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EPIZOOTIOLOGY OF MORBILLIVIRUS INFECTION IN HARP, HOODED, AND RINGED SEALS FROM THE CANADIAN ARCTIC AND WESTERN ATLANTIC

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ABSTRACT: Using a virus neutralization technique, we found phocine distemper virus (PDV) antibody in 130 (83% of 157) harp seals (*Phoca groenlandica*) from the western North Atlantic sampled between 1988 and 1993 inclusive. In contrast, only 44 (24% of 185) hooded seals (*Cystophora cristata*) had antibodies against PDV even though they were sympatric with harp seals and were sampled over a similar period, from 1989 to 1994 inclusive. Antibodies occurred in 106 (41%) of 259 ringed seals (*Phoca hispida*); this prevalence was higher than expected given the solitary behavior and territoriality characteristic of this species. Seropositive ringed seals were found at each of seven locations across Arctic Canada from Baffin Bay to Amundsen Gulf at which samples were collected between 1992 and 1994. However, the prevalence of infection was highest where ringed seals are sympatric with harp seals in the eastern Canadian Arctic.

Key words: Harp seal, *Phoca groenlandica*, hooded seal, *Cystophora cristata*, ringed seal, *Phoca hispida*, morbillivirus, serology, immune response, histopathology, epizootiology.

INTRODUCTION

A novel morbillivirus, phocine distemper virus (PDV) (Cosby et al., 1988) caused an epizootic of unprecedented magnitude that swept through harbor seal (*Phoca vitulina*) populations in western Europe between April and September 1988 (Heide-Jørgensen et al., 1992). Some workers suggested that it may have been introduced by harp seals (*Phoca groenlandica*) emigrating south of their normal range into the North Sea (Goodhart, 1988; McGourty, 1988). Enzootic morbillivirus infection was indeed confirmed in harp seals from the Barents Sea and Jan Mayen (Markussen and Have, 1992; Stuen et al., 1994), but conclusive evidence of an epizootiological link with the epizootic in western Europe awaits isolation of the harp seal virus.

Documentation of morbillivirus infection in the western Atlantic harp seal population has been more sporadic. Henderson et al. (1992) found serologic evidence of infection in three Canadian harp seals as early as 1973, corroborating a report of seropositive harp seals on the west coast of Greenland in 1985 and 1986 (Dietz et al., 1989). More recently, morbillivirus encephalitis was detected in a juvenile harp seal that stranded in the Gulf of St. Lawrence, Canada (Daoust et al., 1993). This was the first indication that morbillivirus infection could play a role in the natural mortality of harp seals.

Hooded seals (*Cystophora cristata*) and ringed seals (*Phoca hispida*) are sympatric with harp seals through much of their range (King, 1983). Based on serologic studies on hooded seals from Jan Mayen (Stuen et al., 1994) and ringed seals from

Greenland (Dietz et al., 1989), infection of these species may be infrequent. Indeed, no serologic evidence of infection was detected in Alaskan ringed seals sampled during the 1980s (Osterhaus et al., 1988), and only a few seropositive animals were found in a limited survey of ringed and hooded seals sampled in eastern Canada (Henderson et al., 1992). Our objectives were to determine the prevalence of infection in free-ranging harp and hooded seals from Atlantic Canada and in ringed seals from the Canadian Arctic, and to determine whether morbilliviruses caused the death of seals that died after stranding along the Atlantic coast of Canada and the United States.

MATERIALS AND METHODS

Adult female harp seals (n = 104) were sampled between 1988 and 1993 while hauled out on pack ice in the Gulf of St. Lawrence, Canada, during the March breeding season (Table 1). Breeding patches were located by helicopter and the seals were approached on foot, captured in nets, and manually restrained for blood sampling. Harp seals from the same population sampled after stranding on the Atlantic coast were mainly juveniles (≤2 yr) as determined by pelage patterns and body lengths (Sergeant, 1991) (Table 1). Live stranded seals retrieved along the coast were taken to rehabilitation facilities and sampled for blood within 24 hr of admission. The blood was collected from either the tarsal venous plexus or the epidural vein into untreated glass tubes and allowed to clot for several hours (Geraci and Lounsbury, 1993). The serum was separated by centrifugation and stored at −20 C. An adult male harp seal killed by Inuit hunters at Salluit, northern Quebec, Canada, was sampled for blood by cardiac puncture.

Capture and sampling of 130 adult female hooded seals was carried out in the same manner as for the adult female harp seals (Table 1). In addition, hooded seals from this population were sampled for blood after they were found stranded along the Atlantic coast from Sable Island, Nova Scotia, to northeast Florida (Table 1). Based on body length, these animals were all juveniles (<2 yr) (McLaren, 1993). One adult male was sampled by cardiac puncture after it was shot by Inuit hunters close to Nottingham Island, Northwest Territories, Canada.

Free-ranging ringed seals were killed by Inuit hunters at seven locations in Arctic Canada ranging from Pangnirtung on Cumberland Sound in the east to Paulatuk on Amundsen Gulf in the west (Table 1, Fig. 1). A blood sample was collected from the body cavity within 1 hr of death and the sample was stored at −20 C. Age was determined by counting dentinal annuli in canine teeth (McLaren 1958); seals were classed as juveniles (≤2 yr) or adults (≥3 yr). The stranded ringed seals were all juveniles and blood samples were collected from them on admission to rehabilitation facilities.

Serology was carried out using a microneutralization test against phocine distemper virus (PDV) and canine distemper virus (CDV) as described by Duignan et al. (1994). In addition, frozen whole blood that was not suitable for the microneutralization assay was tested by a modified plaque reduction assay (Wolf and Quimby, 1973) using PDV (C. Lyons, The Queens University, Belfast, Northern Ireland) and CDV Culture No. VR-128 from the American Type Culture Collection (ATCC), Rockville, Maryland (USA). Both viruses were adapted to Vero cells (Culture No. CRL 1586, ATCC) grown in Minimum Essential Medium with Earle's salts (EMEM, Gibco BRL, Burlington, Ontario, Canada) supplemented with 7.5% heat-treated (56 C for 30 min) fetal bovine serum (FBS, Gibco BRL). Virus stocks were prepared by infecting Vero monolayers in 75-ml flasks at low multiplicities of infection (MOI) of <0.01 plaque forming units (PFU) per cell. The virus was allowed to adsorb for 1 hr at 37 C. After washing, the monolayer was flooded with 20 ml EMEM containing 2% FBS. When cytopathic effects were seen in over 75% of the monolayer, the virus was harvested by freezing the flasks (−70 C) and removing cell debris by centrifugation (5,000 × G for 30 min). Aliquots of supernatant were stored at −70 C. Whole seal blood was prepared for assay by diluting it 1:1 with Minimum Essential Medium and Hepes (14 mM) (Gibco BRL) with 2% FBS. The mixture was then heated at 56 C for 30 min to inactivate complement, and serial two-fold dilutions were made using EMEM supplemented with 2% FBS. An equal volume (100 µl) of virus containing approximately 200 PFU was added to each dilution and after incubating for 1 hr at 15 C, 100 µl aliquots were placed centrally on confluent Vero cell monolayers grown in tissue culture dishes (60 × 15 mm). For CDV, plaque reduction was evaluated after 8 days, while PDV plates were supplemented with culture medium on day 7 and assessed on day 14. Titers were expressed as $\log_2$ of the reciprocal of the highest dilution of serum that gave an 80% reduction in virus plaques per inoculum (Habel, 1969). Antibody titers of $\log_2$

TABLE 1. Sampling locations and dates for harp, hooded, and ringed seals from Arctic Canada and the Atlantic coast of North America.

Location	Year	Juvenile		Adult		Total
		Male	Female	Male	Female	
Harp seals (free-ranging)						
Gulf of St. Lawrence (47°30′N, 62°00′W)	1988 to 1993	—[a]	—	—	104	104
Salluit, Quebec (62°45′N, 75°30′W)	1992	—	—	1	—	1
Harp seals (strandings)						
Atlantic coast (46°25′N, 63°10′W to 40°38′N, 73°08′W)	1988 to 1994	27	22	1	2	52
Subtotals		27	22	2	106	157
Hooded seals (free-ranging)						
Gulf of St. Lawrence (47°00′N, 61°30′W)	1989 to 1994	—	—	—	130	130
Nottingham Island (63°20′N, 77°55′W)	1990	—	—	1	—	1
Hooded seals (strandings)						
Atlantic coast (43°55′N, 60°00′W to 30°57′N, 81°53′W)	1984 to 1994	26	28	—	—	54
Subtotals		26	28	1	130	185
Ringed seals (free-ranging)						
Pangnirtung, NWT[b] (65°40′N, 65°00′W)	1992	17	13	19	27	76
Salluit, Quebec (62°45′N, 75°30′W)	1992	—	—	2	1	3
Arctic Bay, NWT (73°00′N, 85°00′W)	1993	6	10	13	8	38[c]
Eureka, NWT (80°00′N, 86°00′W)	1994	3	3	5	7	18
Resolute, NWT (74°30′N, 95°00′W)	1993	—	—	7	2	9
Holman, NWT	1993	—	—	20	11	31
(70°50′N, 117°40′W)	1994	—	—	21	8	29
Paulatuk, NWT	1993	1	2	3	3	9
(69°30′N, 124°00′W)	1994	10	9	7	12	38
Ringed seals (strandings)						
Atlantic coast (45°00′N, 67°00′W to 40°38′N, 73°08′W)	1981 to 1992	4	4	—	—	8
Subtotals		41	41	97	79	259[c]

[a] Not sampled.
[b] Northwest Territories.
[c] Includes one animal for which the sex was unknown.

4 (1:16 dilution), or greater, were considered positive.

Radio-immunoprecipitation assays (RIPA) were carried out using ^{35}S-labelled CDV protein as described by Duignan et al. (1995a). Test sera included samples from 20 harp, 20 hooded, and three ringed seals that were previously assayed by the virus neutralization test (Duignan et al., 1994). Serum from a dog vaccinated against CDV was used as a positive

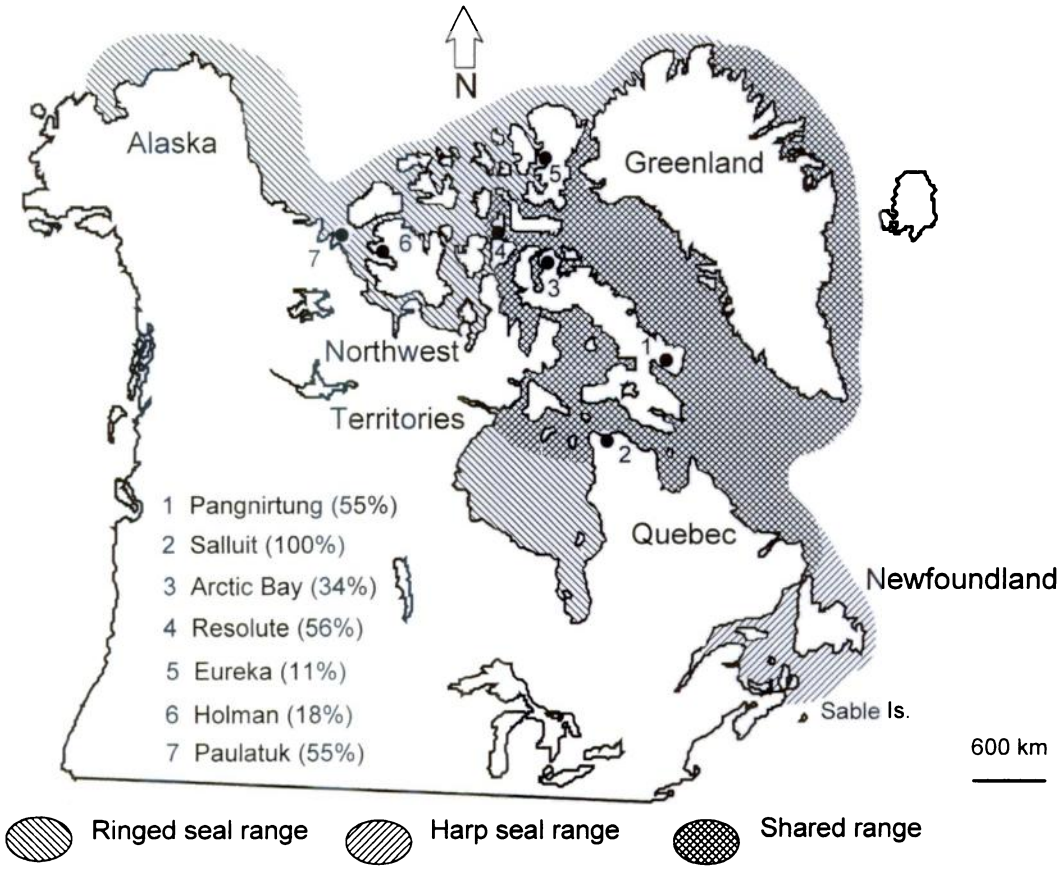

FIGURE 1. Blood samples were collected from ringed seals taken by Inuit hunters from the communities numbered 1 through 7 in Arctic Canada between 1992 and 1994. The shared range of harp and ringed seals in the eastern Canadian Arctic is shown (After McLaren, 1958; Sergeant, 1991). The number in parentheses is the overall PDV antibody prevalence in each sampling area.

control. Canine distemper virus polypeptides in fluorographs were identified based on published molecular weights (Rima, 1983) and by using monoclonal antibodies against the nucleocapsid (N), hemagglutinin (H), phosphoprotein (P), and fusion (F) protein (Örvell et al., 1985). Bands precipitated by test sera were quantitated by using an arbitrary visual scale: 0 (absent) to 6+ (very strong); this was based on the width and intensity of the relevant polypeptide compared to that of the positive control (Miele and Krakowka, 1983).

Frequencies of seropositive animals, and animals with positive RIPA scores, were compared by Yates-corrected Chi-square test and Fisher's exact test on one degree of freedom, and 95% confidence intervals (CI) were calculated for infection prevalences (Martin et al., 1987). Antibody titers against different viruses and between age classes were compared using Student's *t*-test. Statistical analyses were carried out using InStat software (Graph Pad Software, Inc., San Diego, California, USA).

Between January 1991 and December 1994, necropsies were performed on nine harp seals and eight hooded seals that stranded along the Atlantic coast from the Gulf of St. Lawrence (46°25′N, 63°10′W) to Long Island, New York (USA) (40°38′N, 73°08′W). The seals either were recently dead when found or had died shortly after arrival at a stranding response center. Five animals that could not be rehabilitated for medical reasons were euthanized using sodium pentobarbital (240 mg/ml, 0.5 ml/kg intravenous, Vorteck Pharmaceuticals, Dearborn, Michigan, USA, or Livingston Pharmaceuticals, Moncton, New Brunswick, Canada). At necropsy, tissue samples from the eyelid, tongue, trachea, lungs, spleen, peripheral lymph nodes, liver, pancreas, stomach, kidneys, urinary bladder, and brain were fixed in 10% buffered formalin, processed through alcohol and xylene,

TABLE 2. Prevalence of phocine distemper virus neutralizing antibodies in harp, hooded, and ringed seals from Arctic Canada and the Atlantic coast of North America, 1984 to 1994.

Species	Age class		Sex			Total
	Juvenile	Adult	Female	Male	Uk[b]	
Harp	24/49 (49)[a]	106/108 (98)	115/128 (90)	15/29 (52)	0/0	130/157 (83)
Hooded	12/54 (22)	33/131 (25)	42/158 (27)	3/27 (11)	0/0	45/185 (24)
Ringed	36/83 (43)	69/176 (39)	52/120 (43)	52/138 (38)	1/1	105/259 (41)

[a] Number positive/number tested (percent positive).
[b] Unknown sex.

and embedded in paraffin. Sections were cut at 5 μm and stained for both light microscopy and for morbillivirus antigen as described by Daoust et al. (1993).

RESULTS

We found PDV neutralizing antibodies in 130 (83% of 157, 95% CI = 77 to 89%) harp seals; the prevalence was significantly ($P < 0.0001$) higher in adults than in juveniles (Table 2). Only 44 (24%, 95% CI = 18 to 30%) of 185 hooded seals from the same area had antibodies. The association between host species and prevalence was significant ($P < 0.0001$), both for the juvenile age class ($P < 0.01$) and for the adults ($P < 0.0001$). There was no significant association between the sex and antibody prevalence except for juvenile hooded seals in which the prevalence was higher ($P = 0.02$) in females. The mean antibody titer was significantly higher against PDV than against CDV in seropositive adult harp seals ($P < 0.0001$) and hooded seals ($P < 0.0001$). Titers against PDV were also significantly higher in adult harp seals ($P < 0.0001$) and in adult hooded seals ($P < 0.001$) than in juveniles of either species.

Of 104 female harp seals sampled from 1988 through 1993 during the breeding season in the Gulf of St. Lawrence, 103 (99%, 95% CI = 97 to 100%) were seropositive. By contrast, only 32 (25%) of 130 (95% CI = 18 to 32%) adult female hooded seals sampled in the same region between 1989 and 1994 were seropositive, although there was an increase in prevalence between 1989 and 1993 in this species (Table 3).

The prevalence in ringed seals, 106 (41%) of 259 animals (95% CI = 35 to 47%), was significantly lower than in harp seals ($P < 0.0001$) but higher than in hooded seals ($P < 0.001$). The mean antibody titer in adult ringed seals was higher against PDV than against CDV ($P <$

TABLE 3. Prevalence of phocine distemper virus neutralizing antibody in adult female harp and hooded seals from the Gulf of St. Lawrence, 1988 to 1994.

Year	Harp seal		Hooded seal	
	Positive/tested	Prevalence (95% confidence interval)	Positive/tested	Prevalence (95% confidence interval)
1988	8/8	100%	—[a]	—
1989	19/20	95% (85 to 100%)	0/20	0
1990	18/18	100%	3/18	17% (0 to 34%)
1991	20/20	100%	3/20	15% (0 to 31%)
1992	19/19	100%	4/20	20% (2 to 38%)
1993	19/19	100%	10/18	56% (33 to 79%)
1994	—	—	12/34	35% (19 to 51%)
Total	103/104	99% (97 to 100%)	32/130	25% (18 to 32%)

[a] Not sampled.

TABLE 4. Prevalence of phocine distemper virus neutralizing antibodies in ringed seals at seven locations in the Canadian Arctic.

Sampling location	Year	Age class			Prevalence (95% confidence interval)
		Juvenile	Adult	Total	
Pangnirtung	1992	15/30[a]	27/46	42/76	55% (44 to 66%)
Salluit	1992	—[b]	3/3	3/3	100%
Arctic Bay	1993	7/17	6/21	13/38	34% (19 to 49%)
Eureka	1994	1/6	1/12	2/18	11% (0 to 25%)
Resolute	1993	—	5/9	5/9	56% (24 to 88%)
Holman	1993	—	8/31	8/31	26% (11 to 41%)
	1994	—	3/29	3/29	10% (0 to 21%)
Paulatuk	1993	0/3	0/6	0/9	0%
	1994	10/19	16/19	26/38	68% (53 to 83%)
Total		33/75	69/176	102/251	41% (35 to 47%)

[a] Number positive/number sampled.
[b] Not sampled.

0.0001). However, antibody titers in adult ringed seals, measured by the plaque reduction assay, were significantly lower than the virus neutralizing titers in harp ($P < 0.0001$) or hooded seals ($P < 0.0001$). Although seropositive ringed seals were present at all seven sampling locations across Arctic Canada between 1992 and 1994, the prevalence varied by site and year (Table 4). The area with the lowest prevalence was Eureka; however, the association between location and prevalence was not significant when compared to Arctic Bay, the nearest sampling area to the south. Two locations were sampled in consecutive years. At Holman there was no significant association between year and prevalence. However, year did have a significant ($P = 0.001$) relationship to prevalence between 1993 and 1994 at Paulatuk. Phocine distemper antibody prevalence was significantly ($P = 0.004$) higher in ringed seals from areas shared with harp seals (Arctic Bay, Pangnirtung, Salluit, and Resolute) than in those areas where harp seals do not usually occur (Eureka, Holman, and Paulatuk) (Fig. 1).

TABLE 5. Phocine distemper virus neutralizing antibodies in stranded harp and hooded seals.

Year	Harp seals		Hooded seals	
	Number stranded	Prevalence	Number stranded	Prevalence
1988	4	0/1 (0%)[a]	5	1/4 (25%)
1989	2	0/1 (0%)	2	1/1 (100%)
1990	3	1/2 (50%)	10	2/9 (22%)
1991	13	7/11 (64%)	11	4/8 (50%)
1992	10	5/7 (71%)	3	1/2 (50%)
1993	37	10/17 (59%)	26	0/8 (0%)
1994	35	3/13 (23%)	31	0/13 (0%)
Total	104	26/52 (50%)	88	9/45 (20%)

[a] Number positive/number tested (percent positive).

Virus neutralizing antibodies were found in 26 (50%) of 52 harp seals, nine (20%) of 46 hooded seals and three (38%) of eight ringed seals that stranded on the Atlantic coast. Apart from one hooded seal sampled in 1984, all the sera were collected between 1988 and 1994. The total number of harp and hooded seals found stranded increased over the study period (Table 5).

Based on immunoprecipitation studies, virus neutralizing serum from harp and hooded seals each precipitated the N protein of CDV (Figs. 2 and 3). The F and H glycoproteins were precipitated by 18 (90%) of 20 harp seal sera but only by seven (35%) of 20 samples from hooded seals. The association between species and the ability to precipitate F and H was significant ($P < 0.001$). Three seropositive ringed seal sera precipitated the N and F proteins (not shown).

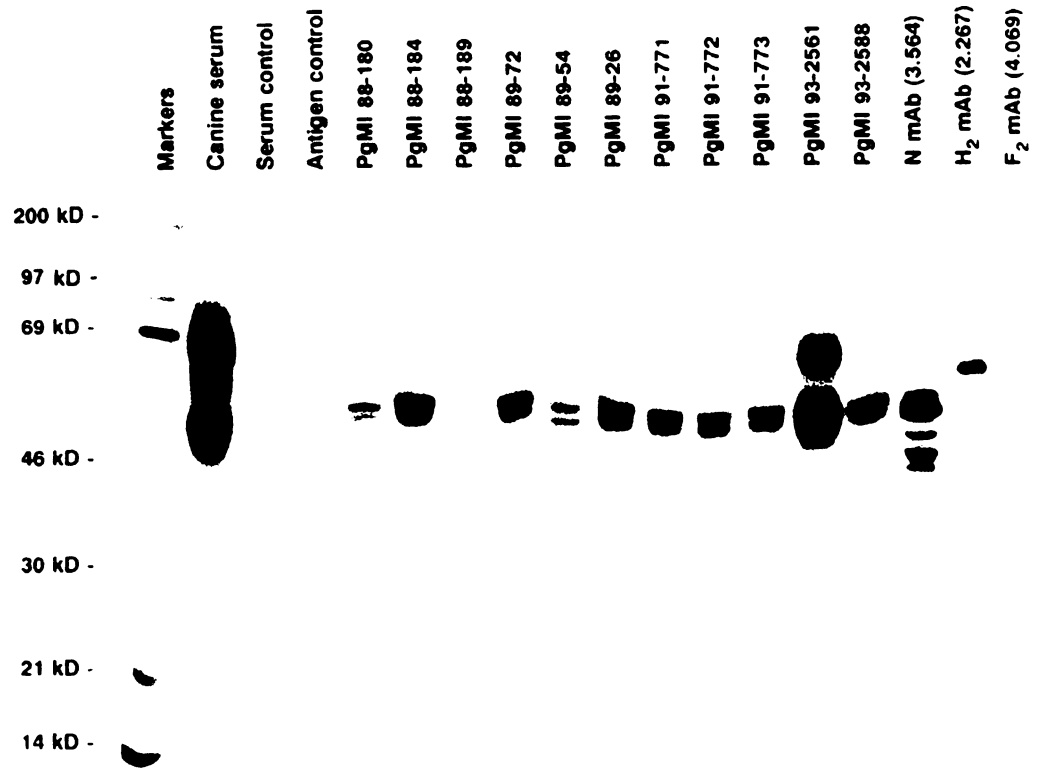

FIGURE 2. Immunoprecipitation of [35]S-methionine labelled canine destemper virus (CDV) antigen with serum from representative adult female harp seals (coded as PgMI-Year-individual number), serum from a dog vaccinated with CDV, monoclonal antibodies against CDV nucleoprotein (N), hemagglutinin (H) and fusion (F) proteins; number in parentheses is a clone designation. The first lane has molecular weight markers with the weight shown on the vertical axis in kilo-Daltons (kD).

Histological changes and positive immunoperoxidase staining consistent with morbillivirus encephalitis were found in one of nine stranded harp seals. Lesions consistent with morbillivirus infection were not apparent in tissues from the stranded hooded seals.

DISCUSSION

From our data, western Atlantic harp and hooded seals, and ringed seals from the Canadian Arctic, have been infected by a morbillivirus similar to PDV since at least 1988. Differential virus neutralization, used here to test harp and hooded seal serum, can be used to reliably distinguish infection in harbor seals by the antigenically-related phocine and canine distemper viruses (Liess et al., 1989). Similar tests also have been used to determine the most likely cause of infection in North American marine mammals such as harbor seals (Ross et al., 1992), Atlantic walruses, *Odobenus rosmarus rosmarus* (Duignan et al., 1994), pilot whales, *Globicephala* sp. (Duignan et al., 1995b), and Florida manatees, *Trichechus manatus latirostris* (Duignan et al., 1995c), from which there were no viral isolates. The modified plaque reduction assay proved to be a reliable method for detecting antibodies in hemolyzed blood from ringed seals sampled after death. The lower mean antibody titers observed in these seals is possibly due to the lower concentration of immunoglobulins in whole blood as compared to serum.

A morbillivirus has not yet been isolated from harp, hooded, or ringed seals, and

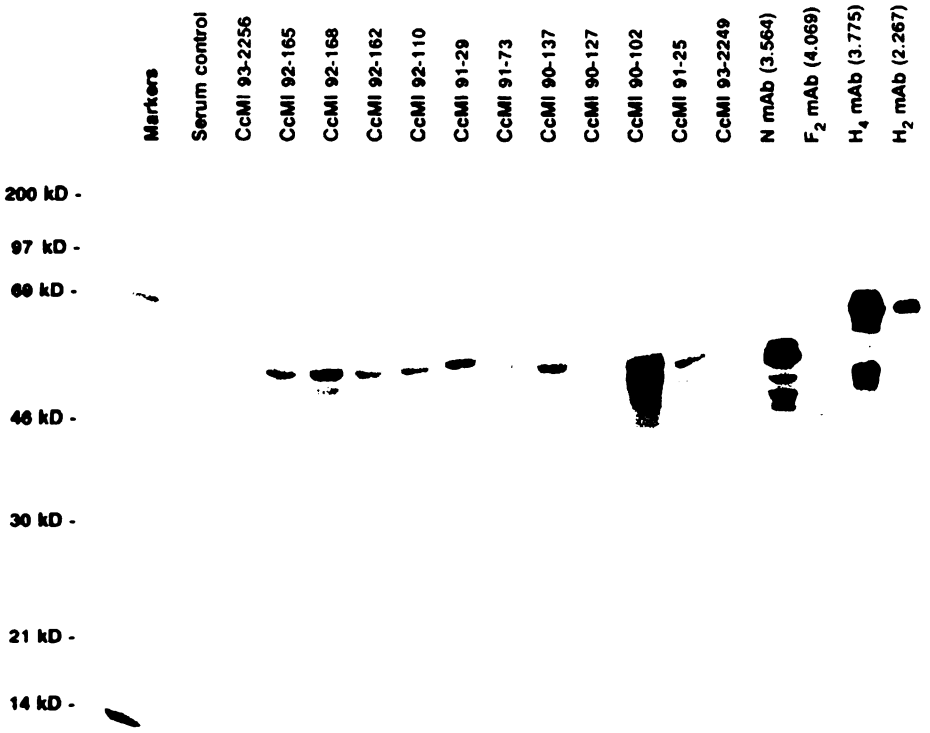

FIGURE 3. Immunoprecipitation of [35]S-methionine labelled canine destemper virus (CDV) antigen with serum from representative adult female hooded seals (coded as CcMI—Year—individual number). Monoclonal antibodies against CDV proteins are the same as in Figure 2.

clinical disease has been described in only one harp seal (Daoust et al., 1993). Thus, immunoprecipitation assays were used to confirm the specificity of the serologic responses, and to compare humoral immune responses to viral antigens. The internal nucleocapsid protein was consistently precipitated by all seropositive seals and, in addition, most of the harp seal sera precipitated one or more of the surface glycoproteins (H and F). In dogs, strong antibody responses against these glycoproteins have been correlated with recovery from CDV infection (Miele and Krakowka; 1983; Rima et al., 1987). By contrast, the responses of hooded seal sera were weak and more typical of the pattern seen in dogs with clinical distemper (Rima et al., 1987) and in harbor seals that died from PDV infection (Rima et al., 1990). This finding, together with significantly lower PDV antibody prevalence, is evidence that hooded seals may be less immunocompetent than harp seals with respect to this virus.

The prevalence of PDV neutralizing antibodies in harp seals was consistently high throughout the study period and equivalent to that found in harp seals in the Barents Sea and Jan Mayen (Markussen and Have, 1992; Stuen et al., 1994). Our findings, together with those from west Greenland harp seals (Dietz et al., 1989), are evidence that morbillivirus infection is probably enzootic in harp seals throughout their range.

Assuming that there is only one morbillivirus circulating among pinnipeds of the North Atlantic, harp seals fit the criteria required of a population to serve as a reservoir for infection. They are numerous, at least four million occur in Canadian waters alone (Stenson, 1995), and they routinely form dense aggregations as part of their

life history (Ronald and Healey, 1981). Under these conditions, a morbillivirus would have ample opportunity to be transmitted between animals in a density-dependent manner. Harp seals also appear to be relatively resistant to clinical distemper, resulting in a high level of herd immunity. A competent immune response may account for this resistance, while antibodies in the milk of lactating females would ensure that their pups are protected during the first weeks of life (Harder et al., 1993). The stranded juvenile harp seal with distemper encephalitis (Daoust et al., 1993) is evidence, however, that there is likely a delicate balance between protection and clinical disease.

Harp seals would seem to qualify as good long-distance vectors of morbillivirus throughout their range and perhaps to other species. Juveniles disperse widely (McAlpine and Walker, 1990), and based on tagging studies, may even traverse the North Atlantic (Sergeant, 1973). Indeed, unusual mass emigrations of harp seals southward along the Norwegian coast between 1986 and 1988 were tentatively linked to the 1988 PDV epizootic in western Europe (Heide-Jørgensen et al., 1992). Seasonally, the high Arctic feeding grounds are shared with walruses, ringed seals, hooded seals, and bearded seals (*Erignathus barbatus*) (King, 1983). Although contact between these species may be infrequent, the high density of pinnipeds along open-water leads and at polynyas, used as migration routes and feeding areas by harp seals, may facilitate casual contact (Stirling et al., 1981). With the onset of winter, harp seals migrate south to Newfoundland and the Gulf of St. Lawrence (Sergeant, 1991) where they share the range of harbor and gray seals (*Halichoerus grypus*), species with enzootic morbillivirus infection (Duignan et al., 1995d). Further elucidation of the epizootiological links between pinnipeds of the western Atlantic and Arctic awaits isolation and characterization of morbilliviruses from each host.

The low prevalence of morbillivirus infection among hooded seals is intriguing. Stuen et al. (1994) found very few seropositive hooded seals in a sample from Jan Mayen and suggested that one explanation may be the preponderance of juveniles tested. In our study, the prevalence of infection was similar between juveniles and adults. We propose three alternative explanations for the result. First, hooded seals, may not be capable of mounting a competent immune response against morbilliviruses. Thus, weak or transient antibody responses against the H and F glycoproteins may escape detection by the virus neutralization test. Second, they may be a dead-end host and allow sufficient viral replication to elicit an immune response but not enough to transmit the disease. Alternatively, they may be highly susceptible to clinical disease and are thus removed from the population. Third, by contrast with harp seals, hooded seals are solitary throughout most of the year (Kovacs and Lavigne, 1986) and may have little opportunity to disseminate viral diseases.

Perhaps of greater interest is the apparent increase in antibody prevalence in recent years among adult female hooded seals in the Gulf of St. Lawrence. Harp seals are sympatric with hooded seals in the western Atlantic, undertaking parallel migrations and utilizing the same breeding grounds (Lavigne and Kovacs, 1988). However, a number of biological characteristics tend to reduce contact between the species. In general, hooded seals prefer deeper water (Reeves and Ling, 1981) and thicker ice floes than harp seals (Sergeant, 1974). However, in the Gulf of St. Lawrence, limited numbers of hooded seals whelp in close proximity to the more numerous harp seals (Kovacs and Lavigne, 1986; Hammill et al., 1992). Assuming that the observed increase in prevalence among hooded seals is real, one possible explanation is that sea ice suitable for whelping was limited in one or more seasons during the late 1980s or early 1990s, forcing harp and hooded seals to share

available resources. Analysis of sea ice charts for the Gulf of St. Lawrence during the month of March between 1985 and 1994 did not support this hypothesis. A second possibility is that infection in hooded seals was linked to an epizootic among New England harbor seals that began in 1991 (Duignan et al., 1995d). It is noteworthy that the harp seal with distemper encephalitis also stranded during the summer of 1991 (Daoust et al., 1993). The most likely scenario is that viral transmission occurs between harp and hooded seals as a chance event. Contact between the species at open-water leads and at breathing holes is not infrequent (K. M. Kovacs, pers. observ.) and now that both populations have grown (Roff and Bowen, 1986; Bowen et al., 1987), interactions are likely to increase.

The ringed seal is the most abundant and ubiquitous marine mammal in the Arctic (Stirling et al., 1981), and we found evidence of morbillivirus infection throughout its range in Canada. The mean prevalence was equivalent to that in harbor seals on the Atlantic coast (Duignan et al., 1995d) and higher than expected given the ecology and behavior of the species (Smith and Hammill, 1981; Smith, 1987). Apart from loose foraging aggregations in open water in summer, adult ringed seals are solitary and highly territorial (Smith, 1987; Kingsley, 1990), characteristics that would not facilitate morbillivirus transmission (Harwood, 1989). A possible explanation of these findings is that ringed seal populations, although highly dispersed, tend to be focally concentrated in areas with habitat that includes stable land-fast ice for breeding and access to open water in the summer (Smith, 1987). Here, adults establish territories and aggressively exclude subadults (Smith and Hammill, 1981). Most of the sampling sites were in areas of preferred habitat (Kingsley, 1990). An exception was Eureka Sound, the most northerly sampling area, which supports a population density almost one-tenth that of Resolute, an area considerably further south (Smith et al., 1979).

Another factor that may influence prevalence is the aggregation of subadult ringed seals in less favorable habitat such as shear zones, polynyas, and areas of unconsolidated ice (Stirling et al., 1981). Such aggregations may provide the best opportunities for transfer of infectious agents between seals sharing breathing holes, and perhaps even facilitate contact with other species utilizing the same resources (Stirling et al., 1981). The higher prevalence of antibodies in ringed seals from the eastern Canadian Arctic, where they are sympatric with harp seals, supports this contention. Juvenile and subadult ringed seals dispersing away from the natal site also may transfer infection between areas (Smith and Hammill, 1981). Indeed, juvenile seals from the western Canadian Arctic migrate as far west as the Beaufort, Chukchi, and Bering Seas (Smith, 1987). As yet, there is no evidence of morbillivirus infection in marine mammals that far west (Osterhaus et al., 1988). However, given the prevalence of antibodies in ringed seals in Amundsen Gulf, at Holman and Paulatuk, it is likely that the virus has already reached Alaskan waters.

In conclusion, we found that morbillivirus infection was enzootic among harp seals of the western Atlantic. Hooded seals also have been exposed to infection, but the lower prevalence of antibodies in this species may reflect either ecological and behavioral constraints on transmission, or the ability to mount an appropriate antibody response to the virus. Casual contact with sympatric harp seals may facilitate transmission of infection to the hooded seal population that might otherwise not sustain enzootic infection. Ecology and social behavior also may be important factors in the epizootiology of morbillivirus infection in ringed seals. Future research needs to be conducted on the nature and relationships of the morbilliviruses infecting each host species in order to gain insight on potential epizootiological links between

these Arctic phocids. Studies also should be directed towards the principal predators of Arctic seals such as polar bears (*Ursus maritimus*) (Stirling and Archibald, 1977), and Arctic foxes (*Alopex lagopus*) (Smith, 1976). This information should help elucidate the importance of these viruses in the population dynamics of Arctic mammals.

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