

THE LACS DES LOUPS MARINS HARBOUR SEAL,

Phoca vitulina mellonae Doutt 1942:

ECOLOGY OF AN ISOLATED POPULATION

A Thesis

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of

The University of Guelph

by

RICHARD JOHN SMITH

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ABSTRACT

THE LACS DES LOUPS MARINS HARBOUR SEAL, *Phoca vitulina mellonae* Doult 1942: ECOLOGY OF AN ISOLATED POPULATION

Richard John Smith
University of Guelph, 1999

Advisor:
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Investigations were undertaken to determine to what extent the Lacs des Loups Marins harbour seal (*Phoca vitulina mellonae*) is distinct and isolated from oceanic harbour seals. The population occurs in the area of Lacs des Loups Marins (Lower Seal Lakes) (56-57°N, 73-74°W), 160 km East of Hudson Bay, on the Ungava peninsula of northern Québec. Written references to the unique appearance and behaviour of this seal date back to 1818. The subspecies was described primarily on the basis of a characteristic morphology and presumed long-time geographic isolation from neighbouring oceanic harbour seals.

A craniometric analysis of *P. v. mellonae* confirmed that it is morphologically distinguishable from oceanic harbour seal subspecies in the Atlantic and Pacific. There was also evidence of behavioural differences: Pupping seems to take place substantially earlier (early May) than in other harbour seal populations at similar latitudes. An analysis of DNA sequences from the mitochondrial control region indicated that the Lacs des Loups Marins animals exhibit some haplotypic divergence from other harbour seals. Analyses of stable isotope ratios in hair and fatty acid signatures in blubber indicated that *P. v. mellonae* feeds exclusively in freshwater. Monitoring of the movements of eight freshwater animals with satellite telemetry over portions of a two year period provided

further evidence that not only are the seals resident within the Lacs des Loups Marins area, but that individual animals exhibit considerable site fidelity. The differentiation exhibited by *P. v. mellonae* is similar to that demonstrated by isolated ringed seal populations in Lakes Saimaa, Finland (*Pusa hispida saimensis*) and Ladoga, Russia (*P. h. ladogensis*).

The totality of the evidence collected provides support for the designation of the Lacs des Loups Marins seal as a distinct subspecies. The population warrants classification as an Evolutionarily Significant Unit. The information gathered on the range of *P. v. mellonae* has implications for future efforts to conserve the population, which is now listed as “vulnerable” by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC).

For John Petagumskum, Sr.,
who knows more about *achikunipih* than I ever will.

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It was the Mauritius pink pigeon that inspired this thesis. Voracious reading of Gerald Durrell as a kid got me thinking about the unique bond that can develop between a researcher and their study animal. As I absorbed the tales of Corfu and other far-away places, I figured the natural and necessary complement to becoming the “world expert” on the arcane aspects of a little known (though wonderful) creature’s biology is a special responsibility for the conservation of that species. I feel very fortunate that this project afforded me the opportunity to explore all of these sides of an incredible animal that exists – almost unknown – in my own country.

This thesis was a long time in coming, and it was only with the support and encouragement of many people that its completion was possible. I hope that my Mom and Dad see a lot of their early teachings in this work. It was their love of the outdoors and our family canoe trips and weekends at Lake Chateaugay that first made me realise that I wanted to become a forest ranger (or some similar occupation!). My sister Lori, my grandparents John and Marjorie Braive, and my late grandmother Joan Smith (who was responsible for our growing up very much aware of our Newfoundland, sea-centred, roots) have always been very supportive of my biological bent.

I’m very grateful to Dave Gaskin for giving me my start in marine mammal biology. The amazing diversity and number of people at Dave’s memorial service last year was testimony to his decency and positive impact on people’s lives. His lab in Zoology

Annex 1, and the Grand Manan Whale & Seabird Research Station, were great places to learn and to discuss marine mammal issues, and were a meeting place for a dedicated group of colleagues and friends that I respect tremendously: Per Berggren, Dave Johnston, Heather Koopman, Aleksija Neimanis, Andy Read, Sue Wallace, Andrew "Sparky" Westgate and Thom Woodley. I had my first "marine mammal experience" with Andrew and Thom, travelling back and forth in very straight lines across the Bay of Fundy. Andrew and Heather aided enormously in the work of this thesis and never doubted its completion (or not that they told me anyway).

My thesis project, and my love of (some might say obsession with) seals in general, would never have come to be without Dave Lavigne -- a trusted advisor, an admired colleague and friend. I remember the exact moment that I decided to work with him. It was the day after the Sandanistas lost the election, and I walked into Mammalogy class to see table after table of stuffed microtine rodents and bats. I observed that it seemed pretty pointless to be studying obscure mammals when a great revolution had just been defeated in Nicaragua. Dave dryly told me to sit down and focus on the lab, because there were plenty of mammal-related matters to worry about. Nearly ten years, and many animal welfare campaigns later, his words seem quite prophetic. Seals are not, as he once told me, "just like small furry whales": they're much more interesting than that. Thanks are due to the other members of my advisory committee – Tom Nudds, Brad White and Bill Leonard -- for their counsel and most especially their patience. Tom also kindly stepped in as co-advisor when needed. Thank you to the members of my examination committee for helpful comments and criticisms: Drs. W. Beamish, V.

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To my friends (and fellow residents of 63 Koch and 134 Paisley), Ian Adams, Paul and Irene Heaven, Mike McMullen, Merrill Stephen, Julie Stewart, and Tim Tinker, I owe more thanks than I can say. They were my home in Guelph. I also owe a debt to a number of organisations, which, though they prolonged my affiliation with the University of Guelph, taught me as much as this thesis project: the Canadian Federation of Students, the University of Guelph Graduate Students' Association (CFS Local 62), CUEW Local 13/CUPE Local 3913 and the International Fund for Animal Welfare (IFAW). I am grateful to the good friends that I met through the student movement --

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Heaven (who, if you analysed their tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios, would likely still show traces of Lacs des Loups Marins brook char feeding), I. Schmelzer, C.A.P. Smith, and A. Westgate -- great friends (and in one case, family) all, provided three years of sterling field assistance. This project wouldn't have happened were it not for them.

I owe the completion of this thesis and this chapter of my life to Jennifer, my best friend. Our relationship began (again) as I was racing out the door for my first field season. She asked me to move in with her over short-wave radio. "In Just – Spring..."

All sampling was done in compliance with University of Guelph Animal Care Committee regulations and permits from the Ministère de l'Environnement et de la Faune of the Government of Québec. This research was funded by the International Marine Mammal Association Inc., Guelph, Ont., the World Wildlife Fund-Canada Endangered Species Recovery Fund, and a Natural Sciences and Engineering Research Council of Canada (NSERC) operating grant to David Lavigne. I was provided with financial assistance by two Ontario Graduate Scholarships, an NSERC Post-Graduate Scholarship and the Norman James Aquatic Mammalogy Scholarship.

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PREFACE

Facts and Fables

You have to go to a windowless building in downtown Pittsburgh, Pennsylvania, in order to see the only known museum specimens of the mysterious Lacs des Loups Marins harbour seal (*Phoca vitulina mellonae*). The story of how these specimens got there is quite incredible: the seal is probably the only endemic Canadian mammal to have a popular adventure story written about its first encounter with science (Twomey 1942). And this story isn't the only one. In fact, upon beginning this thesis project one of the things that struck me was the amazing number and muddled quality of the anecdotes swirling around this subspecies. Separating fact from fiction was sometimes a challenge. As one example, a Hydro-Québec researcher once told me with a straight face that they had concluded the Lacs des Loups Marins seal was herbivorous, and spent much of its time rooting about for vegetation at the bottom of the lake –certainly an unprecedented behaviour for a pinniped and one which the analyses in this thesis found to be false.

Another story that at first blush seemed just as improbable was relayed by a Cree elder in the first year of the project. He told me that the freshwater seal (or *achikunipih*) is almost always solitary, and when disturbed in the middle of the lake will make a beeline back to shore and try to use the contours of the shoreline to escape. Not only did this turn out to be entirely accurate, but the propensity for hugging the shore was exactly the behaviour that allowed us to capture the animals and complete the project.

In addition to its sometimes strange existence at the junction of science and science fiction, the Lacs des Loups Marins seal has been, and continues to be, embroiled in events unfolding in one of the most volatile, and politically complex, regions of Canada.

The Carnegie Museum and Canadian Disinterest

The freshwater seals of Ungava have been known about by Europeans since at least 1757, when Nicolas Bellin first mapped the peninsula. They were the objects of interest by Hudson's Bay Company explorers and fur traders throughout the 19th Century. The Geological Survey of Canada officially took note of their presence in 1898, but it was not until an expedition from Pittsburgh's Carnegie Museum traveled to Lacs des Loups Marins in 1938 that the population was described scientifically.

One of the more puzzling questions surrounding this seal is why it has been known of for so long, with so little work having been done on its biology. Part of the reason for this may be the rather late transfer of the northern Ungava peninsula to full provincial status (1912) and, until the 1970s, the area's comparatively inaccessible and undeveloped nature. In addition, the freshwater seal occupies a uniquely ambiguous legal position: it is a marine mammal (a federal jurisdiction) in freshwater (mostly a provincial jurisdiction) (Anonymous 1990). The province is charged with the seal's management, yet because all governmental marine mammal researchers are employed at the federal level, has minimal expertise in discharging this responsibility. To further complicate matters, Lacs des Loups Marins exists just North of the 55th parallel at the northern extreme of traditional Cree hunting territory. According to the James Bay and Northern

Québec Agreement; however, this is Inuit-controlled land, placing the seals not only in a legal grey zone between the federal and provincial governments, but also between the Cree and the government of Québec (the Cree enjoy considerable autonomy in the region), and between the Cree and Inuit.

When Dr. W.E. Clyde Todd, Curator of Ornithology for the Carnegie Museum wrote to the Canadian government on January 8th, 1937 to request assistance in mounting the expedition to Ungava, the response was astonishing. The letter back to Clyde Todd from Dr. R.M. Anderson, Chief of the Dominion Division of Biology, exemplifies the low priority that the Canadian government still attaches to marine mammal research:

By far the greater part of the aerial surveying in the north
of Canada is in connection with development of
prospecting and mining, and as there is so much pressure
brought to bear for surveys which may throw some light on
developments which have what is called economic
[emphasis original] value, that there is hardly any hope that
any survey party would be sent out by aeroplane for purely
biological collecting.

Anderson went on to say that he is “sorry that [he does] not have many constructive ideas on Hudson Bay exploration”, hopes the Carnegie will “not be disappointed if [the

seals] do not prove to be something ‘new’” and suggests that Clyde Todd should contact the government of Québec, not the government of Canada, regarding specimen collection permits.

Undeterred by Ottawa’s disinterest, the Carnegie team traveled to Lacs des Loups Marins in March, 1938, and were successful in collecting two seal specimens that were used to describe a new subspecies. The expedition was so arduous that the account, when published as the adventure story *Needle to the North*, has been called the “classic narration of the journey-quest” (James 1982, p. 5). The team reached the lake by sledding overland from the Hudson Bay coast, but became dangerously short of food. The photograph of the happy faces of the team members just after two seals were killed, is testament to how quickly the meat of these valuable scientific specimens was rendered into a badly-needed stew. The pelts and skulls made it back to Pittsburgh intact.

The Last Fifty Years

Since 1938, the bulk of research occurring in the area has been instigated by threatened new construction by Hydro-Québec. When Robert Bourassa was re-elected in 1986, the architect of the James Bay hydroelectric project quickly moved ahead with “James Bay II”: huge new proposed impoundments on the Great Whale, Nottaway, Broadback and Rupert Rivers. At the National Energy Board hearings in 1990, Hydro-Québec initially tried to claim that there was no such thing as a freshwater seal (Posluns 1993), while at the same time initiating a variety of investigations of them (Consortium Gilles Shooner & Associés 1991). The Whapmagoostui Cree spent a significant amount of time during

their presentation to the Board speaking about their knowledge of the freshwater seals (Richardson 1991; Posluns 1993). A year later, Hydro-Québec issued a report stating that the freshwater seals were to be found in numerous lakes in the area (Consortium Gilles Shooner & Associés 1991).

The genesis of this thesis also lies in the proposed Great Whale hydroelectric project – which has now been indefinitely shelved by the Québec government. In 1991, the International Marine Mammal Association published a report entitled “Potential Impacts of Hydroelectric Development on Marine Mammals in Northern Québec” (Woodley et al. 1992). Much of this report dealt with the potential impacts on the Lacs des Loups Marins seal, and a later iteration of it was presented in 1994 to the Great Whale project environmental assessment process (Review Bodies 1994). Also in 1994, I authored a status report on the Lacs des Loups Marins seal for the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Smith 1997). The Committee was concerned enough about the possible impacts of development on the Ungava peninsula to list the seal as “vulnerable” (Smith 1997). Around this same time, the International Union for the Conservation of Nature and Natural Resources (IUCN) listed the seals as “suspected but not definitely known to be endangered, vulnerable, or rare due to a lack of reliable information” (Reijnders et al. 1993). This thesis grew out of attempts to provide some of the answers needed to assess the conservation status of this unique Canadian population.

Ironically, the Lacs des Loups Marins harbour seal, which has had stories told about it for hundreds of years, only became the focus of sustained biological investigation at the point when it seemed threatened with possible extinction by the rising waters of Hydro-Québec dams. The animal still has no legal protection. Unlike the United States, Canada has no Endangered Species Act or Marine Mammal Protection Act. There are long-outstanding proposals to establish both federal and provincial parks in the Lacs des Loups Marins area, and the government of Québec has listed the seal as “likely to be designated as threatened or vulnerable” since 1992 (Québec 1992). R.M. Anderson’s comment from 1937 that “I do not think that hair seals are protected any place in Canada, particularly in the open sea” is as true today as it was then.

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THE LACS DES LOUPS MARINS HARBOUR SEAL,

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We hold the highest respect for the freshwater seal; because although it was hard to hunt, it saved the lives of entire families at times past when famine struck. When all else was not available, by miracle a hunter killed a freshwater seal. It was as if the Creator planned it this way.

John Petagumskum Sr., testifying before the National Energy Board, Ottawa, 1990 (Richardson 1991, p. 360)

CHAPTER 1: GENERAL INTRODUCTION

Harbour seals (*Phoca vitulina* L.) are well known for occasionally frequenting lakes and rivers throughout the world (Erlandson 1834; DeKay 1842; Allen 1880; Browne 1909; Grenfell 1910; Prichard 1911; Strong 1930; Dunbar 1949; Fisher 1952; Wheeler 1953; Harper 1956; Harper 1961; Beck et al. 1970; Paulbitski 1974; Roffe and Mate 1984; Williamson 1988). With the possible exception of Lake Iliamna, Alaska, however, the harbour seal (*P. v. mellonae*) population in the area of Lacs des Loups Marins (Lower Seal Lakes) (Fig. 1.1) on the Ungava peninsula of northern Québec, is the only one known for which there exists evidence of year-round residency in freshwater. Much of this evidence is anecdotal and historical, and includes repeated references to the Lacs des Loups Marins seal's restricted distribution and unique morphology and behaviour.

Historical References

The Cree people of Whapmagoostui, who have lived and hunted in the area in question for at least a millennium (Crowe 1991), consider the current range of *P. v. mellonae* to be Lacs des Loups Marins, Petit Lac des Loups Marins, and Lac Bourdel, with some reports of animals having once been in Lac à l'Eau Claire (Clearwater Lake) (Posluns 1993; J. Petagumskum Sr., Whapmagoostui, pers. comm.). This information is corroborated by the Cree toponyms in this area, which make reference to *achikw* (seal) and *achikunipih* (freshwater seal) (Consortium Gilles Shooner & Associés 1991). The Cree contend that the freshwater seal has a number of unique attributes, which are described quite specifically in a recent interview with one of their elders, James Kawapit:

The freshwater seals look different in that their fur is much darker. Their markings are more numerous and are dark.

The marine seals are much lighter in colour. They also have different habits. The other difference is in the taste.

The freshwater seals taste more like fish and their fat tastes different from the marine ones (Posluns 1993, p. 90).

Kawapit's account of the morphological distinctness of *P. v. mellonae* is strikingly similar to that of George Atkinson II who, on July 22, 1818, noted that:

At these ripples is a fishing place where the Indians set nets for seals in the winter; they are quite a different species to those on the sea coast; their skin being covered with short silky hair; yesterday and this day we saw several in the

lakes and rivers; they are in general small and shyer than
the others and much darker in color (p. 61).

Though Atkinson's sighting of seals in Upper Seal Lake (Petit Lac des Loups Marins), during one of the earliest Hudson's Bay Company expeditions into the Ungava interior, is the first written description of these animals, the phrase "Lacs des Loups Marins" is in fact much older. The French cartographer Nicolas Bellin's "Petite Atlas Maritime" (1757) seems to have coined the term, establishing a written record of seals in this area dating back nearly 250 years. Subsequently, other sightings were made in the vicinity of Lac d'Iberville and Petit Lac des Loups Marins (J. Clouston, July, 1820) and Lacs des Loups Marins (W. Hendry, July, 1828; N. Finlayson, July, 1830; Rev. E.J. Peck, July, 1884 in Lewis 1904). Near the turn of the century, during his traverse of the Ungava peninsula for the Geological Survey of Canada, A.P. Low observed seals in Lacs des Loups Marins (July, 1896), and reported that "the Indians kill annually more than thirty, showing that the animal breeds freely in the fresh water" (Low 1898, p. 13).

Written references to the dissimilarity between the Lacs des Loups Marins seals and oceanic harbour seals are not restricted to those of Kawapit and Atkinson. Hendry's (1828) journal makes mention of the "fine quality" (p. 84) of the freshwater seal skins and, in 1888-89, there are a number of specific references to freshwater seal pelts in trade in the records of the Little Whale River post (Hudson's Bay Company Archives, Little Whale River Inventories, Country Produce, B.373/d/22, fo. 14d and B.373/d/23, fo. 13d). During his travels on the Ungava peninsula, Flaherty (1918) was told of seals in Lake Minto (just to the North of Lacs des Loups Marins):

The lake is famous among the Eskimos as the habitat of the fresh-water seal, hunted primarily not as food, but for the pelt, which, much darker, softer, and more lustrous than that of the salt-water variety, is used for their finer garments (p. 119).

More recently, after extensive research among the Inuit of northern Québec, Graburn (1969) described the freshwater seal skins as being among “the softest and most beautifully marked of all ... [that] bring top prices when traded.” (p. 20).

Subspecies Description

The Lacs des Loups Marins seal was brought to the attention of a wider audience in 1942 by the publication of its subspecific description (Doutt 1942) and a popular book entitled *Needle to the North* (Twomey 1942). Both these works were the products of a Carnegie Museum expedition to Lacs des Loups Marins in March, 1938, which resulted in the collection of two type specimens. Doutt was familiar with the anecdotal accounts of *P. v. mellonae* ‘s unusual characteristics and restricted distribution, and he endeavoured to use a more rigorous scientific analysis to evaluate the evidence. The subspecies was described primarily on the basis of its unusually dark pelage and an enlarged coronoid process on the mandible, and on the premise that the population had been isolated for 3000-8000 years, trapped by the Ungava peninsula’s isostatic rebound since the retreat of the Laurentian ice sheet (Doutt 1942). Interestingly, this was an idea that had first been advanced by Low (1898):

The harbour seal is known to travel overland for considerable distances, but its presence in this lake nearly a hundred miles from salt-water at an elevation of nearly 800 feet above the sea, can hardly be due to its migration up such a rough stream as the Nastapoka. Another way in which it might have reached the lake was during the subsidence of the land at the close of the glacial period, when the lake was nearer sea-level than at present by more than 600 feet, and when the deep bay extended inland up the present valley of the Nastapoka to or near the outlet of the lake, with such conditions it would be easy for seals to reach the lake, and having found it full of fish they probably lost the inclination to return to the sea (Low 1898, p. 13).

Radio-carbon dating has recently been used to estimate more precisely the deglaciation date in the coastal hills of the Nastapoca River area to be 7300 years BP (Allard and Séguin 1985).

Doutt's subspecies description was accepted by a number of authors such as Simpson (1944), Anderson (1946), Davies (1958), Scheffer (1958), Banfield (1974), and Bigg (1981). George Gaylord Simpson, in his classic text *Tempo and Mode in Evolution*, actually used the Lacs des Loups Marins seal, and Doutt's estimate of its time of

isolation, as a case study for calculating a rate of evolution (Simpson 1944). In Doutt's words:

I estimated that a new subspecies was produced in about 5,500 years, plus or minus 2,500 years. Simpson (1944, p. 19) points out that this would be about 1,000 generations.

He suggests that in some rodents subspecific differentiation might take place in even less than 300 generations (Doutt 1955).

Other authors disputed the subspecies designation, arguing that the supposed craniological anomalies of *P. v. mellonae* were inconclusive, and that the seals were likely able to travel freely between salt and freshwater (Mansfield and McLaren 1958; Mansfield 1967; Smith and Horonowitsch 1987; also see Honacki et al. 1982; King 1983; Wiig 1989; Reeves et al. 1992). Mansfield (1967) also contended that because Arctic harbour seals are, as a rule, much darker than those from the southern part of the range, the dark colour of *P. v. mellonae*'s pelage is not diagnostic, but rather a characteristic that the freshwater animals share with nearby oceanic harbour seals.

Since Doutt's description, a continued number of seal sightings from all times of the year have been made in Lacs des Loups Marins: In August, 1953 (Doutt 1954); August, 1976 (Power and Gregoire 1978); April, 1984 (Berrouard 1984); and March, 1986 (Smith and Horonowitsch 1987). Other recent evidence, however, from sightings and hydro-acoustic data compiled by Hydro -Québec, indicate that *P. v. mellonae* may be

distributed over a wider area than previously thought and, consequently, have a greater potential to overlap the range of oceanic harbour seals (Consortium Gilles Shooner & Associés 1991).

Implications for Conservation

Though it is difficult to make precise estimates of population size due to a lack of information, it seems clear that the Lacs des Loups Marins seals are few in number (Consortium Gilles Shooner & Associés 1991). The tendency of harbour seals to be distributed in small local populations makes them sensitive to disturbance (Boulva and McLaren 1979; Maine Seal 1994), and there are a number of examples of local harbour seal populations being extirpated, or their numbers reduced, by human activity (DeKay 1842; Allen 1880; Teilmann and Dietz 1993; Reijnders et al. 1993). The likelihood that the Lacs des Loups Marins seal population is similarly vulnerable, and the potential threat of future development -- particularly hydroelectric development -- on the Ungava peninsula, prompted the International Union for the Conservation of Nature and Natural Resources (IUCN) to list *P. v. mellonae* as being "suspected but not definitely known to be endangered, vulnerable, or rare due to a lack of reliable information" (Reijnders et al. 1993). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has designated the population as "vulnerable" (Smith 1997). The government of Québec has also listed the population as "likely to be designated as threatened or vulnerable" (Québec 1992a), and is considering whether to give legal protection to a portion of *P. v. mellonae*'s range (Dubreuil 1983; Québec 1992b). Further investigation of the

distribution of *P. v. mellonae* and the degree to which it is a distinct population is, therefore, extremely relevant to future conservation efforts.

Thesis Description

The objective of this thesis was to test Doutt's hypothesis that the Lacs des Loups Marins seal is an isolated group that is distinguishable from neighbouring oceanic harbour seal populations. This was achieved through the integration of sources of data from investigations of natural history, morphology, molecular genetics, feeding, and range and distribution.

The second chapter of the thesis builds on Doutt's original analysis and contains morphometric comparisons of crania from *P. v. mellonae* and the other four putative subspecies of harbour seal, according to the classification of Bigg (1981). The third chapter is an analysis of the genetic diversity of harbour seals in northeastern North America, including *P. v. mellonae*, accomplished through the comparison of a 500 bp region of the mitochondrial control region. The fourth chapter is an investigation of habitat use by *P. v. mellonae* as revealed by stable isotope ratios and fatty acid profiles. In the fifth chapter, satellite telemetry techniques are used to examine the distribution and range of *P. v. mellonae*. The status report on *P. v. mellonae* that was prepared for the Committee on the Status of Endangered Wildlife in Canada (Smith 1997) is provided in Appendix 1.

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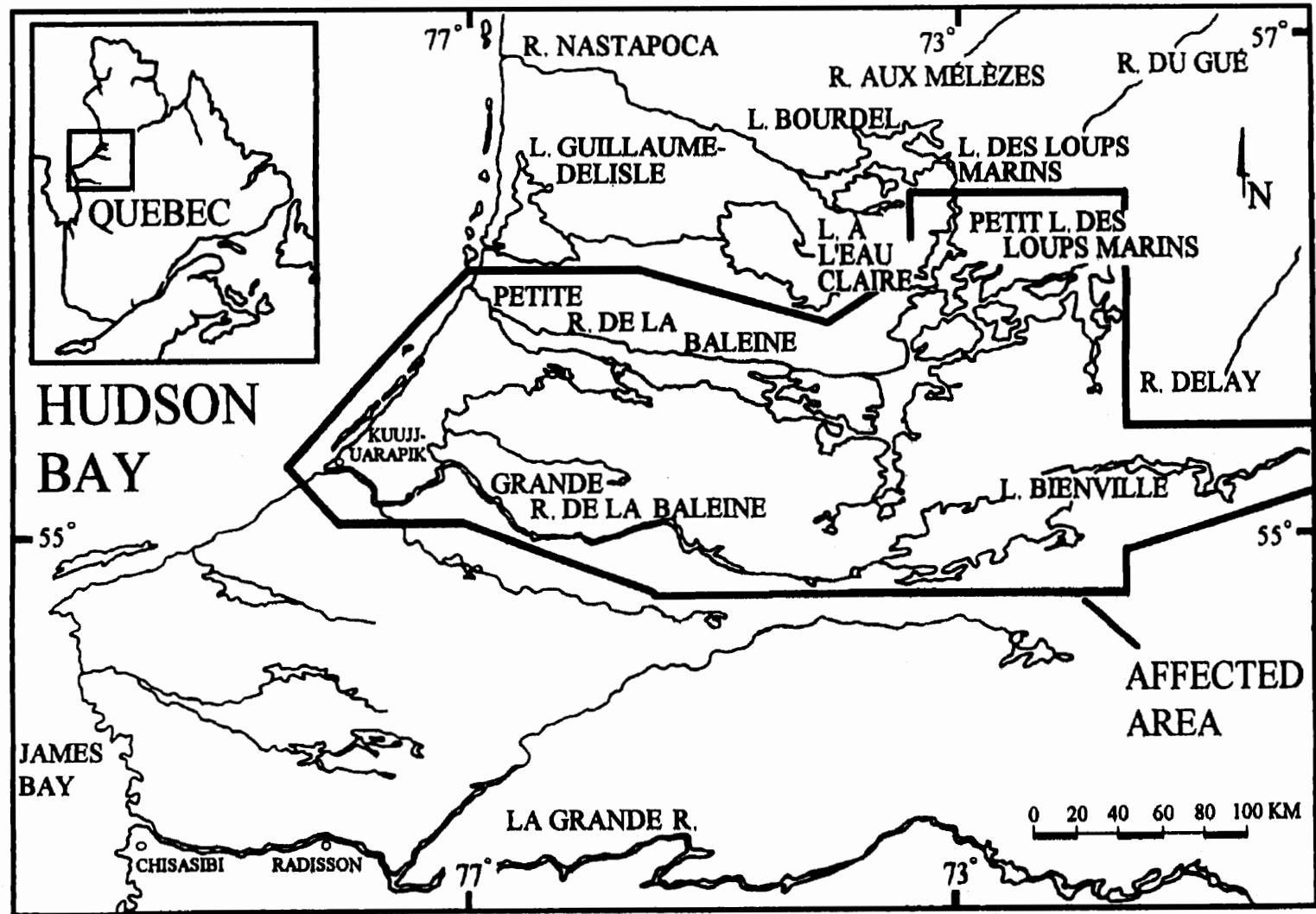
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Fig. 1.1. Known range of *Phoca vitulina mellonae* in relation to Hydro-Québec's proposed Grande Baleine hydroelectric project.



CHAPTER 2: SUBSPECIFIC VARIATION IN CRANIA

OF THE HARBOUR SEAL, *Phoca vitulina* L.

A mythic beast requires a mythic country to inhabit ...
Now known as Nouveau-Québec, Ungava stretches east from Hudson Bay to the Labrador boundary, and north from the Eastmain and Hamilton Rivers to Hudson Strait (James 1982, p. 9)

Introduction

The harbour seal, *Phoca vitulina* (L.), occurs in both the North Atlantic and North Pacific Oceans over a wide range of latitudes (Fig. 2.1). Five subspecies were described by Bigg (1981) on the basis of geographical distribution: *P. v. vitulina* - found from northern Portugal (rare) to the Barents Sea (rare), Iceland, the Faeroe Islands, and Spitsbergen; *P. v. concolor* - found from northern Florida (rare South of Massachusetts) to Hudson Bay, to Admiralty Inlet on Baffin Island and to southeastern and western Greenland, but absent West of Melville Peninsula and northern Baffin Island to the MacKenzie River delta; *P. v. mellonae* - a land-locked population found in the area of Lacs des Loups Marins (Seal Lakes), Québec, Canada; *P. v. richardsi* - found along the central-West coast of Baja California, Mexico, North to the Aleutian Islands, Bristol Bay, and the Pribilof Islands; *P. v. stejnegeri* - found on northeastern Hokkaido, Japan, the Kuril Islands to southern and eastern Kamchatka and Commander Islands, and with an unclear range around the Aleutian Islands (also see Rice 1998).

The phylogenetic relationships among the different populations of *P. vitulina* are poorly understood (Bigg 1981), with the one study of worldwide diversity in harbour

seals having omitted *P. v. mellonae* from the analysis (Stanley et al. 1996). The extent of isolation between *P. v. richardsi* and *P. v. stejnegeri* in the Aleutians has been a matter of contention, with Burns et al. (1984) estimating that the point of demarcation between the two groups occurs near the end of the Alaska peninsula and more recent investigations (O'Corry-Crowe and Westlake 1997; Rice 1998) pointing to intergradation between the groups. The ice-breeding spotted seal, *P. largha*, of the North Pacific, previously regarded as a subspecies of *P. vitulina* (Burns et al. 1984), was elevated to the level of species on the basis of morphological, physiological and behavioural differences (Shaughnessy and Fay 1977; Burns et al. 1984; Delyamure et al. 1984). It is now known that *P. largha* is genetically distinguishable from *P. vitulina* (Mouchaty et al. 1995; O'Corry-Crowe and Westlake 1997).

Pacific and Atlantic harbour seals can be differentiated by a few skull characteristics (Doutt 1942; Chapskii 1969). Differentiation among Atlantic harbour seals is, however, less certain. Stanley et al. (1996) were the first to review the taxonomy of *P. v. vitulina* and *P. v. concolor* since Scheffer (1958), and found that they were also genetically differentiated.

P. v. mellonae was described as a subspecies by Doutt (1942) on the basis of the unusually dark colour of its pelage and the enlarged coronoid process of its mandible. Doutt (1942) and Davies (1958) believed that this seal has been land-locked in the interior of northern Québec for approximately 5000 years, having been trapped in Lacs des Loups Marins since the last ice-age by the isostatic rebound of the Ungava peninsula.

This hypothesis was disputed by Mansfield (1967), who suggested that the supposed morphological anomalies of the *P. v. mellonae* specimens could be artifacts of Doutt's small sample size ($n = 2$) rather than being characteristic of an entire population. Mansfield (1967) also thought it likely that the seals travelled freely between Lacs des Loups Marins and the ocean, only entering freshwater to feed opportunistically. He pointed out that this was a common behaviour of harbour seals (Beck *et al.* 1970; Roffe and Mate 1984; Williamson 1988). The most recent review of the subject (Smith *et al.* 1994), however, which was based on data from this thesis, was unable to reject the hypothesis that the Lacs des Loups Marins seal is a unique subspecies. Rice (1998) subsequently accepted *P. v. mellonae*'s subspecific designation in his review of marine mammal systematics.

Though there remain considerable disagreements over some aspects of pinniped phylogeny, there is an emerging consensus in the literature regarding the biogeographic history of the phocids (Hoberg and Adams 1992). It is suggested that the earliest phocid seals appeared in the North Atlantic approximately 15 million years ago, subsequently dispersing into the Pacific through the Arctic basin during the first opening of the Bering Strait, approximately 3 million years ago (Repenning *et al.* 1979; Wyss 1987). Recent work on the organisation and structure of helminthic parasite faunas among phocid hosts supports these conclusions (Hoberg and Adams 1992).

The fossil record, and parasitological and molecular genetic data indicate, therefore, that *P. v. concolor* is most closely related to *P. v. vitulina*, *P. v. richardsi* is most closely

related to *P. v. stejnegeri* and, following the reasoning of Doutt (1942), *P. v. mellonae* is most closely related to *P. v. concolor*. In the first global examination of harbour seal morphology, the present study investigated these hypothesised relationships using a multivariate analysis of craniometric traits. Such analyses have been extensively used with other marine mammal species to elucidate patterns in infra-specific variation (e.g. Hyvärinen and Nieminen 1990; Ross and Cockcroft 1990; Amano and Miyazaki 1992).

Materials and Methods

Collections of *P. vitulina*, *P. largha* and ringed seal (*Pusa hispida*) crania were examined at the following institutions: Arctic Biological Station, Fisheries and Oceans Canada, Montréal, Québec; Carnegie Museum, Pittsburgh, Pennsylvania; National Museum of Natural History, Washington, D. C.; Canadian Museum of Nature, Ottawa, Ontario; Grand Manan Whale and Seabird Research Station, Grand Manan Is., N.B. Canada; University of Alaska Museum, Fairbanks, Alaska; American Museum of Natural History, New York, N. Y.; Naturhistoriska Riksmuseet, Stockholm, Sweden; Zoologisk Museum, Copenhagen, Denmark; University of Amsterdam Museum, Amsterdam, the Netherlands (Appendix 1).

A total of 303 crania were examined: 5 *P. v. mellonae*, 61 *P. v. vitulina*, 60 *P. v. concolor*, 45 *P. v. richardsi*, 41 *P. v. stejnegeri*, 42 spotted seals (*P. largha*) and 49 ringed seals (*P. hispida*) (Appendix 1). Due to the fragmentary nature of some specimens, only 25 metric and 4 non-metric characters described by an existing experimental protocol (Burns *et al.* 1984) were examined on each skull (Table 2.1).

Measurements were \log_{10} -transformed and the data analysed using the *Statistical Package for the Social Sciences* (SPSS-X).

A MANOVA on the sexed specimens indicated that there was no interaction between taxonomic group and sex (Wilk's $\lambda = 0.53$, $P = 0.31$); thus, data from male, female and unsexed specimens were pooled in subsequent analyses. The effects of individual size differences were minimised using the "C-score" method (Howells 1986), which involved calculating the difference between the Z-score of a single measurement for a given individual, and the mean Z-score of that individual for all the measurements used in the analysis. The means of each study group's C-scored character measurements were calculated, and significant differences between these means analysed using ANOVAs and Tukey-Kramer HSD tests ($P < 0.01$). The data were then submitted to a discriminant analysis (Zar 1984). F-statistics were calculated from the Mahalanobis D^2 distance measures computed between the 7 groups of seals and *a posteriori* classifications made based on the discriminant scores.

Results

The first two functions of the discriminant analysis together accounted for about 83.6% of the variation between the 7 groups of seals (Table 2.1). A plot of the first three canonical variates showed a separation between the 7 groups consistent with the hypothesised relationships: the Pacific harbour seal subspecies were closest in the discriminant space; the Atlantic harbour seal subspecies and *P. v. mellonae* grouped closest together; *P. largha* and *P. hispida* were at some distance from the harbour seal

subspecies (Fig. 2.2). The F-statistics calculated from the Mahalonobis D² measurements indicated that all group means were significantly different from one another ($P < 0.0001$). *A posteriori* classifications, based on the discriminant scores, were 83% for *P. v. mellonae* as compared to 98% for *P. hispida*, 87% for *P. v. concolor*, and 78% for *P. v. richardsi* (Table 2.2).

All 29 characters demonstrated significant subspecific variation (ANOVA; $P < 0.01$, (Table 2.3). When submitted to Tukey-Kramer HSD tests, many more cranial characters ($n = 20$) exhibited significant differences between Atlantic and Pacific Ocean harbour seal subspecies than did characters which exhibited significant variation between subspecies within the same ocean ($n = 5$) (Table 2.3).

In general, the Pacific crania were larger than the Atlantic crania (character CL in Table 2.3). The extent of contact between the premaxillaries and nasals (character PTN in Table 2.3) was found to be valuable in distinguishing Atlantic (little contact) from Pacific (extensive contact) animals. It was also found that the medial length of the nasals which were in contact with the frontals (character NFO) was greater in the Atlantic subspecies than in the Pacific subspecies. The least interorbital width was significantly different between *P. v. vitulina* (larger) and *P. v. stejnegeri* (smaller).

Within the Atlantic ocean, *P. v. vitulina* showed significant differences from *P. v. concolor* in only 4 characters: total length of the nasals (LN), the length of the maxillo-frontal suture to the anterior end of the nasals (MAN), the greatest width of the external

nares (WEN) and the degree of extension of the premaxillaries towards the nasals (PTN) (Table 2.3).

Within the Pacific ocean, *P. v. richardsi* showed significant differences from *P. v. stejnegeri* in only 1 character: the width of the bulla (WB).

P. v. mellonae also exhibited significant differences from the Pacific Ocean subspecies in the degree of the extension of the premaxillary towards the nasal (PTN) and was similar to *P. v. concolor* with respect to this character. When compared to *P. v. concolor*, the population to which it is most closely related, *P. v. mellonae* was found to have upper premolars which are set parallel, rather than obliquely, to the angle of the jaw (SPT), a longer distance between the end of the snout and the anterior edge of the nasals (SAN) and a smaller interorbital width (LIW). Interestingly, the mandible height at the coronoid, one of the primary criteria with which Doutt (1942) described the subspecies, was not significantly larger in *P. v. mellonae* than in *P. v. concolor*.

The crania of *P. largha* and *P. hispida* were well-differentiated (Table 2.3). The height of the foramen magnum (HFM) in *P. largha* was significantly smaller than that of the Atlantic Ocean harbour seal subspecies but not significantly different than that of the Pacific Ocean harbour seal subspecies. The teeth of *P. largha* were generally set parallel rather than obliquely to the angle of the jaw (character SPT).

Discussion

The results of the craniometric analyses support the classification of Bigg (1981): the relatively large amount of variability between the Atlantic and Pacific harbour seal subspecies and relatively small amount of variability between the subspecies within each ocean are consistent with the known biogeographic history of the phocid seals.

According to Davies (1958), "... if *vitulina* differentiation dates from the last glacial, then the separation between Pacific and Atlantic groups would be slightly older than that between eastern and western groups in each ocean." Davies (1958) went on to speculate that the evolution of the *P. vitulina* subspecies was dependent on sequential episodes of dispersal (from the Atlantic via the Arctic) and subsequent vicariance. This view has been supported by other studies of biogeography and pinniped host-parasite associations (Hoberg and Adams 1992) and cladistic analyses (DeMuizon 1982). The molecular genetic analysis of Stanley et al. (1996) indicated that harbour seal populations in the Atlantic and Pacific Oceans and East and West coast populations of these oceans were significantly genetically differentiated, and that Pacific and Atlantic harbour seals have been isolated for 1.7-2.2 million years. Further, in the Atlantic, the pattern of genetic divergence suggests that the colonisation proceeded from the West Atlantic coast of North America to the North and then East to Europe, and the degree of divergence between European and West Atlantic populations suggests this colonisation may have begun from 0.9 to 1.3 million years ago (Stanley et al. 1996). In the Pacific Ocean, genotypes in the Northwest are basal to those in the East, suggesting a West to East colonisation pattern similar to that found in the Atlantic (Stanley et al. 1996). The morphological, behavioural and genetic evidence that *P. v. richardsi* and *P. v. stejnegeri*

have closer affinities with North Atlantic populations of *P. vitulina* than with *P. largha* suggests the importance of multiple events of dispersal and vicariance during the Mid to Late Pleistocene (Hoberg and Adams 1992).

The results of the present study confirm the conclusions of many extant craniometric analyses. The extent of contact between the premaxillaries and nasals was first described by True (1899) to be valuable in distinguishing Atlantic from Pacific animals. The medial length of the nasals in contact with the frontals was used by Chapskii (1969) for the same purpose. In agreement with the observation of Doutt (1942), the degree of extension of the premaxillary towards the nasal (PTN) in *P. v. mellonae* was similar to that of *P. v. concolor*. The significant difference between the least interorbital width of Atlantic and Pacific populations is interesting, considering that it is a measurement which Wiig (1989) noticed to be remarkably small in his *P. v. vitulina* crania from Svalbard. The fact that ~~the eastern and western~~ Atlantic populations showed significant differences in only 4 characters and, when mis-classified by the *a posteriori* analysis, were most often mistaken for each other (87% correct classification for the western Atlantic animals and 92% for the eastern Atlantic animals) (Smith *et al.* 1994), is reflective of Doutt's (1942) difficulty in stating "how specimens [of harbour seals] from the American side of the Atlantic can be distinguished from specimens taken on the European side." That the eastern and western Pacific populations showed a significant difference in only 1 character, and that, in the *a posteriori* classification, these two groups were more often mis-classified as each other than any other two groups (78% correct classification for each group) (Smith *et al.* 1994), is consistent with the confusion which surrounds the

location of the demarcation between these groups (Burns *et al.* 1984). The observation of Shaughnessy and Fay (1977), that "*richardsi* differs from *largha* in the same characters and in the same ways as does *stejnegeri*", was also supported (see characters MW, CW1, DMM, LIW, PWM and PMJ). The small height of the foramen magnum and the fact that the teeth are set parallel to the angle of the jaw in *P. largha* are both characters that have been previously described (Shaughnessy and Fay 1977; Guylack and Robineau 1993).

The results indicated that *P. v. mellonae* is differentiated from other harbour seal subspecies and that, consistent with the biogeographic evidence, is most closely related to *P. v. concolor* (Doutt 1942; Davies 1958). All *P. v. mellonae* crania were correctly classified by the craniometric analysis, and only one *P. v. stejnegeri* crania was incorrectly classified into this group (Table 2.2). These results are similar to those of a smaller craniometric analysis that was undertaken by Hydro-Québec researchers (Consortium Gilles Shooner & Associés *et al.* 1991).

Using a similar analysis, Temte (1991a) was able to differentiate between crania of local populations of harbour seals on the Pacific coast of North America. He found a significant relationship between differences in cranial morphometry and population differences in birth timing, and suggested that these "allochronic", as well as allopatric factors, may be acting to promote population differentiation. With respect to *P. v. mellonae* there is evidence that, in addition to the population's apparent geographic isolation from other harbour seal populations, similar allochronic mechanisms may be at

play. From his conversations with the indigenous peoples of northern Québec, Doutt (1942) reported that the mean pupping date of the population occurred in early May. This date has also been corroborated by more recent work (Consortium Gilles Shooner & Associés et al. 1991). The female *P. v. mellonae* specimen collected by Doutt (1942) on March 22, 1938 was carrying a 60-cm fetus. By applying this information to a prenatal growth curve that was formulated for the *P. v. concolor* population from Sable Island, Nova Scotia (which included a linear increase in length of 3.6 mm per day, and a mean length at birth of between 76 and 85 cm), the mean birth date for *P. v. mellonae* can be estimated as being between 6 and 31 May (Boulva and McLaren 1979). Using a prenatal growth rate of 4.4 mm per day and a mean length at birth of 81.6 cm, such as were observed in *P. v. richardsi* in British Columbia (Bigg 1969), the estimated mean birth date of *P. v. mellonae* is 10 May. Both of these estimates for the mean birth date of *P. v. mellonae* are substantially earlier than for other harbour seal populations at a similar latitude (for example, June 10 in northern Labrador, June 27 at Schleswig/Holstein, Germany, and June 29 at Port Moller, AK) (Temte et al. 1991). If Temte (1991a, 1991b; 1994) was correct in his belief that birth timing in harbour seals has a heritable component and may, therefore, function to create reproductive barriers between adjacent populations, my calculations would further suggest that *P. v. mellonae* is reproductively isolated from *P. v. concolor*.

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Table 2.1. Standardised canonical discriminant function coefficients for first two functions. Percentage variations accounted for by the two functions are also given.

Character	Func 1	Func 2
Condylar Length (CL)	-0.137	0.596
Length of Upper Toothrow (LUT)	0.488	-0.405
Mastoid Width (MW)	0.599	0.061
Cranial Width (CW1)	0.093	0.102
Zygomatic Width (ZW)	-0.633	0.647
Height of Cranium (HC)	0.268	-0.118
Length of Mandible (LM)	0.074	0.103
Mandible Height at Coronoid (MHC)	0.662	0.081
Length of Lower Toothrow (LLT)	0.302	0.068
Depth of Mandible Behind M1 (DMM)	-0.539	0.274
Total Length of Nasals (LN)	1.879	0.617
Length of Maxillo-Frontal Suture to Anterior End of Nasal (MAN)	-1.690	-0.628
Greatest Width of External Nares (WEN)	0.202	-0.123
Width of Snout at Canines (WSC)	0.487	0.177
Least Interorbital Width (LIW)	0.746	-0.214
Greatest Length of PM2 (GLP)	0.643	-0.092
Palatal Width at M1 (PWM)	0.352	-0.006
Width of Bulla (WB)	0.111	0.310
Length of Bulla (LB)	0.051	-0.171
Condylar Width (CW2)	0.370	-0.034
Width of Foramen Magnum (WFM)	0.193	-0.058
Height of Foramen Magnum (HFM)	0.601	0.644
Length of Snout from Anterior Edge of Nasal (SAN)	0.157	-0.541

Width of Bulla from Tip of Auditory Process to Anterior Edge of Carotid Foramen (AAC)	0.265	-0.210
Length of Nasal in Contact With Frontal, Relative to Their Overall Length (NFO)	-0.848	-0.152
Degree of Extension of Premaxillary Towards Nasal (PTN)	0.320	0.860
Shape of Posterior Margin of Jugal (PMJ)	0.492	-0.187
Set of Premolar Teeth (SPT)	0.394	0.443
Variance	59.4%	24.2%

Table 2.2. *A posteriori* classifications based on discriminant scores for five *P.*
vitulina subspecies, *P. largha*, and *Pusa hispida*.

Groups	PVC	PVM	PVR	PVS	PVV	PL	PH	% Correctly classified
<i>concolor</i>								
(PVC)	52		2		4	1	1	87
<i>mellonae</i>								
(PVM)		5						100
<i>richardsi</i>								
(PVR)	1		35	8		1		78
<i>stejnegeri</i>								
(PVS)	1	1	4	32	1	2		78
<i>vitulina</i>								
(PVV)	5				56			92
<i>largha</i>								
(PL)			3	1		38		91
<i>hispida</i>								
(PH)						49	100	
%								
Correctly classified	88	83	80	78	92	91	98	100

Table 2.3. Means of adjusted (\log_{10} -transformed and C-scored) cranial character measurements arranged according to study group (following Amano and Miyazaki 1992). Within rows, means that are annotated with the same superscript letters are significantly different ($P < 0.01$).

Character	PVC	PVM	PVR	PVS	PVV	PL	PH
CL	-0.063	0.061	0.111 ^A	0.182 ^B	-0.209 ^{ABC}	0.031	0.051 ^C
LUT	-0.037 ^{AB}	0.102	0.205 ^{ACD}	0.231 ^{BEF}	-0.182 ^{CEG}	0.089 ^{GH}	-0.197 ^{DH}
MW	-0.044 ^A	0.010	0.163 ^{BCD}	0.241 ^{AEG}	-0.066 ^{BE}	-0.086 ^{CF}	-0.143 ^{DG}
CW1	0.034	0.045	0.120 ^{AB}	0.246 ^{CDE}	-0.033 ^C	-0.186 ^{AD}	-0.162 ^{BE}
ZW	-0.064	-0.087	0.078	0.122	-0.035	-0.173	0.105
HC	0.022 ^A	-0.048	-0.025 ^B	0.187 ^C	0.072 ^D	0.048 ^E	-0.286 ^{ABCDE}
LM	-0.167 ^A	-0.038	0.128	0.157 ^A	-0.110	0.015	0.084
MHC	-0.065	0.202	0.114	0.099	-0.033	-0.070	-0.027
LLT	-0.070 ^{AB}	0.004	0.208 ^{AC}	0.306 ^{BD}	-0.109 ^{CDE}	0.100 ^E	-0.312 ^{ABE}
DMM	-0.172 ^{ABC}	-0.346 ^D	0.192 ^{AEF}	0.153 ^{BG}	-0.112 ^{EH}	-0.380 ^{FGE}	0.407 ^{CDHI}
LN	0.322 ^{ABCDE}	0.230	0.010 ^A	-0.085 ^B	-0.175 ^C	-0.031 ^D	-0.112 ^E
MAN	0.136 ^A	0.120	0.068 ^B	-0.091 ^C	-0.642 ^{ABCD}	-0.044 ^D	0.671 ^{ABCD}
WEN	0.050 ^A	-0.003	0.039 ^B	0.127 ^{CD}	-0.280 ^{ABC}	0.357 ^{ABE}	-0.161 ^{DE}
WSC	0.070 ^A	0.097 ^B	0.108 ^C	0.188 ^D	0.077 ^E	-0.015 ^F	-0.435 ^{ABCDEF}
LIW	0.180 ^A	-0.337	0.021 ^B	-0.138 ^{CD}	0.341 ^C	0.483 ^{BD}	-0.927 ^{ABCD}
GLP	0.203 ^A	0.212	0.115 ^B	0.115 ^C	0.306 ^D	-0.140 ^D	-0.732 ^{ABCD}
PWM	0.073 ^A	-0.119	0.189 ^B	0.247 ^C	0.190 ^D	-0.157 ^{ABCD}	-0.560 ^{ABCD}
WB	-0.030	-0.230	-0.372 ^{ABC}	0.102 ^A	-0.199 ^D	0.221 ^B	0.374 ^{CD}
LB	-0.284 ^{ABC}	-0.260	0.144 ^{AD}	0.349 ^{BE}	-0.447 ^{DEF}	0.260 ^{CF}	0.283 ^C
CW2	-0.259 ^{ABCD}	-0.006	0.133 ^{AE}	0.287 ^{BF}	-0.233 ^{EFG}	0.094 ^C	0.164 ^{DG}
WFM	-0.123	0.728	-0.134	0.042	-0.282 ^A	-0.004	0.519 ^A
HFM	0.230 ^{AB}	0.759	-0.274 ^C	-0.581 ^{AD}	0.791 ^{CDEF}	-0.681 ^{BE}	-0.023 ^F
SAN	-0.290 ^{ABC}	0.201	0.356 ^{AD}	0.119 ^{BE}	-0.275 ^{DEFG}	0.247 ^{CF}	0.038 ^{AG}
GLJ	-0.056 ^A	-0.414	0.112	0.093	-0.188 ^B	-0.150 ^C	0.292 ^{ABC}

AAC	-0.118 ^{AB}	-0.244	0.011 ^C	0.262 ^{AD}	-0.309 ^{CDEF}	0.123 ^E	0.220 ^{BF}
NFO	0.257 ^{ABC}	0.245	-0.318 ^{AD}	-0.509 ^{BE}	0.679 ^{DEF}	0.175 ^{EF}	-0.618 ^{CF}
PTN	0.223 ^{ABC}	1.029 ^{DEF}	-0.562 ^{ADG}	-0.937 ^{BEH}	1.161 ^{ABCDEFGH}	-0.935 ^{CFI}	0.279 ^{GHI}
PMJ	-0.302 ^{AB}	-0.931 ^{CD}	-0.389 ^{EF}	-1.042 ^{GH}	-0.189 ^G	1.100 ^{ACEH}	0.987 ^{BDFG}
SPT	0.343 ^{AB}	-0.982	-0.550 ^{AC}	-0.473 ^{BD}	0.492 ^{CDE}	-0.292 ^E	0.219

Fig. 2.1. Range of the harbour seal (*Phoca vitulina* L.).

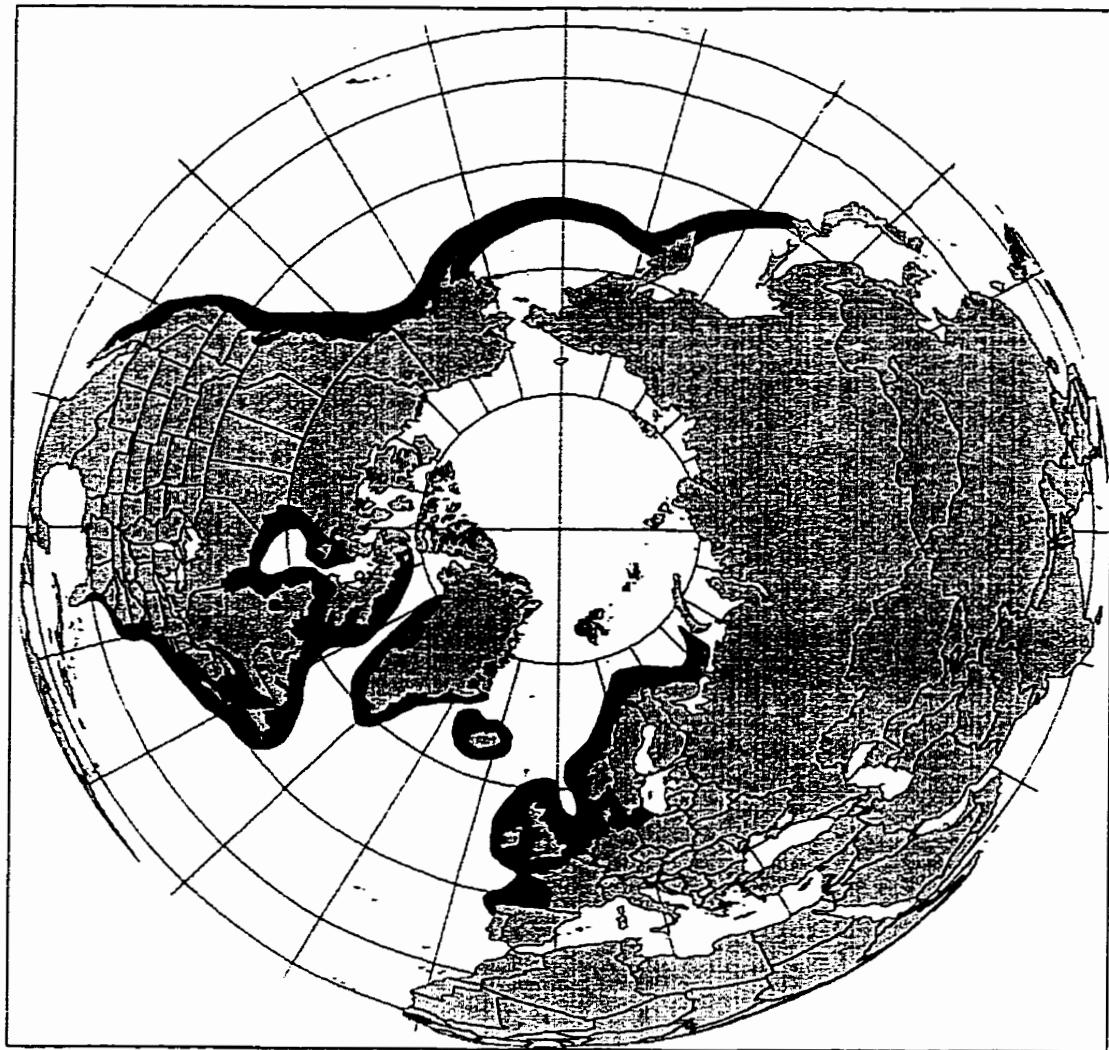
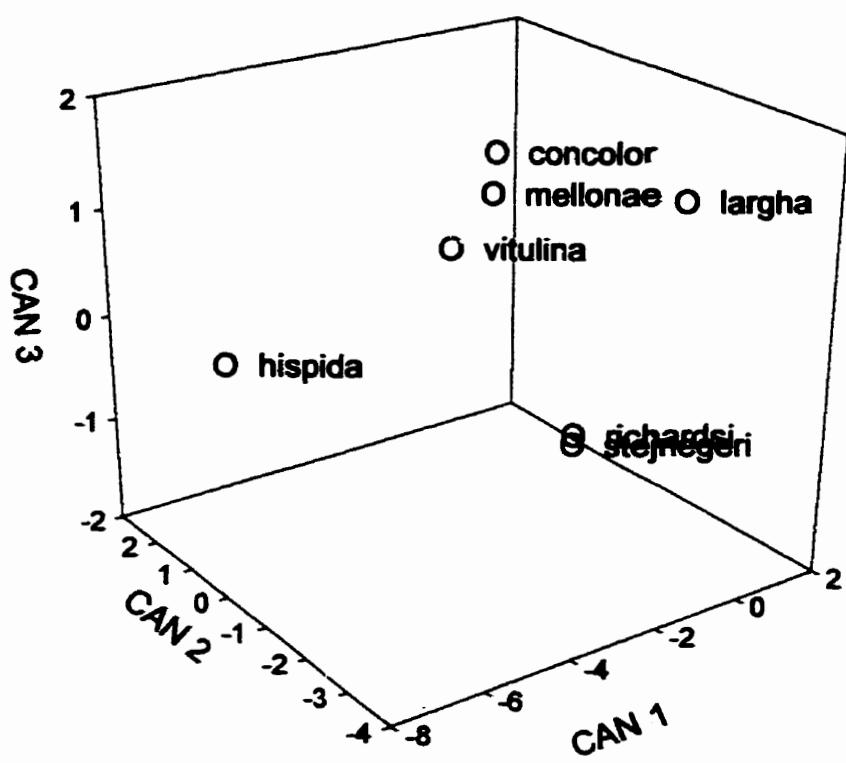


Fig. 2.2. Relative differences between the group means of cranial measurements of 5 subspecies of harbour seal (*Phoca vitulina concolor*; *P. v. mellonae*; *P. v. vitulina*; *P. v. richardsi* and *P. v. stejnegeri*), the spotted seal (*P. largha*) and the ringed seal (*Pusa hispida*) based on plots of first, second and third canonical variates.



Appendix 1

Sources and acquisition numbers of harbour, spotted and ringed seal crania used in these analyses.

American Museum of Natural History

Phoca vitulina concolor: 100, 80201, 144651, 164600, 232379, 232390, 232406, 232414, 232415, 232420, 232424, 232425, 232427, 232431, 232438, 232440, 232441, 232443, 232449

P. largha: 18169

Pusa hispida: 19308, 19310

Arctic Biological Station

P. v. mellonae: LM-89-01, LM-89-02, LM-90-01, LM-90-02

Canadian Museum of Nature

P. v. concolor: A20685, 1984-29-SIV1, 10358, 12502, 52622, 52630, 52631, 52639, 52640, 52641, 52642, 52643, 52644, 52645, 52650, 52651, 52652, 52653, 52654, 52658, 52659, 52660, 52661

P. v. richardsi: 2597, 52662, 52663

Carnegie Museum

P. v. concolor: 6671, 17848, 17849, 18748

P. v. mellonae: 15215

P. v. richardsi: 18738, 57626, 57627, 57628

Grand Manan Whale and Seabird Research Station

P. v. concolor: GM-91-06, PV-92-02, PV-92-03

National Museum of Natural History

P. v. concolor: 180285, 188823, 188826, 504298, 504299

P. v. richardsi: 49550, 81516, 81518, 81520, 146429, 146431, 146435, 146436, 146437, 154015, 154016, 219866, 219868, 219873, 219874, 219876, 219879, 245914, 245915, 253041, 253042, 253235, 250712, 250713, 273532, 504842

P. v. stejnegeri: 21310, 21312, 290653, 290654, 290655

P. v. vitulina: 238153, 238154

Naturhistoriska Riksmuseet

P. v. vitulina: A612932, A630347, A750036, A750039, A750080, A750093, A760005, A763061, A765002, A775002, A775033, A775049, A775071, A775094, A775098, A785015, A895066, A895122, A895155, A895159, A905097, A905100, A915070, A915078, A915079, A915082, A915086

Zoologisk Museum

P. v. concolor: CN79, CN82, CN83, CN84, CN85, CN196

P. v. vitulina: CN159, CN253, CN321, CN751, CN847, CN1085, CN1111, CN1142, CN1146, CN1149, CN1155

Pusa hispida: CN295, CNS85, CN591, CN592, CN618

University of Alaska Museum, Fairbanks

P. v. richardsi: 3409, 3704, 11475, 11627, 11727, 11740, 11742, 11746, 11750, 11751, 11752, 11758

P. v. stejnegeri: 11718, 11720, 11721, 11723, 11724, 11728, 11729, 19127, 19128, 19130, 19134, 19135, 19139, 19141, 19143, 19146, 19149, 19150, 19151, 19152, 19155, 19156, 19183, 19184, 19185, 19186, 19187, 19190, 19191, 19192, 19199, 19202, 19203, 19205, 19206, 19207

P. largha: 11458, 11459, 11593, 11594, 11599, 11602, 11605, 11613, 11634, 11797, 11799, 11801, 11804, 11805, 11891, 16606, 16607, 18602, 18604, 18605, 18610, 18612, 18613, 18617, 18619, 18620, 18621, 18622, 18623, 18624, 18625, 18641, 18642, 18643, 18659, 18666, 18675, 18680, 18683, 18686

Pusa hispida: 2088, 7183, 11565, 11566, 11568, 11575, 11576, 11578, 11579, 11580, 11581, 11584, 11585, 11586, 11587, 11588, 11590, 11892, 11895, 11896, 11897, 11898, 11899, 16599, 16600, 19055, 19058, 19063, 19068, 19080, 19084, 19085, 19095, 19096, 19098, 19100, 19102, 19108, 19118

University of Amsterdam Museum

P. v. vitulina: 11.116, 11.119, 11.742, 12.647, 12.919, 15.146, 15.987, 18.454, 18.455, 19.397, 19.398, 23.713, 23.716, 23.726, 23.735, 23.737, 2090, 2593, 4290, 8276, 8723

P. largha: 24.142

Pusa hispida: 17.184, 21.065, 24.348

**CHAPTER 3: GENETIC ANALYSIS OF WESTERN ATLANTIC,
Phoca vitulina concolor DeKay 1842, AND LACS DES LOUPS MARINS,
P. v. mellonae Doutt 1942, HARBOUR SEALS USING MITOCHONDRIAL DNA**

Does the layman understand what the sight of a piece of strange sealskin means? It means the clue to possible discovery of a new large mammal, and the discovery of any new large mammal is now so rare that even the possibility gives a scientist the jitters (Twomey 1942, p. 4).

Introduction

The original subspecies description of the Lacs des Loups Marins harbour seal (*P. v. mellonae*) was made on the basis of morphological evidence and a presumed geographical isolation of the population since the retreat of the Laurentide ice sheet (Doutt 1942). The most prominent critique of the subspecies designation was that of Mansfield (1967), who noted:

Several seals in company could well have been the founding members of the population in Upper and Lower Seal Lakes, their establishment in these two lakes probably depending on the presence of rapid sections with open water in the winter and an adequate food supply. There is no evidence of migration of these seals, the lakes appearing to be their permanent homes. In spite of this, there appears to be no need to postulate a long isolation by slow emergence of the lakes from the level of the post-glacial

seas, since access to them at the present time is quite possible (p. 256).

Smith and Horonowitsch (1987, p. 8) thought that Mansfield's interpretation "that the area contains a resident population occasionally augmented by wandering seals entering from the sea and undertaking random overland migrations" was a reasonable hypothesis. Mansfield (1967) pointed to Inuit toponyms that seemed to indicate that seals were once more widely distributed throughout the Rivière aux Feuilles drainage system (also corroborated by Consortium Gilles Shooner & Associés 1991), and suggested that:

It may well have been possible that before the turn of the century the watershed lakes were a favored summer resort of young wandering harbor seals, a few reaching Upper and Lower Seal Lakes from time to time. When the rifle came the coastal harbor seals were heavily exploited, resulting in virtual isolation of the lake seals (p. 256).

Analyses of mitochondrial DNA, in particular the control region, have been increasingly used to elucidate population sub-structure in a variety of marine mammal species (see Hoelzel et al. 1991; Maldonado et al. 1995; Mouchaty et al. 1995; Rosel et al. 1995; Malik et al. 1997). The mitochondrial DNA of harbour seals (*Phoca vitulina*) was first analysed by Árnason and Johnsson (1992). In their subsequent study of worldwide mitochondrial DNA diversity in the harbour seal, Stanley et al. (1996) used a limited sample of harbour seals from the western Atlantic (*P. v. concolor*) and no samples from Lacs des Loups Marins (*P. v. mellonae*). Other analyses of harbour seal

genetic diversity have also excluded these two subspecies (Burg 1996; Lamont et al. 1996; O'Corry-Crowe and Westlake 1997). The purpose of the present study was to undertake a preliminary investigation of the extent to which *P. v. mellonae* is genetically distinct from oceanic harbour seals, particularly those from eastern North America (*P. v. concolor*), through the sequencing of a portion of the mitochondrial control region and the comparison of these sequences to the results of Stanley et al. (1996).

Materials and Methods

Sample Collection

Seventeen samples were sequenced for the purposes of the analysis (Table 3.1). Muscle samples were frozen until use, and blood was taken from the hind flippers of captured seals (Chapter 5) in serum separation tubes and centrifuged as soon as possible after collection before being stored in liquid nitrogen.

DNA Analysis

Blood and muscle samples (approximately 0.5 to 1.0 g of muscle tissue) were prepared in 1× lysis buffer (4 M urea, 0.2 M NaCl, 0.5% n-lauroyl sarcosine, 10 mM CDTA (1,2-cyclohexanediamine), 0.1 M Tris-HCl pH 8.0) and ground using a mortar and pestle cooled in liquid nitrogen. DNA extractions were performed according to Guglich et al. (1994).

DNA served as a template for amplification using the polymerase chain reaction (PCR). Two PCR primers (WKT115 5'-ATGACCCTGAAGAA(G/A)GAACCAG-3' and

WKT283 5'-TACACTGGTCTTGTAAACC-3') were used to amplify a 520 b.p. product containing a portion of the tRNA threonine and proline and part of the control region (Lamont et al. 1996). The DNA was amplified under the following reaction conditions: 10 mM Tris-HCl (pH 8.4), 50 mM potassium chloride (KCl), 0.001% Triton X-100, 2.0 mM magnesium chloride ($MgCl_2$), 0.2 mM dNTP's, 0.2 mM of each primer, 1.5 U of Taq DNA polymerase (Perkin-Elmer-Cetus), and 100 ng of template DNA carried out in a 25 μ l volume. Amplification was performed under a temperature regime of: 95°C for 90 s, 52° C for 60 s, 72°C for 60 s for 1 cycle; 94°C for 30 s, 52° C for 30 s, 72°C for 30 s for 25 cycles; 94°C for 30 s, 52° C for 30 s, 72°C for 7 minutes for 1 cycle. PCR products were isolated through a 1.5% low-melting point agarose gel and excised and purified using a phenol-chloroform and chloroform extraction.

Amplified product (2 - 300 ng) was used for cycle sequencing according to the PRISM™ Ready Reaction Dye Deoxy Terminator Protocol (Applied Biosystems Inc., Foster City, CA). DNA sequences were analyzed by the computer program Image Quantification (Molecular Dynamics). The product was sequenced using both primers to confirm the sequence using both strands.

Analysis of Sequence Variation

Two comparisons were undertaken: the first among the 17 sequenced samples ; the second between the sequenced samples and the 34 haplotypes described by Stanley et al. (1996) (GenBank accession numbers U36342-U36375). For both comparisons a published DNA sequence of the grey seal (*Halichoerus grypus*) was used as the outgroup

(sequence from Árnason et al. 1993). DNA from the 17 sequenced samples were reduced to 480 b.p. to align the sequences in the computer program Genetic Data Environment. Next, 385 b.p. of these sequences were aligned with those of Stanley et al. (1996). For each of the two comparisons, sequence variation was estimated using the computer program Phylip 3.5c (Felsenstein 1993). DNA distances of pairwise sequence comparisons were obtained using Kimura's (1980) "two-parameter" model assuming a 2-to-1 transition to transversion substitution in the Phylip program DNAdist. A statistical analysis using the bootstrap method was performed to generate confidence intervals on the phylogenies. The Phylip program Seqboot resampled the original data by replacing characters, in this case nucleotides, and estimated the variation among the replicates using the DNAdist program. Neighbor-joining trees were calculated for the distance measures of each replicate using the program Neighbor. A consensus tree -- a majority rule tree that is constructed according to the groups or clusters that are generated most often in the replicates -- was then created from bootstrap data in the program Consense to estimate the confidence interval at each node. A total of 500 bootstrap data bases were generated to test the phylogenies (Felsenstein 1985). In addition, a parsimony analysis was undertaken using the DNAPars program. A bootstrap of 1000 replicates, using the programs listed above, was applied to the parsimony analysis.

Results

A total of 14 different mitochondrial DNA haplotypes were found among the 17 sequenced samples (Table 3.2). Three of the individuals from Lacs des Loups Marins

(LM-89-01, LM-94-03, and LM-94-04) shared a haplotype, and two of the individuals from Massachusetts shared a haplotype.

Within the 480 b.p. examined, the observed number of pairwise differences among haplotypes ranged from 1 to 19. Corrected DNA distances for comparisons between the 17 sequenced samples ranged from 0.008 to 0.05 (Table 3.2). Lacs des Loups Marins had four unique haplotypes, three of which were similar and grouped together 64.7% of the time (Fig. 3.1). The fourth Lacs des Loups Marins haplotype (LM-90-02) was more differentiated than the other harbour seals that were sequenced, with a mean of 16 ± 0.6 substitutions as compared to a mean of 6.6 ± 0.4 substitutions for all 17 samples (Table 3.2).

When compared with the sequences from Stanley et al. (1996), all *P. v. mellonae* and the majority of the *P. v. concolor* samples grouped with other harbour seals from the western Atlantic (Fig. 3.2). The exceptions were the sample from New Jersey, which was identical to a sample from Churchill, Manitoba from the Stanley et al. (1996) study and which -- as it did in the Stanley study -- grouped with eastern Atlantic Ocean haplotypes (Fig. 3.2). In addition, one of the haplotypes from the St. Lawrence River was similar to one of the haplotypes described in Stanley et al. (1996) and they grouped together close to the eastern Atlantic samples.

The most parsimonious tree generated grouped all of the Lacs des Loups Marins samples together 47.2% of the time.

Discussion

Doult (1942) summarised his hypothesis concerning *P. v. mellonae* in this way:

it would seem that we have a large species, with few generations per century; but it has been thrust into a new environment which would cause it to change more rapidly than would otherwise be the case. Thus, these two factors tend to cancel one another...Thus it seems probable that about 5,500 years, plus or minus 2,500 years, has been the time required to produce a new subspecies under the conditions set forth above (p. 78).

In response, Mansfield (1967) indicated that there is evidence of harbour seals having once been more widely distributed in the Arctic in localised populations, but that they were eliminated by over-hunting. He noted that:

The localized distribution of the harbor seal in the arctic makes its future somewhat precarious. Already in Ungava Bay, southern Baffin Island, and southern Southampton Island it has been eliminated from some local territories, for the Eskimos often know exactly where to find this species in summer (p. 252).

Though there are known to still be small harbour seal populations in estuaries in Ungava Bay, western Hudson Bay and the lower Churchill River, Manitoba (S. Innes, Department of Fisheries and Oceans, pers. comm.), the over-hunting that Mansfield (1967) referred to has obviously contributed to the further isolation of *P. v. mellonae*

from neighbouring oceanic harbour seals. Mansfield's argument was that the Lacs des Loups Marins population is simply a remnant of harbour seal diversity that was once widespread on the Ungava peninsula.

Given that the mitochondrial control region is a neutral marker (Hoelzel et al. 1991) and would exhibit little, if any, change over the 7,300 year period since the retreat of the Laurentide ice sheet (Allard and Séguin 1985), it is not possible to formulate any conclusions regarding the time of isolation of *P. v. mellonae* from the present genetic data. Those selectable morphological and behavioural characteristics that seem to have changed in the population (Chapter 2) do, however, lend weight to Doutt's (1942) contention that the population has been isolated for some time. It is unlikely that a shift in reproductive seasonality, such as *P. v. mellonae* seems to exhibit (Chapter 2), would be possible in the century or so that Mansfield (1967) postulated as the time period over which other harbour seals in northern Québec were eliminated.

Consistent with the arguments of both Doutt (1942) and Mansfield (1967), the Lacs des Loups Marins seals appeared to be most closely related to harbour seals from the western Atlantic Ocean (Figs. 3.1 and 3.2). Though the four unique haplotypes and particular difference exhibited by one individual from Lacs des Loups Marins sample are intriguing, and potentially indicative of a founder effect in the population, it is difficult to formulate any conclusions regarding the genetic relationship of *P. v. mellonae* to harbour seals that used to exist in Arctic Canada without further analysis of historic samples. The samples that were included in the analysis from the closest geographic locations to Lacs

des Loups Marins were the one animal from Churchill, Manitoba and two from Greenland. The Churchill animal was more closely related to animals from the New Jersey coast and the eastern Atlantic (Table 3.2; Figs. 3.1 and 3.2). One haplotype from Greenland was most closely related to haplotypes from Sable Island, N.S., Miquelon and the St. Lawrence. The second Greenland haplotype, though it grouped closely with Lacs des Loups Marins 2, was not supported by a very large bootstrap value (38.8%) (Fig. 3.1).

The number of pairwise substitutions in the combined sample of 17 sequences was very similar to that observed by Stanley et al. (1996) (1 to 23 substitutions in 435 b.p.). Interestingly, Burg (1996) and Lamont et al. (1996) found higher numbers of pairwise substitutions in their sampling of Pacific animals (average of $2.6\% \pm 0.29\%$, and 1 to 16 among 320 b.p. respectively). Lamont et al. (1996) concluded that this relatively large amount of genetic variation in Pacific harbour seals was likely due to the lack of a severe population bottleneck – as has been experienced by other pinniped populations due to over-exploitation -- at some time in the past. In addition, Lamont et al. (1996) concluded that there is limited gene flow among Pacific harbour seals along the coasts of Washington, Oregon, and California and limited, if any, gene flow between Puget Sound and the Pacific coast of Washington. In reference to the work of Temte et al. (1991), Lamont et al. (1996) concluded that the timing of harbour seal births in Puget Sound is most likely genetically regulated, and possibly follows the schedule of harbour seals off British Columbia. Burg (1996) also reported significant structuring of the harbour seal population in B.C. and Alaska. From her analysis, she discerned three significantly

separate groups, suggesting that the Pacific Ocean was colonised by harbour seals twice. One maternal lineage invaded the Pacific approximately 670,000 years ago and is now restricted to southern Vancouver Island, Puget Sound and Japan. A second invasion occurred approximately 380,000 years ago. This group of animals colonised Japan and Alaska and a small group of females moved south from northern B.C. and Alaska to colonise southern B.C.

The conclusion of both Burg (1996) and Lamont et al. (1996) is that there are reproductively isolated groups of harbour seals within *P. v. richardsi*. This conclusion based on genetic evidence confirms previous observations of harbour seals' extreme site fidelity (Boulva and McLaren 1979; Bigg 1981; Kelly 1981). These conclusions are consistent with those of O'Corry-Crowe et al. (1997), who found – through an analysis of the mitochondrial DNA control region – that *P. v. stejnegeri* and *P. v. richardsi* do not occur as genetically distinct clades. It could very well be that, with further analysis of *P. v. concolor* genotypes, similar sub-structuring comes to light.

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Table 3.1: Specimens of *Phoca vitulina concolor* and *P. v. mellonae* used in the analysis of the mitochondrial control region.

Sample Number	Tissue	Collection Location	Collection Date
LM-89-01	muscle	Lacs des Loups Marins	89-08
LM-90-02	muscle	Lacs des Loups Marins	1990
LM-94-03	blood	Lacs des Loups Marins	94-09-07
LM-94-04	blood	Lacs des Loups Marins	94-09-10
LM-95-05	blood	Lacs des Loups Marins	95-09-11
LM-95-06	blood	Lacs des Loups Marins	95-09-14
G1612	muscle	S. Aappilattoq, Greenland	86-05-04
G1618	muscle	Anorluitsoq, Greenland	86-05-11
80-84	muscle	Massachusetts	80-01-18
80-125	muscle	Massachusetts	80-01-23
80-128	muscle	Massachusetts	N/A
80-193	muscle	Massachusetts	N/A
GM-92-05	muscle	Grand Manan, N.B.	92-08-20
NS-93-02	muscle	Nova Scotia	N/A
NJ-94-01	blood	New Jersey	N/A
133-89	muscle	Gaspé, Qué.	89-04-14
140-89	muscle	St. Lawrence River, Qué.	89-08-27

Table 3.2. Kimura's DNA distance measures of 6 *Phoca vitulina mellonae* and 11 *P. v. concolor* assuming a 2-to-1 transition-transversion substitution ratio.

	MA 1	MA 2	MA 3	GR 1	GR 2	GM 1	LM 1	LM 2	LM 3	LM 4	NJ 1	NS 1	SL 1	SL 2
80128 (MA 1)	0													
80193 (MA 2)	.002	0												
8084 (MA 3)	.01	.01	0											
G1612 (GR 1)	.004	.006	.02	0										
G1618 (GR 2)	.01	.01	.02	.01	0									
GM9205 (GM 1)	.006	.008	.02	.01	.02	0								
8901 (LM 1)	.004	.006	.02	.008	.01	.01	.01	0						
9002 (LM 2)	.03	.03	.05	.04	.03	.04	.03	0						
9505 (LM 3)	.01	.01	.02	.02	.02	.02	.02	.008	.04	0				
9506 (LM 4)	.006	.008	.02	.01	.02	.01	.002	.03	.01	0				
NJ9401 (NJ 1)	.01	.02	.03	.02	.03	.02	.01	.04	.02	.02	0			
NS9302 (NS 1)	.004	.006	.02	.008	.01	.006	.008	.04	.02	.01	.02	0		
13389 (SL 1)	.008	.01	.02	.01	.02	.01	.008	.04	.02	.01	.01	.008	0	
14089 (SL 2)	.004	.006	.02	.008	.01	.01	.008	.03	.02	.01	.02	.008	.01	0

Fig. 3.1. Consensus tree of 500 bootstrap neighbour-joining distance trees for 480 b.p. of the mitochondrial control region for 6 *Phoca vitulina mellonae* and 11 *P. v. concolor*. The grey seal (*Halichoerus grypus*) is the outgroup. The number located at the nodes indicates the percentage of bootstrap trees that contain this pattern.

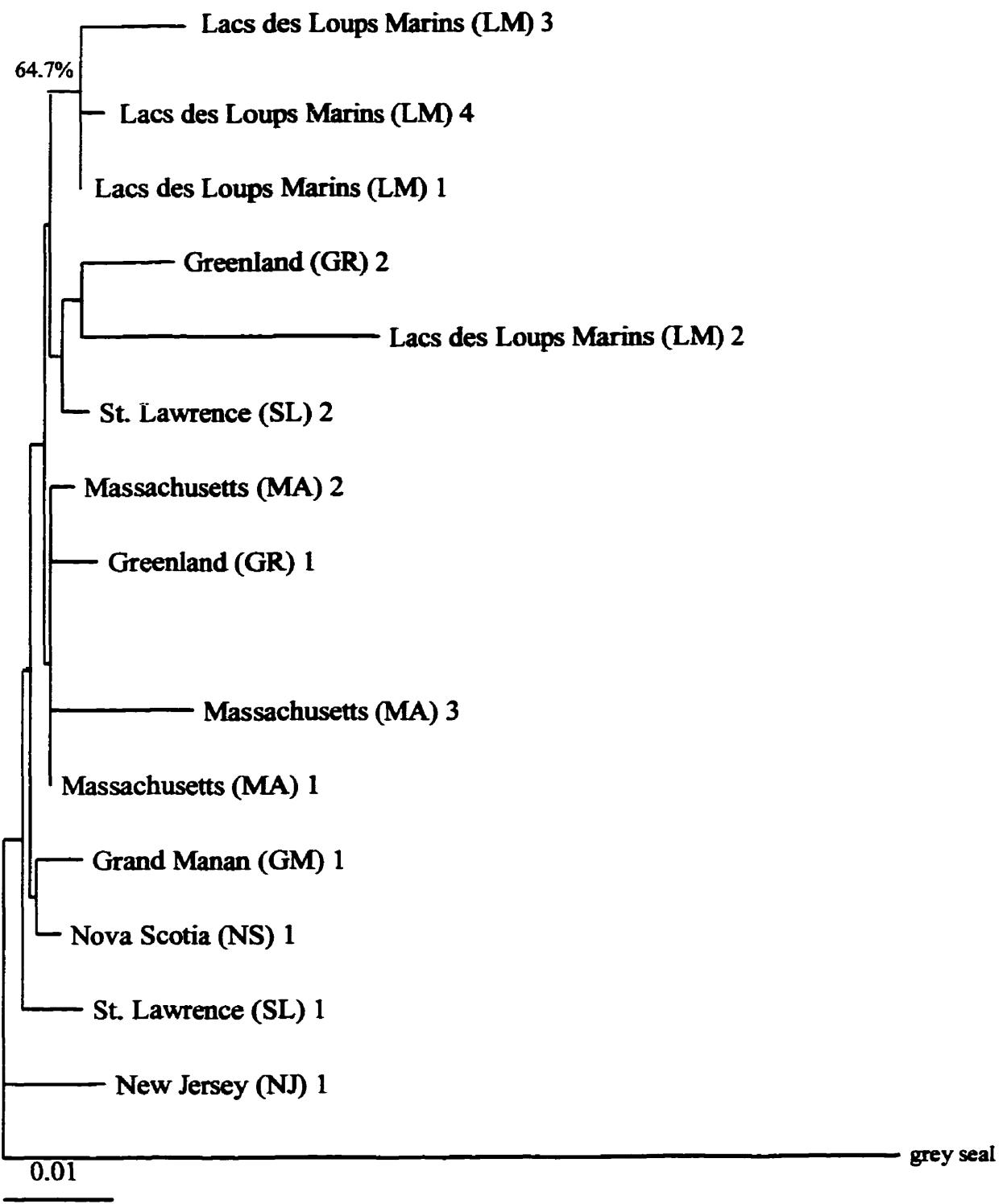
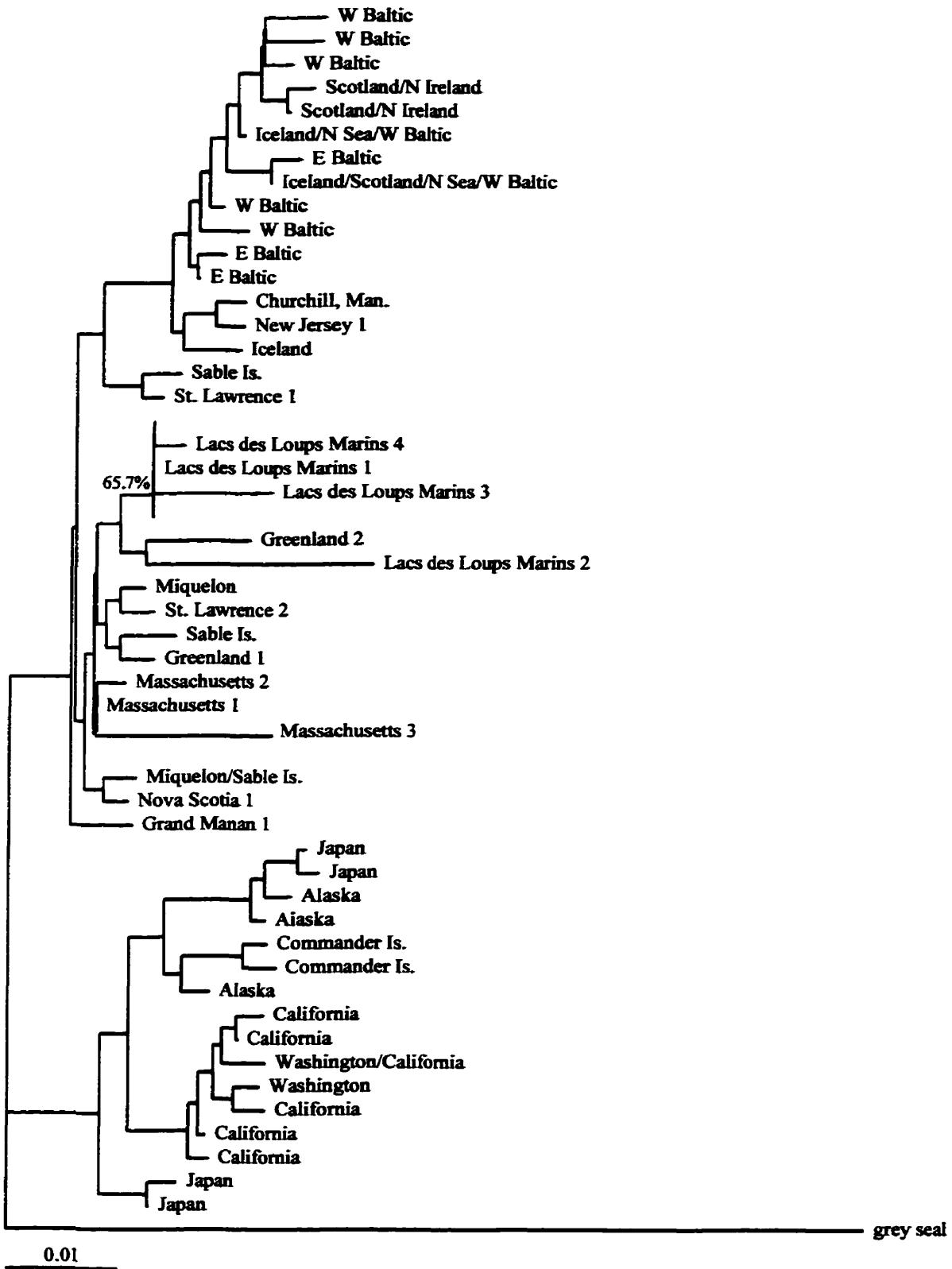


Fig. 3.2. Consensus tree of 500 bootstrap neighbour-joining distance trees for 385 b.p. of the mitochondrial control region for 6 *Phoca vitulina mellonae*, 11 *P. v. concolor*, and 34 harbour seal haplotypes reported by Stanley et al. (1996). The grey seal (*Halichoerus grypus*) is the outgroup. The number located at the nodes indicates the percentage of bootstrap trees that contain this pattern.



CHAPTER 4: DISTINGUISHING BETWEEN POPULATIONS OF FRESH AND SALTWATER HARBOUR SEALS, *Phoca vitulina* L., USING STABLE-ISOTOPE RATIOS AND FATTY ACID PROFILES

No one knows how many years might have passed ... had not the search for *kasagea*, the unknown seal of Seal Lakes of Ungava, received a sharp and sudden impetus. During his 1935 summer work at Great Whale River, [Doutt] ... noticed the sealskin handy-bag which hung from an Indian's shoulder. The bag seemed to be made from the skin of a hair seal, but not the skin of *netchek*, common hair seal of salt water, or any hair seal known to science (Twomey 1942, p. 10)

Introduction

While it is common for harbour seals (*Phoca vitulina*) to feed occasionally in lakes and rivers throughout their world-wide distribution (Reeves et al. 1992), the apparent residency of harbour seals in Lacs des Loups Marins is unique (Smith et al. 1994; Smith 1997). One way to investigate the degree of the Lacs des Loups Marins seal's (*P. v. mellonae*) use of freshwater, and the extent to which this behaviour distinguishes the population from marine harbour seals, is through a study of feeding habits.

The diet of *P. v. mellonae* was examined using biochemical techniques that have proven effective in other, somewhat similar, investigations: stable-carbon and nitrogen isotope ratios in hair (reviewed by Peterson and Fry 1987; see also Lajthe and Michener 1994), and chemometry of fatty acid profiles in the tissue lipids (Grahl-Nielsen et al. 1993; Käkelä et al. 1993).

The stable-isotope approach is based on the fact that stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) in animal tissue are ultimately related to diet (DeNiro and Epstein 1978, 1981). Stable-carbon isotope ratios of primary producers in freshwater food webs are typically less enriched in ^{13}C than those of marine food webs and this difference is passed on to higher-order consumers (Chisholm et al. 1982; Fry and Sherr 1988; Hobson 1990; Hobson and Sealy 1991; Ramsay and Hobson 1991; Walker and Macko 1999). Thus, seals from marine food webs should show relatively more ^{13}C in their tissues than those from freshwater food webs. Any enrichment of ^{13}C in *P. v. mellonae* tissue from expected values for freshwater endpoints would provide evidence of marine input to the diet. When used in conjunction with ^{13}C measurements, stable-nitrogen isotope analysis can provide additional information about the diet of seals as well as their use of marine and freshwater food webs (Hobson and Welch 1992, 1995). Stable-nitrogen isotope ratios in consumer tissues tend to be enriched by about 3‰ compared to dietary values and this step-wise enrichment in ^{15}N in food webs has been used to estimate the trophic levels of animals, including marine mammals (Rau 1982; Minagawa and Wada 1984; Wada et al. 1987; Fry 1988; Hobson and Welch 1992, 1995).

Tissue fatty acid composition is also related to an animal's diet (Hilditch and Williams 1964). Freshwater and marine food webs are characterised by different levels of specific fatty acids, particularly long-chain polyunsaturated fatty acids (PUFAs) (Hilditch and Williams 1964). Primary producers in freshwater environments have significantly lower

n-3/n-6 ratios than their marine counterparts (Sargent 1976) resulting in freshwater fishes having lower n-3/n-6 ratios, lower levels of C₂₀ and C₂₂ unsaturated fatty acids, and higher levels of C₁₈ PUFA than marine fishes (Henderson and Tocher 1987). In pinnipeds, blubber is the most important site of lipid storage (Pond 1978) and the chemical composition of this tissue is thought to reflect that of the animal's diet (e.g. Iverson et al. 1995, 1997). Thus, the fatty acid composition of the blubber of marine seals, which presumably prey exclusively on saltwater fish, should mirror the chemical profile detailed above. Similarly, a freshwater signature in the fatty acid composition of *P. v. mellonae*'s blubber would indicate that it feeds primarily on freshwater fish species.

I analysed the tissues of *P. v. mellonae* and two marine populations of harbour seals (*P. v. richardsi*, eastern Pacific Ocean; *P. v. concolor*, western Atlantic Ocean and eastern Canadian Arctic) to test the hypothesis that *P. v. mellonae* feeds primarily in a freshwater habitat, and is distinguished from its oceanic counterparts by the freshwater signature in its tissue stable-carbon and nitrogen isotope ratios and fatty acid profiles (Smith et al. 1996). I also tested whether stable isotope ratios in *P. v. mellonae* were distinguishable from those in a group of lacustrine *P. v. concolor* which, because of their proximity to the ocean, probably feed in both freshwater and marine habitats (Smith et al. 1996).

Materials and Methods

Sample Collection

Stable-carbon and nitrogen isotope values were examined in three groups of seals: *P. v. concolor* from Kasegalik Lake, Belcher Islands, N.W.T., *P. v. concolor* from the

Northwest Atlantic Ocean, and *P. v. mellonae*. Fatty acid values were examined for the latter two of these groups, in addition to *P. v. richardsi* from the eastern Pacific Ocean.

Most of the hair samples used for stable isotope analyses were garnered from dried pelts in the following collections: the Carnegie Museum, Pittsburgh, PA (Table 4.1; CM accession numbers); the Canadian Museum of Nature, Ottawa, Ont. (CMN accession numbers); and the Greenland Environmental Research Institute, Copenhagen, Denmark (PV-G1). The remainder of the samples that were used in both analyses was fresh/frozen tissue collected from animals that were shot (Department of Fisheries and Oceans Canada, Nanaimo Research Station, samples PV-11 through -26; University of Guelph, samples LM-94-02 and LM-95-04; Greenland Environmental Research Institute, samples PV-1527, -1612 and -1618), found dead (Grand Manan Whale and Seabird Research Station, North Head, N.B., samples PV-92-01 through -05 and PV-93-01), or drowned incidentally in gillnets (Department of Fisheries and Oceans Canada, Institut Maurice-Lamontagne, samples LM-89-01 and -02).

Hair, blood and blubber biopsy samples from LM-94-01, LM-94-03 through -05, LM-95-01 through -03, LM-95-05 and -06, and LM-96-01 through -05 were collected from live animals that were captured and released in Lacs des Loups Marins in August and September of 1994, 1995 and 1996 (Chapter 5). Blood was taken from the hind flippers in serum separation tubes and centrifuged as soon as possible after collection before being stored. Biopsies were taken from the animals' side near the pelvis; the area was first frozen with a small injection of lidocaine hydrochloride (Xylocaine, Astra Pharma

Inc., Mississauga, Ont.) before the application of a 6 mm diameter biopsy punch (Acu-Punch, Acuderm Inc., Ft. Lauderdale, FL).

The fish fauna of Lacs des Loups Marins was sampled in 1995 and 1996 using a scientific sampling monofilament gillnet (length of approximately 42.5m; divided into 7 panels of different sized mesh, ranging from 2.5 cm to approximately 10 cm in 1.25 cm increments). The fish were sampled both to gather a rough idea of the composition of the lake's fish community, and to obtain samples of potential prey or foodweb components for stable isotope analysis.

Stable-isotope Analyses

The collected hair samples were washed in detergent using an ultrasonic cleaner and then rinsed repeatedly in distilled water before being dried in an oven at 60°C. Samples were then soaked in ether, rinsed, and air dried before being ground to a powder in a dental amalgam ball mill (Wig-L-Bug). Fish muscle tissue was freeze-dried and lipids extracted using repeated rinses with 2:1 chloroform:methanol. Samples were then air dried and powdered. Samples for $^{13}\text{C}/^{12}\text{C}$ analysis were loaded into tin cups and combusted in a CN elemental analyser that was part of the Europa Robo-Prep continuous flow mass spectrometer used for ^{13}C analysis of CO₂. Samples for ^{15}N analysis were loaded into quartz tubes with CuO, elemental Cu, Ag wire, and CaO, evacuated and then sealed using a propane torch. These samples were then combusted at 850°C for 2 hours before being allowed to cool slowly. The resultant N₂ gas was introduced directly into a

SIRA-12 isotope ratio mass spectrometer. Stable-isotope ratios were expressed using the following notation:

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

where $X = {}^{13}\text{C}$ or ${}^{15}\text{N}$, $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$ and the conventional standards were PeeDee Belemnite (PDB) carbonate and atmospheric (AIR) nitrogen for carbon and nitrogen samples, respectively. Analytical error for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses was estimated at $\pm 0.3\text{\textperthousand}$. ANOVAs ($\alpha = 0.0001$) were used to compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among the groups of seals.

Fatty Acid Analyses

Immediately after biopsy, blubber samples (approximately 0.5 g each) from LM-94-01 to -05 were placed in 2 mL of 2:1 chloroform:methanol (C:M) with 0.005% butylated hydroxytoluene, in Kimax test tubes with teflon caps. Samples were kept at -20°C until further analysis, at which time an additional 7 ml of the C:M mixture was added to each tube. Blubber samples from the other seals (Table 4.1) were taken from fresh carcasses and frozen until further analysis (also at -20°C). Approximately 0.5 g of each of these samples was placed in 9 mL of the C:M solution in Kimax tubes with Teflon caps. All samples were mashed manually with a glass homogeniser until thin and transparent, then vortexed for 20 seconds and allowed to soak for 24 hours. Samples (total lipid) were extracted according to a modified Folch procedure (Folch et al. 1957; see Iverson 1988).

Fatty acids of total lipids were converted to methyl esters by placing 50 mg of lipid with 1 mL hexane and 1 mL 10% BF₃ in methanol (samples LM-94-01 to -05), or by placing 50 mg of lipid with 1 mL hexane and 1 mL 10% BF₃ in butanol (all other samples) in Kimax tubes, which were then incubated at 100°C for 1 hour and allowed to cool to room temperature. Deionised H₂O (3 mL) was added, and the sample was vortexed and centrifuged at 480 x g for 5 min. The hexane layer was removed, washed with 5 mL deionised H₂O, and dried with sodium sulphate. Samples were flushed with nitrogen and capped tightly.

Fatty acid composition was determined using temperature-programmed capillary gas-liquid chromatography as described in Iverson et al. (1995) (methyl esters) and in Koopman (1994) (butyl esters). Fatty acids were identified using chromatograms of known standard mixtures (Nu Check Prep, Elysian, MN) and from samples earlier identified using silver nitrate chromatography (Iverson 1988). Identified fatty acid components were converted to a mass percentage of the total array of fatty acids plus unknown compounds. The small sample size restricted the number of statistical tests that could be made; thus only individual fatty acids and fatty acid families that have revealed habitat differences in other species (e.g. see Henderson and Tocher 1987; Käkelä et al. 1993) were compared between groups of seals: 18:2n-6, 18:3n-3, 20:1n-9, 20:4n-6, 22:1n-11, total C₁₈ PUFA, total saturates, total monounsaturates, total PUFA and the n-3/n-6 ratio. The three subpopulations of seals were compared using ANOVA on ranked data (equivalent to a Kruskal-Wallis non-parametric test) with $\alpha = 0.05$.

Results

Stable-isotope Analyses

The three sampled populations exhibited different ^{13}C content (ANOVA, $F_{[2,47]} = 142.6$, $p < 0.0001$): *P. v. mellonae* showed the most negative mean $\delta^{13}\text{C}$ value; the Kasegalik Lake sample of *P. v. concolor* showed an intermediate value; and the marine population of *P. v. concolor* showed the most positive value (Table 4.2, Fig. 4.1).

Applying the diet-hair $\delta^{13}\text{C}$ fractionation value for seals of +2.8‰ (Hobson et al. 1996), mean dietary $\delta^{13}\text{C}$ values for these three populations of seals were calculated as -25.9, -21.9, and -18.9‰ for the *P. v. mellonae*, Kasegalik Lake, and marine *P. v. concolor* samples, respectively. Serum $\delta^{13}\text{C}$ values for *P. v. mellonae* were very similar to the values derived from the analysis of hair samples (mean of -27.2‰ after applying the fractionation value).

Stable-nitrogen isotope values of seals from the two freshwater locations were less variable than those from the broader marine sample (Table 4.2, Fig. 4.1). Using the seal diet-hair $\delta^{15}\text{N}$ fractionation value of +3.0‰ (Hobson et al. 1996), mean dietary $\delta^{15}\text{N}$ values of the *P. v. mellonae*, Kasegalik Lake, and marine *P. v. concolor* samples were 9.9, 10.6, and 13.2‰, respectively. The mean serum $\delta^{15}\text{N}$ value for *P. v. mellonae* was identical to the value derived from hair (9.9‰).

One freshwater seal that was marked in 1994 (LM-94-01) was subsequently recaptured in 1995 (LM-95-01). To avoid analysing the same animal twice, the means of this

animal's 1994 and 1995 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (see Fig. 4.1) were used for the purposes of the ANOVA and the calculation of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for *P. v. mellonae*.

The fish species collected included: longnose sucker (*Catostomus catostomus*), cisco (*Coregonus artedii*), lake whitefish (*C. clupeaformis*), sculpin (*Cottus* sp.), lake chub (*Couesius plumbeus*), threespine stickleback (*Gasterosteus aculeatus*), round whitefish (*Prosopium cylindraceum*), ninespine stickleback (*Pungitius pungitius*), brook char (*Salvelinus fontinalis*), and lake char (*S. namaycush*) (Table 4.3). Stable-carbon and nitrogen isotope ratios for the sampled Lacs des Loups Marins fish are also presented in Table 4.3.

Fatty acid Analyses

The blubber of *P. v. mellonae* contained significantly higher levels of 18:2n-6, 18:3n-3, 20:4n-6, C₁₈ PUFA and total PUFA than did the blubber of either *P. v. concolor* and *P. v. richardsi*. *Phoca v. mellonae* also had significantly lower levels of 20:1n-9 and 22:1n-11 and a lower n-3/n-6 ratio than the two groups of marine seals (Table 4.4). The most obvious difference between the freshwater and marine seals examined here was the large proportion of n-6 fatty acids in *P. v. mellonae*'s blubber. Levels of total n-3 fatty acids in these animals were also higher than both marine seal groups, but were closer to the range of values observed for marine seals than were the levels of n-6 fatty acids (Fig. 4.2).

There were some significant differences between the fatty acid composition of the blubber of the two groups of marine seals: *P. v. concolor* (Northwest Atlantic) had higher levels of 18:2n-6, 20:1n-9, 22:1n-11, C₁₈ PUFA and a larger n-3/n-6 ratio in their blubber than did *P. v. richardsi* (eastern Pacific).

Discussion

Results from the stable-isotope and fatty acid analyses both indicated that the diet of Lacs des Loups Marins seals is of freshwater origin. Stable-carbon isotope analysis of seal hair allowed the successful segregation of the three populations of seals from freshwater and marine habitats (Fig. 4.1). As predicted, *P. v. mellonae* showed the most depleted $\delta^{13}\text{C}$ values, which is consistent with a diet derived from freshwater prey during the period when the hair was grown – likely at least half a year. The results from the analysis of *P. v. mellonae* serum, which are similar to the results from the hair analysis, are consistent with a diet derived from freshwater since the last major feeding. The fact that there was no discernible difference between the isotopic signatures of the *P. v. mellonae* samples from 1936-38, 1989, and 1994-96, and that the marked and recaptured animal (LM-94-01, LM-95-01) had a $\delta^{13}\text{C}$ value that was virtually identical in both years (-22.9 in 1994, -22.5 in 1995), is further evidence of prolonged freshwater feeding.

The Cree of Whapmagoostui have long contended that the Lacs des Loups Marins seals feed in freshwater and that these animals taste differently compared to oceanic harbour

seals, making them a favoured target for hunting (John Petagumskum Sr., pers. comm.; Twomey 1942; Posluns 1993). The Cree also consider that this freshwater diet is one of the reasons why the Lacs des Loups Marins seals' pelage is darker and more lustrous than its saltwater counterpart (John Petagumskum Sr., pers. comm.; Posluns 1993). This belief that the pelage of the freshwater animals is quantifiably different has been remarked upon by a variety of authors over the course of nearly two centuries (Atkinson 1818; Flaherty 1918; Doutt 1942; Graburn 1969), and formed one of the bases for *P. v. mellonae*'s subspecific description (Doutt 1942).

Aside from these anecdotal accounts, few previously published data are available on the diet of the Lacs des Loups Marins seal (Smith et al. 1996; Smith 1997). Power and Gregoire (1978) conducted a study in which fish from Lacs des Loups Marins were compared with samples caught in nine nearby Ungava peninsula lakes. After determining that brook char (*S. fontinalis*) was the dominant fish species of Lacs des Loups Marins, and that lake char (*S. namaycush*) and lake whitefish (*C. clupeaformis*) populations in the lake were depressed compared to the other lakes, they concluded that seal predation on the latter two species was responsible for the observed alterations in Lacs des Loups Marins' fish community. Even though brook char showed evidence of high mortality in Lacs des Loups Marins, Power and Gregoire hypothesised that their unusual dominance of the lake's fish fauna was attributable to the fact that their spawning occurs in sheltered tributary streams, making them inaccessible to potential seal predation during this vulnerable period. Despite this interesting hypothesis, these

researchers provided no direct evidence of the prey preference or feeding habits of the freshwater seals.

The lake whitefish and char populations in Lacs des Loups Marins are resident populations (Consortium Gilles Shooner & Associés et al. 1991b), and limited evidence from the stomach contents of the 4 available seal specimens indicates that *P. v. mellonae*'s diet consists, in large part, of these fish species: CM-15213, "well-digested pieces of fish" (Doutt 1942, p.71); LM-89-01, "2 otoliths similar to *Salvelinus* sp., numerous small pebbles, and the dorsal spine of *Gasterosteus aculeatus*" (Consortium Gilles Shooner & Associés et al. 1991a); LM-89-02, "60 otoliths appearing to be those of the genus *Salvelinus*, 3 otoliths of *S. fontinalis* and the pelvic and dorsal spines of *G. aculeatus*" (Consortium Gilles Shooner & Associés et al. 1991a); and LM-94-02, 7 otoliths of genus *Salvelinus* (Smith 1997). However, given that the $\delta^{13}\text{C}$ values of the char and whitefish sampled from Lacs des Loups Marins were even less than those calculated for the mean seal diet, it is clear that a more extensive carbon isotopic survey of potential prey of *P. v. mellonae* is required before any further inferences can be made about the composition of seal diets within Lacs des Loups Marins.

While few isotopic studies have been conducted on fish in Arctic drainages, Hesslein et al. (1989, 1991) demonstrated that variation in isotope values among species can indicate different sources of feeding both within and outside of local lakes. The $\delta^{13}\text{C}$ values for char in Lacs des Loups Marins (Table 4.3) overlap those found for char (*S. alpinus*) at

Char Lake, N.W.T. (Hobson and Welch 1995). Whitefish and stickleback values are similar to those found by Hesslein et al. (1991) in Travaillant Lake, N.W.T.

Phoca v. concolor from Northwest Atlantic marine populations showed $\delta^{13}\text{C}$ values that are typical of marine mammals measured elsewhere in north-temperate regions (Ramsay and Hobson 1991; Hobson and Welch 1992; Hobson et al. 1997). The Kasegalik Lake sample was intermediate in $\delta^{13}\text{C}$ signature between the marine and Lacs des Loups Marins values. Kasegalik Lake is, at some points, less than 2 km from the ocean, and the Arctic char that frequent the lake are anadromous (Sanikiluaq Hamlet Council 1978). Thus, seals collected from Kasegalik Lake had access to both freshwater and marine-derived carbon, either because of their use, or because of their prey's use, of both kinds of aquatic habitat.

The stable-nitrogen isotope values for the marine *P. v. concolor* sample indicated that it occupied at least two trophic levels. This is consistent with published stomach content and scat analyses that have indicated a broad diet consisting of invertebrates as well as planktivorous and omnivorous fish (Boulva and McLaren 1979; Payne and Selzer 1989).

The *P. v. mellonae* and Kasegalik Lake *P. v. concolor* were similar in $\delta^{15}\text{N}$ values, suggesting that they occupy similar trophic positions. The estimated mean $\delta^{15}\text{N}$ values of 9.9 to 10.6‰ for the prey of freshwater seals is in close agreement with those values found for fish in Lacs des Loups Marins (Table 4.3). Freshwater seals also showed less variation in trophic position; probably due to fewer dietary alternatives in high-latitude

lakes compared with Arctic marine systems (e.g. Kling et al. 1992; Hobson and Welch 1992, 1995).

The fatty acid composition of the blubber of *P. v. mellonae* also indicated that the lipid in these seals is derived from a freshwater source. The plot of n-3 vs. n-6 fatty acids (Fig. 4.2) shows that levels of n-6 alone can distinguish the freshwater harbour seals from the two marine populations. The pattern of high levels of n-6, C₁₈ PUFA and low levels of monounsaturated C₂₀ and C₂₂ in the Lacs des Loups Marins seals is typical of the fatty acid composition of organisms in freshwater environments (Henderson and Tocher 1987). Henderson and Tocher (1987) noted that the n-3/n-6 ratio in freshwater fish ranges from 0.5 to 3.8, while in marine fish the value is typically between 4.7 and 14.4. Assuming similar ratios for higher level consumers like seals, this further indicates that *P. v. mellonae* (ratio = 2.05) is feeding in fresh water, whereas *P. v. concolor* (ratio = 7.65) and *P. v. richardsi* (ratio = 6.31) are consuming marine prey.

There are few comparative studies of the fatty acid composition of other mammals in freshwater environments; however, those that do exist have arrived at similar conclusions. Käkelä et al. (1993) examined the fatty acid composition of the blubber of Saimaa ringed seals (*Phoca hispida saimensis*) from a freshwater lake and found that it contained higher levels of 20:4n-6 (3.02 %) than did the blubber of ringed seals (*P. h. botnica*) from the Baltic (0.63 %). However, these authors found the levels of 18:2n-6 and the n-3/n-6 ratio in the blubber of Saimaa seals (4.50 % and 4.58, respectively) to be the same as those of the Baltic seals (4.43 % and 4.53, respectively), and suggested the

presence of a gradient of fatty acids from freshwater to brackish to marine food webs. Käkelä et al.(1995) found the levels of C₂₂n-6 fatty acids in the blubber of freshwater ringed seals from lakes Saimaa and Ladoga to be twice as high as those in marine ringed seals from the Arctic Ocean. In the present study, the separation between marine and freshwater seals on the basis of these fatty acids was even clearer; the blubber of the marine seals contained less than one-tenth the amount of C₂₂n-6 fatty acids observed in the freshwater seals (*P. v. richardsi*, 0.18%; *P. v. concolor*, 0.13%; *P. v. mellonae*, 1.95%). The Amazon river dolphin (*Inia geoffrensis*) is completely riverine and its blubber is characterised by an extremely low n-3/n-6 ratio (0.27), which is primarily the result of high levels of 18:2n-6 (6.61 %) (Ackman et al. 1971). *Inia geoffrensis* blubber also contains low levels of 20:1 (0.52 %) (Ackman et al. 1971), similar to those observed here in *P. v. mellonae* (0.61 %).

The two marine harbour seal subspecies examined exhibited clear marine signatures in the fatty acid patterns of their blubber. Surveys of the composition of the blubber of five phocid seal species revealed n-3/n-6 ratios ranging from 9 to 24 , and levels of 20:1 and 22:1 ranging from 5.0 to 16.6 and 0.7 to 6.5, respectively (Engelhardt and Walker 1974; West et al. 1979). While the fatty acid compositions of the blubber of *P. v. concolor* and *P. v. richardsi* are similar to those of other marine seals, they can also be distinguished from one another on the basis of levels of monounsaturated C₂₀ and C₂₂. These fatty acids originate in marine copepods (Ackman 1980), and the significantly higher levels of these compounds in the *P. v. concolor* sample (Table 4.4) are probably a reflection of variation in the diet of the primary prey species in each area. Levels of

different isomers of monounsaturated C₂₂ fatty acids can also be used to provide further evidence that the Lacs des Loups Marins seals are feeding in freshwater; 22:1n-11 originates in marine copepods, while 22:1n-9 is found in freshwater invertebrates (Ratnayake and Ackman 1979; Bell et al. 1994). The ratio of 22:1n-11 to 22:1n-9 in the *P. v. mellonae* seals (0.56) was much lower than in the *P. v. richardsi* and *P. v. concolor* seals (7.52 and 8.21, respectively), and 22:1n-11 was virtually absent in the freshwater seals, suggesting further that the Lacs des Loups Marins animals are not feeding in a marine food web.

This study has demonstrated the utility of two relatively new analytical techniques for the study of marine mammals with access to marine or freshwater ecosystems. While the present analyses were performed on samples that did not allow year-round inferences of seal diet, they do provide additional evidence that *P. v. mellonae* is resident in freshwater and point to interesting future research possibilities in this unique aquatic ecosystem. Further isotopic analysis of bone collagen would, for example, provide dietary inferences based on the lifetime of individuals (Tieszen and Boutton 1988). In addition, isotopic and fatty acid analysis based on samples collected throughout the year would reveal seasonal dietary patterns.

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Table 4.1. Specimens of *Phoca vitulina richardsi*, *P. v. concolor* and *P. v. mellonae* used in the stable isotope (SI) and fatty acid (FA) analyses.

Specimen	Types of analyses	Location Collected	Date Collected	Sex
<i>P. v. richardsi</i>				
PV-11	FA	Danger Reefs, B.C.	92-10-02	F
PV-12	FA	Danger Reefs, B.C.	92-10-02	M
PV-13	FA	Snake Island, B.C.	92-07-16	F
PV-14	FA	Nanaimo, B.C.	92-05	F
PV-15	FA	Snake Island, B.C.	92-04-30	F
PV-16	FA	Snake Island, B.C.	92-04-30	F
PV-17	FA	Crofton, B.C.	92-10-06	F
PV-18	FA	Miami Island, B.C.	92-10-06	F
PV-19	FA	North Stuart Channel, B.C.	92-10-06	F
PV-20	FA	North Stuart Channel, B.C.	92-10-06	F
PV-21	FA	Miami Island, B.C.	92-10-06	M
PV-22	FA	North Reef (Crofton), B.C.	92-10-07	M
PV-23	FA	Escape Reef, B.C.	92-10-07	M
PV-24	FA	Thetis Island, B.C.	92-10-07	M
PV-25	FA	Miami Island, B.C.	92-10-07	F
PV-26	FA	Danger Reefs, B.C.	92-10-07	F
<i>P. v. concolor</i>				
PV-92-01	FA	Grand Manan Island, N.B.	92-07-10	M
PV-92-02	SI	Grand Manan Island, N.B.	92-07-28	F
PV-92-03	SI	Grand Manan Island, N.B.	92-08-05	M
PV-92-04	SI	Grand Manan Island, N.B.	92-08-20	F
PV-92-05	SI	Grand Manan Island, N.B.	92-08-20	F

PV-93-01	FA	Grand Manan Island, N.B.	93-09-09	F
PV-1527	FA	Anorluitsoq, Greenland	86-05-01	M
PV-1612	FA	S. Aappilattoq, Greenland	86-05-04	F
PV-1618	FA	Anorluitsoq, Greenland	86-05-11	M
PV-G1	SI	Qaqortoq, Greenland	1993	na
CMN-6138	SI	Nettilling Fiord, Baffin Is.	26-03-13	F
CMN-9311	SI	Saguenay Co., Qué.	28-06-04	F
CMN-10358	SI	Cape Dorset, Baffin Is.	28-10-16	F
CMN-20289	SI	Ha Ha Bay, Qué.	50-06-16	M
CMN-20290	SI	Ha Ha Bay, Qué.	50-06-15	na
CMN-20291	SI	Ha Ha Bay, Qué.	50-06-16	M
CMN-20600	SI	Anticosti Is., Qué.	52-06-25	F
CMN-20685	SI	Grand Grève, Qué.	51-07-23	F
CMN-20687	SI	Grand Grève, Qué.	51-07-23	na
CM-13161	SI	Freshwater Lake, Belcher Is.	37-10-11	na
CM-15217	SI	Kasegalik Lake, Belcher Is.	37-07-15	F (?)
CM-15218	SI	Kasegalik Lake, Belcher Is.	38-06-30	F
CM-15219	SI	Kasegalik Lake, Belcher Is.	38-06-30	F
CM-15220	SI	Kasegalik Lake, Belcher Is.	38-06-30	F
CM-15221	SI	Kasegalik Lake, Belcher Is.	38-07-19	F
CM-17679	SI	La Tabatière, Qué.	39-07-01	M
CM-18698	SI	La Tabatière, Qué.	39-12-23	F
CM-18745	SI	Lake, Belcher Is., N.W.T.	Spring 1940	F
CM-18746	SI	Lake, Belcher Is., N.W.T.	Spring 1940	M
CM-18747	SI	Lake, Belcher Is., N.W.T.	Spring 1940	M
CM-18748	SI	Lake, Belcher Is., N.W.T.	Spring 1940	F
CM-19445	SI	Lake, Belcher Is., N.W.T.	40-08-11	F

P. v. mellonae

CM-15211	SI	Lacs des Loups Marins, Qué.	Summer 1936	F
CM-15212	SI	Lacs des Loups Marins, Qué.	Summer 1937	M (?)
CM-15213	SI	Lacs des Loups Marins, Qué.	38-03-22	F
CM-15214	SI	Lacs des Loups Marins, Qué.	38-03-22	M
CM-15215	SI	Lacs des Loups Marins, Qué.	38-03-23	M
CM-17744	SI	Lacs des Loups Marins, Qué.	1938-39	N/A
LM-89-01	Both	Lacs des Loups Marins, Qué.	89-08	F
LM-89-02	Both	Lacs des Loups Marins, Qué.	89-08	F
LM-94-01 (AF1)	Both	Lacs des Loups Marins, Qué.	94-09-04	F
LM-94-02	Both	Lacs des Loups Marins, Qué.	94-09-05	M
LM-94-03 (AF2)	Both	Lacs des Loups Marins, Qué.	94-09-07	F
LM-94-04 (AF3)	Both	Lacs des Loups Marins, Qué.	94-09-10	F
LM-94-05 (AF4)	Both	Lacs des Loups Marins, Qué.	94-09-11	M
LM-95-01 (AF5) (recaptured AF1)	SI	Lacs des Loups Marins, Qué.	95-09-04	F
LM-95-02 (AF6)	SI	Lacs des Loups Marins, Qué.	95-09-07	M
LM-95-03 (AF7)	SI	Lacs des Loups Marins, Qué.	95-09-09	M
LM-95-04	SI	Lacs des Loups Marins, Qué.	95-09-09	F

LM-95-05 (AF8)	SI	Lacs des Loups Marins, Qué.	95-09-11	M
LM-95-06 (AF9)	SI	Lacs des Loups Marins, Qué.	95-09-14	M
LM-96-01 (AF10)	SI	Lacs des Loups Marins, Qué.	96-08-25	M
LM-96-02 (AF11)	SI	Lacs des Loups Marins, Qué.	96-08-27	F
LM-96-03 (AF12)	SI	Lacs des Loups Marins, Qué.	96-08-27	F
LM-96-04 (AF13)	SI	Lacs des Loups Marins, Qué.	96-08-30	F
LM-96-05 (AF14)	SI	Lacs des Loups Marins, Qué.	96-08-31	F

**Table 4.2. Stable-carbon and nitrogen isotope values (mean \pm SD)
of hair and serum from seals from fresh, brackish and salt-water.**

Population	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>Phoca vitulina mellonae</i> (hair)	23	-23.1 \pm 1.4	12.9 \pm 1.1
<i>P. v. mellonae</i> (serum)	10	-24.4 \pm 1.0	12.9 \pm 0.8
<i>P. v. concolor</i> (Kasegalik Lake)	11	-19.1 \pm 1.0	13.6 \pm 1.2
<i>P. v. concolor</i> (marine)	16	-16.1 \pm 1.2	16.2 \pm 3.4

Table 4.3. Fish fauna of Lacs des Loups Marins, Québec: abundance and stable-carbon and nitrogen isotope values (mean \pm SD) from muscle tissue.

Species	Numeric Abundance	Relative Abundance (%)	Stable Isotope Analyses		
			n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
				(‰)	(‰)
<i>Catostomus catostomus</i>	1	0.3	1	-23.7	6.8
<i>Coregonus artedii</i>	41	11.3	23	-25.5 \pm 0.8	10.2 \pm 2.6
<i>Coregonus clupeaformis</i>	76	21.0	25	-22.8 \pm 2.0	8.0 \pm 0.5
<i>Cottus</i> sp.	*	*	16	-21.3 \pm 2.0	8.5 \pm 2.7
<i>Couesius plumbeus</i>	23	6.4	19	-21.3 \pm 1.2	8.4 \pm 1.4
<i>Gasterosteus aculeatus</i>	*	*	18	-24.2 \pm 1.4	6.8 \pm 0.5
<i>Prosopium cylindraceum</i>	23	6.4	15	-20.6 \pm 1.8	8.5 \pm 0.4
<i>Pungitius pungitius</i>	*	*	10	-24.5 \pm 1.3	6.9 \pm 0.2
<i>Salvelinus fontinalis</i>	140	38.7	22	-21.8 \pm 1.3	9.1 \pm 0.8
<i>Salvelinus namaycush</i>	58	16.0	21	-23.4 \pm 0.8	12.2 \pm 1.2

* Specimens were opportunistically obtained using dip-nets and therefore not included in abundance calculations.

Table 4.4. Levels of selected fatty acids in the blubber of three subspecies of harbour seal (*Phoca vitulina*).

	<i>P. v. concolor</i> (marine)	<i>P. v. richardsi</i> (marine)	<i>P. v. mellonae</i> (freshwater)
Fatty acids			
18:2n-6	1.29 ± 0.08 a	1.06 ± 0.15 b	4.78 ± 0.84 c
18:3n-3	0.52 ± 0.12 a	0.44 ± 0.11 a	2.88 ± 0.78 b
20:1n-9	8.77 ± 1.90 a	2.34 ± 0.92 b	0.09 ± 0.16 c
20:4n-6	0.40 ± 0.17 a	0.54 ± 0.15 b	2.69 ± 0.20 c
22:1n-11	3.42 ± 1.78 a	0.63 ± 0.44 b	0.02 ± 0.01 c
Total saturates	15.73 ± 1.36 a	14.54 ± 3.67 a	12.07 ± 1.43 a
Total monounsaturates	58.80 ± 3.76 ab	63.15 ± 5.97 a	49.60 ± 6.38 b
Total PUFA	23.36 ± 2.59 a	19.94 ± 5.30 a	34.26 ± 6.39 b
Total C ₁₈ PUFA	3.94 ± 0.30 a	2.81 ± 0.43 b	10.39 ± 2.02 c
n-3/n-6 ratio	7.65 ± 0.95 a	6.31 ± 1.36 b	2.05 ± 0.29 c

Note: Levels of fatty acids are given as percent wet weight (\pm S.D.) of total fatty acids and unknowns present in the sample. Levels of each fatty acid in a subspecies followed by different letters were significantly different ($p < 0.05$). Sample sizes were 5, 16, and 7 for *P. v. concolor*, *P. v. richardsi*, and *P. v. mellonae*, respectively.

Fig. 4.1. Distribution of stable-carbon and nitrogen isotope ratios in the hair of harbour seals with diets derived from marine (*Phoca vitulina concolor*; Northwest Atlantic), freshwater and marine (*P. v. concolor*; Kasegalik Lake), and freshwater (*P. v. mellonae*) sources. Subscripts 1 and 2 denote the 1994 and 1995 values, respectively, for the one freshwater seal that was marked and recaptured.

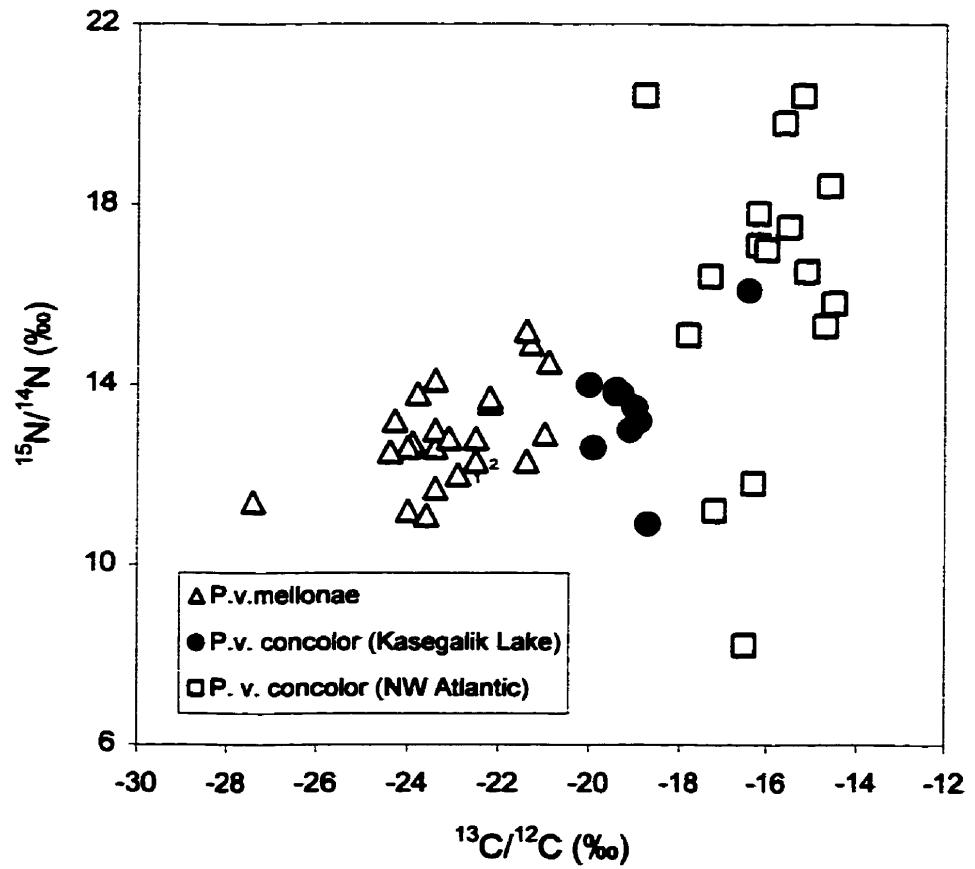
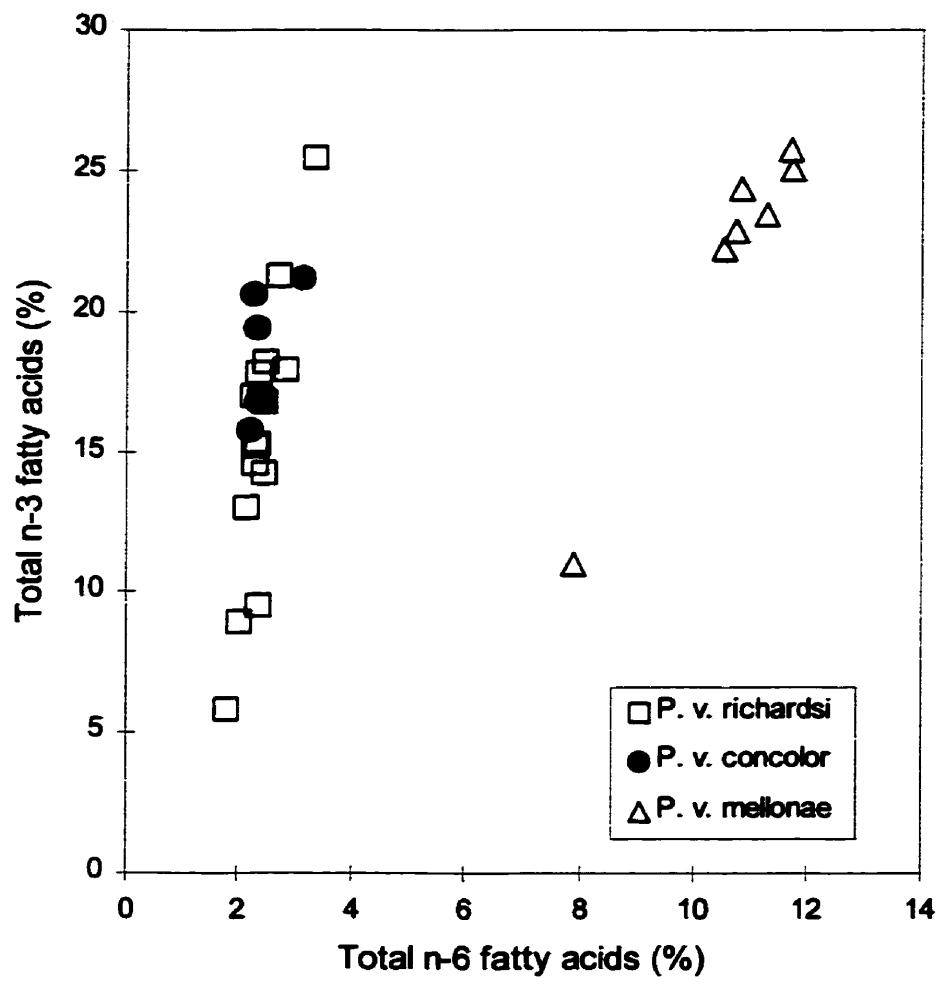


Fig. 4.2. Plot of total n-3 vs. total n-6 fatty acids (as percent of total fatty acids) in the blubber of marine (*Phoca vitulina richardsi* and *P. v. concolor*) and freshwater (*P. v. mellonae*) harbour seals.



CHAPTER 5: MOVEMENTS OF LACS DES LOUPS MARINS

HARBOUR SEALS, *Phoca vitulina mellonae* Doutt 1942,

MONITORED BY SATELLITE TELEMETRY

That there were seals in the inland lakes of Ungava was an old, old rumour on the mainland, and naturally of interest to all biologists (Twomey 1942, p. 9)

Introduction

Available evidence indicates that the harbour seal (*Phoca vitulina mellonae* Doutt 1942) population in the area of Lacs des Loups Marins, northern Québec, has persisted for at least 250 years (Bellin 1757), and is resident in freshwater year-round (Smith 1997). The Cree people of Whapmagoostui, who have hunted in the area for hundreds or thousands of years (Crowe 1991), consider the range of *P. v. mellonae* to be Lacs des Loups Marins, Petit Lac des Loups Marins, and Lac Bourdel, with some reports of animals having once been in Lac à l'Eau Claire (Clearwater Lake) (J. Petagumskum Sr., Whapmagoostui, pers. comm.) (Fig. 5.1). Sightings have been made of the seals in Lacs des Loups Marins at all times of the year (Smith 1997). Recently, evidence has been gathered by Hydro-Québec indicating the presence of these seals throughout a wider range of Ungava peninsula waterways (Consortium Gilles Shooner & Associés et al. 1991).

One of the presumptions upon which the subspecific description of *P. v. mellonae* was initially based is that the population had been isolated for 3000-8000 years, trapped by

the Ungava peninsula's isostatic rebound since the retreat of the Laurentian ice sheet (Doutt 1942). Other authors have disputed this interpretation, arguing that the seals are likely able to travel freely between salt and freshwater (Mansfield and McLaren 1958, Mansfield 1967, Smith and Horonowitsch 1987, also see Honacki et al. 1982, King 1983, Wiig 1989, Reeves et al. 1992). Smith and Horonowitsch (1987) noted that the large waterfalls on the Rivière Nastapoca would seem to make this avenue of exchange with Hudson Bay (a distance of approximately 160 km) unlikely, but that the more placid Rivière aux Feuilles, Rivière aux Mélèzes and Rivière DuGué, that drain toward Ungava Bay (a distance of approximately 300 km), might provide a more likely access to the ocean.

The question of seasonal changes in distribution has also been the subject of regular speculation (e.g. Doutt 1942, Mansfield 1967, Smith and Horonowitsch 1987, Consortium Gilles Shooner & Associés et al. 1991). Consortium Gilles Shooner & Associés et al. (1991) hypothesised that the seals congregate in larger bodies of water, such as Lacs des Loups Marins, Lac Bourdel and Petit Lac des Loups Marins in the winter, but then disperse into the surrounding watersheds in the spring (Fig. 5.1). Unlike ringed seals (*Pusa hispida*), harbour seals do not possess elongated nails on their anterior flippers that can be used to create breathing holes in the ice. As a consequence, any harbour seals that over-winter in Ungava lakes are dependent on naturally occurring ice-free areas. Doutt (1942, p. 71) quoted information relayed to him by his Cree guides:

Open water is the place to get seals when the lakes are frozen. Such places are found in the rivers where steep

hills narrow the channel and make swift water. The holes change rapidly with changes in the weather – warm weather opens new holes and makes old ones larger – cold weather closes up the smaller ones entirely and narrows the larger ones to small dimensions.

This observation of seal behaviour was the same as that provided to me by Cree hunters in Whapmagoostui (J. Petagumskum, Sr., pers. comm.). There have also been suggestions that the Lacs des Loups Marins harbour seals may take advantage of shoreline deformations of ice caused by dropping water for protection – a naturally-occurring analogy to the ice caverns that are excavated by ringed seals (Twomey 1942; Smith and Horonowitsch 1987; Dean Consulting & Research Associates Inc. 1991).

The use of satellite-linked transmitters is an increasingly common method of monitoring the movements and behaviour of marine mammals (Stewart et al. 1989; Lesage et al. 1995; Stewart et al. 1996; Westgate and Read 1998). The objective of the present study was to investigate the seasonal movements of Lacs des Loups Marins harbour seals with satellite telemetry in order to test Doutt's hypothesis that they have a restricted range and are resident in Lacs des Loups Marins throughout the year.

Materials and Methods

Seal Capture and Transmitter Configurations

Harbour seals (*P. v. mellonae*) were observed during field studies at Lacs des Loups Marins in August and September of 1994, 95 and 96. Satellite-linked transmitters were

placed on nine harbour seals that were captured in 1995 and 1996 (Table 5.1). Seals were captured in braided monofilament tangle nets (dimensions approximately 60 m x 3 m, mesh size of 10 cm) that were anchored on land and set perpendicular to the shore. Seals were removed from the net and strapped to a modified stretcher for restraint. Body mass was measured using a spring balance, and a variety of samples were taken (Chapters 3 and 4).

After the area of attachment was thoroughly cleaned and dried using acetone and a towel, satellite-linked transmitters were placed on each seal using five-minute epoxy (Devcon, Danvers, Massachusetts, USA) that was vigorously worked into the pelage. Two different transmitter configurations were used. In 1995, the transmitters were epoxy-cast satellite-linked time depth recorders (TDRs) (Wildlife Computers, Woodinville, Washington, USA), and were placed between the animals' shoulder blades. These TDRs had a 17 cm whip antenna, measured 6 cm x 14 cm x 6.5 cm and weighed approximately 400 g. Each instrument was powered by five 2/3 A lithium cells. To conserve battery life, the TDRs were duty-cycled 8 hours/day, with the exception of the TDR on seal AF5 (5132-95), which was set to transmit every other day. Unfortunately, the conductivity of Lacs des Loups Marins was so low that it was beneath the level of sensitivity of the TDRs' salt-water switch (which prevents TDR transmission when the seal is submerged), so it became necessary to turn the transmitters on permanently, rendering impossible the use of the TDRs' environmental sensors.

In 1996, the configuration of instrument that was used was a flat-board ST-10 transmitter (Telonics, Mesa, Arizona, USA) mounted in a low profile, rectangular, lexan box. These transmitters had a 17 cm whip antenna, measured 13.4 cm x 4.7 cm x 1.9 cm and weighed 200 g. The ST-10s were set to transmit 6 hours out of 48 with a 60 second repetition rate. Because they were substantially smaller than the TDRs, it was possible to attach them nearer to the backs of the animals' heads.

Data Analysis

Location data from each seal were obtained from Service ARGOS, Inc. (Landover, Maryland, USA). Service ARGOS provided information on the quality of the estimated location, and divided the location classes into seven categories: Class 3 (at least six uplinks received in a single satellite pass, position accuracy better than 150 m); Class 2 (five uplinks received in a single satellite pass, position accuracy within 350 m); Class 1 (four uplinks received in a single satellite pass, position accuracy within 1 km); Class 0 (less than four uplinks received in a single satellite pass, position accuracy greater than 1 km); Class A (three uplinks received; no estimate of position accuracy); Class B (two uplinks received; no estimate of position accuracy); and Class Z (a single uplink received; no latitude and longitude provided) (Service ARGOS 1996). Class Z uplinks produced no useable positions for the purpose of the analysis. All estimated locations were filtered using plausibility checks on speed and geographic position. Consecutive positions resulting in an average travel speed of greater than 7.2 km/hour were excluded; for an example of the use of such a filter see Read and Westgate (1997). This filter value was selected based on published travel speeds of phocid seals (Innes 1984). Each

estimated location was also filtered by comparing the geographic location of consecutive positions and excluding those positions that were improbable or impossible based on known pinniped behaviour and the shapes of the animals' satellite tracks. For example, positions that were many km from any body of water, and "spikes" in the animals' tracks (an extremely large position movement between two other, very close, positions) were validated using this filter. If there was any doubt as to the plausibility of a position, it was left in the analysis.

Analysis of movement data was performed using Arcview Geographic Information System (GIS) (ESRI 1994). Only the best position obtained per day from each seal was included to avoid bias associated with multiple daily positions. Positions (filtered, best per day) were plotted on digitised maps of the study area provided by the National Topographic Data Base (NTDB), and consecutive positions connected with track lines. Average daily distance (ADD) traveled was calculated by summing the distance (km) between the best position received each day for all days of the deployment and then dividing this value by the number of days of the deployment.

Two different calculations of home range were performed with the filtered, best per day positions, and plotted on the NTDB maps. Minimum Convex Polygons (MCP) were calculated from each animal's positions (ESRI 1994), and the amount of land within each polygon subtracted from the total polygon area to yield estimates of the amount of the lakes' surface area potentially utilised by each animal. Total area used by all seals was calculated by constructing a MCP around locations of all seals. Though MCP is still

often used by researchers to describe home range, the greatest disadvantage of this method is that the size of the home range estimate can increase indefinitely as the number of locations increases (White and Garrott 1990). Thus, calculations of kernel home range (Worton 1989) were also undertaken for each animal and for the total of all animals captured. The kernel home range method does not suffer from a relationship between sample size and home range size (White and Garrott 1990). It is an estimate of the harmonic mean home range, and weights the points based on the “utilisation distribution.” A point gets a higher weight if it is in a cluster of other points (i.e. a high utilisation area) (Worton 1989; White and Garrott 1990). Kernel home range (cell size: 250 m) was calculated with least-squares cross-validation of h (the smoothing parameter) (see Worton 1989). Arcview GIS allows the calculation of various probabilities of use, and confidence areas of 25%, 50%, 75% and 95% were chosen. The surface area of water within each of these probability areas was then calculated.

Results

A total of 39 seal sightings were made in Lacs des Loups Marins during August and September of 1994, 95 and 96 (Fig. 5.2).

Satellite transmitters placed on the seals provided data from 29 to 177 days (Table 5.1). A total of 1067 locations were received on 438 tracking days. The mean number of positions per day per animal for all location classes ranged from 1.6 ± 0.1 to 3.9 ± 0.2 (Table 5.2). Positions with location classes A, B, 0, 1, 2, and 3 accounted for 50.7% of

all position estimates. Positions that were incorporated into the analyses (non-Z, best per day, filtered) accounted for 20.4% of all position estimates (Appendix 1).

The transmitter on seal 5132-96 only produced 3 position estimates (non-Z, best per day, filtered) likely due to a malfunction soon after deployment (Appendix 1). These positions were therefore excluded from further analysis. Average daily distances traveled ranged from 1.5 to 9.8 km and Minimum Convex Polygon home ranges varied from 100.2 to 625.7 km² (Table 5.2; Fig. 5.3). The size of these home ranges were very much increased by outlying points: estimated locations at a distance from the animals' primary areas of utilisation. The majority of these outlying points were location classes A and B, which are the least precise estimates of location (Service ARGOS 1996). These points often had an IQ value of 0, indicating that the location estimate was of poor quality (IQ is an indicator that estimates residual error on the signal frequency calculation and transmitter oscillator frequency drift between two satellite passes) (Service ARGOS 1996). Examples of such locations are italicised and underlined in Appendix 1. Despite the likely poor quality of some of these locations, they were left in the analysis because of the conservative nature of the filter employed.

From an examination of Figures 5.3 and 5.4, the differences in the movements and ranges of the 8 seals become clear. Seals 5130-95 and 5132-95 had ranges in similar locations, and spent the majority of their time slightly South of the geographic centre of Lacs des Loups Marins. Seal 5131-95 spent the majority of its time in a branch of Lacs des Loups Marins slightly North and West of the centre of the lake, near Lac Bourdel.

Seal 5133-95 was tagged in Lacs des Loups Marins and then spent the next two and a half months in a small river that connects Lacs des Loups Marins and Petit Lac des Loups Marins. Seals 5131-96 and 5133-96 spent the majority of their time slightly North of the centre of Lacs des Loups Marins. Seal 9941-96 spent its time in the southern portion of Lacs des Loups Marins. The two most southern position estimates for this animal, which are well outside Lacs des Loups Marins, and which greatly increased the size of its MCP-calculated home range, are location class B, with an IQ of 0 (Appendix 1). Similarly, seal 9942-96 was tagged near the outflow of Lacs des Loups Marins into the Nastapoca River. This animal spent the majority of its time in this area, with the two location estimates in Lac à l'Eau Claire being location class B, IQ = 0.

There was no evidence of monthly shifts in movement or distribution patterns by the seals (Figs. 5.3 and 5.4). The number of satellite uplinks was dramatically decreased with the onset of ice cover on Lacs des Loups Marins, which usually occurs around the first week of November (Consortium Gilles Shooner & Associés et al. 1991). The predictability with which the transmitters ceased operation – in both years of the study, despite very different transmitter configurations -- around this time is striking. The dates of the last uplinks with numeric location classes for each animal (except 5132-96, which malfunctioned soon after deployment) are as follows: 5130-95 (Nov. 7); 5131-95 (Nov. 11); 5132-95 (Nov. 23); 5133-95 (Nov. 23); 5131-96 (Nov. 03); 5133-96 (Nov. 23); 9941-96 (Jan. 13); 9942-96 (Jan. 18). Given the paucity of location estimates after November 15, it was not possible to test whether there was any movement of seals toward naturally-occurring ice-free areas in the winter. With the exception of the last

position with a numeric location class for 9942-96, which was out of Lacs des Loups Marins on the boundary of the Lac à l'Eau Claire watershed, all positions recorded after Nov. 7 were in similar geographic locations as those recorded prior to the onset of ice cover (Appendix 1).

By combining the locations of all 8 animals (Fig. 5.5) and calculating the utilisation distribution, it was possible to visualise the fact that the seals had two distinct areas of utilisation: seven animals utilised Lacs des Loups Marins/Lac Bourdel proper, and 5133-95 utilised the river between Lacs des Loups Marins and Petit Lac des Loups Marins.

Discussion

These results support the hypothesis that *P. v. mellonae* is resident in the Lacs des Loups Marins area throughout the year. In addition, the results provide evidence that individual seals preferentially utilise specific sites within the lake (Figs. 5.3 and 5.4). Though there were few location estimates available subsequent to the onset of ice cover on the lake, what few satellite uplinks that did occur indicated that the seals remained in the area. Given the site fidelity exhibited by *P. v. mellonae*, and the fact that a large number of animals were captured in the vicinity of the base camp that was utilised over the three years of the study (located at the geographic centre of Lacs des Loups Marins, 56.524° N, 73.78° W), the utilisation distribution of the telemetered harbour seals is clearly partly a function of capture effort. The numeric location-class positions obtained from seals 5133-95 and 9942-96 do, however, provide evidence of some habitat useage outside of Lacs des Loups Marins/Lac Bourdel proper.

Considering that the battery power of the transmitters should have been ample to provide uplinks into January, and that 6 out of 8 transmitters failed concurrent with the onset of ice cover in early November (and the two that did keep transmitting began to do so with much reduced reliability around this time) (Appendix 1), it is reasonable to conclude that it was winter conditions that impaired or prematurely ended transmissions. There are two possible explanations for this: 1) Both configurations of transmitters were more sensitive to malfunctioning in the cold than was expected; or 2) The seals behaved in such a way that they destroyed the transmitters -- such as shearing the antennae as they exited or entered the water through the ice -- or rendered transmissions impossible -- such as spending the majority of their time underneath the ice as suggested by Twomey (1942) and Smith and Horonowisch (1987). The first possibility is unlikely given the extent to which other studies of pagophilic phocids have successfully used the same configurations of transmitters (e.g. Lydersen and Hammill 1993; Lydersen 1995). The second possibility, therefore, seems the most likely explanation and should inform the experimental design of any further field studies in this area.

The results of the present investigation are similar to those that have been undertaken of harbour seal populations in Europe and on the East and West coasts of North America. Harbour seals are well-known for being non-migratory and exhibiting a high degree of site fidelity (Yochem et al. 1987; Thompson 1993). Olesiuk et al. (1995) found that 13 of 15 translocated seals found their way back to their original haul-out sites, some swimming 272 km at swimming speeds of up to 62 km/day. Thompson (1993)

recognised two broad categories of harbour seal movements: 1) those between haul-out sites and the sea, which are primarily for foraging and occur within 50 km of haul-out sites; and 2) those that occur between different haul-out sites, which may involve dispersal and can occur seasonally when seals switch to sites that are more suitable for pupping or are closer to foraging areas. Consistent with this summary, Lesage et al. (1995) reported that one satellite-telemetered harbour seal in the St. Lawrence River remained within 80 km of its capture site throughout the winter, and in November a second animal left the area where it had been captured and moved 520 km to the Baie des Chaleurs where it remained for most of the winter before returning in late March to the capture location. In southern California, Stewart et al. (1989) used satellite telemetry to monitor the movements of a single seal and reported that the animal ranged up to 48 km from its haul-out site, although most trips were within 5 km. Thompson and Miller (1990) and Thompson et al. (1994) observed seals foraging up to 45 km from haul-out sites, but females with pups restricted their movements to within 2 km of haul-out sites during the early part of the lactation period. Other authors have observed foraging to be limited to 20 km of haul-out sites (Bjørge et al. 1995); less than 5.6 km (Suryan and Harvey 1998); and within 30 km (Tollit et al. 1998). Evidence from seals that are resident in freshwater (Lake Saimaa ringed seal, *Pusa hispida saimensis*) indicates that home range size in these animals may be even smaller than oceanic *Pusa* subspecies. Maximum distances traveled by individual Saimaa seals ranged from 3.4 to about 18 km, much shorter distances than ringed seals in the Arctic Ocean, which sometimes swim up to hundreds of km (Sipilä and Hyvärinen 1998).

The range size of harbour seals has been observed to vary according to sex and reproductive condition. Using Minimum Convex Polygon calculations, Thompson et al. (1994) and Van Parijs et al. (1997) showed that female harbour seals restrict their range during the early part of the lactation period (to approximately 5-35 km²) but that they make foraging trips in late lactation and are more widely dispersed when in oestrus (ranges of 50-115 km²). Male home range sizes are generally larger at all times of the year, but also vary seasonally: males continue to travel widely during the early pupping period (ranges of 65-480 km²), but then restrict their ranges to 4-70 km² at around the time that females start to make foraging trips in late lactation. These MCP home range sizes are similar to those observed in Lacs des Loups Marins seals (Table 5.2). Unfortunately, due to a paucity of data points, I was unable to test sex-related or seasonal variations in home range size in *P. v. mellonae*.

Implications for conservation

The results derived from satellite telemetry provide information on the habitat utilised by the Lacs des Loups Marins harbour seal that will be useful to the Government of Québec should it proceed with plans to protect the range of *P. v. mellonae* (Dubreuil 1983; Québec, Province 1992). Such protection should, at a minimum, encompass the watersheds of Lacs des Loups Marins, Lac Bourdel and Petit Lac des Loups Marins (Fig. 5.5).

In light of the evidence that harbour seals rarely venture out of this relatively small area, it is difficult to know how to interpret Hydro-Québec's claim to have recorded

vocalisations of harbour seals in 49 Ungava peninsula water bodies, ranging as far South as the reservoir at LG4, part of the original James Bay I hydroelectric project (Consortium Gilles Shooner & Associés et al. 1991). Hydro-Québec reported the recording of 8 distinctly different kinds of vocalisations: 1) resembling the “click” recorded from harbour seals by Renouf and Davis (1982); 2) vaguely resembling the “passerine call” produced by harp seals (*Pagophilus groenlandicus*) (Møhl et al. 1975); 3) resembling the “chirp” of the harp seal (Møhl et al. 1975); 4) resembling the “tap” of the walrus (*Odobenus rosmarus*) (Stirling et al. 1983); 5) resembling a bearded seal (*Ereignathus barbatus*) vocalisation (Cleator et al. 1989); 6) resembling a Weddell seal (*Leptonychotes weddelli*) vocalisation (Thomas and Stirling 1983); 7) resembling another sort of harbour seal vocalisation (Renouf and Davis 1982); and 8) a new sound not recorded in the literature (Consortium Gilles Shooner & Associés et al. 1991). During the same observations, Hydro-Québec biologists reported that the male and female harbour seals exhibited externally visible sexual dimorphism, with males having a markedly more bulbous forehead than females (Consortium Gilles Shooner & Associés et al. 1991). Hydro-Québec’s findings regarding sexual dimorphism and vocalisations, and the widespread distribution of Lacs des Loups Marins harbour seals, are not consistent with any other data, either historical or contemporary (Boulva and McLaren 1979; Bigg 1981; Smith 1997).

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Table 5.1. Description of harbour seals (*Phoca vitulina mellonae*) that were affixed with satellite transmitters in Lacs des Loups Marins, Québec in 1995 and 1996.

	Seal ID.	Sex	Standard Length (cm)	Body Mass (kg)	Capture Date	Satellite Package	Tracking Period (d)
1995	AF5	F	119	55	4 Sep	SLTDR	81
			5132-95				
	AF6	M	143	70.5	7 Sep	SLTDR	92
			5131-95				
	AF8	M	134	64	11 Sep	SLTDR	80
			5133-95				
	AF9	M	137	64	14 Sep	SLTDR	69
			5130-95				
1996	AF10	M	107	26.5	25 Aug	ST-10	29
			5132-96				
	AF11	F	132	67	27 Aug	ST-10	151
			5133-96				
	AF12	F	99	25.5	27 Aug	ST-10	71
			5131-96				
	AF13	F	130	79.5	30 Aug	ST-10	177
			9941-96				
	AF14	F	121.5	41	31 Aug	ST-10	149
			9942-96				

Table 5.2. Mean number of uplinks per day; number of telemetered positions used in analysis; average daily distance (ADD), and minimum convex polygon (MCP) and kernel home range estimates for 9 Lacs des Loups Marins seals observed in 1995 and 1996.

Seal ID	Mean number of uplinks per day	No. of positions used	ADD (km)	MCP Water (km ²)	Kernel (25) Water (km ²)	Kernel (50) Water (km ²)	Kernel (75) Water (km ²)	Kernel (95) Water (km ²)
5130-95	3.3 ± 0.1	52	9.8	502.5	14.8	29.9	51.0	291.4
5131-95	3.9 ± 0.2	51	7.9	185.5	4.0	7.3	35.5	210.4
5132-95	1.5 ± 0.1	18	5.1	478.0	27.2	83.1	193.8	890.8
5133-95	1.9 ± 0.1	39	4.7	182.0	6.4	11.0	16.8	82.9
5131-96	2.1 ± 0.2	16	1.5	100.2	10.2	34.2	76.5	144.7
5132-96	na	na	na	na	na	na	na	na
5133-96	1.7 ± 0.1	12	2.5	277.5	21.5	42.5	161.4	445.3
9941-96	2.0 ± 0.1	9	1.6	303.9	57.9	126.1	262.9	705.3
9942-96	1.6 ± 0.1	18	1.9	625.7	39.0	75.7	144.5	448.7
All	2.25 ± 0.3	218	4.4	1778.5	20.8	65.1	271.6	672.3

Fig. 5.1. Study area in northern Québec as depicted by National Topographic Data Base digitised maps.

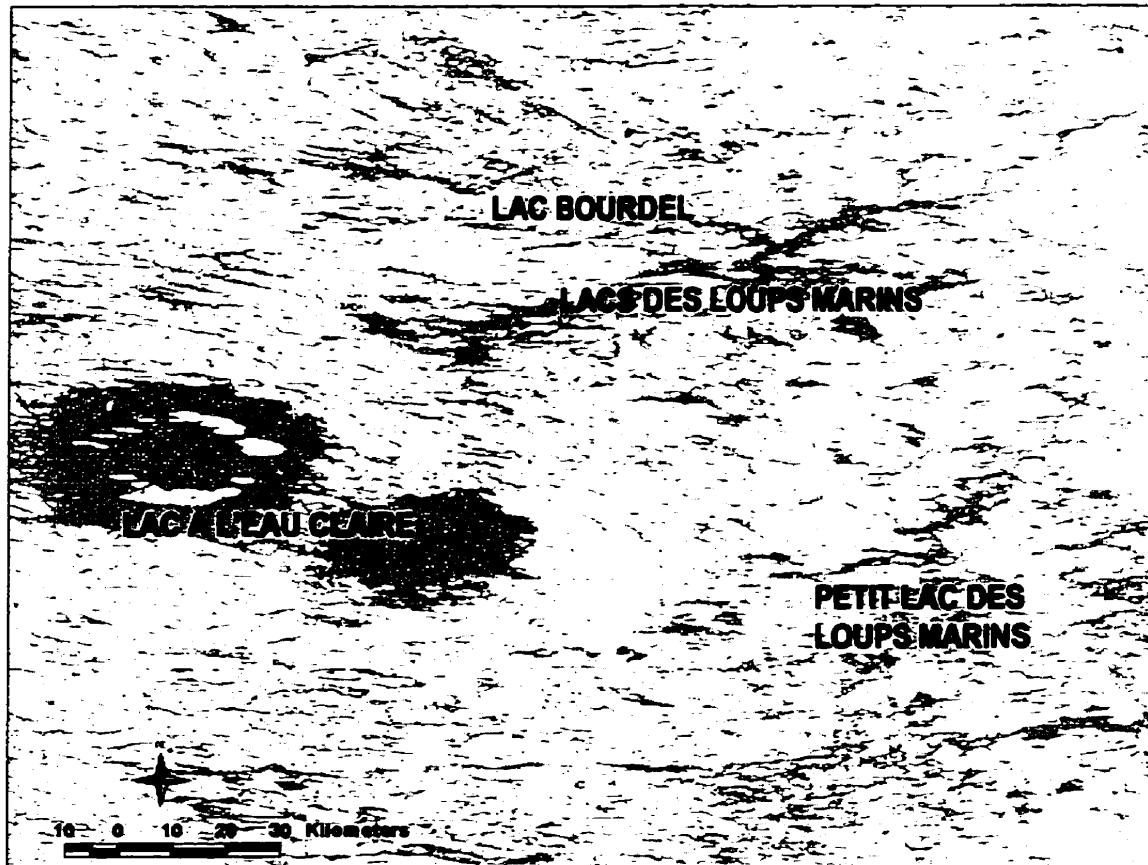


Fig. 5.2. Sightings of Lacs des Loups Marins harbour seals: 1994-96.

Sightings

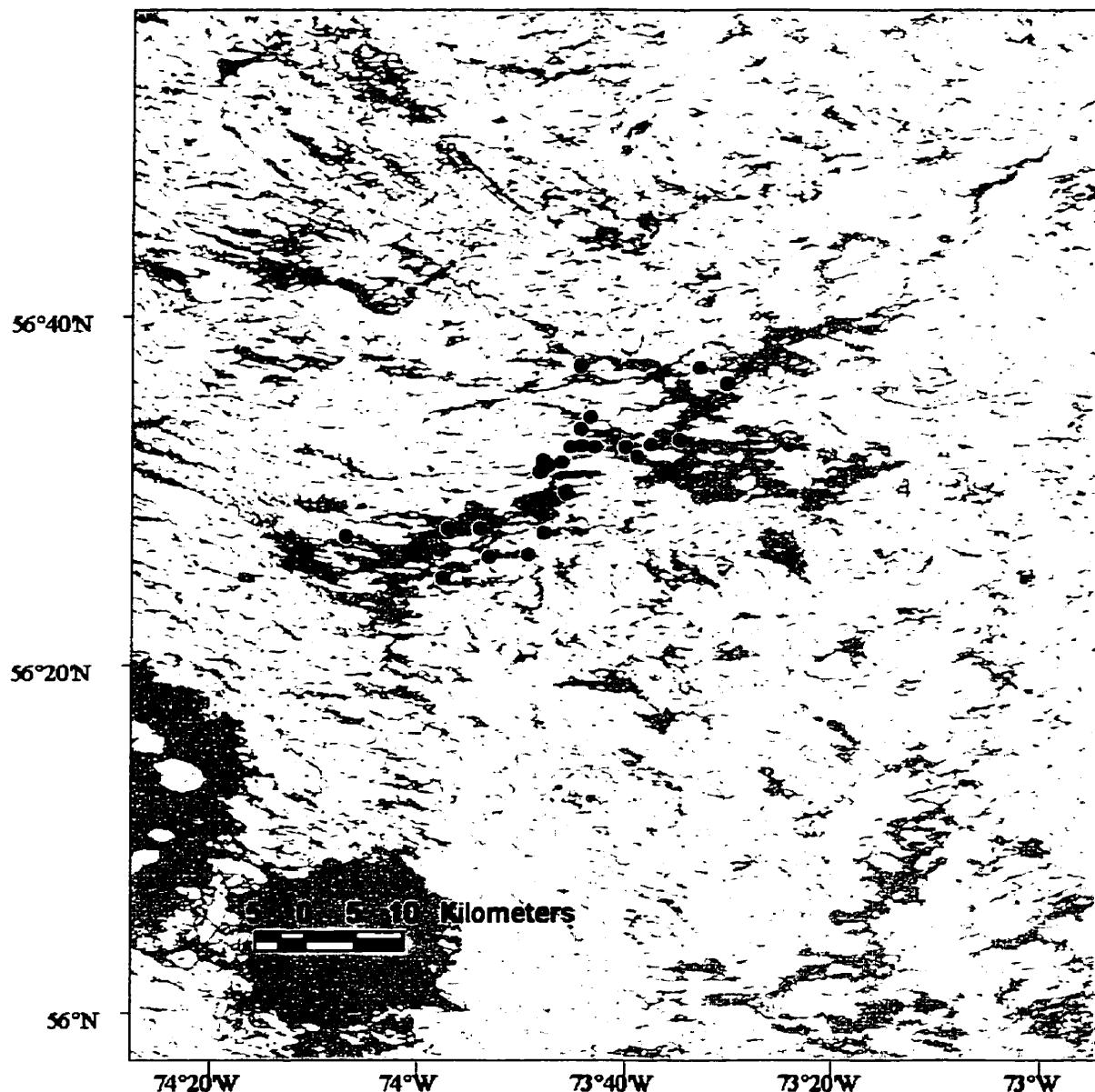
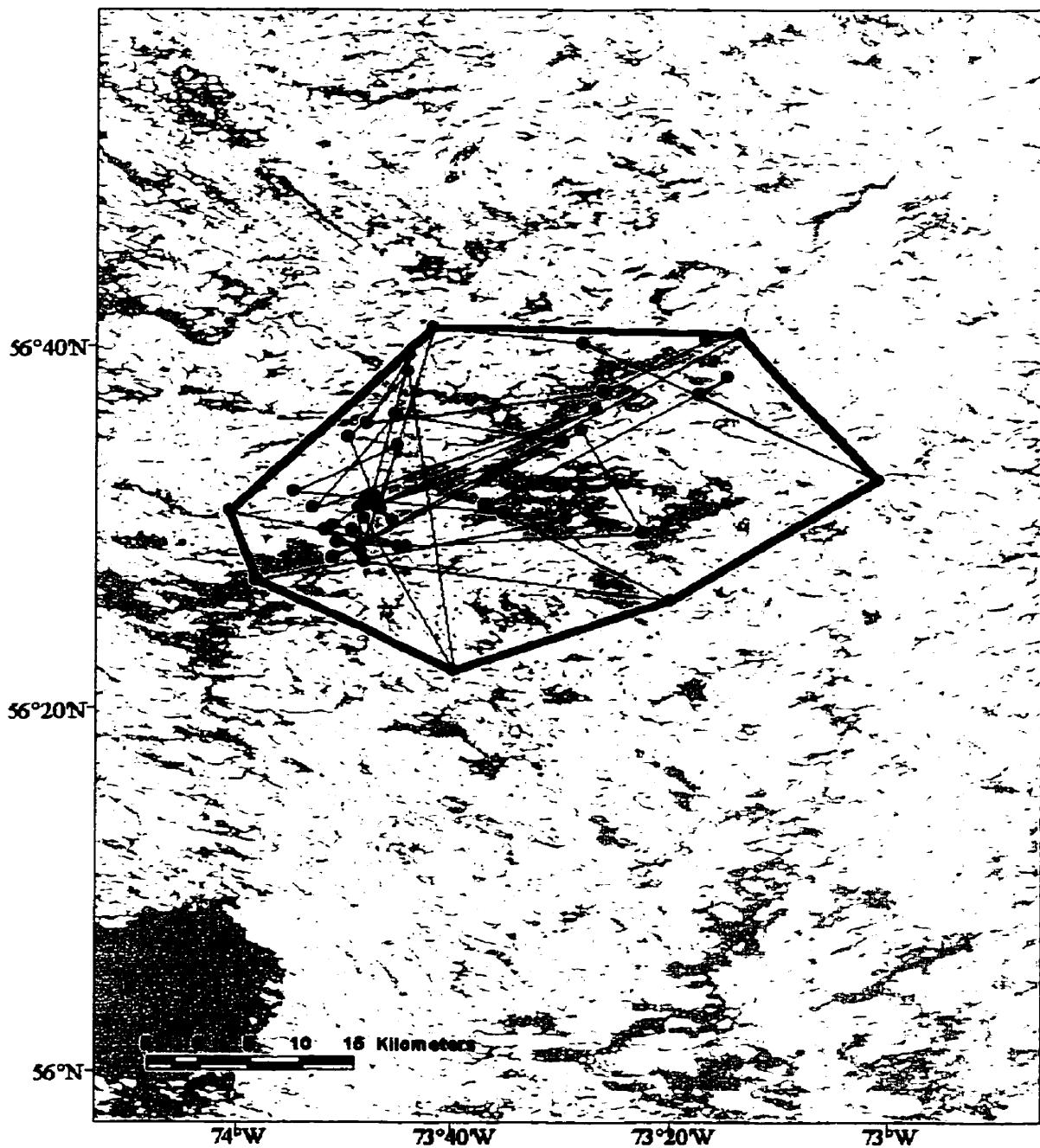
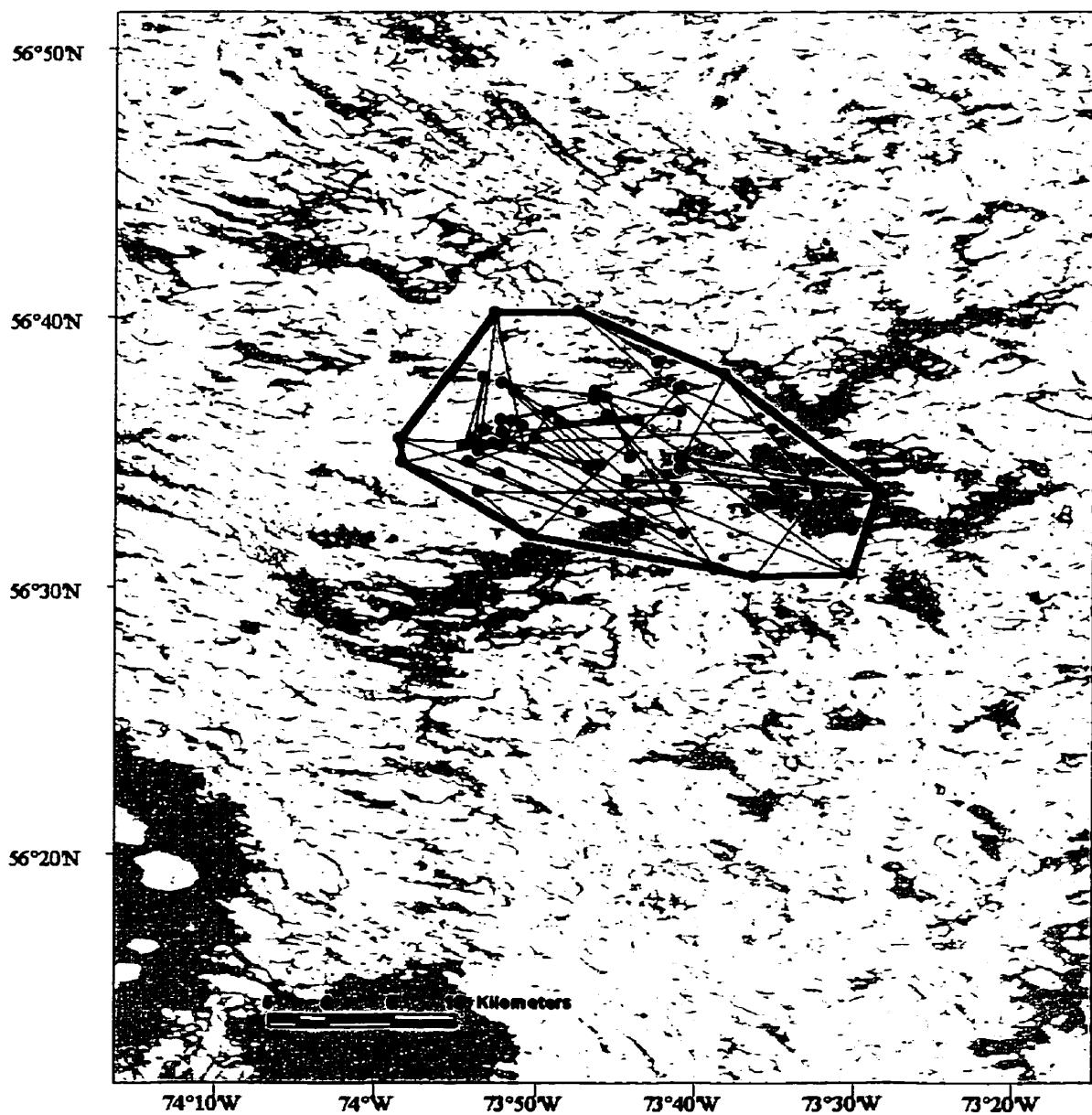


Fig. 5.3. Movements of 8 Lacs des Loups Marins harbour seals as monitored by satellite telemetry in 1995 and 1996. Minimum Convex Polygons enclose all estimated positions.

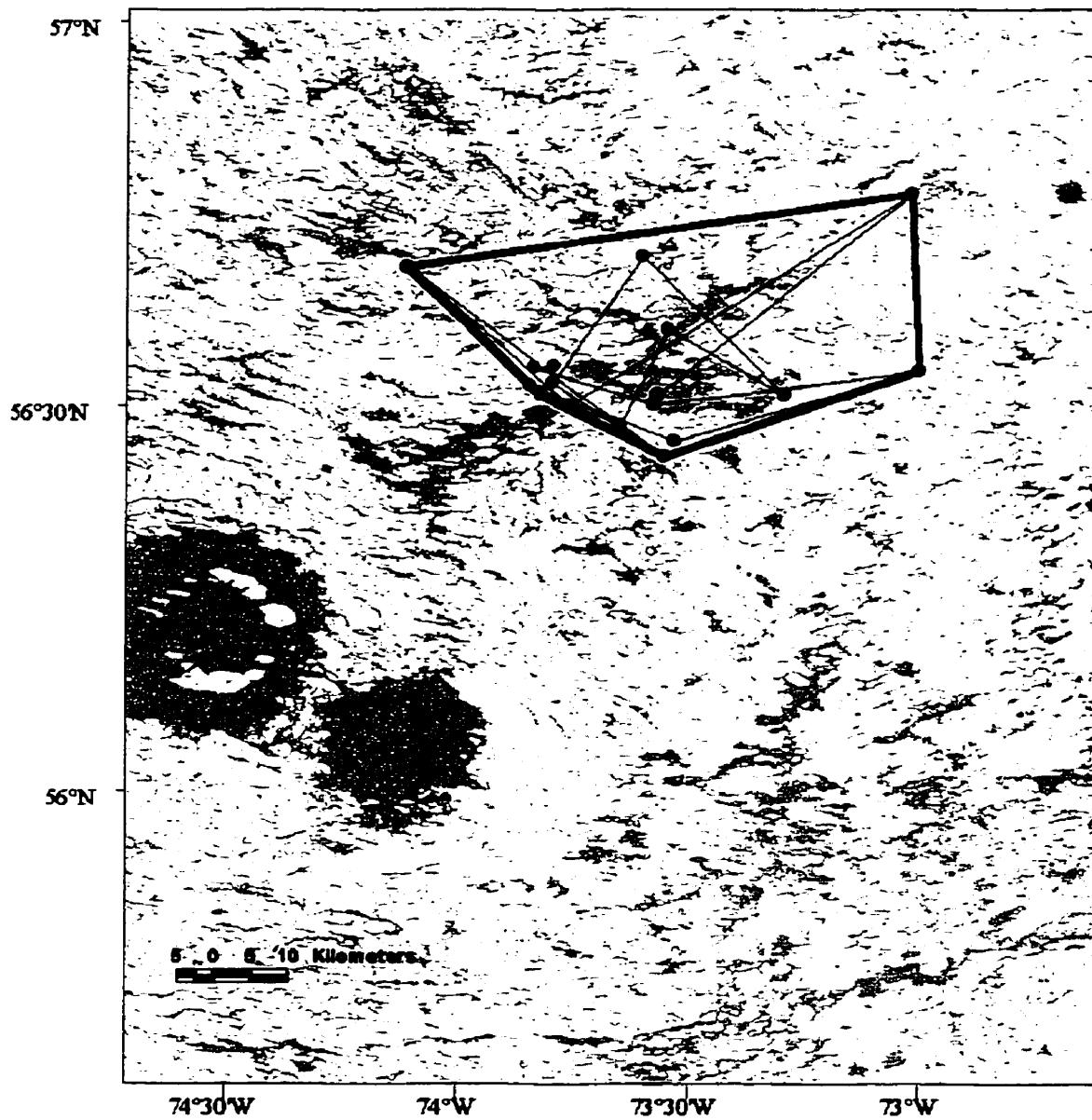
5130-95
[14 Sep 1995 - 20 Nov 1995]



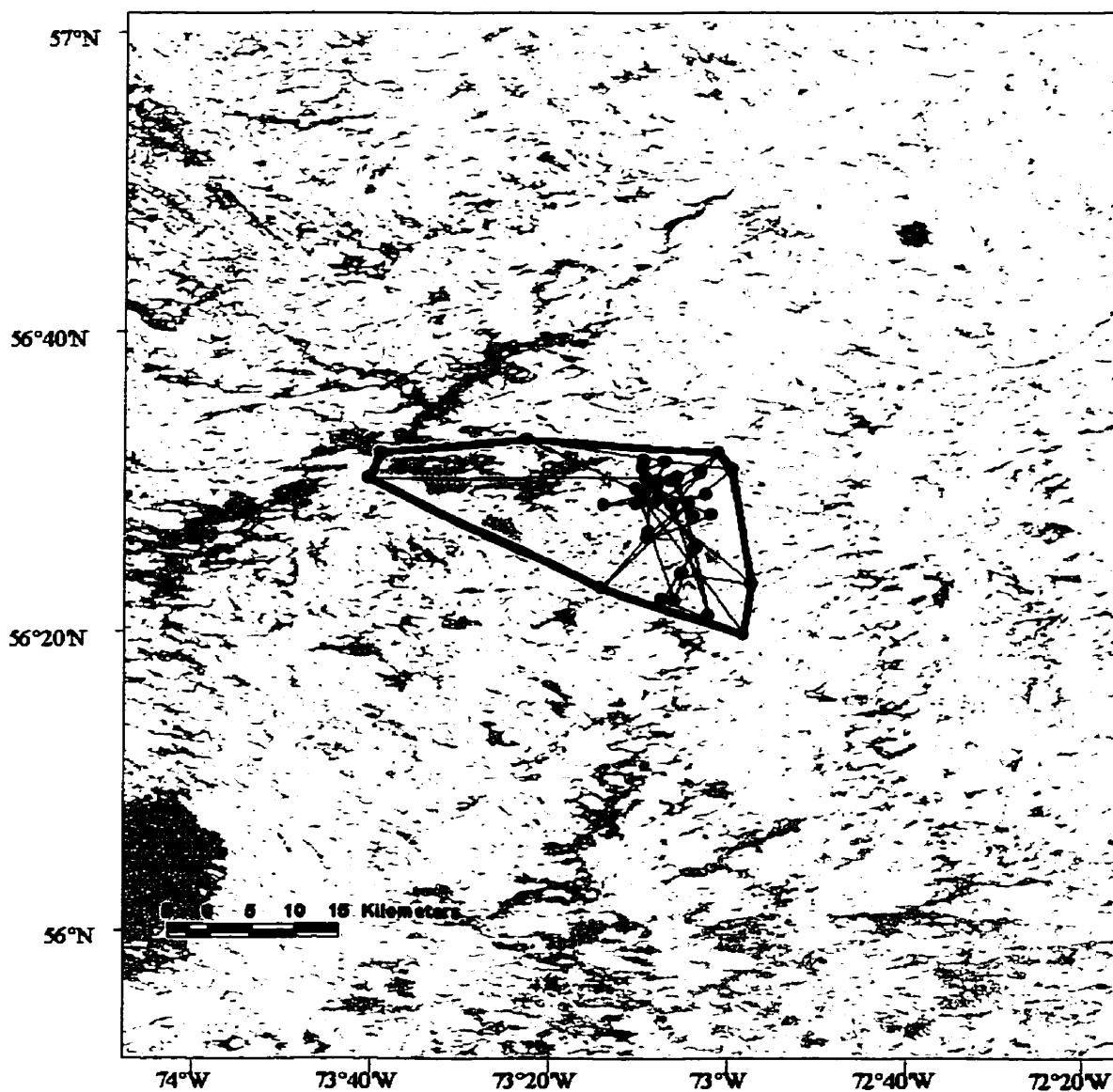
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[7 Sep 1995 - 17 Nov 1995]



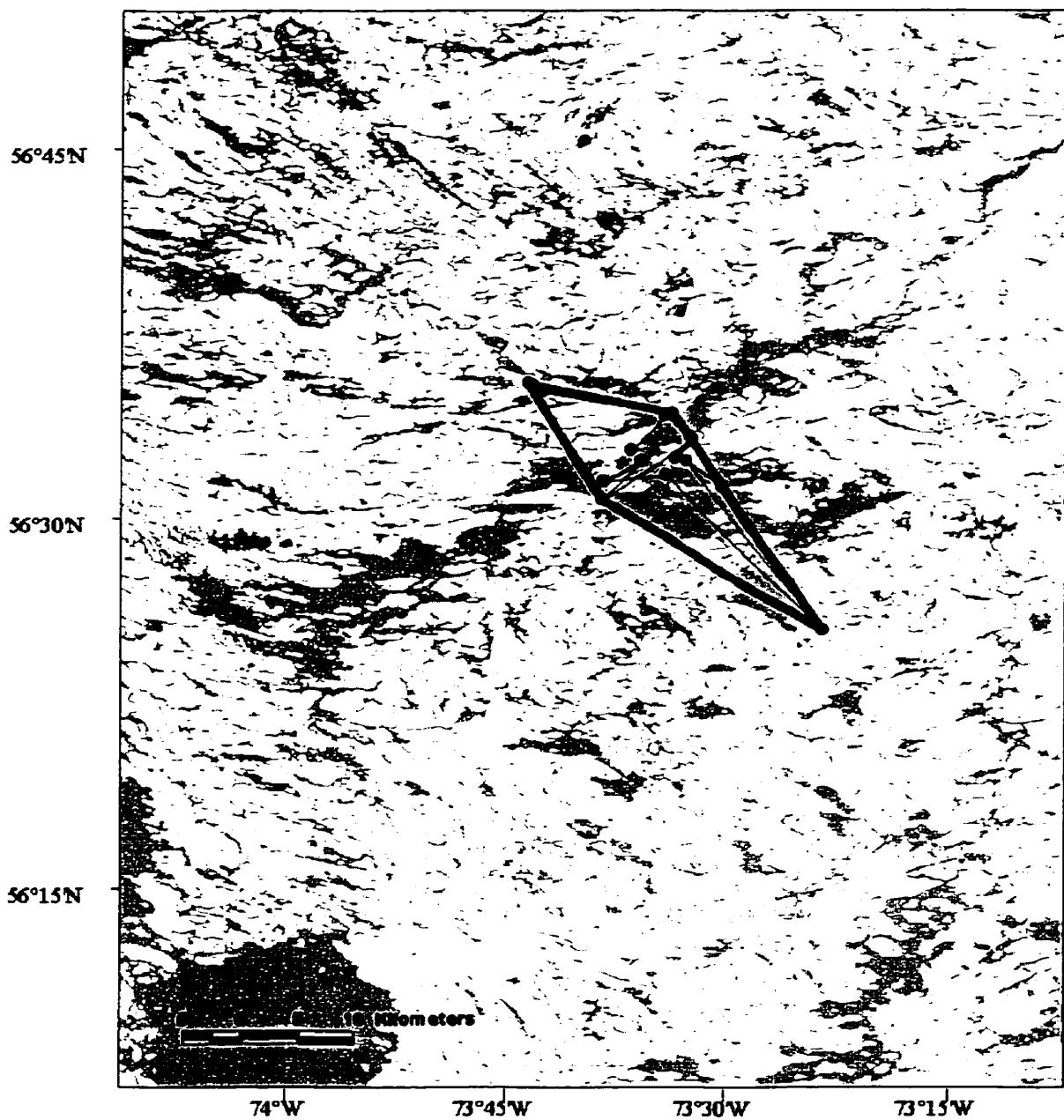
5132-95
[4 Sep 1995 - 23 Nov 1995]



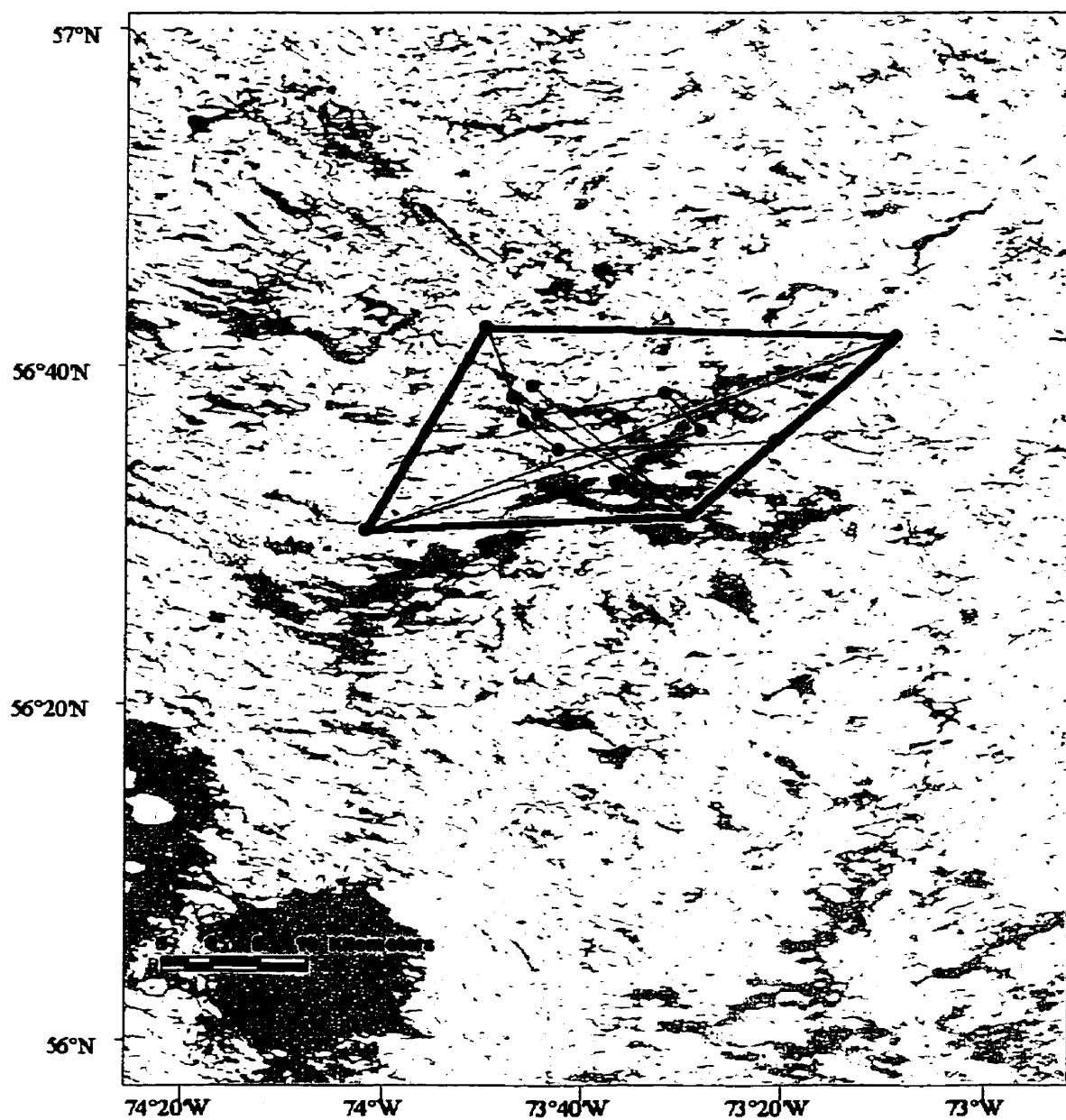
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[11 Sep 1995 - 23 Nov 1995]



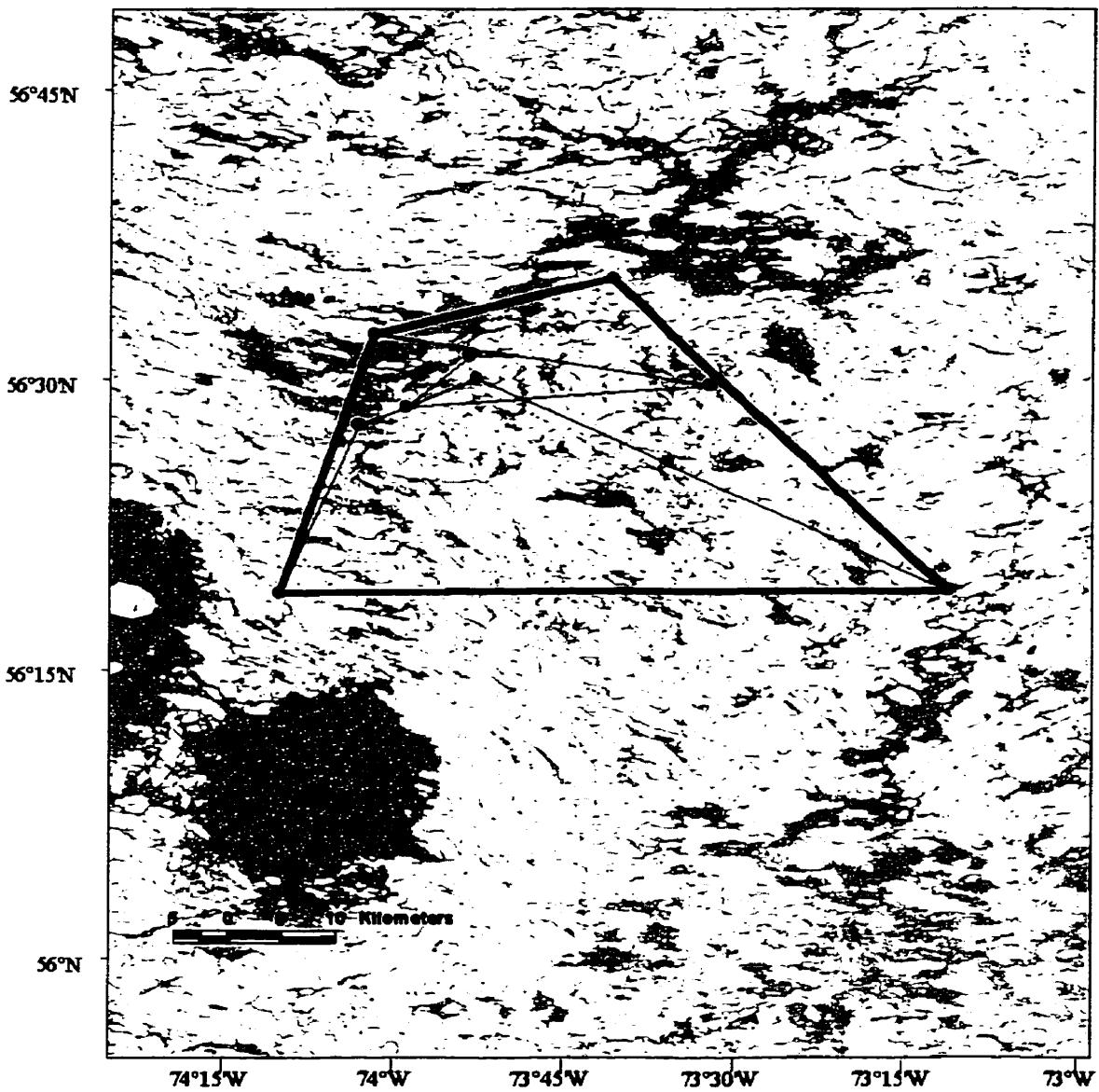
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[27 Aug 1996 - 5 Nov 1996]



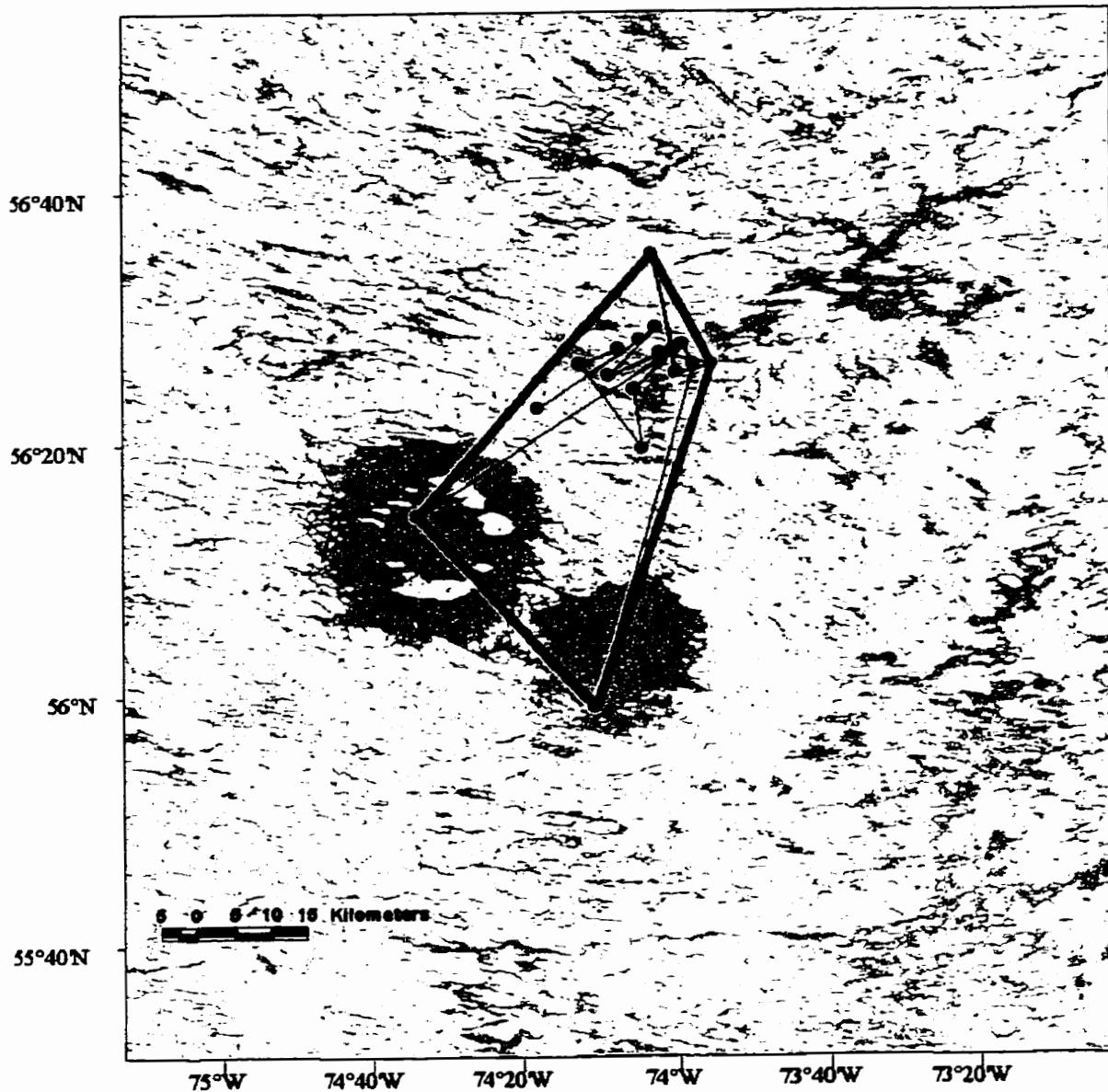
5133-96
[27 Aug 1996 - 23 Nov 1996]



9941-96
[30 Aug 1996 - 13 Jan 1997]

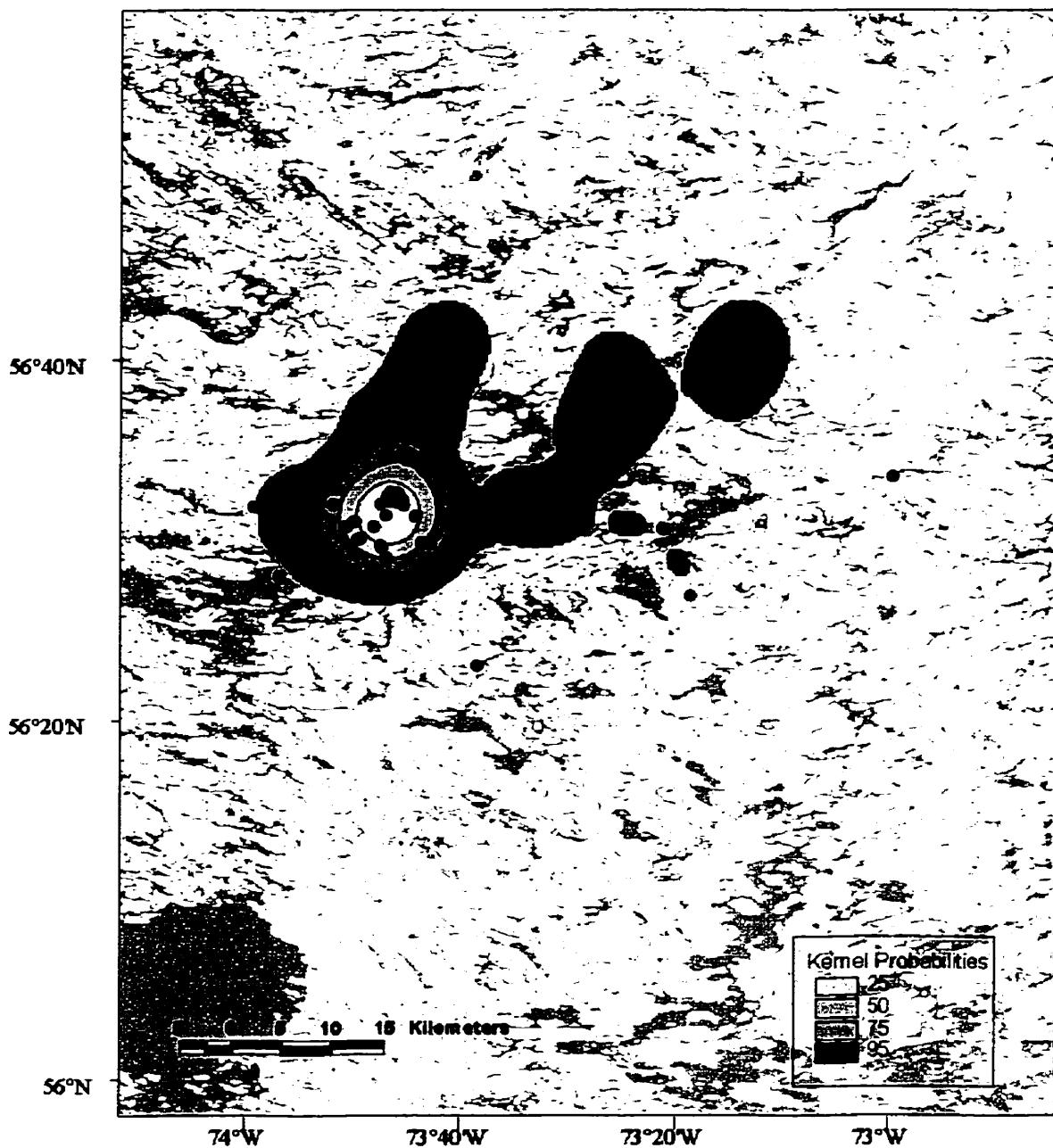


9942-96
[31 Aug 1996 - 18 Jan 1997]

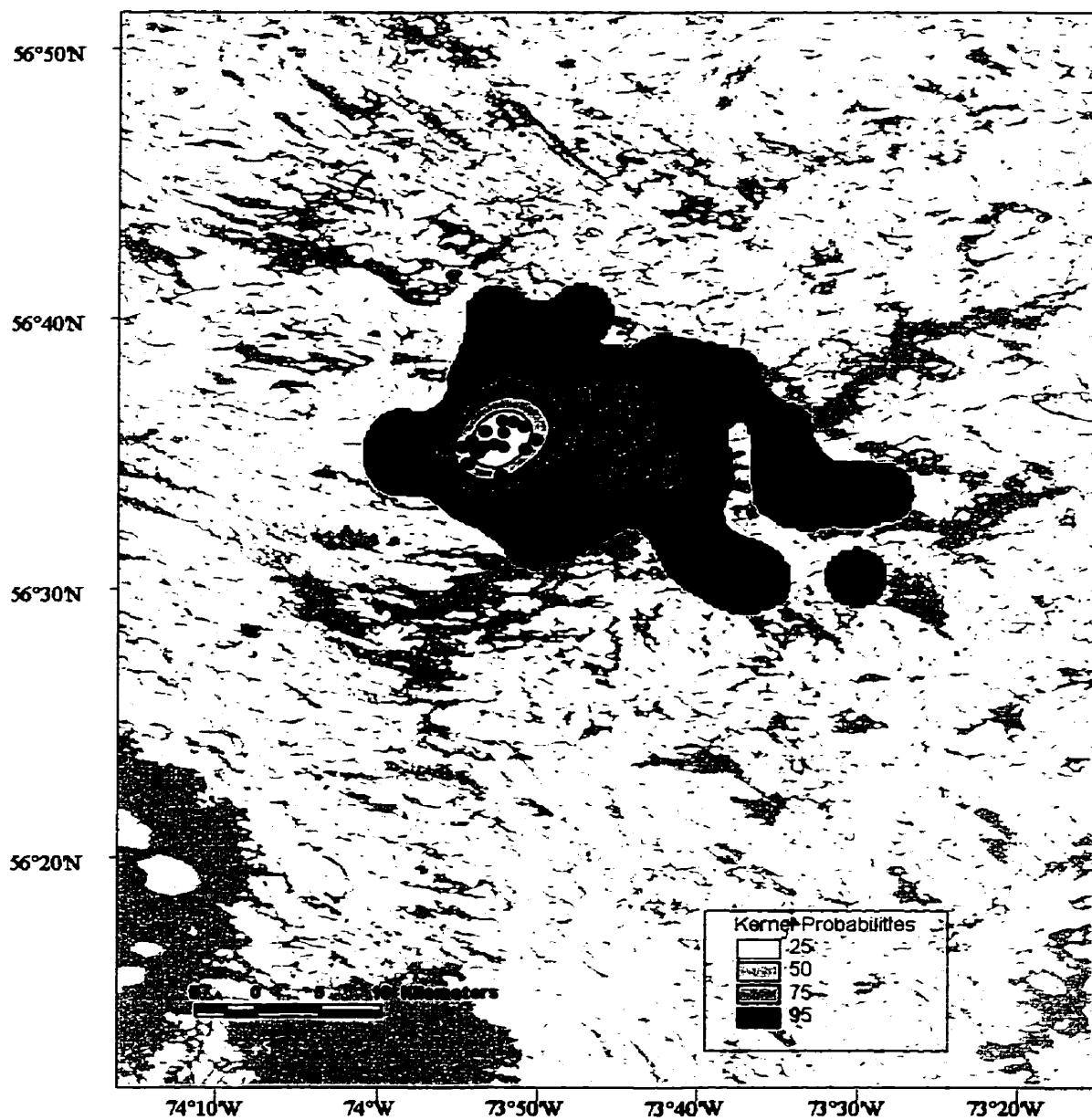


**Fig. 5.4. Kernel home ranges (with confidence areas of 25%, 50%, 75%, and 95%) of 8
Lacs des Loups Marins harbour seals calculated from satellite-telemetered positions:
1995-96.**

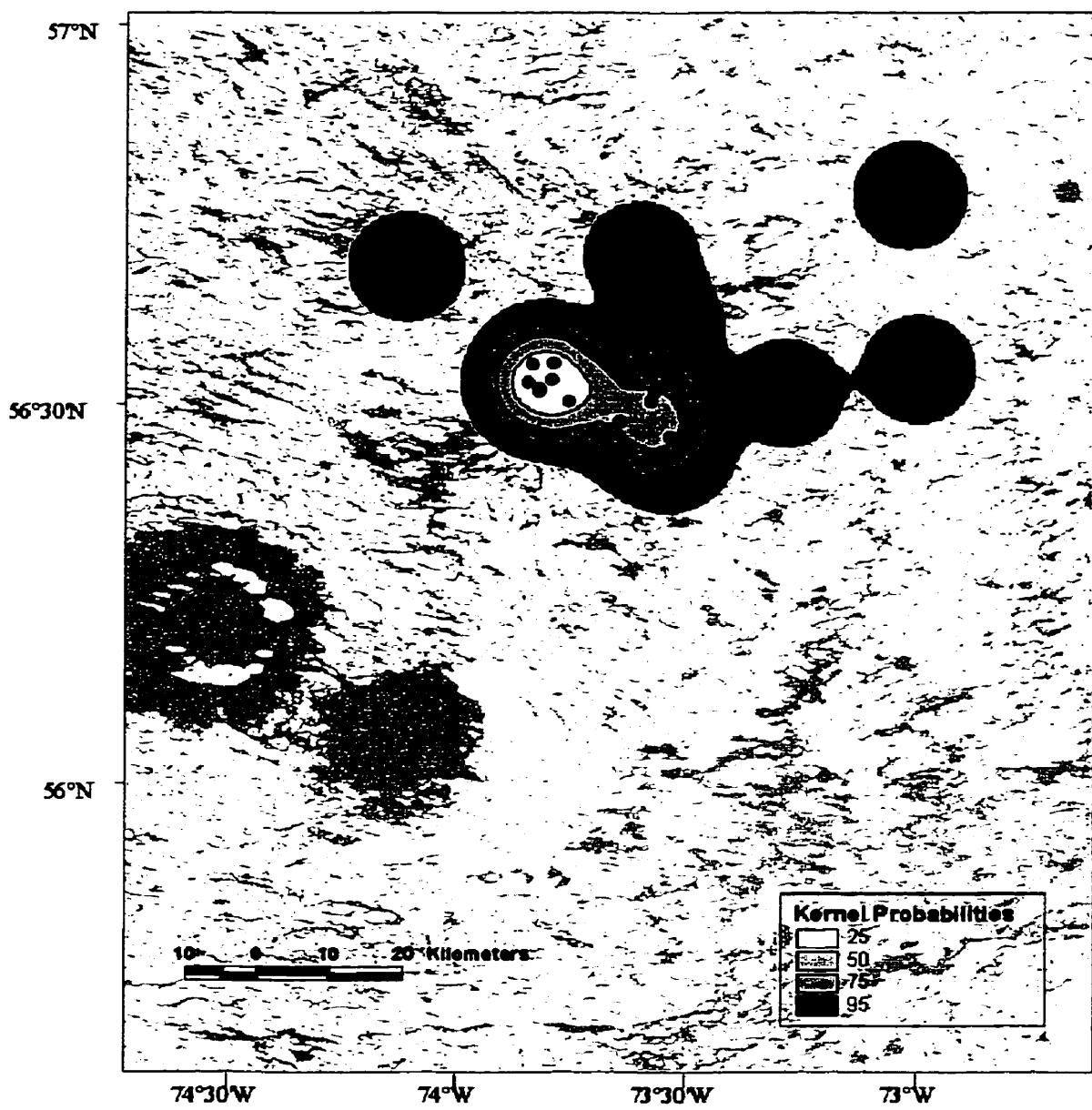
5130-95



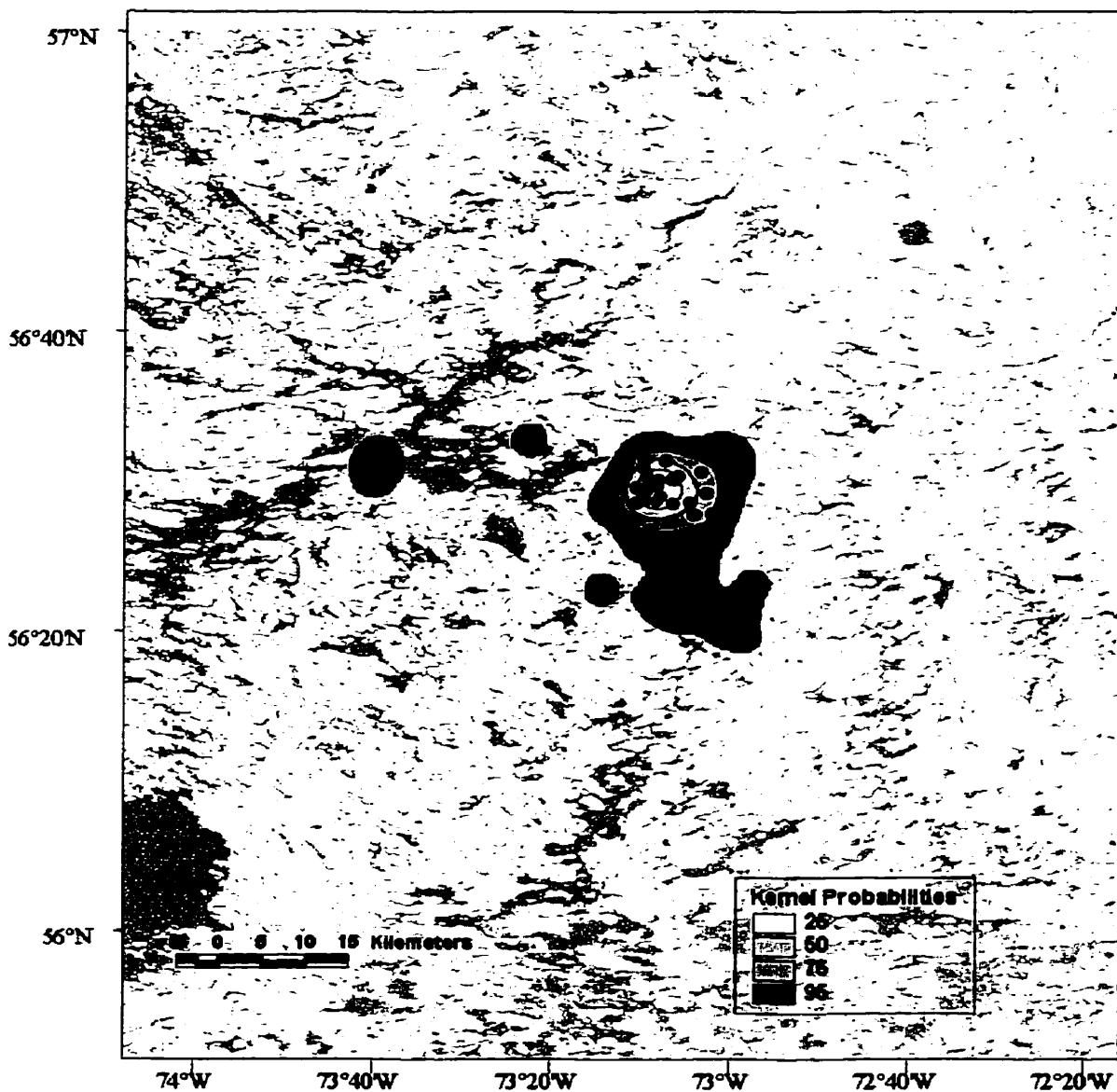
5131-95



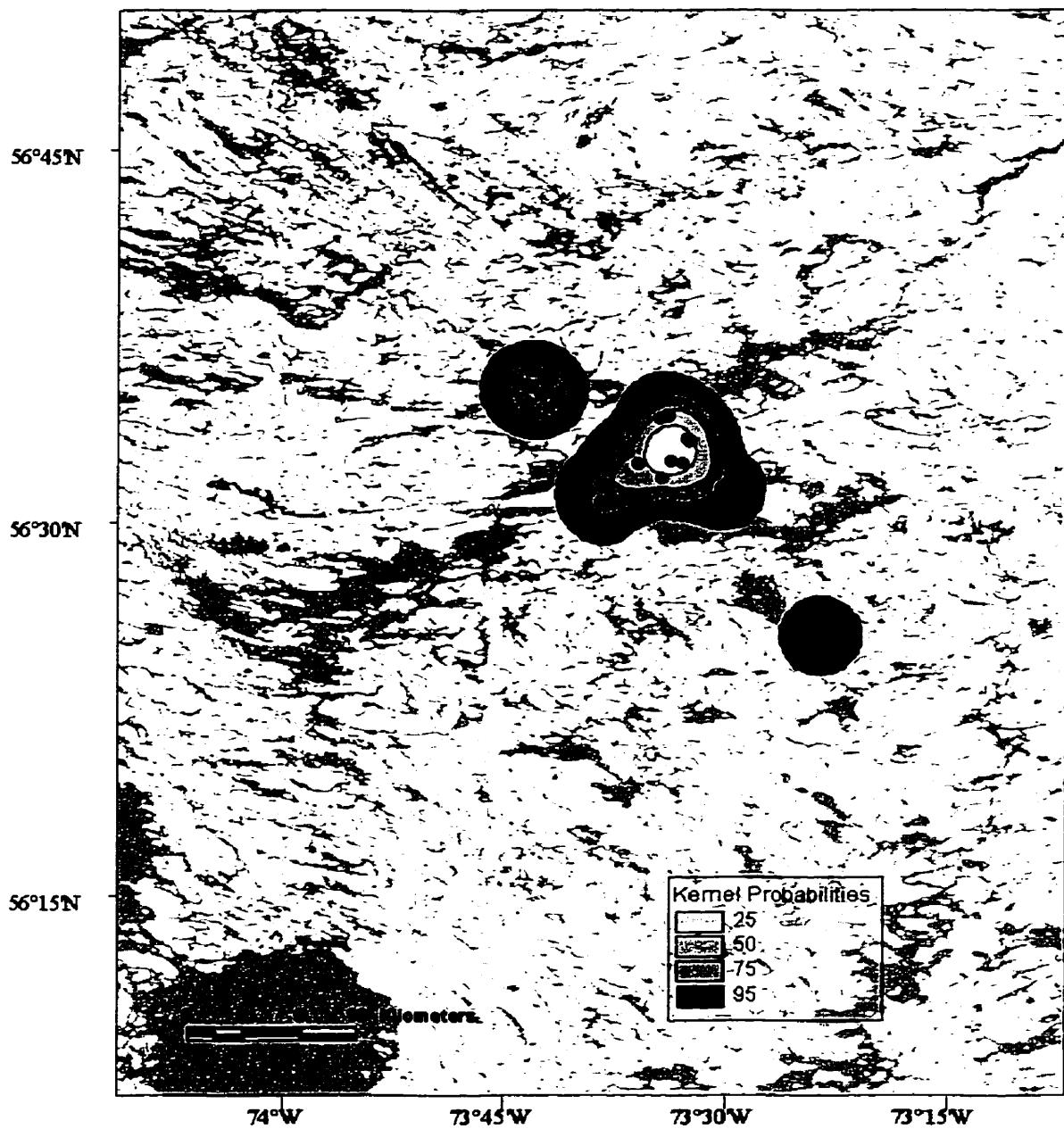
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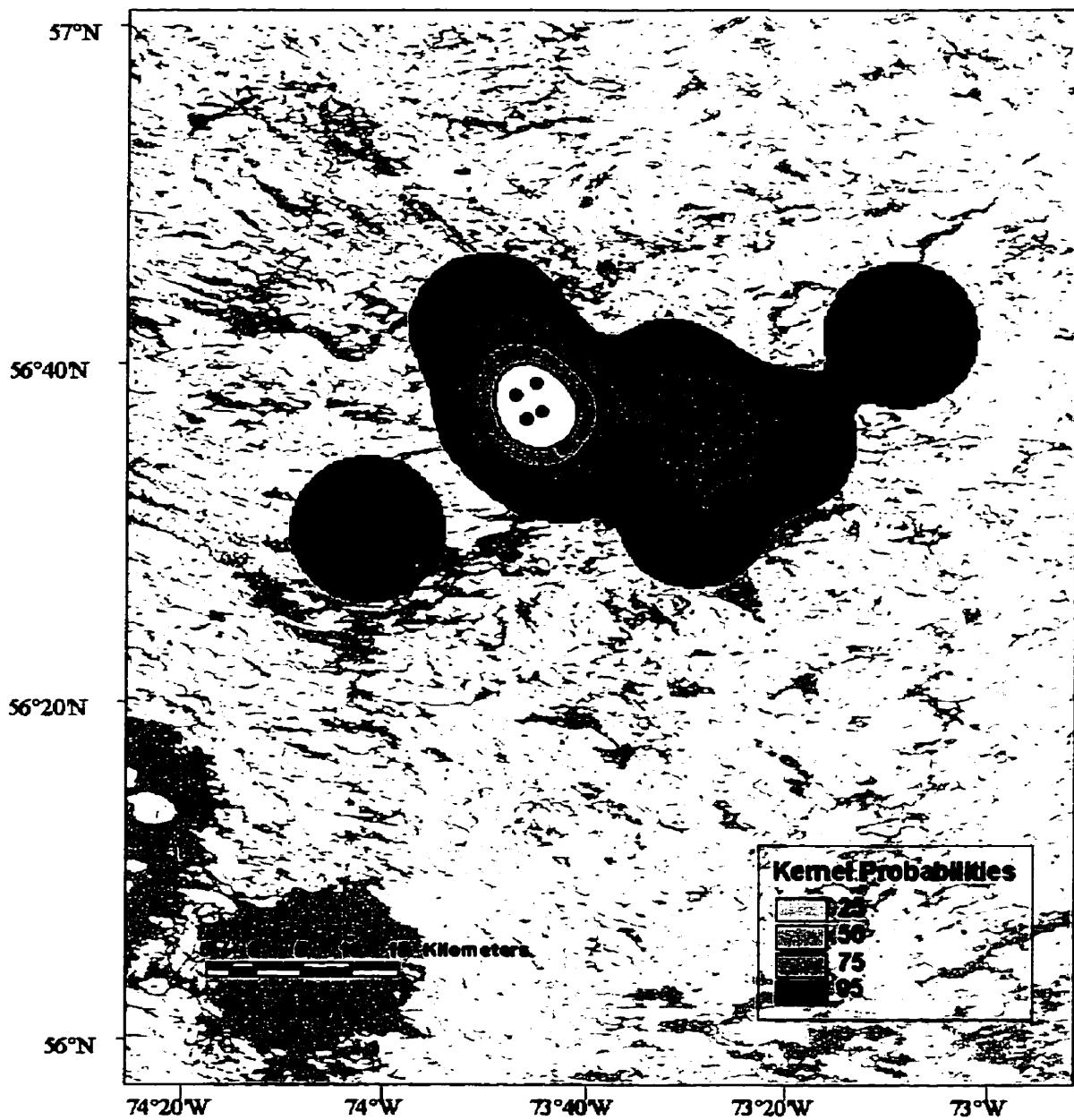
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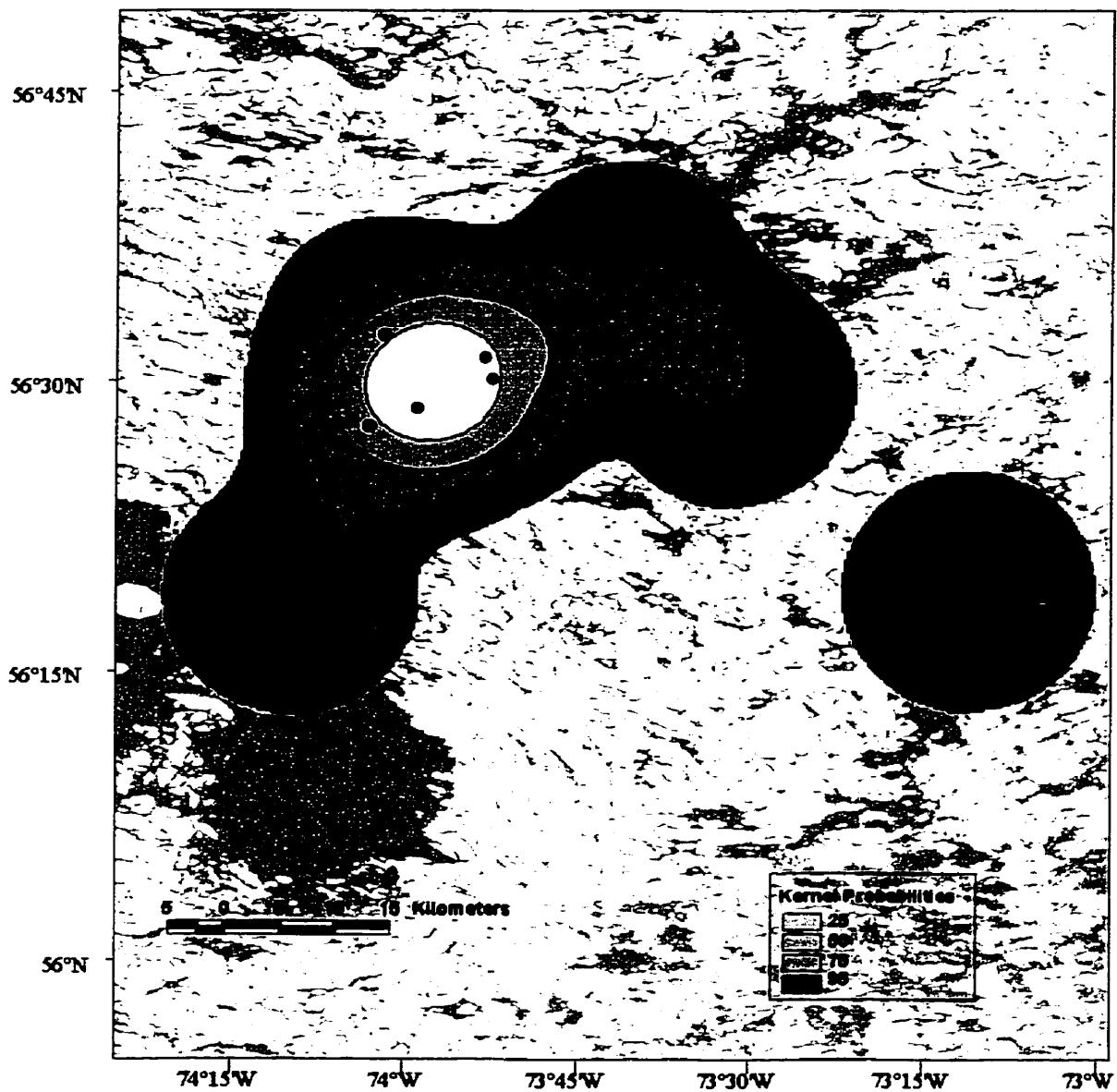
5131-96



5133-96



9941-96



9942-96

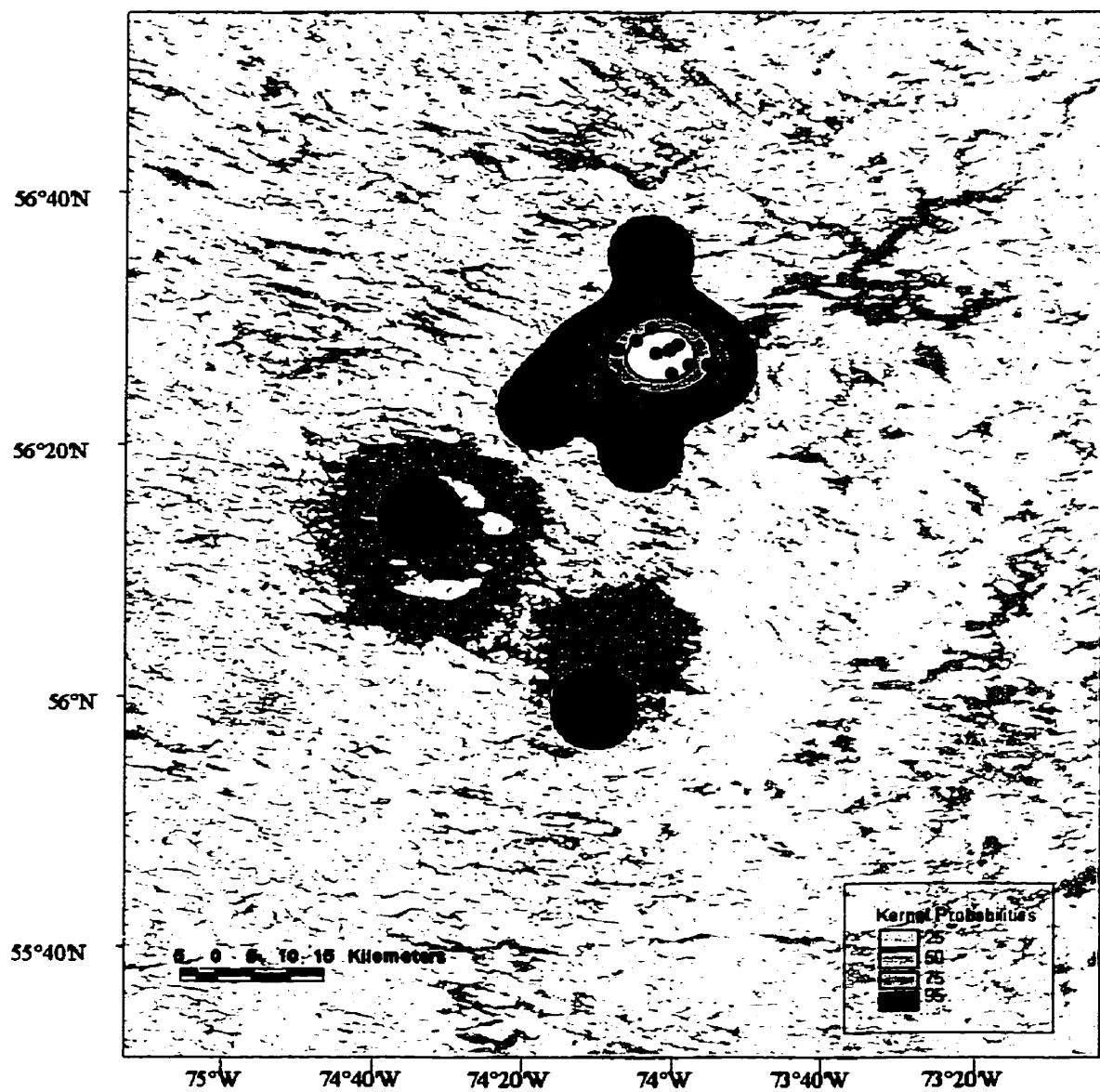
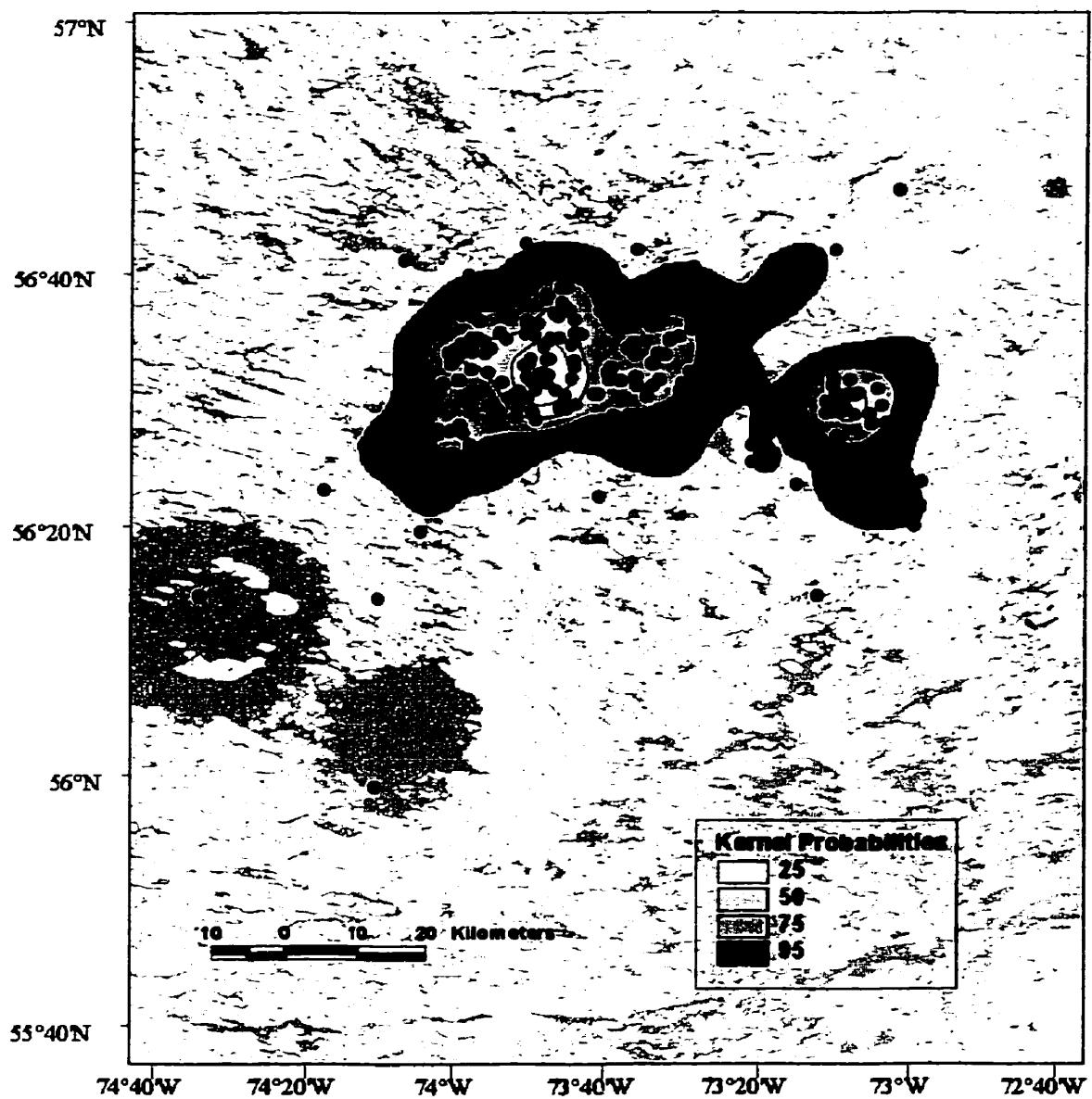


Fig. 5.5. Utilisation distribution (with confidence areas of 25%, 50%, 75%, and 95%)
calculated using combined positions of 8 satellite-telemetered Lacs des Loups Marins
harbour seals: 1995-96.

All Seals



Appendix 1

Position estimates for 9 Lacs des Loups Marins harbour seals used in this analysis.

Positions are filtered, best per day, and do not include locations from class Z (Service ARGOS 1996).

Date	Time (GMT)	Latitude	Longitude	Location	IQ
Class					
<u>5130-95</u>					
14-Sep-95	15:30:00	56.523	-73.780		
14-Sep-95	17:04:11	56.496	-73.851	0	47
15-Sep-95	6:56:13	56.476	-73.796	A	0
16-Sep-95	6:48:24	56.573	-73.732	0	46
17-Sep-95	9:58:38	56.531	-73.897	A	0
18-Sep-95	8:07:42	56.502	-73.470	3	68
19-Sep-95	9:33:56	56.450	-73.956	A	0
20-Sep-95	9:24:24	56.515	-73.999	B	0
21-Sep-95	5:52:56	56.480	-73.734	1	60
22-Sep-95	9:06:38	56.488	-73.353	A	0
23-Sep-95	5:32:34	56.583	-73.440	B	0
24-Sep-95	8:43:14	56.470	-73.839	B	0
27-Sep-95	9:55:10	56.669	-73.190	B	0
30-Sep-95	9:18:20	56.664	-73.245	2	50
01-Oct-95	7:26:59	56.619	-73.406	2	68
02-Oct-95	8:54:57	56.593	-73.782	A	0
03-Oct-95	11:02:21	56.656	-73.711	B	0
04-Oct-95	8:36:19	56.517	-73.782	3	67
05-Oct-95	8:23:45	56.526	-73.770	3	68
06-Oct-95	8:16:49	56.522	-73.787	2	68

07-Oct-95	6:24:35	56.527	-73.780	2	50
08-Oct-95	9:32:13	56.525	-73.777	3	68
09-Oct-95	10:30:18	56.514	-73.761	2	67
10-Oct-95	5:49:56	56.516	-73.771	3	60
11-Oct-95	7:22:14	56.504	-73.743	A	0
12-Oct-95	8:49:20	56.524	-73.779	2	56
13-Oct-95	6:59:42	56.520	-73.766	3	60
15-Oct-95	6:35:53	56.603	-73.420	3	66
16-Oct-95	8:05:35	56.516	-73.868	0	48
17-Oct-95	10:55:28	56.602	-73.735	B	0
19-Oct-95	9:14:31	56.572	-73.471	A	0
20-Oct-95	5:43:55	56.519	-73.763	0	60
22-Oct-95	10:49:00	56.682	-73.671	B	0
23-Oct-95	8:31:38	56.664	-73.436	3	68
<u>25-Oct-95</u>	<u>6:27:43</u>	<u>56.530</u>	<u>-72.982</u>	<u>B</u>	<u>0</u>
27-Oct-95	6:06:04	56.614	-73.259	3	66
28-Oct-95	5:56:07	56.629	-73.214	B	0
30-Oct-95	8:55:58	56.515	-73.595	B	0
31-Oct-95	8:45:09	56.508	-73.566	B	0
01-Nov-95	8:33:02	56.425	-73.310	0	40
02-Nov-95	6:44:42	56.466	-73.791	2	56
03-Nov-95	8:13:07	56.495	-73.809	A	0
04-Nov-95	6:23:30	56.500	-73.837	0	40
05-Nov-95	10:45:15	56.480	-73.720	B	0
07-Nov-95	9:09:30	56.484	-73.831	1	58
08-Nov-95	5:35:27	56.478	-73.799	B	0
09-Nov-95	5:26:22	56.515	-73.798	B	0
10-Nov-95	8:36:37	56.506	-73.789	A	0
<u>11-Nov-95</u>	<u>6:45:42</u>	<u>56.364</u>	<u>-73.649</u>	<u>B</u>	<u>0</u>

12-Nov-95	8:16:44	56.641	-73.714	B	0
15-Nov-95	6:02:01	56.580	-73.813	B	0
20-Nov-95	8:32:28	56.516	-73.768	A	0

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07-Sep-95	16:45:00	56.536	-73.697		
07-Sep-95	18:20:38	56.516	-73.438	0	45
08-Sep-95	16:27:40	56.544	-73.697	A	0
09-Sep-95	14:44:21	56.609	-73.637	A	0
10-Sep-95	14:22:18	56.516	-73.515	1	56
11-Sep-95	15:55:48	56.452	-73.601	0	50
12-Sep-95	13:38:11	56.544	-74.064	0	46
13-Sep-95	13:17:46	56.578	-73.791	0	50
14-Sep-95	14:37:47	56.458	-73.654	B	0
15-Sep-95	16:54:59	56.567	-73.932	A	8
16-Sep-95	16:44:22	56.574	-73.754	0	56
19-Sep-95	12:45:53	56.573	-73.856	1	68
20-Sep-95	12:24:38	56.580	-73.697	1	56
21-Sep-95	17:28:51	56.597	-73.808	0	58
23-Sep-95	14:36:31	56.452	-73.475	A	5
24-Sep-95	14:16:55	56.568	-73.956	A	0
26-Sep-95	10:03:22	56.561	-73.973	B	0
27-Sep-95	16:24:43	56.609	-73.956	B	0
28-Sep-95	16:15:20	56.556	-73.984	A	0
30-Sep-95	12:06:39	56.556	-73.958	A	0
01-Oct-95	17:24:44	56.539	-73.803	0	58
03-Oct-95	14:20:59	56.598	-73.915	3	60
05-Oct-95	13:39:45	56.545	-73.764	0	40
06-Oct-95	11:36:25	56.592	-73.792	1	56

07-Oct-95	16:16:57	56.604	-73.931	0	48
09-Oct-95	12:11:56	56.538	-73.818	0	46
10-Oct-95	11:51:57	56.571	-73.906	2	65
11-Oct-95	17:12:28	56.556	-73.932	A	6
12-Oct-95	17:03:29	56.575	-73.919	1	56
13-Oct-95	12:25:49	56.576	-73.934	0	50
14-Oct-95	15:00:59	56.590	-73.808	B	0
15-Oct-95	15:03:26	56.519	-73.704	B	0
16-Oct-95	16:19:23	56.520	-73.965	A	0
17-Oct-95	14:31:10	56.486	-73.896	B	0
18-Oct-95	11:03:44	56.597	-73.697	B	0
20-Oct-95	17:16:34	56.565	-73.571	A	6
22-Oct-95	16:57:23	56.558	-73.945	A	0
23-Oct-95	13:47:06	56.562	-74.066	0	50
24-Oct-95	11:45:00	56.504	-73.828	A	0
25-Oct-95	14:43:27	56.534	-73.936	A	0
27-Oct-95	12:21:21	56.543	-73.977	0	40
28-Oct-95	17:30:28	56.561	-73.890	0	56
29-Oct-95	11:34:24	56.485	-73.697	A	0
31-Oct-95	14:12:27	56.551	-73.965	0	50
01-Nov-95	15:31:16	56.659	-73.939	A	40
02-Nov-95	16:37:25	56.554	-73.905	A	0
04-Nov-95	14:26:22	56.582	-73.870	1	50
05-Nov-95	17:35:02	56.528	-73.768	1	68
07-Nov-95	17:24:00	56.520	-73.568	0	57
11-Nov-95	11:54:07	56.659	-73.829	1	56
17-Nov-95	11:25:12	56.619	-73.725	B	0

<u>5132-95</u>					
04-Sep-95	21:50:00	56.514	-73.786		
06-Sep-95	0:20:36	56.511	-73.788	A	0
10-Sep-95	6:13:29	56.547	-73.755	0	40
14-Sep-95	0:49:43	56.546	-73.801	0	40
16-Sep-95	6:48:53	56.494	-73.543	2	56
<u>20-Sep-95</u>	<u>0:14:17</u>	<u>56.530</u>	<u>-72.950</u>	<u>B</u>	<u>0</u>
24-Sep-95	7:01:14	56.447	-73.499	0	40
30-Sep-95	5:59:17	56.523	-73.811	B	0
02-Oct-95	0:57:12	56.469	-73.613	B	0
04-Oct-95	1:53:52	56.593	-73.508	B	0
06-Oct-95	6:35:57	56.503	-73.249	B	0
12-Oct-95	5:28:53	56.688	-73.560	B	0
18-Oct-95	0:07:15	56.525	-73.759	2	56
20-Oct-95	1:08:06	56.427	-73.521	B	0
<u>24-Oct-95</u>	<u>6:38:33</u>	<u>56.679</u>	<u>-74.084</u>	<u>B</u>	<u>0</u>
26-Oct-95	6:19:49	56.497	-73.722	1	57
<u>01-Nov-95</u>	<u>6:54:22</u>	<u>56.760</u>	<u>-72.958</u>	<u>B</u>	<u>0</u>
23-Nov-95	0:25:13	56.508	-73.532	0	40

<u>5133-95</u>					
11-Sep-95	17:15:00	56.527	-73.625		
11-Sep-95	19:20:24	56.499	-73.647	A	6
13-Sep-95	1:10:46	56.493	-73.059	0	50
15-Sep-95	6:59:15	56.338	-73.011	1	56
16-Sep-95	6:49:02	56.464	-73.070	0	46
17-Sep-95	4:54:17	56.519	-72.984	1	68
18-Sep-95	6:29:03	56.489	-73.068	0	56
19-Sep-95	6:14:35	56.450	-73.033	1	56

21-Sep-95	5:54:36	56.489	-73.071	A	7
22-Sep-95	1:14:05	56.490	-73.095	0	50
23-Sep-95	0:53:41	56.477	-73.127	1	50
24-Sep-95	0:28:10	56.372	-72.928	1	50
25-Sep-95	6:53:12	56.386	-73.056	1	56
27-Sep-95	6:29:49	56.356	-73.072	0	56
29-Sep-95	6:08:07	56.481	-73.137	0	56
02-Oct-95	0:58:16	56.538	-73.344	0	50
03-Oct-95	0:34:28	56.500	-72.959	B	0
04-Oct-95	0:10:14	56.435	-73.114	B	0
05-Oct-95	5:03:03	56.372	-73.210	0	56
09-Oct-95	0:02:33	56.465	-73.039	2	50
10-Oct-95	5:49:46	56.473	-73.092	1	50
11-Oct-95	1:01:36	56.504	-73.122	0	50
12-Oct-95	0:39:04	56.510	-73.080	2	56
13-Oct-95	6:59:52	56.482	-73.111	2	58
14-Oct-95	6:48:48	56.466	-73.137	0	56
15-Oct-95	6:36:28	56.474	-73.009	3	60
16-Oct-95	6:27:32	56.466	-73.200	1	50
18-Oct-95	6:04:34	56.477	-73.119	1	56
20-Oct-95	5:41:11	56.513	-73.118	2	67
21-Oct-95	0:43:15	56.428	-73.116	A	0
22-Oct-95	0:20:18	56.451	-73.001	0	40
23-Oct-95	6:52:34	56.483	-73.097	1	56
25-Oct-95	6:29:36	56.493	-73.115	1	58
26-Oct-95	6:17:16	56.415	-73.031	A	7
27-Oct-95	6:06:39	56.358	-73.095	B	0
29-Oct-95	1:08:17	56.316	-72.947	B	0
02-Nov-95	6:43:10	56.468	-73.122	2	56

04-Nov-95	0:39:21	56.467	-73.100	0	50
23-Nov-95	0:23:18	56.497	-73.018	0	56

5131-96

27-Aug-96	20:00:00	56.614	-73.718		
29-Aug-96	19:11:11	56.616	-73.724	0	50
04-Sep-96	19:44:38	56.609	-73.704	0	50
08-Sep-96	19:02:50	56.588	-73.520	A	0
10-Sep-96	18:38:43	56.526	-73.447	1	50
12-Sep-96	18:15:43	56.548	-73.501	0	50
<u>17-Sep-96</u>	<u>0:02:56</u>	<u>56.403</u>	<u>-73.311</u>	<u>B</u>	<u>0</u>
22-Sep-96	23:33:26	56.536	-73.531	1	56
02-Oct-96	21:32:48	56.532	-73.618	1	56
20-Oct-96	23:20:33	56.549	-73.566	A	60
22-Oct-96	20:58:08	56.517	-73.620	1	56
24-Oct-96	21:53:03	56.567	-73.491	A	0
28-Oct-96	23:45:38	56.550	-73.516	B	0
01-Nov-96	23:59:14	56.569	-73.493	0	40
03-Nov-96	18:56:24	56.587	-73.531	2	56
05-Nov-96	20:51:00	56.558	-73.579	A	0

5132-96

25-Aug-96	19:02:00	56.565	-73.704		
27-Aug-96	17:51:07	56.571	-73.756	1	50
31-Aug-96	18:48:22	56.561	-73.770	1	56

5133-96

27-Aug-96	20:00:00	56.614	-73.718		
27-Aug-96	23:01:35	56.632	-73.504	A	0

02-Sep-96	20:49:48	56.594	-73.440	B	0
<u>10-Sep-96</u>	<u>22:54:43</u>	<u>56.502</u>	<u>-74.012</u>	<u>B</u>	<u>0</u>
<u>22-Sep-96</u>	<u>23:29:43</u>	<u>56.683</u>	<u>-73.107</u>	<u>B</u>	<u>0</u>
24-Sep-96	19:26:19	56.582	-73.316	B	0
20-Oct-96	18:08:02	56.578	-73.682	A	60
28-Oct-96	22:05:07	56.606	-73.744	3	56
01-Nov-96	19:14:04	56.700	-73.807	0	50
03-Nov-96	21:33:17	56.631	-73.761	1	50
17-Nov-96	21:29:12	56.511	-73.466	B	0
23-Nov-96	18:35:44	56.641	-73.726	0	50

9941-96

30-Aug-96	18:50:00	56.434	-73.868		
30-Aug-96	20:14:49	56.391	-73.966	B	0
07-Sep-96	19:11:40	56.405	-73.513	B	0
09-Sep-96	23:16:30	56.455	-74.011	2	57
<u>25-Sep-96</u>	<u>17:35:42</u>	<u>56.233</u>	<u>-74.155</u>	<u>B</u>	<u>0</u>
17-Oct-96	18:38:12	56.376	-74.037	2	50
25-Oct-96	23:10:23	56.415	-73.858	0	46
<u>06-Nov-96</u>	<u>22:09:15</u>	<u>56.225</u>	<u>-73.169</u>	<u>B</u>	<u>0</u>
13-Jan-97	19:24:56	56.499	-73.657	0	50

9942-96

31-Aug-96	19:50:00	56.455	-74.102		
31-Aug-96	21:36:18	56.435	-74.184	A	0
16-Sep-96	22:22:19	56.322	-74.054	B	0
22-Sep-96	19:51:41	56.402	-74.070	0	52
25-Sep-96	0:30:44	56.454	-73.980	A	0
02-Oct-96	23:14:38	56.449	-74.013	1	57

05-Oct-96	0:11:03	56.434	-73.896	2	66
06-Oct-96	23:26:57	56.422	-73.978	B	0
20-Oct-96	19:47:59	56.580	-74.027	A	60
23-Oct-96	0:18:32	56.452	-73.983	A	0
<u>28-Oct-96</u>	<u>23:47:29</u>	<u>56.239</u>	<u>-74.553</u>	<u>B</u>	<u>0</u>
<u>01-Nov-96</u>	<u>23:58:47</u>	<u>55.982</u>	<u>-74.164</u>	<u>B</u>	<u>0</u>
03-Nov-96	23:15:34	56.434	-73.940	1	50
11-Nov-96	23:39:40	56.461	-73.962	B	0
17-Nov-96	21:25:30	56.420	-74.125	B	0
13-Dec-96	21:57:21	56.482	-74.022	0	50
12-Jan-97	21:03:29	56.466	-74.058	1	57
18-Jan-97	23:54:25	56.379	-74.278	0	42

CHAPTER 6: GENERAL DISCUSSION

After all, does it matter? Does it matter that *Phoca vitulina mellonae* may not be a subspecifically distinct race? Does it matter that this supposedly land-locked race may not have been isolated in the Seal Lakes of Ungava for thousands of years? Such questions are of course important to biologists, and rightly so. But new discoveries have always had a way of consigning old discoveries to the dustbin of history. For the reader of *Needle to the North* the status of *kasagea*, the mythic seal of the Ungava lakes, is secure: we know that *kasagea* is not *netchek*. And we also know that *kasagea* may be attained only after the most arduous of journeys, taken in mid-winter, with the special knowledge of the right assistants and guides, upon completion of a period of patient waiting, and only after coming through the requisite tests and ordeals (James 1982, p. 205).

Subspecies and ESUs

The balance of evidence from this thesis indicates that Doutt (1942) was correct in his subspecific designation of *Phoca vitulina mellonae*. Subspecies were defined by Wilson and Brown (1953) as being “genetically distinct, geographically separate populations belonging to the same species” (p. 99). Expanding on this definition, McIvor et al. (1995) cautioned that:

It is unlikely that any single ecological, morphological, or genetics-based approach will or should answer the question of subspecific status. Rather, an integrated approach should be used involving natural history, morphology, range and distribution, and molecular genetic data (p. 1039).

Just such an “integrated approach” was used in the preceding chapters to address the question of the Lacs des Loups Marins harbour seal’s subspecific status (Table 6.1). As a result of the publication of Smith et al. (1994) – which included a portion of the data presented in Chapter 2 -- the most recent and definitive summary of marine mammal systematics has re-affirmed this status (Rice 1998). The extremely restricted and isolated range of *P. v. mellonae* (Chapter 5), the evidence of year-round freshwater feeding (Chapter 4), significant differentiation in birth timing and morphology (Chapter 2) all corroborate the historical and anecdotal evidence of the population’s distinctness. Though the mitochondrial DNA analysis was preliminary, it did reveal some unique haplotypes in the Lacs des Loups Marins animals (Chapter 3). A larger genetic analysis of harbour seal samples from museums will be necessary before a complete picture can be had of historical harbour seal genetic diversity in the Canadian Arctic, which was likely greater than it is today (Mansfield 1967).

Though the concept of the subspecies is still widely used to describe intra-specific levels of variation, Wilson and Brown (1953, p. 110) astutely observed that “as the analyses of geographical variation become more complete, the trinomial nomenclatorial system will be revealed as inefficient and superfluous.” This dilemma was summarised by Doutt (1955, p. 181) himself, when he stated:

If we recognize as a subspecies every local population
which can be shown to be recognizable, we will eventually
have to name as subspecies the mice from every valley and
every mountainside – perhaps even from every woodlot!

It was “out of a sense of frustration with the limitations of current mammalian taxonomy in determining which named subspecies actually represent significant adaptive variation” that Ryder (1986) advanced the concept of the “Evolutionarily Significant Unit” or ESU. In identifying ESUs, Ryder (1986) noted that the recognition of inevitable uncertainty in the classification of potentially significant populations necessitates that concordance be achieved between sets of data derived by differing techniques (such as natural history information, morphometrics, range and distribution data, as well as protein electrophoresis and molecular genetic techniques).

Since the time of Ryder’s writing, the concept of ESUs has been widely adopted, particularly by conservation biologists, and become an “operational term for a group of organisms that should be the minimal unit for conservation management (Vogler and DeSalle 1994). ESUs have been elucidated for organisms that had previously been classified as species (Moritz 1994; Vogler and DeSalle 1994); subspecies (McIvor et al. 1995); stocks of marine mammals (Dizon et al. 1992); and individual populations of Pacific salmon (Pennock and Dommick 1997; Waples 1998). Moritz (1994) attempted to take the ESU concept further by distinguishing:

between two types of conservation units, both important for management: E.S.U.s, concerned with historical population structure, mtDNA phylogeny and long-term conservation needs; and M.U.s [Management Units],

addressing current population structure, allele frequencies and short-term management issues (p.374).

In contrast, Mallet (1995) advocated uncoupling taxonomic and conservation biology concerns completely, making a strong case for his particular “species definition for the Modern Synthesis” while at the same time noting:

We are much more interested in conserving actual morphological, ecological and genetic diversity than in structuring conservation around a nebulous taxonomic level about which, in the past, there has been so much disagreement (p. 298).

With the exception of Moritz (1994), *P. v. mellonae* fulfills the criteria for ESU designation as laid out by a variety of authors (Ryder 1986; Dizon et al. 1992; Vogler and DeSalle 1994; Waples 1998). The Lacs des Loups Marins seal exhibits the “morphological, ecological and genetic diversity” that pieces of legislation which use the ESU concept, such as the United States Endangered Species Act, are designed to protect (Mallet 1995).

Differentiation and Freshwater Seals

The harbour seal has the widest breeding distribution of any pinniped, with colonies spread over 16,000 km from the East Baltic to Japan (Bigg 1981; Stanley et al. 1996; Rice 1998). Boulva and McLaren (1979) noted that variation in numbers of post-canine teeth suggested that mixing between local harbour seal populations was limited, and Stutz (1967) discussed this lack of mixing with respect to characteristic pelage patterns.

Further research has continued to reveal more reproductively isolated groups within subspecies (see Yochem *et al.* 1988; Temte 1991; Lehman *et al.* 1992; Storr-Hansen and Spliid 1992). In the words of Ray (1976), “*Phoca vitulina* seems to be still actively differentiating if not in the process of developing a species swarm.”

Given that Temte (1991) for example, was able to distinguish significant morphological variation between adjacent *P. v. richardsi* populations – where reproductive isolation seems solely the product of differences in annual birth timing (which he labeled “allochronic” as opposed to allopatric differentiation) -- it is perhaps not surprising that *P. v. mellonae* is measurably differentiated from *P. v. concolor*.

It is instructive in this regard to compare *P. v. mellonae* to the isolated ringed seal populations in Lake Saimaa, Finland, *Pusa hispida saimensis*, and in Lake Ladoga, Russia, *Pusa hispida ladogensis* (Table 6.1). These two subspecies, the Baikal seal (*Pusa sibirica*), the Caspian seal (*Pusa caspica*) – which lives in brackish water -- , and *P. v. mellonae* comprise the sum total of the world’s seal populations that are known to be resident in fresh or brackish water (Rice 1998). Both of the ringed seal subspecies seem to have been isolated in freshwater for a similar period of time as *P. v. mellonae*, and though Lakes Saimaa and Ladoga are substantially larger than Lacs des Loups Marins, they are closer to each other and to the Baltic Sea (approximately 50 km) than Lacs des Loups Marins is to Hudson Bay. Both of these ringed seal populations are few in number, and both exhibit morphology and behaviour that are distinct from each other and from ringed seals in the Baltic (Sipilä and Hyvärinen 1998). It seems clear from

Table 6.1 that a small population of pinnipeds, when isolated for approximately 7,000-9,000 years, can become measurably differentiated.

Implications for Conservation

A number of harbour seal populations throughout the world have been extirpated (e.g. in Lake Ontario), or are threatened and in decline (e.g. in Greenland; Sable Island, Nova Scotia; Hokkaido, Japan; and Tugidak Island, Alaska) (DeKay 1842; Allen 1880; Boulva and McLaren 1979; Boveng 1988; Rougerie 1990; Pitcher 1990; Wada *et al.* 1991; Reijnders *et al.* 1993; Teilmann and Dietz 1993; Ellis 1998). Ironically, one of these populations was likely extirpated by the collecting that resulted in some of the samples used in this thesis. Between 1937 and 1940, the Carnegie Museum, Pittsburgh, PA, collected a number of specimens of harbour seals from freshwater lakes on the Belcher Islands, NWT: there does not now appear to be any seals remaining in this area (Smith *et al.* 1996).

Unless the governments of Canada and Québec act soon to provide adequate legal protection for *P. v. mellonae*, which has recently been listed as “vulnerable” by the Committee on the Status of Endangered Wildlife in Canada (Smith 1997), the small group of seals in Lacs des Loups Marins may yet join the list of extirpated harbour seal populations (Alfonso and McAllister 1994).

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Table 6.1. Comparison of freshwater seal populations in Lacs des Loups Marins and Lakes Saimaa (Finland) and Ladoga (Russia).

Attributes	Lacs des Loups Marins harbour seal (<i>Phoca vitulina</i> <i>mellonae</i>)	Lake Saimaa (<i>Pusa hispida saimensis</i>)	Lake Ladoga (<i>Pusa hispida ladogensis</i>)
Surface area of lake (km ²)	535 ¹	4,400 ²	19,890 ²
Lake shoreline length (km)	1,830 ¹	15,000 ²	N/A
Distance from next nearest harbour seal population (km)	160 ¹	50 ²	50 ²
Likely time of isolation (Years before present)	7,300 ³	8,000 ²	9,000 ²
Number of individuals in population	Most recent estimate approximately 100 ^{1,4}	200 ²	Minimum of 5,000 ²
Population density	Approximately 0.1 seals/km ² ^{1,4}	0.05 seals/km ² ²	0.25 seals/km ² ²
Morphologically distinct	Yes ⁵	Yes ^{2,6,7}	Yes ^{2,6,7}
Behaviourally distinct	Yes ⁵	Yes ²	Yes ²
Haplotypic differences	Yes ⁸	No data	No data
Exclusively freshwater feeding	Yes ⁹	Yes ¹⁰	Yes ¹⁰
Site fidelity in freshwater	Yes ¹¹	Yes ²	Yes ²

Footnotes:

(1) Consortium Gilles Shooner & Associés et al. 1991; (2) Sipilä and Hyvärinen 1998; (3) Allard and Séguin 1985; (4) Smith 1997; (5) Chapter 2 and Smith et al. 1994; (6) Müller-Wille 1969; (7) Hyvärinen and Nieminen 1990; (8) Chapter 3; (9) Chapter 4 and Smith et al. 1996; (10) Käkelä et al. 1995; (11) Chapter 5

APPENDIX 1

STATUS OF THE LACS DES LOUPS MARINS HARBOUR SEAL, *PHOCA VITULINA MELLONAE*, IN CANADA

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January 11, 1996

Status Recommended: Vulnerable

Status of the Lacs des Loups Marins harbour seal, *Phoca vitulina mellonae*, in Canada

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Smith, R.J. 1994. Status of the Lacs des Loups Marins harbour seal, *Phoca vitulina mellonae*, in Canada. Report to the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Canadian Wildlife Service, Ottawa, Ontario K1A 0H3.

The Lacs des Loups Marins harbour seal (*Phoca vitulina mellonae*) is a subspecies that occurs in the area of Lacs des Loups Marins (Lower Seal Lakes) (56-57°N, 73-74°W), 160 km east of Hudson Bay, on the Ungava peninsula of northern Québec. With the possible exception of Lake Iliamna, Alaska, it is the only known harbour seal population that is resident in freshwater year-round. Written references to the unique appearance and behaviour of this seal date back to 1818. The subspecies was described primarily on the basis of its unique morphology and presumed long-time geographic isolation from neighbouring oceanic harbour seals. Estimates of the population's size are imprecise, and range from 100 to 600 animals. Little is known of the seals' habitat requirements other than that they seem to feed exclusively in freshwater, and are likely reliant on some specific environmental features such as under-ice air pockets to sustain them through the winter. Pupping seems to take place substantially earlier (mid-April to mid-May) than in other harbour seal populations at similar latitudes. The only known cause of human-induced mortality is occasional hunting by aboriginal peoples. Both the IUCN and the Québec government have recognized that *Phoca vitulina mellonae* is potentially vulnerable or threatened because of its small population size, restricted range, and susceptibility to disturbance. A COSEWIC status of "vulnerable" is recommended.

INTRODUCTION

Subspecies description

The Lacs des Loups Marins harbour seal, *Phoca vitulina mellonae*, is confined to the area of Lacs des Loups Marins (Lower Seal Lakes), approximately 160 km east of Hudson Bay, on the Ungava peninsula of northern Québec (Figure 1) [Doutt 1942; Anderson 1946; Scheffer 1958; Bigg 1981].

While there are numerous references to harbour seals occurring in freshwater worldwide (Erlandson 1834; DeKay 1842; Allen 1880; Browne 1909; Grenfell 1910; Prichard 1911; Strong 1930; Dunbar 1949; Fisher 1952; Wheeler 1953; Harper 1956; Harper 1961; Beck et al. 1970; Paulbitski 1974; Roffe and Mate 1984; Williamson 1988), with the possible exception of Lake Iliamna, Alaska (Everitt and Braham 1980), *Phoca vitulina mellonae* is the only known harbour seal population resident in freshwater year-round (Atkinson 1818; Clouston 1820; Hendry 1828; Finlayson 1830; Low 1898; Lewis 1904; Flaherty 1918; Twomey 1938; Doutt 1942; Manning 1946; Doutt 1954; Graburn 1969; Power and Gregoire 1978; Smith and Horonowitsch 1987; Consortium Gilles Shooner & Associés et al. 1991).

Written references to the unique appearance and behaviour of *Phoca vitulina mellonae* date back to Atkinson (1818). The subspecies was described primarily on the basis of an unusually dark pelage and an enlarged coronoid process on the mandible (Doutt 1942), with the presumption that the population had been isolated for 3000-8000 years, trapped by the Ungava peninsula's isostatic rebound since the retreat of the Laurentian ice sheet. Other authors disputed this interpretation, however, arguing that supposed morphological anomalies of *Phoca vitulina mellonae* are merely artifacts of a small sample size, and that the seals are likely able to travel

freely between salt and freshwater (Mansfield and McLaren 1958; Mansfield 1967; Smith and Horonowitsch 1987; *also see* Honacki et al. 1982; King 1983; Wiig 1989; Reeves et al. 1992). Other work, the majority of it recent, strongly supports the validity of *Phoca vitulina mellonae*'s subspecific designation (Davies 1958; Consortium Gilles Shooner & Associés et al. 1991; Smith et al. 1994, 1996; Smith 1996).

Taxonomy

Order: Carnivora

Family: Phocidae

Scientific name: *Phoca vitulina mellonae*

Common names: Lacs des Loups Marins seal, Seal Lakes seal, Ungava seal, phoque

d'eau douce, qasigiaq (Inuktitut), achiguanipe (Cree)

DISTRIBUTION

This is clearly a population with restricted distribution (Figure 1). There are historical references to the presence of this seal in Lac Minto, at the head of Rivière aux Feuilles (Flaherty 1918; Manning 1947), Lac Beneta, situated in the basin of Rivière aux Mélèzes (Manning 1947), Petit Lac des Loups Marins (Atkinson 1818; Clouston 1820; Doutt 1942), and Lacs des Loups Marins (Hendry 1828; Finlayson 1830; Low 1898; Lewis 1904; Doutt 1942; Doutt 1954; Power and Gregoire 1978; Berrouard 1984; Smith and Horonowitsch 1987). Several sightings have been made by Hydro-Québec employees and contractors in the Rivière aux Feuilles, Lac Melvin and Rivière Delay (Consortium Gilles Shooner & Associés et al. 1991). Inuit hunters,

interviewed by Hydro-Québec contractors, reported seeing or killing freshwater seals in Lac Guillaume-Delisle, Rivière Nastapoca, Rivière Boniface, Rivière Niagurnaq, Rivière Kuunga, Rivière Longland, Lac Tasialuk, and Lacs des Loups Marins (Archéotec inc. 1990). The Cree nation of Whapmagoostui considers the range of *Phoca vitulina mellonae* to be Lacs des Loups Marins, Petit Lac des Loups Marins, and Lac Bourdel, with some reports of animals having once been in Lac à l'Eau Claire (Clearwater Lake) (J. Petagumskum, Whapmagoostui, personal communication).

Hydro-Québec has recently compiled observations made of these freshwater seals between 1970 and 1990 (Consortium Gilles Shooner & Associés et al. 1991). Though the preponderance of their survey efforts have been concentrated in Lacs des Loups Marins, Hydro-Québec's data nevertheless indicate the presence of seals in Rivière Nastapoca, Lacs des Loups Marins, Petit Lac des Loups Marins, Lac Bourdel, Lac à l'Eau Claire, and Petite Rivière de la Baleine. In addition, evidence from recordings of underwater vocalizations suggests the presence of seals in Rivière aux Feuilles, Rivière aux Mélèzes, Rivière du Gué, Grande Rivière de la Baleine and La Grande Rivière (Consortium Gilles Shooner & Associés et al. 1991).

During the autumn of 1995, 4 seals were captured in Lacs des Loups Marins and affixed with satellite-linked time-depth recorders (Wildlife Computers, WA). All four tags transmitted from early September to mid-November, and during that time all four seals remained within Lacs des Loups Marins or in the immediate vicinity (R.J. Smith, unpublished data).

PROTECTION

Because Canada possesses no specific marine mammal or endangered species legislation, and because it is unclear whether *Phoca vitulina mellonae*, a marine mammal in freshwater, falls within a provincial or federal jurisdiction, the population currently has minimal legal protection. Freshwater seals north of the 55th parallel are listed as a protected species under the James Bay and northern Québec Agreement (Québec 1976); however, this protection does not have the force of law (J. Gunn, Ministère de l'Environnement et de la Faune, Radisson, Qué. personal communication). *Phoca vitulina mellonae* was recently listed by the International Union for the Conservation of Nature and Natural Resources (IUCN) as being "insufficiently known", meaning that it is "suspected but not definitely known to be endangered, vulnerable, or rare due to a lack of reliable information" (Reijnders et al. 1993). The government of Québec has listed the population as "likely to be designated as threatened or vulnerable" (Québec 1992a), and is considering whether to give legal protection to a portion of *Phoca vitulina mellonae*'s habitat (Dubreuil 1983; Québec 1992b). This protection should be a priority given that the proposed Grande Baleine hydroelectric development could have an adverse impact on a large portion of this population's range (Rosenthal and Beyea 1989; Rougerie 1990; Woodley et al. 1992; Smith et al. 1994).

POPULATION SIZE AND TREND

Estimates of the size of this small population are imprecise. A maximum of 500 animals was the "guess" of Doutt (1957), cited in Scheffer (1958). Power and Gregoire (1978) estimated 200 and 600 animals by two different summations. The most recent estimate by Consortium

Gilles Shooner & Associés et al. (1991) was approximately 100 animals, or 0.1 seals/km², in Lacs des Loups Marins and Lac Bourdel. Population trends over time obviously cannot be calculated.

HABITAT

Little is known of the habitat and ecological requirements of this subspecies.

The few dead animals that have been examined were found to have salmonid (*Salvelinus* sp.) otoliths in their stomachs (Consortium Gilles Shooner & Associés et al. 1991; Smith et al. 1996). Comparisons of the stable-isotope ratios and fatty acid profiles of the tissues of *P. v. mellonae* and harbour seals collected from oceanic locations indicate that, over a two year period, *P. v. mellonae* seemed to be feeding exclusively in freshwater (Smith et al. 1996).

Recent investigations found no permanent haulout sites on Lacs des Loups Marins and Lac Bourdel (Consortium Gilles Shooner & Associés et al. 1991). In winter, when the vast majority of the lakes and rivers are covered in ice, the seals may rely on several physical features for their sources of air: areas that remain ice-free because of strong currents, fissures in the ice, and air pockets created by the shoreline's complicated geometry or by the undulations in the bottom of the sheet ice on the lake's surface (Smith and Horonowitsch 1987; Consortium Gilles Shooner & Associés et al. 1991; Dean Consulting & Research Associates Inc. 1991).

None of the habitat of this population is protected. It is entirely on Crown land that could be adversely affected by Hydro-Québec's construction of the proposed Grande Baleine hydroelectric project (Woodley et al. 1992) which, though indefinitely postponed by the current provincial government, has not been cancelled altogether. One of the results of the Grande

Baleine environmental assessment process has been that Hydro-Québec is now required to evaluate properly the likely impacts of the project on the population, prior to construction (Review Bodies 1994). Some of these potential impacts include the disappearance of ice-free areas and under-ice shoreline shelters, upon which the seals may rely in the winter, in water courses with altered flows arising from hydroelectric development. The Grande Baleine project may also affect the distribution and abundance of the seals' prey, and contaminate the animals with methyl mercury released from the flooded, decomposing vegetation (Woodley et al. 1992). The negative effects of this habitat destruction could lead to a decline in the seal population and an impoverishment of its genetic diversity (Alfonso and McAllister 1994).

GENERAL BIOLOGY

Reproduction probably occurs between mid-April and mid-May in the Lacs des Loups Marins area; substantially earlier than other harbour seal populations at a similar latitude (Doutt 1942; Archéotec inc. 1990; Consortium Gilles Shooner & Associés et al. 1991; Temte et al. 1991; Smith et al. 1994). Since the lakes are still iced over at the time of pupping, and no births have been observed on the ice, several authors have postulated that pupping takes place in under-ice shelters (Consortium Gilles Shooner & Associés et al. 1991), like those of ringed seals (*Phoca hispida*) (Smith and Stirling 1975).

The only known cause of human-induced mortality is occasional hunting of the seals by aboriginal peoples (Clouston 1820; Low 1898; Flaherty 1918; Doutt 1942; Doutt 1954; Consortium Gilles Shooner & Associés et al. 1991; J. Petagumskum personal communication).

Seasonal movements of the population are poorly known, though the sporadic

observations of Gilles Shooner & Associés et al. (1991) hint at seals spending the winter months in larger bodies of water like Lacs des Loups Marins, Lac Bourdel, and Petit Lac des Loups Marins, with some dispersal into outlying, smaller bodies of water upon the melting of the ice. These investigators report finding many worn trails between bodies of water frequented by the seals, some as long as 0.15 km, and on inclines as steep as 25°. There is no evidence that animals move between the area of Lacs des Loups Marins and Hudson or Ungava Bays. However, though there are a number of impassable waterfalls on the Rivière Nastapoca, some authors believe that if the seals could move into the more placid rivers that flow north into Ungava Bay, this would be a feasible avenue of exchange between the fresh and saltwater populations (Mansfield 1967; SOGEAM 1985; Smith and Horonowitsch 1987).

Preliminary evidence from DNA sequencing of region I of the mitochondrial D-loop indicate that *P. v. mellonae* has haplotypes that are unique when compared to harbour seals in the eastern Canadian arctic and Northwest Atlantic (Smith 1996).

Animals hauled out in the spring months are usually in small groups, whereas at the end of the summer, they are usually hauled out singly or in pairs: This behaviour is probably related to the moulting process (Consortium Gilles Shooner & Associés et al. 1991).

LIMITING FACTORS

The tendency of harbour seals to be distributed in small local populations makes them vulnerable to disturbance (Maine Seal 1994). There are a number of examples of local harbour seal populations being extirpated, or their numbers drastically reduced, by human activity. For example, a small population that seemed to frequent Lake Ontario was eliminated by the early

1800s (DeKay 1842; Allen 1880); the population in Greenland is practically extirpated (Teilmann and Dietz 1993; R. Dietz, personal communication), an important reason being the intensity with which it has been hunted and entangled in fishing gear; the population in Hokkaido, Japan, is very small, with removals from incidental catches in fishing gear exceeding recruitment (Reijnders et al. 1993). Given such evidence, the Lacs des Loups Marins seal population is likely sensitive even to limited disturbance by humans.

SPECIAL SIGNIFICANCE OF THE SUBSPECIES

This population of harbour seals is unique, in that it is the object of reverence by the aboriginal peoples of northern Québec (Posluns 1993; Archéotec inc. 1990; M. George, Whapmagoostui, personal communication); it is the object of a wealth of historical references, and seems to be unusual in a number of ways, including aspects of its biology (Consortium Gilles Shooner & Associés et al. 1991; Smith et al. 1994, 1996; Smith 1996). The population has also acquired something of a public profile over the last few years (e.g. Dubreuil 1987).

RECOMMENDATIONS

Future research should address how genetically distinct this population is from nearby ocean populations, estimate current abundance and trends in the size of the population, expand our knowledge of the population's range and seasonal movements, and collect basic biological data such as the timing of reproduction, and critical habitat requirements.

This subspecies should be classified as vulnerable by both COSEWIC and Québec provincial legislation, and crucial areas of its habitat protected, possibly through Québec's

ecological reserve programme, or the establishment of a national park.

The recommendations expressed here are those of the author, and not necessarily those of COSEWIC or its member agencies.

EVALUATION

It is essential for the future viability of this subspecies that the potential impacts on the population from the Grande Baleine hydroelectric project, and any other future development in Québec's north, be eliminated or seriously mitigated.

Because of the inaccessibility of the population, there is no known trade in the subspecies, legal or otherwise.

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AUTHOR'S RECOMMENDATION OF STATUS

Because of the population's uniqueness, small size, restricted range, and the possibility of its being adversely impacted by future development on the Ungava peninsula, *Phoca vitulina mellonae* should be classified as vulnerable.

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Figure 1. Known range of *Phoca vitulina mellonae* in relation to Hydro-Québec's proposed Grande Baleine hydroelectric project.

