



Causes of mortality of harbor porpoises *Phocoena phocoena* along the Atlantic and Pacific coasts of Canada

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ABSTRACT: There is increasing public interest in the overall health of the marine environment. Harbor porpoises *Phocoena phocoena* have a coastal distribution, and stranded animals function as sentinels for population and ecosystem health. The goal of this retrospective study was to join datasets from the western Atlantic and eastern Pacific coasts of Canada to investigate causes of morbidity and mortality in this species. A total of 241 necropsy records were reviewed including 147 (61%) from the Pacific region and 94 (39%) from the Atlantic region from 1988 to 2011. A cause of death could be determined with confidence in 118 (49%) of these cases. Of these 118 cases, the leading cause of mortality for both regions, together and separately, was infectious disease. In the Pacific region, this was followed by traumatic and anthropogenic causes, whereas in the Atlantic region, it was followed by emaciation/starvation, mortality of dependent calves, and anthropogenic causes. Pathogens of potential zoonotic significance or indicative of environmental contamination, e.g. *Salmonella* sp. and *Cryptococcus gattii*, were identified. Numerous parasitic species were observed within the lungs, liver, stomach, middle ear, and subcutaneous tissues, although they were usually interpreted as incidental findings. Anthropogenic causes may be underrepresented as they are notoriously difficult to diagnose with certainty, thereby making up a proportion of the 'unknown causes of death' (51%) category. Improved standardization of data collection and documentation is required to better understand harbor porpoise and ecosystem health.

KEY WORDS: Harbor porpoise · *Phocoena phocoena* · Cetacean · Stranding · Mortality · Disease · North America · Canada

INTRODUCTION

There is global interest in the use of marine mammals, particularly odontocetes, as sentinels for monitoring the health of ocean ecosystems (Bossart 2011).

Current knowledge of diseases of free-living marine mammals and of the complex and dynamic ecology of diseases within the marine ecosystem has been enhanced by (1) studies of recent outbreaks of morbillivirus infection causing large-scale mortality in

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cetaceans and pinnipeds (Di Guardo 2012, Duignan et al. 2014); (2) an increasing interest in emerging zoonotic diseases such as brucellosis and toxoplasmosis (Van Bresse et al. 2009); and (3) the potential role of cetaceans as sentinels for persistent organic pollutants in the environment (Kucklick et al. 2011). As it is often logistically challenging to study marine mammals in the wild, it is particularly important to maximize the information obtained during stranding events in order to establish normal life history parameters and monitor anthropogenic causes of morbidity or mortality, emerging infectious diseases, and population demographics (Geraci & Lounsbury 2005). Analyses of causes of mortality of cetaceans have been reported from several regions of the world (Cornaglia et al. 2000, Parsons & Jefferson 2000, Jauniaux et al. 2002, Camphuysen et al. 2008, McFee & Lipscomb 2009, Bogomolni et al. 2010, Arbelo et al. 2013, van der Hoop et al. 2013, Lair et al. 2016).

The harbor porpoise is the smallest cetacean in Canadian waters and has a predominantly coastal distribution, making it an excellent sentinel of Canadian inshore and nearshore waters. Both the Atlantic and Pacific populations are listed as 'Species of Special Concern' by the Committee on the Status of Endangered Wildlife in Canada (http://www.cosewic.gc.ca/eng/sct6/index_e.cfm, [accessed December 2016]). In addition, the Atlantic population is listed as 'Threatened' under the Canadian Species at Risk Act (www.registrelep-sararegistry.gc.ca/default.asp?lang=en&n=24F7211B-1, [accessed December 2016]), largely due to the high incidence of by-catch mortality from entanglement in gill-net fishing gear (Trippel et al. 1996). This cause of mortality has remained a concern despite reduced fishing efforts following the collapse of commercial groundfish fisheries in the North Atlantic in the early 1990s (Lawson et al. 2004, Lesage et al. 2004). Although the numbers of harbor porpoises entangled in fishing nets in the Gulf of St. Lawrence (Fontaine et al. 1994) and in the Bay of Fundy (Trippel et al. 1996) have been estimated in the past, analyses of other causes of morbidity and mortality of harbor porpoises in Canadian waters are limited (Norman et al. 2004). According to Nemiroff et al. (2010), disease (including acute or chronic infection, chronic trauma, and poor nutritional condition) was the main cause of mortality among harbor porpoises found stranded or dead in the Maritime region of Atlantic Canada (i.e. the provinces of New Brunswick, Nova Scotia and Prince Edward Island) between 1990 and 2008. On the basis of existing diagnostic datasets, the objectives of this study were to summarize the causes of morbidity and mortality

of harbor porpoises in the Atlantic and Pacific regions of Canada and to determine whether significant differences exist in these causes between the 2 regions.

MATERIALS AND METHODS

Animals from the Atlantic region of Canada were found along shores of Québec and the Maritime provinces (44–47° N, 59–68° W), whereas those from the Pacific region were found along the coast of British Columbia (48–54° N, 122–133° W). All necropsies in the Atlantic region were performed from 1988 to 2011 by pathologists at the Atlantic Veterinary College, University of Prince Edward Island, Charlottetown, Prince Edward Island, or at the Faculté de médecine vétérinaire, Université de Montréal, Saint-Hyacinthe, Québec. Necropsies in the Pacific region were performed from 1992 to 2010 either by wildlife biologists or veterinarians in the field or, more consistently after 2001, by pathologists at the Animal Health Centre, British Columbia Ministry of Agriculture, Abbotsford, British Columbia, where frozen carcasses were shipped and where laboratory analyses and final reports were completed. Necropsy and sample collection were based on a standard protocol modified according to the state of preservation of the carcass (Geraci & Lounsbury 2005).

Table 1 provides a detailed list of the parameters and information recorded in the necropsy reports, although data were not available for all animals. Parameters included year and month when the carcass was found, location of carcass, body mass, standard length, blubber thickness at 3 sites, sex, relative age based on length, incident type (alive ashore [stranded], dead ashore [beached], dead in fishing net, floating dead at sea), state of carcass preservation, subjective body condition score, gross necropsy findings, histopathological findings, ancillary diagnostic tests, and morphologic diagnoses. For each necropsy report, a primary diagnosis was reached through consensus among 4 pathologists (H.F., P.Y.D., M.J.F., S.R.), who had carefully and independently reviewed morphologic findings and results of ancillary tests. For the purpose of this study, the primary diagnosis (cause of death) is the condition most likely to have initiated the series of events that resulted in the eventual death of the animal based on the information available. In contrast, secondary diagnoses, such as parasitism, include conditions that may or may not have contributed to the animal's death but were not considered the initial problem. The presence or absence of parasites in the lungs (nematodes), liver

Table 1. Parameters recorded in the necropsy reports of harbor porpoises *Phocoena phocoena* found moribund or dead and submitted to Canadian veterinary diagnostic laboratories 1988–2011. Not all parameters were recorded for all animals

Parameters	Details
Year and month when found	
Location	British Columbia (Pacific region); Prince Edward Island, Nova Scotia, New Brunswick, Québec (Atlantic region)
Body mass (kg)	
Standard length (m)	Straight line from tip of snout to tail notch
Blubber thickness at 3 individual sites on the carcass (mm)	Dorsal, lateral, and ventral at axilla
Sex	Male, female, or not recorded
Relative age based on length (Van Bressem et al. 1998)	Calf (<1.18 m) Juvenile male (<1.30 m) Juvenile female (<1.40 m) Adult male (>1.30 m) Adult female (>1.40 m), or with evidence of sexual maturity such as lactation or pregnancy
Incident type	Alive ashore (stranded) Dead ashore (beached) Dead in a fishing net Floating dead at sea
State of carcass preservation	Fresh, moderately decomposed, or autolyzed
Subjective body condition score	Good, moderate, or poor, based mainly on relative degree of convexity or concavity of epaxial muscle mass and, to a lesser extent, on overall thickness of blubber
Gross description of pathological findings	
Histological description of tissues sampled	
Ancillary diagnostic tests	Virology, bacteriology, mycology, parasitology, toxicology, immunohistochemistry, polymerase chain reaction (PCR), performed as required based on gross and histopathological examination of the carcass
One or more morphologic diagnoses	Determined by a trained wildlife pathologist (either the one who performed all of the diagnostic testing or, when the necropsy was performed by a biologist or non-specialized veterinarian, the one who examined the tissues histologically)

(trematodes), stomach (nematodes), pterygoid sinuses (associated with the middle/inner ear complex) (nematodes), and subcutaneous tissue (either plerocercoid cestode larvae or nematodes) was noted based on gross and/or microscopic findings.

The cause of death was assigned to one of the following categories adapted from Bogomolni et al. (2010) and Nemiroff et al. (2010):

- (1) Infectious/inflammatory disease (viral, bacterial, fungal, parasitic, cause undetermined);
- (2) Non-infectious disease (congenital anomaly, perinatal complications, toxicity);
- (3) Emaciation/starvation (based mainly on relative degree of convexity or concavity of epaxial muscle mass and, to a lesser extent, on overall thickness of blubber), with no other clinically significant disease process identified;
- (4) Dependent calves with no clinically significant disease process identified;

(5) Anthropogenic (e.g. gun-shot wound, entanglement in fishing gear);

(6) Trauma (interspecific aggression or exact cause undetermined);

(7) Mishap (animals found stranded or beached with no evident underlying disease process, and a history of adverse environmental conditions such as strong onshore wind and receding tide or the presence of a sand bar between shore and open water combined with the reported presence of prey species in the area);

(8) Unknown.

All statistical analyses were performed in Stata (version 14.1; StataCorp), unless otherwise stated. Fisher's exact tests were performed on categorical variables, for example between causes of death among the Atlantic and Pacific regions. Binomial probability tests were used to identify differences in proportions between 2 groups, for example between

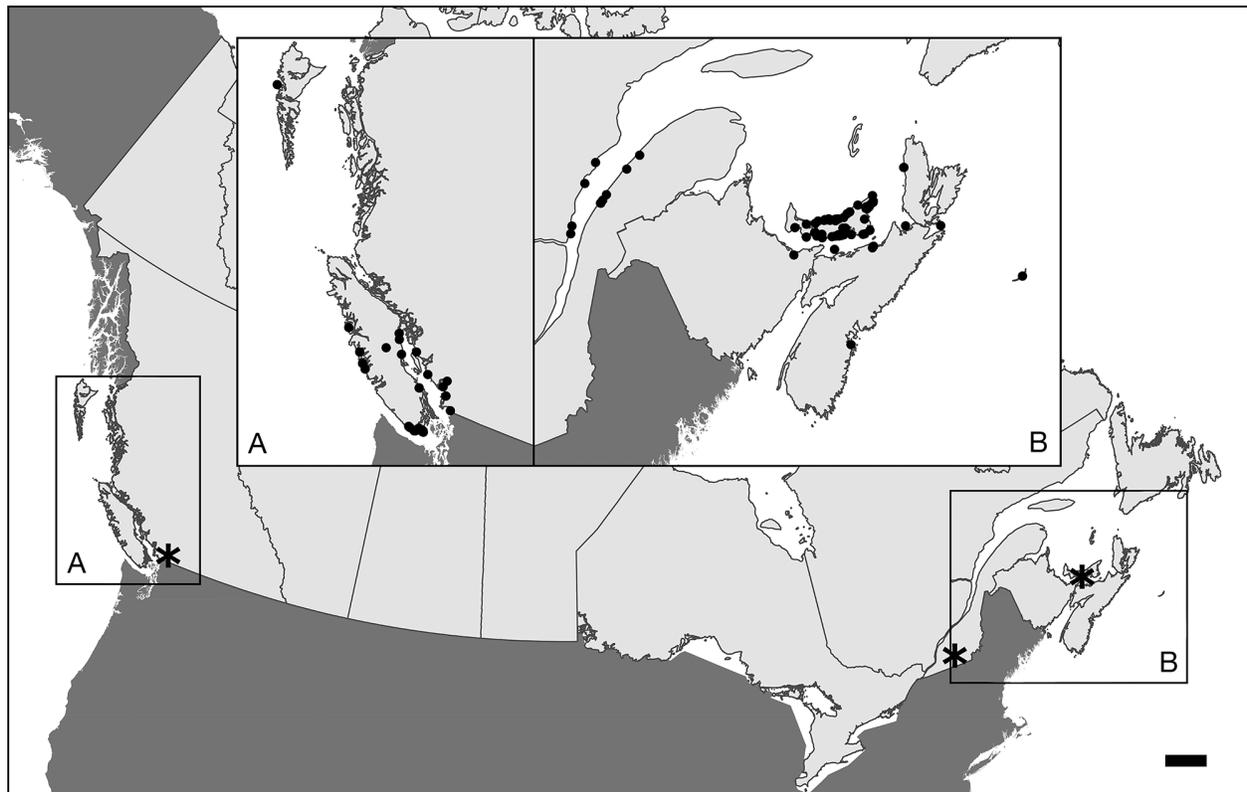


Fig. 1. Recorded locations of harbor porpoise *Phocoena phocoena* mortalities in (A) the northeastern Pacific region 1992–2010 ($n = 84$) and (B) the northwestern Atlantic region 1988–2011 ($n = 94$). Asterisks indicate locations of the Canadian veterinary diagnostic laboratories that examined harbor porpoises. Scale bar = 300 km

sexes or between regions for a specific cause of death. Finally, a simple linear regression was used to estimate the differences in mean blubber thickness (determined by averaging the dorsal, lateral, and ventral thicknesses at axilla) between the subjective body condition scores (BCS) (good, moderate, poor). Statistical significance was set at $p < 0.05$. Maps were generated with QGIS version 2.11 (www.qgis.org/ [accessed March 2016]).

RESULTS

Location, sex, relative age, and incident type

Of 241 necropsy reports reviewed, 147 (61%) were from the Pacific region and 94 (39%) were from the Atlantic region (including 56 that were also part of the study by Nemiroff et al. 2010 in that region). Because of the large expanse of coastline in both regions and the variable extent to which it is frequented by humans, it was not possible to determine what proportion of the total number of stranded har-

bor porpoises was represented by those necropsied. All cases consisted of individual deaths; there were no instances of mass stranding. The approximate location was available for 84 porpoises from the Pacific region and for all porpoises from the Atlantic region (Fig. 1). The majority of animals in the Atlantic region (84/94, 89.3%) were found from May to September, when coastal water in this region is generally free of ice and when members of the public are also most likely to be on beaches. In the Pacific region, which is free of ice year-round, the month when the animal was found was available for only 29 of the 147 cases (19.7%), and it was therefore not useful to assess monthly distribution. However, unpublished data from the Pacific region of the Canadian Department of Fisheries and Oceans suggest that 78% of porpoise mortalities were reported between April and September and 41% of these mortalities were reported in April–May alone.

The majority of carcasses were collected from British Columbia ($n = 147$, 61.0%) and Prince Edward Island ($n = 72$, 29.9%), while 12 carcasses were collected from Québec (5.0%), 9 from Nova Scotia

(3.7%), and 1 from New Brunswick (0.4%). For both regions combined, there were equal proportions of males and females ($p = 0.839$), and the number of calves and juveniles was significantly higher than that of adults ($p = 0.007$) (Table 2); there was no statistically significant difference in age class or sex between the Atlantic and Pacific regions. The type of incident was recorded for 119 animals (49.4%). Of these, the majority were found beached ($n = 94$, 79.0%), followed by dead at sea ($n = 13$, 10.9%), and, in equal proportions, dead in a fishing net ($n = 6$, 5.0%) and stranded ($n = 6$, 5.0%). Stranded animals either died on their own or were promptly euthanized. There was no statistically significant difference in the distribution of types of incidents between the Atlantic and Pacific regions.

Causes of death

A cause of death could be determined in 118 of 241 cases (49.0%) (Table 3). Of these 118 cases, the leading cause of death for both regions, together and separately, was infectious disease. Among cases included in this category, 17 of 29 cases in the Pacific region and 3 of 16 cases in the Atlantic region were tested by polymerase chain reaction for infection by morbillivirus which, by targeting the immune system, can predispose to other infectious diseases. All cases were negative, and no microscopic lesions typical of morbilliviral infection, particularly intranuclear and/or intracytoplasmic inclusions bodies, were observed in any case.

In the Pacific region, infectious disease as a cause of death was followed by traumatic and anthropo-

genic causes, whereas in the Atlantic region it was followed by emaciation/starvation, mortality of dependent calves, and anthropogenic causes. Many more trauma cases were found in the Pacific region ($p = 0.004$), while the Atlantic region had many more cases of emaciation/starvation ($p = 0.021$) and dependent calves found dead ($p = 0.012$) and was the only region to have recorded mishaps. The proportions of porpoises included within the categories of infectious disease, non-infectious disease and anthropogenic causes were similar between regions. In both regions, non-infectious disease and, for the Atlantic region, mishap appeared to play a minor role in overall mortality. More harbor porpoises from the Pacific than from the Atlantic region were included in the 'unknown' category ($p < 0.001$). The proportion of necropsy reports in which autolysis was mentioned as a factor that could have interfered with determination of a cause of death did not differ between the Pacific and Atlantic regions ($\chi^2 = 0.570$, $p = 0.450$) or by province ($\chi^2 = 3.79$, $p = 0.285$).

Nine of the 16 cases classified as 'Emaciation/starvation' were calves. Assuming a birth date around mid May (Westgate et al. 1997), the estimated age of 8 of these calves varied from recently born (teeth not erupted, umbilicus barely healed) to 6 mo; the time of death of one calf was not recorded. Eleven other calves (10 from recently born to estimated 4 mo old; 1 with no time of death recorded) had no clinically significant disease process identified and were not considered emaciated.

For both regions combined, mean blubber thicknesses were associated with the subjective BCS ($n = 85$); they were on average 12.2, 14.0, and 20.0 mm for poor, moderate, and good BCS, respectively. While there was no statistically significant difference in blubber thickness between poor and moderate BCS ($p = 0.673$), there were significant differences between poor and good ($p < 0.001$), and moderate and good ($p < 0.001$) BCS. No statistically significant difference was found in these parameters between the Atlantic and Pacific regions.

Secondary diagnoses

Of the 241 porpoises examined, 153 (63.5%; 95% CI, 57.1–69.6%) had some form of parasitism, which was associated with the cause of death in only 10 cases (Table 3). Adults represented a larger percentage of the animals parasitized (77/153, 50.3%) compared with juveniles (30/153, 19.6%), calves (13/153, 8.5%) and animals of unknown age (33/153, 21.6%)

Table 2. Sex and age breakdown of 241 harbor porpoises *Phocoena phocoena* submitted to Canadian veterinary diagnostic laboratories 1988–2011. Male and female porpoises equally represented within the dataset. Dataset was biased towards younger animals (juveniles and calves)

	Pacific region	Atlantic region	Total	%
Sex				
Female	62	49	111	46
Male	63	44	107	44
Not recorded	22	1	23	10
Age				
Calf	37	41	78	32
Juvenile	26	16	42	17
Adult	46	35	81	34
Not recorded	38	2	40	17

Table 3. Causes of death (primary diagnosis) (number of animals [percentage]) of 241 harbor porpoises *Phocoena phocoena* submitted to Canadian diagnostic laboratories 1988–2011 by region (western Atlantic and eastern Pacific). There were overall unequal distributions in the causes of mortalities between the Pacific and Atlantic regions (Fisher's exact test; $p < 0.001$), and binomial probability tests (p) were used to identify regional differences for specific causes of death. *Statistical significance at $p < 0.05$

Cause of death	Pacific region (n = 147)	Atlantic region (n = 94)	Total (n = 241)	p
Infectious	29 (20%)	16 (17%)	45 (18.7%)	0.072
Viral ^a	1	0	1	
Bacterial ^b	6	1	7	
Parasitic ^c	3	7	10	
Fungal ^d	11	2	13	
Cause undetermined ^e	8	6	14	
Non-infectious	2 (1.3%)	4 (4.2%)	6 (2.5%)	0.688
Congenital anomaly ^f	1	1	2	
Perinatal complications	1 ^g	1 ^h	2	
Saxitoxin intoxication ⁱ	0	2	2	
Emaciation/starvation^j	3 (2%)	13 (13.8%)	16 (6.6%)	0.021*
Dependent calves: no identifiable disease	1 (0.7%)	10 (10.6%)	11 (4.6%)	0.012*
Anthropogenic	12 (8.1%)	9 (9.6%)	21 (8.7%)	0.664
Gun-shot wound	1	0	1	
Entanglement in fishing gear ^k	11	9	20	
Trauma	14 (9.5%)	2 (2.1%)	16 (6.6%)	0.004*
Interspecific aggression ^l	5	0	5	
Cause undetermined	9	2	11	
Mishap	0 (0%)	3 (3.2%)	3 (1.2%)	0.250
Unknown	86 (58.5%)	37 (39.4%)	123 (51.0%)	<0.001*

^aEsophagitis caused by herpesvirus infection based on PCR analysis of fresh tissue samples; thought to have interfered with swallowing

^bSepticemia (3; *Photobacterium damsela*, *Streptococcus phocae*, *Vibrio parahemolytica*), myocarditis (*Salmonella arizonae*), pneumonia (*Staphylococcus sciuri*), peritonitis (*Edwardsiella tarda*), enteritis (*Clostridium difficile*)

^cVerminous pneumonia (7; at least 3 of them complicated by secondary bacterial infection: *Vibrio* sp., *E. tarda*), enteritis (unspecified helminths), hepatic trematodiasis (2)

^dGeneralized infection (8 caused by *Cryptococcus gatti*, 1 caused by *Aspergillus fumigatus*, 1 caused by a zygomycetous fungus, 1 caused by an unidentified fungus), pneumonia (1 caused by a zygomycetous fungus, 1 caused by an unidentified fungus)

^eMeningitis/meningoencephalitis (4; all negative for *Brucella* sp. by PCR; only 1 tested by PCR for morbillivirus and found negative, none of the 4 cases with microscopic lesions typical of morbilliviral infection, such as intranuclear and/or intracytoplasmic inclusion bodies), pneumonia, pleuritis (2), peritonitis (4), polyserositis, metritis, endometritis

^fInterventricular septal defect; hepatic hamartoma

^gMeconium aspiration syndrome in a neonate

^hDystocia (female with intrauterine autolyzed near-term fetus, opened uterine cervix, and marked inflammation of the uterine wall)

ⁱBased on same criteria as in Scarratt et al. (2013)

^jIncluding 9 calves

^kConfirmed by the history in 6 animals; based on the presence of characteristic linear cutaneous indentations and abrasions in 12 animals; in 2 animals, based on otherwise negative laboratory findings and on the nearby presence on shore of carcasses of northern gannets *Morus bassanus* in good body condition and with fish in their stomach, a species commonly affected by entanglement in fishing gear

^lBased either on direct observation of predation or smothering by killer whales or on presence of characteristic lesions of predation by killer whales (skin stripped off caudal region of body, or caudal region missing altogether; obvious teeth marks)

($p < 0.001$). From the total number of submissions, 126 (52.3%) had pulmonary nematodes, 102 (42.3%) had hepatic trematodes, 54 (22.4%) had gastric nematodes, 41 (17.0%) had nematodes in pterygoid sinuses, and 16 (6.6%) had blubber/subcutaneous parasites (either plerocercoid cestode larvae or nematodes). Parasite species identified included *Pseudal-*

ius inflexus, *Stenurus* sp., *Torynurus convolutus* and *Halocercus* sp. in the lungs; *Campula oblongata* in the liver; *Contracaecum* sp. and *Anisakis* sp. in the stomach; *Stenurus minor* in pterygoid sinuses; and *Phyllobothrium* sp. and *Crassicauda* sp. in the blubber. Other parasites noted occasionally were *Pseudal-*

major pulmonary blood vessels (9/241, 3.7%) and intestinal cestodes thought to be *Diphyllobothrium* sp. (3/241, 1.2%). There were no regional differences in the number of animals with some form of parasitism ($p = 0.339$), pulmonary nematodes ($p = 0.509$), gastric nematodes ($p = 0.735$), or hepatic trematodes ($p = 0.505$). The presence of blubber parasites was recorded more often in the Pacific region than in the Atlantic region ($n = 15$ and $n = 1$, respectively; $p = 0.006$). All of the nematodes within pterygoid sinuses were recorded in the Atlantic region; this anatomical location was not examined systematically in the Pacific region.

Salmonella sp. was isolated from 3 animals that died from an unrelated cause: *Salmonella* sp. group B from the small intestine, *Salmonella* sp. (serotype 1:4,12:a) from the lungs, and a non-serotyped *Salmonella* sp. from the lungs. Other bacterial species known to be opportunistic or primary pathogens in humans (Quinn et al. 2002) that were cultured from animals which died from an unrelated cause included *Aeromonas* sp., *Erysipelothrix rhusiopathiae*, *Clostridium difficile*, *C. perfringens*, *Pasteurella multocida*, *Photobacterium damsela*, *Proteus* sp., *Staphylococcus epidermidis*, and *Vibrio* sp.

DISCUSSION

Retrospective studies of causes of wildlife mortality carry a number of limitations, such as sampling biases and the difficulty of distinguishing primary from secondary diagnoses in the absence of any clinical history. However, such studies can provide valuable insight into the life history of the species involved, their habitat, baseline health parameters, and anthropogenic factors that may affect their survival. Male and female harbor porpoises were equally represented in this study, but there was a significantly higher proportion of sexually immature animals (juveniles and calves) compared to adults, which is consistent with previous reports for marine mammals (Barlow & Boveng 1991). In the Atlantic region, Prince Edward Island was markedly overrepresented in terms of the number of harbor porpoises necropsied as compared to New Brunswick, Nova Scotia, and Québec. This was likely because the small size of the province allows easy delivery of carcasses to the diagnostic laboratory at the Atlantic Veterinary College, and compared to the other provinces, most of its shoreline is easily accessed by people, increasing the probability of carcass detection. We did not try to determine specifically whether reported cases of stranding were

more likely to come from the vicinity of cities, although in the Pacific region the harbor porpoises submitted seemed to be predominantly clustered around highly populated centers such as Victoria and Vancouver, presumably because carcasses and stranded animals are more likely to be found and reported in such areas. In their study of cetacean strandings in the Canadian Maritime provinces, Nemiroff et al. (2010) briefly discussed the many factors that can influence the likelihood of stranding events being reported, such as proximity to large cities, higher concentrations of whales in rich feeding areas, and thus larger numbers of observers in these areas, and the proportion of accessible beaches in a particular region.

Cause of death

Unknown

A cause of death could not be determined with confidence in 123 (51.0%) of the 241 cases reviewed. Autolysis was partly responsible for the undetermined results in some cases. An unknown proportion may also be attributed to anthropogenic causes since these can be difficult to diagnose with certainty. In particular, drowning from entanglement in fishing gear may leave little to no evidence, especially if even moderate autolysis has allowed deterioration of the skin surface, thus masking abrasions or small indentations caused by the nets.

In the Pacific region, the larger proportion of undiagnosed cases could be explained in part by inconsistent levels of examination and diagnostic evaluation in the early years up until 2001, when a better system for carcass response and collection was established, and possibly in general by provision of less information to the pathologists on the circumstances surrounding the animals' death. The reverse situation could explain the fact that all causes of mortality identified as mishap were from the Atlantic region, as these diagnoses depended on a detailed history of the circumstances surrounding the animals' death.

Infectious disease

Infectious diseases were the most commonly diagnosed cause of death for the Atlantic and Pacific regions, together and separately. Infectious diseases, particularly pneumonia (bacterial and parasitic), were also a leading cause of mortality in other populations of harbor porpoises previously studied (Baker

& Martin 1992, Siebert et al. 2001). Similarly, they are the most prevalent cause of mortality in the isolated population of beluga *Delphinapterus leucas* in the St Lawrence Estuary (SLE) (Lair et al. 2016) and a substantial cause of mortality in bottlenose dolphins *Tursiops truncatus* in coastal waters of South Carolina, USA (McFee & Lipscomb 2009). However, it is possible that animals of coastal species such as harbour porpoises, belugas and bottlenose dolphins debilitated by an infectious disease seek shallower waters to reduce energetic demands of swimming and are thus more likely to be found after death than animals dying as a result of other causes.

Infectious causes of death in this study included those of a viral, bacterial, fungal, and parasitic nature. Of the bacteria identified, *Vibrio* sp., *Photobacterium damsela*, and *Salmonella* sp. are zoonotic and have been associated with previous exposure to fish (Harper 2002); *Clostridium difficile* generally resides in the large intestine of mammals (including humans), and therefore its presence can be an indication of fecal contamination of water, as is that of *Salmonella* sp. (Daoust & Prescott 2007, Anderson et al. 2015).

Cryptococcosis, responsible for 8 of 13 cases of fatal fungal infection in this study, all from the Pacific region, is due to the basidiomycetous yeast *Cryptococcus gattii* (formerly *C. neoformans* var. *gattii*) and can cause cutaneous, respiratory and neurological disease in immunocompromised hosts, including humans. The disease emerged in 1999 in humans and a variety of other species, including harbor porpoises, in southwestern British Columbia, largely within its coastal Douglas fir (*Pseudotsuga menziesii*) biogeoclimatic zone, highlighting the role that marine mammals can play as sentinels of environmental health (Duncan et al. 2006).

The potential role of environmental contaminants in causing immunosuppression, thus predisposing marine mammals to infectious disease, was not examined in this study. However, there is published evidence of an association between exposure to heavy metals and organic pollutants and increased susceptibility to infectious disease in harbour porpoises and other marine mammals (Bennett et al. 2001, Jepson et al. 2005, Reif et al. 2015, Lair et al. 2016).

Non-infectious disease

Non-infectious causes of death included congenital defects (cardiac malformation, hepatic hamartoma), perinatal complications (dystocia, meconium aspiration syndrome presumably resulting from dystocia),

and saxitoxin poisoning. Cardiac anomalies have been previously reported in marine mammals (Gray & Conklin 1974, Dennison et al. 2011). Poor maternal condition, *in utero* viral infection, or exposure to toxin, as well as chromosomal and genetic alterations have been suggested as possible causes that are well described in humans (Schoen & Mitchell 2010). A hamartoma represents a benign, non-neoplastic cellular proliferation in a localized area that surpasses the normal growth of cells in that area and is presumed to be of congenital origin (Kusewitt 2012). Hamartomas have been reported in a California sea lion *Zalophus californianus* (Blankenship et al. 2008) and in a neonatal harbor seal *Phoca vitulina* exposed to polycyclic aromatic hydrocarbons (Harris et al. 2011). Dystocia has been documented as a cause of death in a variety of marine mammal species including harbor porpoises. Lair et al. (2016) observed a recent increase in occurrence of perinatal complications in the SLE beluga population and discussed the possible role of perinatal environmental stresses, nutritional stress, and endocrine-disrupting environmental contaminants as risk factors. Saxitoxin is a neurotoxin produced by dinoflagellates that is responsible for paralytic shellfish poisoning in humans and is capable of killing marine mammals (Geraci et al. 1989). The 2 porpoises killed by this toxin were from an episode identified in the St. Lawrence Estuary in 2008 that affected a large number of animals of various species (Scarratt et al. 2013). Although comprising a small percentage, the non-infectious causes of mortality found in the harbor porpoises examined in this study could potentially reflect a much larger impact of environmental toxins within the marine environment.

Emaciation/starvation

Evaluation of body condition in small and large whales is often based mainly on the appearance of the epaxial muscle mass; blubber thickness by itself is not considered a reliable indicator of this parameter, although we did see a positive correlation between mean blubber thickness and subjective BCS (Read 1990, Arbelo et al. 2013, Joblon et al. 2014).

Emaciation with no other clinically significant disease process was a common cause of mortality in the Atlantic region, which is consistent with similar studies from Europe (Jauniaux et al. 2002). The cause of this emaciation was unknown, but more than half of the animals were calves that were still dependent on their mother. Separation of mother and calf has been

documented in other cetaceans in areas of high boating activity and could thus be considered a possible anthropogenic cause of mortality (Van Parijs & Corkeron 2001). Fishing vessels are common in both regions included in this study, and the appearance of pleasure crafts in early summer coincides with the approximate birth date of harbor porpoises. In our study, there were more harbor porpoises classified in this category from the Atlantic than from the Pacific region, but the reason for this could not be determined.

Dependent calves: no identifiable disease

A specific cause of death could not be determined for 11 calves that had presumably been separated from, or abandoned by, their mother and had no identifiable disease process such as emaciation. Disorientation and eventual stranding by mishap may have occurred in some of them. Two of these 7 calves had recently been born. The capacity of a newborn animal to cope with sudden food deprivation can vary substantially among species. For example, the amount of fat present at birth in healthy bovine calves is enough to provide energy for at least 7 d of severe malnutrition in a thermoneutral zone (14–16°C) (Schoonderwoerd et al. 1986). In contrast, a newborn piglet has very little fat available for mobilization and relies mainly on glycogen in liver and muscle as an endogenous source of energy (Mersmann 1974). It is unclear where the harbor porpoise fits in this spectrum. The marine environment where and when a harbor porpoise calf is born likely requires a major expenditure of energy for thermoregulation (Koopman 1998). It is therefore possible that the death of a newborn calf would result from acute calorie depletion combined with hypothermia. However, the category of emaciation/starvation included 2 recently born calves with marked atrophy of their epaxial muscle mass, indicating that some newborn harbor porpoises deprived of food may survive for some time on endogenous sources of energy. In the study of the SLE beluga population by Lair et al. (2016), the cause of death of the vast majority of dependent calves examined also could not be clearly determined.

Anthropogenic causes

Anthropogenic causes were among the main diagnosed causes of death in both regions and within

the combined dataset. This is consistent with other studies that have shown that human factors, more specifically boat collisions and fisheries by-catch, are important causes of mortality in cetaceans, including harbor porpoises (Lawson et al. 2004, Lesage et al. 2004, Arbelo et al. 2013, van der Hoop et al. 2013). The overall impact of death from anthropogenic causes is likely underestimated in this study since some cases included in the 'trauma' category were suspected, but not proven, to have been caused by boat collision and since some cases included in the 'unknown' category may have resulted from drowning secondary to entanglement in fishing gear without leaving evidence of this in the carcass. Entanglement in fishing gear was the leading anthropogenic cause of death of harbor porpoises identified in both regions (20 of 21 cases), despite the fact that a conclusive diagnosis of entanglement can be difficult. Ideally, it requires a history of the animal being found within a fishing net or lesions such as linear cutaneous furrows, indentations or abrasions affecting the snout, flippers, and/or cranial part of the torso, and possibly evidence of recent ingestion of fish (Kuiken 1996).

Trauma

All suspected cases of predation were attributed to killer whales *Orcinus orca* and were from the Pacific region, corresponding to regional differences in the range and abundance of this species (Forney & Wade 2006). Predation of harbor porpoises by sharks has been reported in the Atlantic region (Arnold 1972), but no such case was found in this study. Predation by grey seals *Halichoerus grypus* on harbor porpoises has been described in the southeastern North Sea (Leopold et al. 2015). This has been suspected, but not proven, to also happen in the Atlantic region.

Vessel strikes involving both small craft and large ships have been documented as a cause of mortality of marine mammals (Stone & Yoshinaga 2000, van der Hoop et al. 2013). Although it may be difficult to distinguish collisions with boats from other forms of trauma, 2 harbor porpoises in this study had deep lacerations of the dorsal skin suggestive of propeller wounds (Laist et al. 2001). The cases of trauma of unknown origin could have been due to predation or to collision with boats, but also to aggression by whales of larger species (Baird 1998, Haelters & Everaarts 2011, Larrat et al. 2012).

Parasitism

Parasitism was a common incidental finding in harbor porpoises included in this study. Adults were parasitized more often than juveniles and calves, perhaps reflecting an increased likelihood of ingesting parasites from intermediate hosts with age (Measures 2001). Nematodes within pterygoid sinuses, in some cases identified as *Stenurus minor*, were reported only from the Atlantic region. This was likely because this anatomical location was not examined systematically in carcasses from the Pacific region. The pathological effects of this nematode are poorly known. Early reports associated heavy infection with stranding, presumably due to disruption of echolocation, but this has not been conclusively shown, in contrast to other middle ear parasites like the trematode *Nasitrema* sp. (Measures 2001).

Because of a long period of co-evolution, many parasites may be host-adapted, and infections are not necessarily associated with the cause of death (Anderson 1982). In particular, the clinical significance of pulmonary parasitism in odontocetes can be difficult to assess (Lair et al. 2016). Factors allowing pulmonary parasitism to progress to clinically significant disease, including complication by secondary bacterial infection, could be related to immunosuppression caused by organic pollutants, marine algal toxins, concurrent infection with viruses, or environmental stressors such as marine traffic and noise (Jepson et al. 2000, Bossart 2011, Rolland et al. 2012).

CONCLUSIONS

Overall, the leading known cause of mortality for harbor porpoises in Canadian waters was infectious disease, although anthropogenic causes were likely underestimated. Parasitism was commonly observed but was considered a secondary diagnosis in most cases, suggesting caution in interpreting parasitic infection as a significant cause of death. Previous reports of harbor porpoise mortality often indicate that the top 3 causes of death are emaciation, negative fisheries interactions, and infectious disease (Trippel et al. 1996, Jauniaux et al. 2002, Wright et al. 2013, Huggins et al. 2015).

Coastal ecosystems throughout the world have suffered extensively from a wide variety of human activities, since more than half of the world's human population resides within approximately 60 km of the coast (Kennish 2005). Moreover, there is published evidence of a correlation between occurrence

of infectious diseases in harbor porpoises and burdens of environmental contaminants and their associated immunosuppressive effects (Bennett et al. 2001, Jepson et al. 2005). Being typically a coastal species, the harbor porpoise is more likely than other species to be exposed to contaminants and pollutants of industrial and agricultural origin (Lafferty et al. 2004, Kennish 2005, Gibson et al. 2011, Barbosa et al. 2015). This may explain at least partly the relatively high proportion of infectious diseases identified in both regions in this study. However, determination of levels of environmental contaminants in animals included in this study was not attempted. A proper comparison of such levels between the east and west coasts would have required extensive methodology in order to take into account the multiplicity of factors (biological, regional, temporal) influencing the types, chemical profiles, and potential impact of these contaminants (Muir et al. 1996, Westgate et al. 1997). We are not aware of major differences in natural and human-related environmental conditions between waters of the east and west coasts of Canada that should have been considered in the interpretation of our results, except for the fact that, in contrast to the west coast, large water ways of the east coast are frozen in winter. The proportions of deaths from infectious disease were similar in both regions, thus reducing the likelihood of a differential influence of contaminants in these 2 regions.

The proportion of cases of entanglement in fishing gear was also similar in both regions. Negative interactions with fisheries are often considered the leading conservation threat for harbor porpoises and are often the only focus of mitigation measures (Trippel et al. 1999, Read et al. 2006, Gönener & Bilgin 2009). While fisheries interactions undoubtedly play an important role in harbor porpoise mortality, this and other studies (Jauniaux et al. 2002, Hohn et al. 2013) show that other causes are involved and, in particular, demonstrate a knowledge gap regarding the overall impact of infectious diseases on populations of harbor porpoises.

The actual impact of each cause of death on populations of harbor porpoises cannot be predicted based on the current datasets. Nonetheless, considering the very low proportion of carcasses normally recovered from cetacean mortality events (1–2% by some estimates; Brown 1975, Williams et al. 2011), observations of carcasses coming ashore represent a valuable opportunity to study the natural history of these animals and the diseases that may affect their populations.

This study also indicates a need to better understand the pathogenesis of infectious diseases in marine mammals, including the potential contribution of immunosuppression and its various possible causes. The identification of various pathogens of zoonotic significance, some of them suggestive of fecal contamination of coastal waters, highlights the importance of health surveillance in marine mammals as sentinels of ocean health.

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