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A PELAGIC OUTBREAK OF AVIAN CHOLERA IN NORTH AMERICAN GULLS: SCAVENGING AS A PRIMARY MECHANISM FOR TRANSMISSION?

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ABSTRACT: Avian cholera, caused by the bacterium *Pasteurella multocida*, is an endemic disease globally, often causing annual epizootics in North American wild bird populations with thousands of mortalities. From December 2006 to March 2007, an avian cholera outbreak caused mortality in marine birds off the coast of Atlantic Canada, largely centered 300–400 km off the coast of the island of Newfoundland. Scavenging gulls (*Larus* spp.) were the primary species detected; however, mortality was also identified in Black-legged Kittiwakes (*Rissa tridactyla*) and one Common Raven (*Corvus corax*), a nonmarine species. The most common gross necropsy findings in the birds with confirmed avian cholera were acute fibrinous and necrotizing lesions affecting the spleen, air sacs, and pericardium, and nonspecific hepatomegaly and splenomegaly. The etiologic agent, *P. multocida* serotype 1, was recovered from 77 of 136 carcasses examined, and confirmed or probable avian cholera was diagnosed in 85 cases. Mortality observed in scavenging gull species was disproportionately high relative to their abundance, particularly when compared to nonscavenging species. The presence of feather shafts in the ventricular lumen of the majority of larid carcasses diagnosed with avian cholera suggests scavenging of birds that died from avian cholera as a major mode of transmission. This documentation of an outbreak of avian cholera in a North American pelagic environment affecting primarily scavenging gulls indicates that offshore marine environments may be a component of avian cholera dynamics.

Key words: Atlantic Canada, avian cholera, gulls, Laridae, Newfoundland, *Pasteurella multocida*, pelagic, scavenging.

INTRODUCTION

Avian cholera is an infectious disease of birds caused by the bacterium *Pasteurella multocida*. The disease has been reported in a wide variety of birds and mammals globally (Blackburn et al. 1975; Brogden and Rhoades 1983; Botzler 1991); however, it primarily affects densely aggregating waterfowl species associated with freshwater wetlands in North

America (Botzler 1991; Samuel et al. 2007). Recent reports indicate that avian cholera has caused substantial mortality in Snow Geese (*Chen caerulescens*), and has become endemic in Common Eider (*Somateria mollissima*) populations in northern Canada (Samuel et al. 2007; Descamps et al. 2012). Outbreaks have occurred in every month (Friend 1987; Wobeser 1992; Samuel et al. 2005, 2007) and in all four migratory flyways of North America:

Pacific, Central, Mississippi, and Atlantic (Wobeser 1997). The epidemiology of avian cholera in the marine environment is, however, unclear. Avian cholera has affected several species of offshore seabird breeding colonies, including Amsterdam Albatross (*Diomedea amsterdamensis*) and Yellow-nosed Albatross (*Thalassarche chlororhynchos*; Weimerskirch 2004), Cape Cormorants (*Phalacrocorax capensis*; Waller and Underhill 2007), Common Murres (*Uria aalga*; Osterblom et al. 2004), Adelie Penguins (*Pygoscelis adeliae*), Skuas (*Stercorarius* spp.), Kelp Gulls (*Larus dominicanus*; Leotta et al. 2006), and one Southern Giant Petrel (*Macronectes giganteus*; Leotta et al. 2003). Marine birds are also affected outside the breeding season, but this is infrequent (Christensen et al. 1997; Bodenstein et al. 2015).

Outbreak dynamics are driven by carrier birds and the environment (Botzler 1991). There is evidence that some apparently healthy waterfowl species act as carriers and may play an important role in initiating outbreaks, and wetlands or shallow water environments are important for pathogen transmission and maintenance during an outbreak (Botzler 1991; Samuel et al. 2004, 2005). Following introduction of *P. multocida*, transmission can occur by direct bird-to-bird contact, consumption of contaminated water or food, or inhalation of bacteria-laden aerosols (Simensen and Olson 1980; Botzler 1991; Wobeser 1992). Scavenging of infected carcasses may be another important route of transmission, as sporadic mortality in avian scavenging species, including terrestrial (e.g., crows) and marine species (e.g., gulls), has been observed during outbreaks (Hindman et al. 1997; Friend 1999).

The island of Newfoundland is located on the easternmost edge of North America. Because of the cold, nutrient-rich waters surrounding the island, Newfoundland is an internationally important breeding location for seabirds, particularly the family Alcidae (hereafter alcids) (Cairns et al. 1989). Additionally, it supports a large and diverse assemblage of wintering seabirds (Lock et al. 1994), including seaducks (Anatidae, subfam-

ily Merginae) and a diversity of gulls (*Larus* spp.). Large densities of gulls can be associated with offshore oil platforms (Weise et al. 2001), fishing activity along the Grand Banks, and landfill sites in coastal communities during winter months (November–April).

We describe an outbreak of avian cholera that occurred December 2006–March 2007 in the pelagic environment, 300–400 km off the coast of Newfoundland, with subsequent spread to inshore locations of Atlantic Canada. The outbreak affected seven species of overwintering gulls, including an endangered Ivory Gull (*Pagophila eburnea*), and one raven (*Corvus corax*). *Pasteurella multocida* was recovered from 77 of 136 carcasses, and confirmed and probable avian cholera were diagnosed in 85 scavenging birds based on postmortem findings. Despite the large number of nonbreeding seabirds using the area, the outbreak was limited to scavenging species, suggesting an outbreak sustained by scavenging rather than a bacteria-laden environment, as in classical descriptions of avian cholera.

MATERIALS AND METHODS

Surveillance and sample collection

In mid-January 2007, the national wildlife disease scanning surveillance program of the Canadian Wildlife Health Cooperative (CWHC) identified an index case of avian cholera as the cause of seabird mortality observed by workers on vessels and oil platforms on the Grand Banks of Newfoundland and Labrador, Canada. To investigate the extent of the problem, an enhanced surveillance program was initiated by Environment and Climate Change Canada. Carcasses were opportunistically collected directly from offshore oil platforms, offshore supply vessels, and Canadian Coast Guard vessels off Atlantic Canada when marine workers had the means to handle and transport carcasses safely. Because of the large concentrations of gulls wintering in the City of St. John's, Newfoundland, and the city's location at the eastern tip of Newfoundland, systematic surveillance of four gull roosting and feeding areas was conducted in the city. Furthermore, duck populations were monitored at the two main ice-free ponds in the city. Carcasses reported by the public from additional locations in St. John's and other Atlantic Canadian provinces were collected opportunistically. Following col-

lection offshore, carcasses were kept cool (4–8 C) until vessels arrived at port. Carcasses were subsequently transported to Newfoundland and Labrador Forestry and Agrifoods Agency or the CWHC, and upon receipt, were stored at 4 C until necropsy, which occurred within 7 d.

Postmortem examination

Partial necropsies were completed at the Newfoundland and Labrador Forestry and Agrifoods Agency and comprehensive necropsies were done at the CWHC, Atlantic Region, Atlantic Veterinary College, University of Prince Edward Island, Prince Edward Island, Canada. Gross necropsy examinations included determination of species, age, and sex. Birds were categorized into good, moderate, or poor physical condition based on a qualitative assessment combining information from body mass and visual inspection of pectoral muscle mass and subcutaneous and internal adipose tissue stores. Samples for bacteriology were collected from all carcasses submitted individually, and from mildly to markedly decomposed carcasses in multiple specimen submissions. Only carcasses submitted individually and well-preserved carcasses from multiple specimen submissions were selected for histology. Tissues collected for microscopic examination included brain, heart, lung, air sacs, proventriculus, ventriculus, small intestine, large intestine, liver, pancreas, kidney, gonad, and any other tissue with gross lesions. Tissues were fixed in 10% neutral buffered formalin, dehydrated in graded alcohol and xylene, and embedded in paraffin blocks; 5- μ m sections were stained with hematoxylin and eosin (Luna 1968). Selected sections were also stained with a modified Brown and Brenn Gram stain (Luna 1968).

Bacteriologic analysis and serotyping of *P. multocida*

Liver and lung tissue from all birds were submitted for bacteriologic analysis. For birds with gross lesions, tissues from affected organs also were submitted. All fresh samples were cultured aerobically on blood agar (comprised of tryptic soy agar [BD, Mississauga, Canada] and 6% sheep blood) and MacConkey II agar (BD) at 35 C for 24–48 h. Bacterial colonies were identified by selective growth, colony morphology, Gram stain, and biochemical characteristics. Samples from the first five carcasses were screened using API 20E test strips (BioMerieux, Marcy l'Etoile, France). All subsequent isolates were identified based on a combination of catalase, oxidase (Dryslide; BD), indole (Kovac's), and sugar fermentation activity (TSI Slant; Oxoid, Nepean, Canada). Lyophilized isolates were sent

in Aimes transport medium to the US Geological Survey—National Wildlife Health Center in Madison, Wisconsin, US for somatic serotyping according to the Heddleston scheme (Heddleston et al. 1972).

Avian cholera case definition

Birds diagnosed with avian cholera were classified as either confirmed or probable. A confirmed diagnosis of avian cholera required a comprehensive necropsy, including gross examination, histology, and bacteriology. This was done on a representative sample of all the carcasses collected during enhanced surveillance for avian cholera in Atlantic Canada. Comprehensive necropsies were only done on carcasses submitted to CWHC, Atlantic Region. Probable avian cholera was only diagnosed when the specimen was collected from a geographic location where avian cholera had been confirmed in another specimen of that particular species and age class collected on the same date and examined with the comprehensive necropsy procedure described earlier. The diagnostic investigation in probable cases of avian cholera was variable but did not include histology because the majority of carcasses examined were either moderately or markedly decomposed. For moderately decomposed specimens, the diagnostic findings for probable cases of avian cholera included the identification of gross lesions similar to those found in confirmed cases of avian cholera with isolation of *P. multocida* from the lesions or only with gross lesions similar to those found in a confirmed case of avian cholera without bacteriologic culture. For markedly decomposed specimens, a diagnosis of probable avian cholera required isolation of *P. multocida* from multiple tissues, and these specimens only received a partial necropsy because their state of preservation precluded gross examination to identify lesions consistent with those of confirmed cases. The probable avian cholera diagnosis was assigned at CWHC, Atlantic Region and the Newfoundland and Labrador Forestry and Agrifoods Agency.

Marine bird abundance along the Newfoundland and Labrador Shelf

Weighted mean abundance (number of seabirds/km² surveyed) for large scavenging gulls, Black-legged Kittiwake (*Rissa tridactyla*), Northern Fulmar (*Fulmarus glacialis*), Dovekie (*Alle alle*), and murre species (*Uria* spp.) along the Newfoundland and Labrador Shelf were extracted from Fifield et al. (2010). Unfortunately, seaduck estimates were not included. These estimates of abundance represent data from 2006–09, collected November–February, the months during

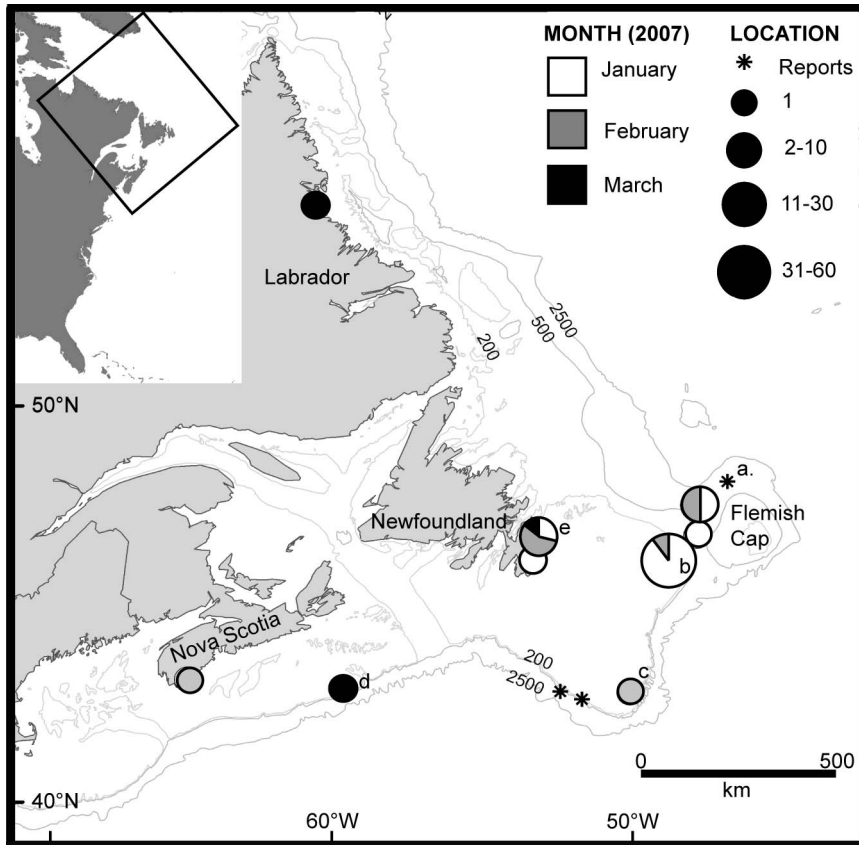


FIGURE 1. Locations where confirmed and probable cases of avian cholera were diagnosed during the outbreak, 2006–07. The number of cases per region is identified by the size of the pie chart, and the month in which cases were detected is designated by color. The outbreak was initially reported in December 2006 at point a, and the offshore oil platforms in the Jeanne D'Arc Basin are at point b. The tail of the Grand Banks is at point c, the offshore production platform near Sable Island is at point d, and the city of St. John's, Newfoundland and Labrador is located at point e.

which most carcasses were recovered offshore. Estimates of species abundance were examined in relation to relative species composition of carcasses from which avian cholera was determined to be the cause of death (confirmed and probable cases) to ascertain whether the detected mortality reflected species abundances or was biased to certain species or groups.

RESULTS

Outbreak descriptions

The first reports of unusual gull mortality were from the vicinity of the Flemish Cap (48°14'N, 45°56'W) and northern Flemish Pass (47°00'N, 46°45'W) during mid-December 2006 (Fig. 1). Numerous gull species,

particularly Great Black-backed Gulls (*Larus marinus*) and Glaucous Gulls (*Larus hyperboreus*), were noted landing and dying on Canadian Coast Guard patrol vessels. First indications of bird morbidity in the vicinity of the northeastern-most oil platform in the Jeanne d'Arc Basin (46°47'N, 48°01'W) occurred at the end of December 2006, at which time many gulls were noted landing and roosting on the oil platform, an atypical behavior (Weise et al. 2001; Fig. 1a). These birds were uncoordinated and unable to fly prior to dying. The first gull carcasses were collected in early January 2007 from this platform and submitted for postmortem examination. Continued gull mortality in the

TABLE 1. Species composition of birds submitted and diagnosed with avian cholera due to *Pasteurella multocida* during a 2007 outbreak in Atlantic Canada.

Species	No. carcasses submitted	No. carcasses with <i>P. multocida</i> ^a	Avian cholera diagnosis	
			Confirmed ^b	Probable ^c
Glaucous Gull (<i>Larus hyperboreus</i>)	35	29	10	24
Great Black-backed Gull (<i>Larus marinus</i>)	57	32	10	29
Herring Gull (<i>Larus smithsonianus</i>)	6	2	0	0
Iceland Gull (<i>Larus glaucoides</i>)	3	2	1	1
Lesser Black-backed Gull (<i>Larus fuscus</i>)	1	1	0	0
Ivory Gull (<i>Pagophila eburnea</i>)	1	1	1	0
Black-legged Kittiwake (<i>Rissa tridactyla</i>)	10	8	2	6
Dovekie (<i>Alle alle</i>)	7	1	0	0
Thick-billed Murre (<i>Uria lomvia</i>)	15	0	0	0
Raven (<i>Corvus corax</i>)	1	1	1	0
Total	136	77	25	60

^a Because of marked postmortem decomposition of some carcasses and prioritization of laboratory testing, bacteriology was not done on all specimens.

^b Specimens had gross and microscopic lesions of avian cholera and confirmatory isolation of *P. multocida* from tissues with lesions.

^c Histology not done on specimens because carcasses were decomposed. Specimens had to be the same species and age class as another specimen collected on the same day from the same location as a confirmed case. Moderately decomposed specimens had gross lesions as defined by confirmed cases plus isolation of *P. multocida* or only gross lesions as defined by confirmed cases. Markedly decomposed specimens had *P. multocida* isolated from multiple tissues but only partial necropsy during which gross lesions were not recorded.

Flemish Cap area occurred throughout January and February 2007, with increased mortality at the original site, and two other oil platforms further west and south in the Jeanne d'Arc basin. During late February 2007, there were reports of Great Black-backed Gull and Glaucous Gull mortality along the tail of the Grand Banks (43°25'N, 49°51'W; Fig. 1c) and along the southern shelf (43°35'N, 52°15'W and 43°20'N, 51°31'W). A confirmed case in a Great Black-backed Gull was detected on an offshore platform near Sable Island, Nova Scotia (43°57'00"N, 56°54'57"W; Fig. 1d). Additionally, there were confirmed cases of avian cholera in gulls along coastal regions of Newfoundland, particularly in St. John's. Individual cases were confirmed in Ferryland (47°01'N, 052°53'W) and coastal Nova Scotia (43°42'N, 65°06'W; Fig. 1). Reports of mortality decreased dramatically in mid-February 2007, and the final confirmed cases occurred in mid-March 2007 in St. John's and Northern Labrador (56°22'5"N, 62°5'21"W; Fig. 1). Despite enhanced awareness of avian cholera in the region, no reports of sick and dying waterfowl

or waterfowl carcasses were reported or submitted by the public in Atlantic Canadian coastal communities.

Serotyping

From January to March 2007, 136 carcasses of 10 species were submitted for examination as potential cases of avian cholera (Table 1). All carcasses but one were overwintering seabirds, and the majority (103/136) were scavenging gulls. Of these, *P. multocida* was isolated from 77 carcasses in multiple organs (usually heart, liver, lung, and spleen). All *P. multocida* isolates serotyped ($n=77$) were somatic serotype 1, including those from scavenging gulls, Kittiwakes, a Common Raven (*Corvus corax*), and a Dovekie. One Great Black-backed Gull was positive for *Pasteurella bettaye*, but was negative for *P. multocida*.

Postmortem findings

Thirty-eight carcasses collected during the enhanced surveillance underwent comprehensive necropsy to determine the cause of

death, constellation of lesions, species affected, and geographic extent of the outbreak. Avian cholera was confirmed as the cause of death in 25/38 of these specimens (Table 1, Supplementary Material Table S1), and 24/25 of the confirmed cases were in species of gulls. In instances involving multiple avian cholera mortalities in a gull species, all age classes and both sexes were represented except for Black-legged Kittiwakes, which included only two adult females as confirmed cases of avian cholera. The majority of birds with confirmed avian cholera were in good body condition (21/25) and the most common gross findings were acute fibrinous and necrotizing lesions affecting the spleen (16/25), air sacs (12/25), and pericardium (11/25), as well as nonspecific hepatomegaly (15/25) and splenomegaly (17/25).

Specific gross and microscopic lesions in gulls dying of confirmed avian cholera represented three time frames, including peracute septicemia (21/24), acute fibrinous or necrotizing lesions (20/24), and chronic lesions (1/24). In cases of peracute septicemia, some affected individuals had no gross lesions (5/21), whereas others had acute fibrinous or necrotizing lesions in combination with peracute septicemia (16/21). The microscopic changes of peracute septicemia consisted of colonies of Gram-negative coccobacilli within the lumina of blood vessels and in perivascular tissues throughout the body with no associated inflammatory response. Gulls with acute lesions most commonly had fibrinous exudate partially or completely covering mucosal and serosal surfaces of air sacs and the serosal surface of the pericardial sac. Microscopically, fibrinous lesions consisted of thick, unorganized fibrin exudate enmeshed with colonies of Gram-negative coccobacilli and a few macrophages or heterophils. In addition, acute fibrinous or necrotizing lesions were identified in the brain, lung, spleen, liver, trachea, or intestine of several birds. Chronic lesions were only found in one Great Black-backed Gull that was also emaciated. Scant to abundant broken feather shafts were in the ventricular (i.e., gizzard) lumen of the majority of birds from the family Laridae with a

confirmed diagnosis of avian cholera (17/24). In addition to the confirmed cases of avian cholera, there were 60 probable cases. The majority of these were in Glaucous Gulls (24/60) and Great Black-backed Gulls (29/60), and these specimens were included in the analysis of other aspects of this outbreak. A Common Raven found dead in the coastal community of Lockeport, Nova Scotia (43°41'49.3"N, 65°6'55.2"W) was the only nonmarine bird diagnosed with avian cholera, and it had similar lesions as those described in the gulls. See Supplementary Material Table S1 for additional information concerning lesions by species.

The cause of mortality in the majority of alcid carcasses examined was emaciation (21/22). The only other diagnosis in this group was for a Thick-billed Murre in good body condition that died of traumatic injuries. *Pasteurella multocida* was isolated from the heart and lung of one emaciated Dovekie collected from offshore oil platforms in January 2007, but there were no gross or microscopic lesions compatible with avian cholera in the heart, lung, or other tissues of this bird. Therefore, the cause of death was most likely starvation and not avian cholera. Because this bird did not have avian cholera based on the case definition, it was not included in further analyses.

Carcass composition does not reflect seabird densities

A comparison of bird population density along the Newfoundland and Labrador shelves and of species distribution of birds with a diagnosis of avian cholera indicated there was a bias toward mortality in large scavenging gulls (Table 2). Compared to scavenging gulls, there was a higher relative abundance of other species, such as Black-legged Kittiwakes, murre, and Northern Fulmars (Fifield et al. 2010; Table 2).

DISCUSSION

The outbreak of avian cholera in Atlantic Canada between December 2006 and March

TABLE 2. Species composition of carcasses diagnosed with avian cholera as compared to seabird density on the Newfoundland and Labrador Shelf during the winter (November–February).

Species	Bird density ^a (birds/km ²)	Carcass species composition ^b (%)
Large scavenging gulls ^c	0.95±0.57	89.4
Black-legged Kittiwake (<i>Rissa tridactyla</i>)	2.45±1.87	9.4
Northern Fulmar (<i>Fulmarus glacialis</i>)	1.91±1.53	0
Dovekie (<i>Alle alle</i>)	0.93±1.30	0
Murre spp. (<i>Uria</i> spp.)	3.05±0.75	0

^a Weighted mean seabird density on the Newfoundland and Labrador Shelf during winter (November–February) 2007–10 (Fifield et al. 2010).

^b Confirmed and probable diagnosis of avian cholera.

^c Large scavenging gulls, as defined by Fifield et al. (2010), include Herring Gull (*Larus argentatus/smithsonianus*), Great Black-backed Gull (*Larus marinus*), Iceland Gull (*Larus glaucoides*), Glaucous Gull (*Larus hyperboreus*), and less common Eurasian visitors, Lesser Black-backed Gull (*Larus fuscus*), Yellow-legged Gull (*Larus michahellis*).

2007 is the first known report of an outbreak in a pelagic environment, although other marine bird mortality has been reported on St. Lawrence Island, Alaska (Bodenstein et al. 2015) and among Common Eiders wintering along Danish sea ice (Christensen et al. 1997). This pelagic outbreak is unique in that the host range was primarily restricted to scavenging gull species, which were important in transmission, perpetuation, and spread of the outbreak. Finally, this comprehensive investigation documented a substantial expansion in the number of gull species with confirmed avian cholera, including Glaucous Gulls, Ivory Gulls, Iceland Gulls (*Larus glaucoides*) and Black-legged Kittiwakes. Previous confirmed cases of avian cholera have been diagnosed in Great Black-backed Gull and Common Raven (Samuel et al. 2007).

The highest mortality occurred in the pelagic environment along the continental shelf; however, mortality was also identified in coastal regions of Atlantic Canada, extending from southwestern Nova Scotia to Labrador. The continental shelf is the primary foraging area for various seabirds during winter (Lock et al. 1994; Fifield et al. 2010). The large spatial scale of this outbreak, extending over 1,200 km north and west of the first reported cases (Fig. 1), appeared to follow the distribution and movement patterns of gulls (Lock et al. 1994; Fifield et al. 2010). The first records of mortality appeared to coincide with influx of northern breeding gulls

into the continental shelf; the final confirmed case, in Northern Labrador, appeared to coincide with the onset of northward migration (Lock et al. 1994; Olsen and Larsson 2007; Fifield et al. 2010). Carcasses were collected only from man-made structures and vessels; however, there were numerous reports of dead gulls from other areas. Because of the implications of dead birds on offshore production platforms, increased vessel traffic associated with them, and their role in providing sick gulls a place to land, the offshore component of this outbreak might have gone undetected if not for the presence of these man-made structures. However, because of the sparse vessel traffic beyond the continental shelf and north of the Orphan Basin (49°36'41"N, 47°57'20"W), it is likely that the actual extent of mortality was larger than was detected by opportunistic and enhanced surveillance.

Contaminated water is important in transmission of *P. multocida* during outbreaks (Botzler 1991). However, ocean dynamics would rapidly dilute ocean water contaminated with *P. multocida* from sick or dead birds. Thus, it is unlikely that this pelagic outbreak was perpetuated by contaminated water, unlike outbreaks that occur in wetlands or shallow water environments (Friend 1987; Botzler 1991; Samuel et al. 2004). Rather, a more direct mode of transmission, such as scavenging, would have been required to sustain this pelagic outbreak. This hypothesis

is supported by the fact that avian cholera was diagnosed primarily from large, aggressive scavenging gulls, the majority of which had feather remains in their ventricular lumen compatible with scavenging. Feather remains were also present in the lumen of Kittiwakes, a traditionally non-scavenging species. One Ivory Gull, a small but aggressive scavenging species (Mallory et al. 2008b), was also affected, providing further support for scavenging as the main mode of transmission. The only nonmarine bird diagnosed with avian cholera was a Common Raven, also a scavenging species throughout its range (Boarman and Heinrich 1999). There were much higher densities of non-scavenging species (e.g., alcids) in the affected pelagic areas on the Newfoundland and Labrador Shelves (Fifield et al. 2010) compared to all scavenging gull species combined, yet few carcasses of non-scavenging species were collected and no individuals of these species were diagnosed with avian cholera. Indeed, there was an unrelated mortality event of alcids identified shortly after this outbreak (Tranquilla et al. 2010), suggesting that alcids would have been detected if they had been involved in the outbreak. Additionally, there were high numbers of waterfowl in ice-free ponds in St. John's, yet none were affected by the avian cholera outbreak despite the presence of sick or dead gulls on some of these ponds.

Mortality in scavenging species (including crows, raptors, and gulls) during avian cholera outbreaks is usually secondary to mortality in colonial or densely aggregated waterbirds, a consequence of scavenging on carcasses of the species primarily affected (Zinkl et al. 1977; Brand 1984; Williams et al. 1987; Hindman et al. 1997; Samuel et al. 2007; Barbosa and Palacios 2009). There are a few reports of outbreaks primarily involving scavenging species (Kaschula and Truter 1951; Parmelee et al. 1979; Leotta et al. 2003), but it is unclear what the primary mode of transmission was in these cases. In this outbreak, gulls and other scavenging species were primarily affected, and scavenging is a proposed likely mechanism for the transmission, perpetuation, and spread of this disease.

The three main serotypes circulating in North America are 1, 3, and 4, and detections vary between years and geographic locations (Samuel et al. 2007). The origins of the *P. multocida* strain(s) causing this outbreak are unknown; however, the somatic serotype, type 1, may provide some suggestion. It is possible that there is a link between this outbreak and a massive outbreak that occurred in the eastern Canadian Arctic in the summer of 2006, killing >30% (>3,000) of breeding female common eiders. Limited numbers of other species were also affected, including Herring Gulls and Brant (*Branta bernicla hrota*; Mallory et al. 2008a; Buttler 2009). Although the likelihood and duration of carrier status of gulls is unknown, it is possible that a carrier bird originating from the eastern Arctic may have brought the strain of *P. multocida* serotype 1 from the eastern Arctic to Atlantic Canada, and initiated the offshore mortality event. Candidate species include those with breeding ranges that extend into the eastern Canadian Arctic and with wintering ranges or migratory routes that include the Canadian east coast (e.g., Great Black-backed Gulls, Glaucous Gulls). However, without further genotypic analysis (e.g., Blehert et al. 2008; Subaaharan et al. 2010) of isolates collected from Atlantic Canada, the Canadian Arctic, the St. Lawrence Estuary, and other historical outbreaks across Canada to evaluate possible sources of the recent emergence of avian cholera in Canada's Atlantic coast as well as the eastern Arctic, we can only speculate about the origin of this outbreak.

Despite the shift from traditional outbreak patterns, the range of lesions in the pelagic gulls examined from this die-off are consistent with those described from outbreaks of avian cholera in avian species more typically affected by the disease. As several of the gull species involved in this outbreak represent new records, and current literature on avian cholera outbreaks in the Arctic do not provide detailed description of the lesions encountered in affected avian species, it was relevant to provide detailed diagnostic information in the context of this investigation. Furthermore, recognizing the remoteness of these locations

and lack of access to diagnostic laboratories, if avian cholera continues to emerge in the Arctic, recognition of these lesions in any future mortality events could assist in making a preliminary diagnosis of avian cholera and selecting appropriate samples to send for confirmatory diagnosis. This is significant due to heightened public health and food security concerns that are encountered in local Arctic communities that rely on marine species for food (e.g., Bodenstern et al. 2015).

This outbreak description highlights the potential role of scavengers in the maintenance and spread of avian cholera. An outbreak of avian cholera with epidemiologic characteristics unlike those in classical descriptions of the disease (Wobeser 1992; Friend 1999; Samuel et al. 2007) demonstrates the high variation in host range and environment, highlighting the complex dynamics of this disease. Outbreak descriptions have inherent biases across a hierarchical series (McClintock et al. 2010); here biases range from the highest level (geographic areas visited) to the lowest (pathogen detection) because of numerous logistic constraints. Thus, to assess avian cholera dynamics adequately, a more targeted approach, rather than response to outbreaks, is necessary, which may illuminate factors governing the epidemiology of this disease.

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SUPPLEMENTARY MATERIAL

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