their metabolic rate, diverting energy from growth and fat deposition, which in turn results in smaller and less nutritious fish (Piatt *et al.* 2020); and (iii) improved escape ability of fish, since swimming speed increases with temperature in ectotherms but not endotherms (temperature-dependent predation success; Cairns *et al.* 2008, Dell *et al.* 2014, Grady *et al.* 2019). Fundamental to these processes is the "metabolic asymmetry" between ectotherm prey, which respond directly to increased temperature with increased metabolism, and endotherm prey (in this case seabirds), which maintain their metabolic rate over a range of environmental temperatures (Dell *et al.* 2014). Oceanographic changes in the Gulf of Maine in 2012 reduced the abundance of the high-lipid copepod *Calanus finmarchicus*, which is an important food for forage fish (Johnson *et al.* 2013). Forage fish would therefore have been squeezed between declining quality of food and increased

metabolic demand from higher temperatures, likely resulting in lower survival and poorer body condition. This is the "ectothermic vise" of Piatt *et al.* (2020), in which ectothermic prey are trapped between rising energy demands and decreased food supply, both due to warmer temperatures.

Although the Florida and Cape Cod events were widely separated in space, they overlapped somewhat in time, as illustrated in the distribution of beached birds by 10-day periods (Fig. 8). We expected to confirm that the incursion into Florida was unprecedented, but eBird data, records of the Florida Ornithological Society Records Committee, and a previously-overlooked Florida band recovery in 2003 from a bird banded in the Bay of Fundy, indicated that the 2012/13 event may have been indistinctly foreshadowed in the early 2000s by a slight increase of records in Florida. Veit & Guris (2008) had also drawn attention to increasing numbers of birds off Southern New England coasts in the early 2000s. They proposed either a southward shift in range or an increase in the population (or possibly both) as driving this trend. That fewer Razorbills, as reflected in both eBird and band recoveries, were involved in the 2003 event is probably due in part to the smaller population size at that time. As indicated above, the Razorbill population in eastern North America has certainly been increasing in recent decades, but the increase has been steady, not abrupt enough to account for a dramatic southward shift at one time.

Other cold-water species were also recorded in larger numbers than usual off the southern US coast in the same winter, notably White-winged Scoter *Melanitta deglandi*, Black Scoter *M. americana*, Red-throated Loon *Gavia stellata*, and alcids such as Little Auk and Thick-billed Murre (BirdCast 2012). Thus, the phenomenon calls for explanations beyond the specifics of Razorbill biology; clearly there was a major bottom-up shift in the marine ecosystem involving a variety of normally cold-water marine birds.

Effects of the wrecks

Robben *et al.* (2014) proposed that the Gulf of Maine/Bay of Fundy Razorbill population (some 7000 individual birds, including pre-breeders) was the major source of displaced birds, and that this region "probably suffered a large loss of population." Eighty-six percent of the Razorbills breeding in this region do so on MSI, where numbers increased by 40% (from 1772 pairs to 2550) between 2012 and 2015 (A.W. Diamond, unpubl. data). Most of the birds that died in Florida were juveniles, suggesting that mortality preferentially affected young birds. A survival analysis from MSI band resighting data through 2016 using program MARK showed a pronounced dip in survival of juveniles but not adults in 2013 following the winter under discussion. This confirms this suggestion, at least for the MSI colony (Fig. 9). The mortality of adult Razorbills at Cape Cod later that winter, which involved more than twice as many beached birds as found in Florida, has also not yet been reflected in lower breeding numbers (as described above) and did not affect adult survival at MSI (Fig. 9). This suggests that the local breeding population was not the only contributor to this wreck.

Not all Razorbills that usually winter in the Gulf of Maine and Bay of Fundy are local breeders—indeed most cannot be (Clarke *et al.* 2010)—but no other Razorbill colonies are monitored as intensively as MSI, so we cannot assess effects on other colonies. That four of the six band recoveries in Florida were from colonies in the Gulf of Maine supports our suggestion that this population dominated the irruption, but other colonies certainly contributed (two were banded in Quebec). The lack of band recoveries among the 264 victims of the Cape Cod wreck (and 78 more birds during the following four winters) might indicate a more northern origin for these birds. Colonies further north are much larger, so a smaller proportion of birds is banded; banding effort has also been low since 2006 (A.W. Diamond unpubl. data). Preliminary results of tracking studies confirm that some Newfoundland breeders do over-winter in the Cape Cod area and as far south as North Carolina (S.I. Wilhelm unpubl. data, M. Dodds unpubl. data).

The preponderance of adults among the Razorbill carcasses at Cape Cod indicates a different distribution of age-classes just before the breeding season, compared to those earlier in the winter in Florida. Atlantic Puffins similarly would have been gathered in the rich feeding grounds of Massachusetts Bay prior to dispersing to breeding colonies. Most puffin carcasses (70%) were adults, and many had moderately or extremely worn flight feathers, a condition that would have both hindered diving ability and compromised their ability to escape the storms.

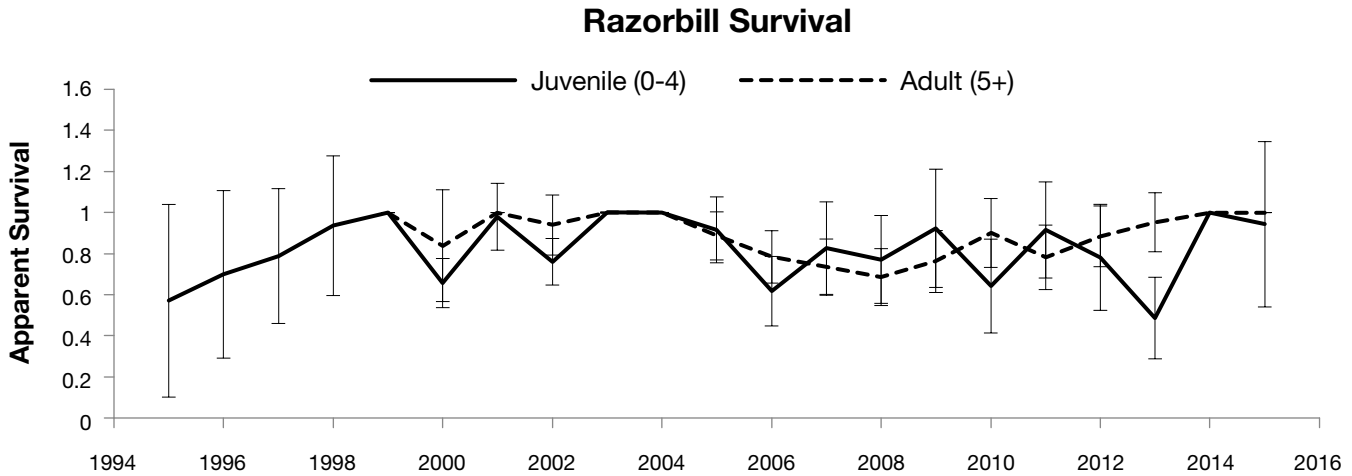

Fig. 9. Apparent survival (mean ± 95% confidence interval) of adult (> 4 years old) and juvenile (1–4 years old) Razorbills at Machias Seal Island, New Brunswick, Canada, from program MARK.

Singularity of the wrecks

Neither the Florida nor the Cape Cod wreck has been repeated in subsequent winters, despite the persistence of both marine heatwaves in the region and ECWSs at Cape Cod. Summer temperatures in the Gulf of Maine were almost as hot in 2016 as in 2012, so if oceanographic change drove the two wrecks in winter 2012/13, similar phenomena would be expected in winter 2016/17. Examination of eBird observations, beach surveys, and band recoveries was used to test of this hypothesis; none of these sources of data showed comparable increases in numbers of Razorbills or Atlantic Puffins in subsequent winters. The only clear difference between winter 2012/13 and later years is the devastation caused by Hurricane Sandy in late fall 2012. Sandy caused enormous damage to the northeastern US during and following landfall in New Jersey on 29 October, including a "catastrophic storm surge into the New York and New Jersey coastlines" (Blake *et al.* 2013). This, in addition to the enormous waves (10 m) and extreme winds (39 kt or 72 km/h according to Miles *et al.* 2015; 70 kt or 130 km/h at landfall in Jew Jersey according to Blake *et al.* 2013), would have stirred up sediment over large areas of the continental shelf, further exacerbating the difficulty of feeding underwater. We suggest that the disruptive effects of Sandy on the coastal shelf ecosystem (Trembanis *et al.* 2013, Warner *et al.* 2017) persisted well into the period that Razorbills would normally expect to find food there. The extreme turbidity (Miles *et al.* 2015) caused by such an exceptional storm would displace fish from their habitat (Secor *et al.* 2018) and impair the foraging success of any visual forager such as pursuit-diving seabirds, leaving the birds no option but to continue further south in search of clearer water. The high energy demands for growth and poorly developed foraging skills of inexperienced juvenile Razorbills might account for their higher representation in mortalities in Florida.

Mortality in the Florida wreck was evidently high, especially of juveniles, but far more Razorbills were beached in the Cape Cod wreck, where mostly adults were involved. The greater intensity of the local beached-seabird survey on outer Cape Cod during winter 2012/13 compared to SEANET surveys is valuable, since our understanding of the magnitude of this seabird "wreck" was enhanced by this local survey; most seabird "wrecks" are local or, at most, regional in scope. National results from SEANET/WHER (Fig. 5) suggest that the pronounced winter mortality of Razorbills, Atlantic Puffins, and several other seabirds in the northeastern US probably extended at least from Georgia to southern Maine. Additional local intensive efforts from this region, i.e., sampling locations more than only once a month (*contra* Harris *et al.* 2006), would have augmented our knowledge of the magnitude of seabird mortality from the six ECWS in this region during winter 2012/13.

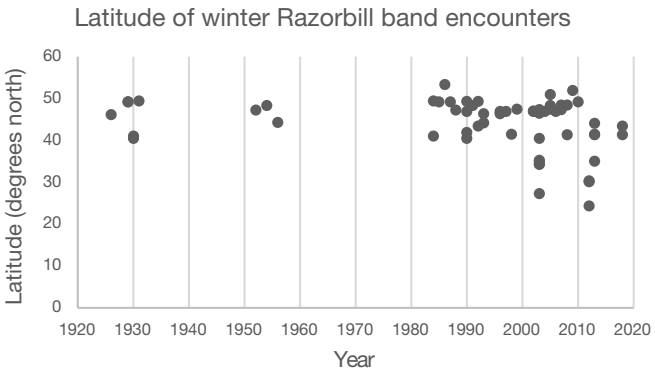

Fig. 10. Winter encounters of Razorbills banded in North America by latitude and by year, using all encounters up to 20 July 2018. Encounters south of 40°N are confined to 2003 and 2012/13.

Sources of data

Citizen-science programs such as eBird, beached-bird surveys, and, to a limited extent, CBCs contributed to characterizing these events. The beached-bird surveys are intended to provide a baseline of seabird mortality rather than to track MMEs (for more information about the SEANET program, please visit https://www.anecdata.org/projects/view/462), but they did reveal considerably higher mortality of Razorbills in the winter 2012/13 especially at Cape Cod (Fig. 4). The full extent of the Cape Cod event was exposed by intensive beach surveys conducted by DBM, a professional ornithologist who lived locally and devoted much more effort than could be expected from a citizen-science volunteer.

Band recovery data more generally suggest that Razorbills have been moving further south in winter since the early 2000s. Of 55 recoveries in winter (November–March) for all years through to December 2016, 30 (55%) took place in Newfoundland & Labrador during early and mid-winter (where there is a legal murre hunt that takes some Razorbills), with smaller numbers between Labrador and New York later in the winter; this pattern has persisted through most recent years. Plotting the latitude of all winter recoveries against year (Fig. 10) showed an increase in recoveries in southern states after 2000; more precisely, in the winters of 2002/03 and again in 2012/13. Notably, there were no recoveries south of 40°N until 2003, when there were four (two adults from New Brunswick to North Carolina, one three-year-old from Newfoundland & Labrador to North Carolina, and one juvenile from New Brunswick to Florida); this is one more than in winter 2012/13. Band recoveries, therefore, suggest that the southward irruption in 2012/13 had been foreshadowed ten years previously but went unnoticed, perhaps (in part at least) because eBird technology had not yet become widely adopted.

Atlantic context

The Cape Cod wreck overlapped in time with the largest wreck of Atlantic Puffins ever recorded at that time: over 3 000 birds in eastern Scotland and northeast England (Harris & Elkins 2013, though this was eclipsed in 2014 (Morley *et al.* 2016)). Victims were emaciated, and they evidently starved in conditions that disrupted feeding behavior, including protracted strong winds, unusually cold temperatures (below freezing), and wave heights of 5–8 m that challenged the birds' thermoregulation and disrupted normal feeding behavior. The UK wreck also accounted for several hundred Razorbills and Common Murres. Thus, the MMEs in eastern North America were evidently part of an extremely challenging winter for auks on both sides of the North Atlantic.

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REFERENCES

ANDRES, M. 2016. On the recent destabilization of the Gulf Stream path downstream of Cape Hatteras. *Geophysical Research Letters* 43: 9836–9842. doi:10.1002/2016GL069966

ANKER-NILSSEN, T., HARRIS, M.P., KLEVEN, O. & LANGSET, M. 2017. Status, origin, and population level impacts of Atlantic Puffins killed in a mass mortality event in southwest Norway early 2016. *Seabird* 30: 1–14.

ARBIB, R.S., JR. 1981. The Christmas Bird Count: Constructing an "ideal model". *Studies in Avian Biology* 6: 30–33.

BIRDCAST 2012. *Forecasts: Gulf of Maine, meet Gulf of Mexico: Razorbills (and others) invade Florida and the Gulf of Mexico.* Ithaca, USA: Cornell Lab of Ornithology. [Accessed online at http://birdcast.info/forecast/razorbills-invade-florida/ in Sep 2013.]

BLAKE, E.S., KIMBERLAIN, T.B., BERG, R.J., CANGIALOSI, J.P. & BEVEN II, J.L. 2013. *Tropical Cyclone Report: Hurricane Sandy, 22–29 October 2012.* AL182012. Silver Spring, USA: United States National Oceanic and Atmospheric Administration, National Weather Service, National Hurricane Center.

BRINKLEY, E.S. 2013. The changing seasons: Strangers in a strange land. *North American Birds* 67: 216–228.

CAIRNS, D.K., GASTON, A.J. & HUETTMANN, F. 2008. Endothermy, ectothermy and the global structure of marine vertebrate communities. *Marine Ecology Progress Series* 356: 239–250.

CAMPHUYSEN, C.J. & HEUBECK, M. 2001. Marine oil pollution and beached bird surveys: The development of a sensitive monitoring instrument. *Environmental Pollution* 112: 443–461.

CHAPDELAINE, G., DIAMOND, A.W., ELLIOT, R.D., ROBERTSON, G.J. 2001. *Status and population trends of the Razorbill in eastern North America.* Occasional Paper No. 105. Ottawa, Canada: Minister of Public Works and Government Services Canada, Minister of the Environment, Canadian Wildlife Service.

CHEN, K., GAWARKIEWICZ, G.G., LENTZ, S.J. & BANE, J.M. 2014. Diagnosing the warming of the Northeastern US coastal ocean in 2012: A linkage between the atmospheric jet stream variability and ocean response. *Journal of Geophysical Research: Oceans* 119: 218–227.

CLARKE, T.C.R., DIAMOND, A.W. & CHARDINE, J.W. 2010. Origin of Canadian Razorbills (*Alca torda*) wintering in the outer Bay of Fundy confirmed by radio-tracking. *Waterbirds* 33: 541–545.

COURCHESNE, S.J. 2015. *SEANET blog.* February 2015. North Grafton, USA: SEANET, Cummings School of Veterinary Medicine, Tufts University. [Accessed online at https://seanetters.wordpress.com/2015/02/ on 03 Mar 2016.]

COURTER, J.R., JOHNSON, R.J., STUYCK, C.M., LANG, B.A. & KAISER, E.W. 2013. Weekend bias in Citizen Science data reporting: Implications for phenology studies. *International Journal of Biometeorology* 57: 715–720. doi:10.1007/s00484-012-0598-7

CROXALL, J.P., BUTCHART, S.H.M., LASCELLES, B. & STATTERSFIELD, A.J. 2012. Seabird conservation status, threats, and priority actions: A global assessment. *Bird Conservation International* 22: 1–34.

DAVIS, R. 1994. Southern Atlantic Coast Region. *National Audubon Society Field Notes* 48: 196–199.

DELL, A.I., PAWAR, S. & SAVAGE, V.M. 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology* 83: 70–84. doi:10.1111/1365-2656.12081

DUFF, J.P., HARRIS, M.P. & TURNER, D.M. 2013. Mass mortality of puffins, linked to starvation. *Veterinary Record* 173: 224. doi:10.1136/vr.f5407

EBIRD 2018. *eBird: An online database of bird distribution and abundance [web application].* Ithaca, USA: eBird, Cornell Lab of Ornithology. [Accessed online at http://www.ebird.org in Aug 2018.]

FEY, S.B., SIEPIELSKI, S.M., NUSSLÉ, S., ET AL. 2015. Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proceedings of the National Academy of Sciences* 112: 1083–1088.

GASTON, A.J. & JONES, I.L. 1998. *The Auks: Alcidae.* Oxford, UK: Oxford University Press.

GJERDRUM, C., FIFIELD, D.A. & WILHELM, S.I. 2012. *Eastern Canada Seabirds at Sea (ECSAS) standardized protocol for pelagic seabird surveys from moving and stationary platforms.* Canadian Wildlife Service Technical Report Series, no. 515. Ottawa, Canada: Environment Canada, Canadian Wildlife Service, Atlantic Region.

GRADY, J.M., MAITNER, B.S., WINTER, A.S., ET AL. 2019. Metabolic asymmetry and the global diversity of marine predators. *Science* 363: eaat4220. doi:10.1126/science.aat4220

GREENE, C.H., FRANCIS, J.A. & MONGER, B.C. 2013. Superstorm Sandy: A series of unfortunate events? *Oceanography* 26: 8–9.

GREENLAW, J.S., PRANTY, B. & BOWMAN, R. 2014. *The Robertson and Woolfenden Florida Bird Species: An Annotated List.* Special Publication no. 8. Gainesville, USA: Florida Ornithological Society.

HARRIS, M.P. 2014. Aging Atlantic Puffins *Fratercula arctica* in summer and winter. *Seabird* 27: 22–40.

HARRIS, M.P. & ELKINS, N. 2013. An unprecedented wreck of Puffins in eastern Scotland in March and April 2013. *Scottish Birds* 33: 157–159.

HARRIS, M.P. & YULE, R.F. 1977. The moult of the Puffin *Fratercula arctica*. *Ibis* 119: 535–541.

HARRIS, M.P., WANLESS, S. & JENSEN, J.-K. 2014. When are Atlantic Puffins *Fratercula arctica* in the North Sea and around the Faeroes flightless? *Bird Study* 61: 182–192.

HARRIS, R.J., TSENG, F.S., POKRAS, M.A., ET AL. 2006. Beached bird surveys in Massachusetts: The Seabird Ecological Assessment Network (SEANET). *Marine Ornithology* 34: 115–122.

HEUBECK, M., AARVAK, T., ISAKSEN, K., JOENSEN, A., PETERSEN, I.K. & ANKER-NILSSEN, T. 2011. Mass mortality of adult Razorbills *Alca torda* in the Skagerrak and North Sea area, autumn 2007. *Seabird* 24: 11–32.

HILL, C., BEATON, G., CLICK, J., ET AL. 2014. 2013 Annual Report of the South Carolina Bird Records Committee. *The Chat* 78: 1–7.

HILL, C., BEATON, G., CLICK, J., ET AL. 2016. 2015 Annual Report of the South Carolina Bird Records Committee. *The Chat* 80: 18–25.

HIRSCH, M.E., DEGAETANO, A.T. & COLUCCI, S.J. 2001. An east coast winter storm climatology. *Journal of Climate* 14: 882–899.

HUETTMANN, F., DIAMOND, A.W., DALZELL, B. & MACINTOSH, K. 2005. Winter distribution, ecology and movements of Razorbills *Alca torda* and other auks in the outer Bay of Fundy, Atlantic Canada. *Marine Ornithology* 33: 161–171.

JOHNSON, C., HARRISON, G., CASAULT, B., SPRY, J., LI, W. & HEAD, E. 2013. *Optical, chemical, and biological oceanographic conditions on the Scotian Shelf and in the eastern Gulf of Maine in 2012.* Research document 2013/070. Ottawa, Canada: Fisheries and Oceans Canada, Canadian Science Advisory Secretariat, Maritimes Region.

JONES, T., PARRISH, J.K., PETERSON, W.T., ET AL. 2018. Massive mortality of a planktivorous seabird in response to a marine heatwave. *Geophysical Research Letters* 45: 3193–3202.

KOOPMAN, H.N., WESTGATE, A.J., SIDERS, Z.A. & CAHOON, L.B. 2014. Rapid subsurface ocean warming in the Bay of Fundy as measured by free-swimming basking sharks. *Oceanography* 27: 14–16. doi:10.5670/oceanog.2014.32

KRATTER, A.W. 2018. Twenty-seventh report of the Florida Ornithological Society Records Committee: 2016–2017. *Florida Field Naturalist* 46: 96–117.

KRATTER, A.W. & SMALL, S. 2007. First record of Northern Fulmar (*Fulmarus glacialis*) for Florida, and notes on other North Atlantic seabird specimen records in 2004–2005. *Florida Field Naturalist* 35: 22–25.

LEBARON, G. 2007. *Audubon's Christmas Bird Count from 19th century conservation action to 21st century citizen science*. Proceedings of the Citizen Science Toolkit Conference. Ithaca, USA: Cornell Lab of Ornithology.

LINK, W.A., SAUER, J.R. & NIVEN, D.K. 2006. A hierarchical model for regional analysis of population change using Christmas Bird Count data, with application to the American Black Duck. *The Condor* 108: 13–24.

LINNEBJERG, J.F. 2012. *Foraging ecology of breeding seabirds in Greenland.* PhD dissertation. Aarhus, Denmark: Aarhus University.

LUCAS, Z., HORN, A. & FREEDMAN, B. 2012. Beached bird surveys on Sable Island, Nova Scotia, 1993 to 2009, show a decline in the incidence of oiling. *Proceedings of the Nova Scotian Institute of Science* 47: 91–129.

MILES, T., SEROKA, G., KOHUT, J., SCHOFIELD, O. & GLENN, S. 2015. Glider observations and modeling of sediment transport in Hurricane Sandy. *Journal of Geophysical Research: Oceans* 120: 1771–1791. doi:10.1002/2014JC010474

MILLS, K.E., PERSHING, A.J., BROWN, C.J., ET AL. 2013. Fisheries management in a changing climate: Lessons from the 2012 ocean heat wave in the Northwest Atlantic. *Oceanography* 26: 191–195.

MONTEVECCHI, B., CHARDINE, J., RAIL, J.-F., ET AL. 2013. Extreme event in a changing ocean climate: Warm-water perturbation of 2012 influences breeding gannets and other marine animals in the Northwest Atlantic and Gulf of St. Lawrence. *The Osprey* 44: 14–19.

MORLEY, T.I., FAYET, A.L., JESSOP, H., ET AL. 2016. The seabird wreck in the Bay of Biscay and South-Western Approaches in 2014: A review of reported mortality. *Seabird* 29: 22–38.

NATIONAL CENTERS FOR ENVIRONMENTAL INFORMATION (NCEI) 2018a. *Storm Events Database.* Barnstable County, USA: NCEI. [Accessed online at https://www.ncdc.noaa.gov/stormevents/ on 10 Oct 2018.]

NATIONAL CENTERS FOR ENVIRONMENTAL INFORMATION (NCEI) 2018b. *Local Climatological Data: Chatham Municipal Airport, MA.* Silver Spring, USA: NOAA, NCEI. [Accessed online at https://www.ncdc.noaa.gov/cdo-web/datatools/lcd on 10 Oct 2018.]

NATIONAL CLIMATIC DATA CENTER (NCDC) 2018. *National Climatic Data Center website.* Asheville, USA: NOAA. [Accessed online at www.ncdc.noaa.gov in Aug 2018.]

NEVINS, H.M. & CARTER, H.R. 2003. Age and sex of Common Murres *Uria aalge* recovered during the 1997–98 Point Reyes tarball incidents in central California. *Marine Ornithology* 31: 51–58.

NEWTON, I. & LITTLE, B. 2009. Assessment of wind-farm and other bird casualties from carcasses found on a Northumbrian beach over an 11-year period. *Bird Study* 56: 158–167.

NGHIEM, S.V., HALL, D.K., MOTE, T.L. ET AL. 2012. The Extreme Melt Across the Greenland Ice Sheet in 2012. *Geophysical Research Letters* 39: L20502. doi:10.1029/2012GL053611

NISBET, I.C.T., VEIT, R.R., AUER, S.A. & WHITE, T.P. 2013. *Marine Birds of the Eastern United States and the Bay of Fundy.* Nuttall Ornithological Monographs, vol. 29. Cambridge, USA: Nuttall Ornithological Club.

NOAA 2013a. *Hurricane Sandy (Atlantic Ocean).* Silver Spring, USA: National Weather Service, NOAA. [Available online at https://www.nasa.gov/mission_pages/hurricanes/archives/2012/h2012_Sandy.html.]

NOAA 2013b. *Service Assessment: Hurricane/Post-Tropical Cyclone Sandy, October 22–29, 2012.* Silver Spring, USA: National Weather Service, NOAA.

NORTHEAST REGIONAL CLIMATE CENTER (NRCC) 2020. *Northeast Regional Climate Center website.* Ithaca, USA: Cornell University. [Accessed online at http://www.nrcc.cornell.edu/ in Aug 2018.]

PIATT, J.F., PARRISH, J.K., RENNER, H.N., ET AL. 2020. Extreme mortality and reproductive failure of common murres resulting from the northeast Pacific marine heatwave of 2014–2016. *PLoS One* 15: e0226087. doi:10.1371/journal.pone.0226087

PITTMAN, S. & HUETTMANN, F. 2006. Seabird Distribution and Diversity. In BATTISTA, T., CLARK, R. & PITTMAN, S. (Eds). *An Ecological Characterization of the Stellwagen Bank National Marine Sanctuary Region: Oceanographic, Biogeographic, and Contaminants Assessment.* NOAA Technical Memorandum NCCOS 45. Silver Spring, USA: Center for Coastal Monitoring and Assessment, NOAA.

PRANTY, B. 2013. *113th CBC Florida Regional Summary.* New York, USA: National Audubon Society.

PROCTOR, N.S. & LYNCH, P.J. 1993. *Manual of Ornithology: Avian Structure & Function.* New Haven, USA: Yale University Press.

PYLE, P. 2009. Age determination and molt strategies in North American alcids. *Marine Ornithology* 37: 219–225.

RICHARDSON, D.E., PALMER, M.C. & SMITH, B.E. 2014. The influence of forage fish abundance on the aggregation of Gulf of Maine Atlantic cod (*Gadus morhua*) and their catchability in the fishery. *Canadian Journal of Fisheries and Aquatic Sciences* 71: 1349–1362. doi:10.1139/cjfas-2013-0489

ROBBEN, T., BROKER, S. & ROBBEN, S.N. 2014. Oceans changing: Do seabirds tell us something about ocean changes? *Bird Observer* 42: 273–284.

RONCONI, R.A. & WONG, S.N.P. 2003. Estimates of changes in seabird numbers in the Grand Manan archipelago, New Brunswick, Canada. *Waterbirds* 26: 462–472.

SATELLITE APPLICATIONS AND RESEARCH (STAR) 2016. *NOAA STAR Ocean Color Science Team.* College Park, USA: Center for Satellite Applications and Research, Center for Weather and Climate Prediction, NOAA. [Accessed online at http://www.star.nesdis.noaa.gov/sod/mecb/color/index.php in Sep 2016.]

SCHOONOVER, J., DEWAR, W.K., WIENDERS, N. & DEREMBLE, B. 2017. Local sensitivities of the Gulf Stream separation. *Journal of Physical Oceanography* 47: 353–373. doi:10.1175/JPO-D-16-0195.1

SEABIRD ECOLOGICAL ASSESSMENT NETWORK (SEANET) 2010. *SEANET protocol: A guide for SEANET volunteers.* Version 3.1. North Grafton, USA: Tufts Cummings School of Veterinary Medicine. [Accessed online at http://www.tufts.edu/vet/seanet/ on 10 Apr 2014.]

SECOR, D.H., ZHANG, F., O'BRIEN, M.H.P. & LI, M. 2018. Ocean destratification and fish evacuation caused by a Mid-Atlantic tropical storm. *ICES Journal of Marine Science.* 76: 573–584. doi:10.1093/icesjms/fsx241

SOUTHERN, J. 2017. Briefs for the files. *The Chat* 81: 38–59.

STEVENSON, H.M. & ANDERSON, B.H. 1994. *The Birdlife of Florida.* Gainesville, USA: University Press of Florida.

SULLIVAN, B.L., AYCRIGG, J.L., BARRY, J.H., ET AL. 2014. The eBird enterprise: An integrated approach to development and application of citizen science. *Biological Conservation* 169: 31–40.

TREMBANIS, A., DUVAL, C., BEAUDOUIN, J., SCHMIDT, V., MILLER, D. & MAYER, L. 2013. A detailed seabed signature from Hurricane Sandy revealed in bedforms and scour. *Geochemistry, Geophysics, Geosystems* 14: 4334–4340. doi:10.1002/ggge.20260

UNDERWOOD, L.A. & STOWE, T.J. 1984. Massive wreck of seabirds in eastern Britain, 1983. *Bird Study* 31: 79–88.

VAN PELT, T.I. & PIATT, J.F. 1995. Deposition and persistence of beachcast seabird carcasses. *Marine Pollution Bulletin* 30: 794–802.

VEIT, R.R. & GURIS, P.A. 2008. Recent increases in alcid abundance in the New York Bight and New England waters. *New Jersey Birds* 34: 83–87.

VEIT, R.R. & MANNE, L.L. 2015. Climate and changing winter distribution of alcids in the Northwest Atlantic. *Frontiers in Ecology and Evolution* 3: 38. doi:10.3389/fevo.2015.00038

WARNER, J.C., SCHWAB, W.C., LIST, J.H., SAFAK, I., LISTE, M. & BALDWIN, W. 2017. Inner-shelf ocean dynamics and seafloor morphologic changes during Hurricane Sandy. *Continental Shelf Research* 138: 1–18.

WEATHER PREDICTION CENTER 2018. *Daily Weather Maps.* College Park, USA: National Centers for Environmental Prediction, NOAA. [Accessed online at https://www.wpc.ncep.noaa.gov/dailywxmap/index.html in Aug 2018.]

WEATHER UNDERGROUND 2018. *Provincetown, MA Weather Conditions.* Brookhaven, USA: The Weather Company. [Accessed online at www.wunderground.com/weather/us/ma/provincetown in Aug 2018.]

ŽYDELIS, R., DAGYS, M. & VAITKUS, G. 2006. Beached bird surveys in Lithuania reflect marine oil pollution and bird mortality in fishing nets. *Marine Ornithology* 34: 161–166.