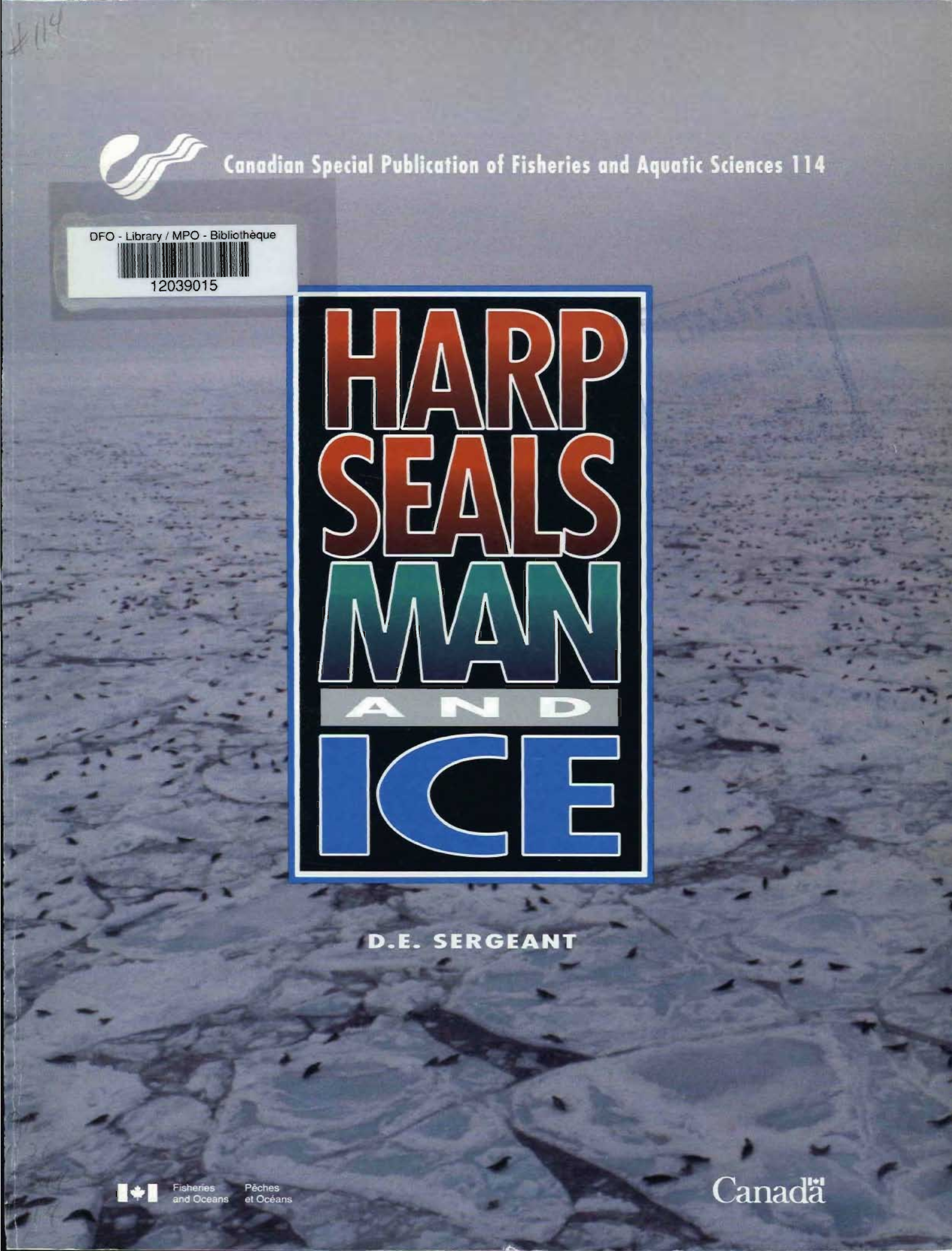

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HARP SEALS MAN AND ICE

D.E. SERGEANT

Fisheries and Oceans   Pêches et Océans

Canada

Harp Seals, Man and Ice

Frontispiece: Moulting patch of harp seals at the "Front" ice, Newfoundland, April 25, 1976.

Canadian Special Publication of Fisheries and Aquatic Sciences 114

Harp Seals, Man and Ice

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Contents

Sergeant, D.E. 1991. Harp seals, man and ice. Can. Spec. Publ. Fish. Aquat. Sci. 114: 153 p.

This book reviews the biology and population dynamics of the harp seal, *Phoca groenlandica* Erxleben, the history of its hunting over several centuries, and its eventual conservation. This is one of the most abundant of the world's hair seals, which has long been an important resource for peoples living on seasonally ice-bound coasts of the North Atlantic Ocean. The author treats the biology of the species as a whole, not only on the coasts of eastern Canada, but also of Greenland and northern Europe, and the history of the hunt in all these regions. Knowledge of the behaviour of pack ice on these coasts gives a background to both the ecology of the seals and the economies of the hunt.

Advances in knowledge of the biology and population dynamics of harp seals led to their successful management as a hunted species, but popular sentiment, concerned with hunting practices, brought about a loss of markets so that catches greatly decreased. Consequently, many present problems are those of an abundant predator species, interacting with human finfish fisheries.

Ce livre donne un compte rendu de la biologie et de la dynamique des populations du phoque du Groenland *Phoca groenlandica* Erxleben, l'historique de la chasse au cours des siècles et des efforts actuels de conservation de l'espèce. Une des plus abondantes parmi toutes les espèces de phoques à poil ras, le phoque du Groenland constitue depuis longtemps une importante ressource pour les habitants des côtes de l'Atlantique Nord bloquées par les glaces une partie de l'année. L'auteur examine la biologie de l'espèce, non seulement sur la côte est du Canada, mais aussi sur les côtes du Groenland et du nord de l'Europe; il traite aussi l'historique de la chasse dans ces régions. Des renseignements sur le régime du pack sur ces côtes mettent en contexte l'écologie du phoque du Groenland et le côté économique de la chasse.

L'accumulation de connaissances sur la biologie et la dynamique des populations du phoque du Groenland a mené à une gestion équilibrée de la chasse, mais les pressions exercées par le grand public, préoccupé par les méthodes de chasse, ont entraîné la perte de marchés. Le nombre d'animaux tués a donc nettement diminué. Par conséquent, nous faisions face à un problème de prédateurs abondants dans les pêcheries de poisson exploitées par un autre prédateur, l'homme.

Introduction and Acknowledgements

The great interest aroused concerning the hunting of harp seals since about 1965 has made the writing of a book on the biology of the species a prime need, since no work exists in the English language which attempts to cover the scope of the species' biology and fisheries. A great amount of research has, however, been carried out, increasing exponentially since the early 1950's, in Canada, Denmark, Norway and the Soviet Union, all countries which have possessed or administered important fisheries for harp seals. I have tried to piece this information together, but since my first-hand research has been in the western North Atlantic, I necessarily give more weight to this area.

The writing of a book gives a spurious finality to research. In fact research has opened as many problems as it has solved. Thus, practically nothing is known of the behaviour of harp seals, how they navigate, the nature of groups of animals, and the bearing of these features on their migration, whether for instance they home to the area in which they lived the previous winter, and so on. To gather such information in the wild is clearly difficult when applied to an active, migratory species which in addition whelps not on land but on pack ice, and which when brought into captivity is in a totally artificial environment. Nevertheless great credit is due to Soviet investigators of the Polar Research Institute of Fisheries (PINRO), Arkhangel'sk who in 1966 began studies by drifting investigation on the natal pack ice of harp seals in the White Sea (Popov 1966, 1967). Professors Keith Ronald and David Lavigne with many co-workers at the University of Guelph, Ontario took this technique to the ice in the Gulf of St. Lawrence in 1976. In addition this group have pioneered the holding of this species in captivity, and studied many aspects of its behaviour and physiology in the field and in the laboratory, with many resulting publications which are paramount in their field, work which has been summarised in a semi-popular book by Lavigne and Kovacs (1988). This study, by contrast, has an ecological emphasis which reflects my interests, and on population dynamics which reflects the tasks of a government scientist. During my 35-year research career, the Federal government resources in eastern Canada concerned with harp seal research shifted in 1955 from St-John's, Newfoundland to the Arctic Unit, Montreal, which later became the Arctic Biological Station at Ste-Anne-de-Bellevue; and moved back in 1978 to St. John's, with back-up from St. Anne's for the Gulf of St. Lawrence. A new fisheries research station at Mont-Joli, Quebec, the Institut Maurice-Lamontagne, which like St. John's is closer to the seals, has now replaced Ste. Anne's in this field of work.

My acknowledgments are, first, to my present and past scientific colleagues in the study of sea mammals within the Federal Department of Fisheries and Oceans (the former Fisheries Research Board of Canada). Drs Dean Fisher, Arthur Mansfield, Ian McLaren, Edward Mitchell, Tom Smith and Robert Stewart have provided much stimulus and constructive criticism in the course of these studies. Dr. Mansfield in 1962 and 1963 aided with aerial surveys, and in 1964 and 1966 headed teams of workers carrying out capture/recapture tagging from a helicopter and an icebreaker respectively. In 1969, Dr. Smith opened up the possibility of collecting data from hunters in the estuary of the St. Lawrence. Dr. M.M.R. Freeman provided first-hand data on harp seals from the Canadian high arctic.

In the 1950's, Mr. John Clowe and Mr. Charles Rose were my field companions and taught me the skills of working and travelling on ice. During the 1960's and later, Brian Beck, Dr. Paul Brodie, Ingram Gidney, Clive Nicol, Hank Killiaan and C.W. Britton, and especially Wybrand Hoek carried out much of the aerial survey, the collecting and analysis of specimens and the tagging of seals, and contributed ideas in field and laboratory discussions. Dr. Edward Grainger and Dr. Gerald Hunter identified food organisms of harp seals, as did Dr. Don McAllister of the National Museum of Natural Sciences, Ottawa. Within the Department of Fisheries and Oceans, I am grateful to many people within the Economics Service for providing catch statistics, and to many officers of the Conservation and Protection Service for observations and collections made on sealing voyages. Among them, over many years Mr. Stanley Dudka and Mr. Tom Curran helped us in our tagging, cooperated fruitfully in the use of helicopter time, and contributed a host of useful observations in their diaries. Mr. G.W. Stead, Chief of the Marine Services of the Department of Transport, provided us with the use of the icebreaker *d'Iberville* at the "Front" ice in 1966. Officers of the Meteorological Branch of the Department of Transport, encouraged by Mr. M. Monsinger, provided many field sightings of seals from ships and the air, and their ice charts were essential to a study of seal behaviour. The Bureau of Translations of the Secretary of State provided translations of Russian papers on seals which were beyond my capacity or time to translate. Mr. Paul Montreuil, past director of the Magdalen Is. fisheries laboratory of the Quebec Government, provided observations and unpublished analyses resulting from his studies of the food and parasites of seals. Dr. J.M. Olds, M.D., of Twillingate, Newfoundland and the late Dr. Yves Jean, of the Quebec Department of Fisheries, forwarded valuable observations on observed seal mortalities. Captain V. Torraville, Montreal, provided general knowledge from his long years of seafaring and seal hunting. Mr. Gordon Williamson, now resident in Scotland, provided information from a sealing voyage.

I acknowledge a great deal of help and discussion from among the sealing industry: among management particularly from the late Mr. J.M. Grieve of Bowring Bros. Ltd., St. John's, Newfoundland, Mr. Karl Karlsen of Halifax, Nova Scotia, Mr. Arne Steierstol and Mr. Bernard Nygaard of Carino Ltd., Halifax and St. John's, and Mr. Christian Rieber of G.C. Rieber A/S, Bergen. Among sealing captains who took responsibility for the care of a biologist or technician or both on board I thank Captains Wilfred Barbour, Fred Hounsell, and particularly (on several voyages) Harold Marø. In many conversations I have absorbed some of their great knowledge of seals and sealing. From Norway, I add especially Capt. Guttorm Jacobsen of Tromso.

I acknowledge the scientific stimulus and exchange of my colleagues overseas, especially the following: in Denmark, Mr. F.O. Kapel, Copenhagen; in Norway, Mr. T. Øritsland and Mr. I. Christensen, Fiskeridirektoratet, Bergen and Dr. N.A. Øritsland, University of Oslo; in the Soviet Union, Dr. A.V. Yablokov, Academy of Sciences of the USSR, Moscow, R. Sh. Khuzin, PINRO, Murmansk, Yu I. Nazarenko in PINRO, Archangel'sk and L.A. Popov, VNIRO, Moscow.

In 1978 Dr. Don Bowen and Dr. Keith Hay began full-time studies on seals and whales at St. John's, Nfld. and in 1986 — Dr. I.-Hsun Ni and Dr. Gary Stenson. Their contributions to harp seal research are reflected in the bibliography of this book, while both Dr. Bowen and Dr. Stenson have taken much time to provide critiques of its earlier version.

In 1980–81 I profited by a sabbatical at Cambridge University, used in part to work on this book, and express my thanks to Corpus Christi College, the Dept of Applied Biology, and (especially for access to historical works), to the Scott Polar Research Institute.

Lois McMullon, followed by Dora Godard, typed successive drafts with intelligence and patience. Wybrand Hoek, Joseph Lovrity and Françoise Cartier drew the Figures. To all these people I express my gratitude.

Chapter I. Origins and Names

Summary

The harp seal is a member of the hair seal family Phocidae which inhabits pack ice of the North Atlantic. Usually considered a member of the genus *Phoca*, it is sometimes placed in the separate genus *Pagophilus*. Its nearest living relative is the ribbon seal, *Phoca* (*Histriophoca*) *fasciata*, of the North Pacific.

The ancestral harp seal probably evolved during the Pliocene in the North Atlantic. A few Pleistocene fossils show an expected southward displacement, which persisted immediately after melting of the last ice sheet began. Subfossils from this time (10 000 yr before the present) are found in the shallow Champlain Sea of the St. Lawrence valley. From about 4 500–2 500 BP a population inhabited the Baltic Sea and was hunted by Neolithic man. This population must have invaded from around the Norwegian coast. The cause of its extinction is unknown but may have been a change from a continental to an oceanic climate, or competition from grey seals, or both factors.

Classification and Evolution

The harp seal belongs to the group of hair seals, family Phocidae, which are characterized by negligible external ear or pinna, hind flippers which do not turn forward, and the absence of an underfur. The eared seals, Otariidae, by contrast, have all these features. The naked-skinned walruses, Odobaenidae, are an offshoot of the Otariidae.

The hair seals have been separate from the eared seals for most if not all of their evolutionary history. McLaren (1960a) reviewing their history suggested that the Phocidae arose probably from an otter-like ancestor "in the extensive and permanent lacustrine systems of Tertiary Asia, and (that they) invaded the seas through marine transgressions in the Miocene". The eared seals and the walruses on the other hand probably arose from a bear-like ancestor and in the North Pacific (McLaren 1960a; Repenning et al. 1979).

For accounts of seals of the world the reader is referred to books by King (1983) and Scheffer (1958). Figure 1 will serve to give an impression of the skeletal structure of a harp seal from its mounted skeleton.

The subfamily Phocinae to which the harp seal belongs is characterized by white-coated young and all extant species are cold-water animals. McLaren (1960b) therefore postulated a northern origin for them. One other subfamily of the hair seals, the Monachinae, includes three species of the tropical monk seals and four species of Antarctic seals, all of thich have dark-coated young. The hooded seal *Cystophora*, placed in its own subfamily, and a northern ice breeder, has this same feature.

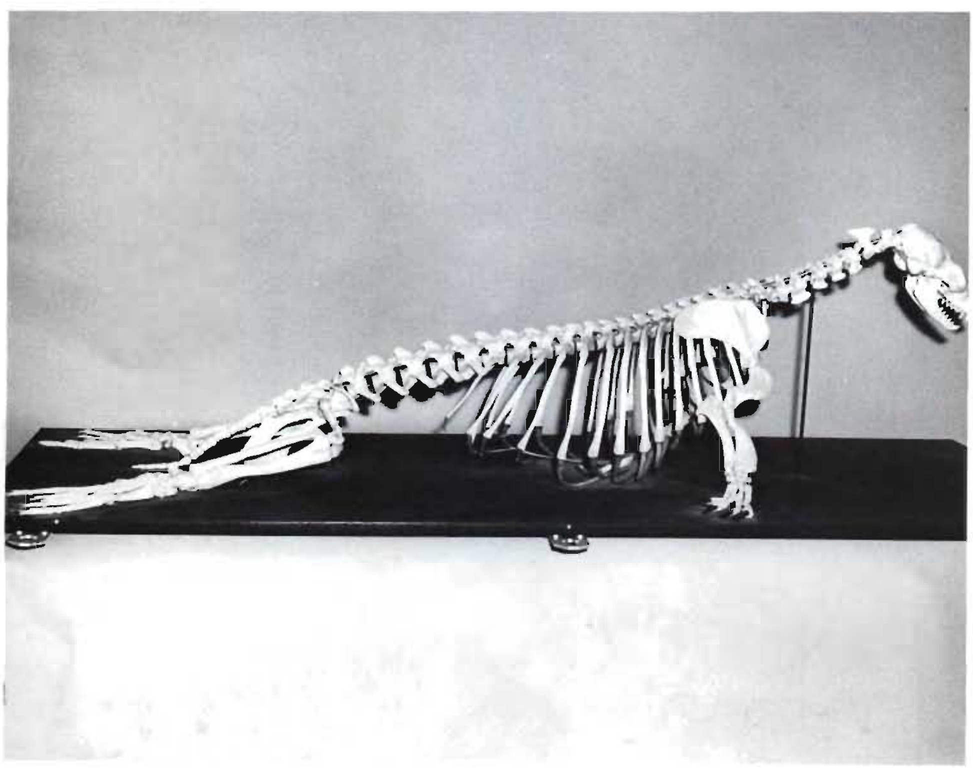


FIG. 1. Mounted skeleton of harp seal. Courtesy Prof. K. Ronald, Guelph University.

The genus *Phoca* of Linnaeus 1758 has been subdivided into several genera by most later workers, who recognized deep differences between modern species of hair seals, indicative of long evolutionary history. Among these new genera was the harp seal, *Pagophilus*.

We now meet two interrelated problems which beset biologists studying the real relationships of animals and giving them names. The so-called *Law of priority* states that the first validly distinguished name following the publication of the third edition (1758) of Linnaeus' scheme should be the name recognized by biologists. In the case of the generic name of the harp seal, this definition requires some historical research.

Miller and Kellogg (1955) cite the history of the hitherto accepted generic name as follows:

> Subgenus *Pagophilus* Gray (harp seals).
> 1844 Pagophilus Gray, in The Zoology of the Voyage of H.M.S. Erebus and Terror, . . . Vol. 1, p. 1, p. 3 (Type, *Phoca groenlandica* Erxleben.) 1904 *Pagophoca* Trouessart, Catalogus Mammalium. . ., Suppl., Fasc. 1, p. 287. (Substitute for *Pagophilus*, assumed to be a homonym of *Pagophila* Kaup, 1829. This is not in conformity with the provisions of the International Code, Article 36, with accompanying recommendation, and Opinion 25 of the International Commission of Zoological Nomenclature, Smithsonian Inst. Spec. Publ. 1938, p. 59–61, July 1910).

This means that Gray distinguished harp seals as a distinct genus *Pagophilus*, which name has priority over *Pagophoca*. Most later western authors have followed this decision. However, Soviet authors, following Ognev (1935), continue to use *Pagophoca*.

However, Burns and Fay (1970) studied large numbers of skulls of several members of the Phocidae: the ribbon, harp, harbour and ringed seals. They concluded that these four species were sufficiently alike to be regrouped in the genus *Phoca*, which would leave the established generic names (e.g. *Pagophilus* for harp seal) as subgenera. Their classificatory scheme is shown in Fig. 2.

Burns and Fay (1970) found that the skulls of the four species showed great variability in various characters, so that in various ways each appeared to be related to all the others. Only the ribbon seal *Histriophoca* stood out as probably the latest derivative of a primitive *Phoca* seal. The idea of earlier workers was that the arctic ringed seal, *Pusa hispida*, is closest to the primitive ancestor, on the grounds of its skull form, small size and arctic habitat. This appears to be invalid: the harp, ringed and harbour seals now all have equal claim to primitiveness. The majority of present workers seem to favour the genus name *Phoca* for all of these seals.

These difficulties of comparative morphology could be resolved if we had a sufficiently complete fossil record, but the record is rarely complete or completely examined, palaeontology being an expensive occupation of largely cultural value. We do know that by the middle Pliocene (more than 5 million years [my] ago) the Phocidae had radiated to produce numerous genera closely resembling modern genera. Fossils of these animals are found in the

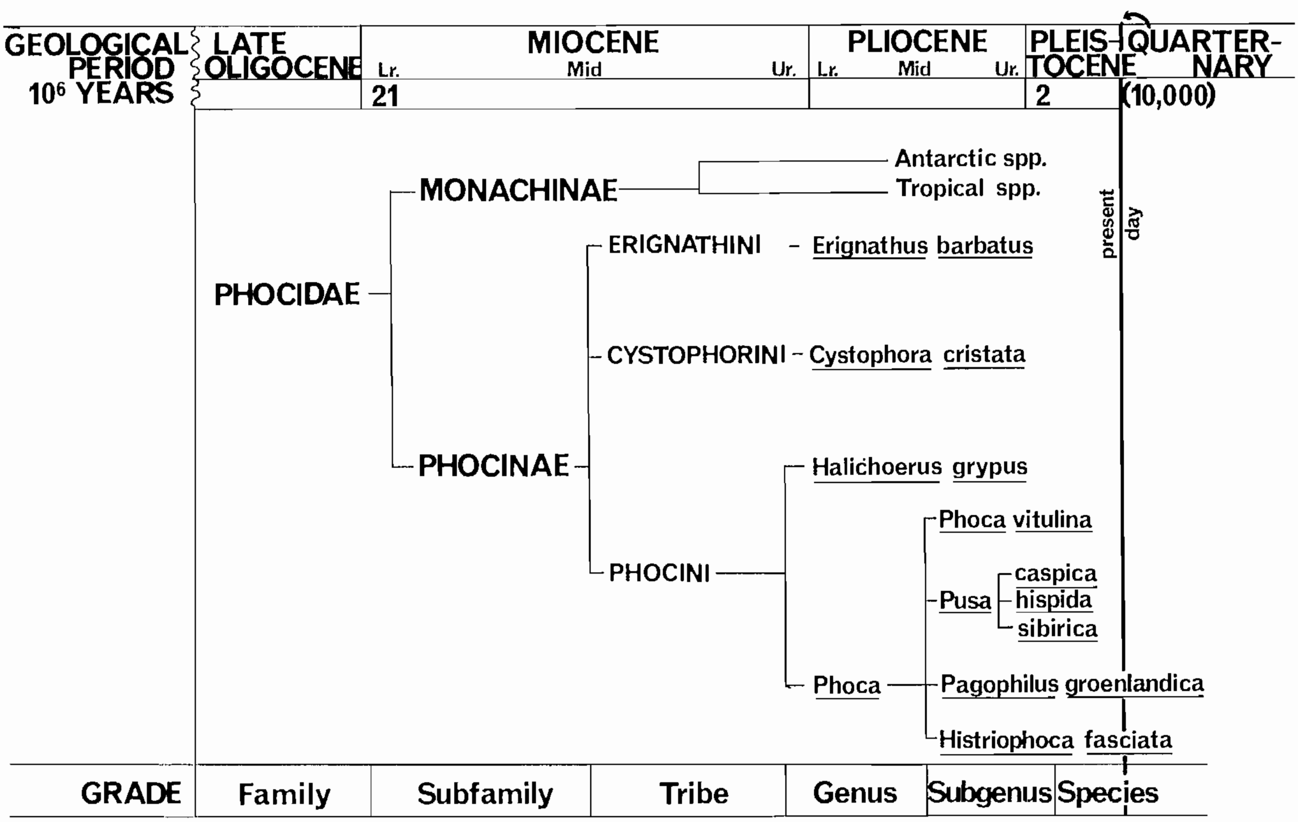


FIG. 2. Geological history of the Phocidae, with supposed age of the present-day species.

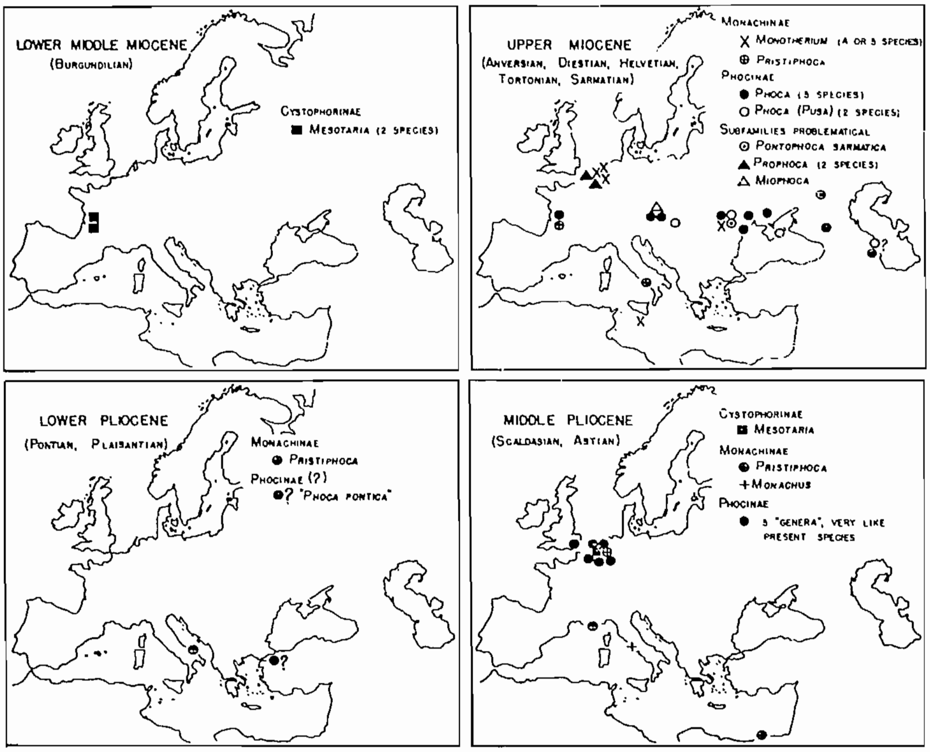


FIG. 3. Fossil Phocid genera from Europe (from McLaren 1960b).

Antwerp basin in Belgium, which was the delta of the Rhine at the time (Fig. 3), and on the east coast of USA. Unfortunately their relationships to modern genera remain in need of reworking, according to Barnes et al. (1985).

A more involved argument for the date of origin of modern harp seals *Phoca* (*Pagophilus*) *groenlandicus* is based on the supposed date of separation of its closest living relative, the ribbon seal *Phoca* (*Histriophoca*) *fasciata* which lives in the north Pacific.

Comparative anatomical studies of modern Phocinae by Chapskii (1955) as well as Burns and Fay (1970) show that *Pagophilus* and *Histriophoca* are closely related. McLaren (1966) argues that the ancestral ribbon seal passed from the North Atlantic to the North Pacific but found the pack-ice breeding niche in the Pacific pre-empted by ice-breeding harbour seals *Phoca largha* and was thus forced to occupy a niche in deeper water where it lives today. Meanwhile *Phoca largha*, he thinks, colonised the North Atlantic among other areas, giving rise to the shore-breeding harbour seal, *Phoca vitulina*. He dates the invasion of the North Pacific by *Phoca largha* as after the end of the Miocene. Therefore the arrival of *Histriophoca* was later.

In fact, *Histriophoca* could not have got into the North Pacific until the Bering Strait opened in mid-Pliocene (3.5 my ago) or later. Since modern *Histriophoca* and *Pagophilus* differ sharply in colour pattern, the origin of modern *Pagophilus* must have been mid-Pliocene or later.

Most authors suppose that the modern species of hair seals had evolved by the Pleistocene, the beginning of which is placed 2 my ago.

Past Distribution

Pleistocene fossils of harp seals seem to be very rare, presumably because during periods of glaciation the sea-level was lowered, and resulting marine sediments now lie well below modern sea-level.

There were found however in Europe a jaw of a ringed seal, and another of a harp seal in caves, respectively, of middle Aurignacian age (ca. 25 000 yr) and late Magdalenian age (ca. 18 000 yr) - in the last or Würm glaciation — from the river valleys of the Dordogne region of south-central France, about 200 km from the present coast (Harlé 1913). It is not clear whether these animals were transported inland by man or swam upriver, but in any case a great southward displacement of these two arctic species had occurred. This would be expected: Kurten's (1972, p. 66–67) map reconstructing the geography of Europe during the Würm glaciation shows tundra along coasts as far south as those of present-day southern France and south-west Britain.

Post-Pleistocene (Quaternary) fossils of harp seals are by contrast common and occur in two areas where the species is not found at the present day. One is the former Champlain Sea which now forms the fertile plain of the St. Lawrence valley (Elson 1969). Immediately after the end of the last glaciation, the crust of the formerly ice-covered northern land remained depressed and the newly rising sea rushed in, forming a temporary extension of the Gulf of St. Lawrence which extended above Ottawa. In the deposits of this age (12 000 - 10 000 BP), near Ottawa and Montreal, nodules of clay contain fossils of smelt *Osmerus* sp., capelin *Mallotus villosus*, Atlantic salmon, sculpins *Artediellus uncinatus* and sticklebacks *Gasterosteus aculeatus*. Also found are bones of white whales, *Delphinapterus leucas*, and of harp and ringed seals (Harington 1977). This is the sort of fauna one would now find 500 km downstream in the estuary of the St. Lawrence at Tadoussac where the surface water is unusually cold, or in the low arctic.

The second locality where harp seal bones have been found in profusion is the Baltic Sea, where they are associated with those of other seals still found in the Baltic — ringed, harbour and grey seals. Figure 4 shows the chronology. The first postglacial deposits of west Sweden, those of the Yoldia Sea (Fig. 5b) show subfossils of typically arctic sea mammals (Freden 1975). At this period also, harp seal subfossils are known from the Elbe estuary (Kellogg 1922). A freshwater phase, the Ancylus Lake, (Fig. 5c) intervened in the Baltic as the result of land uplift. The only seal bones in its deposits were those of ringed seals (Forstén and Alhonen 1975), a species which lives in several northern lakes today.

A new marine phase followed (Fig. 5d), the Litorina (Littorina) Sea, after which the Baltic gradually attained its modern shape. The earliest *Atlantic* stage of the Litorina Sea (about 6 000 BP) had a mild-climate fauna of sea mammals and birds resembling that of the modern North Sea (Lepiksaar 1964). In the succeeding *sub-Boreal* (about 4 500 BP), a more continental period with warm summers and cold, dry winters, abundant fossils of harp seals appear (Fig. 6). These must have invaded *de novo*, and by way of the Scandinavian coast, since a direct connexion with the White Sea was by now blocked. Since, in a big southward invasion of harp seals along the Norwegian coast in the winter of 1902–03, animals reached Helgeland in west Norway, Jylland in Denmark (Nansen 1925), Scotland and even S.W. England (Sim 1903; Clark 1946), it is quite plausible to imagine a colonisation of the Baltic by this route, and the presence of a few bones at times later than the sub-Boreal might represent such abnormal migrations. Most writers agree that the sub-Boreal harp seals were dwarfed (see especially Forstén and Alhonen 1975 for measurements), which suggests an isolated population living in a suboptimal environment such as a large estuary (for example white whales, *Delphinapterus leucas*, living in the White Sea and in Hudson Bay are dwarfed, Sergeant and Brodie 1969). At any rate, harp seals were very numerous —for example, second in numbers after grey seals *Halichoerus grypus* in Denmark (Møhl 1971) — and were the frequent prey of Mesolithic man (Clark 1946). Thus, a harpoon head made from elk (*Alces alces*) bones was found in the ribs of a skeleton of a harp seal found in a drained bog at Närpes, Finland (near the present coastline of the Gulf of Bothnia) in 1935. Waterbolk (1968) sees the shift to sea-mammal hunting in the Baltic which began in the Atlantie period as the result of the contemporary development inland of impenetrable oak forests in place of pine and birch, and a rise in sea level extending swamps on the north German plain. The Mesolithic sea mammal hunters had no domestic animals other than dogs, but traded with farming cultures further south (Clark 1946).

The harp seals of the Baltic died out gradually about 3 000 BP (Sellstedt et al. 1966) from unknown causes. Since none of the other three seal species present was exterminated, excessive hunting does not seem a very likely cause of their extinction.

Climatic change may have been responsible, especially away from continentality and towards mild winters, since the young harp seal needs a dry pelage in order to survive the first few hours or days of life, and dryness is afforded by snow but not by rain (p. 12). This hypothesis would fit the sub-Boreal as peak period of harp seal abundance in the Baltic, which had a continental climate and came between wetter periods before and afterward (Fig. 4).

A third possibility is that one or other of the still-existing Baltic seal species, invading, produced competition with harp seals for a limited ecological "niche". Relative shifts of abundance of the various species have been described in Denmark (Møhl 1971) and at Gotland (Clark 1946). Suspicion would attach most closely to the grey seal, which in the present-day Baltic has its young on the pack ice in March, the same season as present-day harp seals (Hook and Johnels 1972), whereas in the present-day Gulf of St. Lawrence, grey seals whelp in January.

The most plausible explanation would combine both these factors. In a mild Atlantic climate, rain would decrease the fitness of the small harp seal pup to survive, but would favour the large grey seal pup, with lower proportionate heat loss (p. 12). The grey seal was present to the south and west whence it could reinvade the Baltic in climatically suitable periods; whereas for the harp seal, colonisation was likely a chance event from a source population to the north. The little arctic ringed seal which can tolerate brackish and even fresh water survives in the upper reaches of the Baltic and some adjacent lakes to the present day.

The Gulf of St. Lawrence contains grey, harbour, (rarely) ringed, harp and hooded seals; ringed seals formerly occurred in the Saguenay Fjord and northward along the Quebec north shore. This is a larger mix of species (five) than could apparently survive in the Baltic (present day: grey, harbour, ringed = 3 species). The Gulf of St. Lawrence is however open to the north as well as the south, allowing not only the southerly species (grey, harbour) to migrate out in winter, but arctic species (harp, hooded seals) to migrate out in summer by way of the Strait of Belle Isle.

Apart from the St. Lawrence extension and the Baltic population, the geographical range of the harp seal at various dates after the end of the last ice age did not differ greatly from that at the present day but extended somewhat further south at times.

Thus, Kellogg (1922) recorded a subfossil harp seal from South Berwick, York Co., Maine near the coast on the border with New Hampshire, in post-Pleistocene marine mud at a depth of 30 ft (9 m) from the surface.

Norton (1930) recorded two scapulae, two humeri and several other bones of hooded seals *Cystophora cristata* from post-Pleistocene clay in Westbrook, Maine about 14 ft (4 m) below present surface, and a skull and skeleton of a walrus from post-Pleistocene clays in Portland, Maine. These clays contained the molluscs *Mya*, *Macoma*, *Mytilus*, *Cardium*, *Saxicava* and *Leda* spp. Corresponding clays with bones of seals, walruses and

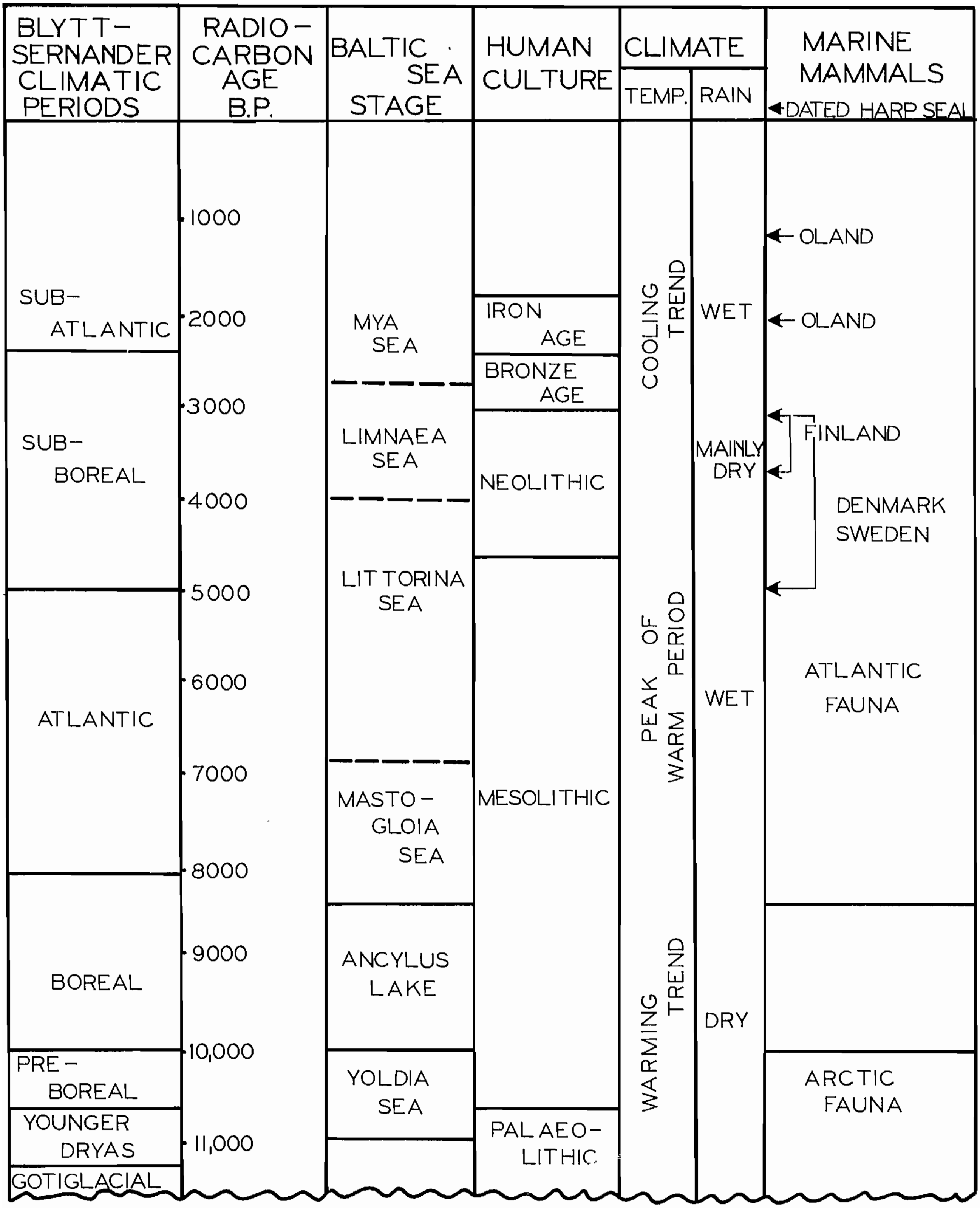


FIG. 4. Chronology of Quaternary Baltic Sea, from various sources.

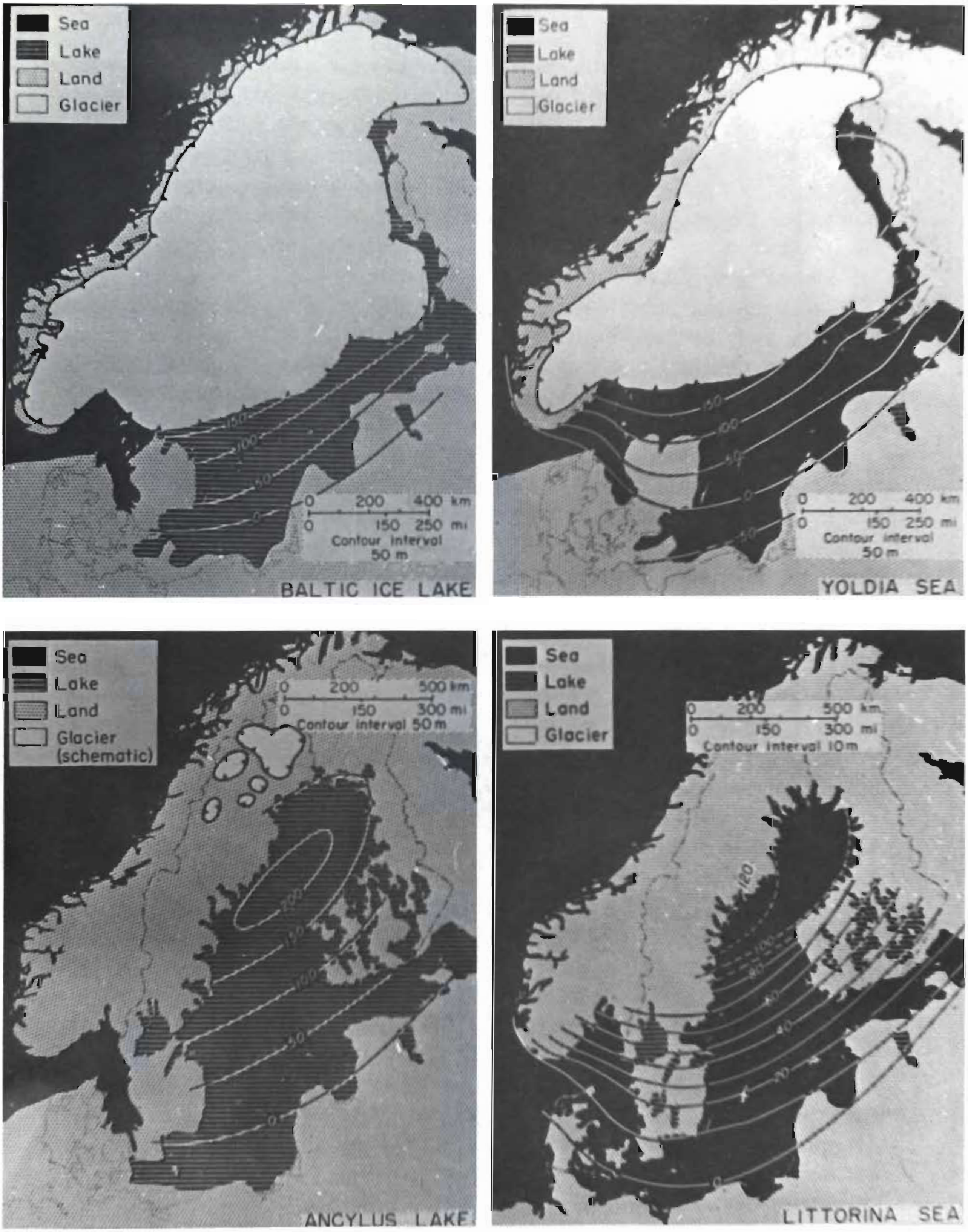


FIG. 5. Post-glacial history of the Baltic Sea (from Flint 1957).

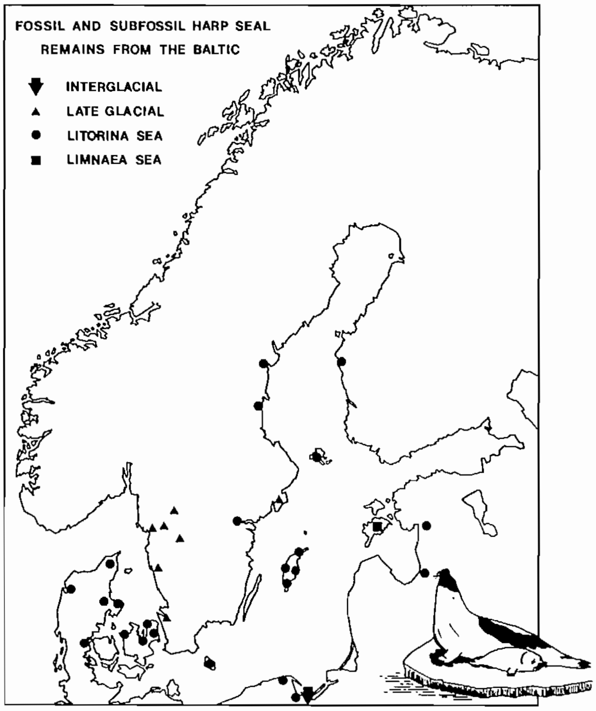


FIG. 6. Subfossil harp seal remains from the Baltic (after Møhr 1952).

whales were reported as occurring at Rivière du Loup, Bic and Matane on the south shore of the St. Lawrence estuary.

Turner (1870) figures the jaw of an immature harp seal found in a red clay of Pleistocene or post-Pleistocene age at Grangemouth in the Firth of Forth, Scotland. The layer was covered with 80 ft (24 m) of clays, gravels and sands, and underlain directly by a glacial till. *Tellina (Macoma) baltica* occurred in an overlying sand. Several other specimens of harp seals had been collected from nearby localities.

These deposits all presumably refer to the period about 10 000 BP immediately following the disappearance of ice at this latitude, the same period as the post-glacial Baltic.

Going back only 5 000 yr, Waters (1967) found bones of grey seals at Martha's Vineyard, Mass., with harbour seals arriving about 1 500 BP. Loomis and Young (1912) however found bones of 12 harbour seals and 7 harp seals (and also many codfish) in shell-heaps of 500 – 1 000 BP Maine, pointing out that the harbour seals were probably under-represented through being hard to catch. At the present day, grey seals are found at Nantucket (near Martha's Vineyar) but rarely in Maine, while harbour seals are abundant in Maine, so past and present distributions are in agreement. Harp seals do not now regularly reach Maine, so that the species was either more abundant or the ice reached somewhat further south round Nova Scotia. Similar conclusions are reached by McAlpine and Walker (1990) in a study of present and recent (Quaternary) occurrences of harp seals in the Bay of Fundy and at New England.

Moving north, Dr. Elmer Harp of Darmouth, New Hampshire (Harp and Hughes 1968) studied the Dorset Eskimo archaeological site at Port au Choix, northwestern Newfoundland of about 2 000 – 1 500 BP. He found abundant seal bones which could be identified as those of harp seals. Archaeologists have not been able to determine how they were caught, except that harpoons were used. Fishermen now do not catch harp seals regularly from Port au Choix by any means except by shooting in spring time from boats in loose ice.

The Norse sites in West Greenland of ca. 1 000 BP contain the expected seal bones: chiefly those of harp and hooded seals at the southern site near Julianehaab, and of harp and harbour seals at the northern site near Godthaab (Koch 1945; McGovern 1985 (Table 1). Hooded seals drift westward round Kap Farvel at the present day, but harp seals reach the Godthaab region from Newfoundland (Ch. IV).

Vernacular Names and Other Terminology

Four languages, Newfoundland-English, Canadian French, Norwegian and Russian have names for some or all age categories of harp seals, based on a long history of hunting. These names are listed in Table 2. The Greenlandic names are *Atak* for the adult pelage and species generally, and *Agdlagtok* for the immature; equivalent Danish names in Greenland are *Sortside* (Svartside) and *Blaaside* (Jensen 1928). The eastern Canadian Inuit (Eskimos) call the species *Qairulik* (A.W. Mansfield, pers. comm.) and the Icelanders call it *Vofuselur* (Saemundsson 1939).

Apart from seal names, one set of geographic terms not found in atlases is rooted in sealing usage. *Gulf* and *Front* are terms for the two ice-coasts of Newfoundland separated by the near land-barrier at the Strait of Belle

TABLE 1. Percent of bones of each seal species at the Norse settlements in Greenland (means of several farms) from McGovern (1985).

Norse — Nearest Modern Settlement(s)	Seals				
	Harp	Hooded	Harbour	Ringed	Bearded
Western (= northern; Godthaab)	61	0	30	1	7
Eastern (= southern; Julianehaab, Narssaq)	64	23	7	2	4

MAP ILLUSTRATING NAFO'S CONVENTION AREA AND 200-MILE FISHING ZONE BOUNDARIES

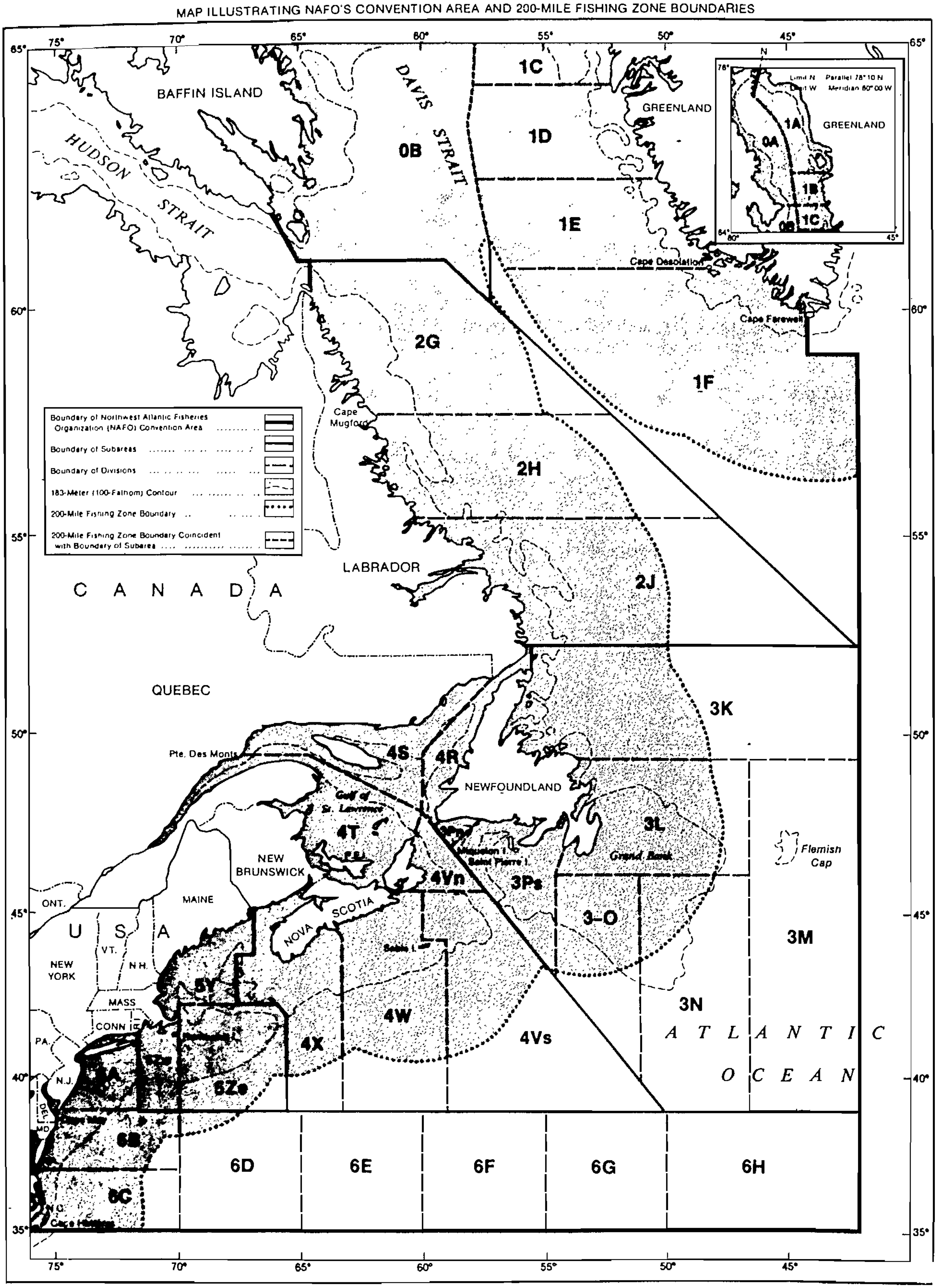


FIG. 7. NAFO (formerly ICNAF) fishing areas.

TABLE 2. Vernacular names of harp seals *Pagophilus groenlandicus)* and their age categories.

Age category	English	Canadian French	Norwegian	Russian
Species	Harp seal	Loup-marin de glace Phoque du Groenland	Grønlandssel	Lysun, Kosha
Fast-furred young	Fast-haired whitecoat	Blanchon	Hårfast Hvitunge	Zhelenets = yellow young
Loose-furred young	Loose-haired whitecoat		Ikke hårfast Hvitunge	Belek = whitecoat
Moulting young	Ragged-jacket		Lurv	Khokhlusha
Moulted young	Beater	Brasseur	Gråunge	Serka
One-year immature	Rusty (bedlamer)		Brunsel	Serun
Immature	Bedlamer	Tacheté	Gråsel	Konzhuya
Adult	Old Seal - old dog (male) - bitch (female)	Coeur	Gammelsel	Krylan (male) Utelga (female)
Melanistic adult male	Smutty harp			Ogar'

Isle. The *Gulf* (of St. Lawrence) has strict geographic boundaries and equates with NAFO (formerly ICNAF[1]) fishing areas 4R to 4T (Fig. 7). The *Front* is limited seaward and southward by the varying ice border and roughly equates with ICNAF subareas 2J and 3K. It can be defined as the ice mass, lying seaward of the coast of southern Labrador and northeast Newfoundland from January to April or May. The terms were used by the sealing industry and are convenient because of their brevity. Other Newfoundland sealers' terms used here are the verb to *be jammed*, of a sealing ship caught in tight ice; *running* ice caught in a current, and *slob* ice, equivalent to the *slush* ice of international usage (See Armstrong et al. 1973). *Fast* refers to seal fur attached firmly to the skin as compared with *loose*.

[1] The International Commission for the Northwest Atlantic Fisheries gave place to the Northwest Atlantic Fisheries Organisation in 1979.

Chapter II. Physiology and Behaviour

Summary

Harp seals have a keen sense of smell, an excellent tactile sense with the vibrissae, and see clearly underwater, though probably less clearly in air. They produce a large variety of underwater sounds during the whelping season. They swim with either dorsal or ventral side upward at considerable speed and as they grow become capable of diving to increasing depths, probably to 200–250 m. Heat loss is controlled very briefly by the foetal coat in the newborn young after which the blubber layer takes over, heat exchange taking place through the thinly-furred skin of the fore and hind limbs. Fat thickness increases to a maximum in winter, decreasing rapidly in females during lactation, and steadily in all animals during April (the season of moult) with a slow recovery during the summer. Harp seals are social animals at all ages except the first year and group size increases towards adulthood.

Senses and Locomotion

Because its ethmoturbinals are large and complex, and because of the activity of its nostrils, one can easily believe that the harp seal has a keen sense of smell. The role of this sense in recognition of the pup by the mother is discussed on page 76.

Since the males of harp seals, like those of ringed seals *Phoca hispida,* have a strong smell as detected by human beings when the animals are hauled out on ice in spring (March–April), there is probably an advertising function of the secretion, warning adolescent males away from the adults at whelping season. The secretion comes from sebaceous glands to the side of and below the eyes (Dr. T.G. Smith, pers. comm.).

In common with other Phocidae the harp seal has large eyes. Walls (1963) showed how these function. Under water the pupil is large, allowing the faint light of deep water to reach the sensitive retina. The harp seal has rod photoreceptors only and so probably lacks colour vision. A large reflecting tapetum probably increases the sensitivity to light (Nagy and Ronald 1970). The shape of the cornea, which would make the animal short-sighted in air, gives a good acuity underwater, without the necessity for accommodation by the lens. In air, the pupil contracts to a horizontal slit, reducing the myopia that would otherwise develop and reducing the amount of light let through. Seals possess no nasolacrymal duct, and therefore weep continuously in air; the secretion is oily and bathes the corneal surface. The effect of this to man in a young whitecoat is to increase its pitiable appeal.

On ice the harp seal progresses between a man's walking and running speeds by means of an action typical of phocid seals. The weight is transferred alternately to the sternum and the pelvis, the animal "humping" like a caterpillar (Harrison and King 1965, and Fig. 60). The claws of the fore-flippers dig in to give an extra pull, and

FIG. 8. Tracks of harp seals on an ice floe.

the track of the seal on the ice is marked by the paired claw-marks on either side of the imprint of the body (Fig. 8).

In water the animal swims swiftly by means of strong lateral oscillations of its hindflippers placed palm to palm, assisted by a lateral body movement (Howell 1930). Since the seal's eyes are set high on its head it can see more underwater by swimming on its back, and living under zero gravity, it swims either way up without giving much importance to the question. Its upward-placed eyes, however, allow warning of danger on the ice when it emerges, and when it is basking.

Without a range-finder I have not been able to measure the swimming speed of groups and herds of harp seals disturbed by a ship as they dive below loose ice floes and re-emerge in a wide lead. However, I once estimated that they covered 100 yards in 10 seconds, or ca. 20 m.p.h. (32 km per h). They give the impression of powerful speed and grace, of an animal which is completely at home in the water. A noticeable feature is the way the animals throw their head high into the air as they emerge from swimming (on their back as well as forwards) in order to respire. I speculate that this behaviour may keep their nostrils free of water when they respire in rough seas, although Dr. T.G. Smith thinks it is just the result of their momentum.

Nor do I have accurate times of diving and knowledge of depth of diving. Indirect knowledge of diving depth comes from the nature of food taken, which may include bottom flatfish and diurnally deep-living redfish, *Sebastes marinus* (Ch. IV). This kind of evidence has suggested that adults may be able to dive to some 150 fathoms (280 m) and immatures probably less. Newly independent juveniles are likely quite shallow divers (Sergeant 1973a); on May 11, 1971 two restrained young harp seals two months old, both weighing 18 kg, and each attached to a float with excess line, made dives of from 2 to 3 min and surfacings of 15 to 35 s.

The physiology of diving in seals is quite well known (Harrison and King 1965). The blood volume is very high, proportionately 75% more than that of a man (which partly accounts for the very bloody nature of sealing). Also the muscles have a high content of oxygen-holding myoglobin, which give them a deep red, almost black, colour, especially in older animals. When the animal dives, the heart rate is automatically reduced to a very slow rate by the action of the vagus nerve and sympathetic nervous system on the heart; a sphincter in the posterior vena cava cuts down the rate of blood flow and only the essential organs such as the brain remain supplied with oxygen. The heart-rate rises slowly in the course of dive as a little blood is let through, and when the animal surfaces, the heart rate becomes "normal" and the tissues are again supplied with oxygen.

Many investigators have noted a curious above-surface behaviour of harp seals which simulates the diving behaviour. When a nursing adult female seal is captured, as by a net being thrown around her, she ceases to struggle and goes into a trance-like state which includes a very slow rate of heart-beat. When the net is removed the animal makes off at high speed in the usual way. I noted that the animal only ceases to struggle if the net covers its head including the nose, so that the stimulus for this behaviour may be not unlike the stimulus releasing bradycardia underwater. Pups, when patted on the nose, often go into the same trance-like state.

Life in Cold Water

How does a warm-blooded seal maintain its existence in sea water which has a freezing point of −1.6°C and is a good conductor of heat? Clearly its blubber layer plays an important part in reducing heat loss. However, as shown by Laurence Irving and J.S. Hart (1957) when the seal is submerged, the superficial tissues are cooled to just above the temperature of the water and a gradient of temperature from 0°C to the body temperature of 36–37°C is found in the top 60 mm of body tissue. The arterioles in the skin contract but allow enough blood to pass for the tissues to survive (Harrison and King 1965). Irving and Hart studied the temperate-living harbour seal as well as the harp seal and found greater cold adaptation in the harp seal: immersed in water below 10°C the harbour seal increased its metabolism (to make up for heat loss to the water) but down to 0°C the harp seal did not. The metabolic rate of the harp seal was the lower one. The metabolic rate of all seal species, they found, was quite high, equal in air and in water, and the respiratory quotient showed that fat was metabolized. The seal's hair has slight insulating properties both wet and dry. The temperatures of the web of the flipper fluctuate, being cool when the animal is resting, but warm after heavy exertion. Thus, the flippers dissipate heat, probably by a heat-exchanging system involving blood vessels near the skin which can be opened or closed. This is a very important adaptation for a well-insulated animal which needs to get rid of excessive heat after unusually great energy production. Such a mechanism is found also in the flukes and flippers of whales and porpoises (Scholander and Schevill 1955).

Davydov and Makarova (1965) extended the study of temperature regulation to the young harp seal. Measuring surface temperatures of newborn and older young, they found that the skin temperature was at first high but gradually lowered as the blubber insulation developed. Thus, in a newborn young, the difference between skin and deep (rectal) temperature was only 2–3°C, in a fat whitecoat — 5–9°C, while in a fully moulted "beater" the adult pattern had developed. In air, the temperature of the surface of the beater was only high where the fat was thin — the neck, throat and forehead. If a newborn pup were made to swim in warm water of 15°C, its surface temperatures decreased equally all over the body. If a well-moulted "ragged jacket" were given the same treatment, very little decrease of skin temperature occurred. However, both groups showed a similar fall in skin temperature if immersed in ice water, so that the adult mechanism is not fully developed in the "ragged jacket" stage. These findings do not mean that the young animals, prior to the beater stage (p. 27), cannot enter the water (for we have frequently seen that they do); but they do their rate of heat loss will be higher than that of older animals. One can see that the "beater" stage is the stage at which entry into the water is normal. A consequence of the heat loss through the skin and wetted hair of the newborn animal is that the foetal coat or lanugo is a good insulator only at air temperatures below zero. Thus the newborn whitecoat is easily able to handle snow but rain likely causes mortality through rapid heat loss.

In the southern Gulf, but not on the Front, rain and freezing rain often occur in early March, making the going very slippery in some years on the Gulf ice. It is possible that a slightly higher mortality of newborn animals in the Gulf, as compared with the Front (Ch. VI) may be due to this factor. By contrast the grey seal (*Halichoerus grypus*) whelps on land or ice. Its northern limit lies at the southern limit of whelping of harp seals in the Gulf of St. Lawrence and in the White Sea, where it whelps in January and November, respectively. The young grey seal has a white coat and is often exposed to rain, cold and wind. However this seal is much larger than the harp seal. Its pup is born at a weight of ca. 14.5 kg (Corbet and Southern 1977), and its rate of heat loss is therefore proportionately less.

Hearing and Underwater Sound

Like many Phocid seals, above water the harp seal makes a low moaning or complaining sound which one can hear at the moulting patches, while the newborn young make a very plaintive hunger call pitched at 1 KHz (Terhune and Ronald 1971) with overtones of 12 KHz — between the keys of middle C and A above. Among a multitude of these calls in a seal patch, one can detect individual differences, and it seems very likely that the adult female learns to detect the call of its own offspring. If, as suggested on p. 76, an olfactory bond is set up between mother and young, the olfactory sense could take over the job of recognition at close quarters. Several authors — Fogden (1971) for grey seals and Nazarenko (1970) and Terhune et al. (1979) for harp seals — concur that adult female seals recognize their pups using visual and auditory clues, with olfaction at close quarters.

It has been found both by the team of W.E. Schevill and W. Watkins from Woods Hole Oceanographic Institution, and by K. Ronald, J.M. Terhune and Bertel Møhl working from Guelph University, that harp seals during the whelping season make a great variety of underwater sounds. An isolated harp seal in captivity made faint clicking sounds, i.e. short pulses, with varying harmonic emphasis on a fundamental of 2 KHz and repetition rate up to 130 per second (Schevill et al. 1963). In the restricted conditions of the experiment the clicks made by a variety of seals, Phocidae and Otariidae, were faint and the investigators were sceptical of their use for echo-location. Schevill (1968) remained sceptical until their use for echo-location should be unequivocally proved. Proof would involve experimental demonstration that food could be found or an obstacle avoided in the absence of all sensory clues except hearing, and that the animal should fail to so orient if hearing were blocked. However, Schevill et al. (1963) noted that blind seals of various species in good health are well-known, so that echo-location could not be ruled out.

However, other sensors could be important in Phocid seals, such as the vibrissae. These have a rich innervation and a complex shape, causing them to vibrate when the seal swims, so that "the vibrissae of the ringed seal may be the most important sense organ during diving in the complete darkness under the ice" (Hyvärinen and Katajisto 1984).

Watkins and Schevill (1979) and Møhl et al. (1975) noted that many Phocid seal species become vocal during the reproductive season, the harp seal among them. They found that harp seals in March produce underwater calls at about 1–3 KHz frequency, lasting 0.1–1 s, usually repeated from 2 to 14 times in a short space of time, and detectable by the hydrophone at ranges up to perhaps 30 km. Terhune and Ronald (1986) detected mass calling using a hydrophone at 60 km from the main herd with seals present at intervals along this distance. They believed that the many seals of a whelping patch could attract further seals to join them by the mass sound produced.

Although the frequency of calls might be ascending or descending, they usually increased in amplitude, and ended abruptly. Watkins and Schevill (1979) pointed out that the increasing amplitude over time, abrupt end and regular repetition rate are the reverse of the characteristics of random sounds in the sea, such as a blow of ice on ice, which start abruptly, die out gradually, and are random in occurrence. They are therefore extremely distinctive to our ears, and presumably to those of other seals. Similarity of all calls in a sequence, and difference from those in another sequence, would allow much variation to be detected between calling individuals. Terhune and Ronald (1986) stressed the importance of the repetition rate, and thought that individual calls might be detected by other seals up to ca. 2 km.

William Curtsinger and Bora Merdsoy were the first diver-photographer naturalists to brave the cold water and the considerable hazard of moving ice floes to study the behaviour of the herds in the reproductive season both above and below water (Merdsoy et al. 1978). While the adult females are on the ice suckling, and approaching oestrus, males are usually in the water (and often on the ice) in groups. These observers found that the adult males threatened each other underwater and vocalized, issuing streams of bubbles as they did so. These are doubtless the vocalizations analysed by the acousticians. The males also threatened by pawing with their foreflippers, as had been observed by Bertel Møhl with an animal in captivity (Møhl, et al. 1975). A male seal once threatened the divers, arching his back in an agressive display. Displaying males usually swam on their backs at the surface with eyes underwater, able to observe other males in the water. Streams of bubbles from 30 m or more depth indicated the presence of other males in a three-dimensional water world under the ice.

A male, or occasionally a group of males, were seen to approach a female with a pup, and attempt to copulate, usually being driven away by an aggressive display of the female. But copulation was once seen on the ice. On another occasion the pair, after some biting and skirmishing on the ice, entered the water together. In the water the disturbance created by a mob of other males often caused the male to leave the female and return their aggression; however, once, a pair were seen to pass to a remote underwater ice pinnacle where copulation apparently took place. Thus, copulation occurs indifferently on ice or in the water: on ice, chiefly when the leads are closed up by action of wind or currents.

Harp seals must be loosely polygynous; it would be impossible to hold a fixed position long in a pack-ice world where leads constantly form and close between the floes. Dominance by large, experienced males must occur.

The Moult

Hair seals moult their skin and hair once a year. Change in pelage colour (p. 28 – 29) can occur after each moult.

Harrison and King (1965, p. 127) describe the moult of Phocidae as characterized by an increase in vascularity of the skin and in the functioning of the sweat glands followed by the development of new hairs. The upper layer of skin develops a stratum granulosum (which is normally absent in hair seals) and the resulting cornified cells (stratum corneum) are shed in patches which carry away the old hairs.

A special study of the moult in harp seals seems not to have been made. On 15 and 16 April 1953, I noted advanced moult in a number of seals of all ages shot at the icefields on the Front. The moult was most noticeable around the face, in the axillae and flanks and the midline of the back. Several old males had raw patches of skin with cracks where bending occurred, as at the neck. These were later interpreted as wounds due to fighting in the preceding mating season. On 17 April 1966, in the northern Gulf, the moult stage attained was highly variable in all age groups, from fast-haired to advanced moult, most commonly being in an early stage with the skin peeling. On 28 April 1968, at the Front, we noticed no rawness and cracking of the skin although the moult was in progess in many animals. It was either in an earlier stage or much less intense, but the reasons for the very marked difference from April 1953 can only be speculative in the absence of much more thorough study. The ecology of animals in moult is discussed on pages 43–44.

Fatness

Blubber thickness may be measured directly or a condition factor, defined as girth/length × 100, determined. The latter is a measure of variation in blubber thickness, if most fat deposition is in the blubber, as is true in seals. In practice we have more measurements of condition factor (Fig. 9) than of fat thickness (Fig. 10) but the two curves are in fair agreement.

Fatness increases during heavy feeding (or feeding on a fat prey, capelin — see Table 27) in late winter, falls during whelping and again during moult, and the animals are still in very lean condition during the summer. They fatten steadily in late summer and by December are fat. In detailed analysis, adult females show a steady fatness from December to late February, which might be expected of animals in late pregnancy, while adult males appear still to be fattening up to late February. The fall in fatness of adult females during lactation is shown dramatically, and is succeeded by a short fattening in early April before the loss due to the moult. This must be due to a short period of feeding, the existence of which we had guessed from the absence of adult females from the moulting patches till late April and was confirmed by adult females with full stomachs taken in nets off northeast Newfoundland during that season. Summer curves appear to be much the same for all segments of the population.

One consequence of the leanness of harp seals during summer is that a high proportion of harp seals shot by Eskimos in the arctic in open water in summer sink; Dr. T.G. Smith collecting in Cumberland Sound in July obtained a figure of about 50% of all shot seals sinking and Riewe and Amsden (1980) 60% for a sample of 61 in Jones Sound. By contrast, fat harp seals shot in the water in winter off the Quebec North Shore invariably float. Some Baffin Island Inuit have developed a technique which reduces the wastage. The animal is shot, if it is still, from a canoe at rest, or if from among a herd of swimming seals, from a canoe moving at speed, but in either case the canoe moves up as fast as possible and the seal is hooked before it can sink.

Social Behaviour

Adult harp seals appear to be social throughout the year except at time of reproduction. Young harp seals

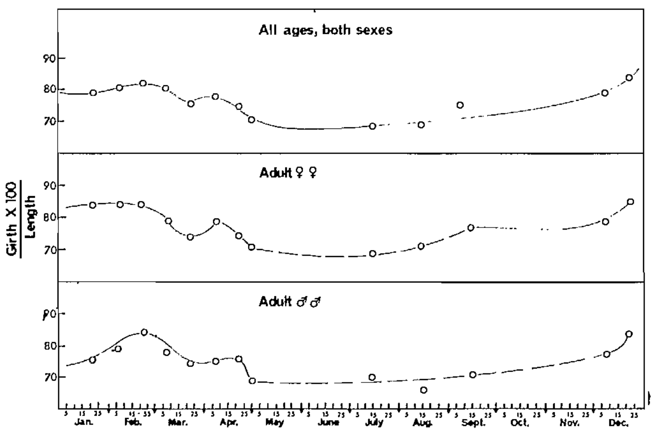


FIG. 9. Variations in condition factor of harp seals through the year (from Sergeant 1973b).

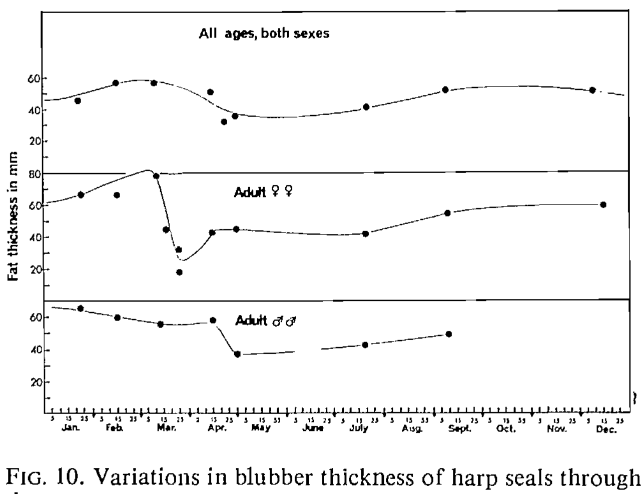


FIG. 10. Variations in blubber thickness of harp seals through the year.

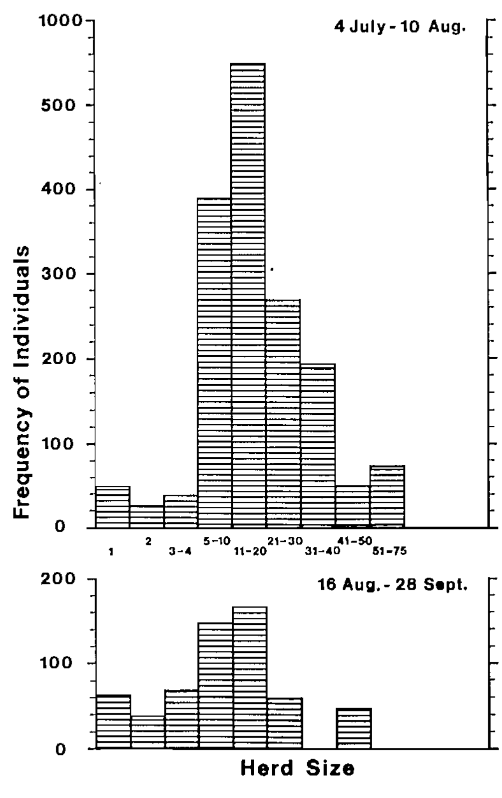


FIG. 11. Distribution of herd sizes of harp seals in Lancaster Sound for two periods in summer 1976 (from Johnson et al. 1976).

begin life as solitary animals (p. 85 - 87) and groupings increase in size towards adulthood when they may reach 15-20 animals (Smith et al. 1979); see p. 52. Sizes of mainly adult groups were studied by Johnson et al. (1976) using aerial surveys in summer in Lancaster Sound (Fig. 11). Group size varied from 1 to 75 animals with most individuals in groups of 5-30 animals. The mean size of groups decreased from about 8 in July-August to 5 in August-September, due to an increase in number of solitary seals, possibly younger animals.

Nothing is known of the duration or structure of these summer groups. When animals are disturbed into leads of water from the moulting concentrations in late April, similar groups, with a size commonly of about 20-30 animals, are seen; groups of the same kind are also observed among wintering animals in the St. Lawrence estuary. There seems no reason, therefore, why groups should not persist throughout the social phase of the life history from April to February. Aggressive behaviour is only detectable between adults at the whelping patches; it is not seen at the moulting groups, and as a result these have a much higher density than the whelping patches of adult females (p. 42).

Further evidence of the increase of sociality with age comes from the age composition of netted catches in the Strait of Belle Isle, representing the autumn migration of the main herds past this region into the Gulf of St. Lawrence (Fig. 28). The representation by age increases annually from a few yearlings to a maximum at 4-7 yr, equivalent to the first age of attainment of sexual maturity. This not only indicates an increasing attachment of young seals to the main herds as they attain sexual maturity, but suggests that the hormones initiating sexual maturation and sociality are the same. Yet most younger animals arrive at the wintering areas with little delay (p. 37).

Chapter III. Age, Reproduction and Growth

Summary

Annual layers in the canine teeth, the structure of which is described, allow accurate age determination of harp seals. Both sexes may live over 30 yr. The reproductive cycle is described and the age-specific parameters of reproduction reported. Both sexes mature sexually at between 4 and 8 yr but the median age of maturity is density-dependent. The sexes are nearly equal in numbers in all age-groups. Mating follows whelping in March but implantation of the embryo is delayed to early August so that effectively gestation lasts 7 mo. Adult males rapidly acquire the full black saddle and nose, sometimes passing through a melanistic blotched phase. Adult females retain a spotted pelage for some years before acquiring, first a light grey saddle and nose, and then a similar pelage to the adult male. Adults of both sexes at 7–8 yr of age attain similar mean asymptotic body lengths of about 169 cm or 5 ft and body weights of about 130 kg in winter, 100 kg in spring after fasting. The species therefore shows little sexual dimorphism in body size, sex ratio or longevity and is relatively slow-growing and long lived.

Age Determination

In 1951, R.M. Laws 1952, 1962) discovered that transverse sections of the canine teeth of the elephant seal *Mirounga leonina* showed clear growth layers in the dentine. Independently V.B. Scheffer (1950a) showed that growth layers could be seen on the surface of the cementum of the teeth of fur seals. Sectioning has become the more widely used method for age determination, and layering in either dentine, cement or both tissues is usually clear in Phocidae. The canine tooth, being single-rooted and larger than the incisors, shows the structures in greatest scale. If the canine is short and dentine is the tissue exhibiting clear layering, transverse sections are generally adequate and can be cut by relatively simple machines (Fig. 12). However, there are now available diamond saws with water cooling which allow the precise cutting of thin longitudinal sections, useful for examining cementum, often laid down at the base of the root of the teeth, as in grey seals *Halichoerus grypus*.

The canine tooth of a harp seal at birth consists of a hollow cone formed by a thin enamel covering a shell of dentine. The tooth grows inward and downward throughout life by adition of concentric cones of dentine deposited from the pulp cavity, and thin shells of cementum laid over the surface of the root by cementoblasts. The cementum layers are too thin to be useful for age determination in harp seals. The pulp cavity however remains open until old age, so that layers of dentine are laid down for many years. By collecting teeth at different times of year, and by collecting teeth from animals tagged when young, often after several years, it is possible to determine that the layering is annual and that certain zones or parts of the annual layering are laid down at certain seasons (Bowen et al. 1983).

In many but not all harp seals, a striking vacuolated zone is laid down in April about the time of the moult; if present, this forms the best marker for counting annual layers (Fig. 13). The rest of the layering is of two types: opaque dentine material, found to be laid down in the migration northward in May–June, and clear dentine, laid down during the remainder of the year from July to March (Bowen et al. 1983). The significance of the difference in structure has not been clearly elucidated, but it may well be, as the Soviet worker G.A. Klevezal' maintains (Klevezal' and Kleinenberg 1967), that the clear material is better calcified. Certainly this entire period is the one in which feeding shows the least interruption

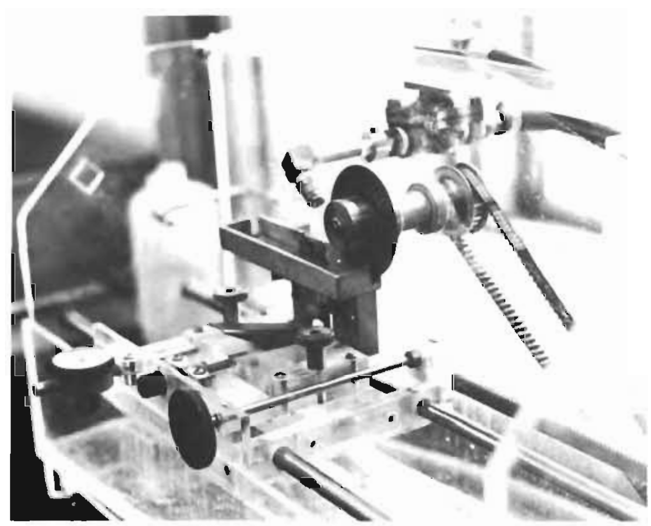


FIG. 12. A machine used for cutting transverse sections of harp seal teeth at the Arctic Biological Station, Ste-Anne-de-Bellevue (courtesy Mr. Bote Bruinsma).

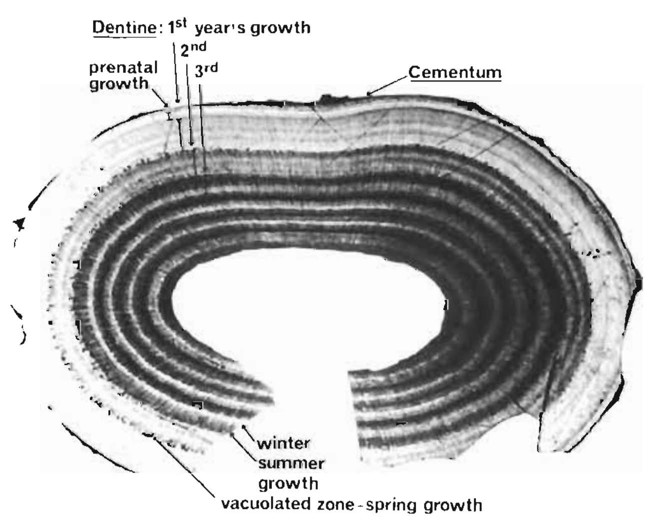


FIG. 13. A harp seal tooth in thin transverse section showing growth zones and annual layers.

(Ch. V). At any rate, the structure allows very rapid age determination of a harp seal from which one canine tooth has been collected. Given an accurate age, the time relations of maturation, pelage changes and so on can easily be determined for any animal. Also the technique finds important application to population studies (Ch. VIII).

Two representative age frequencies obtained by this method are shown in Fig. 28. The maximal age attained by a harp seal may exceed 30 yr, but many teeth cannot be aged beyond 15 or 20 yr, due to irregularities in the later layers which are very narrowly separated. It is possible also to exaggerate the greatest ages, since there is no longer a seasonal pattern discernible in the later layers, and consequently no means to decide whether an annulus represents an entire year, or less. So far, known age teeth, from tagged animals, are available up to an age of 10 yr.

Reproduction

The reproductive development and the reproductive rate through the year have been studied thoroughly by Dr. H.D. Fisher (1954) from whom I quote freely, adding original data.

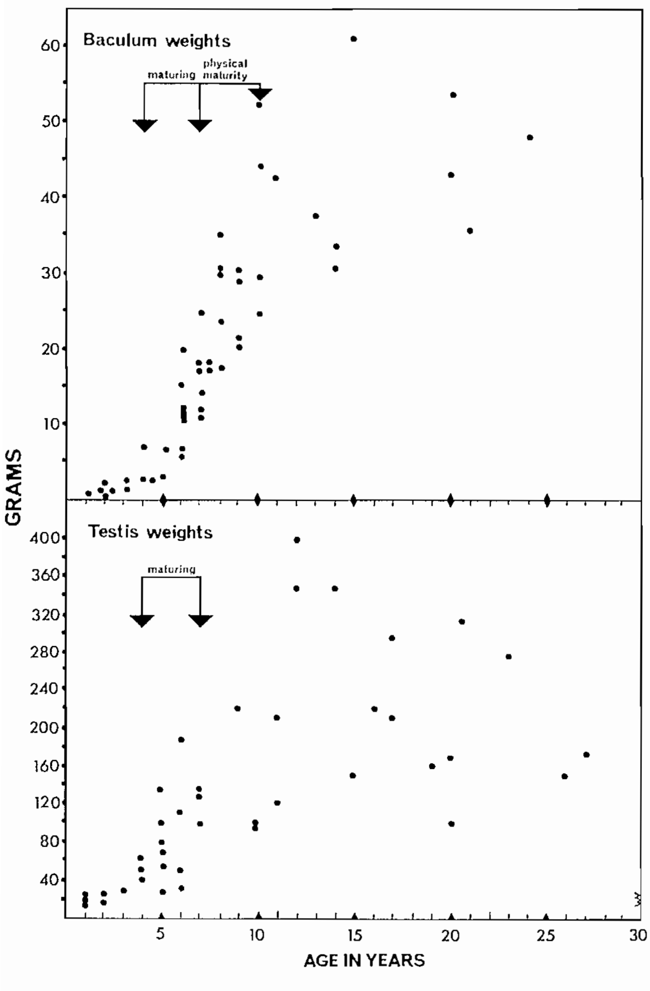


FIG. 14. Growth in weight of testis and baculum of harp seals (original).

By way of introduction, the females whelp over a 2- or 3-wk period in early spring in any one population of harp seals (p. 73–75). They lactate for 10 d following parturition, and then immediately come into oestrus (Ouellette and Ronald 1985) and mate. One month later, adults and immatures carry out their annual moult or change of the hair coat.

The Male

The reproductive state of the male can be determined from the size and histological structure of the testis and from the size of the penis bone or baculum which is peculiar to the Carnivora. Growth of the testis and baculum was measured in relation to age in the northwest Atlantic in 1952–57 (Fig. 14). Interpretation followed from histological studies of testes carried out by Fisher (1954), which showed that males could be classified into three groups. Juveniles aged 1–3 yr showed no testis maturation. Adolescents aged 4–7 yr showed a rapidly growing testis and baculum and some production of spermatozoa, but little sexual activity, as evidenced by small epididymal ducts. Adults aged 8 yr and up showed completion of growth of testis, full sperm production and enlarged epididymal ducts. This age coincided with a testis weight of about 125 g (Table 3). Completion of baculum growth at about age 10 in 1952–57 (Fig. 14) probably indicated the age of physical maturity, when body growth ceased.

However, Yakovenko and Nazarenko (1967) studying the White Sea herd in the period 1958–64 showed a significantly earlier age of sexual maturation in the male (Table 3). They found fully developed testes with sperm in the epididymis in the great majority of 4-yr-old males, and all older males. A comparable state was reached with Newfoundland animals in 1952–57 no earlier than 7 yr. Evidently the "adolescent" group found in our area was not present in the White Sea. Since the Newfoundland population in 1952–57 was large while that of the White Sea was heavily reduced, one may conclude that maturation may be delayed in male harp seals by high stock densities. We will see this phenomenon also in females (p. 19–20). Our data for males in the northwest Atlantic at later dates are based on poorly fixed testes and are probably not adequate for further comparison. Ni et al. (1987) using critical criteria, especially histology of testis and epididymis, found a mean age at sexual maturity in the mid-1980's of 4.4 ± 0.7 yr, about the same as for females in the same years (p. 119).

The males come into breeding condition well ahead of the actual mating season, which at the Front takes place between about March 20 and the beginning of April. Indeed, if one moves about among the females of a whelping patch in early March, one becomes aware of groups of males, perhaps 20 or more, lying on the edge of the leads of water. They can be recognized not only by their uniform black saddles and noses but by a strong, rank odour which the females show much less noticeably. The males, according to Fisher, go out of season very quickly after the end of March, which may be an important factor controlling the regularity of the whelping season. Mating behaviour was described on p. 13.

TABLE 3. Testis weight in grams, indicating age at reproductive maturity, of male harp seals from the Northwest Atlantic and White Sea. White Sea data from Yakovenko and Nazarenko (1967). Both sets of data from March and April.

Age (yr)	Northwest Atlantic 1952–57			White Sea 1958–64		
	N	Range	Mean	*N*	Range	Mean
1	3	10–20	15	5	9.0–18.2	14.2
2	2	15–25	20	6	16.0–24.3	20.3
3	1	30	30	14	16.0–96.0	42.5
4	3	40–60	50	17	78.0–220.0	137.5
5	6	30–140	80	14	82.0–220.0	157.5
6	3	30–190	90	5	132.0–216.0	164.6
7	3	100–135	120		(No Data Cited for Older Ages)	
8		No Data				
9						
10	5	100–225	158.5			
11						

The Female

Most important in studying the reproductive development and cycle of the females are the ovaries. In mammals the ovaries are small rounded bodies lying in sacs, the *bursae fabricii*, at the head of the oviducts. The oviducts unite to form the *uterus*. An egg cell or *ovum* is formed in a jelly-filled *Graafian follicle* which after discharge of the egg cell develops into a *corpus luteum* or yellow body which has important functions in maintaining pregnancy. If the egg is shed and not fertilised, a rather small corpus luteum (*c.l. of ovulation*) is formed which does not persist long (Fig. 15a). If fertilization occurs the corpus luteum grows larger and remains throughout pregnancy (Fig. 15b). Immediately after birth it begins to be resorbed. The yellow-brown luteal cells are then replaced by fibrous tisue and fibrous blood vessels and it shrinks in size to become a small, star-shaped corpus albicans or white body, (Fig. 15c). In harp seals, the *corpus albicans* resulting from pregnancy persists for about 3 yr. Since an adult female seal mates and is fertilised a few weeks after its last pregnancy has ended, in April it usually shows a new corpus luteum, perhaps not fully formed, as well as the still quite large and little-changed corpus albicans of the last pregnancy (Fig. 15c), and smaller scars from previous years' pregnancies. One can, in fact, tell quite a lot about the present reproductive state and past reproductive history of the female by examining the ovaries.

A young immature female seal shows small ovaries with very small follicles. As it approaches sexual maturity the follicles enlarge, particularly during the reproductive season (Fig. 15b). As early as January, immature females of about 2–5 yr of age may show this feature. The older of these seals will become mature and be fecundated for the first time in the coming spring.

The new corpus luteum starts to form after mating in March and by the second half of April becomes filled with luteal tissue, though it has not yet reached maximal size. It doubles in size by the following January.

If the reproductive tract of a pregnant female is examined during the spring and early summer, no embryo can be detected, though careful study may show a very small, flattened disc located about halfway down the oviduct — the unimplanted blastocyst — which is the embryo in an early stage of development. Harp seals, like many other seal species and some other Carnivora, in fact show delayed implantation or embryonic diapause. The length of this period is calculated below (p. 22–23).

A study of the ovaries and corpora lutea in relation to age, first carried out by Fisher, showed that females matured between the ages of 5 and 8 yr, with a peak at 6 yr. I restudied this feature a decade later in both Gulf and Front populations, and separated Fisher's data into the two areas, adding data of my own. I came to the conclusion that the median age of attainment of sexual maturity had shifted downward about a year (Fig. 16). (For 4-yr-old animals, the change was highly significant: $P = 0.012$). I related this change to the decrease of population in the decade between. I also thought that the two populations showed differences, the harder-hunted Front showing the lower age at first maturity. This difference, however, was not significant ($P = 0.126$). Further analysis by Bowen et al. (1981) using a technique of measurement devised by J.P. DeMaster (1978) confirmed that the age of attainment of sexual maturity declined as

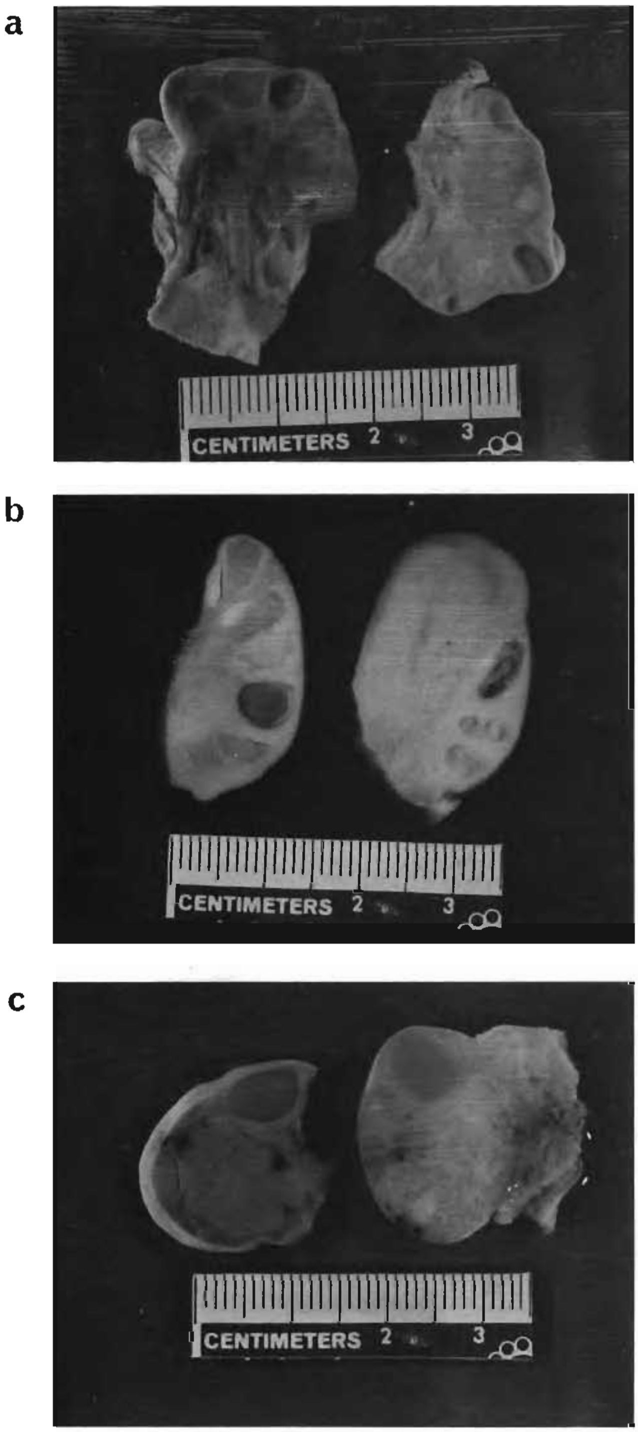


FIG. 15. Slices of ovaries of harp seals showing (a) corpus luteum of ovulation, (b) c.l. of pregnancy, (c) corpus albicans.

the population declined (see below, p. 20). A similar change had been observed in the northern fur seal *Callorhinus ursinus* (Scheffer 1955) and the southern elephant seal *Mirounga leonina* (Carrick and Ingham 1962). The physiological lower limit of maturity may be close to 4 yr for 50% of wild female harp seals, since data from the White Sea collected in 1958–64 by Yakovenko and Nazarenko (1967) agree very closely with those for the Front in 1961–62 (Fig. 16). The White Sea population was heavily exploited up to 1965, and the samples therefore came from the period when the population was at its lowest.

Table 4 shows the maturity status of nearly 1000 female harp seals collected from net fisheries in the northern Gulf of St. Lawrence in January, 1965–69. The age is expressed as the age at the previous reproductive season, in April of the preceding year. The females are classified, on the basis of examination of the ovaries, into four categories. Immatures have follicles only; matures either have a large and functional corpus luteum, are pregnant, and will whelp the following March; or will not whelp in the current season, and either have a regressed corpus luteum (i.e. they have ovulated during the current reproductive season, and have perhaps miscarried), or have one or more corpora albicantia, having been pregnant in previous seasons but not this one. Since the data were collected two months before the date of parturition, few further losses of embryos can be expected.

The analysis shows that the annual percentage of females in 1965–69 which were going to whelp rose to a maximum at age 8 after which it remained at about 90% at subsequent ages. Thus for whatever reason — infertility, loss of embryo, or missing the current season — about 10% of mature females failed to reproduce each year.

Bowen et al. (1981) reanalysed all data on female reproduction up to 1980 and found a change in median age at female sexual maturity from 6.2 yr in 1952 to 4.5 yr in 1979.

They reanalyzed fertility rates for all adult females of age 8 and up and found a steady change from 85 to 94% between 1952 and 1979 as measured in January. Both parameters had therefore changed with decreasing population size and were, presumably, under some form of control by density of animals.

Lett et al. (1981) obtained a similar result but included both moulting animals obtained in early pregnancy (all from the Front) and wintering animals obtained in January in late pregnancy (all from the Gulf) in their samples. They therefore in effect show two curves in their figure, one for the Gulf and one for the Front, both of which show the same trend towards a higher fertility with time; that is a higher fertility as population size is reduced.

The Sex Ratio

Table 5 shows estimated sex ratios for a number of age-groups of harp seals. Juveniles, whether whitecoats or beaters, show a slight excess of males. The figure of 53% males obtained agrees closely with that obtained for the White Sea by Sivertsen (1941).

Samples of older animals are less satisfactory because of the risk of segregation. Samples taken at the icefields from moulting animals are known to be deficient in females up to about 25 April (Sergeant 1965); therefore only samples after this date are used. These show a slight excess of males, but there is always the possibility that a few females have still not joined the groups.

Large samples of wintering animals from the St. Lawrence estuary show considerable variability in sex ratio from month to month and year to year (Table 6).

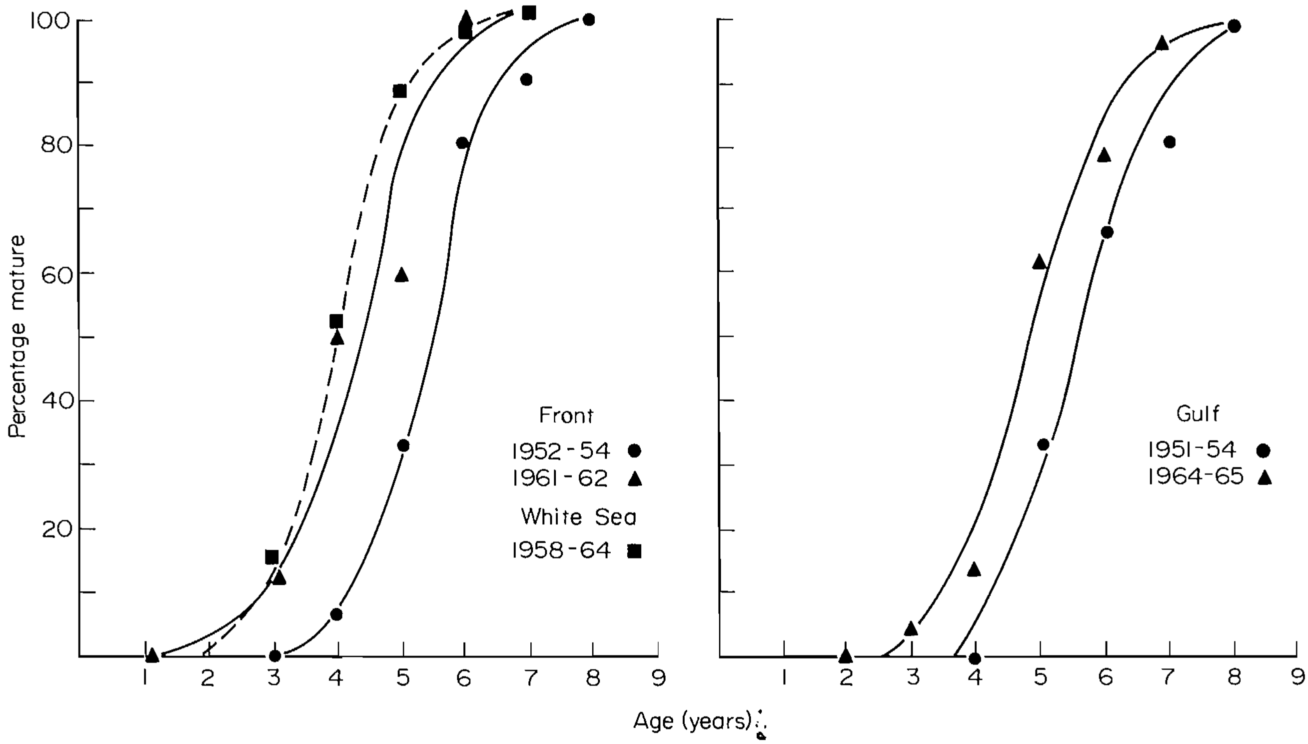


FIG. 16. Age-specific maturity of female harp seals in Gulf and Front regions over time and in White Sea (from Sergeant 1966).

TABLE 4. Maturity status of female harp seals collected in January, 1965–69, on the north shore of the Gulf of St. Lawrence.

Age at previous reproductive season (yr)	Number				Total	Percent pregnant
	Immature	With regressed corpus luteum	With corpus albicans only	Pregnant		
0	25				25	
1	35				35	
2	69				69	
3	77			2	79	2.5
4	74	1		21	96	21.9
5	35	4		65	104	62.5
6	14	1		81	96	84.4
7	7	5		66	78	84.6
8	3		2	51	56	91.1
9	4			50	54	92.6
10	7	5		43	48	89.6
10+	7	12	9	207	235	88.1
Total	350	28	11	586	975	

TABLE 5. Sex ratios of western harp seals.

Years	Dates	Area	Age class (yr)	Number of Males	Number of Females	Percent Males	Observers
1949-73	Mar. 1-17	Gulf, Front	0 (Whitecoat)	560	579	51.9	H.D. Fisher (1954, p. 48); author and colleagues
1965-66	Mar. 29 - Apr. 17	Gulf, Front	0 (Beater)	148	131	52.7	Author, G.R. Williamson
1953-68	Apr. 27-30	Front moulters	1-30	306	262	53.9	H.D. Fisher and author
1969-82	Dec. - Apr.	Gulf winterers	1-30	382	203	65.3	Author
1983-86	Dec. - Apr.	Gulf winterers	1-30	428	400	53.5	Author
1971, 1977	Jan. - Apr.	Front winterers	1-30	136	166	45.0	Author
1981	December	Gulf migrants	1-30	66	80	45.2	Author

TABLE 6. Sex ratio of harp seals in the St. Lawrence Estuary in winter and in spring contrasted.

Year	December to Early March[a]				Late March[b] and April				Out off date[c]
	Male	Female	Total	Female%	Male	Female	Total	Female%	
1969	49	49	98	0.500	14	19	33	0.575	April 21
1971	70	18	88	0.205	9	27	36	0.710	April 14
1978	115	53	168	0.315	38	7	45	0.184	April 24
1983	53	67	120	0.558	4	27	31	0.870	April 9
1984	116	103	219	0.470	28	47	75	0.626	April 2
1985	196	118	314	0.375	—	13	13	100.0	March 29
1986	26	16	42	0.380	—	7	7	100.0	April 5
Overall	625	424	1049	0.404	93	147	240	0.6125	

[a] Latest, March 17.
[b] From March 20.
[c] End of catching.

There is generally an excess of males during early winter months, and a transient excess of adult females in late March, interpreted as a feeding migration after lactation (p. 67-68). A fine-scale heterogeneity in distribution in this area was shown to exist by Sergeant (1973b) based on samples taken over a 30 km width in 1969. These showed that adult females in winter were concentrated in the western part of the area, perhaps due to better feeding conditions. All later samples were taken from the eastern part of the area, which might have led to the excess of males (in both immature and adult portions of the catch). These kinds of variations make estimation of an adult sex ratio difficult. Taking into account other samples of adults — from moulters, southward migrants and other winterers — (Table 5) it seems unlikely that the adult sex ratio has changed far from parity.

Foetal Growth

For studies of delayed implantation and foetal growth, members of the Arctic Biological Station collected a number of uteri of harp seals in Cumberland Sound, Baffin Island in June to August, 1966 and July-August, 1969. We lacked material from late September to December but material from west Greenland in the Copenhagen Museum studied by Erna Mohr (1942) partially filled this gap. Material for early January was purchased from fishermen operating net fisheries on the north shore of Quebec in 1969, and a number of later foetuses came from animals killed in the estuary of the St. Lawrence between January and late February 1969. Crown-rump length in smaller foetuses, nose-tail length in older foetuses, is plotted against time in Fig. 17.

The arctic material shows that foetuses are first observed in about the first week of August, so that implantation has occurred somewhat earlier. Since birth occurs in the first week of March, the main gestation period of the harp seals is approximately 7 mo. Since mating occurs in mid-March, the period of delayed implantation is somewhat less than 4-1/2 mo. Stewart et al. (1989) have made a more detailed analysis of foetal growth for the Northwest Atlantic population.

Growth in Weight

Details of growth of the young seal aged 1–4 wk are given in Ch. VI. What follows applies to older animals.

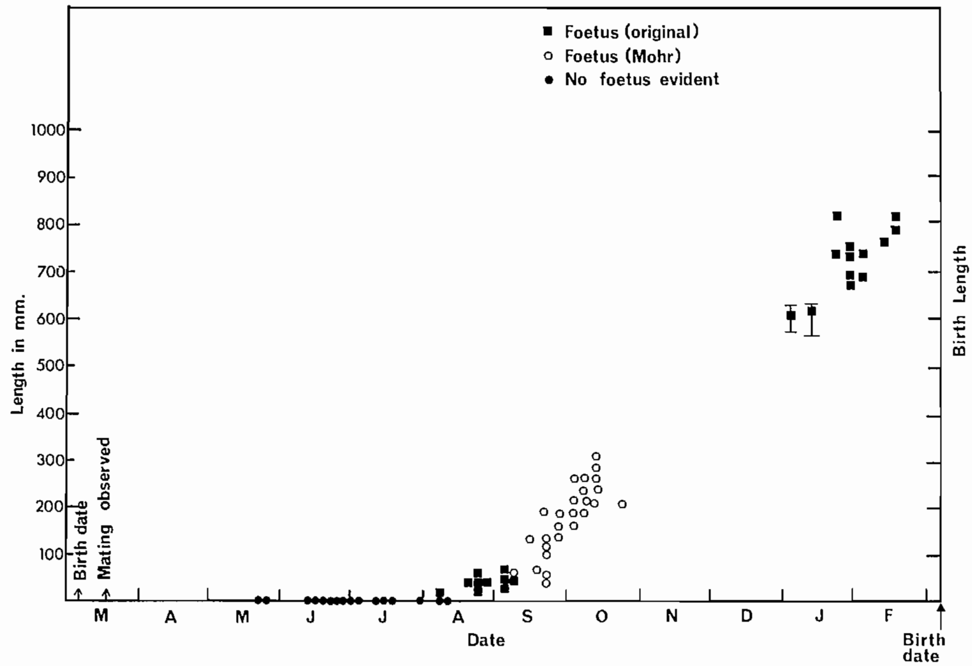


FIG. 17. Foetal growth of harp seals of the western population.

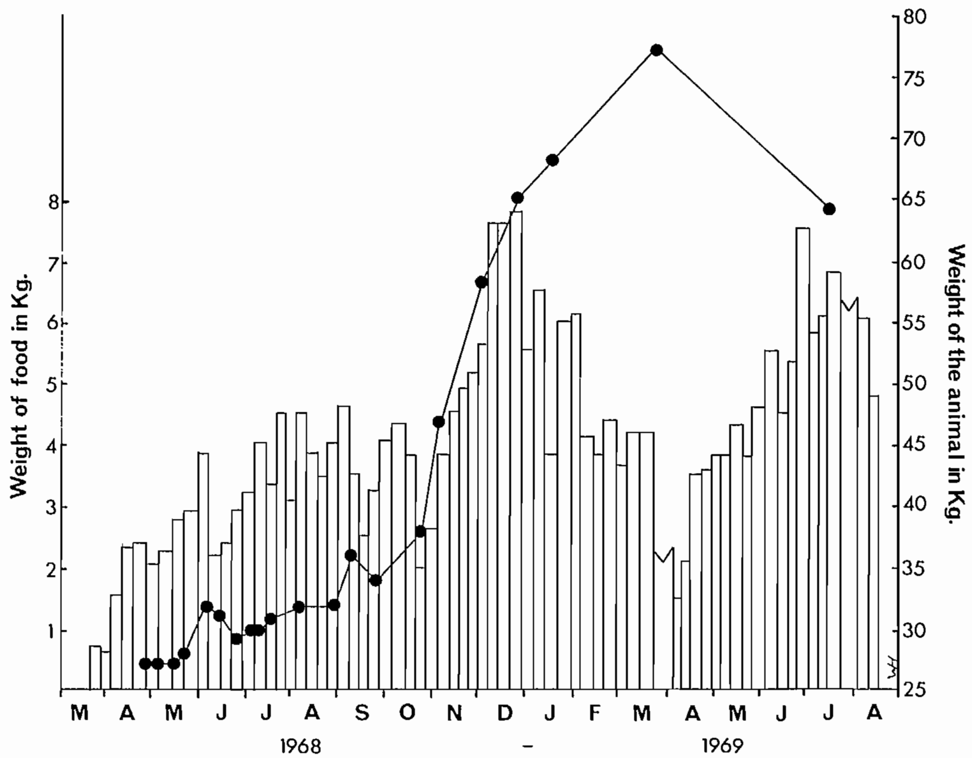


FIG. 18. Weight changes (points) and weight of food ingested (histogram) by one of two young harp seals in captivity (from Geraci 1972).

Dr. J.R. Geraci (1972) reared two young harp seals in captivity for over 1 yr at a surfeited feeding rate (Fig. 18). Starting at weights of 25–35 kg, at 1 yr they attained 75–85 kg. In nature such rapid growth has not been recorded. Ten 1-yr-old animals taken in the estuary of the St. Lawrence in January 1971 ranged from 41–61 kg with a mean of 55 kg (Fig. 19a). Four 2-yr-old animals weighed 56–72 kg with a mean of 68 kg. In Geraci's experiment both animals showed a maximum food intake in the winter months and a minimum in March or April at 1 yr of age. Possibly this alternation represents an innate cycle since it fits well with feeding cycle observed in nature (Ch. IV). However, experimental manipulations such as variation of thiamin fed as a supplement could have affected food intake.

Age-specific weights of older animals come from three sets of weighings: by H.A. Williamson at Nain, Labrador in December 1965, and two by the Arctic Station: in the estuary of the St. Lawrence in January to March 1969 and 1971 and at the Front on a research cruise in late

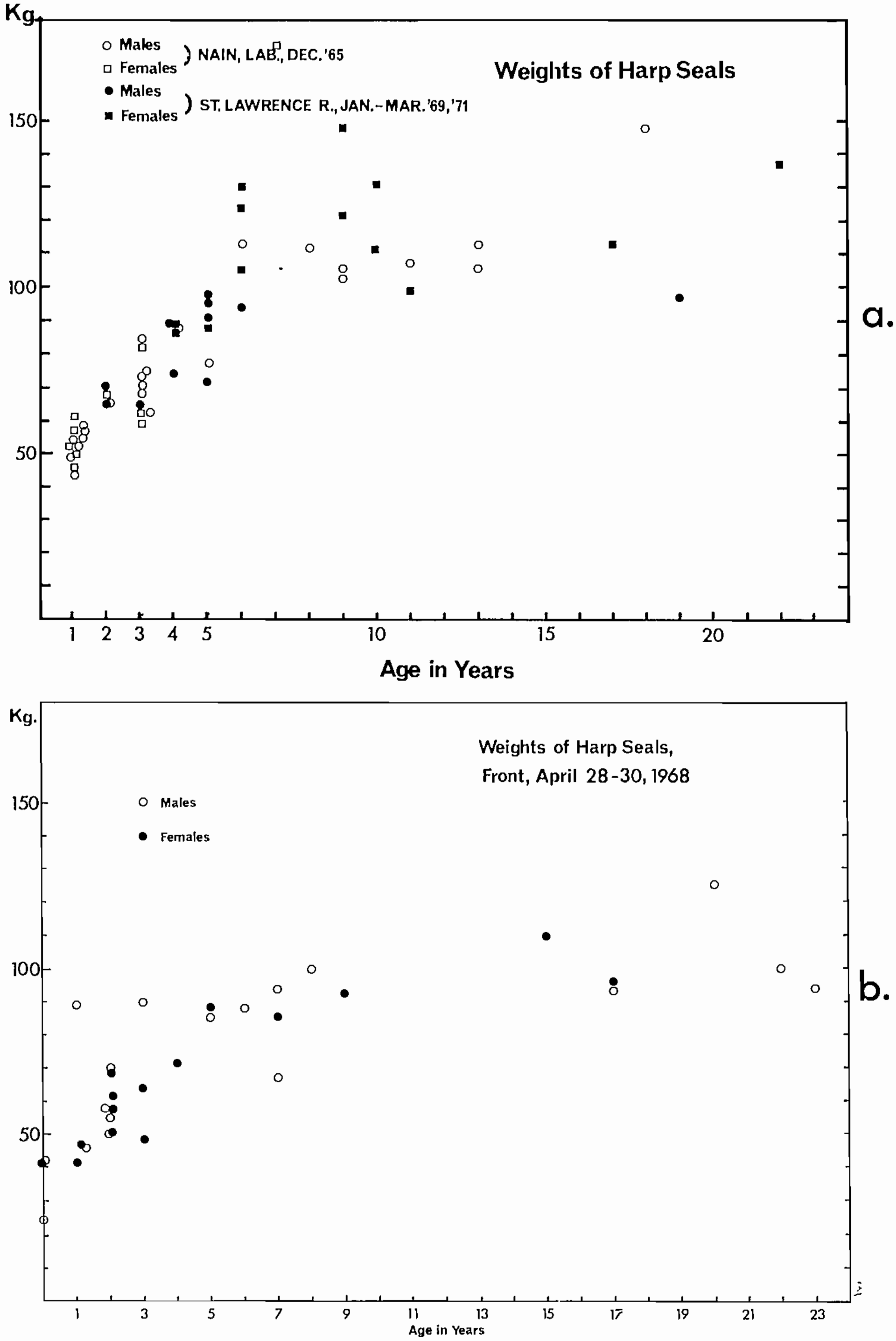


FIG. 19. Weights of harp seals (a) in winter, (b) in spring.

TABLE 7. Mean body lengths of adult moulting harp seals, from Khuzin (1963a) and original (including data of T. Øritsland) during late 1960's.

Locality	N	Male		N	Female	
			Khuzin 1963a[a]			
White Sea	100	184.75	(171.1)	300	183.4	(169.3)
Jan Mayen	142	179.22	(166.0)	137	176.31	(162.8)
Front	83	176.52	(163.5)	127	175.75	(162.3)
			Original			
Front	22	163.5		120	162.3	
Gulf	20	167.1		22	165.6	

[a] Original figures (and scaled down by the ratios of 0.9263 for males, 0.9232 for females, to agree with original data for the Front).

TABLE 8. Condylobasal length of skull of harp seals (in mm) from Khuzin (1963a, 1967) and Yablokov and Sergeant (1963).

	Khuzin 1963a	Yablokov and Sergeant 1963	Khuzin 1967		
			6–8 yr	10–12 yr	16+ yr
			Males		
White Sea	216.9 ± 1.16	214.8 ± 1.15	215.8 ± 1.04	218.0 ± 1.3	221.9 ± 0.88
Jan Mayen	214.8 ± 1.35	215.7 ± 1.07	214.1 ± 1.20	214.1 ± 0.97	219.3 ± 0.87
Newfoundland	208.3 ± 0.83	211.3 ± 1.28	206.0 ± 1.15	211.0 ± 1.31	214.0 ± 0.94
			Females		
White Sea	209.6 ± 1.10	209.3 ± 0.96	208.2 ± 0.81	210.7 ± 1.40	213.5 ± 1.60
Jan Mayen	208.8 ± 0.66	209.3 ± 1.16	205.5 ± 0.69	209.8 ± 0.85	210.0 ± 1.27
Newfoundland	204.5 ± 0.91	204.5 ± 0.71	201.0 ± 1.11	204.0 ± 0.49	206.0 ± 0.79

April 1968. Each set of weighings refers to about 30 animals. Of the three sets, the first and second refer to fat, winter animals and are combined (Fig. 19a), but the April set refers to lean, moulting animals in which it is clear (from reduced fat thickness) that the age-specific weights are lower (Fig. 19b).

For the winter animals the asymptotic weight appears to be about 130 kg and for the spring animals, 100 kg. The data agree with Dorofeev's (1960) findings that adult male pelts lose about 20 kg from late March to early May. Innes et al. (1981) find a mean body weight averaged throughout the year of 118.5 kg.

Growth in Length

Innes et al. (1981) found that length, as a function of age, gave the most precise measure of body size of harp seals. Lean core (body) weight and total body weight were more variable; weight of sculp and blubber thickness exhibited greater variation with age and sampling date. Part of this greater variation of weight, clearly, is due to seasonal variation in fat thickness. These authors had data on length at age for 204 animals from the late 1970's. Best fit was found with a Gompertz curve with the formula: $L(cm) = 169 \exp(-0.497 \exp(-0.432t))$, where t = age in years.

These authors could not detect a sexual difference in any of their measurements of body growth. However, Khuzin (1963a) measuring body length in adult harp seals from all three populations in the early 1960's found that males were consistently larger by amout 2 cm (1.5%) (Table 7).

Khuzin (1963a) found that size decreased in the order: White Sea - Jan Mayen - Front, with the Front being closer in body length to Jan Mayen than Jan Mayen to the White Sea. (Since Khuzin measured body length along the curve of the back rather than in a straight line, I have included in Table 7 conversion factors for both sexes obtained from my own measurements and those of T. Øritsland[2] obtained from the Front in the 1960's.)

[2] Unpublished and kindly given to the author.

Using craniological measurements Khuzin (1963a, 1967) and Yablokov and Sergeant (1963) were in agreement that the size of animals decreased in the direction White Sea - Jan Mayen - Newfoundland (Table 8). Here, however, the difference between males and females is a little larger, about 4%, and the White Sea and Jan Mayen animals are closer together in size than Jan Mayen and Newfoundland animals are. Taken together, the size differences would argue that each population is somewhat isolated from its neighbouring one, but it is difficult to discover the biological meaning of the cline of decrease in size from northeast to southwest. Some of the difference could be phenotypic, since Innes et al. (1981) found that adults of the Newfoundland/Gulf population had increased in size from an asymptotic length of about 161 cm in the 1950's to 169 cm in the 1970's (compare my figure of about 165 cm in the late 1960's in Table 7). Body growth therefore increased as the population declined in size.

Juvenile Pelage and Growth

H.D. Fisher (1954, p. 24) writes:

> "The harp seal is born with the white foetal hair still "fast". The amniotic fluid imparts a yellowish tinge to this coat at birth which fades as the hairs fluff out from the effect of the stretching of the skin caused by the rapid fattening during the suckling period of about two weeks, and possibly with bleaching by melted snow and ice. The white hair begins to loosen by about 10 days after birth, revealing the short spotted pelage, which grows in before the white coat is shed. Pups in the process of shedding the white coat are referred to by sealers as "ragged jackets"."

Stages of growth and moult are shown in Fig. 20a-d.

Chapskii (1964) describes this growth in great detail for young harp seals in the White Sea. A summary of his findings (Fig. 21) indicates changes in body length, total

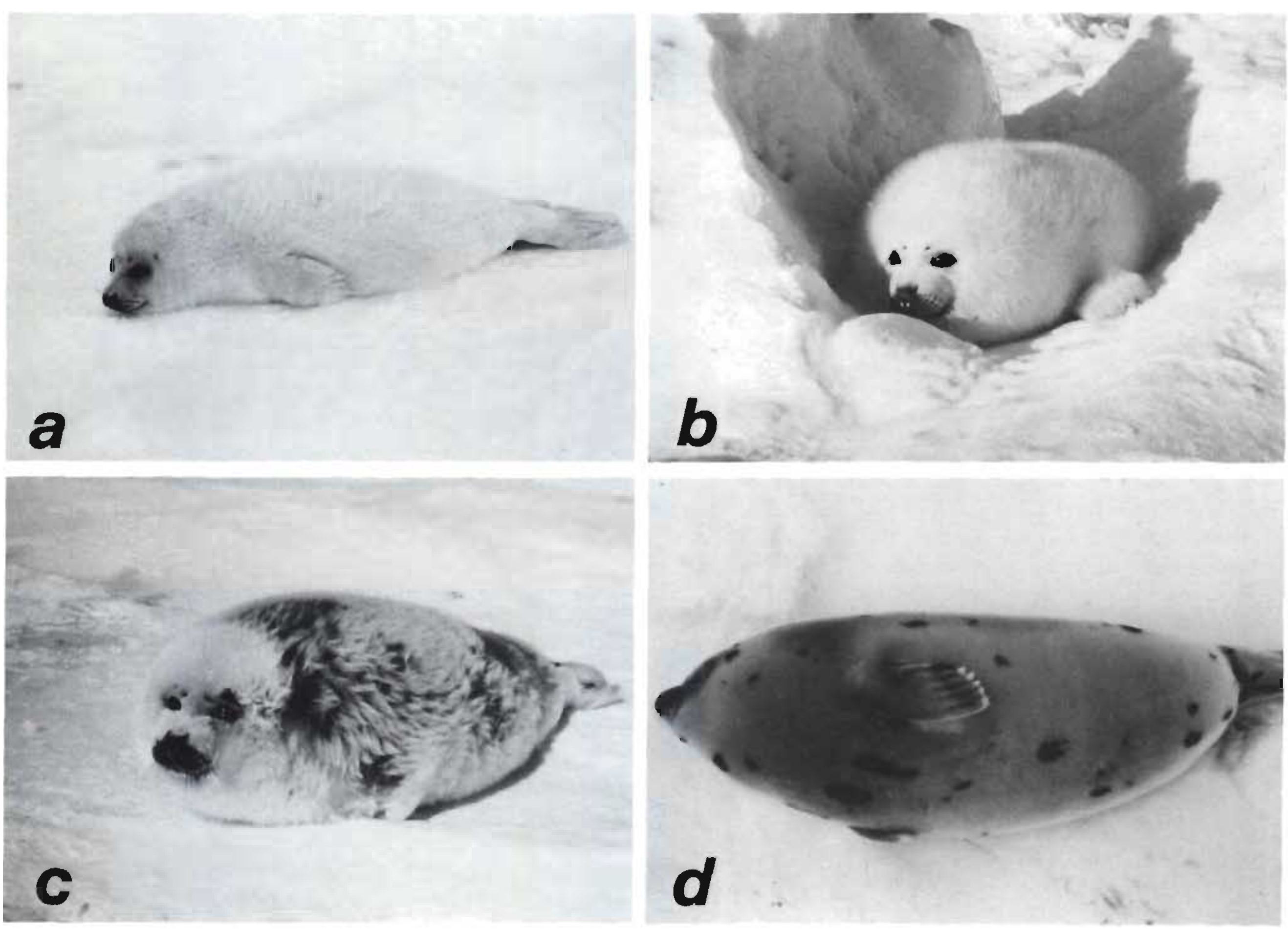


FIG. 20. Stages of growth and moult of juvenile harp seals (a) yellowcoat, (b) fat whitecoat, (c) ragged jacket, (d) beater.

weight and pelt weight (blubber and skin) with time and age, as well as the stages of growth.

There is some disagreement between different authors about the length of each growth period, partly because of the difficulty of defining it. The whitecoat is fast-furred for 5-6 d according to Sivertsen (1941) — who also worked in the White Sea — 10 d according to Chapskii; it is loose-haired for 6-14 d according to Sivertsen and 10-18 d according to Chapskii. The ragged jacket stage lasts from the 18th to the 30th day according to Chapskii. There is better agreement on the end of the moult and onset of "beater" pelage: 28 d according to Sivertsen and 30 d according to Chapskii.

Observations on known-age animals by Stewart and Lavigne (1980) gave the following mean ages in days for each stage, with additional categories:

Category	Approx. age in days	Category	Approx. age in days
Newborn	0	Greycoat	9 or 10
Yellowcoat	1	Ragged Jacket	15
Thin whitecoat	2 or 3	Beater (start)	18
Fat whitecoat	6	Beater (on ice)	30

Myers and Bowen (1989, fig. 3) using resightings of known-age pups and a probability curve of the frequency of each stage by date, obtained the following duration (in days) of the various stages:

Newborn, Yellowcoat	5	Grey coat	7
Thin whitecoat, Fat whitecoat	4	Ragged jacket plus beater	(Up to 30)

These data agree that transition to the ragged jacket stage has occurred at 15-16 d. The beater stage of course persists through the first year of life, till a moult at 13 mo of age.

Stewart and Lavigne (1980) observing births on the ice of the Gulf of St. Lawrence determined that pups weigh 10.8 ± 0.65 kg at birth and grow at a rate of 2.5 kg/d during the intensive part of the nursing period that lasts about 9 d. Lactation then becomes less frequent or ends and the pup increases in weight more slowly to a weight of about 35 kg at 18 d, which must mark final weaning.

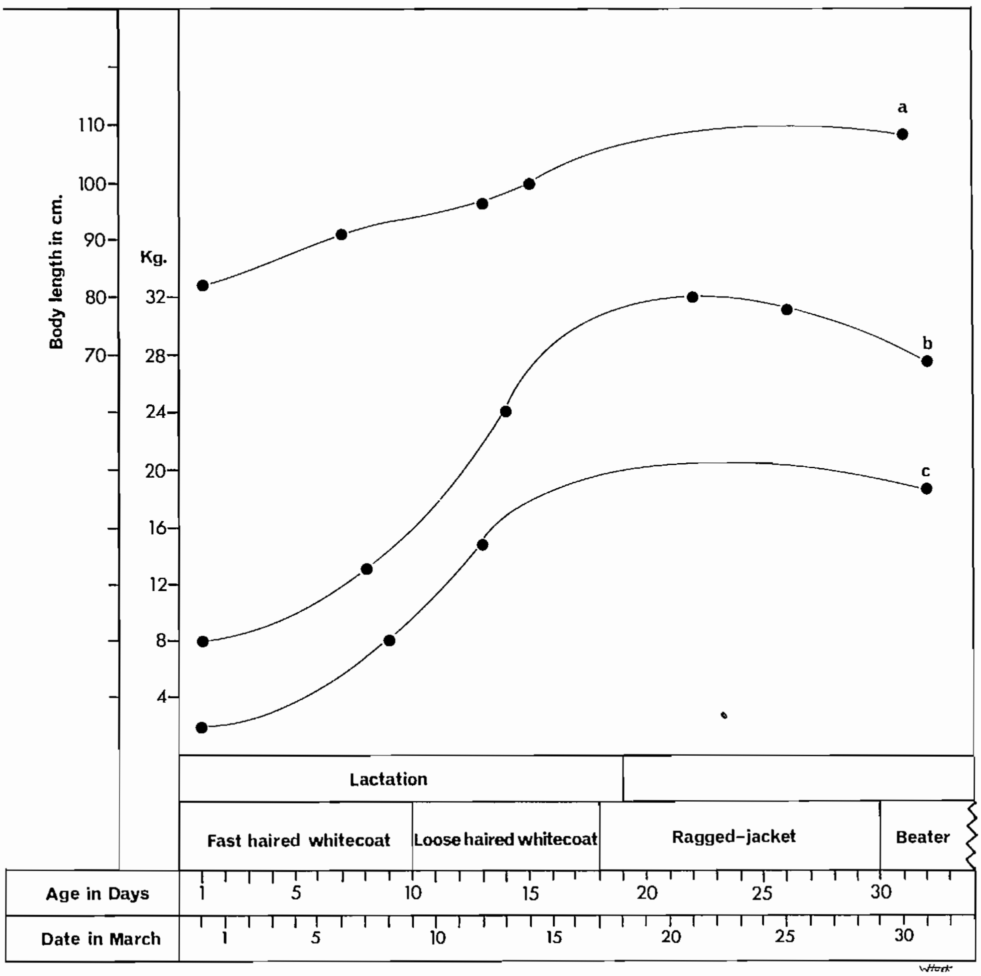


FIG. 21. Growth of juvenile harp seals in the White Sea (after Chapskii 1964). (a) body length; (b) total weight; (c) weight of pelt with blubber fat.

The beater then loses weight steadily, and at an age of about 30 d weighs about 31 kg. At this stage it regularly begins to enter the water and feed independently. Kovacs and Lavigne (1985) give a mean weight at birth of 9.9 $\pm$ 1.7 (1 SD) kg, and a daily weight increment of 2 kg, except for a smaller gain the first day of life, until weaning at ca. 12 d. Further details of pup growth and lactation are given in Ch. VI.

Pelage Pattern

Immature harp seals 1–3 or more years of age have a spotted pelage. When a seal with dry pelage is examined, the spots are normally olive brown, and contrast with the silver background of belly and sides. The back is frequently brownish olive showing less contrast. On 1-yr-old immatures, the spots are frequently rusty brown. As with the beaters, there is a lot of variation in the degree of spotting and the size of the spots. This is typically the pelage of the immatures of both sexes but it persists into the youngest adult stage of females (Fig. 22a). The next older group of adult females have a light nose and saddle (Fig. 22b), but oldest females and all adult males have an identical pattern: a fully developed black saddle and black face markings on a silvery grey background (Fig. 22c). They cannot therefore be distinguished apart in the field in spring, except for a wider head in the male and the male's ranker smell.

The saddle (German) or harp (English) gives the species its name. The Russians liken it to a pair of birds' wings, so three different similes have been employed.

Age Changes in Pelage Type

Studies by H.D. Fisher (1954) on the western populations and by Potelov and Mikhnevich (1967) on the Greenland Sea population are in good agreement (Fig. 23). In males, the change in colour pattern takes place rapidly so that intermediate colour conditions last only 1 or 2 yr. The Soviet workers found spotted males

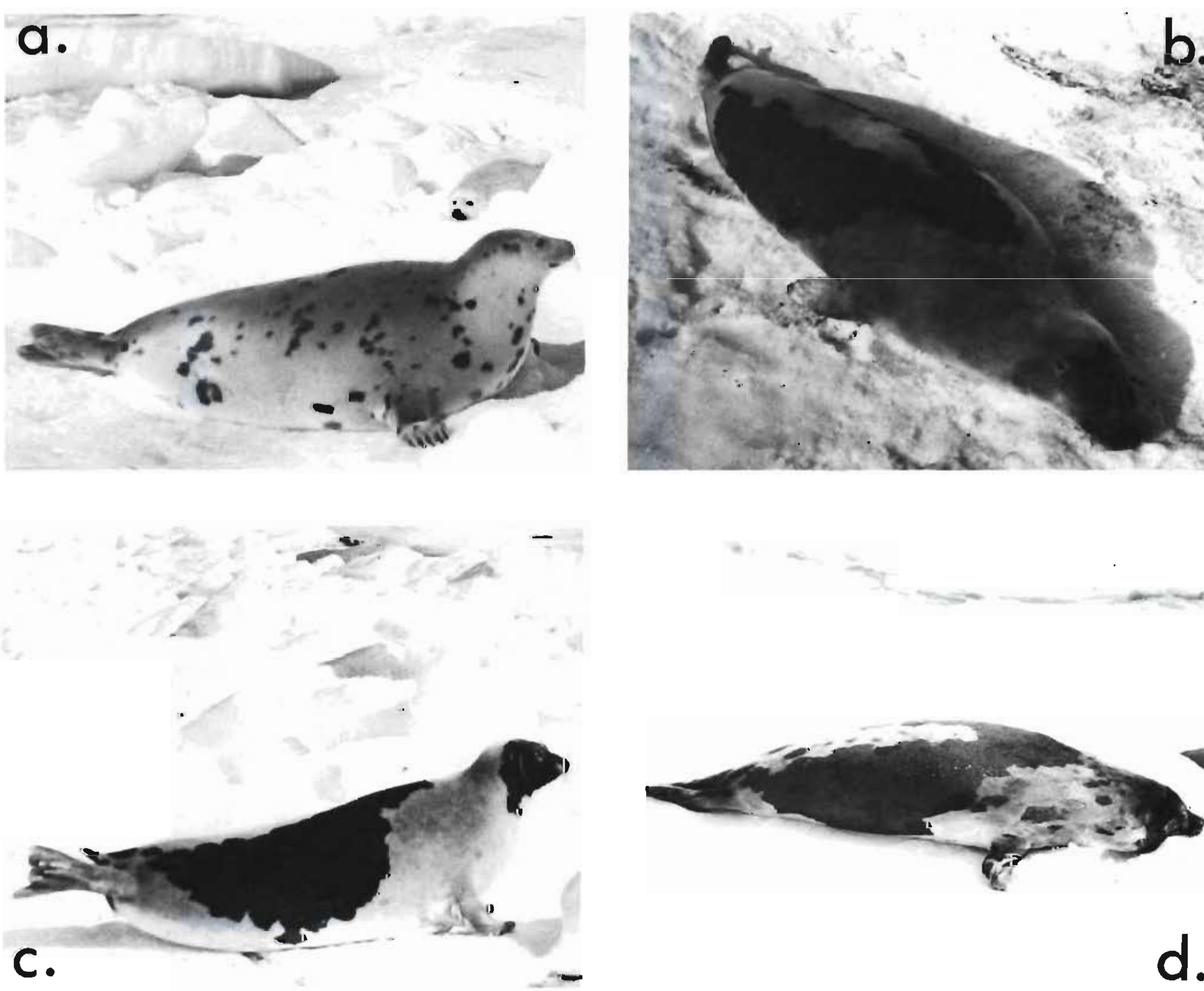


FIG. 22. Pelage of (a) young spotted adult female, (b) older adult female, with light grey nose and saddle, (c) old adult female with black nose and saddle, (d) young adult male, with spotting and dark saddle.

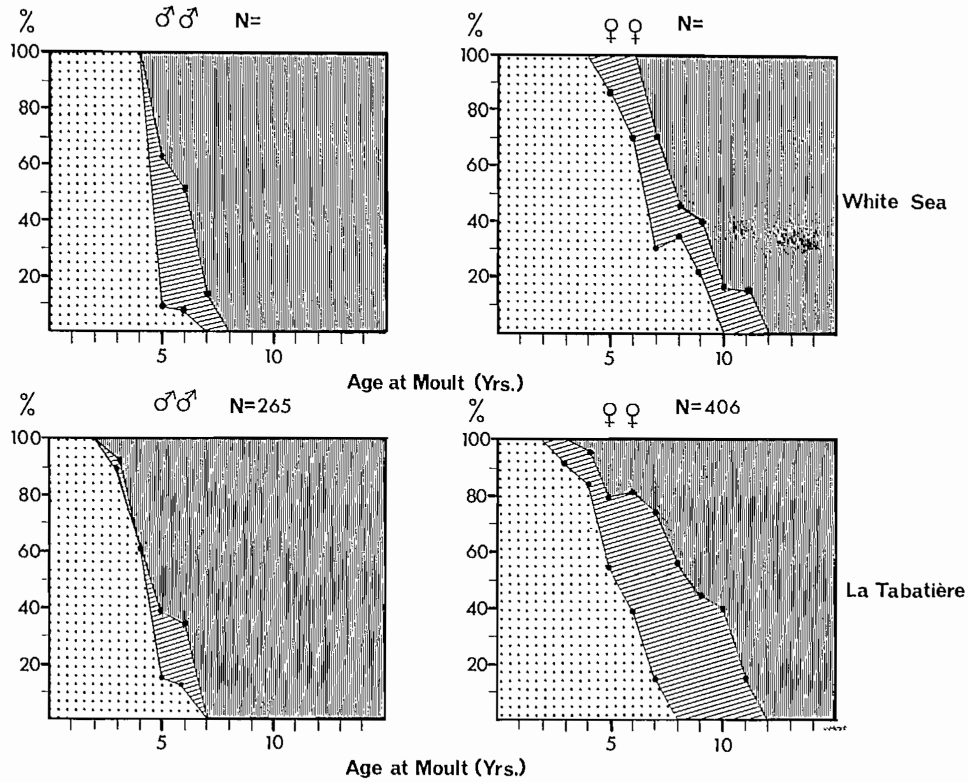


FIG. 23. Changes in colour pattern with age in males *(left)* and females *(right)* in White Sea *(above)* and Newfoundland *(below)*. Data from Potelov and Mikhnevich (1967) and Fisher (1954). Stippled — bedlamer pelage; hatched — light saddle; dark — dark saddle. Percentage reversed for two later categories.

up to an age of 7 yr, and all males had a fully formed saddle from 8 yr old and upward, with intermediate stages occurring between 4 and 7 yr. Chapskii (1967) studied the intermediate stages of the males in detail and recognized three: dark spotted males with indistinct saddles, dark-backed males with saddles, and spotted males with saddles (Fig. 22d). He confirmed that these all occur as intermediate stages in animals aged between 4 and 7 yr and in any one animal probably last less than 3 yr. The melanistic phase is rare enough that it cannot occur in all animals, indeed some animals change directly from the spotted to the fully saddled phase. The intermediate stages coincide in general with the onset of sexual maturity in the male, but in individuals the colour change cannot be directly related to maturity status and its causation is obscure, possibly influenced also by growth hormones.

In females the change to full saddle pattern is much slower and passes through an intermediate stage in which the face mask and the saddle are light grey in colour. Spotted females and females with light saddles are therefore younger than those with dark saddles but their exact age cannot be guessed. By age 11 yr, all have attained dark saddles (Fig. 23)[3]. In agreement with this finding, the number of spotted and light grey females is generally quite low, depending on the age structure of the population. Some percentages are shown in Table 9. For Gulf entrants in January 1965 (row a) the percentage of spotted females was high, in agreement with a high percentage of young adult females in the sample (Fig. 28 lower). However, for whelping females at both the Gulf in 1964 (row b) and the Front in 1962 (row c) the percentage of

TABLE 9. Distribution of pelage pattern in adult female harp seals: a — Gulf entrants, January 1965, females 5 years and up; b — Whelping near Magdalen Islands, March 1964; c — Whelping off Labrador coast, March 1962, from Popov and Timoshenko (1965).

	Spotted		Faint saddle		Dark saddle		
	Number	%	Number	%	Number	%	*N*
a	81	50	38	24	42	26	161
b	56	7	91	12	632	81	779
c	?	13	?	23	?	64	?

[3] Roff and Bowen (1986, fig. 2) showed, from *moulting* samples at the Front in 1981–83, that many female harp seals did not gain dark saddles at all. (They did not attempt to assign ages precisely over 10 yr, due to errors in age determination.) This finding is difficult to relate to the distribution of pelage colours among *whelping* females, shown in Tables 9 and 19. It may be due to (a) a selection towards younger animals, especially of females, in moulting animals in April and (b) age-changes over time in the composition of the herds (also seen in the data of Table 19). The quota in 1972 and thereafter at Newfoundland led to increased survival of younger age-classes, implying an even greater proportional rarity of old females in a moulting sample.

spotted females was low and that of dark-saddled females, high. This was partially due to low recruitment rates caused by high exploitation rates of pups, since comparable samples for 1978–80 show a much higher proportion of spotted females (Table 19). Thus, visual sampling of adult female harp seals by observers at the whelping patches can give a good idea of the general age structure of the population.

Chapter IV. The Harp Seal's Annual Cycle: Distribution and Migrations

Summary

Three stocks of harp seals inhabit the North Atlantic ocean, whelping respectively at Newfoundland, Jan Mayen I., and in the White Sea, near the southern limits of their respective ranges. Of these, the western or Newfoundland stock is more isolated from the other two than they are from each other, as judged from differences in skull form, and cross-over rates of tagged animals. Yet the White Sea and Jan Mayen stocks which mix have whelping seasons 4 wk apart. The Newfoundland stock is itself divided into two substocks, whelping in the Gulf of St. Lawrence (Gulf substock) and east of Labrador and northeast of Newfoundland (Front substock). These two substocks intermingle and are not genetically separable, but generally preserve their ratio of relative numerical size of about 1:2, which is probably set by the relative amount of accessible whelping habitat.

Harp seals whelp on thick first winter ice in spring. Variation in birth date is from late February in the Gulf of St. Lawrence and the White Sea to early March on the Front and late March at Jan Mayen. All three stocks exhibit a constant sequence of events in spring; whelping is followed after 10 d of intensive lactation by mating after which the female deserts the pup. Moulting of adults and immatures takes place, in very much the same locations as whelping, after a further lapse of 4 wk. Adult males and immatures haul out first on the ice to moult, and later the adult females.

Because of the down-current drift of pack ice, harp seals must penetrate the ice for some distance before whelping, utilizing a major longitudinal lead or channel (at Newfoundland) and then smaller leads running transversely into the ice. This is a special migration. After the end of whelping, further up-current migration is required for the animals to find suitable ice for moulting. This movement grades into the northward migration.

Harp seals are found in all seasons close to pack ice. Seasonal migrations are greatest in the western North Atlantic where seasonal changes in ice distribution are greatest. Here, the older the animals, the further they penetrate into arctic waters in summer, so reducing the overlap of age groups.

The effect of climatic change in the 20th century on the distribution of whelping sites of this species has been small. In the west, this is because the Gulf Stream – Labrador Current system is stable. Greatest year-to-year changes are seen in the Gulf of St. Lawrence at the southern margin of the range, where ice in any one season may be thick or almost absent. An effect of 20th century climatic changes on the population of the Barents Sea – White Sea cannot be excluded, but these changes are compounded with those of catch.

Distribution

The harp seal is exclusively a North Atlantic species, where it is easily the most abundant seal. It may well be the second commonest in the world, coming after the crabeater seal *Lobodon carcinophagus* of the Antarctic. The reasons for this abundance are discussed on page 72.

Its general distribution as a seal of the subarctic pack-ice has been well-mapped by Nansen (1925) whose famous illustration is reproduced in Fig. 24. However, since its habitat is the seasonally shifting pack-ice its distribution is a shifting pattern which no single map can illustrate (Chapskii 1961).

The limits of its range are as follows. Rarely, animals may winter along the eastern United States seaboard to the Delaware river, New Jersey (Rhoads 1903, cited by Hall and Kelson (1959)) and Virginia (37°N, Goodwin 1954). Rarely, animals pass through the Canadian arctic archipelago towards the North Pacific at Aklavik (154°W) where one was caught in a fish net in 1924 (R.M. Anderson in Bethune 1934)[4], and Queen Maud Gulf (Anderson 1947). Similar exceptional records no doubt come from the Siberian arctic and King (1964) cites some from western European coasts. Most remarkable of these was a female captured 400 km from the sea on March 5, 1886 in the Mulde river, a tributary of the Elbe; she gave birth to a young animal at Dessau on March 13–14 (Nehring 1896). Nehring thought that this female had been released in the Elbe by a sealing vessel, but the timing seems unlikely, so it may have been a real wanderer.

The foci of distribution are the three whelping areas located around Newfoundland, Jan Mayen I[5] and in the White Sea (see Fig. 24). The degree of isolation of these three whelping populations has been investigated by two complementary methods: the study of skull and body dimensions (Khuzin 1963a; Yablokov and Sergeant 1963) (p. 25–26) and a variety of tagging experiments (Rasmussen and Øritsland 1964; Popov 1971c; Sergeant 1965, 1973c) (p. 62). Agreement of these methods is good. The eastern and central populations show a small degree of cranial differences and some cross-migrations of tagged animals, whereas the western population is the most readily distinguished by means of skull dimensions, and only one cross-movement has yet been demonstrated beyond the southeast coast of Greenland (p. 62). That is to say, isolation is most pronounced east and west of Greenland due to the large land barrier which splits the subarctic region of the North Atlantic.

Large-scale tagging in 1978 at Newfoundland, however, showed that 4/259 or 1.5% of tagged harp seals of the western stock recovered at Greenland passed round Kap Farvel to be taken from settlements in east Greenland between 65° and 67°N, in the summers of 1978 and 1979 (Larsen and Kapel 1979). At the same time, four animals tagged at Jan Mayen by Norwegian investigators in 1978 were recaptured in the same area (see Fig. 25).

[4] Shown in fig. 5 in Doutt (1942).

[5] The ice here is known to Norwegian sealers as the West Ice (*Vestisen*), being on the west side of the Norwegian Sea. It is in fact part of the East Greenland ice, known to the Danes as *Storis* after it passes Kap Farvel westward. We had better stick to Jan Mayen.

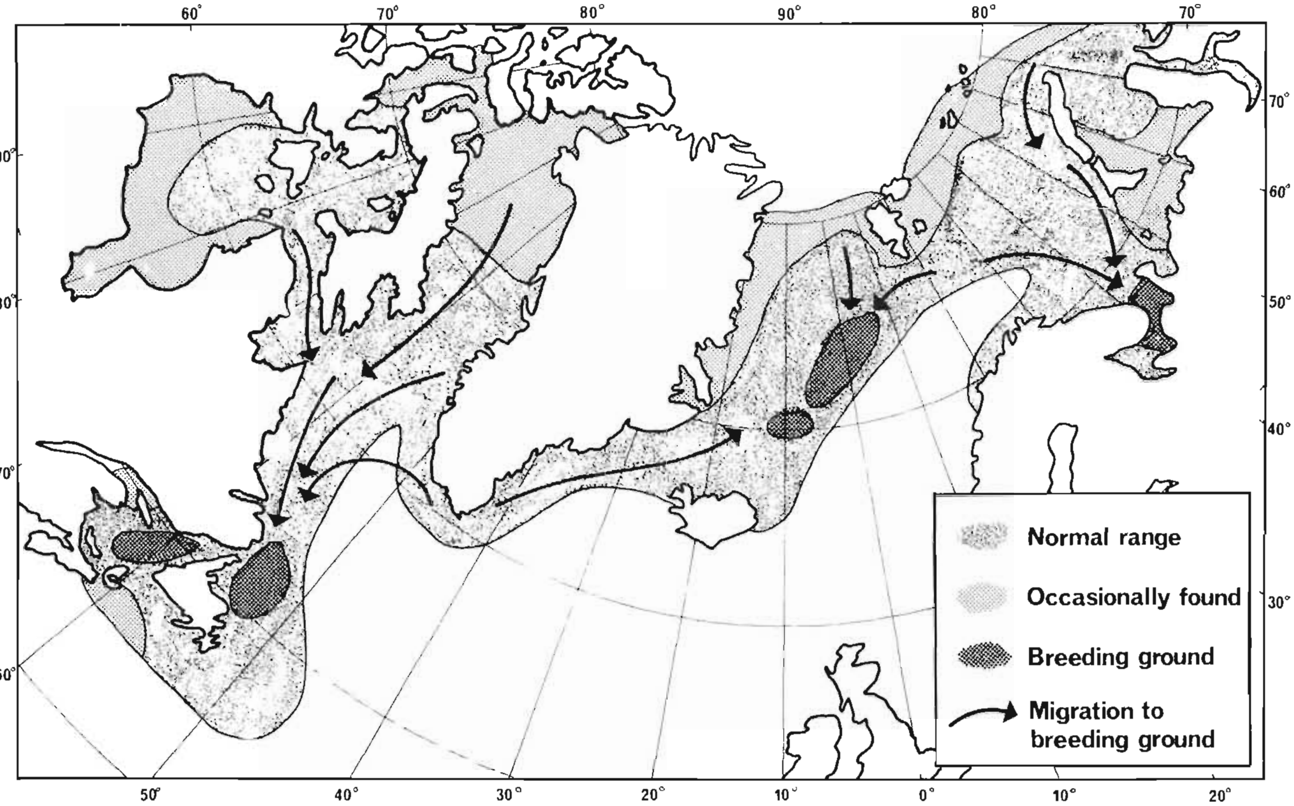


FIG. 24. Frijtjof Nansen's (1925) map of the distribution and migrations of harp seals.

It is not clear whether this overlap is a new phenomenon, or is due to the large scale of recent tagging at Newfoundland. The latter seems more probable since the previous rate of movement of tagged animals in summer from the western herds east of Greenland was 1/84 or of the order of 1%. Such a rate of cross-movement, evidently, is not enough to produce a genetic identity of populations east and west of Greenland, whereas the two populations east of Greenland show close morphometric similarity with a mixing rate estimated at 10% (based on very small numbers of tag recoveries, see Sergeant 1973c). Here there is evidence of migration of immatures from Jan Mayen to the White Sea (Rasmussen and Øritsland 1964).

A new set of recoveries of harp seals tagged at Jan Mayen is shown in a study by Ulltang and Øien (1988; Fig. 25). In "normal" years (1977–85) recoveries of young seals tagged at Jan Mayen in March came mostly from East Greenland, with a few rounding Kap Farvel, and from north Iceland, and a very few from north Norway (Fig. 25a).

In 1986–88, a period which included a big southward emigration of harp seals along the Norwegian coast in 1987, there were more recoveries at Norway than at Greenland, and these included both young and older seals (Fig. 25b). Clearly, then, harp seals of Jan Mayen origin joined the emigration at Norway. But they were not necessarily the majority in this migration. Since no seals were tagged concurrently in the White Sea, one cannot directly estimate the composition of the emigrants, but indirect estimates (see p. 59) give a majority coming from the White Sea.

In all these tagging experiments it must be remembered that it is young seals which are tagged, and that young seals can be expected to wander rather widely. It is likely that on reaching sexual maturity at about 5 yr their migrations become more stereotyped. While evidence on this from recaptured adult animals is hardly yet large enough to be analyzed, evidence from age frequencies is suggestive (see p. 34). (What this evidence cannot show is the possible extent of permanent transfer to another population. We will probably only get at this by study of genetic relatedness between populations.)

The whelping dates, and subsequent phases of the spring cycle, of these three populations are quite differently timed. Earliest to whelp is the White Sea herd which gives birth in the last days of February. The Gulf of St. Lawrence and Newfoundland animal whelp respectively in the first and second weeks of March, and the Jan Mayen animals, at the end of March (see Ch. VI). The timing of the moult, which follows whelping by about one month, varies accordingly (Fig. 26). Stimuli triggering whelping at the appropriate time are likely connected with ice conditions, since in years of reduced ice formation, whelping is delayed (Fig. 54). Whelping occurs when winter ice formation is ending, after which the seasonal pack-ice on which the young are born will last just those few weeks necessary for their growth. Selection for the biologically correct season is therefore rigorous.

The western or Newfoundland population is itself divided, into groups whelping east of Labrador (the so-called "Front" ice) and in the southern Gulf of St. Lawrence, with sometimes an intermediate group or

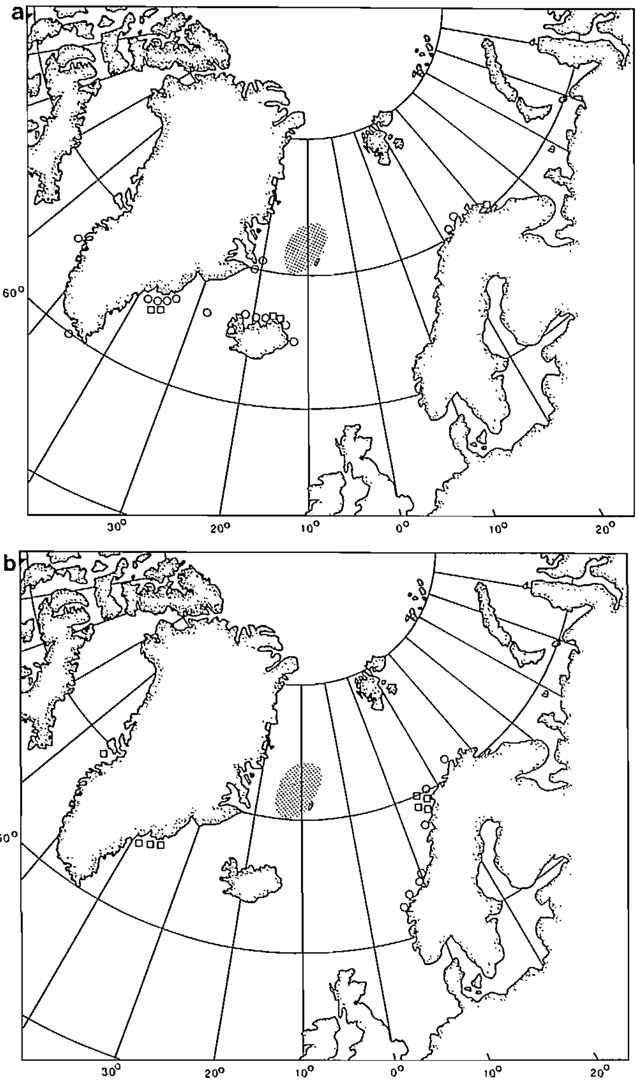


FIG. 25. Harp seals tagged at Jan Mayen (hatched area). (a) Recoveries in 1977–85; (b) in 1986–88, excluding recoveries in tagging area. Circles-recoveries of animals within 1 yr of tagging; squares — recoveries after 1 yr or more (redrawn after Ulltang and Øien 1988).

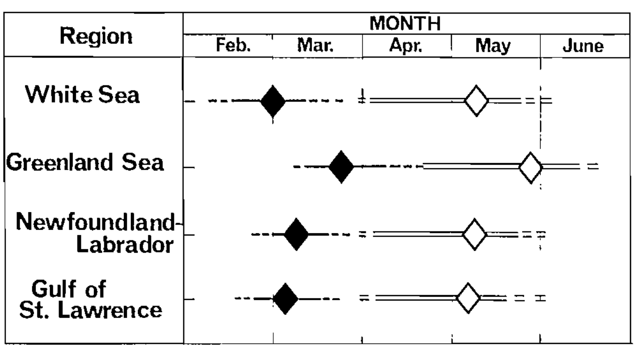


FIG. 26. Whelping (solid diamonds) and moulting dates for the four harp seal populations (after Khuzin 1967).

groups whelping in the northern Gulf, the so-called "Meccatina patch" (Fig. 27, p. 41). The southern Gulf and Front patches differ by about 5 d in mean whelping date (p. 74–75). Large-scale tagging shows that there is widespread migration of immatures from Gulf to Front from one year to the next (p. 54). Also, in extreme conditions when no ice forms in the southern Gulf of St. Lawrence, many of the Gulf breeders depart to whelp northward, perhaps as far as the Front (p. 56).

Mixing of immature seals also occurs between the Jan Mayen and White Sea populations, yet their whelping seasons are separated by 4 wk, and must therefore be under environmental control. (Yet they live at the same latitudes, so the stimulus can scarcely be the light cycle.) The explanation of this paradox will probably turn out to be that as animals mature they progressively return to their home waters, so that it is the home environmental cycle which affects their reproductive timing. But the timing stimulus for this cycle is unknown.

Migrations

A. The Newfoundland–Gulf of St. Lawrence Population

The most highly migratory population of harp seals is the western one, since in the western North Atlantic seasonal variations of sea temperature, and therefore extent of ice, are most marked. For example, on the north coast of Prince Edward Island (46°N) summer temperatures are high enough, reaching ca. 20°C at the surface, for human swimmers to throng the summer beaches and oysters (*Crassostraea virginiana*) to spawn in the lagoons; while at the same place, in winter and early spring, harp seals whelp and moult on the pack ice. One wonders what a palaeontologist would make of such mingling of biocoenoses, from their hard remains![6] In summer, these same seals may be swimming in Jones or Lancaster Sounds at 75 to 76°N lat., so that their round trip twice annually can span 30 degrees of latitude, equivalent to 1 800 miles (3 000 km) in a straight line — far more for animals following indentations of the shoreline.

1. Southward Migration

In the autumn the seals leave the arctic in a long front just ahead of formation of local pack ice, exploring and feeding in and out of the bays first of Baffin Island and then of the Labrador coast. On this migration they are easily taken in nets, and by sampling at past net fisheries we learned details of the movement.

The most northerly fishery was at Port Burwell, Killinek Island in northernmost Labrador at 60° 30′N. In 1964, a fishery conducted by the then Canadian Department of Northern Affairs for the benefit of the local Inuit began with a net set on October 24, hauled daily when weather permitted. Seals were taken beginning at this date and continuing to December 12, when the net was removed due to ice formation. A total of 1 463 seals were

[6] In the Flensburg Fjord, southern Baltic, harp seal subfossils from the sub-Boreal period (Fig. 4) are found in association with European oysters *Ostraea edulis* (Mohr 1952).

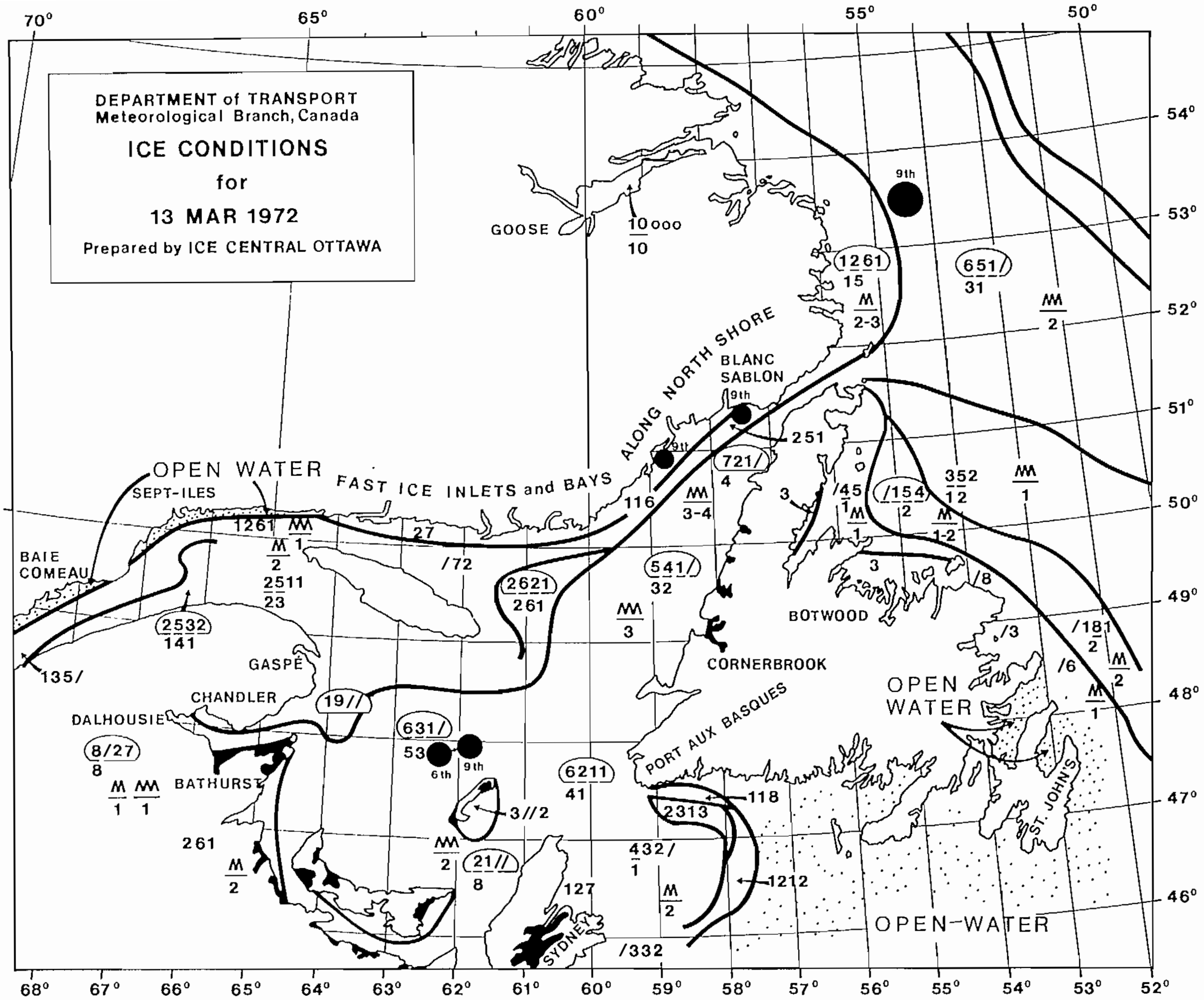


FIG. 27. Ice conditions 13 March 1972 and positions of whelping patches as seen by author in Gulf March 6 and 9 and reported by a sealing industry plane on the Front and in the Strait of Belle Isle March 9. All seal patches are on 6/10 first year ice (6---/4---) with 3-5/10 medium or larger floes (6---/4---) and close to the landward or western border of this thickness and concentration of ice.

taken, of which about half were found to be harp seals from jaws examined by the author. The remainder were mainly ringed and bearded seals with a very few harbour seals.

In Hebron, Nutak (two now deserted settlements) and Nain in northern Labrador, samples collected in the early 1950's were of harp seals only and showed relative absence of younger animals in October–November as the main herds moved south (Sergeant 1965; Fig. 28).

Enquiries made in communities in southern Labrador: St. Lewis, Pinsent's Arm and Square I. whence age samples from net fisheries had been obtained in the 1960's showed netting to take place from late November to the New Year.

As stated by Sergeant (1965) and Beck (1965), the net fisheries on the lower North Shore of Quebec took place from about December 26 to January 15. However, in the 1970's, we obtained tags from these fisheries as early as December 15. As pointed out by Sergeant (1965) the amplitude of a migration and therefore fishery, will vary with the size of the population migrating. Recent protection, and therefore increase of the fishery, could have led to an earlier start of the fishery; only the peak should be constant. If the peak should vary in time an effect of climatic change could be suspected, but this change has not been detected. Net fisheries are usually ended by local ice formation and may be interrupted by an early freeze-up (Beck 1965). A high catch in the 1960's was about 6 000 seals, before the herd of harp seals passed through or freeze-up occurred.

The main body of seals seems to move just ahead of the ice, and is said to avoid ice at this time. The slush or slob ice is made up of finely-packed crystals, too thin for a seal to rest upon and probably unpleasant for it to penetrate with its snout.

The young animals are still largely absent from these migrations. Thus when the herds entering the Gulf pass the Quebec north shore, samples show the proportion of seals in each age group reaching a peak at 4 or 5 yr (Fig. 28). From tag recoveries it is clear that some young seals

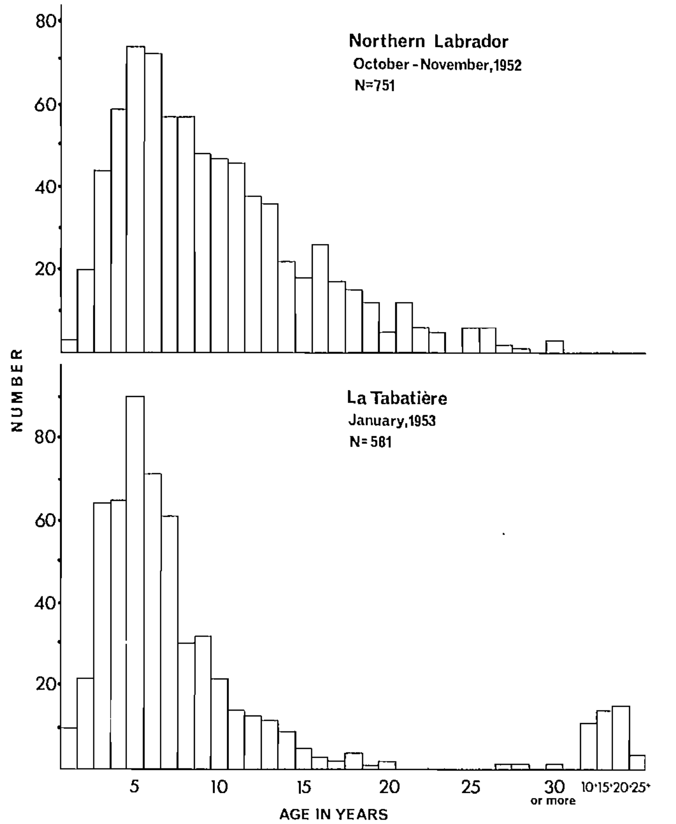


FIG. 28. Age samples in the same season from Hebron, Nain and Nutak, Northern Labrador and La Tabatière, Québec north shore. Note relative absence of immatures among main herd of southward migrant seals.

lag behind in Greenland, moving south later than the main herds. The delay however is not long. Tagged immature animals are taken at points intermediate between summering and wintering ones between November and February, and age samples taken from December and January from shore fisheries in northeast Newfoundland show the expected percentage of young animals (Fig. 29), which actually precede the adults. However, a few tagged animals remain in west Greenland waters as late as March. Age samples from the icefields in April, whether from the Gulf or the Front, show a very high percentage of one and two year animals, but these percentages are exaggerated due to selected catches of the young animals.

Tag recoveries show that animals which winter in the Gulf of St. Lawrence are animals born in the Gulf. However, age samples from the estuary of the St. Lawrence show a consistent shortage of 1–3 yr animals (Fig. 30). Many Gulf-born immatures, in fact, winter on the Front, as tags again show. The adaptive value of the eastward displacement of immatures is probably the result of the very much higher biomass of capelin, a major food, here than in the Gulf of St. Lawrence (Ch. V).

It is important to remember that this whole southward migration comes some two to three months ahead of the whelping season, and is followed by a period of heavy feeding in the wintering areas. Indeed, feeding is probably continuous from the summer through the leisurely fall migration and the winter, as evidenced by the annual cycle of fat thickness (p. 24–25).

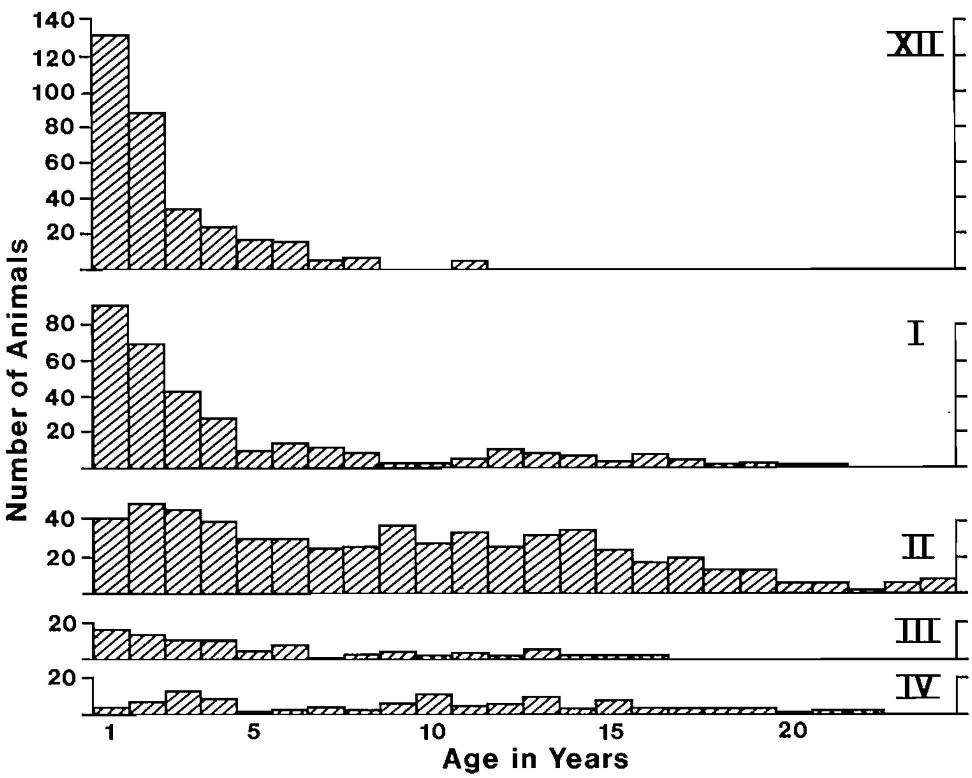


FIG. 29. Monthly age composition of shore catches from White Bay, Newfoundland, 1971 and 1973–1977.

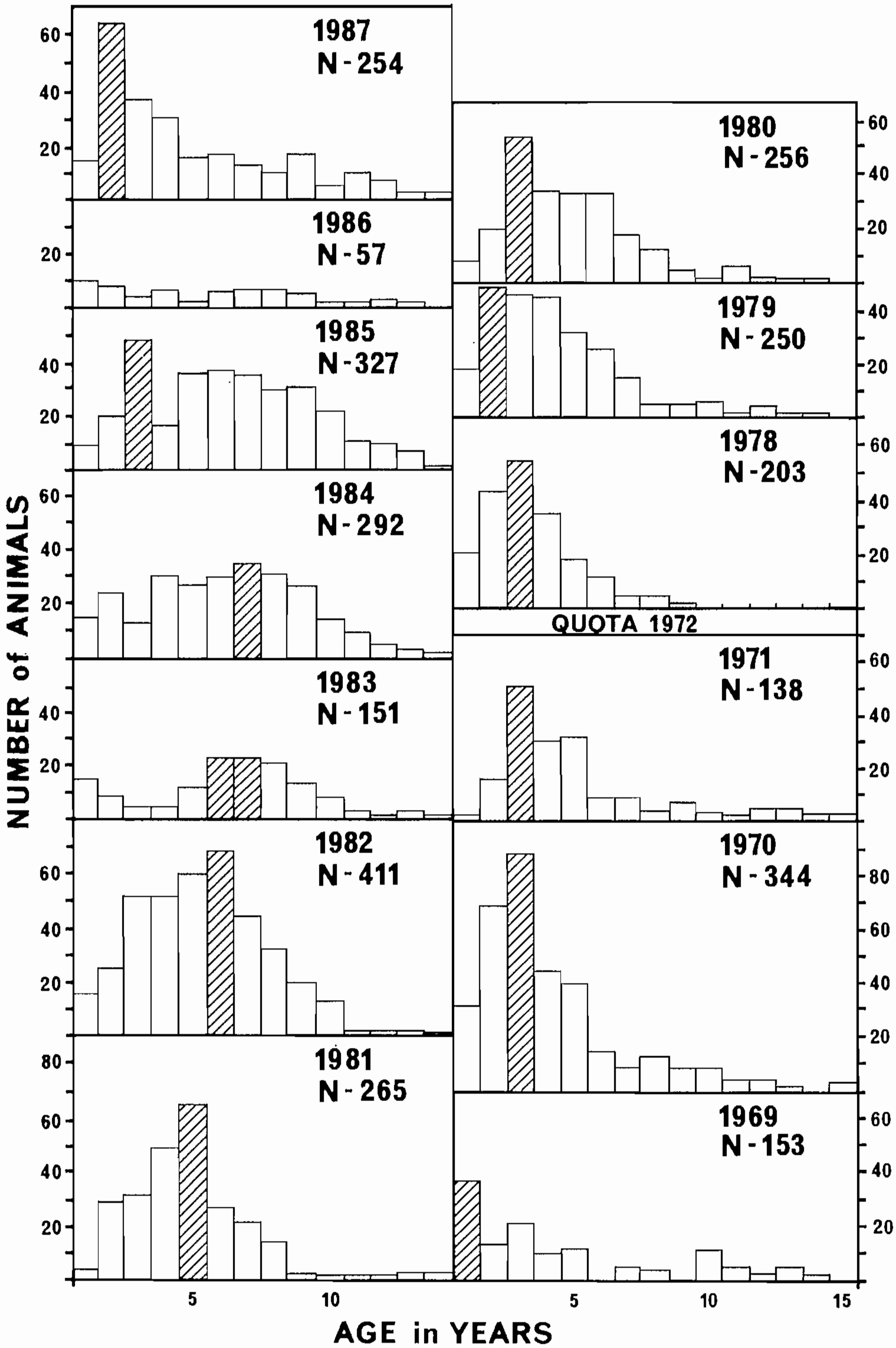


FIG. 30. Age composition of harp seals from the St. Lawrence estuary, 1969–71 and 1978–87. Largest age classes, from whatever year, are hatched.

2. *Wintering*

Knowledge of wintering locations of harp seals comes largely from winter fisheries for them, and this information is probably biased towards the occurrence of animals close to shore. Records at sea are remarkably few, apparently because harp seals are wary and hard to see from ships. Most records come from sealing captains. Thus, Captain Harold Marø told me that he saw feeding harp seals off Fogo I., northeast Newfoundland in February 1965. Also, there are sporadic winter net fisheries in the region of Fogo and Twillingate before the "slob" ice arrives in late January.

Fisheries for southward migrant harp seals using nets have existed for many years at St. Anthony and other settlements in White Bay, Newfoundland. Age samples from this area (Fig. 29) show mostly younger animals passing in December–January, with adults increasing slowly later in the winter, the reverse of the order of migration into the Gulf.

An offshore winter fishery developed in Notre Dame Bay–White Bay after the quota in 1972 allowed a sufficient escapement to make such a fishery profitable. It was conducted principally from long-liners in February, and took mostly immature animals aged 1–5 yr (Fig. 31). This, then, must be the principal wintering area of immatures of the Front herd, swollen by immatures of Gulf origin. They haul out to moult in just this area, the southern edge of the ice-fields, in early April. It is possible that this fishery, taking mostly seals hauled out on loose ice, is selective of immatures.

It seems unlikely that the adults migrate further south, since they are netted in this region in February, and must migrate north again in early March to mount the southward-moving ice fields ready for reproduction and mating. Thus early accounts (Robinson 1897) that the wintering grounds of the Front herd lay over the Grand Bank seem very unlikely; we have no recent observations from this region other than occasional young seals drifted offshore by ice in the spring.

From 1969 to 1987 we studied the winter occurrence and feeding of harp seals in the estuary of the St. Lawrence. Napoleon Comeau (1954), a turn of the century sportsman, described a hunt at Godbout and Point des Monts on the north shore of the middle estuary. It still occurs here and also further upstream between Les Escoumins and Tadoussac. This is a relatively small fishery, the hunters taking in total 500–2 000 animals each winter by shooting from small boats. It has probably existed since the first French and Basque fishermen in the late 16th century found the Indians pursuing it (Tremblay 1945). We were able to purchase our data and processed specimens from a family of seal hunters at Les Escoumins, trained to collect what we needed.

The animals caught in the estuary include both immatures and adults, with some fine-scale segregation which may indicate the existence of preferred feeding areas for the adults (Sergeant 1973b). There is great biological richness in these waters due to intense upwelling or water mixing, due to the shoaling at the landward end of the Laurentian Channel and the resulting tidal and current action (Dickie and Trites 1983). The principal food of

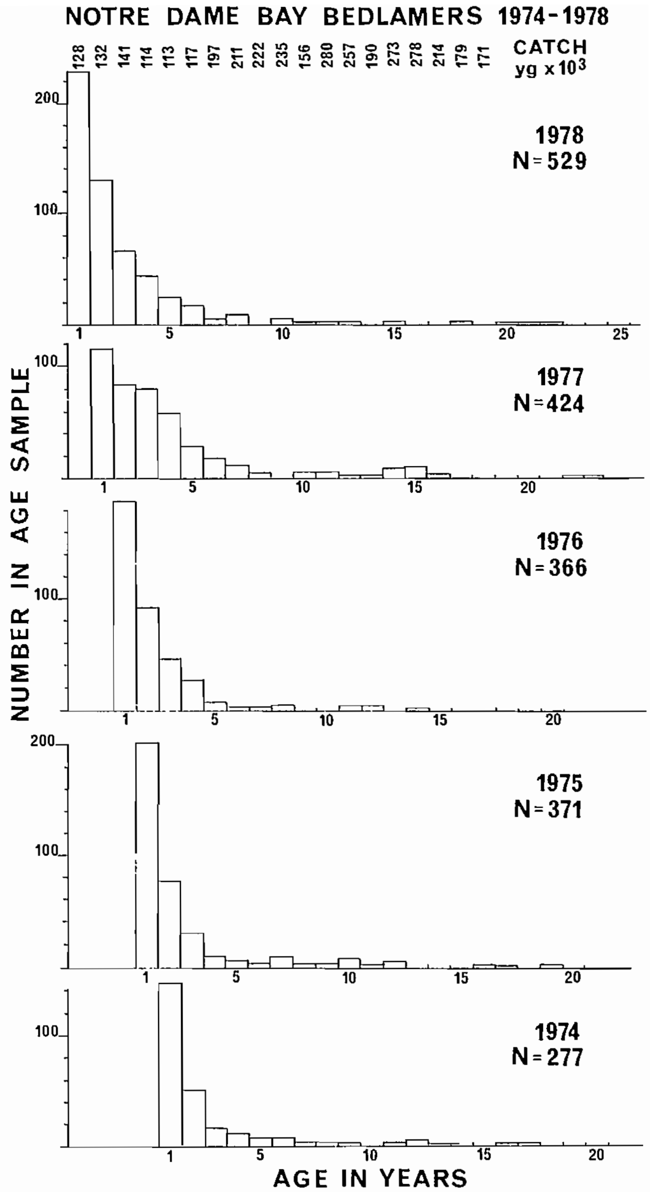


FIG. 31. Age composition of harp seals taken in offshore winter-spring hunt in Notre Dame Bay, Newfoundland, 1974–78.

the seals here all winter is capelin (Ch. V). The adult females in January and February all contain large foetuses and when whelping time comes in early March they (and the adult males) desert the area, returning in late March, after lactation has ended, with greatly reduced fat thickness. In early April, too, some of the newly moulted young arrived. However at this date catches cease, showing that the northward trek has begun.

3. *Whelping*

a. Location of Whelping Ice

Ice formation in eastern Canadian waters reaches its peak in late February and the seasonal pack-ice of the Gulf of St. Lawrence reaches a thickness of about 50 cm.

Studies by ice physics researchers from McGill University and the Canadian Defence Research Board have shown that the ice is formed, for the most part, in the brackish water of the south side of the St. Lawrence estuary and is fed by the Gaspé Current into the southern Gulf. Ice must also spread northwards from Northumberland Strait, as successive ice charts suggest. In some 40–60 d after formation the ice passes through Cabot Strait to be destroyed in the open Atlantic. In its path, however, lie the Magdalen Islands causing eddies and blocking ice drift. It is therefore no accident that whelping groups of harp seals always start to form up west or northwest of the Magdalen Islands, as for example at 47°17′, 62°58′ on February 27, 1959 (Mr. Paul Montreuil, in litt.). With normal, westerly winds, their drift goes past the Magdalen Islands, either northabout or southabout or both, and continues past Bird Rocks, through Cabot Strait. Eventually, many young seals are liable to reach the northeast coast of Cape Breton Island, where there is a regular spring hunt. In some years, easterly winds push the whole ice-mass southwest towards Prince Edward Island or even into Northumberland Strait. The correct forecast of such variations is (or was[7]) a question of much importance to a sealing operator and even to a researcher, who had to decide ahead of time whether to position a chartered helicopter at the Magdalen Islands, or to keep it at Charlottetown.

Since 1969, forecast of whelping areas by a Canadian researcher has been enormously aided by the ice charts made from aircraft and satellite surveys by the Meteorological Branch of the Department of Transport (now Ice Forecasting Central of Environment Canada). Repeated comparison of ice conditions and seal whelping sites allows one to predict the sites of the latter with considerable acuracy (Fig. 27). The seals always whelp on 1-yr winter ice (the thickest type found in the Gulf) of about 6/10 to 7/10 floe density. This is relatively restricted in extent in the southern Gulf in early March, the remainder being thinner ice.

Ice formation on the Front is more complex. In the Labrador Current, going from south to north, the ice thickens gradually from the pancake ice and slush of the "northern slob" in the vanguard to the young ice, which is still too thin to hold seals. Next comes the regular winter ice on which the seals will whelp, and lastly the arctic or multi-year ice, full of icebergs, which will not reach the region of Belle Isle till April, and is unsuitable for harp seal whelping, in part due to shortage of leads. Melting and ice destruction by seas occurs in the same order, so that by late April only the arctic ice is left. Ice of greater thickness can cut through thinner ice under current or wind action, so that great complexities can develop.

From the standpoint of the seals, and the sealers, the most important variations that can develop are between different wind patterns at the whelping season in early March. If winds have blown steadily from the west and northwest on the Labrador coast in February, ice is pushed out from the coast and more forms inside it; the ice belt is of great width and the seals whelp somewhere in the middle, about 30 miles (50 km) from shore (Fig. 32, 34). They will be free of the natural risk of ice-rafting caused by wind-driven pressure of ice on the coast, and sealing ships can reach them rather freely except after very severe winters when the ice is too thick.

By contrast, if low pressure systems generate easterly winds in the region, almost no ice is formed on the southern Labrador coast and the swell probably destroys what is already there (Soule and Challenger 1949). Ice further to the north is pinned against the coast at the sharp bend at Cape Harrison. The seals have only the ice close to the coast upon which to whelp (Fig. 33). They may well be so close upon the rocks that the ships cannot easily reach them. In 1965, snowmobiles pulling sleds were able to do so from Cartwright on the Labrador coast. The seals are then subject to the risk of ice-rafting.

As in the Gulf, the variations are endless. After a whelping close to shore west of Spotted Island in early March 1966, the wind changed to the northward on March 15 and the whole ice mass carrying seals and ships was swept down to Belle Isle in 3 d. The whelping ice usually ends up pinned in the triangle formed by White and Notre Dame Bays where the seals complete their development; however, in some years, seal patches may pass into the Strait of Belle Isle.

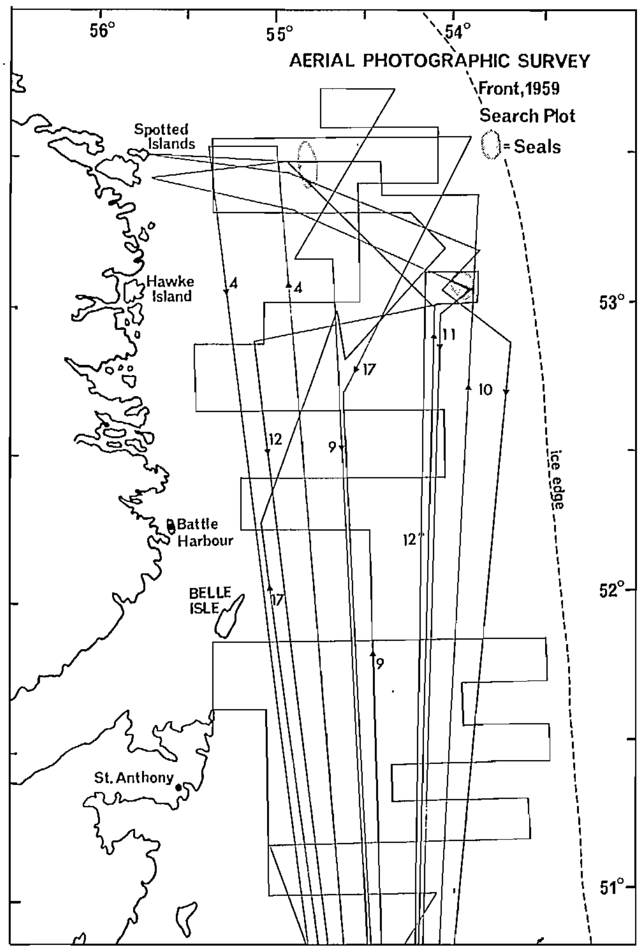


FIG. 32. Aerial search pattern (with date in March) and sites of harp seal whelping patches on the Front in 1959, a year of extensive ice.

[7] In the 1960's but not in the colder 1970's (see p. 40 et seq.).

We once surveyed from the air the coast of mid-Labrador from Cape Harrison northward to Hopedale during mid to end March, lured by groups of harp seals in the water just north of Hamilton Inlet (Fig. 33). In that year, 1960, ice to the southward was not extensive and the seals whelped near the Gannet Islands. We were unable to find whelping patches in the northern region and there were no cracks in the ice, which was solidly frozen to the coast except for a shore lead. Evidently, harp seals need the opening cracks of moving ice in order to penetrate to whelping sites, and this kind of ice is not found north of Hamilton Inlet in March.

There is normally moving ice in the Strait of Belle Isle in early March, due to tidal action. Harp seals can therefore penetrate shoreward here. There is then frequently a wide shore lead between fast ice and pack ice, reaching northward as far as Roundhill I. at 53°26′N, 55°37′W), (south of Spotted I., Fig. 34). The harp seals, in seasons of extensive pack ice, can thus reach this far north and no further from northernmost Newfoundland, by travelling *inside* the pack ice. They probably then whelp outward within the pack. However, if there is no pack ice, harp seals must mount consolidated pack and fast ice shorewards, on which to whelp.

Breathing holes (the "bobbing holes" of Newfoundland sealers) are found in new ice formed in cold weather between pre-existing floes. These holes are not bored by the seals in ice, but are formed in leads of water which begin to freeze immediately after opening. The seals keep the holes open and eventually this ice becomes thick enough for the seals to climb out on it. Whelping ice is normally about 50 cm thick and somewhat hummocked; the greatest density of pups is found on broken, hummocky floes and the least on thin ice and flat, unsheltered floes or parts of floes. Part of this distribution is due to movements of the pups, since hummocks and hollows give the pups protection from wind.

The Front ice is much more broken into smaller floes than Gulf ice, due to greater effect of the north Atlantic swells. It is also much more hummocked than the Gulf ice, giving greater shelter for the pups.

Formation of whelping concentrations proceeds up-current, that is to the north or northwest on the Front and normally to the northwest in the Gulf. Since drift accelerates down-current as the ice loosens, and islands

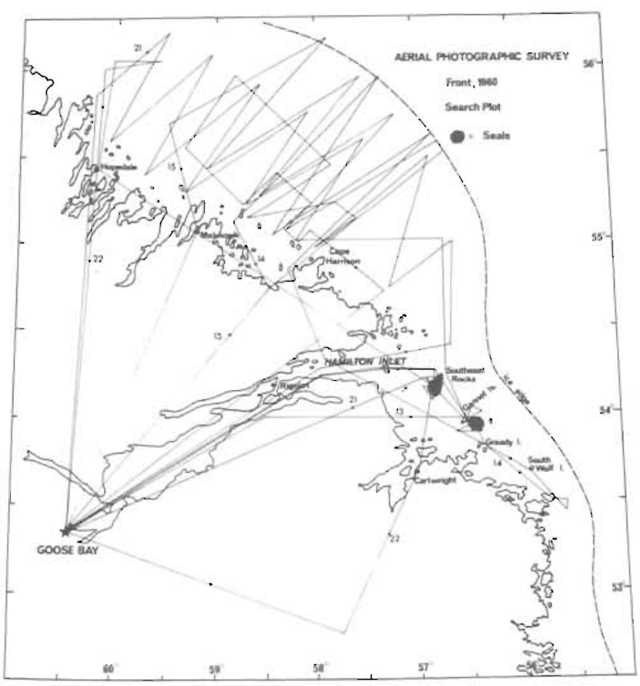


FIG. 33. Aerial search patern and harp seal whelping sites in 1960, a year of little ice south of Hamilton Inlet.

FIG. 34. Mosaic of Landsat satellite photos of northern Newfoundland and southern Labrador on 11 March 1973, showing the extensive shore lead from Belle Isle north to Spotted I., and pack ice eastward. Location of seal patch 10 March shown. (Inset: the shore lead seen from a plane, 7 March 1973.)

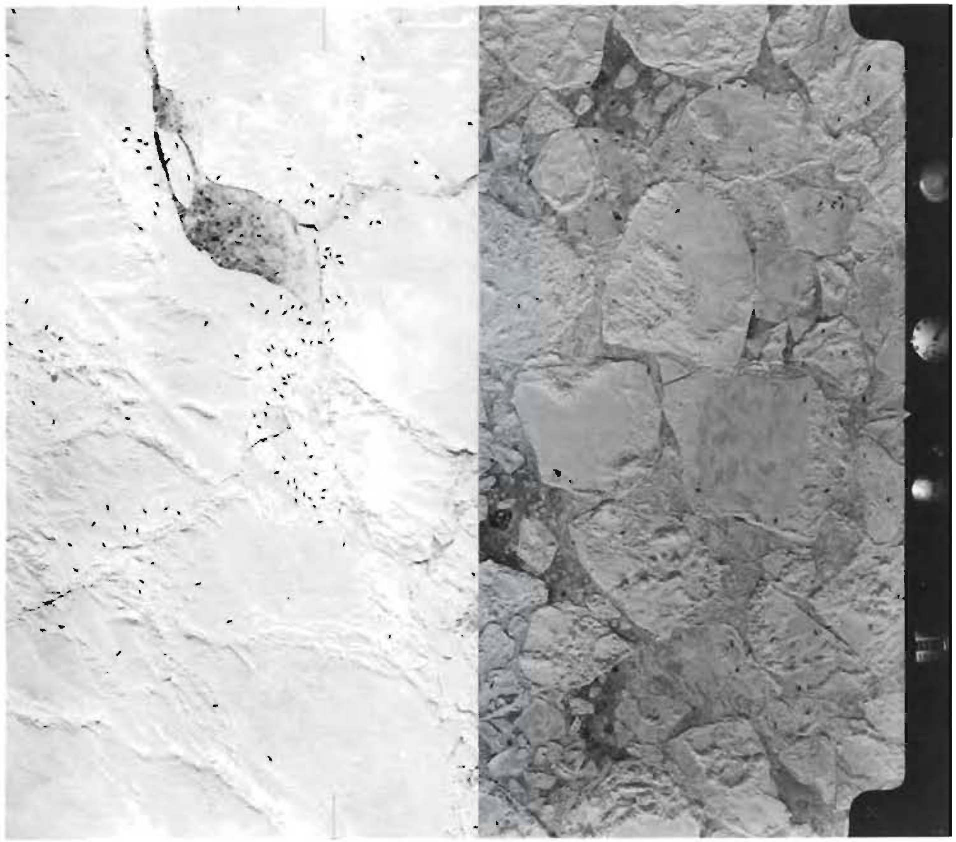


FIG. 35. Gulf (left) and Front ice in early March. Photos: Atlantic Aviation Ltd., Halifax, North of Bird Rock, Magdalen Is. on 9 March 1959, Kenting Aviation Ltd., 52°30′N, 55°07′W, 10 March 1964. Both taken with 6″ (20 cm) lens at 500 ft (150 m).

may break up the floes, it often happens that a single initial focus of whelping soon develops the appearance of several discrete patches of seals. Typical Gulf and Front ice are shown in Fig. 35, detail of Front ice on Fig. 37.

b. Frequency of Various Whelping Patterns

For the Front, I have data for the 21 years, 1959 to 1980 exclusive of 1968 (Table 10). Of these years, 15 or 71% found harp seals whelping far from land, under high pressure weather patterns and extensive ice. In 5 years (1960, 1962, 1965, 1966, 1978) seals whelped close to land in the vicinity of the Spotted Is. or the Gannet Is., Labrador. In 1969, an extreme inshore location was found, whelping taking place near George I., Hamilton Inlet. Contrasting extreme ice distributions are shown in Fig. 36. There was a much greater tendency to whelp offshore in the 1970's (9/10 years) than in the 1960's (5/10 years), which correlates with a cold period of sea temperatures in the 1970's, reaching its peak in 1973 (Sergeant 1982). For the Gulf, from 1959 to 1980 (Table 11), I have 19 years' data during which pupping occurred around the Magdalen Is. in 15 years, on the north coast of Prince Edward I. in 3 years and, in the manner typical of an extremely mild season, in Northumberland Strait once. Between 1972 and 1980 harp seals whelped northwest of the Magdalen Is. in every year, then in 1981 once more came ashore at Prince Edward Island. The 1970's therefore were, here too, a cold decade.

Inshore whelping on the Front was correlated in the Gulf with whelping on the coast of Prince Edward I. in 1960 and 1965, and extreme inshore whelping on the Front was correlated in the Gulf with whelping in Northumberland Strait in 1969. Therefore it seems that persistent low pressure systems, moving through the Gulf and along the Labrador coast, generate easterly winds and reduce the amount of whelping ice in both areas. Conversely, periods of high pressure and cold temperatures with northwest winds in February and early March generate extensive ice fields in both areas, leading to offshore whelping on the Front and whelping well northwest of the Magdalen Is. in the Gulf.

A by-product of cold winters, such as occurred especially through the early 1970's, was to reduce the effectiveness of the trap net fishery for seals which took place on the Quebec shore of the northernmost Gulf of St. Lawrence in December and early January. This fishery failed in only 1 year (1956) between 1950 and 1971, but thereafter failed for 3 consecutive years 1972 to 1974. Apparently, early freeze-ups in December in such years necessitate lifting of the nets before the seals pass through.

TABLE 10. Distribution of whelping patterns on the Labrador coast.

Year	Offshore or Inshore	Location	Source
1959	Off	S.E. Spotted I.	Aerial photo survey (Sergeant and Fisher 1960)
1960	In	Gannet Is.; S. Wolf I.	Aerial photo survey (Sergeant and Fisher 1960)
1961	Off	E. of Harvre Bay Mar. 13	Khuzin 1963a — ship
1962	In	Spotted I.	Dr. J. Olds, pers. comm.
1963	Off	E. Belle Isle	Popov and Timoshenko 1965
1964	Off	S.E. & N.E. Belle Isle, Mar. 7–10	Aerial survey
1965	In	Gannet Is. (severe rafting)	Many obs., in litt
1966	In Off	Spotted I., changing Mar. 13–16	Pers. obs., ship
1967	Off		Øritsland 1971
1968	No data		
1969	Far in	George I.	W. Hoek, obs., ship
1970	Off	45 km off Hawke I., Mar. 14	Øritsland 1971; H Killiaan; diary
1971	Off	45 km N. Grady, Mar. 9	Curran and Lett 1977
1972	Off	65 km E. Roundhill, Mar. 9 35 km E. Spotted I., Mar. 11	Curran and Lett 1977
1973	Off	25 km E. Spotted I., Mar. 5 45 km N.E. Spotted I., Mar. 7	Curran and Lett 1977
1974	Off	40 km N.E. Belle Isle, Mar. 19 70 km E. Francis Hbr., Mar. 10	Curran and Lett 1977
1975	Off	50 km N.E. Spotted I., Mar. 8 40 km E. N.E. Belle Isle, Mar. 11	Curran and Lett 1977
1976	Off	52°53′N, 54°28′W, Mar. 14	Curran and Lett 1977
1977	Off	52°45′N, 54°54.5′W	Curran and Lett
1978	In	20–30 km N.W. Cartwright, Mar. 10	W. Hoek, tagging
1979	Off		D. Bowen, tagging
1980	Off		D. Bowen, tagging

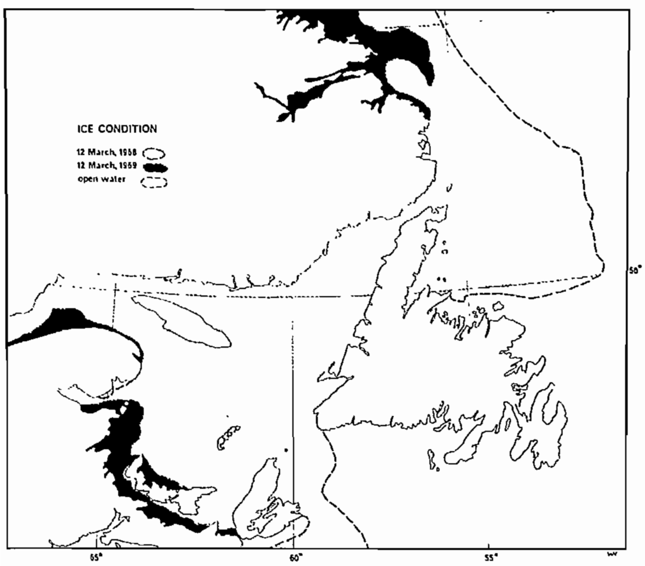


FIG. 36. Ice cover in early March in the heavy ice year 1968 and light ice year 1969 (from Anon, Canada, 1970 and 1971).

c. The Meccatina Patch

Variably, a patch or patches may form in the northern Gulf, apparently often off Meccatina I., giving it its name (Fig. 27). Because this patch was not a prime target for sealing ships, little is known of its regularity. I document some knowledge on location and size of patch from Arctic Biological Station records.

In 1962 D. Welch and J. Christopher were on board M/V *Theron* which on March 20 steamed from Corner Brook, Nfld. to some reported seals southwest of Pte Riche, Nfld. There were a few scattered whitecoats of which 20 were taken. On March 21 the ship steamed further north and at 1400 "picked up a small patch of whitecoats... one hundred were taken including one ragged jacket". The Strait of Belle Isle was blocked solidly; the ship could not penetrate it on March 22.

In 1965 there appeared to be a patch formed off Anticosti I., which moved on to the west coast of Newfoundland; here 19 635 young seals were taken between Rose Blanche and Cape Norman, i.e. along the whole west coast.

In 1966 the industry aircraft located a patch 20 × 6 miles (30 × 9 km) in the northern Gulf which was reached by 5 ships starting on March 31st. By then the young were full beaters. Total catches of beaters by 6 ships and northwest Newfoundland landsmen were 22 626.

In 1967 a photographic survey conducted by Douglas Fleet found a patch 5 × 7 miles (8 × 10 km) at 51°06′N, 57°38′W. Analysis of photographs gave an estimate of 20 000 adult seals. Catches of young by ships in this patch were 35 000.

TABLE 11. Distribution of whelping patterns in the southern Gulf of St. Lawrence.

Year	Magdalen Is.	Prince Edward I.	Source
1959	Brion I. - Bird Rocks	—	Aerial photo survey
1960	—	N. Shore, Malpeque	(Sergeant and Fisher 1960)
1961	- No data -		
1962	- No data -		
1963	- No data -		
1964	N. and S. of Magdalen Is. Mar. 1-10 (3 gps)	—	Aerial survey and tagging
1965	—	N.W. Coast (47°16′N, 63°50′W), Mar. 6	
1966	Deadman I.	—	Original ship voyage
1967	W. of Island	—	D. Fleet, diary
1968	- No data -		
1969	—	Northumberland Strait and N. side island	B. Beck, tagging[a]
1970	(1) 30 km Amherst I. Mar. 8	(2) Pups off E. Pt. Mar. 8	Aerial survey
1971	W. side Havre Aubert, Mar. 12	—	D.E.S., diary
1972	20 km W. Old Harry, Mar. 9 20 km N. Fatima, Mar. 4	—	W. Hoek, diary
1973	20 km W. Pt. au Loup, Mar. 17 45 km NNW. Grindstone, Mar. 5	—	W. Hoek, diary
1974	30 km NW. Grindstone, Feb. 28	—	W. Hoek, diary
1975	30 km W. Grindstone, & 15 km N. Deadman I., Mar. 10	—	W. Hoek, diary
1976	N.W. Magdalen Is. Brian I.	—	S. Dudka, diary
1977	85 km 335°Mag Grindstone, Feb. 27	—	S. Dudka, diary
1978	15 km 330°Mag Grindstone, Feb. 25. W. Coast Is., Mar. 7	—	W. Hoek, tagging
1979	75 km 370°Mag Grindstone, Mar. 1	—	W. Hoek, tagging
1980	7 km 305° Mag Grindstone, Mar. 2	—	W. Hoek, tagging
1981	(Started W. of islands)	N.E. Coast, Mar. 2	W. Hoek, diary

[a] See Fig. at p.p.

In sum, a patch may or may not form in the northern Gulf. Its size may be substantial (20 000–35 000 pups). It is not known if the seals colonize the ice from the southern Gulf or from the Front by movement of ice with seals on it southward into the Gulf; perhaps both mechanisms occur.

d. Density of Animals in Ice

Measurements of densities come from aerial photographs taken in the course of surveys of numbers. Table 12 shows densities of whelping females and Table 13 — densities of moulting animals, taken from aerial photographs of the kind shown in Fig. 35 and 37.

Densities of whelping adults vary greatly because of several factors. Large ice floes limit colonization by whelping females to the edges of the floes and to areas accessible from occasional breathing holes. If the ice floes are broken up, more edge results and the density of females is greater. Since easterly swells break up the ice more on the Front than in the Gulf, the mean density is higher on the Front, by a factor of 3:2 (Table 12). A second variable is the date of survey. Three surveys of the same whelping group over three successive days of March 1959 (Table 12) showed that the density of adults decreased. This is probably because as the young grow larger, the females desert them for longer periods.

Mean densities of moulting seals in April are ten times greater than for whelping adults in March (Tables 12 & 13 and Fig. 37) but remain variable. The greater density of moulting seals than of the most dense whelping groups shows that the whelping females are dispersed. The aggressive behaviour of females one to another keeps them spaced apart. Aggression is expressed by posturing with

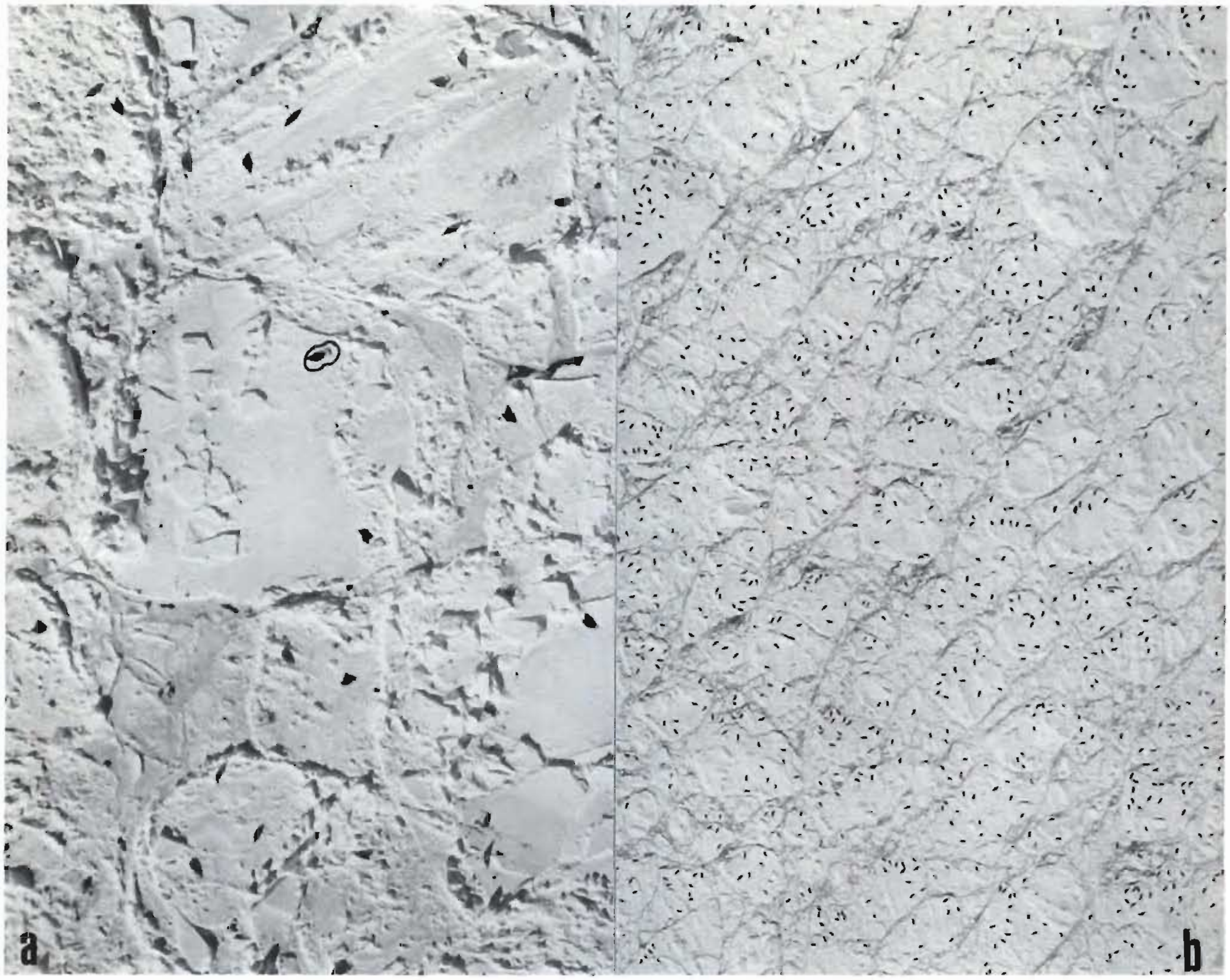


FIG. 37. Density of (a) whelping and (b) moulting seals as seen from the air.

the head raised vertically (Fig. 38) and snarling. This behaviour is used against other females, and under human disturbance, against a man, a passing ship or a low-flying aircraft. If a man approaches too close to a young seal, the female may attack him. The young, spotted females more readily stand their ground and attack while older females more readily enter the water.

4. Moult

March is the time of whelping, lactation and mating, so that the adults are all together. The females leave for a short period of fattening in end March - early April while the adult males begin their moult, remaining around the area of the whelping patch. The immatures by this time are congregated in the southernmost area of pack ice. On the Front the ice is drifting southward and melting at its leading edge. The immature animals are therefore forced to change position every few days, swimming a few hundred kilometres northward to haul out again

FIG. 38. Aggressive posture of one adult female harp seal to another. Gulf of St. Lawrence, 11 March 1954.

TABLE 12. Harp seals. Densities of whelping females from aerial photographs.

Year	Date	Locality	Group	No/km^2
1959	Mar. 6	Gulf	1	802
	Mar. 9	Gulf	1	539
	(Mar. 9	Front	1	1 040)
	(			)
	(Mar. 10	Front	1	760)
	(			)
	(Mar. 12	Front	1	705)
	Mar. 10	Front	2	774
	Mar. 11	Front	2	656
1960	Mar. 7	Gulf	1	1 811
	Mar. 8	Gulf	1	896
	Mar. 13	Front	1	2 047
	Mar. 13	Front	2	2 186
1964	Feb. 28	Gulf	1	314
	Mar. 1	Gulf	1	351
	Mar. 4	Gulf	1	299
	Mar. 3	Gulf	2	170
	Mar. 10	Front	1	438
	Mar. 10	Front	2	417
1967	Mar. 2	Gulf	1	1 045
	Mar. 10	Gulf	2	385
Mean		all obs. (19)		823
Mean		Gulf (10)		661
Mean		Front (9)		1 002

on the ice (Fig. 40). In this way the immatures and adults mix together (fig. 41) and begin the northward migration which proceeds through the month of May.

In the Gulf of St. Lawrence some adult and immature seals are found in early April on the disintegrating ice between Prince Edward I., the Magdalen Is. and Cape Breton I. From here they may make a feeding stop around the Magdalen Is., where herring and other foods are taken (Sergeant 1973a), leaving as the ice disappears in the southern Gulf. They then move to ice fields along the Quebec north shore. On April 8, 1966 from *Theron* west of Flat I. (50°50′N, 58°44′W) we saw a dense patch of moulters extending along ca. 30 × 7 km of ice, which I estimated at ca. 250 000 animals. When this ice became tight enough that the moulters could be taken, I found this patch to consist of all age groups (Fig. 41 centre; Fig. 83). To my knowledge this is the only large age sample of moulters to have been taken in the Gulf, and it shows that late in the season the immatures are fully represented in the Gulf. By late April or early May the Gulf of St. Lawrence seals are passing through the Strait of Belle Isle, followed somewhat later (May–June) by the year's crop of juveniles.

TABLE 13. Densities of moulting harp seals at the Front in 1962, from aerial photographs. Each day starts a new set of seal groups.

Date	Group	No./km^2
April 13	1	2 155
April 13	2	10 781
April 13	3	6 763
April 20	1	20 702
April 21	1	3 894
April 21	2	18 812
April 21	3	9 978
April 23	1	4 118
April 23	2	12 634
April 26	1	4 997
April 26	2	3 605
April 26	3	20 028
April 26	4	7 158
Mean	(13)	9 663

The hauling out of animals on the ice for the moult follows a well-defined pattern. The first moulting animals were usually taken at the Front in end March and the first days of April. At this time, patches were either of old males or of immatures of both sexes. Later these groups coalesced, but the percentage of females remained very low until late April (Fig. 41, upper). On this basis, a closing date of April 25 was set for the seal fishery in the Gulf and at the Front in 1968, thereby protecting the adult females. The late arrival of the adult females at the moulting patches is due to their heavy feeding after the end of lactation (p. 67).

5. *Northward Migration*

Young harp seals were seen at the outer edge of the ice between 52° and 54°N on 24 May 1963 by Dr. E.H. Grainger on the icebreaker *Labrador* (Sergeant 1968). Goudie (1973) described very large numbers of harp seals entering Ujutok Bay, 70 km west of Hopedale, Labrador (55 1/2°N) in late June 1923. They were in troops of 50 to 100, and apparently fed on capelin early in the morning.

FIG. 39. Moulting seals on the Front, [@ 51°50′N, 53°38′W] on April 16, 1976.

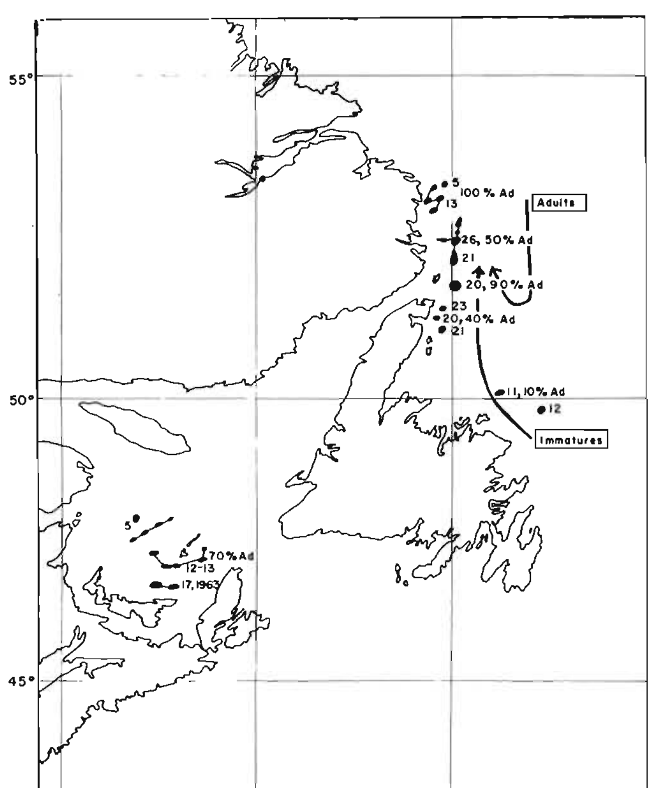


FIG. 40. Distribution of moulting seals in April 1962 (and 1963) on dates specified (from Sergeant 1965).

Foy et al. (1981) showed that the migration passed the north-central settlements of Makkovik, Postville and Hopedale (54°30′ to 55°30′N) between 21 May and 21 June, 1979 to 1981. Harp seals were captured both in the bays and offshore, among the outermost islands. Age samples showed that animals taken offshore were composed mainly of age-classes 0–3, and especially young of the year, while animals taken in the bays were aged from 2 to 25 years.

In 1954, Malcolm S. Gordon (in litt., Nov. 14, 1955) saw 7–8 harp seals, 5 km E. of Hopedale on July 3, and 15–20 in all stages (beaters, bedlamers, harps) in Port Manvers Run, N. of Nain (56 1/2°N), on July 6. Boles et al. (1980) saw a herd of 100–200 harp seals off northern Labrador at 58°20′, 60°45′W on Aug. 13, 1979, and coastal residents reported to them generally rare summering of harp seals in Groswater Bay (54°10′N) and near Nain.

Harp seals therefore summer in small numbers off northern Labrador, but the great majority migrate further north. Harp seals must go seaward, probably along the edge of the pack ice, to reach west Greenland. There are very few surveys in this area and they have detected few seals. MacLaren Marex (1979a) ran shipboard surveys in Davis Strait in April and May 1978; they saw immature harp seals in April, but only hooded seals in May.

In the rest of this account, coastal areas only will be discussed, except in Lancaster Sound, even though we may only be seeing from there the fringes of a widespread migration through icefields. Satellite photographs show the "Middle Pack" in Baffin Bay to open by means of

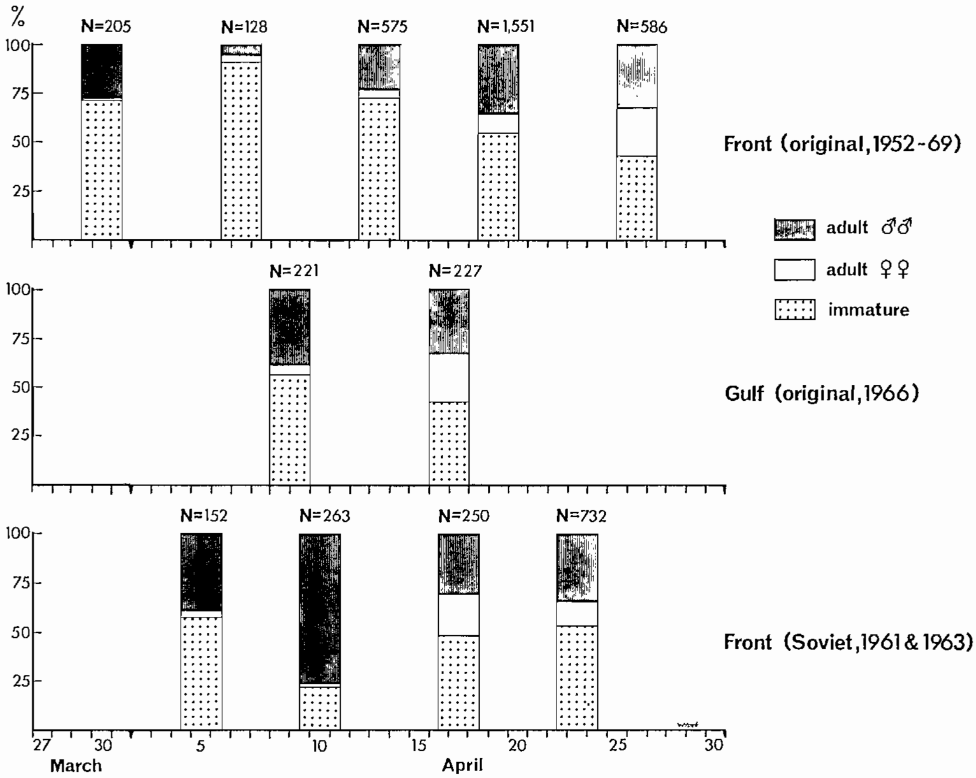


FIG. 41. Composition of moulting groups in Gulf and Front areas by date.

a shore lead on the northwest coast of West Greenland in late June and July, and more rarely (and later) by a lead along the Baffin I. coast. It is likely therefore that in the more northern part of the summer range, harp seals will be channelled to the coasts along these leads.

6. Summering

a. Greenland

It has long been known that harp seals coming from Newfoundland arrive at the coastal settlements of southwest Greenland in early summer (Jensen 1928). Hansen and Hermann (1953, p. 87) state that "just at the time when the capelin concentrate in great shoals at spawning time, the harp seals arrive migrating from the whelping fields at Newfoundland. The seals are very thin at this time after the long fast of the reproductive season and fall greedily upon the capelin" [author's translation].

It is useful to provide a summary of place names, their latitudes, the administrative districts used by Denmark in Greenland, and the statistical regions used by the International Commission for the Northwest Atlantic Fisheries (ICNAF, now Northwest Atlantic Fisheries Organisation, NAFO), which compiles figures for fish and also seal catches. This is done in Fig. 42. There are a number of major settlements in west Greenland, which are shown in the Figure, (and very many more minor ones which are not shown) but only two settlements in east Greenland.

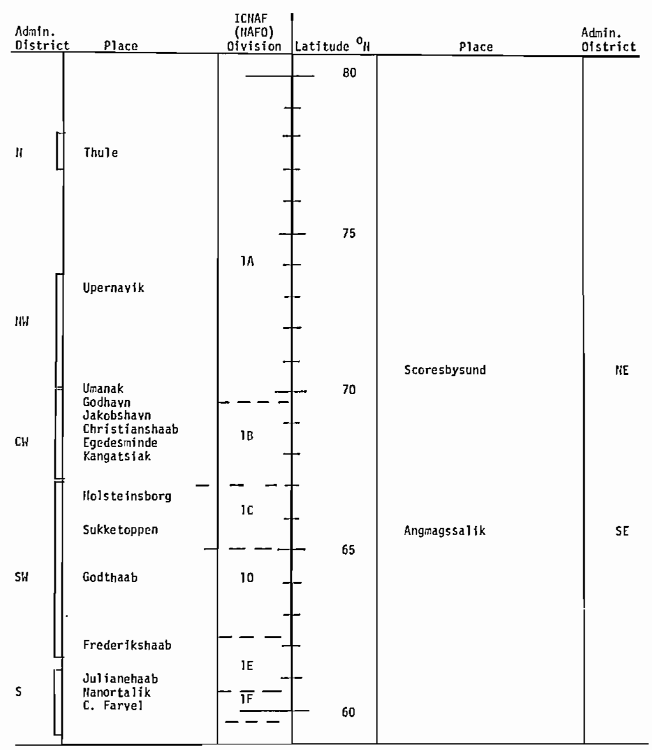


FIG. 42. Latitudes of different Greenlandic localities, their administrative districts and ICNAF (NAFO) divisions (West Greenland only).

Detailed knowledge of summering and migrations in Greenland waters is derived from three sources: catches by district and season, age samples, and tagging recoveries.

Catches: An analysis of catches by district and half month was performed by Rosendahl (1961) summarized by Sergeant (1965) and again by Kapel (1975a). Rosendahl's chart for harp seals is shown as Fig. 43. It shows a peak of catches in June for all localities in west Greenland north to Christianshaab, but from Jakobshavn northward to the limit of large catches at Upernavik harp seals were caught throughout the later part of the year with a peak in August. Such a peak may well represent best catching weather. At Kangâtsiak on the outer coast of central-west Greenland there was even a small peak of catches in December–January.

Age samples: Age samples covering the year 1953 were collected from 609 harp seals from a wide variety of localities in west Greenland and aged by the Greenland Fisheries Investigations. They were generously made available to me by Dr. Paul Hansen. At this time, there was no Danish specialist on seals working in Greenland.

In 1962, Hr. Ph. Rosendahl arranged for collections to be made and sent to me for analysis. Samples totalling 358 animals were collected at Sarqaq in the Vaigat (69°N) and at Tasiusaq, Upernavik district (73°N). Kapel (1975b) later republished the earlier data in extenso and made comparisons with age samples collected by himself in 1970 to 1972. The later samples did not have so wide a geographical spread, but more care was taken to keep them representative of the catch by date. In spite of these differences, the age samples of different years for the same regions are similar. A further set of age samples, almost

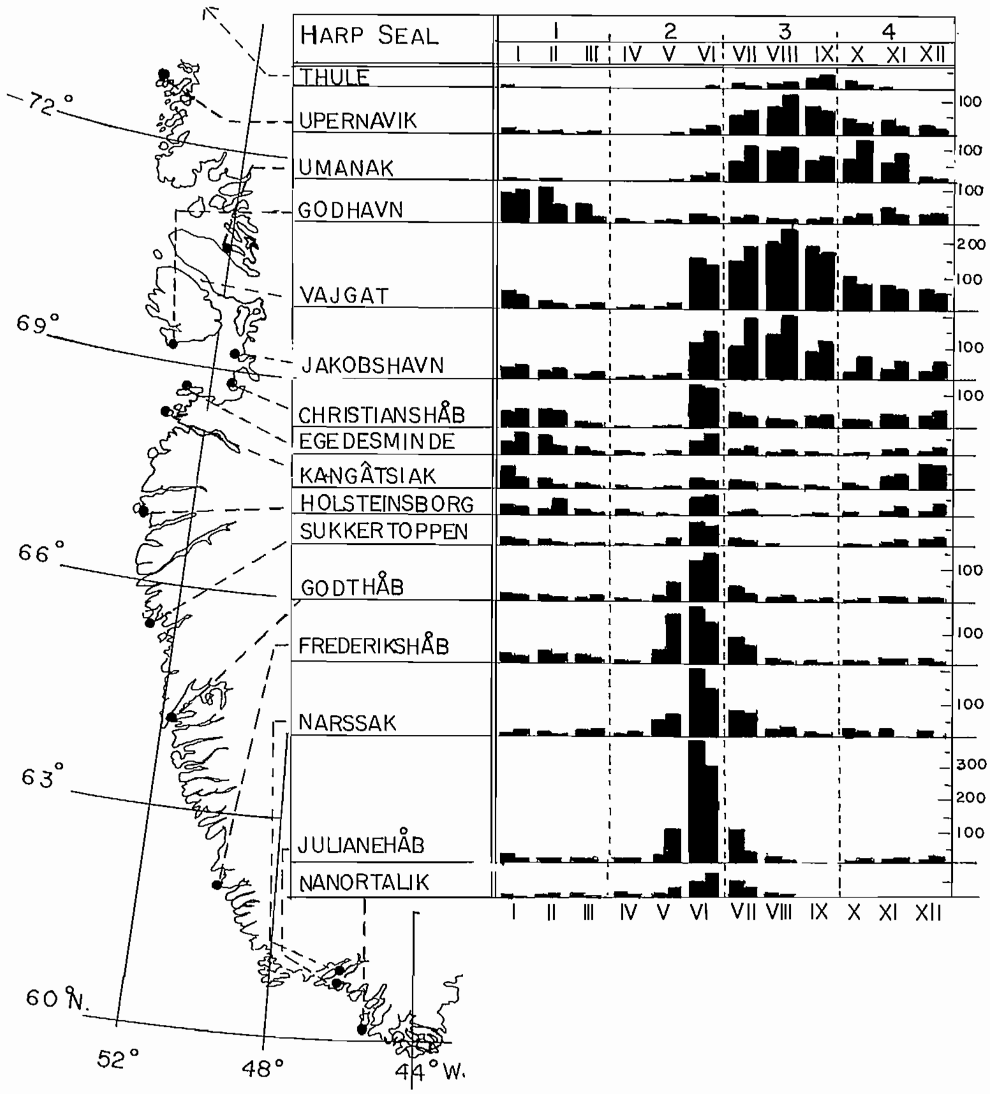


FIG. 43. Catches of harp seals on the west coast of Greenland, 1948 to 1951, by district and half-month (from Sergeant 1965, after Rosendahl 1961).

exclusively from northwest Greenland, was collected and analysed by Kapel and Geisler (1979), and again there were few differences.

Figure 44 analyzes samples from 1953 and 1962. Hansen's data are grouped for regions where the age samples were small, that is, in all districts except Umanak and Upernavik. The following information emerges: From Julianehaab to Holsteinborg districts, i.e. the entire southern half of the sampled coastline, all age classes are represented. From Egedesminde to Christianshaab in the central region of west Greenland, mostly young adults aged 7-9 yr are represented. From Jakobshavn to Godhavn the mean age drops further with a peak shown at 1-3 yr. In Umanak district, nearly half the sample is made up of 0-group animals i.e. young of the year, indicating that this is where the young summered in 1953. In Upernavik the age rises again to a peak at one year, but the sample is still mainly of young animals.

From Rosendahl's samples of 1962, juveniles of the 0 group predominate both at Sarqaq in the Vaigat, and at Tasiusaq in the northern Upernavik district. The former site comes at the northern end of the Jakobshavn district and close to the Umanak district. Therefore as compared with 1953, in 1962 the mean age seems to have been slightly lower in the Vaigat and Upernavik districts. However, the basic age distribution in northwest Greenland remained unchanged. By far the biggest age samples in west Greenland, representing nearly 70% of Hansen's age samples and 100% of Rosendahl's, come from Disko Bugt (69°N) and northwards. Most of these summering animals are young or immatures less than 5 yr old. The adults for the most part disappear before this northern part of the west Greenland coast is reached.

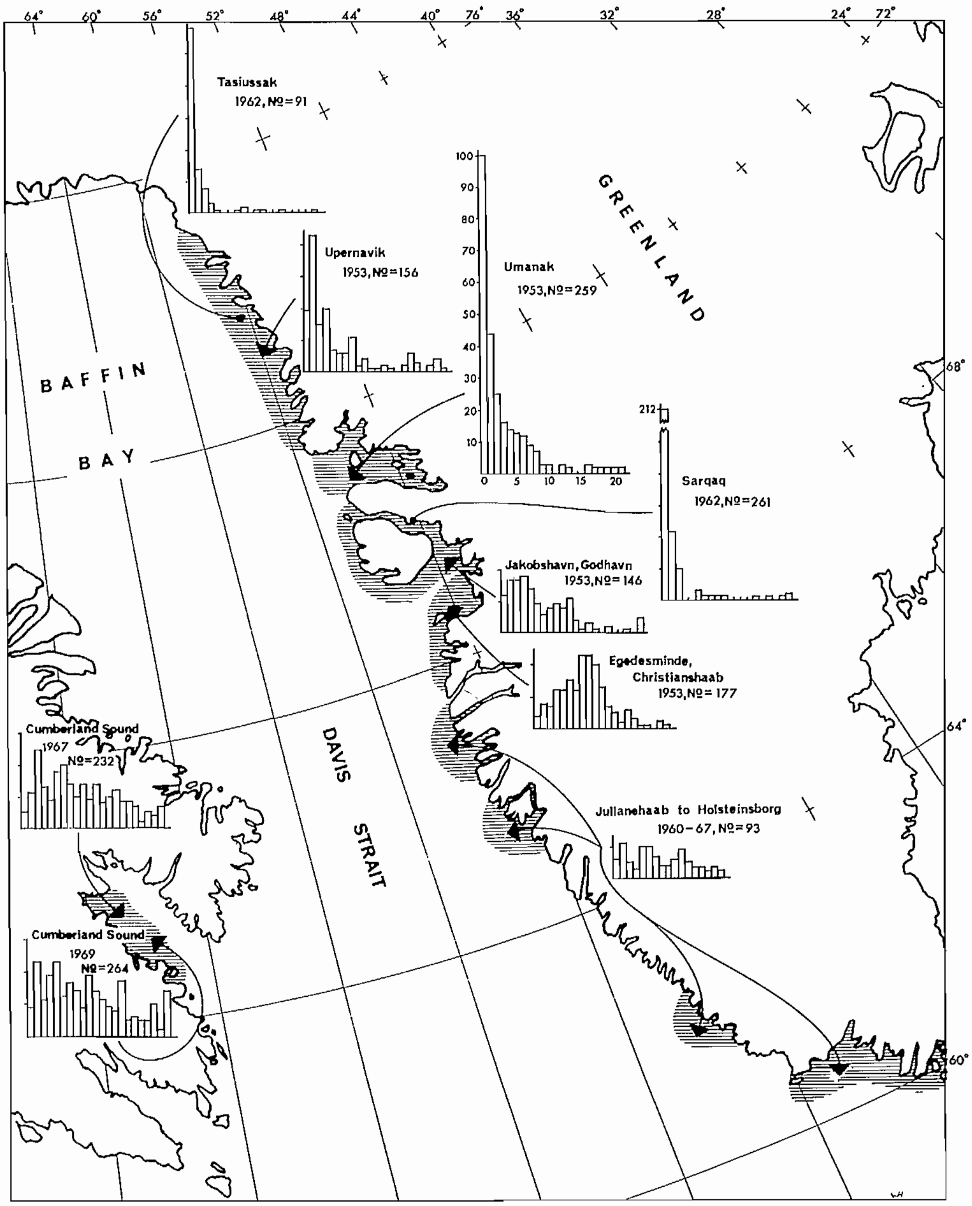


FIG. 44. Summering of harp seals by area and age in West Greenland and Baffin Island in the 1950's and 1960's. Age starts with underyearling (0 gp) at left.

Kapel (1975b) reanalyzed the 1953 sample and compared a sample collected in northwest Greenland in 1972. The 1972 sample was carefully compared with catch figures for each locality as to season of catch, and found to be more representative than Hansen's. Nevertheless the age-samples do not change their composition; from the Vaigat, from Umanak and from Upernavik districts, animals aged 0 to 5 and especially 0 group animals dominate. Kapel and Geisler (1979) repeated the analysis for Disko Bugt, Umanak and Upernavik districts with samples from 1976 and 1977 and the same results were obtained. Indeed, 0 group animals were even more in excess, doubtless because in these first Greenlandic age samples taken after imposition of the 1972 quota restriction (p. 99) on catch of young at Newfoundland, the numbers of escaping young had increased.

Since the proportion of older ages of seals in age samples at south and central-west Greenland was quite high in 1953 (Fig. 44) we do not need to assume that the catches in northwest Greenland, highly biased to young seals, are highly selective. There must be a great majority of young animals present.

Kapel and Geisler (1979) give catches of harp and hooded seals at Greenland from 1975 to 1978. For 1975, a year with complete data, catches in central west Greenland northward accounted for 69.6% of total west Greenland catches of harp seals. Thus, although recent age sampling has been somewhat biased to this area, it seems clear that most of the summering animals in Greenland are juveniles and immatures. This is also shown by catch statistics in Greenland, which separate spotted animals (*blaasider*) from those with saddles (*sortsider*). These, as we know (p. 7) are broadly speaking immatures and adults, respectively. As catch statistics since 1963 show (Table 14), Greenland catches show a catch of at least 70% and, in the 1970's over 80% of immatures.

Tag and brand recoveries: Because of a high loss rate of tags in the past, knowledge of migrations of harp seals tagged as young at Newfoundland referred mainly to the 0 group animals with a rapidly decreasing number of one to three year and older animals. From the knowledge gained from age samples, we would expect recoveries of the younger animals to come mainly from the northern

TABLE 14. Arctic catches of harp seals, western North Atlantic.

Year	West Greenland[a] Immature	Adult	Unseparated or total	Percent immature	Arctic Canada	
1954				—		
1955			16 313	—		
1956			11 490	—		
1957			13 591	—		
1958			17 571	—		
1959			9 623	—		
1960			16 944	—		
1961			12 558	—		
1962			8 966	—		
1963	7 951	2 072	10 023	0.793	362[b]	
1964	6 888	2 252	9 140	0.753	1 413	Average
1965	7 042	2 209	9 251	0.761	1 590	
1966	4 987	2 042	7 029	0.709	1 320	1 768[c]
1967	2 686	1 529	4 215	0.637	1 041	
1968	5 004	2 022	7 026	0.712		
1969	5 051	1 332	6 383	0.791		
1970	4 113	1 634	5 747	0.716		
1971	—	—	5 001	—		
1972	4 705	886	5 591	0.841		
1973	7 000	1 700	8 700	0.805		
1974	5 081	1 341	6 422	0.791		
1975	5 119	850	5 969	0.857		
1976	6 727	1 060	7 187	0.936		
1977	8 011	1 927	9 938	0.806		
1978	6 432	1 230	7 662	(0.839)		
1979	7 278	1 613	8 891	(0.819)	3 620[d]	
1980			12 270		6 184	
1981			13 605		4 672	
1982			17 244		4 268	
1983			18 739		—	

[a] 1 April to 31 March up to 1965 inclusive. Sources: Gronlands Fangstlister; ICNAF/NAFO Statistical Bulletin 1961–83.
[b] 1 July to 30 June. Sources: Hudson's Bay fur returns, unpublished Royal Canadian Mounted Police game reports.
[c] Smith and Taylor (1977) average for years 1962–71. Excludes arctic Quebec.
[d] Department of Fisheries and Oceans, Yellowknife and Winnipeg 1979–83. Excludes arctic Quebec.

TABLE 15. Recaptures of tagged harp seals in West Greenland 1951-74.

Month	Total number	Numbers in ICNAF Subarea					
		1-F 60°-61°N.	1-E 61°-62°30′	1-D 62°30′-64°15′	1-C 64°15′-66°15′	1-B 66°15′-68°50′	1-A 68°50′-N′ward
V	3	1	2				
VI	9	3	3	1		1	1
VII	11	2				1	8
VIII	18					1	17
IX	14					1	13
X	8					2	6
XI	2					1	1
XII	1					1	
I	5				1	1	3
II	2				1	1	
III	—						
IV	1					1	
Summer	2				1		1
Fall	1						1
Late in year	6						6
?	1				1		
Total	84	6	5	1	4	11	57

part of the catching field of West Greenland. This is true except for the months of May and June. Then, just after arrival of the young animals, recoveries are mainly in extreme southwest Greenland (Table 15 and Fig. 45).

Larsen and Kapel (1979) analyzed results of large scale Canadian tagging of harp seals at Newfoundland in 1978 as recovered in Greenland up to early 1979. The seals were tagged with "Rototags" of coloured plastic, a much more long-lasting type of tag than metal tags previously used. The pattern of recoveries is unchanged from earlier experiments, with a preponderance of returns from central west Greenland (Disko Bay) and northward. However a new feature has been a small number of returns in year one from east Greenland, all in the Angmagssalik district (p. 31). This new feature is presumably the result of the much larger scale of tagging and consequent increased number of returns. From the same year of tagging, 1978, four recoveries of seals tagged as young at Jan Mayen by Norwegian workers were also obtained in the Amgmagssalik and Scoresby Sund districts of East Greenland; and Norwegian workers report recoveries in west Greenland of animals marked at Jan Mayen (Ulltang and Øien 1988). Therefore, there is an overlap in summering range of these two herds. This discovery also suggests that some of the harp seals previously found to have arrived early in the summer at southwest Greenland probably pass to southeast Greenland later in the summer.

b. Arctic Canada

We have a good deal of information from the 1970's from aircraft and ship surveys in this region, as well as some age samples and tag and brand recoveries, which throw light on seasonal movements and the age classes of seals involved. *Hudson Bay, Hudson Strait and eastern Baffin Island:* MacLaren Atlantic Ltd. (1978) recorded a number of sightings of harp seals from surveys in Ungava Bay and Hudson Strait. It is known that, from here, numbers of animals pass into northern Hudson Bay extending as far as the Sleeper Is. (Manning 1946; personal observations) and the Belcher Is. (Freeman 1967) in the east, and Rankin Inlet on the west side.

Manning (1946) saw harp seals in July and August 1944 at Port Harrison and the Nastapoka River in eastern Hudson Bay and at Driftwood and Gilmour Is. and the King George, Sleeper and Marcopeet Is. On M/V *Calanus* on September 15, 1958 we saw 2 adult females which had been caught by a Port Harrison boat at the Sleeper Is.

There is also a remarkable record of a few beater seals taken at Fort George (now known by its Cree Indian name, Chisasibi), James Bay in 1976; the record, given to us by Mr. R.G. Greendale, was supported by a pelt.

Sutton and Hamilton (1932) observed harp seals in some numbers on the south coast of Southampton I. in September 1929 (up to September 27) and obtained

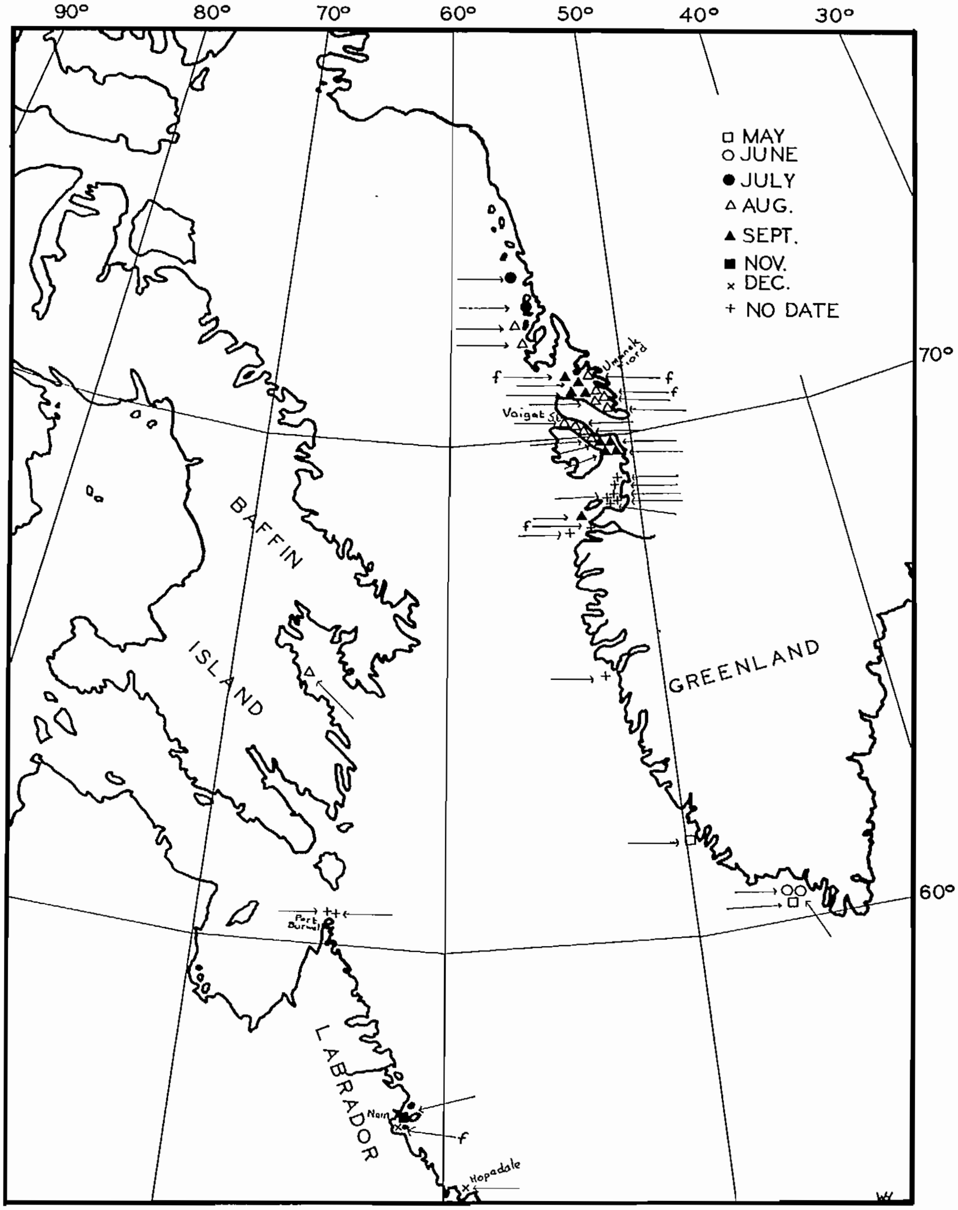


FIG. 45. Recoveries during the same year in northern waters of harp seals tagged at Gulf and Front in March 1966.

reports in this area in late May or early June, and on July 24, 1930. They recognised the species as a summer migrant here. We have received a few recent tags from Coral Harbour, Southampton I.

The majority of the harp seals move up the west side of *Davis Strait*, leaving northernmost Labrador in early June and reaching Cumberland Sound by mid June (MacLaren Marex 1979b). They pass through pack ice and appear to utilise a shore lead. Numbers are high in Cumberland Sound through the summer and there is much hunting of these animals from Pangnirtung and its camps (Fig. 46).

In autumn, with freeze-up of the inner sounds, the animals move to southern Cumberland Sound around the Lemieux Is., where numbers peak in early November; there is then a build-up off Frobisher Bay in late November–early December, and by early December they are passing northern Labrador again. Southward movement out of an area occurs as fast ice builds up from the coast and pack ice thickens. MacLaren Marex (1979c) also found a small number of harp seals, evidently animals one year old and upward, wintering along the pack ice edge in Davis Strait in April, 1978.

MacLaren Atlantic (1977) observed seals near shore between Frobisher Bay and Resolution I. from August 18 to September 11, 1977. Harp seals were more numerous (176 seen) than ringed seals (30 seen). More than 86% of harp seals were in groups of four or more, with one group of 100 offshore near the mouth of Frobisher Bay. Smith et al. (1979) observed and collected harp seals in

FIG. 46. Inuit hunters from Pangnirtung flensing two adult harp seals at Kangilo Fjord, Cumberland Sound, Baffin I. on 7 August 1979.

the inshore waters of the Hall Peninsula, between Cumberland Sound and Frobisher Bay, in summer and autumn, 1979. They found juvenile and bedlamer seals solitary or in small groups of 3–5 animals, adults in larger groups of 10–20 animals. Foods in five stomachs were some polar cod *Boreogadus saida,* and more pelagic Crustacea (*Mysis oculata, Parathemisto libellula, Sergestes arcticus*). A similar distribution of food organisms had been found in a few stomachs collected in Cumberland Sound (Sergeant 1973a) — a rather high proportion of pelagic Crustacea in the diet as compared with fish, which cannot be as abundant here as in the high arctic (see below).

The catch of harp seals in the Canadian arctic in the early 1980's averaged about 5 000 harp seals a year (Table 14). Catch statistics and tag and brand recoveries show that the great majority, about 95% of these catches, came from eastern Baffin Island, and more than half of them from Cumberland Sound. Adding in catches from Quebec and Labrador, excluded above, Stewart et al. (1986) obtain about 7 200 harp seals caught in the Canadian arctic annually in the late 1970's–early 1980's, out of 61 000 seals of all species, mostly ringed seals.

The Arctic Biological Station investigated the age composition of harp seals in Cumberland Sound from samples collected in 1967 and 1969 (Fig. 44). These showed all age classes present but there was a clear deficiency of the youngest 1 or 2 yr olds. R.E.S. Stewart (in litt., 29 October 1979) obtained very much the same age distribution from Cumberland Sound in 1976 and 1977. Peak ages were 4 and 3 yr, respectively. The same result is obtained from tag recoveries from the mass tagging of 1978, which show a peak at 3 yr of age. The missing year-classes are those which have moved to West Greenland. Table 16 shows that the percent of tag returns from West Greenland of all arctic returns is extremely high in the first 2 yr but falls steadily thereafter to a figure of about 55%. This ratio cannot be translated directly into the proportion of animals on each coast — West Greenland or arctic Canada — since not only are the catches larger in West Greenland, but we do not know the relative efficiencies of return of tags in each area.

Lancaster and Smith Sounds: From these areas of the arctic, we have almost no knowledge of age distribution from age samples. We know from catch statistics (Rosendahl 1961) that some harp seals regularly reach Thule, northwest Greenland, where Rosendahl showed a peak of catching in September. Vibe (1950) states that harp seals reach Thule in June, and stay well into October, migrating in and out of the fjords, and leaving when the first ice forms.

On the western side of the "North Water"[8], harp seals are well known to summer in Lancaster and Jones sounds. Until recently, observations were necessarily from the coast or from ships. Miller (1955) states that harp seals migrate into Tay Sound (innermost Eclipse Sound) together with narwhals in end July–early August, are numerous in Guy's Bight and northernmost Navy Board Inlet and fairly numerous in Eclipse Sound; and that they leave Tay Sound about September 25, driven out by ice. Ellis (1957) saw herds of harp seals in Adams Sound (close to the settlement of Arctic Bay) and in the main Admiralty Inlet outside, on September 9, 1954. Dr. Leslie Tuck (unpubl. MS) working from the cliffs of Cape Hay, northern Bylot I. in the summer of 1957 watched "an immense constant stream of herds spaced about half a

[8] A semi-permanent body of open water (polynya) of large size in northern Baffin Bay, so named by the 19th century whalers.

TABLE 16. Recoveries from Arctic Canada (AC) and from West Greenland (WG) of harp seals tagged in the Gulf and on the Front ice in March 1978.

Year of recovery	Age (yr)	Gulf		Front		Total		N	Percent at Greenland
		WG	AC	WG	AC	WG	AC		
1978	0	12	0	40	1	52	1	53	.98
1979	1	18	2	42	2	60	4	64	.94
1980	2	15	7	22	9	37	16	53	.70
1981	3	7	7	9	2	16	9	25	.64
1982	4	7	2	8	7	15	9	24	.63
1983	5	4	3	5	5	9	8	17	.53
1984	6	3	2	2	2	5	4	9	.55
1985	7	2	—	—	1	2	1	3	.66
Totals		68	23	128	29	196	52	248	

mile apart''. There was no return movement up to August 20th when his observations here ceased. On August 22 and 23, harp seals were moving into and out of Navy Board Inlet. Greendale and Brousseau-Greendale (1976) working from the same site saw harp seals pasing in summer 1976 from 3 July up to the end of their observations (mainly devoted to narwhals) on July 31st. They estimated only 16 000 animals passing during this period. They described animals passing as 95% saddled adults and 5% spotted beaters or bedlamers. Group sizes of adults were 5 to 100 but there were solitary juveniles. Thus, in spite of a lack of age samples, we can be reasonably sure that it is mainly adult harp seals which occur in this area.

Extensive observations were made from aerial surveys in the 1970's by scientists working for consultant companies carrying out ''environmental impact'' studies for oil companies in Lancaster Sound. Generally, this type of survey covered a defined area of interest to the oil company, within which area observations were extremely thorough.

Johnson et al. (1976) and also Renewable Resources Consulting Services Ltd. (no date) studied a block of Lancaster Sound lying between 80° and 83°10′W from May 1 to September 28, 1976 by means of coastal flights and offshore transects. This belt includes Cape Hay and also the mouth of Navy Board Inlet, where harp seals were found to be abundant. Harp seals were commonest in this region in July, arriving July 4 to 5, and again in September, with a fall-off in numbers in August, suggesting a movement further west. Distribution was markedly coastal, in close proximity to the receding land-fast ice in July, although almost all seals were in the water. Group sizes were accurately quantified with most animals travelling in groups of 11–20 but ranging from 1 to 75 (Fig. 11); group size did not much change between July and September. Surveys ended before harp seals left Lancaster Sound.

In flights out of Resolute in early August 1973, I did not see harp seals in Admiralty Inlet, but in Maxwell Bay on the north side of Lancaster Sound there were herds of harp seals, a few thousand in number, accompanying several hundred white whales (*Delphinapterus leucas*) and many seabirds, probably mostly *Fulmarus glacialis* L., into the bay on August 3rd. The ice at the head of the bay had just gone out and I had the impression that seals, whales and birds were feeding heavily on a prey — probably *Boreogadus saida* — suddenly freed from the safety of the ice. (In neighbouring Radstock Bay the shore ice was still solid and a herd of white whales waited just outside).

In Jones Sound, Dr. M.M.R. Freeman kindly sent the unpublished results of studies of marine mammals made by him from the catch at Grise Fjord, Ellesmere Island in summer 1965. Among these were 15 harp seals caught between 26 August and 19 September. From the lengths of the seals, I judged that all were adults save two. Freeman found remains of *Boreogadus saida* in the stomachs of 3 seals taken on September 6. Judging from otolith sizes, and comparing these with otoliths from intact fish, the arctic cod eaten measured from 12.5 to 17.5 cm in length. Cod eaten by white whales were larger, and it is probable that in the observation at Maxwell Bay described above, white whales, harp seals and seabirds were all feeding on different-sized fish.

R.E.S. Stewart (in litt.) obtained an age sample of 54 animals from Jones Sound in 1977. This had a bimodal frequency with peaks at 4–5 and 20–21 yr, i.e. had an older age distribution than animals examined by him in Cumberland Sound the same year.

Finley (1976) worked further west in Barrow Strait in July and August 1975. Harp seals were seen starting from breakup on July 6th, between Cornwallis Island and Prince Leopold Island. While one herd of 519 animals was seen on ice, the remainder of the animals were in the water of Barrow Strait offshore but never far from pack ice. Group size was smaller than described by Johnson et al. (1976), observations of singletons being commonest. Density was low and a minimum estimate of numbers was some 2 000 present. Finley and Johnston (1977) extended these observations of harp seals south to Bellot Strait in August–September 1976. Over 100 harp seals were seen here in late August and early September. This must mark the normal limit of penetration southwestward of harp seals from Lancaster Sound in an average open summer.

As to the season when harp seals clear the high arctic, Webb (1976) in a survey from Bylot Island south to Cape Dyer on September 23-24, 1976 found harp seals between Navy Board Inlet (where we have noted their presence all summer), Pond Inlet and Home Bay, mainly at the north end of this area. He also had observations at Broughton Island on September 26th, where the Inuit stated that seals passed in September, October and November.

On September 5, 1963 Canadian Transport Department ice observer A.W. Smith observed 400-500 harp seals close to Grise Fjord from the icebreaker *Labrador*. On September 28, at 76°01′N, 77°W (60 km east of the Devon I. coastline) the ship passed for one hour through harp seals, estimated at 10 000 in number. Transport's latest reported sightings from the area came from southeast of Devon I. on October 2 to 4, 1962.

We are now back where we started, with the migration south along the Baffin and Labrador coast to the wintering area.

7. Mixing of Gulf and Front Herds

Large-scale marking of young seals was carried out in the Gulf in 1966-70, 1972-77 and 1978-80; on the Front in 1978-80. From recoveries of tags in Gulf and Front areas in subsequent winters the degree of cross-over was calculated. Since catches of immature and adult seals have always been much larger on the Front than in the Gulf (Table 17), the cross-over rates from Gulf to Front are given as a proportion of total catch. Figure 47 shows the results, for both raw and corrected data; Table 18 shows full data for the 1978-80 experiment.

Front-tagged animals show a return to the Front which increases from 88% at age 1 to 100% at age 5. When corrected for catch, this reduces to from 50% to some 80% (Table 18).

Gulf-tagged animals, when corrected for the ratio of catches, show a return to the area of birth which also increases with age. In this there seems to have been a change with time. The corrected data show 95% of the Gulf

TABLE 17. Relative catches of immature-plus-adult harp seals in Gulf and Front regions. Data from ICNAF (NAFO) statistical bulletins.

	Mean Catch (%)		
Time Period	Front	Gulf	Total
1964-67	50 775 (84.5)	9 260 (15.4)	60 035 (100.0)
1968-71	33 427 (87.9)	4 614 (12.1)	38 041 (100.0)
1973-78	27 305 (82.5)	5 802 (17.5)	33 107 (100.0)
1979-83	19 063 (83.7)	3 720 (16.3)	22 784 (100.0)

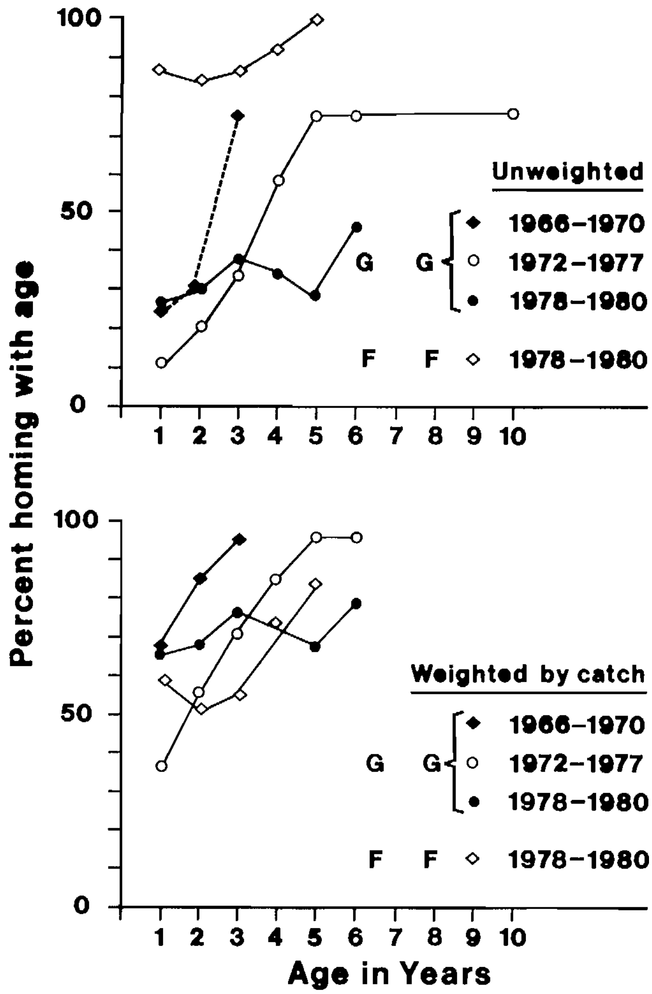


FIG. 47. Percent tagged young seals homing to native ice (Gulf or Front) by age, over time.

animals homing at 3 yr in the late 1960's, 75% of the 3 yr olds and 95% of the 5 yr olds homing in the early 1970's; and only 70% of both these age-groups homing in the early 1980's. This means that an increased percentage of animals, especially older ones, crossed to the Front at the later time, since there had been no change in the age when sexual maturity is attained (p. 119).

A check on these results is possible from other approaches.

(1) For females tagged (as adults) in the Gulf in the late 1970's, 4 were recovered or observed in the Gulf in subsequent years, 1 at the Front, for a homing rate of 0.8. This small sample agrees with our corrected results for juveniles.

(2) There have been 20 recoveries from Gulf-born and none from Front-born animals in the southernmost wintering area of the harp seal in the estuary of the St. Lawrence. A few Front-born animals have been found in the northern Gulf, and this must be the southern limit of their penetration of the Gulf at 1 yr and up.

In sum, the data suggest the capability of harp seals to home with increasing accuracy towards adulthood to a level of 0.8 or greater.

TABLE 18. 1978–80 marking experiment, returns to Gulf and Front areas in winter.

Age (yr)	Year of tagging	Raw Data: Gulf to Gulf Yes	Total	Ratio	Front to Front Yes	Total	Ratio	Corrected[a] Gulf to Gulf	Front to Front
1	1978	32	116	0.275	145	167	0.868		
	1979	30	108	0.277	45	46	0.978		
	1980	13	56	0.232	32	39	0.820		
	Mean			0.268			0.880	0.653	0.531
2	1978	29	91	0.319	60	74	0.892		
	1979	4	5	(0.800)	13	24	0.541		
	1980	12	53	0.226	23	23	1.000		
	Mean			0.302			0.842	0.688	0.509
3	1978	23	56	0.410	8	10	0.800		
	1979	3	11	0.272	10	11	0.909		
	1980	6	16	0.375	20	23	0.864		
	Mean			0.385			0.864	0.763	0.532
4	1978	12	26	0.462	6	7	0.858		
	1979	1	10	0.100	8	9	0.889		
	1980	3	10	0.300	14	14	1.000		
	Mean			0.347			0.933	0.732	0.731
5	1978	2	7	0.286	8	8	1.000		
	1979	2	7	0.286	6	6	1.000		
	Mean			0.286			1.000	0.673	0.837
6	1978	3	7	0.428					
	Mean			0.428			0.428	0.793	—

[a] By relative catch-rates.

If mixing occurs between two sub-herds, decreasing towards sexual maturity, it is important to know whether the two sub-herds retain a significant genetic isolation or not. Two methods have been used to study the question. Lavigne et al. (1978) studied genetic variability of young seals from Gulf and Front using starch-gel electrophoresis of soluble enzyme systems from a number of tissues. Gene frequencies were found to exhibit no differences between Gulf and Front animals.[9]

Sergeant (1978) studied the distribution of ages of adult females assessed from pelage types at whelping sites in the Gulf and on the Front; this can readily be done during marking of pups. The younger, spotted females and pale-saddled animals can readily be separated by eye from the older dark-saddled females (p. 29). Since hunting of young was at a considerably higher intensity at the Front than in the Gulf between 1972 and 1978, if the populations were isolated the Front should show an age structure with relatively more old animals. Results in 1976–78 however showed that there was no difference between the two areas (Table 19). That the method is valid is shown by comparable counts in the Gulf in 1964, a period when exploitation of young was high. As compared with the Gulf in 1977–78, the Gulf in 1964 exhibited far fewer young spotted and pale-saddled animals, demonstrating a much lower recruitment to whelping ages in the period prior to the 1972 quota (Table 19).

TABLE 19. Distribution of pelage type among adult, whelped females in late February to mid-March. Number and (percent).

Area	Years	Spotted	Light saddle	Dark saddle	Total
Front	1976–78	110 (14)	276 (36)	384 (50)	770 (100)
Gulf	1977–78	216 (18)	351 (30)	609 (52)	1 176 (100)
Gulf	1964	56 (7)	91 (12)	632 (81)	779 (100)

[9] With far fewer gene loci studied, Jan Mayen and northwest Atlantic animals did show differences. A properly conducted genetical study of all three populations remains a desideratum which requires full cooperation among Canada, Norway and the USSR.

The results discussed above show that the Gulf and Front substocks mix sufficiently that they can be treated as a common stock for the purpose of management, i.e. that a hunting regime concentrated at the Front will not deplete the Front stock differentially, presumably because there occurs an influx of Gulf-born immatures, which remain with the Front-born animals thereafter.

8. Site Tenacity

The results of aerial photographic surveys of whelping animals do not tell us very much about the constancy of numbers whelping from year to year in each subarea, Gulf and Front, because errors in the census compound with any variability that may occur.

However, evidence is available from the exceptionally mild year 1969 (Fig. 54). The number of seals whelping in the Gulf was closely studied by researchers from the Canadian government carrying out marking, by the sealing industry and by humane society observers. There was no ice in the Gulf except in Northumberland Strait and shore ice on the north coast of Prince Edward I. It was generally agreed that no more than 40 000 animals whelped here, a skill of 32 000 having left ca. 6 600 survivors. The number at that time expected to whelp in the southern Gulf was ca. 100 000. Probably, the remainder searched for ice, and finding none in the northern Gulf, passed through the Strait of Belle Isle and whelped together with the Front herd on the coast of Labrador at Hamilton Inlet (But see p. 130). Age samples of animals migrating into the Gulf and taken at the net fishery in La Tabatière in 1975 and 1976, when the 1969 age class should have been dominant, do not show any marked shortage of animals in it.

In 1981, however, although ice was of minimal extent and thickness in the Gulf, harp seals whelped off the west coast of the Magdalen Is. and drifted to the north coast of Prince Edward I. Here storms destroyed the small amount of ice and young harp seals died due to starvation and loss of body reserves (Dr. J.R. Geraci, in litt.). Age samples of harp seals in the estuary of the St. Lawrence in the years 1985 and 1986 show an extremely small 1981 year-class (all seals taken here are of Gulf origin, as shown by tag recoveries), showing that the 1981 Gulf year-class was reduced by shortage of ice, presumably by the mechanism observed by Geraci.

Under unusually heavy ice conditions, it is not possible for harp seals to move from the Front to the Gulf before whelping, since the Strait of Belle Isle is then blocked by ice. Whelping merely occurs further south along the east coast of Newfoundland.

B. The Jan Mayen Population

The Jan Mayen population of the three lives closest to the arctic. The whelping grounds are described as follows by Robert Brown (1868):

"Early in March (the seal) is found by the sealing ships in immense numbers in the proximity of the dreary island of Jan Mayen off the east coast of Greenland, not far from the 72nd parallel of north latitude; but of course the longitude varies with the extent which the ice stretches out to the eastward, though the common meridian is between 6° and 8° west of Greenwich. They are never found far inwards on the fixed ice, but on the margin of the icebelt which extends along the whole of the eastern shores of Greenland, stretching as far as the longitude of Iceland, and sometimes even for a hundred miles to the eastward of that island and of Jan Mayen island into the ocean. The general direction of its sea margin is towards the north-east... The nature of the ice, which can easily be perceived by the experienced sealer, determines whether the Seals will be found far from the margin of the ice. Thus, if there is much new, light ice, it is probable that the seals will have taken the ice at a considerable distance from the seaboard margin of the pack, as it is well known that instinctively they select ice of a strong consistence for the safety of their young when in that helpless condition in which they are unable to take to the water. Again, they often take the ice where it stretches out to sea in the form of a long, broad promontory, with apparently this end in view, that their young may easily get to sea when able to do so; this is the great clue which guides the sealer in the choice of the ice where he may find his prey."

Nansen (1925) gives a map (Fig. 48) which shows the variation in site of whelping over a number of years. He amplifies the description of whelping ice as follows:

"A good distance from the outer edge of the drift ice, the females go on to the floes about the middle of March or later. They choose snow-covered ice of medium thickness, that is not so easily broken by storm and sea, and where their young ones have a

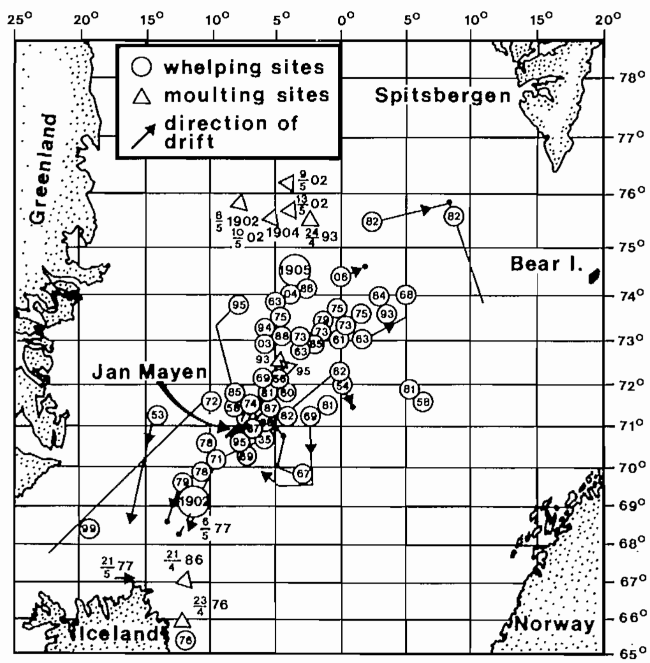


FIG. 48. Locations of whelping and moulting patches of harp seals at Jan Mayen I. in the late 19th and early 20th centuries (from Surkov 1960, after Nansen 1925 and Wollebaek 1907 [86 - 1886, 03 - 1903, etc.]).

little soft snow on which to lie. These floes are usually about three feet in thickness. As a rule the seals do not choose the older, thicker and more uneven floes, which are more difficult to ascend and more easily become compact. It is also quite an exception for them to give birth to their young on bare, newly-formed ice, or what is known as bay-ice".

Thus, the harp seals whelp on the fringe of winter ice lying seaward of the heavier arctic ice of the east Greenland pack, on which the hood seals, abundant in the area, whelp.

The main whelping season of this herd is in late March (Fig. 26). Thus in the early 1870's, when the arrival of steam sealers forced earlier entry to the whelping ice, and competition occurred between Scottish and Norwegian sealers, both groups sought a starting date of early April, which would have guaranteed fat whitecoats (Bentinck 1875; Melsom 1871). Capt. Soutar stated that "the seals pup between the 25th and the end of March, but sometimes even later" and Capt. Adams that on the 1st April "there would be one and a quarter inches of fat upon (the young) all over" when they would be 5 or 6 d old, whereas if sealing were delayed till 5 April, the seals (presumably the adult females) would have taken to the water (indicating the end of lactation). This whelping period is about 4 weeks later than in the White Sea (ut supra).

Predation of young seals by polar bears (*Ursus maritimus*) is quite common at this sealing ground (Nansen 1925).

Nansen (1925) describes in general terms the migrations of this herd:

"Towards the end of April, the multitudes of seals at the "Jan Mayen breeding grounds" begin to disperse. The young ones of the year... set off in herds towards the outer edge of the ice where there are plenty of crustaceans in the water, and here they frequently mount the "streams" of small ice that are detached from the more compact edge of heavier floes... The majority of adult seals proceed to the north and north-east along the edge of the ice, while some of them go southward to the sea south-west of Jan Mayen, and many of them every spring and early summer visit the banks off the coast of Iceland... After the seals have left the breeding grounds, they begin to moult at the end of April and in May. The old seals then congregate on the ice in large numbers. As mentioned previously, it is especially these "he-seal" flocks, as they are called, that are hunted during this period. Naturally there may also be females among these male seals, and a few young seals... When the moult is ended, the seals disperse in rather small herds over the drift-ice in the whole of the vast expanse of sea of the east coast of Greenland, from Denmark Strait or farther south, and Iceland northward towards Spitsbergen, and also most probably in (the) Barents Sea. Presumably they live in those regions the greater part of the year, until they again begin to assemble at the breeding grounds in the following spring".

To provide some specific detail, Rasmussen and Øritsland (1964) using tag recoveries showed that the young drift passively in the disintegrating pack towards northwest Iceland in the east Greenland current (Fig. 49).

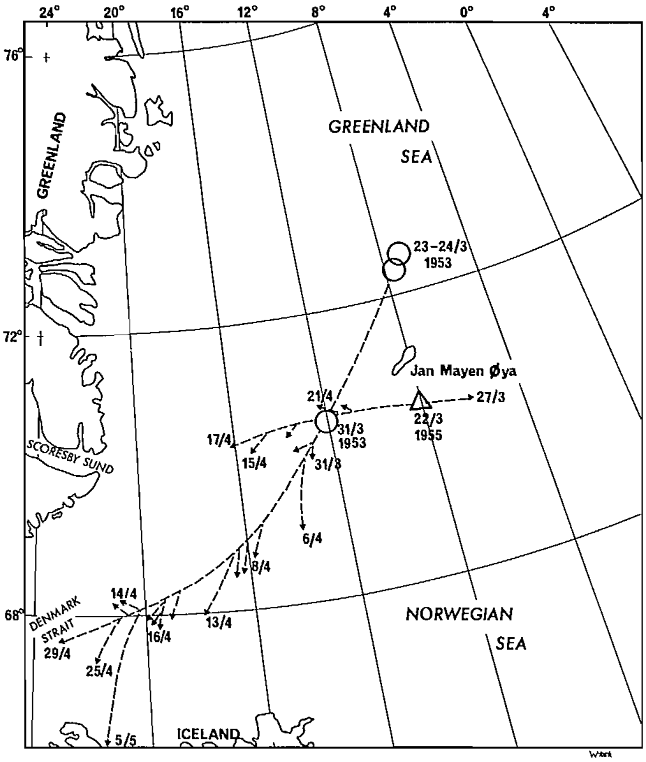


FIG. 49. The dispersal of weaned harp seal pups in the Jan Mayen area in 1953 and 1955. Tagging localities are plotted as circles (1953) and triangle (1955). Arrows indicate recaptures within the first six weeks after tagging (from Rasmussen and Øritsland 1964).

As at Newfoundland (Ch. VI) the young must afterward begin an active movement northward and probably in toward the coast, for they have not yet been found drifted round Kap Farvel with the East Greenland ice in summer[10]. R.W. Gray (1889) found juveniles on 1st May, 1888 at 72°10′N, 8°04′W, with crustacean remains, probably from seal faeces, in the water. Gray (1935) described adults, especially males, on heavy ice at 76°N where "they may lie on ice for weeks in fine weather", which sounds like moulting behaviour, and Khuzin (1964) found moulting groups at the ice edge from 24 April to 15 May between 75° and 76° N; these consisted mainly of adult males until the middle of May. Gray (1887) found adult harp seals moving east along the ice edge at 76°07′N, 36°E on July 19, 1886, and at 76°26′N, 27°03′E on July 22nd, and again at 75°07′N, 5°15′W on July 26th. Johansen (1912) also met them in the outer drift ice at 75°N, 4°34′W on 31 July, 1906 and at 75°N, 8°W on 30 July, 1908. There were none, and no bones of harp seals at archaeological sites, in east Greenland between 75° and 83°N. However, Bartlett (1934) met harp seals at the edge of the fast ice close to Shannon I. (75°N) on the east Greenland coast on July 9, 1930. Pedersen (1930) took old and young specimens in the fjords of Scoresby Sund (70°N) during September and

[10] But see p. 32 for later data.

October 1927 and 1928 and Degerbøl (in Stephensen 1933) a specimen between Angmagssalik and Scoresby Sund in August 1932. We now have tag recoveries of young animals of the Jan Mayen herd from both these settlements (Larsen and Kapel 1979).

C. The White Sea Population

As before we turn to Nansen (1925) for a general account of the annual cycle of this herd. (For the geography see Fig. 50.)

> "The eastern tribe of saddlebacks that live in (the) Barents Sea, and also to some extent in (the) Kara Sea, has its breeding grounds in the outer part of the White Sea near Mezen Bay, and south-westward at the entrance to the White Sea itself... In the late autumn there is a great migration of seals to the south, and according to certain Russian sources it begins to appear in the White Sea as early as the beginning of November, whilst according to other reports it does not arrive until the beginning and middle of December. The herds come both from the east, along the coast from Nova(ya) Zeml(ay)a and also from the north across the Barents Sea. They include both adult and young seals... Simultaneously with the gathering of these multitudes of seals near the breeding grounds in the White Sea, considerable numbers of seals may also arrive in other districts, e.g. off the Murman Coast in December and January (especially in 1902) and often in February and March also. Thus in many years large numbers of seals came to Ribachi Peninsula from January to April. The people there consider that these seals come from the north, "from Spitsbergen". Many of the female seals are pregnant; newly-born pups have also been found on the shore... At times the herds cover large areas of ice... According to information given by some Russians, the saddlebacks also assemble in late autumn in Cheskaya Bay, east of the Kanin Peninsula".

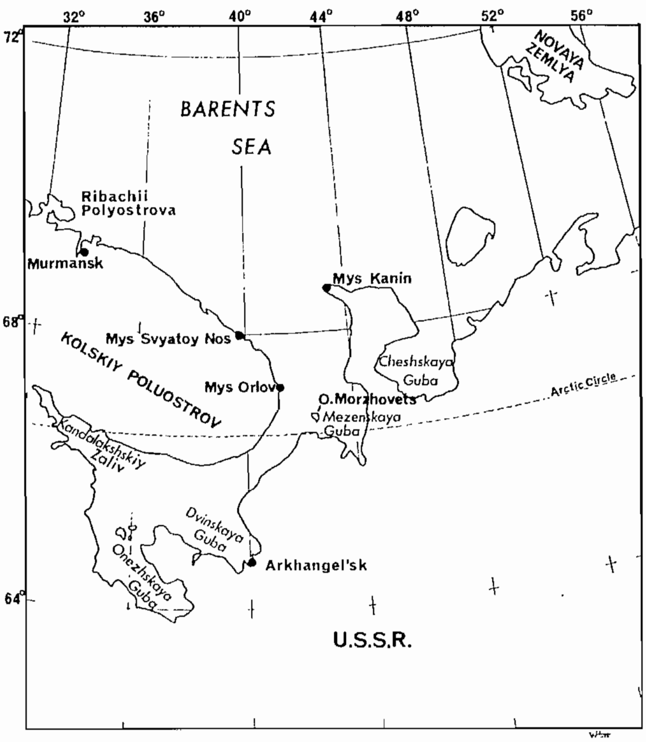


FIG. 50. Geography of the eastern herd of harp seals in winter-spring.

> "During the period between the middle of February and the end of March, the young ones are brought forth on the ice. The males are also present at the breeding grounds for the purpose of mating, which takes place on the ice about three weeks after the birth of the young ones. According to a Russian source (Smirnov) the earliest mating was observed on March 10th. After mating comes the moulting, which may last from the beginning or middle of April to about the middle of May. Generally from the beginning or middle of April till about mid May the seals set out again for the north in great multitudes from the White Sea. As a rule the young ones leave first, then the older ones, and lastly the full grown seals. Some of them proceed to the north-west along the ice off the Murman Coast to Ribachi Peninsula, and on to Varanger Fjord and East Finmark, where they usually appear during the period from April (or even March) to June, when they disappear. They usually arrive off East Finmark at the same time as the capelan, which approaches the coast followed by multitudes of cod".
>
> "The seals that go there are to a large extent the young ones that are born in the White Sea the same year. But it is impossible to draw any hard and fast line between this spring migration of seals coming from the east, and the winter migration of seals which has been discussed previously, and which the inhabitants believe to come from the north. In certain years the seals also migrate farther westward along the coast of Finmark... There were particularly large swarms of them in the winter and spring of 1902 and 1903 as far south as the coast of Vesteraalen and Helgeland... These flocks of seals mainly consisted of young seals from the previous spring, but there were also many old seals and full-grown males among them".
>
> "The majority of those that come out of the White Sea in April and May proceed to the north-east along the edge of the ice, and as by degrees the limits of the ice recede northward and eastward, the herds of seals follow them towards the coasts of Nova(ya) Zeml(ay)a and northward toward Franz Josef Land and Spitsbergen, and to some extent also into the Kara Sea".
>
> "In summer and the early part of autumn they almost disappear from the southern part of (the) Barents Sea, and only a few solitary seals are to be met with in the White Sea or along the Murman coast, and the north coast of Russia towards Nova(ya) Zeml(ay)a".

Wollebaek (1907), Smirnov (1924), Naumov (1933), Chapskii (1938, 1961), Sivertsen (1941), Dorofeev (1960), and Nazarenko (1970), provide more detail on the annual cycle. Whelping occurs from late February through the first half March in the pack ice of the White Sea or of its entrance the Voronka (funnel) and Gorlo (neck) (Fig. 51). This is winter ice of the current year and about 40–90 cm in thickness (Popov 1971a), as in the southern Gulf of St. Lawrence. The females whelp first to the south and in larger patches (Popov 1969). Nazarenko (1970) gives the limits of usual whelping as 65°25′–65°55′N, and 38°30′–39°40′E. The young seals usually drift northward out of the White Sea towards independence on their natal ice at a speed of about 5km/d (Chapskii 1961) though in a cold spring with north winds such as that of 1966 this drift may be much delayed (Popov 1971a, Bianki and Karpovich 1969).

The sequence of moulting of older animals as described by authors such as Naumov (1933), Sivertsen (1941) and Surkov (1957) is the same as for the western herds. At the beginning of moult in late March, the adult males are found hauled up in the White Sea near the whelping sites, the immatures on the northern outskirts. The animals mix late in April and the adult females arrive. Moulting continues into May. After completion of moult in late May the adults move actively northward to the fringes of the pack-ice in the Barents Sea where they spend the summer, their distribution shifting with the edge of the pack-ice (Fig. 52). Tag recaptures show that adults may reach southeast Spitsbergen by late June (Rasmussen and Øritsland 1964).

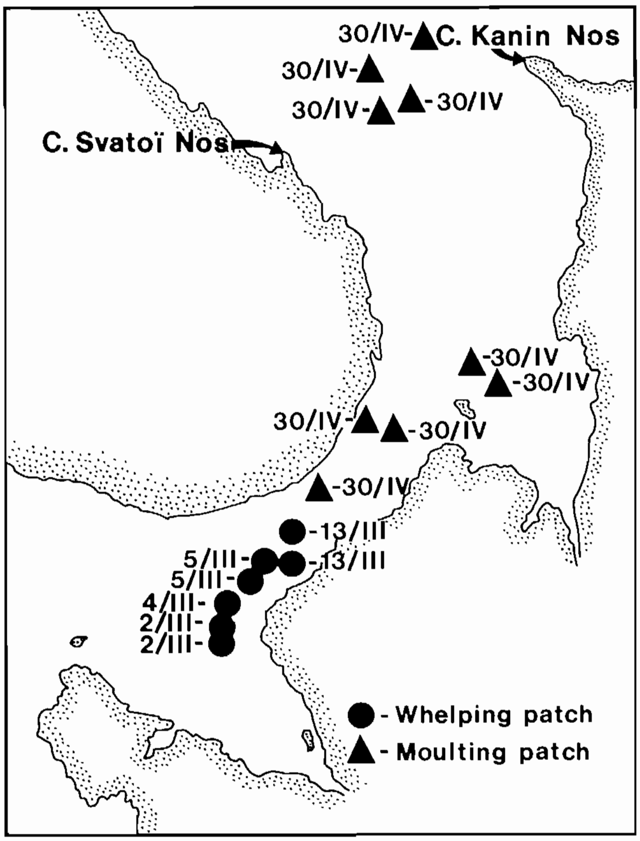


FIG. 51. Positions of whelping patches (circles) and moulting patches (triangles) in the White Sea in March–April 1972 (from Anon. Soviet Union 1972).

The southward migration begins in late September and brings some animals of all age classes close to shore along the west coast of Novaya Zemlya, where they may remain from November to February. However, normal distribution in winter usually extends west to the Murman coast, and in severe winters, can be displaced west towards Finmark.

Large variations can occur however in the range of wintering. Thus in 1978–84 (and later), harp seals were again reported to have followed capelin into the East Finmark fjords (Bjørge et al. 1981, T. Øritsland, in litt. 10 April 1987). Immatures and females arrived in February, the former remaining to late April, while adult males arrived in mid-March, and adult females returned from mid-April to mid-May. More than 10 000 drowned annually in cod gill nets in 1979 to 1981. Most probably, this renaissance of the problem reflects the increase of the eastern herd following protection in 1965 (p. 92-93) to an estimated million or more animals in 1981 (Bjørge et al. 1981). This agrees with the calculations of Borodin (1978) who estimated the population at 0.7 million in 1972, and calculated that 8–10 yr would be necessary for restoration to maximal sustainable yield production, defined by him as 220–240 thousand females, or about 1 million total herd. This time period would bring us to 1980–82.

During the interim between 1903 and 1977, little was heard of incursions of harp seals westward to Norway except for a small-scale displacement as far as Finmark in winter 1962/63 (Øynes 1964). It was just in this period, from the 1920's to the 1960's, that the eastern herd received heavy exploitation. It is also true that the period of the 1920's and 1930's was one of warm climate in the north-east arctic (Jones et al. 1986; Fig. 53), which would have tended to displace the spawning of capelin eastward towards the Russian and away from the Norwegian sector (Stergiou 1984). Therefore, we cannot fully separate these two influents of climatic and population change on the westward displacement of the White Sea harp seals in winter.

In January 1987 there occurred a particularly heavy emigration or invasion along the whole Norwegian coast, with more than 60 000 seals caught in fishing gear, especially from the Tromsø area (69°30′N) (Wiig 1988b). Although a few animals were caught bearing tags put on at Jan Mayen in spring 1985 and 1986, calculations and biochemical analyses showed that most animals must have come from the White Sea where no tagging had taken place[11]. One animal reached Shetland, others Denmark, the Netherlands and Germany (Duguy 1987). Six reached the Atlantic coasts of France as far as the Loire (Duguy

[11] Thus, (purely as illustration) if production in the West Ice = 100 000, 500 tags were put on in March 1987, and there were 10 000 young seals caught at Norway, then the number of West Ice tags taken should have been 50, assuming all seals came from the West Ice (and no tag loss). Actually there were 6 tags reported. Therefore, only perhaps 10% of seals may have come from Jan Mayen.

This conclusion was confirmed by comparison of fatty acid composition of eye lens and jawbones from animals from the 2 herds, which showed differences believed genetically determined; analysis of the composition in animals taken on the Norwegian coast showed that these resembled White Sea animals (O. Grahl-Nielsen, Kjemisk Institutt, Universitet i Bergen, writing in *Bergens Tidende,* 17 December 1987).

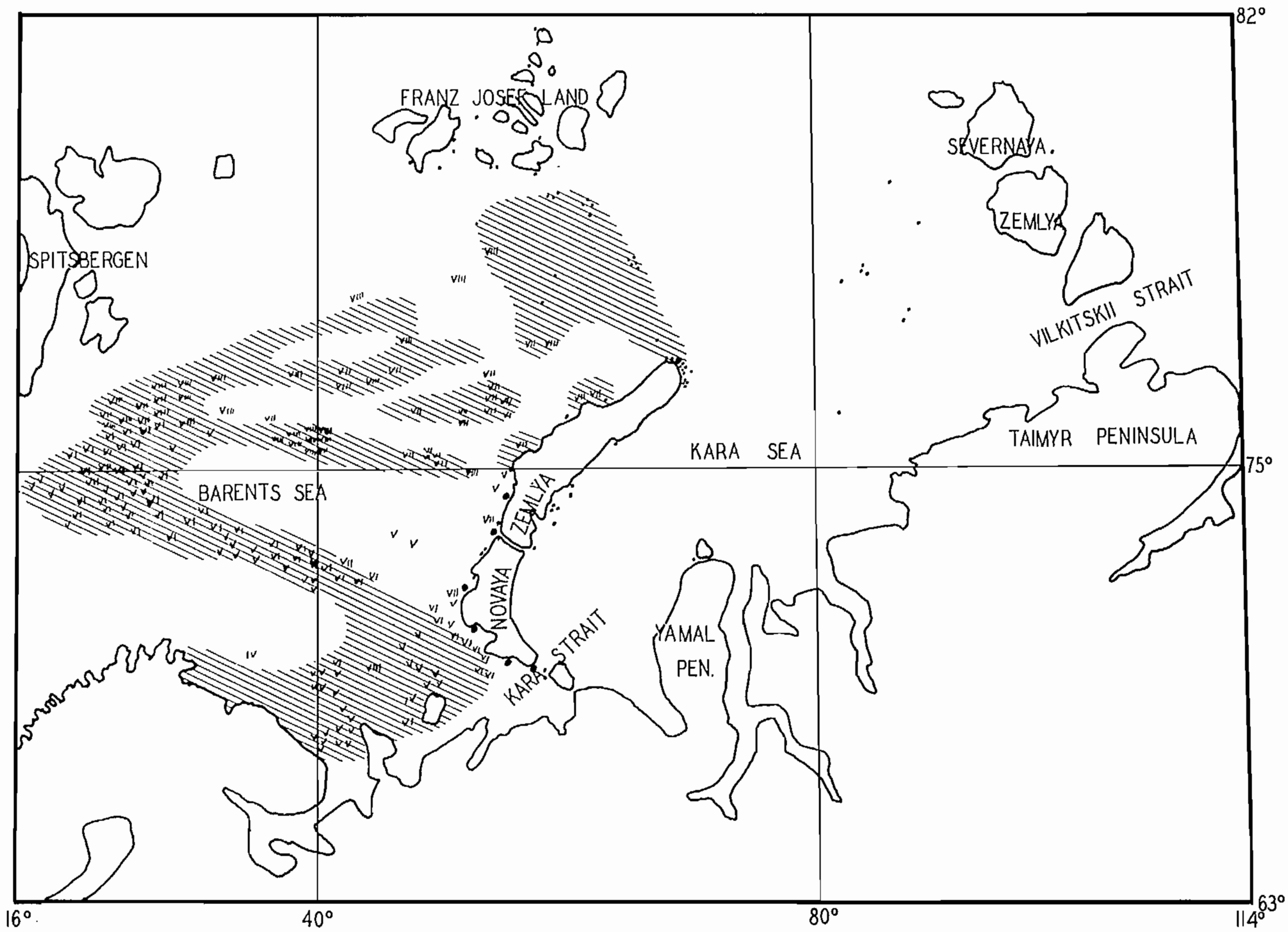


FIG. 52. Summer distribution of the eastern herd of harp seals (from ships' catches compiled by Chapskii 1938).

1988). No harp seals had been known to reach France in recent times (Duguy 1987). Most emigrating animals were young, 1–2 yr old, but adults also occurred (Wiig 1988b). Most animals were described as thin or starving. Many remained along the Norwegian coasts in the summer of 1987.

Haug et al. (1990) describe the age composition of 97 harp seals sampled from the netted by-catch in north Norway, about half taken from the Tana estuary in east Finmark and half from Troms Co., in January–February 1988. Most animals were immatures with a peak age of 3 yr at both sites, but adults up to 25 or 28 yr were also present.

Although there had been a severe winter in north-east Europe in December–January 1987, ice conditions in the southern Barents Sea proved to have been normal, unlike 1902–03, when ice reached close to the Murman coast (Chapskii 1961). Heavy overexploitation of capelin stocks had occurred in the Barents Sea by 1986, when the fishery was closed, and may have been the cause of this second extraordinary migration of the century (see p. 000).

Effect of Climate upon Whelping Sites

Chapskii (1961) stated that in the second half of the 1930's, the whelping sites shifted further into the White Sea. This statement rests on the documentation of Sivertsen (1941) on the locations where Norwegian ships encountered whitecoats during the period 1925 through 1937 (Table 20). At this period these ships were limited to hunting north of a concession line which ran across the Funnel at 67°10′N. They obtained many whitecoats in the years 1925, 1928, 1930 and 1933 (and according to captains, in earlier years), but not in 1929, 1931–32, 1934–37. Sivertsen therefore believed that the main foci of whelping had shifted further south into the White Sea, and that the well-known climatic amelioration of the 1930's (Fig. 53) had been responsible.

In view of the changes observed at the Front between the 1960's and 1970's (p. 40), I have tried to determine whether contemporaneous changes in whelping site may have occurred in the White Sea. Information comes from the drifting camps "Toros I to IV" for 1966, 1967, 1968 and 1970 (Popov 1966, 1967, Khuzin 1970, Yakovenko 1970). Later charting (Anon USSR 1969 to 1976) comes from aerial surveys. Most useful recent chartings (Anon USSR 1977 to 1979) show the positions of whelping patches at various dates (e.g. Fig. 51).

Analysis of these chartings show that in all recent years 1966 to 1979, whelping patches have formed up either in the northern part of the White Sea or in the Funnel (Voronka), and have for the most part been carried north-

TABLE 20. Locations of whelping in the White Sea in the 1920's–1930's (from Sivertsen 1941).

Year	Location B = basin, F = funnel	Source
1925	Outer F	Sivertsen 1941, fig. 3
1926	—	—
1927	—	—
1928	Outer F and B, northeast	Sivertsen, fig. 4
1929	Outer F and B, northeast	Sivertsen, fig. 5
1930	Outer F and B, northeast	Sivertsen, fig. 6
1931	Outer F and B, northeast	Sivertsen, fig. 7
1932	Outer F and B, northeast	Sivertsen, fig. 8
1933	Outer F and B, northeast	Sivertsen, fig. 9
1934	Outer F	Sivertsen, fig. 10
1935	Outer F	Sivertsen, text p. 27
1936	Outer F	Sivertsen, text p. 27
1937	Outer F	Sivertsen, text p. 27

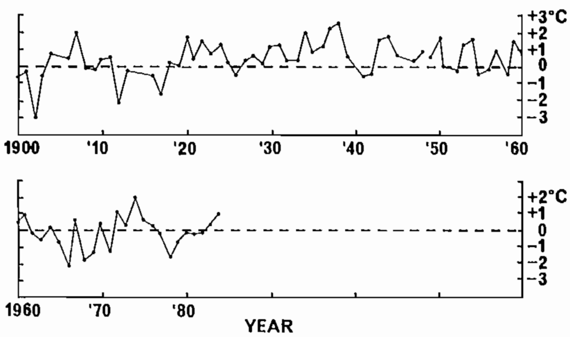


FIG. 53. Mean annual air temperature anomalies for the Barents Sea (70°–75° N. Lat., 10°–50° E. Long.) for 1900–83. Baseline mean 1931–50 (from data in Jones et al. 1986).

ward by ice drift (Table 21). Only in the year 1966, documented by Popov (1971a) and by Bianki and Karpovich (1969), did persistent northerly winds keep the whelping ice and young seals in the White Sea. With these conditions, Norwegian ships, if they had had the same limit, which they did not in the 1960's–1970's, would have been able to catch whitecoats in all years except one, a year of cold conditions in the Basin of the White Sea.

Thus it seems likely that the Norwegian analysis, which showed more difficult catching through the 1930's, could have confused overexploitation with climatic change, since the herds were rapidly decreasing during the 1930's (Ch. VII), and a whelping herd decreasing in size would have been less likely to extend out of the White Sea basin where it would become accessible to them.

In comparing the sites of whelping one must also note that the Norwegians in the 1920's–1930's had no aerial survey (the Russians were then doing aerial counting, but mainly of moulting herds); while in the 1960's and 1970's, using aerial survey, the Russians were able to find the

TABLE 21. Locations of whelping in White Sea in 1960's–1970's. Data from Popov (1966, 1967) and Anon, (1969 to 1979).

Year	Location B = basin, F = funnel	Source
1966	B, northwest	Popov 1966, Toros I drift
1967	F	Popov 1967, Toros II drift
1968	F, south	Anon. 1969, marking site Khuzin 1970, fig. 1 Yakovenko 1970, Toros III drift, fig. 1
1969	—	
1970	F	Anon. 1970, Toros IV drift
1971	—	
1972	B, northeast	Anon. 1972, fig. 1 [see Fig. 00]
1973	F & B, northwest	Anon. 1973, fig. 1 (aerophoto)
1974	F	Anon. 1974, fig. 1
1975	F	Anon. 1975, fig. 4
1976	F	Anon. 1976, fig. 3
1977	B, northwest	Anon, 1977, fig. 3
1978	B, northeast	Anon, 1978, fig. 3
1979	B, north	Anon. 1979, fig. 1

whelping seals at an earlier date. It is the later drift of these patches which must be compared with the earlier locations; one cannot compare ship-borne observations with those from aircraft.

Discussion

a. Significance of the Whelping Sites

The relative constancy of the main whelping site in the Gulf of St. Lawrence, with the seals whelping northwest of the Magdalen Is., shows that whelping sites are selected for their ability to delay the drift of the young to open water for 30–40 d. This is true for all other sites, and requires that the adults migrate far into the ice through leads to reach suitable sites (Dorofeev 1960). Simultaneously, Darwinian natural selection has speeded growth of the young seal, since the sites must be at the limit of open leads in the pack ice in early spring so that the adults can reach them. For the sites to be safely reachable by the adults, a balance of melting over freezing must be beginning in the leads, i.e. the season must be spring. This does not give very much time for growth and development on ice.

It is also true that when the young become independent, e.g. in April in the Gulf of St. Lawrence, their principal food of Euphausiacea, especially *Thysanoessa* spp., are swarming in surface waters at their season of reproduction. However, there is a smaller and later spring productivity of phytoplankton in the area of the ice edge than further south on the Newfoundland shelf and banks (Drobysheva 1964) so that to some extent, the harp seals which require ice as a substrate must make do with the best trophic conditions that they can get. In summer they must leave these regions, which are high in production of capelin all the year round, to other mammalian predators — the great whales especially — and travel northward to where other foods, such as polar cod, replace the capelin.

Of the 3 other herds, only the Front herd has no physical barrier to slow the ice drift, and we have seen how its adult animals must migrate far north into the pack ice to find the initial whelping site. The Jan Mayen herd may well have the drift of its whelping ice slowed by the island itself; and the White Sea seals have the drift of their whelping ice slowed by the constriction of the Funnel. In all these situations some risk ensues: that severe rafting may occur when the ice passes the land barrier or constriction (p. 81), causing pup mortality.

b. Stock Relationships

The Gulf and Front whelping groups retain a relatively constant ratio of size of about 1 Gulf animal to 2 Front animals. This is probably maintained by the relative amount of suitable whelping ice to be found in each area. As we have seen, the Gulf herd is not a self-contained entity in winter since many of its immatures winter on the Front, while the converse is not true. This suggests that the Gulf is not as rich a feeding environment as the Front (see p. 72).

Knowledge of relationships between the 3 main stocks is based chiefly on differences in skull and body sizes discussed on p. 26. Published knowledge from cross-overs of marked seals was summarized by Sergeant (1973c). Referring to recoveries after 1 yr or more:

— One juvenile seal marked in the Gulf of St. Lawrence was recovered off the Norwegian coast, as compared with many hundreds recovered from west Greenland (and more recently tens from east Greenland), (Sergeant 1973c).
— Of 8 recoveries of harp seals marked at Jan Mayen, 7 were from the same area and one from the White Sea, (Rasmussen and Øritsland, 1964, and see also p. 32).
— Of 6 recoveries from the White Sea, all were from the Barents or White seas, (Sivertsen 1941; Popov 1971c).

This evidence all refers to movements of immatures; thus we know that immatures can wander between all three populations (or areas) but we gain the impression that movement between populations close together (Jan Mayen and White Sea) is greater than between populations further apart (Newfoundland and northeastern Atlantic). This agrees with the evidence from morphometry. We do not know what degree of mixing between herds is shown by adult seals, but we know that adult seals show more site fidelity than immatures.

Future research will require biochemical and genetical studies, to study the resemblances between the three main stocks, and simultaneous mass marking in all three areas to test the actual mixing between them. This will clearly demand wider international collaboration and planning than hitherto.

It is possible that, as the seal populations increase towards their asymptotes, and extend over wider geographical areas, the degree of movement between them will increase. This is suggested by the apparent extension of western Atlantic harp seals in recent years to summering in east as well as west Greenland. It is possible also that the seasonal spread of distribution will widen. Thus, more observations of summering herds of harp seals in the Gulf of St. Lawrence have come in the 1980's than previously.

Orientation

Long migrations are forced upon the harp seal by its necessity to stay at the ice-edge year round. It must therefore have developed an accurate method of orientation. How is this done?

Senses used in orientation might be vision, olfaction or hearing, with the former two prime suspects of value for distance orientation. If vision is poor above water, it seems unlikely that the sun or stars could be used for orientation, even though this ability is well known for many birds and for fish (Hasler 1966). More likely, as Nansen (1925) suggested, a dark "water sky" or its converse, the white "ice blink" (reflection in the sky) could be used for distance orientation. Olfaction might detect land odours, which could emanate also from ice on which particles settle. In spring, a northbound seal could keep land and ice on its left, and in fall, with the reverse migration, on its right in order to orient accurately between Belle Isle and West Greenland or Baffin Island. Although land is all round the Gulf of St. Lawrence, ice tends to be on the west side of the northern Gulf owing to the Coriolis force.

Circumstantial evidence and one experiment described later have not given clear results on what sense is used in the Gulf of St. Lawrence:

(1) In spring 1969, owing to unusual absence of ice in the southern Gulf, many adults whelped and presumably mated deep in Northumberland Strait (Fig. 54). Mr. Charles Bartlett, Manager of the Prince Edward Island Game Park at North Rustico, accompanied by Conservation Officer Walter Stewart (in litt. Sept. 22, 1970) on March 27–29, 1969, saw up to 21 adult harp seals at the head of the Hillsborough River, a tidal estuary which runs northeast from the south coast of Prince Edward Island and ends close to the north coast of the island. On March 30, 1969, at least four adult harp seals were found in the woods between the northern head of the Hillsborough River and Savage Harbour on the north coast of the island. These inlets are separated by only 1 mile (2.5 km).

The animals had clearly taken a blind alley northward instead of turning east or westabout round Prince Edward Island. That they wandered into the woods suggests to me that they received some stimulus to continue further. This coult have been an innate sense of direction, based perhaps on the sun or stars; or the sight or smell of the sea or the smell of a herd of harp seals a few miles to the north. We cannot separate these possibilities.

(2) An experiment in orientation of the young is discussed

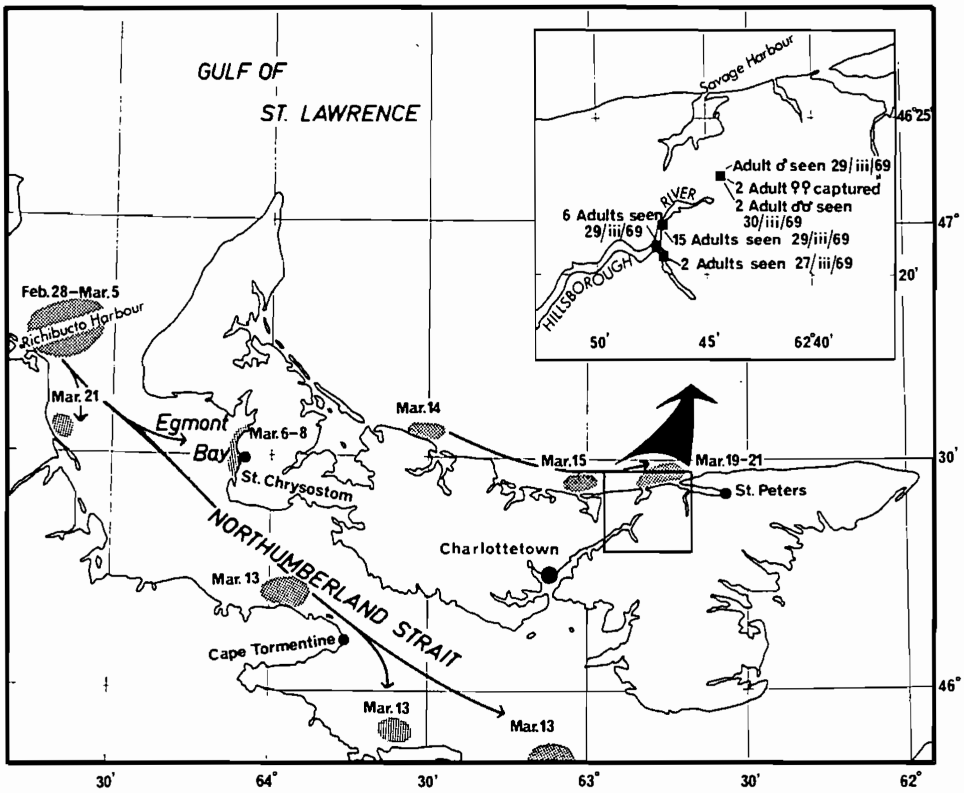


FIG. 54. Whelping sites of harp seals around Prince Edward I. in 1969, and locations of adults which moved into the cul-de-sac of the Hillsborough River.

on p. 83 to 85. No knowledge was gained of the mechanisms used but at least one naive animal, held in captivity for four weeks, was able on release to orientate correctly northeastward in late April. A second returned the following year to join other, undisturbed immatures.

Thus, rather weak evidence suggests that both adults and young in spring possess a tendency to orientate northward. This tendency is expressed in adults between late March and, presumably, the end of the northward migration in June or July; in the young, between independence in early April and the same culmination of the northward migration. A reverse orientation, to the southward, must prevail in both age groups in the fall, from October to December of January.

Chapter V. Food and Feeding

Summary

Food of juvenile harp seals after independence consists of pelagic Crustacea and fish. Older age classes, having the ability to dive to greater depths, also take benthic Crustacea, cephalopods and fish. Although harp seals take many food species, capelin (*Mallotus villosus*) is the most important fish taken in the subarctic, and polar cod (*Boreogadus saida*) the most important fish in the arctic (Fig. 55). Euphausiids and the shrimp *Pandalus borealis* are the chief Crustacea taken in subarctic waters; under-ice Amphipoda and a variety of Decapoda in the arctic. Separation of the adults of the western herd to arctic waters of eastern Canada, juveniles and immatures to subarctic waters of West Greenland, in summer reduces intra-specific competition for food. In spring, when all age classes are closely grouped in the natal area, feeding of adults is reduced at times of whelping, mating and moult. This may reduce intra-specific competition, as does the later migration north of the young. There is evidence of recent food shortage in the Gulf of St. Lawrence in winter, where capelin stocks are small. Also many immature harp seals born in the Gulf after migrating to the arctic return south to the Front to winter together with the seals born on the Front, in the region of a large capelin stock. Both features seem to have increased with increasing stock size.

Estimates of food consumption from animals held in captivity are variable but based on energetic calculations, it is estimated at about 2.6 kcal $\times$ $10^3 \cdot yr^{-1} \cdot animal^{-1}$, or about 2.2–2.5 kg/d for a highly calorific (oily) fish such as capelin or polar cod. Because estimates of the composition of the diet are reasonably consistent, at least in terms of frequency of major components, it is possible to estimate the annual consumption of different categories; for example the quantity of capelin (assumed to be about 0.25 of total food by volume) consumed by the northwest Atlantic herd (assumed to number 2 million) is about 0.4 $\times$ 10^6 tonnes annually. More of this would be consumed at Newfoundland than at Greenland.[12]

Introduction

It is difficult to obtain samples of harp seals for food analysis. Most harp seals killed by man are taken while resting on ice some hours after feeding, since recently hauled-out animals are wary and readily reenter the water. Consequently, few seals killed in this way contain food remains, and the data obtained are often from single animals out of a great many. By contrast, harp seals taken in the water, as by netting, shooting or formerly by baited hooks (as at the Magdalen Is.), show more frequent food remains, on which quantitative studies can be made.

[12] An estimate from Wiig's data (p. 70) is about twice as great, presumably based upon a doubled estimate of daily feeding rate.

Western Herds

Sergeant (1973a and 1976) summarized knowledge of the food of harp seals of the western North Atlantic and this will be a condensed account with additional information. The food captured is extremely varied, ranging from Crustacea, especially Euphausiacea, Decapoda and pelagic Amphipoda, through pelagic fishes such as capelin, Atlantic herring (*Clupea harengus harengus*) and arctic cod (*Boreogadus saida*) to bottom fish such as cod and flatfishes (Pleuronectidae) and even the large spiny redfish (*Sebastes marinus*), sculpins *Myoxocephalus* sp. and sea raven (*Hemitripterus americanus*).

Sergeant (1973a) believed that immediately after weaning the young seals fed mainly on Euphausiids with some capelin. Rowsell (1977) examined the stomachs of 76 beaters (juveniles) killed throughout April, 1977 by the crew of a longliner outsider Twillingate, Notre Dame Bay, Newfoundland. Thirty-two stomachs or 42% contained food of which 21 or 68% contained fish, in one case identified as capelin. The remainder held unidentified Crustacea. Capelin was found in stomachs of 8 migrant beaters at Blanc Sablon, Gulf of St. Lawrence in June (Sergeant 1973a).

The immatures in winter were found to feed mainly on capelin, although additional material from the moulting fields in more recent years emphasises shrimp. Sergeant (1976) reported that 0 and 1 yr old animals on the northeast Newfoundland Shelf between 50°30′ and 52°N, 53°30′W in early April, 1976 were taking shrimp *Pandalus borealis* over 180 m of water, presumably at or close

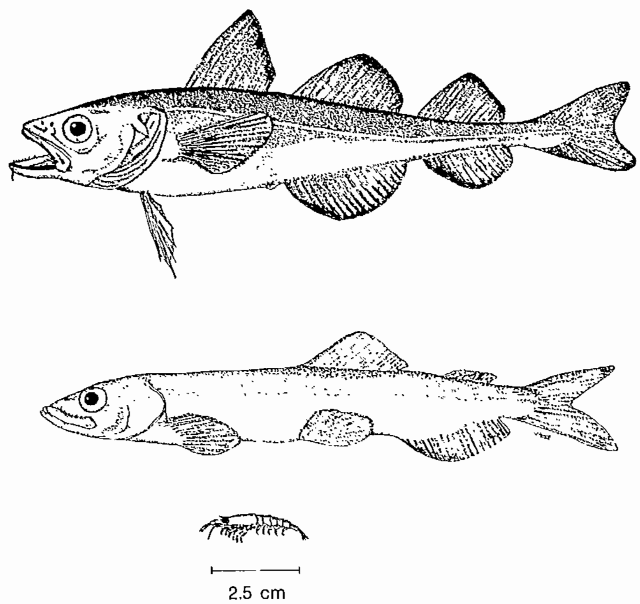


FIG. 55. Three important food species of harp seals: polar cod *(Boreogadus saida)*, capelin *(Mallotus villosus)* and a euphausiid *Thysanoessa* sp.

to the bottom. Bergflodt (1977) reported *Pandalus*, exceeding capelin in abundance, in many stomachs of moulting seals, or its remains excreted by them, from catches on April 10 and 11, 1977 east of Cape Bauld at 52°12′N, 54°06′W. Previously, principally lactating female harp seals had been found taking *Pandalus borealis* in the Gulf, and mixed with other species of shrimps, on the Front.

Capelin are taken as the dominant food and in large quantity by animals of all ages in the St. Lawrence estuary near Les Escoumins, Quebec between December and April. Food data were collected over seven seasons at this site (Table 22). Subsidiary to capelin in these stomachs were other fish (e.g. cod, herring, barracudina *Paralepis rissoi,* blennies, etc.), shrimp (mostly the pelagic *Pasiphaea tarda*) and unidentified cephalopods in that order of abundance (Table 23). The food seems to be taken mostly pelagically at this locality, where depths are about 200–300 m over the Laurentian Channel. The quantity of capelin taken can be compared from year to year since the fish, being maturing subadults, are of a uniform size with nose-tail length of about 16.5 cm. The mean annual number of capelin varied more than threefold, and when it was low, the percentage of stomachs containing other types of foods: shrimps, other fishes and cephalopods — increased (Table 22). (Unfortunately there are no year-by-year studies of the size of the capelin stock in the estuary of the St. Lawrence.) Based upon the rate of digestion of herring and capelin, Murie (1984) showed that the seals fed with a peak of activity in the early morning hours, although her data would not have ruled out an evening peak also (p. 70). In the St. Lawrence estuary in samples taken between 1969 and 1982, among juveniles aged 1–5 yr females ate slightly more than males (Table 24) but adult females aged 6–30 yr ate much more than adult males. Most adult females here are pregnant, and this is the last period of feeding before the season of births, mating and moult. Consequently the fattening produced is highly important, especially for these females.

Goudie (1973) observed herds of harp seals feeding in June in a bay near Hopedale, Labrador, probably on capelin, with an early morning peak of activity. Foy, de Graaf and Buchanan (1981) quantified feeding on the Labrador coast near Makkovik, Postville and Hopedale. In late May and June 1979 and 1980, juveniles were found to occur near the offshore archipelagoes of small islands. Stomachs of these animals contained mainly euphausiids. Immature and adult harp seals occurred chiefly in the bays where they consumed large quantities of capelin. However, those immatures and adults captured further offshore had more varied diets, including euphausiids, bottom-living decapod shrimps and a variety of fish. In autumn (Nov.–Jan.) in the bays, a variety of small fish species — small Gadidae, capelin and polar cod *(B. saida)* — dominated stomach contents, with invertebrates secondary.

Studies on the feeding of harp seals at West Greenland were reported by Kapel (1973), Kapel and Geisler (1979) and Kapel and Angantyr (1989). This last paper provides a large amount of information from a huge coastline, being based on 661 stomachs collected from 13 localities, ranging from Nuuk(=Godthaab) at 64 N. to Qaanaaq near Thule at 77 N. Lat. It also includes an offshore locality on the West Greenland banks. The animals studied were of known age. Reports also came from hunters as in previous studies. Capelin was confirmed as the dominant food in southwest and central-west Greenland (as defined in Fig. 42), with Crustacea, especially euphausids and amphipods, as other important food items, especially for young seals. In north and northwest Greenland, polar cod *(Boreogadus saida)* was confirmed as the dominant food species, with Arctic cod *(Arctogadus glacialis)* also taken, together with pelagic euphausiids and amphipods (*Parathemisto* spp.). In southwest Greenland a large variety of fishes, including large benthic species such as gadoids and flatfish, were taken, as well as prawns *(Pandalus borealis)* and squid *(Gonatus fabricii)*; this food complex is very similar to that taken in nearly the same years (1986–88) on the coasts of north Norway (p. 69), which is also at the southern climatic perimeter of the harp seal's range. Offshore, on Store Hellefiskebanke, harp seals took sand eels(*Ammodytes* sp.) in summer. Capelin were taken en masse in southwest Greenland in early summer (as described on p. 46), but also from late

TABLE 22. Feeding success of harp seals in the St. Lawrence River near Les Escoumins in winter over 7 yr.

Year	Months	No. of stomachs	Percent With capelin	Percent Other items	Percent Empty	Mean no. of capelin	Difference between means[a]
1969	I–IV	89	92.2	3.3	4.4	47.7 ± 38.9	
1971	I–IV	69	89.4	21.0	10.5	44.8 ± 44.3	–
1978	III–IV	67	98.5	14.1	1.4	28.5 ± 21.0	+
1979	XII–III	92	99.1	4.1	0.8	29.8 ± 23.7	–
1980	XII–II	41	91.3	30.7	2.1	18.3 ± 20.5	+
1981	XII–II	60	96.7	7.7	1.2	64.4 ± 42.9	+ +
1982	XII–II	54	77.2	32.9	8.9	19.9 ± 29.5	+ +
Mean						32.3	

[a] Significance of diff. between adjacent means; using t-test: –, non-significant; +, significant at 0.01 level; + +, at 0.001 level.

TABLE 23. Items other than capelin found in harp seal stomachs in the St. Lawrence estuary, January–April 1969, 1971 and 1978–1982 (Sergeant original) and 1983 (Murie 1984).

Fish	
White barracudina (*Paralepis rissoi kroyeri*)	32 & 20 fish 2 stomachs, 1969
Cod (*Gadus morhua*)	Frequent
Skate (*Raja* sp. indet)	1971
Eelpout (*Lycodes vahlii*)	1981
Herring (*Clupea harengus*)	
Grenadier (*Coryphaenoides rupestris/carnatus*)	1982
Lumpsucker (*Cyclopterus lumpus*)	
Alewife (*Alosa pseudoharengus*)	Up to 19 cm
Longfin hake (*Urophycis chesteri*)	33–35 cm
Blenny (Pholidae or Stichaeidae)	
Flounder (*Heterosomata* sp.)	
Redfish (*Sebastes* sp.)	
Smelt (*Osmerus mordax*)	
White hake (*Urophycis tenuis*)	
Silver hake (*Merluccius bilinearis*)	
Rockling (*Enchelyopus cimbrius*)	
Cephalopoda	
Octopods (*Bathypolypus arcticus*)	
Squid (*Loligo peali*?)	1981
Crustacea Decapoda	
Shrimp (incl. *Pasiphaea tarda*)	Frequent

summer through early winter at Godhavn and in the Vaigat (see Fig. 43). Altogether 23 species of fish were identified in stomachs, besides 8 of decapod, 4 of euphausid, 2 of amphipod and 1 of mysid Crustacea, and 2 of cephalopod Mollusca. Off southeast Baffin I., between Cumberland Sound and Frobisher Bay, Smith et al. (1979) found the food in five stomachs to be some polar cod *(Boreogadus saida)* and more pelagic crustacea *Mysis oculata, Parathemisto libellula, Sergestes arcticus.* A similar distribution of food organisms had been found in a few stomachs from Cumberland Sound (Sergeant 1973a) — a rather high proportion of pelagic Crustacea as compared with fish, which cannot be as abundant here as at higher latitudes. In the high arctic, at Grise Fjord in Jones Sound, Freeman (pers. comm.) reported finding polar cod of lengths 125–175 mm[13] in the stomachs of mostly adult harp seals killed in early September. This fish must be a major component of the diet of harp seals in Lancaster Sound, where I saw the seals from the air feeding in schools, together with while whales *(Delphinapterus leucas)* among the disintegrating ice of bays in early August (e.g. Maxwell Bay, Devon I., August 8, 1973). Foy et al. (1981) cite unpublished observations of K.J. Finley and E.J. Gibb on feeding of harp seals at Pond Inlet and Grise Fjord. Of 63 stomachs, 95% contained food, with fish accounting for over 99% of the biomass. The most numerous prey species were polar cod *(B. saida)* and *Arctogadus glacialis,* seasnails (Cyclopteridae), eelpouts (Zoarcidae), Greenland halibut *(Reinhardtius hippoglossoides)* and sculpins (Cottidae). Mostly adult harp seals are present in this area. Vibe (1950) found *B. saida* in one stomach of a harp seal in Smith Sound on July 23, 1941, and the Thule Inuit told him that this was the principal food of harp seals caught here in summer.

[13] As deduced from otolith sizes.

TABLE 24. Comparison of food eaten by sex of harp seals in St. Lawrence estuary, 1969–82.

Sex	Age (yr)	*N*	Number of capelin eaten: Mean	Range	Sign of difference between means[a]
M	1–5	192	29	1–181	
	6–30	91	36	1–137	
F	1–5	96	41	1–165	+
	6–30	69	59	1–245	+ +

[a]As in Table 22.

Adult female harp seals feed little during lactation (Stewart and Murie 1986), presumably because they cannot leave the pups for long periods and can therefore dive only straight down or within a small radius of the pup's site. They therefore lose fat thickness rapidly. During April this cohort of animals is the last to join the moulting herds (p. 43). On the Front, food samples from the area of St. Anthony, Newfoundland were collected from a winter-to-spring fishery in 1971. There was a large catch of adult females on 3–7 April, which had fed heavily on a variety of bottom-living Crustacea (Sergeant 1973a). Comparison of locations of inshore and offshore catch showed that moulting patches on 2nd April occurred

60 km southeast and northeast of this female feeding area.

Similarly, in the estuary of the St. Lawrence, annual collections showed that there is a temporary high female sex ratio in late March and early April (Table 3). This is due to the sudden arrival of many adult females which have whelped, finished lactation, and then returned to a rich feeding area one hundred of km distant from the whelping areas of the Gulf. The food in here is mainly capelin (p. 66).

During the moult, little food is found in the stomachs of animals resting on the ice, but shooting cannot succeed till the animals are well-dried and sleepy, when digestion will have taken place. Moulting animals take to the water en masse at intervals, particularly during dull weather, and some feeding takes place at this time, since faeces can be found in the gut of animals among those shot on the ice. This would indicate feeding within the last 12 h (Murie 1984 — see p. 70). Samples taken from harp seals at the Magdalen Is. in the water between March and May, 1956 showed a steady increase in feeding intensity (chiefly on herring) during this period (Table 25).

Feeding off north-central Labrador is relatively intensive during May–June and November–January (Foy et al. 1981). However on the Quebec north shore during the southward migration in December–January, capelin and euphausiids were found in the stomachs only in small numbers (Sergeant 1973a).

Using moulted young seals as experimental animals and introducing live smelt *(Osmerus mordax)* and Mysids to them in tanks, we found (Sergeant 1973a) that small prey are taken singly and by suction, with little manipulation. The fish were taken tail-first, and it is evident from the positions of the fish in the stomachs that capelin in the St. Lawrence estuary are taken in this way. Large fish must be held in the mouth and bitten since the spiny heads e.g. of sea ravens and sculpins (Cottidae) are sometimes found on the ice fields among harp seal herds, and redfish are found on the ice rejected entire. In the estuary of the St. Lawrence, we very rarely found redfish in hundreds of stomachs of harp seals, although the stomach of a single hooded seal *Cystophora cristata* was full of redfish.

The presence of *P. borealis* shrimp (in stomachs) and redfish (on the ice), as well as an episode involving the taking of flatfish by moulting seals on the Grand Bank, suggested that adult harp seals can dive to some 150 fath (270 m), and immature and young weaned seals to some 180 m (Sergeant 1973a). These conclusions need to be tested by the use of attached transmitters with pressure-sensitive recorders, as developed for fur seals (Kooyman et al. 1976), since some of these food organisms can move well above the sea bottom.

Central Herd

Gray (1889) reported stomachs of adult harp seals in the Greenland Sea to contain the amphipod *(Para) themisto libellula* and the euphausiid *(Mega)nyctiphanes norvegica,* Pedersen (1930) found polar cod, *Boreogadus saida,* in stomachs of harp seals from Scoresby Sund, East Greenland, in the summers of August 1927 to 1929, during which period he saw 45 harp seals killed. Stephensen (1933), reporting on collections of M. Degerbøl, found numerous euphausiids, *(Thysanoessa inermis* and one *Meganyctiphanes norvegica*) in the stomach of a harp seal from Kangerlugsuak (68°N, 32°W).

Rasmussen (1957) described the weaned young as feeding on *Boreogadus saida* at the edge of the icefields off east Greenland in April. Surkov (1960) quoted M. Ya. Yakovenko as having observed *Themisto* (*Parathemisto libellula*?) in the stomachs, and remains of Crustacea in the intestines, of harp seals at Jan Mayen I, presumably during the spring hunt. He saw crustacean remains in faecal masses in July northwest of Jan Mayen I. More details are given by Sivertsen (1941) citing the observations of Per Høst at Jan Mayen I. in late March 1932, who found 57 *Gammarus locusta* (probably *G. wilkitzki*

TABLE 25. Stomach contents of harp seals from the Magdalen Islands, March to May 1956. F = females, M = males (from Sergeant 1973a).

		Percent stomachs containing					Empty stomachs	
Time period		Herring	Flatfish	Redfish	Gadidae	Invertebrates	Percent	Number
March	F	19.3	3.4	—	—	2.3	75.0	44
	M	28.6	—	—	—	—	71.4	14
April 1–15	F	47.7	2.3	2.3	2.2	—	45.5	11
	M	57.1	28.6	—	—	—	14.3	7
April 16–30	F	76.7	11.7	—	1.6	—	10.0	20
	M	66.9	5.6	—	—	1.7	25.8	62
May	F	92.9	—	7.1	—	—	—	7
		73.9	10.9	8.7	2.2	—	4.3	23
Overall	F	43.8	4.8	0.8	0.6	1.2	48.7	82
	M	62.7	7.1	1.9	0.5	0.9	26.4	106
	Both	54.3	6.4	1.5	0.6	1.0	36.1	188

Birula), 28 *Parathemisto libellula,* 2 *Gammaracanthus loricatus,* 1 *Eusirus cuspidatus* and one euphausiid *Thysanoessa raschi.* Tencati and Geiger (1968) collected most of these species of pelagic amphipod under drift ice off northeast Greenland.

The harp seals of the central herd thus show unique features associated with their high arctic and pelagic location. During whelping, adult seals feed on under-ice living amphipod Crustacea rather than bottom-living decapod Crustacea. Young very early turn to *Boreogadus saida*, although it seems very likely that they will prove to be finding abundant Euphausiacea at the edge of the East Greenland current. Also the subarctic fish species capelin, herring and cod have not been recorded in the seals' diet. Saemundsson (1939) stated that many harp seals visit the north and northwest coasts of Iceland during "ice summers" and chase away the cod. Wollebaek (1907) and others gave the same story for east Finmark. Naumov (1933) made clear that the inverse correlation between occurrence of harp seals and of cod, together with other temperature-water fish, was due to incursions of arctic water, from which the fish retreated, but with which the seals were associated.

Eastern Herd

According to Sivertsen (1941) the weaned pups in the White Sea during April take largely Crustacea (the euphausiids *Thysanoessa raschi* and *T. inermis* and the amphipod *Anonyx nugax*). At the same time of year 1-yr-old immatures take the same Crustacea together with bottom-living Decapoda, identified as *Crangon crangon,* and significant quantities of capelin, *Mallotus villosus.* Sivertsen attributed the increasing quantities of fish in the diet to the superior swimming abilities of the 1 yr olds. He was able to find stomach contents in only two adults of many examined, a male in March containing euphausiids, and a female in early April containing *Crangon.* Knowledge of the food of adults comes from other authors: Naumov (1933) states that the young seals eat mainly invertebrates and the adults, mainly fish of small size such as capelin, haddock and herring. Chapskii (1961) states that in summer at the ice edge in the Barents and Kara seas the food is mainly polar cod, *Boreogadus saida.* The same fish is important along the coasts of Novaya Zemlya during November to February, the seals varying their wintering grounds according to the locations of abundance of the fish. He states that in the winter of 1902–03 when the seals visited the coast of Murman in unusually large numbers the food was mainly herring. Wollebaek (1907) states that when harp seals visited the coast of east Finmark in spring 1901 they took large quantities of spawning capelin and some Atlantic cod, *Gadus morhua.* Wiig (1988a) states that harp seals taken in Varanger Fjord in winter 1984 were also full of capelin, capelin roe and a little cod. When they invaded southward in winter 1986–87, foods were a wide spectrum of fish such as herring and sei *(Pollachius virens),* shrimp and squid — but many seals were then starving (Wiig 1988b). Wiig (1988b) believes that the large concentration of capelin normally found in the Barents Sea is an optimal food resource for this socially-feeding seal species.

The food of the eastern herd is therefore qualitatively similar to that of the western herds of harp seals, including pelagic and benthic crustacea and fish. Seasonally, shift to a higher arctic location produces a change from capelin to arctic cod as the main fish food species, again as in the western North Atlantic.

Haug et al. (1990) describe the food of 354 harp seals taken as netted by-catch from the north Norwegian coast in January–February 1986 and 1988 following exceptional migrations southward. Feeding was opportunistic, with a variety of gadoids taken (cod *Gadus morhua*, haddock *G. aeglefinus*, pollack *Pollachius virens* and Norway pout *Trisopterus esmarkii*). Herring and capelin were also taken, plaice (*Pleuronectes platessa*) and prawns (*Pandalus borealis*). Empty stomachs were few. The main food comprised gadoids, especially saithe. Nilssen, Grotnes and Haug (1990) confirmed fishermen's reports

TABLE 26. Frequencies of different food items found in harp seals. This table is a summary of all data discussed in the text, for all feeding areas.

	Number of occasions		Number of occasions
Fish		*Crustacea*	
Capelin	23 (24%)	Euphausiids	14
Herring	6	Decapods	12
Cod, haddock, saithe, pout	6	Mysids	5
Polar Cod	6	Amphipods	4
Flatfish	6	Indet.	1
Redfish	4	*Mollusca*	
Arctic cod	1		
Barracudina	1	Cephalopods	4
Lanternfishes	1		
Sandeel	1	Invertebrates	26 (41%)
Indet.	1		
Fish	56 (59%)		

TABLE 27. Calorific value of some foods of harp seals (Wiig 1988c).

Item	Kcal/g
Capelin	1.5–2.4
Herring	2.0–2.4
Cod	1.0
Polar cod	1.0
Crustacea	1.0

that fish entangled in nets were bitten and the soft abdominal parts removed, and that fish were probably scared away from gill-netting grounds in the fjords by the seals.

Composition of the Food

Table 26 summarizes all observations on food items recorded as taken by harp seals. Since the observations were widely scattered in space and time, an approximately quantitative estimate of the composition of the food is obtained by summing the frequencies of observations of each component. About two-thirds of the food appears to be fish, one third invertebrates. The most frequent food species is capelin, comprising about one-quarter of the observations. The volume of polar cod eaten is probably not much less, since observations of feeding were biased towards the wintering area[14] and against the high arctic. Also, as Lavigne et al. (1985) observe, the percentage of feeding in the summer 6 mo is greater than 50%, because of starvation periods at whelping and moult in the winter 6-mo period. The calorific value of fish per unit weight exceeds that of Crustacea (Lavigne et al. 1985), and that of oily fish such as capelin and herring exceeds that of cod and polar cod (Wiig 1988c) (Table 27). Wiig goes on to estimate food needs of harp seals according to composition of the food (Fig. 57).

How Often and How Much Do Harp Seals Eat?

D.J. Murie (in Murie and Lavigne 1985) and Murie (1984, 1987)) ingeniously measured rate of food consumption in harp seals in the laboratory. She fed intact herring to harp, grey and ringed seals and sacrificed them at fixed times after feeding. Digestion of otoliths in the stomach began after 1 h (95% confidence limits: 0–5 h) and was complete by 8 h (limits 4–14 h). If the small intestine were examined, too, the mean limits were between 3 h for no loss, to 13 h for complete digestion of otoliths.

Murie (1984, 1987) applied these findings to the examination of the state of digestion of capelin in the stomachs of wintering seals caught in the St. Lawrence estuary, where capelin made up 86% of the food items by frequency and 77% by weight, and contributed 88% of the gross energy of the food. She was able to show that the volume of contents in the stomachs of the seals, which were caught mainly in the middle of the day, had a single peak, and that therefore the harp seals fed on aver-

[14] About 19/30 (63%) of datable records discussed above referred to the wintering period December to May.

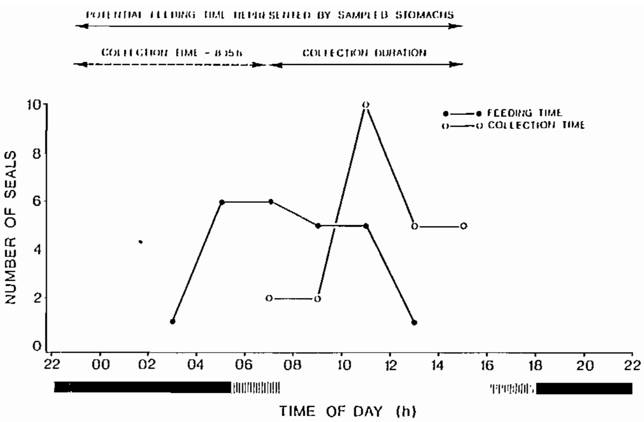


FIG. 56. Deduced feeding time of harp seals in the St. Lawrence estuary (from Murie 1984). Night and dawn/dusk periods are shown for January.

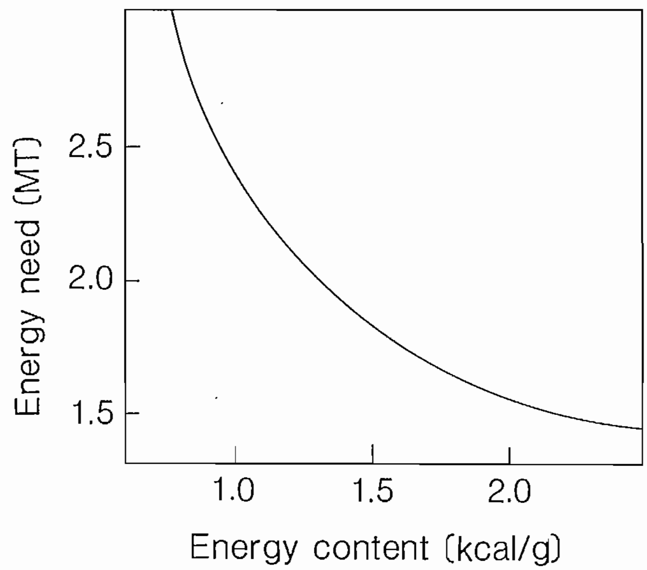


FIG. 57. Annual food needs of a stock of 1 million harp seals, with different mean energy content of food (from Wiig 1988c).

age in the early morning — about 4 h before the mean time of collection of the seals by the hunters (Fig. 56).

One deficiency in these findings is minor. Murie did not correct for the size difference between the otoliths of herring, the experimental fish, and capelin. Capelin is a smaller fish and I assume that its otoliths are smaller. If this is so, the otoliths would have been digested faster than those of herring, so that the animals will have fed later than reported by Murie. However, the early morning peak will remain.

Secondly, these animals were collected in January. If there were a secondary period of crepuscular feeding in the evening (ca. 1700 h in January) complete digestion of otoliths will have occurred before examination of stomachs the following day about 15 h later, and it would not be detectable. We cannot therefore rule out 2 peaks of feeding a day, and an increase of the quantity of food calculated to be eaten by Murie assuming a single daily feeding period.

Our own observations on these winter stomachs from the St. Lawrence sometimes showed a mass of newly eaten capelin in the stomachs, and a residue of vertebrae at the pylorus from previous feeding. This seems to indicate that more than one feeding episode can occur per day.

Our own extensive data over 7 yr (1969, 1971 and 1978–82) at this site, partly described in Sergeant (1973a) showed an overall mean of 32.3 capelin in the stomach (Table 24). These fish were of very uniform size, averaging 16.0 cm in fork length. Murie finds, from knowledge of fresh capelin at Newfoundland in February to April (Winters 1970), that the equivalent mean weight is about 18 g. However, I find the mean volume of stomach contents to be 27.4 mL per fresh capelin which must be close to 27.4 g. The mean weight of a fresh meal of capelin on this basis is 885 g. According to Murie, the capelin represent 0.77 of the diet by weight so that the mean intake per meal will be 1 149 g of all items. The weights of 20 harp seals collected by us in the St. Lawrence estuary in January 1971 ranged from 49.0 to 148.3 kg for animals aged 1 to 30 yr, with a mean weight of 118 kg. Mean age was 5.7 yr, modal age 3 yr — about the same as in the complete 1971 food sample. From these data, mean daily ration would be 0.97% of total weight for 1 daily feeding, 1.94% for two daily feedings.

Murie (1984) states that the food consumed by a free-living harp seal with good blubber thickness in the estuary in January 1983 (when we did not sample) was 1.3–2.5 kg, the lower figure for a young seal, the higher for a large or adult seal. From her weighings, this translated into 1.8–2.0% of its body weight.

Other routes to calculate the quantity of food eaten by harp seals are by using the data on food eaten by captive animals, and by using basic data on the metabolism and therefore the food energy needed by mammals the size of harp seals with the same growth and reproductive characteristics.

For captive animals, Geraci (1972) maintained two young harp seals aged 1–15 mo in tanks with a mean *at libitum* diet of fish (smelt) of 3.9–4.0 kg per day, with the seals' body weights averaging about 65 kg. The animals gained weight faster than in nature, to weights of 65 and 80 kg at 15 mo of age. This ration represents 6–7% of body weight per day. The animals were in small tanks with little exercise.

Keiver et al. (1984) using four juvenile (<1 yr) animals determined the maintenance energy requirements, i.e. those allowing neither weight loss or gain, to be 2658 kcal/d for seals fed 2 meals per day; more for seals fed 4 meals, because food was then digested less efficiently. Now winter capelin is a fish of high calorific density, because it has a high fat content (Winters 1970; Jangaard 1974). According to calorific data summarized by Lavigne et al. (1985), to convert from energy to mass for such a high energy food, one divides by 2.6. If we do this, the feeding rate on capelin for the captive seals was 1 kg per day. The mean weight of the animals was given as 56.1 kg, so that the feeding rate was about 1.8% of body weight per day of high calorific fish.

Lavigne et al. (1985) take the energetic approach. Energy costs were estimated for basal metabolism and activity from body mass, assuming that harp seals have the same basal metabolism per unit mass as other large mammals. The higher energy needs of young seals were taken into account. The energy costs of swimming were calculated from assumed swimming at 1 m/s for 18 h/d, with empirical estimates available of energy cost in relation to body size and swimming speed of harp seals.

Lavigne et al. (1985) then built a mathematical model for a population of harp seals of stable age distribution, took into account the variable calorific value of different food components (fatty fish or chitin-rich Crustacea, which have a much lower calorific value), and came up with ranges of estimates of annual food consumption per animal. The per capital gross energy required was relatively constant at 2.3–2.6 × 10_3 kcal per year, which translated to 0.8–0.9 t/yr of oily fish, or 2.2–2.5 kg/d.

Keiver et al's (1984) results are much lower (1 kg/d) than those calculated by Lavigne et al. (1985) (2.2–2.5 kg/d), which must be because the latter made the calculations for adult as well as juvenile seals and also allowed for growth and reproduction. Geraci's (1972) feeding results are very high, but resulted in much higher growth than in nature. Murie's (1984) results would suggest that one or two daily feedings take place in nature, or that in many years, the St. Lawrence estuary provides suboptimal feeding.

A Decline in Feeding Rate in the St. Lawrence Estuary

Although harp seals appear to concentrate in the St. Lawrence estuary for the purpose of feeding, this is not always a good feeding ground. To begin with, there is a big variability in success of feeding on capelin from year to year (Table 22). When I compared the data on feeding by age group for the pre-quota period 1969–71 and for the post-quota period 1978–82 (Table 28), I found a sharp decrease in mean number or weight of capelin taken by adult harp seals, aged 6 yr and up ($P = 0.0001$),

TABLE 28. Harp seals in the St. Lawrence estuary. Food consumption before and after the 1972 quota.

Age of seals (yr)	Mean body weight (kg)	Mean no. of capelin in stomach		Equivalent mean weight (g)		Food weight / animal weight	
		1969–71	1978–82	1969–71	1978–82	1969–71	1978–82
1–5	66.8	32.25	30.92	583.7	559.7	0.0087	0.0084
6–30	115.5	62.01	36.83	1122.4	666.6	0.0097	0.0058

though there was a statistically insignificant decrease for immatures ($P = 0.7715$). The feeding level was already low for immatures, when their higher metabolic rate is taken into account, and I found evidence in 1969 from reciprocal distributions in space in the estuary that the immatures were apparently being forced by the adults to the poorer feeding areas (Sergeant 1973b)[15]. The Gulf stocks of capelin are small as compared with those, for instance to the northeast of Newfoundland (Jangaard 1974), and northeast Newfoundland is a wintering ground for many of the immatures of the Gulf herd, as determined from tag recaptures (p. 54). This movement increased in intensity in 1978–80 (Fig. 47). Murie (1984) working in 1983 showed that adult female harp seals did not increase their weight between feeding in the estuary in January, a period of intensive feeding, and when sampled at the Gulf whelping ice in March, although one might have expected such an increase. Lastly, Stewart and Lavigne (1984) showed that in 1976 these lactating females had large food reserves, but in 1978 to 1980 their food reserves were scarcely adequate for completing lactation.

We are therefore faced with a paradox: the estuary is a prime feeding ground in the Gulf, but in some years food can be inadequate to fatten the animals. This was true in the period 1978 to 1982 or 1983. Two things had happened in this period: the seals' population had increased (Ch. VIII), and a major decline of the capelin stock took place at least in the northeast Newfoundland shelf in 1978–80 (Leggett et al. 1984) which could have affected the Gulf spawning capelin also. The Front must be a better feeding ground for harp seals than the Gulf, because many of the Gulf immatures choose to winter there. Presumably, the adults of the Gulf herd winter in the Gulf because there is no way that they can make an extra migration halfway through the winter, when the Strait of Belle Isle is blocked, or because it is energetically a better choice to spend the winter in the Gulf, taking into account feeding and migration.

Calculation of Food Consumption

In order to know the total annual consumption of a particular food item by a herd of harp seals, we need to know the size of the herd, the percentage consumption by weight or volume of the item, and the daily food consumption by weight. For the northwest Atlantic, we have reached the point where such a calculation is probably realistic.

The annual production of young harp seals in the northwest Atlantic has now passed 500 000 (Ch. VIII) implying a herd about 4 times as great, i.e. 2×10^6 animals.

Annual consumption of food, if it were all taken as oily fish such as winter capelin, has been estimated (p. 106) as about 800–900 kg per animal. If capelin represents one quarter of this (Table 26), and the seal population is 2 million animals, consumption of capelin would be about 400 000 to 450 000 tons per year. Of this consumption, perhaps three-quarters might be consumed by the whole herd during the 6 winter months in Newfoundland waters; one-quarter by the juveniles and immatures in Greenland waters.

Discussion

Harp seals are probably as major a predator of capelin in the western North Atlantic as are the major whale species combined which prey upon this fish (fin, sei, minke and humpback whales) (Winters and Carscadden 1978). However, harp seals prey upon capelin when ice is present nearby as a resting substrate. This period is about 6 mo, from November to or December to May or June for eastern Canada (less fasting periods when whelping and, partially, when moulting, totalling about 1 mo). In the reciprocal period, the whales prey upon the capelin stocks, but run the risk of being beset by ice in the winter period. The resource is thus shared between these major mammalian predators, although there are additional and probably more important major fish predators on capelin such as cod.

By contrast with capelin, herring is not an important prey species for harp seals since herring mainly occur away from the ice margins. The only area of important predation on herring by harp seals so far identified is or was at the Magdalen Is., where Sergeant (1973a) from the data shown in Table 25 assessed it as perhaps 20 000 tonnes per year in the 1950's. However, this herring stock was greatly reduced by heavy fishing pressure in the 1960's and has not recovered much to date, so that it cannot yet again rank as an important food fish for harp seals.

The abundance of the harp seal is due first to its trophic level as predator on forage fish such as capelin and polar cod as well as invertebrates; and second to its migrations, such that it feeds seasonally on different fish stocks, both in the subarctic and the arctic. This is not to say that it could not live all the year in an area such as the Gulf of St. Lawrence; increasingly, in recent years (as the population has increased), rare herds of harp seals have been seen there in summer (W. Hoek, pers. comm.). But living in ice-free waters is presumably made difficult by competition from the temperate-water seals, such as grey seals, which inhabit these waters in summer, and the great whales such as fin and minke whales.

[15] This evidence could not be checked in later years since the fishermen had increased their efficiency and fished within a smaller area.

Chapter VI. The Young Seal

Summary

The majority of young seals are born in the first week of March in the Gulf of St. Lawrence, on average 5 d later on the Front, with a total spread of about 10 d for 95% of births. Birth weight is about 11 kg and the young are weaned at ca. 10 d having attained a mean weight of 34 kg. The moult of the young takes place between ages of 10 and 20 d and by 30 d the fully moulted young begin to feed, now having a mean weight of 30 kg.

Mortality of newborn animals is low, less than 5% in the first month. In early life two occasional sources of mass deaths are rafting of icefields close to shore when many young (and sometimes some females) are crushed, and very thin ice just after birth, when the young drown or cannot be fed. Swimming ability is precocious and abnormally early breakup of ice, after weaning, causes little added mortality. In extensive tight ice, young move over ice to the seaward edge. Moulted young exposed normally to disintegrating ice swim northward until new icefields are found, then drift passively southward until it disintegrates. Experimental release of young seals in the Gulf of St. Lawrence did not elucidate the sensory clues used in the first northward migration.

Birth

In the course of one of our marking expeditions, Mr. W. Pinckard observed a birth near the Magdalen islands on March 1, 1964, and gave the following description to Dr. A.W. Mansfield:

> "The cow was lying on a small slab of ice in obvious labour. At the moment before birth, she clawed at the ice with the fore flippers and rolled on her side, all this while (10 minutes from when first observed) she growled, grunted and whined. The pup appeared tail-first for about half of its length, then remained in this position for about 30 seconds. The cow thrashed from side to side, then the pup was completely born in one last convulsion by the cow. The placenta appeared immediately and was still attached to the pup at least one half-hour after. The pup made no attempt to suckle in the observed period".

Stewart et al. (1981) described two more births in detail. In these two, delivery of the placenta was not observed, for observation periods of 17 and 1 min after delivery.

The placenta is not eaten by the female but is left on the ice, often to be devoured by gulls *Larus marinus, L. hyperboreus,* etc. or crows *Corvus americanus.* Lavigne and Stewart (1979) give the weight of the placenta as 1.3 ± 0.4 kg (12% of newborn pup weight) with an energy content of 1 430 ± 438 kcal.

Season of Births and Length of Lactation

A. Introduction

It is very difficult to determine birth dates in harp seals because unpupped females disturbed by man vanish into the water to reappear elsewhere. Observing females and pups from ships, it is extremely difficult to remain for days or weeks with individual animals and examine their growth. However, Soviet investigators first solved this problem by mounting drifting expeditions serviced by helicopters on the ice of the White Sea (Popov 1966, 1967), and investigators from the University of Guelph have more recently done the same thing in the Gulf of St. Lawrence (Stewart and Lavigne 1980).

The normal weight of stillborns is about 8–9 kg. This agrees with the data of Chapskii (1964) who gives the birth weight as about 8 kg with a pelt weight of 3 kg. Dorofeev (1960) gives the birth weight as 9.5 kg. However, Lavigne and Stewart (1979) weighed 10 neonates which were still wet from their birth and averaged 11.2 ± 1.0 kg in weight. Stewart and Lavigne (1980) find 10.8 ± 0.65 kg for 40 living neonates in the Gulf of St. Lawrence. This shows that the stillborns average below living birth weight.

In the normal course of research from ships, in different years and even within one season, one meets with different age-groups of young seals at any one date. However, one way to determine birth dates is to make use of data on the mean weight of pups and of their pelts at different dates and to average the results for different groups. Knowing the weight of the newborn pup and its pelt, one can extrapolate back to the birth date. The end of lactation likely corresponds with the age at which the weight of the pup and of its pelt reach an asymptote.

B. Northwest Atlantic

Figure 58a and b shows summed data on weights of young and of their pelts for the Gulf and Front over several years of study. Extrapolating back from the data on early weight increase of pups, a pup weight of 10 kg and a pelt weight of 3 kg would give mean birth dates of about March 9 for the Front and March 3–4 for the Gulf. Weighings on the Front in 1952 were from an earlier-pupped group and would give an earlier date there.

Figure 58b shows that maximal pelt weights are attained about March 20 in the Gulf and March 25 on the Front. These two sets of dates would suggest a lactation period of about 16–17 days.

Stewart and Lavigne (1980) studied growth in marked pups observed from birth in the Gulf of St. Lawrence in 1979, and used the data on growth in length and weight of these animals to calibrate comparable data from young of known pelt type but unknown age. Six categories were

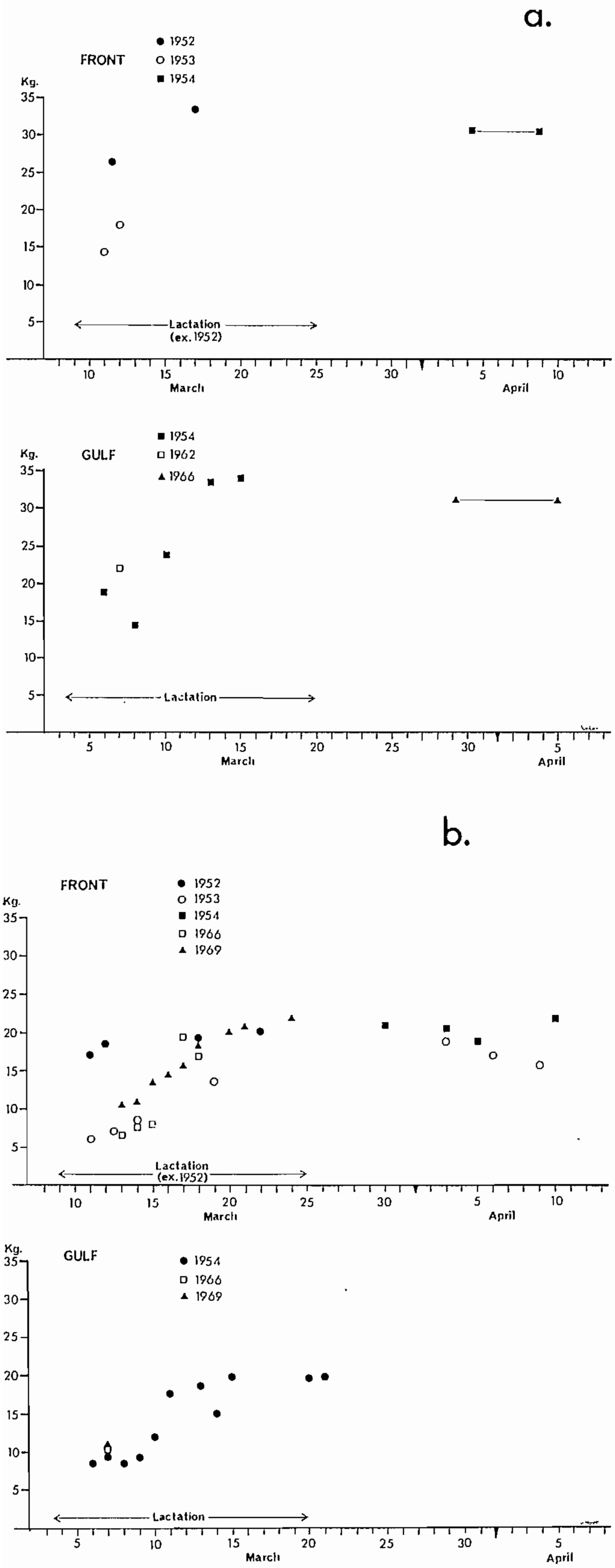


FIG. 58. Weight increase of young harp seals, Front and Gulf (a) total weight (b) pelt weight.

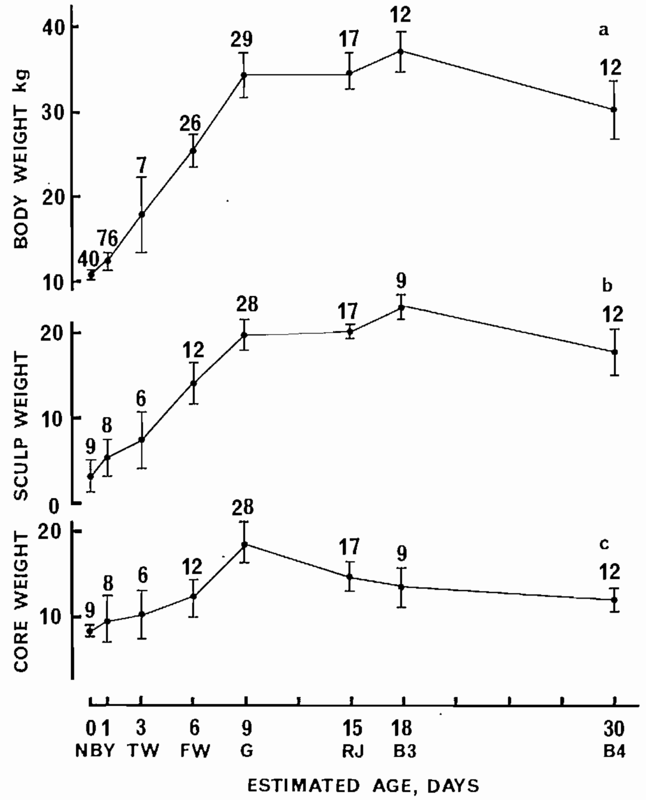


FIG. 59. Mean total body weight (a) sculp weight (b), and core weight (c), as a function of pup age. Vertical bars represent 95% confidence intervals. The number by each point is sample size (from Stewart and Lavigne 1980). Explanation of pup categories in text p. 00.

recognized: newborns and yellowcoats, thin whitecoats, fat whitecoats, greycoats (with moult showing under the lanugo), ragged jackets, March beaters and April beaters. Growth in total weight, core- and sculp-weight are shown in Fig. 59 for these categories. The main addition to previous work was to show that pelt weight continued to increase (at the expense of core weight) after weaning had been attained. Mean daily weight gain was estimated at ca. 2.8 kg, from a mean neonatal weight of 10.8 kg to a weight at weaning of 34.4 ± 2.6 kg. Kovacs and Lavigne (1985) from growth studies estimated a lactation period of 12 d.

A third method of estimating the lactation period is given by observational data on whelping and either the onset of mating, which according to Popov (1966) marks the end of lactation, or the observed end of lactation itself.

1. Whelping

In the Gulf in 1959 females were beginning to haul out on February 27 with some bloodstains indicating first births (P.L. Montreuil in litt. to Dr. H.D. Fisher, 28-II-59). In 1966 a large patch seen from an aircraft was estimated to be about half-pupped on March 4, and when the same patch was entered by ships on March 7 the young were estimated to be about 4–5 d old, i.e. many births must have taken place March 2–3. On March 3, 1967 our helicopter settled on a large patch which proved to have just begun to whelp, since the large majority of females moved away leaving a few scattered females with pups. These young were weighed on March 4 and 5 and were estimated at 3 d old, i.e. born on March 1–2. On March 3, 1969, many animals had whelped in one patch in the Gulf.

Owing to the effect of sealing it is difficult to place mean date of whelping, but the whitecoat industry for many years required pelts on average 4–5 d old and settled on a starting date of March 7 in the Gulf which suggests that many animals in the Gulf whelp March 2–3. This is probably earlier than the mean date since the ships could, after the starting date, go on to later-whelped groups. Stewart and Lavigne (1980) estimate a mean whelping date in the Gulf in 1979 of March 3.

The end of whelping may be quite late. In 1965, when the Gulf quota had been taken on March 12, whelping was still taking place. In 1967, many new pups were found on a sealed-over patch on March 14 after the quota had been reached on March 11. In 1970, with no aircraft disturbance and before a late starting date of March 20 for ship sealing, one large patch was whelping between March 8 and 17, an unusually late date.

On the Front, the whitecoat industry agreed on a starting date of March 12, confirming that the mean date of births is about 5 d later than in the Gulf. Variability occurs, as in the Gulf, from group to group of seals and from year to year. Very often there is a "southern patch" which whelps earlier than the "northern patch". On March 11, 1952 on board *Blue Seal* I weighed large fat whitecoats near Belle Isle, but on March 11, 1953, on board *Algerine* north of Belle Isle, I met with pups which were still thin (Fig. 58a). From other reports the seals in question came respectively from a southern and a northern of two patches in each year. The difference in mean weights was between 25 and 15 kg and the mean birth dates of the two groups must have been close to March 3 for 1952, March 9 for 1953.

In 1966 the majority of young studied in Hamilton Inlet on March 13 were about 4–5 d old giving a birth date of about March 8–9, and births were still taking place.

Late births occur on the Front too. In 1969 W. Hoek met with whitecoats still attended by females off Hawke's Harbour, Labrador, on March 30, and similar reports have been obtained in other years.

In sum, whelping in the Gulf may take place between about March 1 and 17, with a median date of about March 2 or 3. The mean date on the Front is 4–5 days later than in the southern Gulf. The whelping curve is very likely left skewed, with a late tail.

2. *Mating*

I have observed mating in the Gulf on March 14; our tagging party in 1966 observed mating in the Gulf on March 20 and 21, and in 1970 observed sexually active males March 16–18; Fisher (1954) observed mating on March 21. On the Front, Fisher (1954) from male reproductive condition estimated the time of mating to extend between March 20 and end March or early April.

3. *End of Lactation*

In the Gulf I observed females attending pups only in the morning and evening on March 15, 1954 and in a late-born patch there were still females with pups on March 22. On the Front I observed adults with pups up to March 19, 1952. W. Hoek observed no adults with pups in a patch on March 23, 1969, and Popov and Timoshenko (1965) observed females with pups up to March 23–24, except for a few females with late-born pups on March 31. These data, summarised in Table 29, would suggest that the end of lactation occurs on average about March 15–20 in the Gulf, about March 20–25 on the Front. This method therefore provides an estimate of lactation length of about 12–17 d.

The method using growth in weight of whitecoat pelts over-estimates the lactation period, if pelt weight continues to increase (at the expense of core weight) after weaning. The observations of the time between birth period and weaning period probably tend to overestimate it also since late observations of suckling may refer to

TABLE 29. Observed mean dates of birth, weaning and mating and length in days of lactation (boxes) deduced from them.

Area	Birth	Weaning	Mating
Gulf	March 2–3	March 15–20	March14–21 (16–18)
		13–17	12–18
Front	March 7–8	March 19–24	March 20–31
		12–16	13–
West Ice	March 18–20		March 30–April (5)
			12–
White Sea	March 1		March 10
			10–

late-whelping females. The true period therefore is less than 15 d, and may be as short as 9 d as concluded by Stewart and Lavigne (1980). Earlier authors, who apparently used the last of the 3 methods described, gave: 10–12 d (Rasmussen 1957 following Sivertsen 1941) 3 wk (Dorofeev 1960), 19 d (Chapskii 1964 — see Fig. 21), and ca. 3 wk (Popov 1966).

C. Other Areas

The *Jan Mayen* population has the latest whelping season. Rasmussen (1957) gives the mean birth date as March 18–20 and the period of mating as from end March to early April. The *White Sea* has the earliest season. The whelping season here was given to me by Dr. L.A. Popov (in litt., Nov. 16, 1969) as 20 February to mid March with a peak of February 25 to March 10. Sivertsen (1941) gives the peak as February 20 to March 5 and Nazarenko (1970) as February 25 to March 5. Popov (1966) observed mating on March 10, while Sivertsen reported it between March 4 and 12 in different years.

D. Discussion

Since the White Sea and West Ice lie at nearly the same latitude but their harp seal populations differ by three weeks in whelping date, it is difficult to believe that light cycle regulates implantation time and therefore whelping date, especially since a degree of mixing has been observed between these two populations. Yet it would seem necessary for whelping to be regulated by a seasonally varying external factor. An explanation of this dilemma could be that wandering and displacement occur mainly among young immature seals, which as they mature increasingly migrate with the main herd to new home waters. In just these years of adolescence a light cycle or other environmental stimulus could synchronise the reproductive period of the herd.

Whelping must also be "triggered" by an immediate factor such as, most likely, the condition of the ice. Dr. A.W.H. Needler pointed out to me that probably the adult female can delay whelping for several days, a necessary adaptation if good ice is not available. At least, evidence of harp seals whelping on shore is extremely rare, a feature which would be observed if no such adaptation were present.

It is very remarkable that a century or more of ship sealing has not disrupted the whelping herds of harp seals, when one considers that a species like the Mediterranean monk seal (*Monachus monachus* is extremely sensitive to such disturbance to its whelping (Sergeant et al. 1979), and the same is true for the Hawaiian monk seal *M. schauinslandi* (Kenyon 1980). An answer was suggested by Gentry (1980) discussing the social life of the northern fur seal *Callorhinus ursinus* L. He asked why fast-learning fur seals return year by year to the same rookeries for reproduction and haul-out where they will be disturbed by man. He concluded that the "categorical imperative" for a socially-breeding species was the complex sequence of breeding activities, that the species had no choice but to return to traditional sites en masse for reproduction, and that this need over-rode the human disturbance. The same must be true for harp seals; they must return to much the same ice-fields, and in large aggregations, for successful breeding. With this standpoint and comparing the sensitivity of the solitary or indifferently social monk seals, it appears that (apart from the advantage to man of sheer density of animals), highly social Pinnipeds better withstand exploitation by man than those much less social in their reproductive behaviour.

Lactation

Lactation and Pup Growth

I was rarely able to observe undisturbed behaviour of females and young. However, on March 10, 1953 the ship *Algerine* arrived in a group of seals at the Front in an 120 km/h northerly gale which precluded sealing that day, and I was able to observe the seals from shipboard, as also occasionally after landing from helicopters at other times. The majority of mothers with very small pups stay with the pups all day and only rarely enter the water. Suckling occurs at any time as the result of the pup's nuzzling. The mother and pup show frequent "nosing" and I speculated that this behaviour may set up an olfactory bond. W. Hoek in 1968 shot a film sequence which showed a female emerging from a hole in the ice, sniffing a pup and rejecting it as strange, moving to a second pup and suckling it (Fig. 60).

Nazarenko (1970) studied in detail this question of how the mother finds the pup and showed that the mother first returned to the site where she had left the pup, using spatial clues. If the pup had wandered, or had been removed by man, she followed its scent trail to its termination, as far as 150 m. She could also detect and respond to the characteristic cry of her own young by emerging from the water. Nazarenko believed that the auditory and scent recognition by the female of its pup were set up in the first 4 or 5 d.

As the pup grows older, the female deserts it more frequently and milk meals become larger and less frequent. This feature was well-studied by the first Soviet drifting expedition in the White Sea (Popov 1966) where it was found that young 4–6 d old take on average 700 mL of milk, older whitecoats 1 litre and pups near the end of lactation, 800 mL. Popov gives the daily weight gain of pups in early lactation as 1.5 to 1.8 kg rising to 2.5 kg to 3.0 kg and falling again to 0.5–1.0 kg near the end. Stewart and Lavigne (1980) found a mean daily weight gain in the Gulf of St. Lawerence of 2.7 kg from birth to greycoat stage. The volume of milk in 8 neonate stomachs averaged 245 mL and in one ragged-jacket stomach, 170 mL. Popov (1971a) found a daily weight loss of 0.6 kg in starvelings 7 d old or older, as did Worthy and Lavigne (1984) on young pups held in captivity.

This very rapid growth is based on an exceedingly rich milk. Published analyses of harp seal milk are shown in Table 30. Cook and Baker (1969) further report on the composition of its ash and fatty acids. Harp seal milk is approximately 12 times more fatty and 25 times richer in protein than cows' milk, according to Dorofeev (1960). Lavigne et al. (1982) showed changes in the composition of harp seal milk during lactation; fat content increased

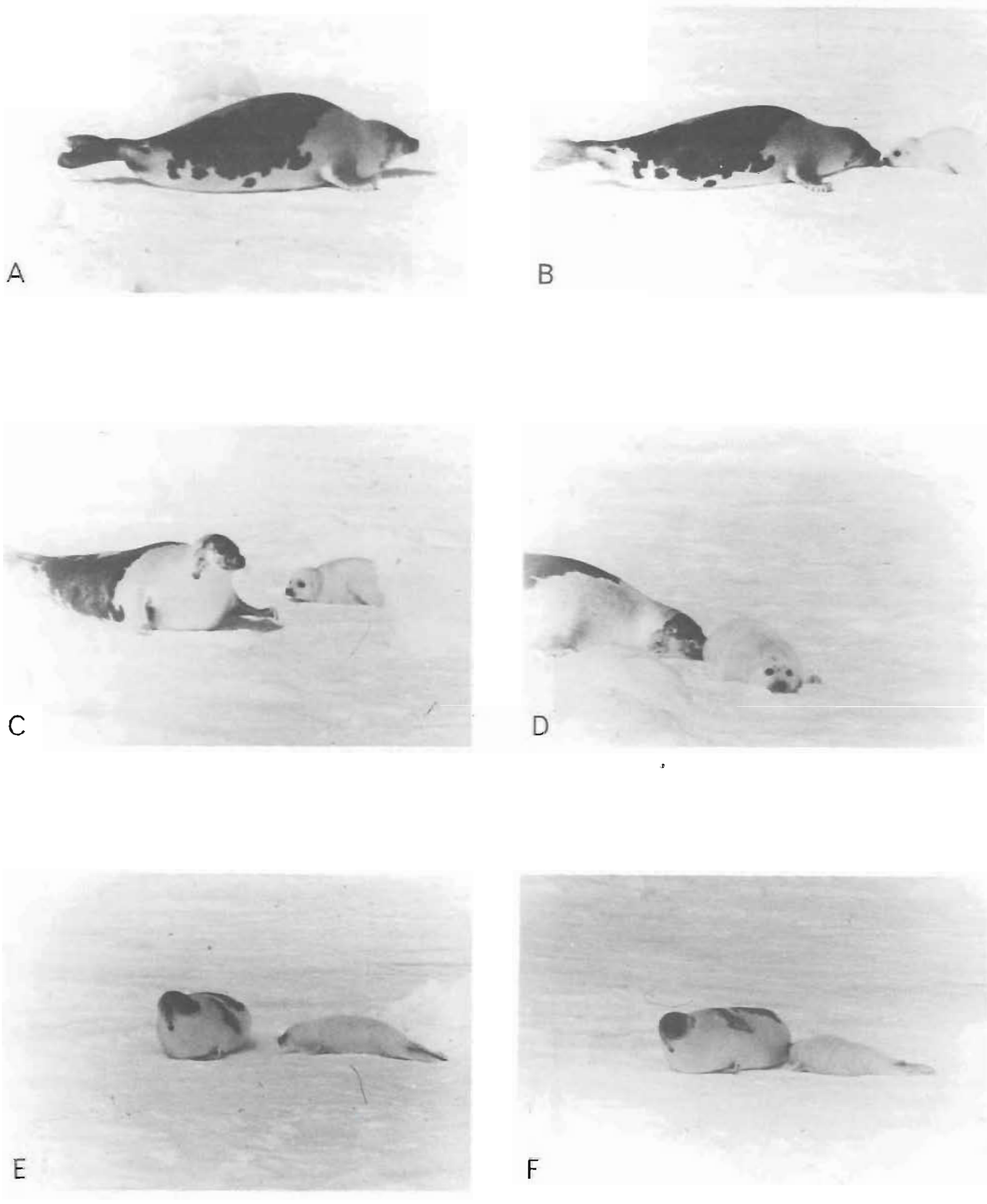


FIG. 60. Still pictures from film sequence showing adult female newly climbed out (A), nosing and rejecting one pup (B & C), nosing and accepting a second (D) and suckling it (E & F). (Photos W. Hoek; Gulf 1968).

TABLE 30. Analysis of milk of harp seals.

Author	No. animals analyzed	Percent				
		Water	Protein	Fat	Ash	Lactose
Sivertsen (1941)	2	44–45	10–12	43	0.8–0.9	nil
Dorofeev (1960)	1	42.8	8.4	44.5	no data	no data
Cook and Baker (1969)	3	40–45	6.0–7.5	47–53	0.3–0.5	0.3–1.0

while water content decreased, hence energy content increased. Protein and ash remained constant.

Lactation and Time of Day

Popov (1966) and his colleagues, counting females and pups from ice level, found that females were practically absent in the morning hours and returned to the ice in the middle of the day and especially in the evening. In fog and snow most of the females stayed in the water, coming up on the ice only to feed the young. However, they preferred to stay on the ice on clear and windless days and basked in the sun after feeding the young. On such days, Popov found, 70–80% of the females were present on the ice in the evening and 45–55% in the daytime, while in snowstorms the daytime percentage fell to 10–11%. Popov thought that he had missed some hidden whitecoats and so had slightly overestimated the percentage of females present under each weather condition.

Timoshenko (1982) and co-workers placed a 240 x 130 m frame marked with strips of material and flags on the ice of the White Sea, so that the number of pups and adults could be counted from the ice or the air, on March 1, 1980, when all the pups were newborn (yellow). At 1500–1530 h, the number of adults was 16/31 pups = 51.6%, and from aerial photos at 1542 h 20/31 = 64.5%.

On March 10–14, 1968, Dr. D.H. Pimlott and I counted the number of attendant females from a low-flying helicopter over rather smooth ice in the southern Gulf (Table 31). The percentage of females was highest at 89% for a patch of newborn young. In other patches with older young, on an overcast morning the percentage of attendant adults was 25%, on a clear morning it was 62–71%, and on a hazy (light overcast) afternoon it was between 60 and 77%. Our data therefore support Popov's that more females attend in clear weather, but we find a larger percent of females can be present in the daytime than Popov or Timoshenko. Clearly many more observations are needed, under as undisturbed conditions as possible.

TABLE 31. Diurnal movements of adult seals, observed from a helicopter in 1968.

Date (March)	Time	Weather	Number		Percent
			adults	young	adults
10	0845–0930	Overcast	141	364	25
13	0800–0950	Clear	116	178	65
13	1315–1500	Light overcast	132	191	69
*14	1415–1430	Light overcast	102	114	89

The complexity of these variations shows how difficult it is to count adult whelping harp seals. When the percentage of attendant females is highest, not all of the females have whelped, and unless these unwhelped animals are lying out one has missed them. On the other hand, as the percentage of young born increases, females having older young will increasingly tend to be in the water. The data also show why observes are often puzzled that patches of seals often seem to decrease in size. At first the massed adults are conspicuous. Later, especially on cloudy days, one may fly over a patch of young and see only scattered adults, missing the inconspicuous young.

Energetics of Early Life

Figure 58a showed that growth occurs to a mean maximum weight of about 34 kg at weaning, after which the weight decreases as the young lives on its body reserves. Figure 21 taken from Chapskii (1964) referring to the White Sea showed essentially the same curves for total and pelt weights, and in addition showed growth in body length which is continuously positive. [I have substituted the Newfoundland trade terms for growth stages in place of the Russian ones.]

Young in a late stage of moult or fully moulted (beaters) were weighed in the Gulf on April 1–5, 1966 and on the Front on April 4–9, 1954. In each case the mean weight was close to 31 kg (Table 32). Therefore, in a period of approximately 20 d following weaning, the young have lost approximately 3 kg of weight. During this period, they have been relatively inactive, and have shed the white hair coat or lanugo. Stewart and Lavigne (1980) obtained similar figures (Fig. 59).

On the Front in 1953, I examined stomachs of beaters on April 2, 3, 5, 9 and 10 and the first food remains were found on April 5. Stewart and Lavigne (1980) found food (*Pandalus* shrimps) in 50% of stomachs of 12 beaters taken at the Front in mid-April. Full independence, therefore, as defined by the beginning of independent feeding, begins at about 28 d of age. As soon as adequate proficiency in feeding is gained, body weight will stabilise and begin to increase again. W.D. Bowen (in litt.) from examination of stomach contents in 1980–84, states that "most pups do not begin to feed until at least the third week of April in most years".

TABLE 32. Weights of moulted juvenile harp seals, Gulf and Front, age ca. 4 wk.

Area	Year	Dates in April	Sex	N	Weight in kg Range	$\overline{X}$
Front	1954	4-9	Both	41	17.7-40.4	30.8
			MM	26	17.7-39.0	30.7
			FF	15	24.5-40.4	31.0
Gulf	1966	1-5	Both	105[a]	17.7-45.4	31.3
			MM	53	17.7-45.4	30.8
			FF	48	21.3-40.8	32.1

[a]4 unsexed.

Stewart and Lavigne (1984) showed that the female appeared to lose little core weight during lactation but loses a mean of 24 kg of sculp weight (i.e. blubber) from her mean weight (129 kg), at a rate of about 3.17 kg per day. This represents a loss of about 250 000 kcal of energy (200 000 for lactation and 50 000 for her maintenance) of which 194 000 kcal goes into milk. The pup gains 2.78 ± 0.19 kg per day of which 1.95 ± 0.13 kg per day goes to the sculp (i.e. the pup's blubber) and 0.83 ± 0.11 kg to the core. That is, two-thirds of the mass gain of pups is blubber. In fact the females must lose more core mass than shown by Stewart and Lavigne to account for weight increase of the pup's core.

Stewart and Lavigne (1980) showed that after weaning, the core weight of the pup decreases, while sculp weight increases, before independent feeding begins. Therefore the weaned ragged-jacket/beater burns protein rather than fat for a while. Sivertsen (1941) had reported similar weight changes. The later authors deduced that maintenance of a thick blubber is important in the beater, presumably for insulation.

Kovacs and Lavigne (1985) give further figures for pup body growth and also changes in organ weights. The liver (a source of fat reserves) fluctuates in size with the pup's gain and loss in body weight. Worthy and Lavigne (1983) confirmed this by studying in captivity the energetics of captive weaned pups starved for various times from 1 to 10 wk. Pups were sampled at various dates, and their tissues (carcass, viscera and blubber) analysed for lipids, protein, water and ash. They found that core proteins and lipids formed an important part of the energy source for the first 2 wk, then diminished so that blubber supplied 90% of the total energy at 6-8 wk; core proteins were again mobilized at 9-10 wk of fasting. The mean decrease of weight in 10 wk was from 32 to 15 kg (in 2 wk — to 27 kg). Feeding led to a higher rate of weight gain if started at 4 wk (0.29 kg/d) than at 1-2 wk (0.17 kg/d) after fasting began. In nature fasting lasts about 2 wk before independent feeding begins. This work confirms that the blubber layer is maintained preferentially during the normal fasting period, so allowing the pup to enter the water to feed with adequate thermoregulation. It also suggests that the other adaptations allow pups which start feeding late to make up their deficiencies and survive.

Worthy (1987) showed experimentally that after independent feeding begins, growth is preferentially in the core and not in the blubber. Comparison with the work of Worthy and Lavigne (1983) suggests that, after a normal fasting period of ca. 2 wk, this metabolic pathway would allow replenishment of the somewhat depleted core proteins and lipids.

Stewart and Lavigne (1980) stated that there was no significant difference in total body weight of pups of different age-groups between different years of study. However, Stewart and Lavigne (1984) found very different initial and final body weights of adult females during the same series of years. This kind of adaptation would tend to reduce and regularise pup mortality from year to year. Such mortality is extremely difficult to measure, however, once the young seals leave the natal ice.

Early Mortality

As Popov (1971a) points out, quantification of mortality of young in their first year is only possible (with present techniques) during the first month of life, when investigators can remain on the ice floes with the whelping groups.

In the course of tagging pups we have investigated mortality in the first few days of life by counting the number of living and dead pups. In the larger counts every living pup had been tagged. The results are shown in Table 33. The mortality rates observed were 1% or lower, and were significantly ($P < 0.01$) lower on the Front than in the Gulf. Sources of mortality were not closely studied but appeared to include birth difficulties, (e.g. a placenta over the head), genetic abnormalities producing undersized young, and a rare category of apparently normal fat pups.

Kovacs et al. (1985) estimated a mortality of 1.1-1.4% in the Gulf in 1983-84 over the first 2-4 wk, including stillborns and starvelings.

From studies during three drifting expeditions (in 1966-68) in the White Sea, Popov (1971a) and team divided sources of mortality of pups into three categories: stillborns, pups deserted by the mother at birth or at later ages, and pups dead from injuries. Stillborns could be distinguished from pups abandoned by the mother at birth by the presence or absence of covering membranes. In the second category, Popov studied weight loss in three pups which had been deserted soon after birth by the mother, and one in which the mother had been shot. These weighed between 8 and 11.1 kg when studies began. Weight loss was at the rate of about 0.4 kg per day and death occurred at weights of 6-8.8 kg, which is below the normal weight at birth, and at ages 9-10 d. These data would suggest that pups deserted at later ages might survive for a long time.

Indeed, pups deserted in this way become the well-known "starvelings" which are noted by all visitors to the icefields. Thus a tagged specimen was recorded in the Gulf of St. Lawrence on 7 May, 1967 which weighed only 31 lb (16 kg). Possibly, mortality of such young occurs during the northward migration when the metabolic demands become high.

TABLE 33. Early deaths of whitecoats, Gulf and Front, 1966 and 1968.

Area and date	Living Young Number	Dead Young Number	Dead Young %	Observer(s)
Southern Gulf, March 7–8, 1966	417	4	1.0	Author on sealing ship *Theron*
Gulf, March 7–11, 1968	2219	15	0.7	Tagging party from helicopter
Front, March 13, 1966	330	1	0.3	Author on *Theron*
Front, March 8–13, 1966	3581	9	0.3	Tagging party from icebreaker

It is also possible that some of the early emaciated young are siblings, since twinning is found in foetuses of about 1% of harp seals examined in January.[16] If twins are born alive, the larger or dominant animal may soon exclude its twin from suckling, since the female lies on its side. Thus, a fast-furred starveling and a moulting, fat pup weighing 90 lb (41 kg) were found on the same ice floe on March 24, 1952. The former could, admittedly, have been deserted by another female. However, Peterson and Reeder (1966) observed three births of live twins to northern fur seals *Callorhinus ursinus L.* and in the best-documented example, one twin was rejected by the mother and did not even begin to nurse. The "nosing" behavious described above (p. 00) between mother and pup harp seal suggests that here too the subordinate twin would be ignored very early.

Traumas observed by Popov (1971a) in pups included injuries to flippers, lips and eyes and deep, bleeding wounds; the former category he thought caused by the female (possibly under stress), and the latter caused by the claws of an adult male acting aggressively to the pup when ready to mate with the female. Popov was able to quantify the three categories of dead pups as follows:

— stillborns 0.8 to 1.1% over 3 years
— emaciated 1.0 to 1.1% in 1968 only
— traumatised 1.2% in 1968 and 2.7% in 1966

for an estimated total of 4 to 5% of deaths during the whole lactation period.

Two kinds of mortality have been thought to occur due to environmental hazards: drowning in loose ice during storms, and crushing due to rafting of ice. Our data show that mortality due to stormy conditions in loose ice is probably low. By contrast, crushing due to rafting of tight ice near shore is a very real hazard.

Mortality of Young in Loose Ice

In Ch. IV it was shown that the whelping ice is normally thick enough and so placed that it persists well beyond the four weeks needed for the young to reach independence. However, sometimes it becomes broken up by storms and dispersed at sea before they reach this stage. Do the pups then survive? Most sealing observers have thought not. Sivertsen (1941, p. 58) for example cites observations of a sealing captain in the White Sea as follows:

> "During a violent southeast gale that blew at the beginning of April, S/S *Sverre* observed near Cape Kanin a number of larger floes drifting out of the White Sea full of young seals. The skipper was of the opinion that the floes would be destroyed by the sea and most of the young seals lost".

Results of a marking experiment which we carried out in March 1966 happened to give relevant information. Young seals were marked on March 16 to 21 from a helicopter using metal tail tags in the south-east Gulf of St. Lawrence. The first group marked on March 16 and 17 consisted mostly of fast-haired pups located on broken ice close to the leading edge of the ice, near the border of open water. On March 18 the helicopter pilot reported that the marked seals had moved out off St. Paul's Island into the open Atlantic swell and that the ice floes were breaking up. On March 19 to 21 another group of harp seal pups were marked, mostly at a later stage of moult, and with mating adults. These young were located on larger ice floes further to the south and thus further from drift and break-up around Cape Breton Island.

First recoveries of the marked seals were obtained from shore fishermen in the Gulf of St. Lawrence in March to June 1966 with later recoveries from the arctic (mostly west Greenland) in the first summer, and from southward migration and first rewintering at 1 yr of age. Table 34 shows recovery rates for the two groups of seals.

The first and younger group of tagged seals gave slightly lower recovery rates than the second group for both recovery periods, first spring and first year, indicating that they had suffered slightly higher natural mortality first. However, the difference in natural mortality between the two groups was only about 10%, in spite of the fact that this group had been forced to swim at a precocious age, and is not significant ($P = 0.50$ for Gulf recoveries). Moreover individuals of the first group were picked up very soon in the northern Gulf on April 7, 8 and 9, having moved some 300 km (180 miles) northward across open water to a band of ice extending along the north shore of the Gulf westward from the Strait of Belle Isle (see below, p. 83). Other of these marked animals were recovered on the northwest coast of Cape Breton Island up to April 10, and round the Magdalen Islands mostly up to April 14 with one to

[16] In samples taken in the Gulf of St. Lawrence over 12 winters, twin foetuses were recorded in one out of 370 near-full-term females, but it is likely that this is an underestimate due to under-reporting.

TABLE 34. Comparison of recoveries of two groups of young harp seals marked in March 1966. Recoveries (a) from the Gulf of St. Lawrence in March–June 1966; (b) in the rest of the first year of life, comprising returns received as of July 1967; (c) combined.

Date of marking	Number marked	Number recovered a	b	c	Recovery rates % a	b	c
March 16	274	20	10	30			
March 17	241	7	9	16			
Group 1	515	27	19	46	5.2	3.7	8.9
March 19	578	35	21	56			
March 20	189	9	10	19			
March 21	113	5	8	13			
Group 2	830	49	39	88	5.9	4.7	10.6

April 21, while a moribund animal was found on the shore of Prince Edward Island on April 21. It seems likely that early separation and breakup of ice from the main icefields by current and/or storms is a hazard to which young harp seals are to some extent adapted and which causes little mortality. This conclusion is supported by observations that swimming behaviour in young may start very early. Inadvertent swimming is commonly seen in young pups when a ship passes through a whelping group and displaces pups. On March 7, 1967, a pup observed from a blind on the ice repeatedly entered the water of a large breathing hole when its mother had disappeared through it. The pup was no more than 3 or 4 d old.

Mortality Due to Ice-Rafting

Mortality of young harp seals and sometimes of accompanying adults due to severe rafting of pack-ice in contact with land and under pressure from wind or current was well-documented by Sivertsen (1941, p. 70–72) in the narrow Funnel of the White Sea.

This phenomenon occurred in the two seasons 1962 and 1965 at the Front. Research personnel or Fisheries officers were present on ships and did not report any such seal destruction due to rafting on the Front during the whelping seasons of 1951 through 1964, and 1966 through 1970. Thus, severe rafting with seal deaths was seen at the Front in 2 out of 11 yr in this period.

In early May of 1962 the St. John's Biological Station received reports of large numbers of harp seals drifted ashore at Twillingate and adjacent points in Notre Dame Bay, Newfoundland. I contacted Dr. J.M. Olds of the Notre Dame Bay Memorial Hospital, Twillingate, who sent back the following telegraph message: "Around three thousand dead, round (i.e. entire[17]) seals picked up in vicinity. Well developed whitecoats 87 per cent, old harps 13 per cent, bedlamers nil. Many crushed heads, also some multiple fractures to spine and ribs, no evidence of epizootic or man-inflicted wound". This evidence suggested that a group of young seals with some of the attending adults had been crushed by rafting ice.

[17] In what follows, words in parentheses are the author's.

The Front herd of seals in 1962 pupped very close to land in the vicinity of South Wolf I. and Spotted I., Labrador (Fig. 61) and deaths due to ice-rafting were later reported to me by sealing captains. There had been strong northerly winds in the middle and later part of March, when the Front young would have completed their moult. Subsequently the carcasses must have drifted to Notre Dame Bay which is the most common route of drift of seal patches on the Front.

In 1965, fisheries officers were on board Canadian sealing ships at the Front and their diaries gave good documentation. The location of the seal patch was again very close to shore in the vicinity of South Wolf I. (Fig. 61). Mr. George Furey on M/V *Algerine* wrote on or about 15 April:

"The weather this spring was very bad. . . Northeast gales prevailed, snow storms and zero weather being the order of the day, and rafting ice. . . Numbers of seals were killed along the ice edge by rafting ice, crawling into cracks and getting crushed."

Mr. J.J. Mulcahy on board M/V *Arctic Endeavour* wrote that the young seals moulted around the first week in April, taking to the water at this time. However, where the seals were on fast ice, they did not get in the water before about 19 April.

Subsequently Mr. James N. Court of Kegaska (Kégashka) on the north shore of Québec at 50°11'N, 61°16W', wrote to the Quebec Department of Tourism, Fish and Game as follows:

"Around two weeks ago (i.e. in early July, 1965) we discovered a lot of dead seals in the water and around the beaches. These seals came in with a south wind. In a small area around here I have counted forty-two and according to rumour these dead seals are along the coast everywhere. Most of these seals are young harps (i.e. fully-moulted young) although there are some raggety jackets. The seals have been in the water a long time, all being

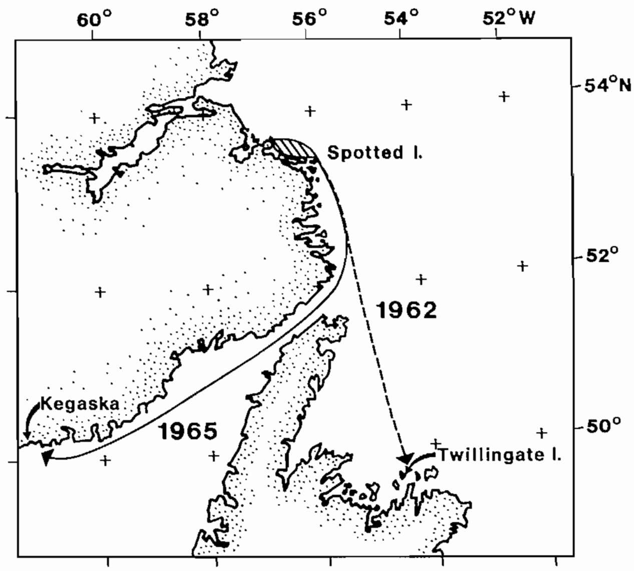


FIG. 61. Sites of ice-crushing of young (and once, attendant adult female) seals, 1962 and 1965, and drift of carcasses.

tainted, and the sea gulls have eaten them in places. One thing we have paid special attention to here, the seals have their heads missing, and it looks as if they have all been crushed off in about the same place, across the neck. According to the blubber the seals must have been healthy at time of death''.

There is little difficulty in relating these carcasses, drifted south by the Labrador Current, to the deaths described two and a half months earlier by fisheries officers. The Labrador Current water is extremely cold, and the ice had probably held the carcases for some time. The state of moult of young is in agreement with the date of deaths in the two accounts, and a description of crushing occurs in both.

Without special enquiry, I have not received reports of severe rafting followed by widespread deaths of young seals and attendant females in the Gulf, and therefore suppose it is rare. However, sealing captains and, later, fisheries officers, reported small-scale ice crushing to occur in the Gulf and in 1969 (as the result of special enquiry about deaths of young seals) we received one documentation. District Protection Officer D.T. MacNeil, Sydney, Nova Scotia wrote (letter of April 14, 1969):

> "I have made enquiries along the Gulf of St. Lawrence coastline (of Cape Breton Island) regarding mortality of harp seal pups. The only area reporting such mortality was Pleasant Bay, Inverness Co. (ca. 46°15'N, 61°20'W) Fishermen in this area saw a number of drowned carcasses and also reported seeing pups being crushed in a small patch of whelping ice shorebound by a northwest wind. A few carcasses washed onto the beach in Pleasant Bay. . . This mortality occurred about mid-March''.

The level of the 1965 mortality on the Front cannot have been high in comparison with the normal hunting mortality rate, since this year-class was relatively strong in subsequent age samples (e.g. that of 1970 shown in Fig. 91). The catch in 1965 was 189 000 young in place of 273 000 in 1964, and 256 000 in 1966, or a mean reduction of 75 000 = 28%. The relatively strong survival of this year class (Fig. 91, lower) shows that the additional natural mortality of young due to ice rafting was less than 75 000 animals.

In summary, the mortality due to ice-crushing cannot be quantified from the data on hand, but in some years can be quite severe. It affects mostly the young and to a lesser extent the adult females.

It seems significant that all reports of ice-crushing came from the 1960's and none from the 1970's. Crushing can only occur when the seals whelp close to land. Such whelping occurred during a mild period of the 1960's whereas in the harder climatic period of the 1970's harp seals almost without exception whelped far offshore (p. 40). What seems surprising is that in the 1960's harp seals did not therefore whelp further north. However, as our aerial surveys along the Labrador coast in March 1959 showed (Sergeant and Fisher 1960), even when there is little ice south of Hamilton Inlet, the ice north of Cape Harrison (ca. 55°N, 58°W) is of an arctic type affording no leads capable of being penetrated by harp seals, even when (as observed in that year) they showed some readiness to explore north.

For the White Sea, in addition to the documentation of Sivertsen (1941), Popov (1971a) describes his impressions from the drifting expeditions of 1966–68 and Bianki and Karpovich (1969) add further details for the year 1966. Variability of ice conditions in March–April was as follows:

	Ice	Winds	Weather
1966	Firm (50–90 cm)	Light, N.E. and N	Cold
1967	Very thin	Strong, S.	Warm.
1968	Thin (30–40 cm)	Light, S.	Normal

In 1968, Popov believed conditions to have been within normal limits, in spite of rather thin ice, leading to good pup survival. In 1967, as a result of abnormally thin ice and strong south winds which moved the ice out of the White Sea rapidly, he believed that pups died due to having to enter the water prematurely. But in 1966 abnormally cold weather occurred. Northerly winds persisted for two months and the resulting tightly packed ice kept the young in the White Sea and its bays and gulfs. Under these conditions, pups drowned in nets, moved into woodland, up rivers and near settlements, and were picked up in an emaciated state. Popov believed that the food base under these conditions was subnormal. It is normal for southerly winds and currents to carry the young rather rapidly out of the White Sea (p. 61).

It is interesting to test these conclusions against comparative survival rates of year-classes 1966–68 for the White Sea as obtained from samples of moulting seals. These are available for 1970 and 1971 (Anon. 1970, 1971) but not for years adjoining. These show that the strongest year-class of the three was that of 1967 for both sexes (Table 35 lower). These results suggest that delayed ice break-up causes pup mortality, while rather early break-up does not.

First Movements of Young Seals

Prevalence of easterly winds on the Front during March will pack the ice into the coast, usually into the White Bay – Notre Dame Bay region of northeast Newfoundland, where it makes the movement of sealing ships so difficult that the area is known to the trade as "ice triangle''. I was on board the sealing vessel *Blue Seal* jammed here from 26 March to 8 April, 1952 and noted a movement of young seals over ice eastward toward open water. Carroll (1873) observed the same type of movement. Under similar conditions in late April 1961, I flew over a good part of the Norwegian sealing fleet jammed in the triangle and noticed that a large number of young seals had reached the ice edge and were concentrated along it.

Under these rather extreme conditions, therefore, the young must have a form of directional orientation towards the ice edge where they will find food. Having arrived there they do not yet need to move northwards, and they allow themselves to be carried passively southward with the drift of the Labrador Current, reaching the eastern bays of Newfoundland, where they remain,

TABLE 35. Age samples of moulting seals from the White Sea. Numbers and percent total sample of youngest age classes (from Anon. 1970, 1971).

Year class	1970 Male	1970 Female	1970 Total	1971 Male	1971 Female	1971 Total	Combined Male	Combined Female	Combined Total
					Number				
1970	—	—	—	22	23	45	—	—	—
1969	18	36	54	13	16	29	31	52	73
1968	39	27	66	13	13	26	51	40	92
1967	39	34	73	22	18	40	61	52	113
1966	28	19	47	20	13	33	48	32	90
1965	24	8	32	22	22	44	46	30	76
					Percent				
1970	—	—		8.3	14.0				
1969	6.1	18.7		4.9	9.8				
1968	13.3	14.0		4.9	8.0				
1967	13.3	17.7		8.3	11.0				
1966	9.5	9.9		7.6	8.0				
1965	8.1	4.1		8.3	13.5				

as our tagging has shown, until late April or early May (Sergeant 1965).

The converse situation may occur equally early in life, when the ice disappears from round a young harp seal. As described above (p. 80), marking showed that, under these conditions, the young swim actively northward towards the next belt of ice, ceasing to travel when they reach it. In the Gulf it is commonly found that the first field of ice to melt is the natal field round Prince Edward Island or the Magdalen Islands and the young swim to the next icefield which they usually find towards the Strait of Belle Isle (Fig. 62). Marking, as in 1968 and 1969, may even show that some of the young born in the southern Gulf penetrate an ice-free Strait of Belle Isle and, having reached ice around Cape Bauld, the northeast tip of Newfoundland, drift back south with the ice so that Gulf-born young are recovered in the White Bay triangle, (Fig. 62). In such circumstances, the Gulf young are separated from the Front-born young only by the width of the ice extending east of Belle Isle. If the Front ice is not pressed to the coast by onshore winds, it will have so many leads that these young can scarcely be isolated from each other.

In summary, harp seal pups are capable of swimming long distances even before or generally after the fully moulted "beater" stage is reached. The stimulus to do so is the disappearance of ice, when they migrate northward and seek out a new belt of ice, coming to rest again when they meet it.

The orientating mechanisms of these first direct movements are a fascinating subject for future study and at present remain a subject for speculation. Ehrenfeld and Carr (1967) showed that young green turtles *Chelonia mydas L.* could find their way from the beach back to the sea, even if the sea were invisible, but could not do so if the horizon were blocked off. They were therefore probably responding to brightness of background, brighter over the sea.

There are two types of background to which young harp seals could respond. When one looks from the ice towards open water, one observes a dark "water-sky" and conversely, when looking from open water, one can detect the presence of ice in the distance by a white "ice-blink". Nansen (1925) quotes Carroll (1873) that embayed seals in tight ice were observed moving in a straight line toward distant open water, and Nansen suggested that they might respond to the dark water-sky.

Ehrenfeld (1967) has shown that the eye of green turtles is so constituted that the animals have poor visual acuity and could not therefore use sun or stars as accurate guidance cues for long distance travel in the manner shown for migrating birds (Griffin 1964). A study of the eye of phocid seals shows that they likely have low acuity in air, especially at low levels of luminance (Walls 1963; Schusterman 1972). However, even with low acuity, they might be able to appreciate the relative direction and azimuth of the sun

An Experiment on Orientation

In 1970 we took the opportunity to carry out an experiment on the orientation of these young seals, perhaps the first such experiment to be carried out on a marine mammal. Yet the results were few and puzzling.

The logistics and costs were considerable, but nothing went wrong. On March 16 and 18 the young seals, then loose-haired whitecoats about 2 wk of age, were picked up by Sikorsky-55 helicopter[18] and transferred (by sling or inside the aircraft) to a snow-filled seal-pool which had been built some years before at the Quebec Government's

[18] This was a piston-engined helicopter which could carry 6 passengers plus gear. We used it before there became available to us in about 1972 the smaller but faster and vibration- and noise-free jet helicopters.

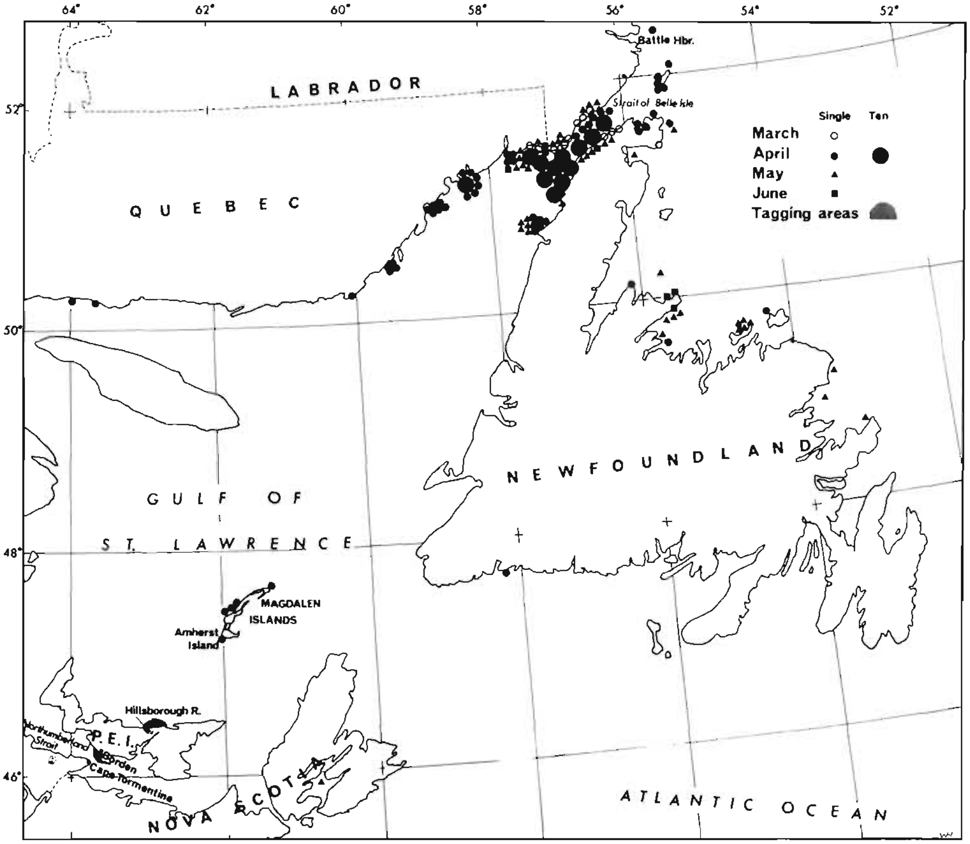


FIG. 62. Movements of young seals from the southern Gulf in their first spring, as shown from results of tagging in 1969.

marine biological laboratory in the Magdalen Islands (Fig. 63). Thence they were transferred by truck, DC-3 aircraft and truck again to the Prince Edward Island Wildlife Park at Rustico, where they were looked after for a month in a snow-filled paddock by Mr. Charles Bartlett and staff. They started feeding in early April and were fed pieces of mackerel together with thiamin tablets to counteract thiaminase enzyme in the fish. In mid-April we chartered the small steel sealing vessel *Polarfish* of Halifax, her hold empty, and sailed to Charlottetown where we loaded on 25 seals and two bales of straw.

FIG. 63. Captive fat whitecoats at the Magdalen Is., March 1970.

Young harp seals, by the way, are conveniently handled by bundling them into sacks, in which they can breathe but not bite. The seals sat in the hold, as in a barn, in small groups divided by the partitions normally carried to prevent the ship's load from shifting, and probably enjoyed less wave motion that the scientific party quartered forward.

We had brought a number of devices to attach to the seals and trace their movement. Most important was a specially made stretchy corset (Fig. 64) with large flipper holes, attached by lacing along the ventral side (a job which proved to require three people) using string which we though would soon rot and release the corset if the seal escaped with it on. The corsets had been devised for attachment of instruments at the University of Guelph. By means of strong monofilament nylon we attached a shaped polyethylene float some metres away to allow for diving. To the float we could attach a number of devices: flashing xenon lights, helium balloons, or a small radio transmitter.

In practice the seals travelled so little distance when released from the ship that we could trace them easily with the float alone. The balloons made too much drag in a wind, but the xenon flashing ligths were excellent for night releases. The radio would probably have been more effective with a better directional antenna; yet it costs so much to tie up even a small ship for long periods that satellite tracking radio-tagged seals will probably prove to be the more effective way of tracking radio-

FIG. 64. Waistcoat made for beater harp seals by Guelph University, used in 1970 for attaching tracking devices.

tagged seals. After experimental release all animals were recaptured by hooking the nylon line with a crook and drawing them on board, and then released freely.

The results were curious. The young seals, after a few moments of surprise after being dumped unceremoniously into the strange new medium, swam actively away from the ship and then took up a constant heading into the wind, even if it were quite light (5 knots). In the one flat calm available to us, they loafed and mostly made no apparent movement, although one animal out of eight released at the point possible showed some northerly movement.

All releases were made in open water, except those in the southermost Gulf (George's Bay) where one animal was released close to a small icefield which had a well-defined edge. Released within 100 m of the ice edge it swam parallel with it into the wind and only moved in to shelter or hide at the ice edge when about 20 m from it. Details of releases and behaviour are shown in Table 36 and Fig. 65.

In spite of these uncertain results, the animals had not lost their ability to move northwards. There were four recaptures, two short-term (Fig. 65) and two after a year. One of nine animals released at the entrance to Bay of Islands, Newfoundland tangled in a herring net within 4 days. The second recapture was of an animal released on a clear night but out of sight of land 30 miles northwest of Bonne Bay. When released experimentally it had headed west into a light breeze in calm water. After free release it was recaptured after 10 days, 10 km off Big Brook in the Strait of Belle Isle, having made good a distance of 125 miles (200 km) in a northeast direction between April 21 and May 1.

One animal released in Northumberland Strait was recaptured in Notre Dame Bay, Newfoundland at 11 mo of age in early February 1971, while one animal released in Bay of Islands was recaptured at the site of release at 13 mo of age on 15 April 1971. All one can say of these two long-term recaptures is that the animals behaved as do normal Gulf one-year olds, some of which show a homing pattern while others cross to the east side of Newfoundland.

The experiment therefore, tells us little about how young harp seals orient northwards in spring, except that

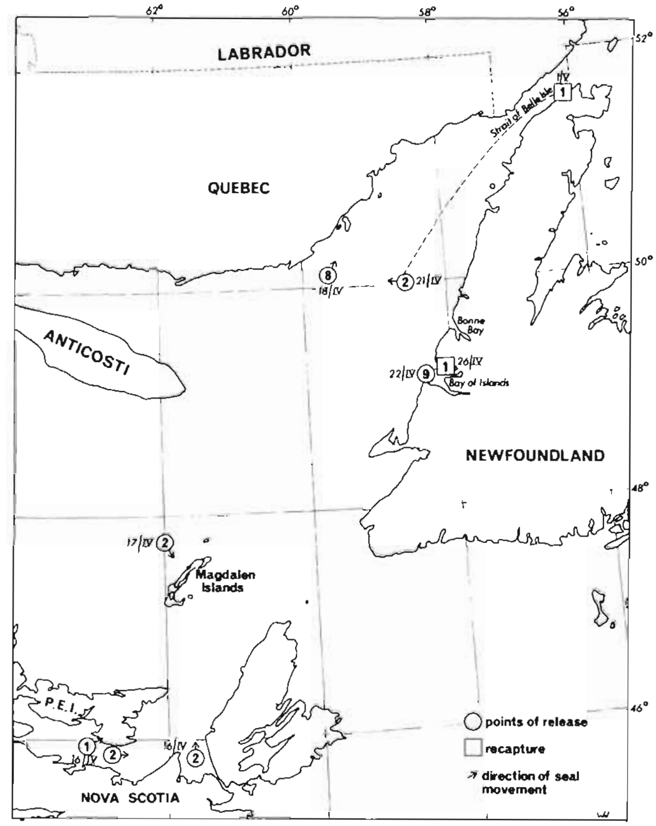


FIG. 65. Sites of experimental releases of 26 young harp seals in the Gulf of St. Lawrence in April 1970 (circles) and sites of recoveries of two of them (squares).

they are capable of normal orienting behaviour even when they have been reared away from the sea to an age of about 5 weeks, and they apparently detect ice only at short range. This last observation would suggest that their use of vision is small.

Could wind be used as an orienting mechanism? When published meteorological data for the Gulf in April, 1970 became available it was found (Fig. 66) that prevailing winds at all sites would have allowed the young, heading into the wind, to orient northward. However, this neat pattern is not retained when we examine a series of several years' April wind patterns.

Heading into the wind could be useful to an animal merely seeking ice since the ice itself drifts downwind. It could hardly be a sufficiently accurate method of long distance orientation for a species with such well-demonstrated ability to orientate.

The Solitary Young Seal

It has repeatedly been observed that the young harp seal in the spring is a solitary animal. While it is not easy to make observations on the herds of migrating harp seals in the spring, the migrations of the young appear (from catches) to be somewhat separate from, and later than, those of the rest of the herds. Thus, tagged in the Gulf, young are frequently taken in the Strait of Belle Isle up to early June while the adults leave when the ice clears in early May. At the Front on April 29–30, 1968 we found

TABLE 36. Experimental releases of young harp seals — Gulf of St. Lawrence, 1970. For sites of releases, see Fig. 20.

Date Apr.	Time EST	Locality or Lat. N.	Long. W.	Wind Dir.	Wind Strength (knots)	Sun	Stars	Animal Tag No.	Animal's behaviour
16	0900	Off Pt. Prim, PEI, 4 mi.		NE	10	+	NA	1384	Swam steadily ENE
16	1220	Between Pictou I. and PEI shore		NE	10	+	NA	1384	Swam steadily E, 150 yards in 5 min. (1 knot). Recaptured 6 Feb. 71 at 49°40′N, 55°40′W (Front)
16	1315	Between Pictou I. and PEI shore		E	10	+	NA	1399	Swam steadily E
16	1800	On ice edge in George's Bay		N	15	+	NA	1371	Circled ship from SW to W to N, then into wind till 20 yards from ice, then into ice
16	2000	On ice edge in George's Bay		N	15	NA	+	1389	Headed into wind
17	1200	24 m NW Grindstone I.		SE	10	+	NA	1363	Headed into wind
17	1215	24 m NW Grindstone I.		SE	10	+	NA	1394	Headed into wind
18	1545	50°08′	59°30′	Nil	Nil	+	NA	1381	No clear direction, ? North
18	1545	50°08′	59°30′	Nil	Nil	+	NA	1392	Idle, generally NE and N
18	1545	50°08′	59°30′	Nil	Nil	+	NA	1385	
18	1545	50°08′	59°30′	Nil	Nil	+	NA	1390	Released in a group, one went N, 2 idled
18	1545	50°08′	59°30′	Nil	Nil	+	NA	1391	
18	1545	50°08′	59°30′	Nil	Nil	+	NA	1383	
18	1545	50°08′	59°30′	Nil	Nil	+	NA	1378	Idled
18	1630	50°08′	59°30′	Nil	Nil	+	NA	1366	
21	2000	50°01′	58°31′	W	5	NA	+	1380	Went into breeze, recaptured 1 May 1970 at 51°35′N, 56°15′W
21	2000	59°01′	58°31′	W	5	NA	+	1379	Went into breeze. Behaviour on release not followed.
22	0330	Off Lark Hbr., Bay of Is., Nfld.		W	10	NA	+	9 controls	Included one local recapture and one at same site after 13 mo (15 April 71)

TABLE 37. Segregation of young and older harp seals in the St. Lawrence estuary from January to April 1969. One-year-old seals were categorized by age-reading, adult and immature seals by pelage. Tadoussac is the upstream or western locality.

Age-class	Number of animals collected at A Tadoussac: Number	A Tadoussac: %	B Escoumins and Bergeronnes: Number	B Escoumins and Bergeronnes: %	Calculated percent of each age-class present at B
One-year-olds	3	4.9	30	41.7	89.5
Older immatures	15	24.6	32	44.4	64.3
Adults	43	70.5	10	13.9	16.5
Total	61	100.0	72	100.0	

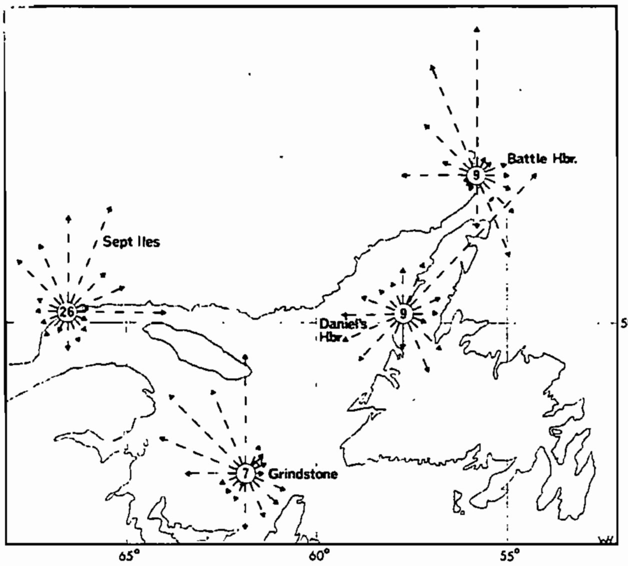


FIG. 66. Summary of winds at selected hourly weather reporting stations, April 1970: frequency in hours of winds from different compass points (one bar or space - 10 h), and of flat calms (number at centre) (from Sergeant 1970).

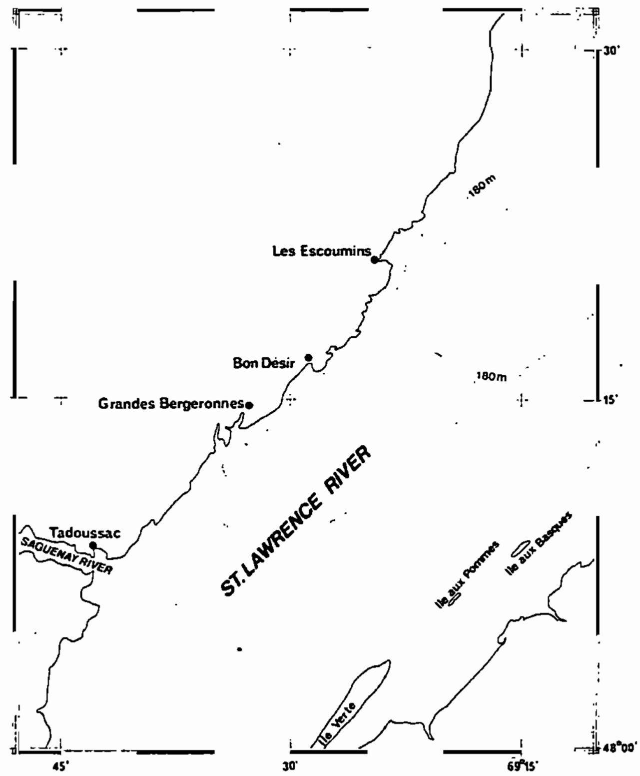


FIG. 67. Geography of St. Lawrence estuary near the Saguenay fjord.

a few young only among the herds of moulting adults and immatures. On the late spring ice of the Labrador coast, the presence of scattered young is noted after the main herds of older animals have passed north.

The general separation of young from older animals continues into the summer period, and even into the first winter. Feeding seals were sampled in the water by hunters in the region of Tadoussac and Escoumins, Quebec in January–March, 1969, an extent of some 35 km east and west (Fig. 67). One-year-old animals were well represented in the samples, probably because the little-hunted 1968 year-class had survived unusually well. Analysis of catch by location (Table 67) showed that these 1-yr-old seals were on the whole segregated from the older animals, with older immatures in an intermediate position, and Dr. T.G. Smith, who with Mr. W. Hoek carried out initial hunting in January 1969, noticed that the under-yearlings were solitary (at an age of 10 mo) as compared with the older animals. The feeding of all animals however was of the same nature — on capelin fish. The evolution of sociality in older animals was discussed on p. 15.

Chapter VII. History of Exploitation and Management

Summary

The Jan Mayen population, first to be exploited, was reduced to a depleted state by the 1870's, and remained so for 100 yr until effective protection in the late 1970's, with a recent quota of 25 000 seals taken mainly by Norway. The present population has been estimated to be about 300 000 animals.

The White Sea population was overexploited during the first half of the twentieth century, until catches were reduced and regulated by the USSR in 1965, with a strict quota catch taken by the USSR thereafter. The population was believed to have reached about 1 million (producing about 200 000 pups) by 1980, and to be rising at about 5% per annum.

The western population was overexploited by Newfoundland through the nineteenth century, but recovered in the first half of the twentieth. New exploitation by Canada and by Norway after 1946 reduced the population again until closure of the Gulf of St. Lawrence to ships and introduction of an effective quota in 1972 halted the decline. It is now estimated to number about 2.5 million, close below its maximum sustainable yield level, producing about 500 000 pups per annum, and to be rising slowly (see Ch.. VIII).

In the history of exploitation of harp seals there was a tension between the need to take the young as the most valuable product and the need to prevent undue disturbance of whelping or moulting and to conserve the stock. This generally resulted in the adoption of a starting date and a closing date for sealing as first conservation measures. In no population however were conservation measures introduced in time to prevent depletion. Effective controls on catch were applied to populations below the size giving optimal yields.

The western populations, which supported the most diverse hunting, have been hunted from ships (in the 1960's, also, aircraft) in spring and by shoremen all the year. Hunting in the summering and wintering areas consisted chiefly of shooting from boats. On the fall migration, nets, which might be complex, were used from shore. Boats or small craft were used at the floating ice in spring, or men might simply walk out on ice.

Parallel shore-hunting techniques evolved, apparently independently, in different areas; and more efficient hunting techniques using mechanisation replaced labour-intensive techniques on board ships.

The Jan Mayen Population

The Jan Mayen or "West Ice" population was the first to be hunted by ships from Europe, as an offshoot of the Spitsbergen hunt for Greenland whales *Balaena mysticetus* L. (Jackson 1978). Our knowledge of the catch at Jan Mayen in the eighteenth and first two-thirds of the nineteenth centuries is poor, but the first record of a voyage for seals was in 1720, and during the 18th and 19th centuries ships from Schleswig-Holstein, Germany (Oesau 1937), Holland, Denmark, Britain and later Norway took part. Petermann (1869) gives a catch in 1868 of 136 750 seals by 22 British, 15 Norwegian, 5 Danish and 5 German ships. The trade was then rapidly passing to south Norway (Melsom 1871), only the Dundee fleet giving competition into the 1870's (Brown 1874, 1876 cited in Allen 1880). In 1875 the total number of ships was 60, of which 27 (with 2 000 men aboard) came from Norway, 12 of them steamers; 20 steamers and a few sailing vessels from Britain; 5 steamers from Germany, 2 from Sweden and one from Holland. The hunt began in late March before the adult females had completed whelping and the adult females were taken (Bentinck 1875) since "the young are worthless until 3 or 4 weeks old". Brown (1868) writing mainly of the period 1812 to 1865 speaks of "upward of 200 000 seals, the bulk of which are whitecoats, being taken". However two sets of catch data, in 1868 and 1874 (Buckland 1875; Allen 1880), show that at that time the catch was composed of 55 and 63% whitecoats. The Norwegian catch reached 135 000 in 1874 but declined thereafter and has never regained this value (Fig. 68) although heavy hunting has been continuous since the mid-nineteenth century, except for a short period during the second world war.

Competition for a limited supply of seals in the 1870's is shown by the disappearance of the Danish, Dutch and German hunting, and by attempts between Britain (the Dundee fleet) and Norway — that of the Oslofjord — to agree on a starting date which would reduce the shooting of adult females before birth of the young (Melsom 1871; Bentinck 1875). Such an accord was realized in 1876 (Allen 1880; Nansen 1925), but it was too late for the herd; the damage has been done and only Norway was left with the remainder. It was not long, therefore, before Norwegian ships began to explore for further stocks. Nevertheless, profits from catches in this field in the 1860's allowed sealing owner Svend Føyn to finance his experiments in developing a harpoon cannon for the hitherto elusive balaenopterid whales (Tønnessen and Johnsen 1982).

About 1900 the Norwegian hunting in the West Ice passed from the ports of the Oslofjord, which took up the more lucrative but also more capital-intensive whaling, to the ports of Sunmøre in western Norway (Vollan 1951) and those of Troms in the north, from where it continued to be prosecuted until the 1980's. Numbers of the smaller sealing vessels went to this ground (Backer, 1948) while the larger vessels went, while political conditions permitted, to the White Sea and then to Newfoundland. Sailing vessels persisted as late as 1920 at which time major capital investment in motor vessels took place in Sunmøre made possible by high seal oil prices during and just after the first world war (Iversen 1927).

The Jan Mayen field maintained its importance for Norwegian sealing, in spite of the decline of its harp seal stock, because it is the centre of abundance of the hooded seal *Cystophora cristata* which became relatively more valuable as improvements took place in seal fur dressing (C. Rieber in Vollan 1951). Recent (1970's) quotas for the area for Norwegian ships were 15 000 harp and 30 000 hooded seals (Øritsland 1976). The Soviet Union started sealing in this area in 1955, but their sealing there was small scale and intermittent; recent quotas for the Soviet Union under a sealing treaty with Norway were 1 500 harps and 4 500 hoods (Øritsland 1976). Since the combined quotas were divided between individual ships they were not fully taken, since not every ship can always get its quota, and it is possible that recent lowered catches halted the population decline. The West Ice harp seal quota increased to 25 000 in 1980, of which 21 000 was allocated to Norway and 4 000 to the USSR (ICES 1987). Yet Norwegian effort and catch were declining (Fig. 69) so the economics of the industry could not have been attractive in recent years.

Since the Jan Mayen seal hunt was prosecuted for 100 yr before we have reliable figures for total catch in any one year, we can have little knowledge about the size of the initial stock. Dorofeev (1956) believed that it numbered no more than a million animals, and believed that numbers were kept low by high predation from polar bears, and by wave action and swell, both causing mortality of seal pups. It could also be argued that there is a relative scarcity in the East Greenland ice of a stock of schooling fish such as capelin which can serve as food as compared with the other three seaboards.

Brown (1868, 1869) described the British hunt. British ships assembled at Bressa Sound, near Lerwick in Shetland to take on Shetland apprentices and their last fresh provisions. It was then about a week's steaming to the first loose ice. There was considerable variation from east to west and from north to south in the position of the floe-edge from year to year. Nevertheless the ships always sailed first to Jan Mayen I. Sailing ships left earlier, in late February from Hamburg (Petermann 1869). The ships followed the ice edge and tested it for sign of seals; young could be heard at night in still weather. Adult females were shot and whitecoats clubbed; boats took the skins from the "pans" to the ships, showing that work was in quite loose ice. In good conditions a ship could be loaded in a week, and it returned to Britain to unload before proceeding to the Davis Strait whale fishery. With gales and break-up of the floe, the ships could be driven out to sea, and men left on the ice. However, other ships were usually close by, so that loss of life was rare. Also, so far out to sea, little rafting occurred to crush ships. The main risk was being caught outside the ice in severe storms, one of which sank 4 to 5 ships and drowned 600 men on March 29, 1774 when the boats had been put out in loose ice and sank (Scoresby 1820). "Black frost" or severe icing conditions with a northerly storm could still be dangerous in modern times, sinking 5 Norwegian sealing ships without trace on 4–5 April, 1952. The following year and thereafter, a large sealer, the *Norsel*, went into service as meteorological and hospital ship at this catching field.

Hooded seals were rarely pursued in the first half of the nineteenth century, doubtless because they whelped further into the ice where sailing ships could not easily go. In May some ships would work the old harps northward during moulting season but the seals were thin and sank when shot in the water. Such ships would move up to 80°N in summer pursuing Greenland whales.

Table 38 shows some 19th century catch and effort statistics. Figure 68 shows Norwegian and Russian catches from 1850 to 1967, and Fig. 69 Norwegian catches by age type from 1946 to 1981. Figure 70 shows a group of West Ice sealers, ca. 1959.

If we use the data on middle European catching up to 1870, and north European catching thereafter, we can see that the catch fell from about 135 000 in at least some of the 1860's to about 20 000–35 000 thereafter, at which level it remained for 100 yr until regulated. There was no quota control of catching at the West Ice till 1971 (Øritsland 1976), so control of catch during the century 1871–1970 must have been by effort, i.e. number of participating ships.

A remarkable feature of this herd is that, after overhunting, it survived a further century of hunting on a reduced population without becoming extinct. The harp

TABLE 38. Some nineteenth century catches of harp seals at the West Ice (Jan Mayen) field (from Brown 1874, 1875, 1876, per Allen 1880; Buckland 1875; Melsom 1871; Petermann 1869).

	Britain		Germany		Denmark		Norway	
Year	Ships	Seals	Ships	Seals	Ships	Seals	Ships	Seals
1760			19	44 722				
1790			—	45 000				
1850			12	48 800				
1864							10	47 000
1865							10	59 000
1866							10	38 000
1867							15	78 000
1868	22		5		5		15	54 000
1868	———	———	136,750	———	———	———		
1872							26	Mean 90 200
1873							27	
1874		46 252					35	
1875		45 295						
1876		53 776						

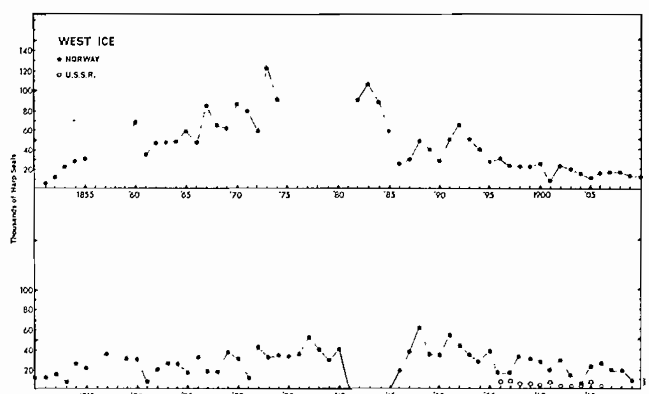


FIG. 68. Catch figures (Norway and USSR only) for the Jan Mayen harp seals, 1851 to 1969 (from Rasmussen 1957; Khuzin 1969).

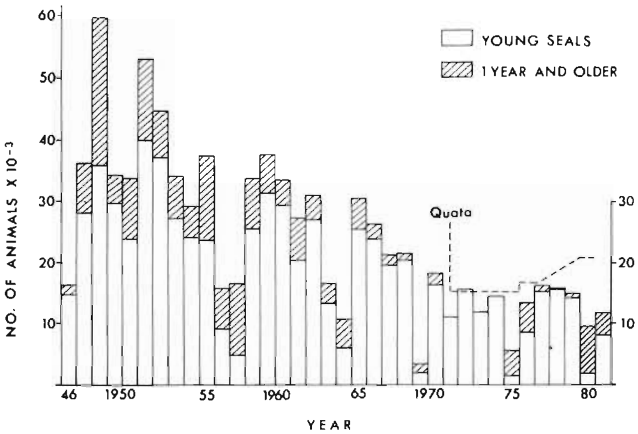


FIG. 69. Jan Mayen catches by age type, 1946-81. From Øritsland 1976, with additions from Norwegian statistics (Anon. Norway, 1951-1984).

FIG. 70. Norwegian sealers in the West Ice ca. 1959 (Photo courtesy B. Berland, Zoologisk Museum, Oslo).

seal can perhaps achieve this because many adult females can escape at whelping time, and are absent when moulting animals are shot.

Ulltang and Øien (1988) show that catch per unit of effort of harp seals at Jan Mayen reached a minimum in about 1965 and then started to increase. From marking experiments they estimate production of young in about 1980 to have been 40 000-50 000 and increasing. With application of reasonable natural birth and death rates and the decreasing catch levels they calculate 1988 production to have been between 53 000 and 69 000 young. (This would give a total population of 250 000-350 000 animals.)

The White Sea Population

Shore Fisheries

Sdobnikov (1933) describes a net fishery for harp seals which took place at that time on the Murman coast between February and May, also taking other seal species and white whales. It was ended by thaw in the rivers. Nets were 100-200 m long according to site, and 10 m deep, with 20 cm mesh and 3 mm ply. The kholkhozy (cooperatives) involved exported the blubber to Murmansk and used some leather locally; the meat was not used.

Allen (1880, citing Schultz 1873) described the shore fisheries of the White Sea, taking place on both coasts and also around the Kanin Peninsula. On the eastern shore ("winter coast") hunters would assemble in late February as soon as young seals became available, hunting over 230 km of coast and setting up winter huts on the shore. In late March they followed the moulted young to sea in 22-foot long sailing vessels equipped with iron keels so that they could be hauled up on the pack ice, and supplied with provisions for several men. Men on snowshoes sought the seals, and the boats followed. The seals were then shot on the ice and brought to the coast for skinning (the description of herds of seals suggests that moulting adults as well as beaters were hunted).

On the western coast of the White Sea there was a smaller hunt. The men were organised in groups of 4 of whom 3 went out on the ice, one seeking seals while the other two followed hauling a small boat. The seals were shot in water leads and hooked up into the boat. A similar fishery is described by Yablokov (1962). There are considerable similarities between these descriptions and net hunting practised on the Quebec north shore, as well as with shore hunting practised in the Magdalen Is. and in northeast Newfoundland (p. 93).

Although harp seals frequently invade the coast of Finmark, and sometimes further west and south along the Norwegian coast (p. 58) there is no hunting directed towards harp seals on this coast. Indeed, the Norwegian government now provides the fishermen compensation for by-catches of harp seals in gill nets for cod and other species in this area, at considerable cost in most recent winters, and very high cost in years of seal invasions (as in early 1987).

Offshore Fisheries

Heavy hunting of seals in the White Sea by ships began in the 1920's and 1930's, first from Norway and then by the Soviet Union. In this period a Soviet concession allowed Norwegian sealing in the northern half of the White Sea (Sivertsen 1941). A maximum of over 400 000 seals was taken out in 1925 (Fig. 71). The stocks could

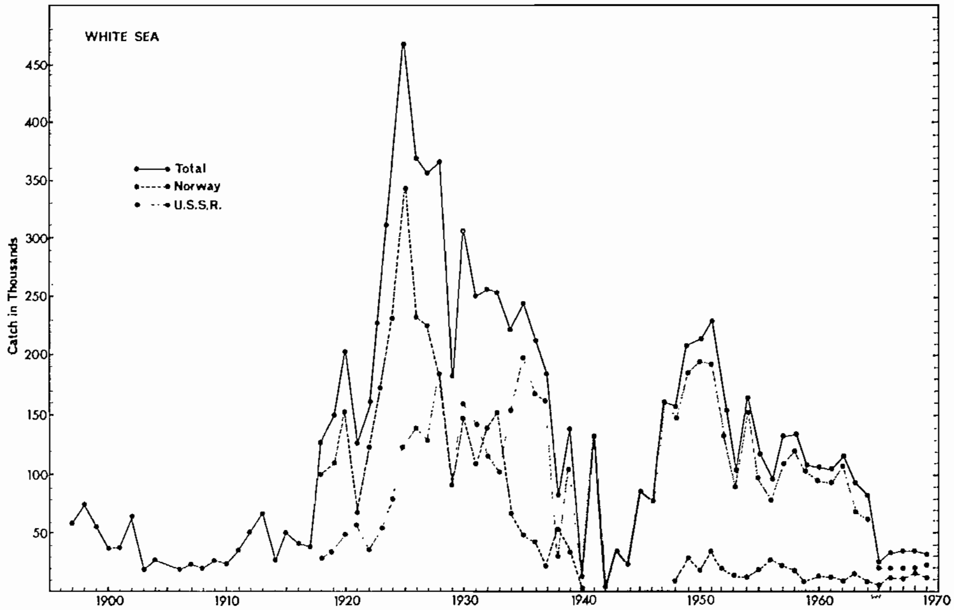


FIG. 71. Catches of harp seals of the White Sea herd, 1895 to 1965. From Yakovenko (1963, 1967) and Norwegian statistics (Anon. Norway, 1951–1984).

not stand this sort of pressure and catches were falling fast in the late 1930's (Dorofeev 1956; Yakovenko 1963).

The rest given by the second world war was not long enough to allow the stock to recover fully, although the Soviet Union reserved the White Sea thereafter for its own catching industry, allowing Norwegian catching only outside its confines. Following 1950, catches declined once again and there were intensive studies by Soviet scientists which resulted in urgent calls for curtailment of the hunt (Nazarenko and Yablokov 1962; Yablokov 1962; Yakovenko 1963).

One of the reasons for the rapid decline of the White Sea herd had been the practice of Soviet ships to take large numbers of whelping females. It was calculated in retrospect (Benjaminsen 1979) that production in 1965 had been reduced to 100 000 pups. As a result of this strong decrease, in 1964 Soviet authorities banned the killing of adult females, and in 1965 prohibited sealing by their ships in the White Sea and eastern Barents Sea. This protection has lasted to date, with restricted quotas of young seals taken by coastal cooperatives using aircraft. At the same time catching continued of immature and adult seals by Norwegian ships outside agreed coastal limits.

Soviet biologists argued that a 10-yr rest was needed to allow the abundant year-classes expected around 1970 to reproduce in their turn some 5 yr later. Nevertheless a moderate quota of young was applied in 1965, together with a small catch of moulting adults and immatures from which were made studies of age composition and maturity (Nazarenko annd Timoshenko 1974; and Soviet statistics 1969–79, from which Fig. 72 is drawn). It proved possible slowly to increase the catch, which reached 35 660 in 1979 (Anon, U.S.S.R. 1979), and the seal population was calculated to be increasing at about 5% per annum to a level of about 800 000 in 1978, producing 172 000 pups (Benjaminsen 1979), and 1 million in 1980 (Bjørge et al. 1981). It was projected to reach a level producing 220 000–240 000 pups in 1980–82 (Borodin 1978). At the same time, studies were made on the whelping patches by drifting expeditions (Popov 1966, 1967). Many of the young caught were now taken alive by helicopter as fat whitecoats and allowed to grow into beaters on land, when they were slaughtered under controlled conditions (Ponomarev 1973).

During 1965 to 1984 Norway maintained a concession to catch seals outside the White Sea and these were both young (mostly beaters) and older seals (Table 39). The number of ships decreased slowly over the years, but catch per effort increased, especially for older seals. This presumably reflects an increase in availability of bedlamers (immatures) due to increasing production and consequent escapement.

The combined catches from the White Sea herd reached a peak of 64 000 for the U.S.S.R. and 18 000 for Norway,

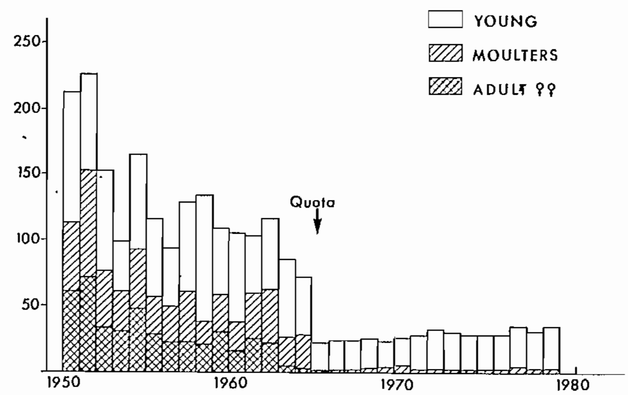


FIG. 72. Russian catches in the White Sea 1950 to 1979 (from Nazarenko and Timoshenko 1974; and Anon. USSR, 1969–1976, 1977–1979).

TABLE 39. Five-year means of Norwegian catches of harp seals and mean catch per ship from the White Sea herd, outside the White Sea, following the Soviet quota.

	Mean number of			
Years	Ships	Young	Older	Total
1965–69	7.0	6 663.6	4 813.8	11 477.4
per ship		951.9	687.7	1 639.6
1970–74	6.2	4 667.8	6 045.6	10 713.4
per ship		752.9	975.1	1 728.0
1975–79	4.2	3 031.2	6 616.6	9 647.8
per ship		721.7	1 575.4	2 297.1
1980–84	4.0	4 370.4	11 047.2	15 417.6
per ship		1 092.6	2 761.8	3 854.4

or 82 000 in all, in 1983 (Anon. Norway, 1984). In 1984, Norway's catch fell sharply and the total catch was 74 000. This presumably reflects a reduction in west European purchases of seal pelts which affected the Norwegian more strongly than the Russian catch.

The Western Herds

A. Landsmen

The geographical extent of hunting by landsmen is shown in Fig. 73.

Icefield Fishermen

The earnings of a landsman are variable, depending on the degree of his participation and luck. Probably the most consistently important fishery taking seals on or around the icefields is at the Magdalen Is. (Îles de la Madeleine), Quebec, because as mentioned earlier (p. 38) the seal patches almost invariably drift eastward close by the shore of these islands; nevertheless, in the 1970's, the islanders' catches were poor because the patches were too far out to sea (Sergeant 1982). The Magdalen islanders (Madelinots) have no tradition of sealing from large vessels, probably because their shores are icebound in March, and unlike Newfoundlanders they could not leave home to join a ship at a distant port, until aircraft gave them transportation. However, they have long used small craft to take young seals around loose ice in late March and April. Most of their seals have been taken by men walking out on the ice on foot or on snowmobile or by a combination of this activity closer to shore and small craft further out. During the decade of the 1960's Magdalen islanders joined aircraft as sealing crew, until the dangers and abuses of sealing by this method, very conspicuous from the land, brought about its prohibition.

Another form of fishery, a hook and line fishery for harp seals, was carried out at the Magdalen Is. through April and May, but was prohibited as cruel in the early 1960's. An extremely arduous form of sealing practiced at the Magdalen Islands is to lift heavy clinker-built boats over the ice to take young seals, or to shoot adults in pools

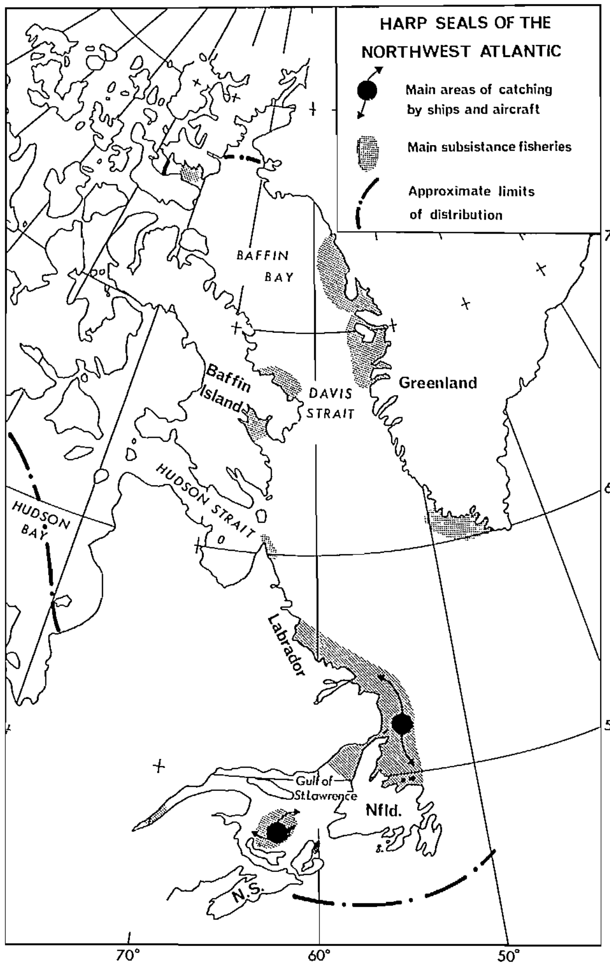


FIG. 73. Distribution of hunting effort on the northwest Atlantic herds of harp seals.

between the ice floes in late March. Yablokov (1962) described the same form of sealing in the White Sea, which must have arisen independently. The Magdalen Is. boats were also used to take young grey seals at the colony at isolated Deadman I. (Ile Corps Mort) in January. Needless to say, when ice starts to "run", it is useful to have a boat in which to row ashore. Many landsmen have perished around Newfoundland, or have (in recent years) required expensive search and rescue operations by air and sea, when they ventured out on to pack ice on foot and the tide or wind changed.

Summer Fishermen

When the seals reach north to West Greenland in summer, they are hunted extensively by the Greenlanders. There are no modern descriptions of this hunting but motor boats have replaced the kayaks described by the Greenlandic painter-hunter Jakob Danielsen as used at Godhavn, Disko I. in the early years of the century (Rosendahl 1967). Historically changing catches are shown in Fig. 92, in good times exceeding 20 000 animals.

A good description of hunting at Cumberland Sound, Baffin I. is given by Anders (ed., 1967). He states that harp seals occur from mid-June to mid-January and in summer are at least as common as ringed seals in the Sound although much rarer to the northward on the outside coast. They are hunted in summer from powered canoes (Fig. 46). Most seals, harp or ringed, are hunted among the archipelagoes because the islands give protection from the wind, allowing the seals to be seen. Harp seals raise their heads higher in the water than ringed seals and surface for a longer period but are liable to sink when shot, the loss rate being from 70% in early June to 40% in mid-September. Thus they are best hunted by shooting from a fast-moving boat and being picked up at once. Catches in 1962–71 in Cumberland Sound were about 1 000 (Smith and Taylor 1977) and in the early 1980's 2 500, all traded. Before this period, skins of harp seals were used locally for sleeping platforms and few animals of this species were hunted.

Autumn Fishermen

As the seals moved south they were netted at settlements all the way south from northernmost Labrador to the north shore of Quebec (Fig. 74). On the Labrador coast nets were generally simple ones. Complex traps were used at the settlements of La Tabatière, Cheverie, and Harrington Harbour on the Quebec north shore. Their structure is shown in Fig. 75, taken from Beck (1965). The nets were strung on heavy cables running between islets and arranged in the form of baffles. Most net fisheries lasted for a few weeks only, from the onset of migration till freeze-up, when the nets had to be lifted. This net fishery evolved during the late eighteenth century and catches from it peaked in the 1950's and in value during the 1960's (Baril and Breton 1982). There were small-scale spring net fisheries in the Strait of Belle Isle.

Winter Fishermen

In the vicinity of St. Anthony, Newfoundland along the shores of White Bay and around the Great Northern Peninsula, net fisheries persisted through the winter from January to April or May when ice conditions allowed.

At the extreme westward limit of the harp seal's winter range at Escoumins and Tadoussac in Quebec, close to the estuary of the Saguenay river, a number of fishermen take seals in the winter by shooting from powered canoes or boats rather like the summer Inuit hunters. This fishery has existed since at least the middle of the eighteenth century when it was practised on this coast by Indians (Tremblay 1945), with a catch in 1750 of nearly 1 000 seals. (Catches since 1979 again reached nearly this figure with the formation of a hunters' cooperative at Escoumins.) There was a very similar small boat fishery in the nineteenth century at Pointe des Monts near Godbout (Comeau 1954). This also has persisted on a small scale to the present day.

In winter the seals are fat and do not sink. Prevailing northwesterly winds keep open a band of water between the Quebec north shore and the newly-forming pack ice. Hydrographic conditions at the west end of the deep Laurentian Channel result in upwelling of cold, productive water and the seals find good feeding, chiefly on capelin, which probably accounts for their concentration

FIG. 74. Net fishermen at La Tabatière, Québec, 1964 (Photos by Fred Bruemmer; from B. Beck 1965).

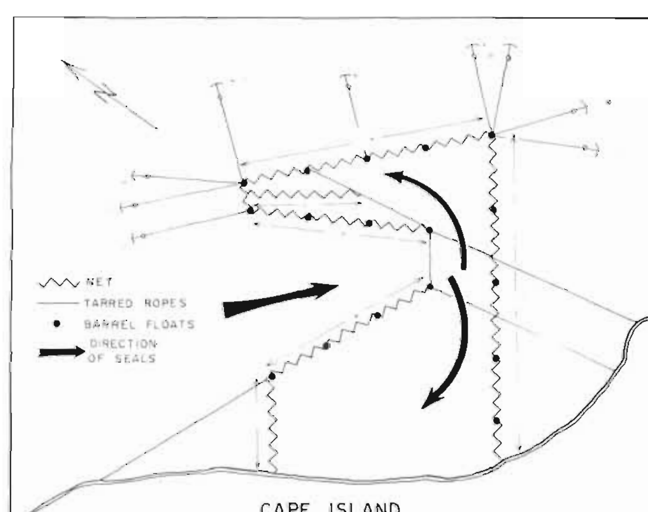


FIG. 75. La Tabatière seal trap (from B. Beck 1965).

and the long-continued hunting in this area, from mid-December to early April. Samples collected by the hunters have been valuable for studying feeding habits (Ch. V) and the winter third of the annual cycle of growth and reproduction.

Since 1972, increased and predictable escapement of young seals due to the quota allowed development of what appears to be a totally new fishery. This is a hunt of immature and adult seals in Notre Dame Bay by motor boats and long-liners from many ports in northeast Newfoundland. This fishery recently took up to 25 000 seals older than one year, principally in February. Age samples showed that these were mainly young bedlamers (Fig. 31). Young seals were taken, mainly as beaters, by the same fleet in late March and April. This was, in the late 1970's, the second largest individual seal fishery of Canada after that of the large ships taking their quota of young seals. The long-liners measured from 35 to 65 ft (10–20 m) long, with cabin forward, and had powerful engines and freezing capacity. Like wooden sealing ships, they were sheathed with greenheart wood and strengthened in the bow with extra frames, but used the rest of the year for fishing (W. Penney and I.-H. Ni, in litt., July 25, 1985).

Discussion

At different times of the year, then, different groups of inshore fishermen were recently taking harp seals at some point in their annual migration between the Saguenay in the south to Thule or Jones Sound in the north. This fact makes impossible regulation of landsmen's catch by season. However, most shoremen's catches of seals were limited, either by annual variations in location of whelping sites and in ice movement, by the restrictions imposed by venturing out onto the ice on foot or vehicle or into the ice in small craft, or by the short time of appearance of migrating seals. Thus, hunting by shoremen was less efficient and requires less regulation than hunting from larger ships. As the fishery became more valuable, an increasing problem in eastern Newfoundland was to determine the point at which a shoreman became a deepsea sealer. At present the limit set is for a vessel of 65 ft (20 m). Although vessels over 35 ft (10 m) require licenses, their numbers are not regulated. Because of the smaller investment in long-liners than in large vessels, and their versatility, they were recently one of the more profitable platforms for hunting seals in eastern Canada (Dunn 1977) and in 1976 there were 200 of them.

B. Offshore Fisheries

The history of exploitation of the northwest Atlantic seal stocks will always be associated with the great days of sail and steam in Newfoundland. In the harsh climate of northern and eastern Newfoundland, the shore is icebound and codfish remain in deep, offshore water during the long winter months. The seal fishery, coming at the end of a long inactive winter, provided a release and a challenge, as well as a very welcome addition to the economy. At the height of the fishery in the mid-nineteenth century, thousands of men went to the fishery in hundreds of boats (Table 40), outfitted by other thousands of boat-builders, carpenters, coopers and sailmakers, while processing and selling of the catch occupied many merchants. The seal fishery was not much diminished in the later twentieth century but being divided between two countries its importance was less evident; moreover the efficiencies of modern catching and processing meant that fewer men were involved. Nevertheless it still benefitted hundreds and gave an important supplementary income for thousands of men in Newfoundland, Quebec and the Maritime Provinces (Dunn 1977). For a social history of Newfoundland (and other) sealing, see Busch (1985).

Sealing began in the late eighteenth century mainly as an affair of net fisheries, which survived to the present day in their most developed form on the north shore of Quebec, as described above. On the northeast coast of Newfoundland net fisheries were less productive because the seals keep further offshore. There was, therefore, an early tendency for the people to follow the seals into the ice and from early, open shallops, they soon developed larger, decked sailing vessels which reached their greatest numbers and catching power in the 1850's. Additional vessels sailed from New Brunswick, Prince Edward Island and Nova Scotia to the Gulf of St. Lawrence, with catches little documented. Although Newfoundland statistics lumped all seals together, one can calculate that in those days more harp seals were taken than at any subsequent period (Table 40 and see p. 107). It is not surprising therefore that catches began to fall (Fig. 76) before the time steamers entered the fishery in the 1860's.

The great development of steamers came in the second half of the nineteenth century (Fig. 77). These were outfitted by wealthy shipowners, causing a shift of the fishery to the main ports of Newfoundland. In addition, steamers came to prosecute the hunt from Scottish ports, discharging their cargo in St. John's and then proceeding to the bowhead fishery in Baffin Bay (Jackson 1978).

Newfoundland regulations soon led to a latening of the starting date and to development of a closing date. Carroll (1873) suggested that the disturbance of seals was so great,

TABLE 40. Some nineteenth century statistics for the Newfoundland seal fishery (from Allen 1980; Mosdell 1923).

Year	Vessels		Men	Seals	Value
	Sail	Steam			
1763	First voyage			5 000	
1765					£6,089
1804			1 600	156 000	
1807	30				
1834	375		9 000	440 828	$298,796
1853	392		14 931	685 530	
1857	379		13 600	530 000	£425,000
1866	177	5	8 909		
1871	201	13	9 791	486 262	$1,458,282
1873	104	20	11 000	526 000	

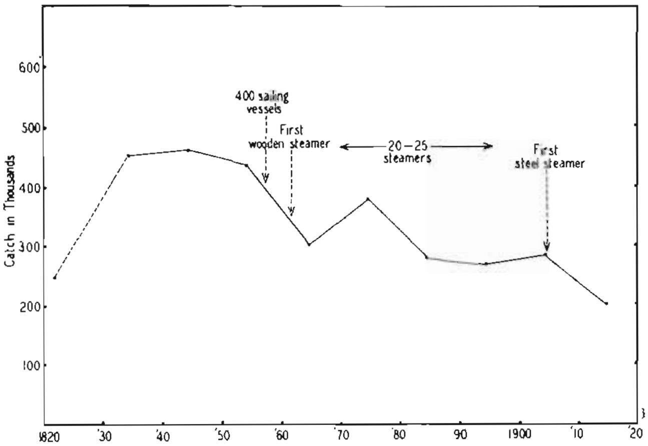


FIG. 76. Catches of seals by decades in Newfoundland, 1820 to 1920.

FIG. 78. The steel steamers *Florizel* (left) and *Imogene,* 1910. Courtesy E.A. Bowring (the ships carry Bowring's funnel insignia).

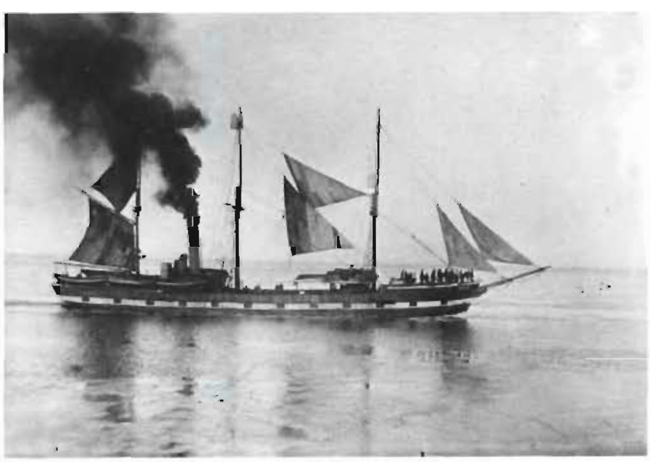


FIG. 77. The wooden sealer *Iceland* ca. 1900.

coming from 150–200 sailing vessels and 20 steamships and 10 to 10 000 men with 700–800 sealing guns, that laws would be needed to regulate the fishery. An Act of the General Assembly of Newfoundland of 1883, the *Seal Fishery Amendment Act*, set sailing dates of March 1st for sailing vessels and March 10 for steamers, and by 1922 the sealing season was fixed between March 15 and May 1 (England 1924).

The last great phase of the Newfoundland fishery started in 1906 with the introduction of steel steamers. These great coal burners gained fame for breaking ice, as did their skippers for taking bumper catches of whitecoats, a fame which remains part of the Newfoundland saga (Fig. 78). But, strangely, the overall catches of seals at this time were decreasing. This was due to a combination of the first world war, when many of the steel steamers were sunk, and the unprofitability of the ships themselves. It is one thing to have an efficient piece of seal-catching machinery, another to find profitable employment for it for the rest of the year. A steel steamer was too small and too heavily built to be a profitable freighter, and its main off-season use was for arctic exploration and supply duties, a role which sealing vessels have played from the turn of the century to the present day in arctic and Antarctic. But the market for arctic exploration and supply ships is limited.

During the interwar period, the 1920's and 1930's, the seal fishery declined (Fig. 79). Various opinions have been presented on whether this decline represented a decline in the seal stocks or not. Sir Wilfred Grenfell (1919) for instance, who travelled as a sealer in 1910, thought that it did; George Allan England (1924) who travelled to the seal fishery in 1922, though it did not. I am inclined to agree with both observers; that is, that up to about 1910, the fishery had reduced the seal population, but that after the first world war the losses due to World War I of the steel ships, and the various succeeding depressions, so reduced sealing effort that the stocks began to recover. The catch during the 1920's and 1930's averaged about 130 000 young and 30 000 older harp seals, much less than in the 1950's and 1960's (Fig. 79). The second world war finally gave an almost complete rest to the seal stocks.

One cannot pass over these times without giving credit to the statistical documentation of L.G. Chafe (Mosdell 1923) who kept full records of seal catch and participation in sealing (what is now called by fisheries biologists "catching effort") over a period of 40 yr beginning in

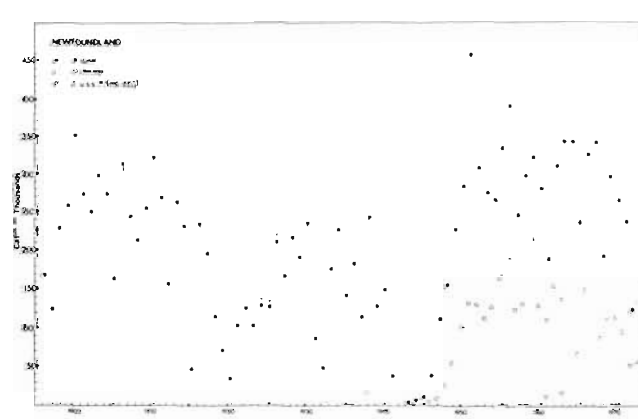


FIG. 79. Catches of harp seals at Newfoundland icefields, 1895–1973. Source: Chafe's Sealing Book (Mosdell 1923) and Canadian and Norwegian fisheries statistics.

1895. This documentation was continued later by the Newfoundland Fisheries Board, which became, after Confederation in 1949, the Newfoundland office of the Department of Fisheries of Canada. Unfortunately later economists and statisticians outside Newfoundland did not follow Chafe's desirable consistency of documentation, and even now Quebec does not give landings by species of seal.

The last phase of sealing in the Northwest Atlantic was characterised by the arrival of Norway and the replacement of Newfoundland sealing techniques by Norwegian ones.

Newfoundland sealing was geared to the maximal production of oil. This was achieved by taking fat whitecoats and legislation was even enacted to allow ships to reach the whitecoats at the best time — March 15 — when, as we now know, the Front whitecoats are nearly weaned and weigh some 70 lb (32 kg) each on average. The season in the Gulf started a week earlier. The pelt was sold for leather, for a fat whitecoat is moulting. Sealers were paid by shares and the share was based on weight of catch; weighing was performed at the dockside watched over by the master-watches as representatives of the crew who ensured that the men got their due.

This was indeed the universal sealing technique during the nineteenth century, by Scottish and Norwegian sealers alike, and the Newfoundland practice represented the last vestige of the old way. However, during the 1920's and 1930's, American and Norwegian sealing processors began to pay more attention to the pelts as furs and this attention culminated after the Second World War in a highly-developed fur industry. Many of the techniques evolved quite recently, in the 1950's and 1960's, for fur dressing is a complex business (see Rieber, p. 340 et seq. in Vollan 1951). One development after 1945, for example, was the use of antioxidants to prevent the irreversible yellowing of pelts which is due to oxidation (rancidity) of the oils that soak them. While this yellowing does not matter, and may even be aesthetically desirable, on after-ski furs derived from old seal pelts, it is unacceptable on first class whitecoat or beater furs and dyeing in deep colours is needed to hide it. Another very important Norwegian development was the use of deep-freezing of pelts on board. Newfoundland ships stowed pelts in snow; when the weather began to warm in April the snow melted and the oil began to run, so that the ships had to turn for home. Norwegian ships, with refrigeration, could stay out as long as fuel and supplies allowed.

Actually two techniques — deblubbering and refrigeration — were developed from Norway. In some ships coming from north Norway, the pelts were deblubbered on board, salted, and the blubber put in tanks. This required a great deal of hand work, and since defatting is better done by machines ashore, this technique was discontinued and the large Norwegian ships later all had refrigerated holds and the pelts were deblubbered ashore. The only disadvantage of frozen pelts is that unloading is rather slow.

Large Norwegian ships first began to explore the western North Atlantic sealing grounds in 1937 (Vollan 1951). They were impelled in this direction by the approaching exhaustion of the White Sea sealing grounds. After the Second World War they came again and soon built up in numbers. Before the 1972 quota reduced their participation, some 13 to 15 Norwegian vessels, including the largest and most modern sealing ships to be found at that time, came annually to the western catching fields.

As an accident of the Second World War, the Norwegian sealing technique was introduced to Canada, where it competed with and almost replaced the traditional Newfoundland technique. Several Norwegian sealing ships and their crews had escaped the German occupation by being over at the Newfoundland sealing grounds in April 1940. They gave distinguished war service by supplying allied bases in Greenland, and after the war some of these sealing men and one owner settled in Nova Scotia.

The method of operation of Norwegian sealing differed greatly from the Newfoundland way. Newfoundland sealing was not only an industry, it was a game; the skipper and crew who could first get a bumper crop and be first ship home with the first crop of flippers not only added to their fortunes but also their fame. The Newfoundland sealing ship was thus crammed to the bursting point with sealers who slept two or more to a bunk.

On opening day, they deployed over the ice in military formation, trying to cut off their rivals in the next ship, and practically all the whitecoats were taken in the first few days (Fig. 80, lower). The seal pelts were "panned" and the pans marked with distinctive flags. The succeeding days were spent by skippers in picking up their pans, and many pans were lost, though if a rival ship came across pans that looked pretty well lost, it often recovered them. This may have led to lawsuits, but at least saved waste.

The Norwegian ships, on the other hand, operated with smaller crews and worked more steadily. The backbreaking labour of "double-panning", making larger pans out of smaller ones to save ship manoeuvring, was dispensed with. In its place, the ship used great wires of half a mile or more in length provided with loops at intervals to which the piles could be attached using "straps" with an eye and a toggle. The winchman then hauled them in.

Since the Norwegian ships used smaller crews, their pay was better. It was based not on weight, but on the assessed value of each type of pelt, which depended on market conditions. In Norway, especially, great attention was paid to quality and each pelt was individually assessed. A representative of the processing firm, valuing pelts as they were unloaded, was watched by the skipper and a representative of the crew.

The Norwegian method at first spread slowly in Canada, but eventually almost totally supplanted the Newfoundland method as the older Newfoundland-style ships and skippers lived out their working lifespans. The higher payments attracted Newfoundland crews to man the newer vessels. While most of the pelts went to Norway for their final treatment the first stages of de-blubbering, de-oiling, treating with antioxidant and salting in vats was done in Canada. By 1969 there were two plants equipped for this treatment, one in Nova Scotia and one in Newfoundland. As well as the pelts taken by the ships,

FIG. 80. *(Upper)* Shades of former glory. M/V *Arctic Prowler* leaves St. John's for the icefields, March 6, 1953. This type of sealer was an ex World War II boom defence vessel; *(Lower)* Men from *Algerine* "double-panning" (making larger piles of pelts) in tight ice, March 13, 1953. Note the gaffs, then used to kill seals.

pelts taken by landsmen at scattered points were collected, often by a sealing ship at the end of the season, and taken to the plants.

The share earned by a sealer varied very widely, depending on the success of his voyage. In 1966 a good share in Canada for nearly two months of work was $2,000 while the skipper might earn $17,000. At the same time a good share in Norway was $4,000 (Anon. Norway 1966) for a transatlantic voyage which lasted nearly 3 mo, and income tax could be calculated over a two-year period to allow for good and poor seasons. Little increase in crew shares for Canadian ships was shown by Dunn (1977) for the year 1976, but the length of a voyage following the quota of 1972 was reduced to only one month.

Prior to the quota, the arrival of Norwegian sealing ships had two consequences for the fishery and the seals. First, it resulted in longer voyages. Newfoundland ships could not stay out very late, as explained above, and though they sometimes made second and even third trips for moulting seals, not many such voyages were made. On the other hand, the Norwegian ships with refrigeration and large fuel reserves could stay out almost indefinitely. During the 1950's, if they did not make good catches of young, they took very large catches of old seals, following them north along the Labrador coast in May.

These catches, up to 100 000 seals in a season, were clearly destructive, and the governments of Canada and Norway agreed in 1961 to gradually earlier closing dates, after which sealing would be prohibited till the start of the following season (Table 41). First set at May 5, the closing date for the Front was moved back to April 30, then to April 25 and in 1969 (temporarily) to April 23, (although in 1970 it regressed again to April 29, as compensation to the industry for a late starting date). After imposition of a quota in 1972 the closing date lost its importance, since the great reduction in effort, and a division of the quotas between ships, allowed them all to take their quota as young seals, the voyage ending generally by mid-April.

A second consequence of the Norwegian arrival, and one which led to an unresolved difficulty, is that the fishery started earlier. Whereas the old Newfoundland fishery took the fattest whitecoats and could begin (on the Front) about March 15, the Norwegian processing industry required whitecoats with fast furs, which are ideally aged about 4–5 d and can be taken starting about March 7 in the Gulf and March 12 on the Front.

As is well known, a great volume of protest developed since 1965 based on the premise that the taking of a cuddly whitecoat (which makes a plaintive, human-sounding cry) away from its mother and killing it is an act of barbarism which civilised people should not tolerate. The popular clamour against taking young whitecoats forced the Canadian government in 1970 to legislate that the moulted "beater" young would be taken instead of the whitecoats. The same had been done in 1968 as the result of a surplus of whitecoats on the market, but not in 1969. This alternation did not continue subsequently because the industry did not like to lose the market for the silky whitecoat pelts and after a quota came into force in 1972, the surplus of whitecoat pelts disappeared. The stiff-haired beater pelts have fewer uses.

In 1971 a quota came into force for ship catching at the western icefields. Divided equally between Canadian and Norwegian ships, it was 200 000 harp seals of all ages. Canada divided its 100 000 seal quota equally between the Gulf and Front. Because of a large landsmen's catch

TABLE 41. Legal starting and closing dates for sealing at Newfoundland.

Season in effect	Starting date		Closing date	
	Gulf	Front	Gulf	Front
1951	March 5	March 10	None	
1961	March 5	March 10	May 5	
1963	March 5	March 10	April 30	
1964	March 5	March 10	April 25	April 30
1965	March 7	March 12	April 25	April 30
1968	March 18	March 22	April 25	April 25
1969	March 7	March 12	April 23	April 23
1970	March 20	March 22	April 23	April 29
1971	March 12	March 12	(23)	April 23
1972	—	March 12	—	April 25

at the Magdalen Is. and a shortage of seals, the ships did not attain their quota here and so the Canadian quota was not attained.

In 1972, the quota was reduced to 120 000, again divided equally between both nations. Canada also closed the Gulf to ships, so that all catching was on the Front. Neither nation's ships succeeded in taking their quota. Subsequently, further regulation consisted in increasing the quota, according to biological advice, to 165 000 seals by both large ships and longliners, and apportionment of an increasing share of it to Canada. Results of this protection will be discussed in Ch. VIII.

Chapter VIII. Population Dynamics, Size and Yields

Summary

Direct counting of the population by aerial photographic survey of moulting adults and immatures was the first method used, pioneered by Soviet researchers in the 1920's in the White Sea. In the western North Atlantic it has given low results as compared with other methods, presumably because many seals were in the water at times of survey.

Four other methods have been developed in Canada to estimate annual production of young from which the total population may be calculated. These methods are: direct aerial photographic survey of whelping adults or young seals; tagging and recapture of young; study of comparative survival to one or more years of age in age samples after varying levels of kill of year-classes of young; and study of maximum kill levels of young, where these are known (from the first three methods) to be intensive. Results of all four methods are compared for the western North Atlantic herds.

Photographic estimates of adult whelping animals or moulters appear to give under-estimates of numbers at all times, because of animals which are in the water. Pups can be counted if "ground-truthing" is used to take into account the completeness of births at time of survey. Marking and recapture of pups is an excellent technique for estimation of numbers if random samples of the animals can subsequently be obtained. Studies based on age sampling, including cohort analysis, allow retrospective tracing of population history.

Production of the western populations in the late 1960's is now estimated to have been about 200 000 for the Front, 100 000 for the Gulf of St. Lawrence or 300 000 in all, with a sustainable yield of no more than 150 000 or 50% of production. Production in the early 1960's was probably about 400 000 and in the early 1950's perhaps 500 000, but earlier estimates are more tenuous. The decrease is explained by a mean annual catch of about 230 000 young, plus about 50 000 older animals.

Following imposition of a quota in 1972, escapement in the western herd started to rise immediately and production subsequently, the increase continuing to date. An aerial survey on the Front alone in 1983 gave a minimal estimate of 295 000 pups; capture-recapture tagging estimates in both areas of 534 000 pups. This is close to the production that would allow maximal sustainable catch. Other direct evidence such as the changing levels of catch of juvenile seals at Greenland shows that production in the mid 1980's again approached levels of the early 1950's, before sealing became heavy. The maximum sustainable yield for the northwest Atlantic is estimated at about 200 000 young and 40 000 older animals.

Approximate estimates of total populations (excluding pups) at time of writing (1988) are: about 2.5 million animals for the western herds, 1 million for the White Sea herd, and 350 000 for the Jan Mayen herd.

Rational Exploitation

This is a large and difficult but important subject and the greater part of the effort of a fishery biologist is bent towards determining the level of best management of the stocks of the chosen species for the use of man. First it is necessary to explain a few concepts.

Exploitation or cropping of a population for sustained yield is achieved by taking that part of the population which would otherwise be lost by natural deaths. There is of course a residuum of natural mortality which must be allowed for. As Slobodkin (1967) has expressed it, a "prudent predator" takes that part of the population which is going to die anyway. Man is supposed here to be the prudent predator, even if he has rarely proved to be so in the history of exploitation of sea mammals.

A wild population unexploited by man reaches a natural equilibrium population at which births are just balanced by deaths. (This population will probably fluctuate with quite large oscillations, but for the purposes of the argument we will assume it to be at a plateau.) If man crops a portion of the population, at a fixed rate, a new level of population will be set up lower than the maximal possible population, because the maximal population can only exist if no cropping takes place at all. If too much cropping takes place, the population will go to extinction. Somewhere in between is the optimum cropping level, giving the maximal sustainable (or equilibrium) yield.

Since adult male harp seals are probably promiscuous, one could in theory crop quite a lot of males (as is done for instance in the cropping of adolescent male fur seals). However, in practice, it is not possible to isolate adult male harp seals. Even at the moult, they are usually mixed with immatures of both sexes.

It is clearly imprudent to take the reproductive females. In practice, management of harp seals has been designed towards maximizing the harvesting or cropping rate of the young up to the optimum level and protecting as far as possible the older animals. The adults are protected quite simply by imposing a closing date for sealing during the moult, and by prohibiting the taking of whelping female when with their young.

While the practice of taking the young of harp seals is traditional and due to their equal or greater value as compared with older animals, it is a rational form of exploitation (up to a point) since the natural mortality rate of young animals is generally greater than that of older animals and likely to be density-or resource-dependent (see Ch. IX); meaning that it rises as production of young increases, due to interaction between them or shortage of food.

How to find the optimal take of young is a question that must be solved by mathematics. We need to find how many young are produced, not an easy question to answer in practice. We must also find the birth rate and the death rates of the various age groups of seals and then draw up a mathematical model of the population which must be in balance and must closely fit reality.

Mortality rates of the older age-groups, from age one upward, can be determined from age tables of the population. This is the sort of thing that actuaries draw up for human beings from records of their birth dates, but the task with animals is a little more difficult.

It is fortunate that harp seals are very easy to age from periodic layers in their canine teeth. Having collected teeth from various samples of the population one can then age them and construct age samples which show death rates. The fishery worker spends a lot of his or her time doing this. However, various sorts of bias occur in the sampling, since animals group themselves in different ways, and these biases must be allowed for — best, by collecting as many different kinds of samples as possible and finding the most consistent answers. In this way, we have determined that immature and young adult harp seals die at the rate of about 10% per annum. However, we do not know accurately the natural death rate of the young, because they do not mix with and are cropped separately from the older animals.

As a result of this last problem, empirical methods of calculating sustainable yield are useful, and in harp seals the great variability of (unregulated) catches of young pre-1972 were very useful for this purpose, as explained on p. 106.

Whether the young are exploited as whitecoats or beaters makes very little difference to the yield, since the mortality between the whitecoat and beater stages of the young (separated by only 3 wk) is very small. This question is therefore one essentially for the fur trade, although humane considerations have entered very powerfully in recent years in exerting pressure on the outcome.

The picture of idealized exploitation described above has been very far from realisation in most of man's history of exploitation of harp seals, as I have outlined above. However, the species has had one ally on its side: ice which is hard for underpowered ships to penetrate and in which seals must be sought for.

Nansen (1925) explained well the variability of catch levels at Jan Mayen. If exploitation starts too early the unwhelped seals disperse, and dispersed seals can be taken only in small numbers. In some years, natural conditions are such that dispersed whelping occurs in any case. In such years, catches are low. In yet other years, ships may be unable to find the whelping concentration (spotting aircraft at the White Sea and Newfoundland have removed this last possibility but are not used at Jan Mayen).

For these reasons, harp seals have escaped the rapid overexploitation suffered by the great whales in various parts of the world. Moreover thanks to widespread public pressure (whether accurate or not), the responsible governments eventually became very sensitive to the question of overexploitation. This was particularly true for eastern and western herds, where local communities of people dependent on sealing for all or part of their income required that the hunt be sustainable in perpetuo. Successful attempts to make it so were frustrated by sociopolitical causes which had more to do with humane killing than with conservation. The story is ably told by Janice Henke (1985).

Population Dynamics

Productivity of a harp seal population depends on the balance between its fertility and mortality rates.

Fertility rates were discussed on p. 20 where an increase in age-specific reproductive rate (decline in median age at first reproduction) and increase in fertility of adult females of the western herds were shown to have occurred between the early 1950's and the late 1970's, presumably as the result of the thinning of the population. Current rates are probably near maximal in physiological terms. (p. 119).

Mortality rates are hard to measure from age samples (catch curves) because of selectivity in catching. Lett and Benjaminsen (1977) calculated instantaneous total mortality rates from moulting samples, using age 2 and up, since age 1 animals were variably represented from year to year. Levels of fishing (hunting) mortality of immatures and adult were much lower in the 1970's than in the 1960's, following quota regulation and reduction of hunting effort by large ships. The authors therefore set up 2 simultaneous equations which enabled them to calculate instantaneous natural mortality ($F + M = Z$, where F = Fishing, M = natural mortality, Z = total mortality) by difference. Their value for M was 0.114 0.068. Benjaminsen and Øritsland (1975) calculated it at 0.106; Winters (1978) at 0.10 and Ugland (1985) at 0.105.

The vexed question of mortality in the first year remains unresolved. Lett et al. (1981) looked at the possible forms of variation in density-dependence in harp seals: age of whelping, pregnancy rate, and pup mortality rates. They calculated the number of age 1 animals from sequential population analysis, and number of pups from application of maturity ogive and pregnancy rates (both density dependent) relative to population estimates derived from a sequential population model. Escapement was determined by subtracting catch from estimates of pup abundance for 1950–76. Natural mortality of pups was calculated from the equation: $M_0 = \ln (ESC/N_1)$, where ESC = escapement and N = abundance at age 1. Due to high year-to-year variability the estimates were averaged over 5-yr periods. Values of pup mortality were found to be high in 1952-56 and 1957-61 when the absolute value of escapement was high (300 000 to 350 000), and low in 1962 to 1966, 1967 to 1971 and 1972 to 1976 when it was lower (140 000 to 200 000). The later values were from 0 or negative to 0.1; earlier values to 0.5. The authors therefore believed that density-dependent mortality occurred in the first year, although they could not invoke an explanation other than possible competition for food between juveniles. At any rate, their estimates of recent juvenile mortality were as low as those of older age-groups.

Note that the high inverse correlation between levels of catch and survival shown from successful use of the survival index method (p. 8-15) during the 1960's implies that natural mortality of young was constant, and therefore probably low, during this decade in the northwest Atlantic, which does not deny Lett et al.'s (1981) thesis.

Roff and Bowen (1983) do not reach a conclusion whether juvenile mortality is equal to or exceeds adult natural mortality and in their modelling of population use rates of both $M_0 = M$ and $M_0 = 3M$. Their most probable values of M, in their simulations constrained by a time series (1967–80) of estimates of pup production, were 0.075 and 0.0725 for $M_0 = M$ and $M_0 = 3M$, respectively.

Population Estimates: Techniques and Results Especially in the Western North Atlantic

I reviewed this subject nearly 20 yr ago (Sergeant 1975). Techniques devised to date are as follows:

A. Counting or estimating production of young seals.
1. Photographic aerial survey of whelping adults, or young born.
2. Marking and recapture of young seals.
3. Totalling catches of young seals where it is known that few survived the catch.
4. Calculating young produced by plotting catch of young against relative strength of the same year-class subsequently as shown in uniform age-samples (the so called "survival index" method).

B. Counting the population, less young, as moulting animals.

C. Catch and effort analysis.

D. Sequential population analysis.

Direct aerial counting methods were pioneered in the white Sea by Soviet scientists so these will be discussed first.

1. Photographic Aerial Survey

It is convenient to consider photographic aerial survey as a whole and to consider first adult and immature animals (moulters), and then adults and young (whelping patches). These groupings on ice have had obvious appeal as directly accessible to population counting and the methods not surprisingly were the first to be employed. Dorofeev and Freiman (1928) censused moulting herds of harp seals in the White Sea. They recognized that the great majority of the adult and immature seals assembled on the ice only late in the moulting season, in late April and the first 10 d of May. Technical problems led all four attempts in 1927 to be incomplete; that of April 29 gave an estimate of 700 000 seals and the authors estimated that 50% needed to be added to account for missing immatures and adults not yet hauled up, giving 1 050 000, plus a second patch of unknown size, so that the number calculated was a minimum one. Dorofeev (1956) states that in 1928, surveys showed a stock of 3 to 3.5 million seals which would have produced about 500 000 pups. According to Surkov (1957), these were the combined estimates from two flights made in 1928. Surkov discussed errors due to seals being in the water; he believed them to be small in the ideal weather conditions used for survey (when seals tend to bask in the sun) and in the absence of sealing.

Surkov (1957) repeated the surveys in 1952 and 1953, a period when stocks were under heavy pressure and believed to be decreasing rapidly. The age-sex composition of moulting seals was analysed from samples taken at the same time as the aerial survey. In 1952, three times and in 1953, twice, complete aerial surveys were run. Up to 16 moulting patches were found, surveyed, and sampled photographically. Sometimes 2 consecutive counts were made within hours, and proved to be closely comparable. Computations gave a stock size of 1.2 to 1.5 million, or less than half that of 1928 (when Surkov accepts an estimate of 3 million). These new estimates therefore demonstrated severe reduction of population of white Sea harp seals. Surkov recommended renewed census after 5 years.

This was done (Surkov 1963) and the 1959 estimate was 1.2 million. Yakovenko (1969) however had criticized certain assumptions used, e.g. that age and sex composition had remained unchanged. Yakovenko (1969) himself reported on census made in 1962 and 1963. He attempted in 1963 to count both whelping and moulting concentrations *in toto*, the former on March 1–2 with pupping in full progress. He estimated the number of whelping females at 65 000. On April 23 and 24, photography of all moulting groups gave 165 000 animals in 76.1 km^2 (2164.7/km^2). In 1962, about 90% of moulting animals were counted. Therefore the two surveys had high precision. Between 1962 and 1963, the decrease, as estimated from moulting surveys, was from 179 000 to 165 000, or 14 000 animals, representing the surplus of catch and natural mortality over production.

Yakovenko (1969) calculated the declining trend in the early 1960's from kill figures and estimates of fertility and mortality rates and related these to actual counts. He then calculated the rate of increase that would occur under protection, estimating that in 1970 the herd would number 427 000, and would increase its rate of growth after 1970 when protected cohorts started to increase.

Retrospective cohort analysis by Benjaminsen (1979) showed that the decrease in 1962–63 was indeed rapid but that the minimum pup production reached in 1965 was about 100 000. This shows that aerial estimates, as one might expect, tend to underestimate numbers.

A similar, but later, history of surveys occurred in the western North Atlantic, the method used here first being aerial photographic survey of whelping adults. Dr. H.D. Fisher (1954) carried out photographic surveys of whelping patches in the Gulf and on the Front in 1950 and 1951, obtaining a calculated total of about 729 000 whelping adults in the two areas combined, 381 000 on the Front and 348 000 in the Gulf (though the figures were greatly extrapolated from incomplete counting). I repeated these surveys in 1959 and 1960 and was able to estimate only some 327 000 whelping adults, 214 000 on the Front and 102 500 in the Gulf (Sergeant and Fisher 1960). Whatever the comparability of the surveys, they showed a marked decline. Heavy catching of adults, as well as excessive catching of young, were pointed to as causes. In 1961, a closing date for catching of adults was introduced by Canadian, Norwegian and Danish governments in the northwestern Atlantic icefields. [At that time occasional ships chartered by Denmark for Greenlandic hunters came to the Front.]

Once a quota had been introduced by Canada and Norway in 1972, a more accurate level of population estimation was required in order to determine existing population and, if possible, the current trend. Soon after this time, Lavigne and Øritsland (1974) showed that the reflective properties of the pelage of a harp seal pup to ultra-violet light would allow pups to be detected more clearly from the air on white snow using this sensor than from black and white photographs. The technique merely required a UV — sensitive lens to be fitted to a survey camera. At the same time, advances in navigational techniques made it much more feasible to run parallel survey lines over a whelping patch. Disadvantages were that their lens could be fitted only to a 70 mm camera; this was used to calculate the ratio of pups to adults, and a regular 24 × 24 cm survey camera was used to estimate the total number of adults at a higher altitude.

A preliminary survey was carried out in 1975 (Lavigne 1976) and suggested production of between 197 233 and 257 602 animals. Total coverage, however, was only believed to have been obtained in the Gulf of St. Lawrence, for an estimate of 46 000 ± 5 158 animals. A full census was carried out in 1977 (Lavigne et al. 1980) and this, by chance, was more successful on the Front, where production was estimated at ca. 200 000 pups. If the ratio of Front/Gulf production of .63/.37 found by Lavigne (1976) in 1975 is applied, the Gulf production would have been 117 469 for a total of 317 460 pups in 1977.

Aerial survey, even at its most sophisticated, has disadvantages, chiefly of cost (especially over the extensive northwest Atlantic icefields); usually at least 2 and probably 3 consecutive years' surveying is required, at a cost estimated at Canada in 1978 of about $250,000 a year for a 2-yr survey, using one aircraft for each area, plus helicopters for ice-level "truthing" in order to estimate missed pups, provide real pup density counts, and assign growth stages to pups.

Nevertheless aerial photo survey was continued in Canada, harp seals being counted in 1983 at the same time as a full set of surveys for hooded seals (*Cystophora cristata*) in the same icefields. Because the surveys were designed principally to count the black hooded seal pups, a return was made to use black and white light imagery. The harp seal survey was a pilot study only, but nevertheless seems to have located all patches and photographed the major one. Close attention was paid to the validation of the counting procedure, as well as to the distribution of births of harp seals over the whelping season. Simultaneously, a mark-and-recapture experiment was carried out. This set of experiments is described below (p. 174).

2. Mark and Recapture Analysis

This is a well-known technique in the estimation of animal populations. A sample of the population is marked, allowed to mix fully, and the population sampled again for marks. The ratio of total to marked animals sampled the second time, multiplied by the initial number marked, is an estimate of the population. Strictly:

$$N = \frac{(M + 1)(n + 1) - 1}{(m + 1)}$$

where N is the estimate, M is the number marked, n is the number sampled the second time, and m is the number of tags recovered in the second sample (Chapman 1951). The population must be closed, all animals must have equal probability of being caught for marking, marking must not affect catchability, animals must not lose their marks before recapture, and all marks must be reported. Of these requirements, the one most likely violated in early experiments was the completeness of reporting of marks; non-reporting increases the estimate spuriously. The source of the second sample for harp seals is of course the catch.

Harp seal pups can be marked in large numbers at the whelping patches from a helicopter or icebreaker; the requirement of mixing before recapture can be achieved if marks are sought from a fishery which takes the animals at some distant point, when they have migrated actively some distance. Such a fishery exists taking Gulf-born seals in the Strait of Belle Isle some years in April. On the Front, it is usually necessary to depend on shore fisheries which take seals which have drifted passively in the ice without much re-sorting, and tags are not always then well mixed. Estimates are also possible from succeeding years, when the young animals from the two area have mixed, so that the estimates are of the whole population of young combined.

In later experiments, studies of non-returned marks were carried out by sampling fishing communities where sealers lived; and double-tagging of individual seals was used to test loss rate of marks over a year or more.

Marking experiments were carried out in the Gulf from a helicopter in March 1964, and at the Front from an ice-breaker in 1966, each time with a team of 6 men. There were active fisheries in each area and marks were recovered immediately after marking, in the Gulf from ships and aircraft, on the Front from ships alone, as well as from landsmen in all areas. Aircraft, which went out daily taking sealers to the ice, took tags more randomly than from ships, which showed great variability in catch of marked animals from day to day (Table 42), and between individual ships. Therefore aircraft recoveries were used as the best estimate of production. Table 42 shows that an estimate from aircraft returns for the Gulf production in 1964 was 127 336 ± 6 927 pups, which will be high by the amount of unreturned tags, though since late returns were rare these must have been few.

By comparison, the estimate from ships in the Gulf was 154 072 ± 9 142 in 1964; 127 009 ± 5 298 (from another set of markings) in 1966. At the Front, for ships, it was 188 913 ± 4 755 in 1966. Thus a combined estimate in the mid-1960's from capture-recapture tagging was 316 000 ± 10 700.

In the 1970's a brightly coloured plastic tag (Dalton Rototag) was introduced for the marking of young seals, and this tag proved to be much more durable than the metal tags we had previously used, due to its low weight. Also, the imposition of quota catching allowed tagging to be carried out on a large scale in Gulf and Front areas with possibility of good escapement. On the Front, in order to get offshore, helicopters had to be carried on board or refuelled from a ship. As far as possible, tagging was carried out so as to avoid subsequent catching by adjacent ships and landsmen. It was necessary to ensure that

TABLE 42. Marking and recapture from ships and aircraft of harp seals in the Gulf of St. Lawrence, March 1964, and at the Front in March 1966.

Date of marking	Number marked	Subsequent recoveries by			
		Ships	%	Aircraft	%
March 1	548	10	1.8	214	39.0
March 2	637	16	2.5	242	37.9
March 3	620	254	41.0	154	24.8
March 4	839	500	59.6	121	14.4
March 7	110	—	—	74	67.2
March 11	90	—	—	71	78.9
	2 844	780	27.4	876	30.8

1964 — Gulf: Aircraft catch = 39 252

N = 127 336 ± 6 927

Ship catch = 42 256

N = 154 072 ± 9 142

1966 — Front: Front catch = 54 955, M = 3 581, m = 1 042

N = 188 913 ± 4 755

tags were not retained by the sealers but sent in in full, and the reward was therefore raised. However, it was found necessary nevertheless to carry out surveys in selected fishing communities to assess the percentage of tags retained (Bowen 1979; Bowen and Sergeant 1983). The following numbers of seals were tagged in this program:

Year	Gulf	Front	Total
1978	4 378	5 000	9 378
1979	2 680	2 884	5 564
1980	3 362	3 615	7 247

The high Front total the first year was fortuitous, the result of whelping taking place on easily accessible shore ice, near Cartwright, Labrador (see p. 40; Fig. 61).

Bowen and Sergeant (1983) assessed results of the 3-yr experiment. Corrections were made for both loss of tags (determined by putting 2 tags on a percentage of animals), and for non-reporting of tags (between 20 and 30% of those put on in different years). Both short-term returns, if considered relatively random, and long-term recoveries from wintering immature seals, were used. X^2 tests showed that long-term recoveries from 1978 and 1979 tagging experiments gave the most random returns. These led to estimates of 506 000 ± 77 000 and 489 000 ± 71 000 pups produced in both areas combined.

1 and 2 Aerial photo survey and capture–recapture tagging compared

We carried out simultaneous aerial photo survey and tag and recapture marking in the Gulf of St. Lawrence in 1964. Aerial photographic survey on March 1–4 was based on adults, since an early start to catching prevented full photography of young. It gave an estimate of 93 000 animals in 2 patches. Capture–recapture tagging analysis as described above (Table 42) gave an estimate of 127 336, that is, 37% greater.

In 1983 a capture–recapture tagging experiment was carried out in Gulf and Front regions in order to check on the results obtained in 1978 to 1980 (Bowen and Sergeant 1985). Recoveries in the same season had to be used since by 1984 the seal catch had fallen to too low a level to provide adequate recaptures of 1-yr-old seals for analysis. The recaptures in 1983, however, were well dispersed. The resulting estimate was 534 000 ± 33 000.

Intensive aerial photo surveys of hooded seals were carried out at the Front and in Davis Strait in 1983, together with the deployment at the ice from ships and helicopters of teams whose task was to assess growth stages of hooded seal pups at fixed dates. Opportunity was taken the same season to carry out an aerial photographic estimate of harp seals at the Front (Myers and Bowen 1989). The "ground-truthing" team carried out an assessment of the growth stages of harp seal pups at different dates. They also marked a number of newborn and yellow-coated pups. This data allowed calculation of the length of each of the older stages up to grey coats (but not of the longer-lasting ragged jackets and beaters, p. 27). This, in turn, allowed construction of a curve which showed what percentage of each stage was on the ice at each date (Fig. 81). An assumption had to be made about the rate of entry into the water of ragged jackets and beaters, though few of these stages had been reached at date of survey, March 17, so that the correction was small.

The photographs were taken using visible light (black and white) and great care was taken to test the performance of the reader against known numbers of pups. He

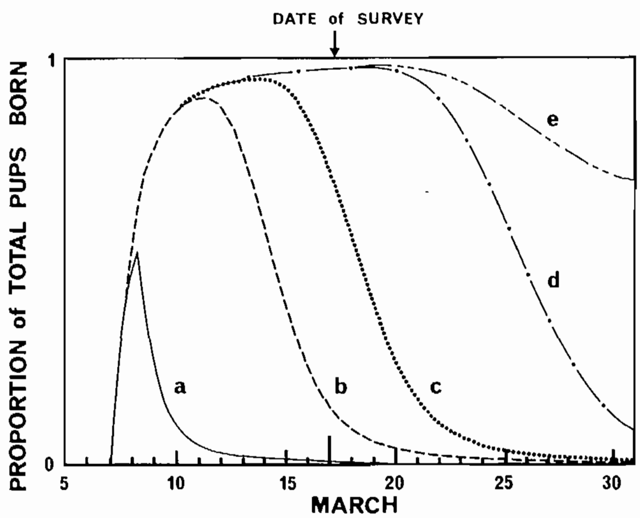


FIG. 81. Predicted proportion of the total pup production in the main patch on the Front in 1983 under the assumptions of model 1 (peak pupping March 7; all grey stage pups visible; ragged jackets leave ice at a constant rate of 0.0154/day; giving 0.975 of pups born, and 0.973 on ice). a, (——) newborn and yellow pups; b, (- - -) newborn, yellow and thin white pups; c, (. . . .) newborn, yellow, thin and fat whitecoats; d, (- . -) newborn, yellow, white and grey pups; e, (——) newborn, yellow, white, grey, ragged-jacket and beater pups (from Myers and Bowen 1987).

was shown to have a learning curve, i.e. experience allowed detection of more pups on the photos, up to an asymptote.

Results of the 1983 aerial photo survey were corrected for a series of negative biases: for pups which had not been born at survey date or had left the ice as beaters (estimated together as less than 3%); for errors in analysing the imagery (10%) and for difficulties in photographing all whelping concentrations known at the Front (not less than 10%). The summed corrections upward were 25% so that the direct count of 235 000 pups was corrected upward to 295 000[19]. In addition an unphotographed patch gave an additional 20 000–30 000 animals for a total in excess of 330 000.

The capture–recapture estimate was, as stated above, 534 000 in both areas together. Bowen and Sergeant (1985) calculating pup production in the two subareas separately found that approximately 0.72 of the pups were born on the Front in 1983. Front production from capture–recapture tagging was therefore 384 500 or 15–20% larger than the fully corrected estimate from aerial survey of pups.

Thus even with considerable improvement in detecting negative biases in aerial survey, and reducing positive bias (primarily due to unreturned tags) in capture-recapture analysis, the two methods remain with a considerable difference in means.

3. Maximum Catch of Young

During the late 1960's, in the northwest Atlantic, catching effort was large and the catch of young seals was high and uncontrolled. Under favourable ice conditions and if catching began at an early date — it was sometimes delayed to increase catches of beaters — most young seals of an age class could be killed. Evidence for this state of affairs came from studies by T. Øritsland (1967) who showed that, as the catch of whitecoats rose through these years, that of beaters (i.e. survivors) fell (Fig. 82). Øritsland (1971) calculated catches of the 1967 year-class as immatures by multiplying the catch of one-plus year animals by the percentage of one, two etc. years in successive years' samples of moulting animals. These he added to the catch of young in 1967 to estimate total removals of the year-class. The estimate up to 1970 was 296 000 pups for Gulf and Front combined. Since catches of the age class were not completed for many years, this figure would rise slowly with time to an asymptote. It may be compared with the estimate of 316 000 obtained from capture–recapture tagging in 1966 (p. 8-10). Presumably, not all the year-class was killed over time.

4. Catch and Survival Method

This method, which I formalised (Sergeant 1971) requires that catch of young fluctuate widely, a state of affairs which held true during the period of uncontrolled

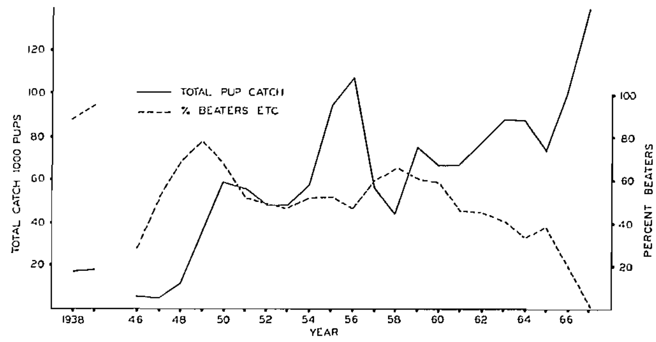


FIG. 82. Total Norwegian catches of harp seal pups on the Front, and percentage of beaters and ragged jackets in these catches. Both curves smoothed to a 3-yr sliding average (from Øritsland 1967a).

catch of young seals, but became no longer true when relatively steady quotas were applied. Therefore, like the method just described, it may be considered a historic method[20]. It quantifies the survival of a year-class from annual age samples (e.g. that shown in Fig. 83) and plots this index or figure against the catch of the year-class as young seals (Fig. 84). Since total removal of a year-class would produce a survival index of 0, the point where the curve cuts the X axis representing catch is an estimate of production.

The method suggested itself very early, after a high catch of pups in the northwest Atlantic icefields in 1951 depressed the strength of this age class, relative to all adjacent ones, in succeeding age frequencies; but it required a series of years of data for quantification. Plotting survival indices for year-classes 1960 to 1969 in this way gave a remarkably straight line fit (Fig. 84) which meant that annual production of pups was relatively constant and that catch, not natural mortality, was the main determinant of survival, at least at 1960's levels of production.

Various age samples were used for these studies, either a single series from one site (Fig. 85), when percent representation could be used, or the whole set available in one year, when an index of survival had to be used (Fig. 84).

Resulting estimates of production of young seals were about 100 to 110 000 (Gulf) and 320 to 350 000 (total) in the late 1950's (Fig. 85) and about 350 000 in the early 1960's (Fig. 84). The later total is somewhat higher than given by other methods. There is probably always an upward bias in the result of this method, owing to inaccuracies of age determination. When one has adjacent year classes, one showing high survival and the next low, errors in age determination will smooth the frequency, reducing the high figure and raising the low one. The result will be that the curve is flattened and will produce too high an estimate of production.

Exactly what is the frequency of errors in age estimation cannot be told at present, when the only method of assessing such errors is to compare different readers'

[19] 20% may be missed using black and white photography according to Ni and Stenson, cited by Bowen (in litt.), giving a total correction of 33% upward. The estimated total is then 310 000.

[20] Request by scientists for experimental large variation in the catch of young in the 1970's did not meet with managerial sympathy.

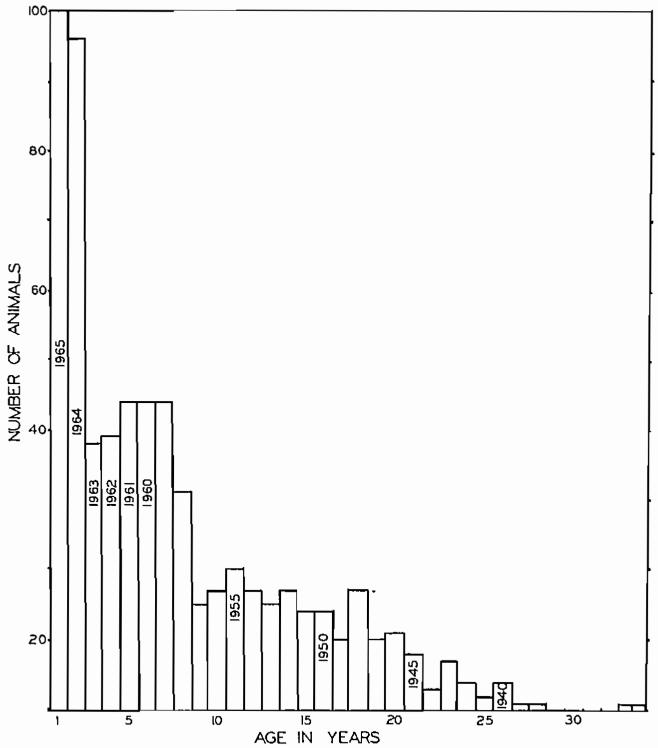


FIG. 83. Age frequency of moulting harp seals in the northern Gulf of St. Lawrence, April 1966.

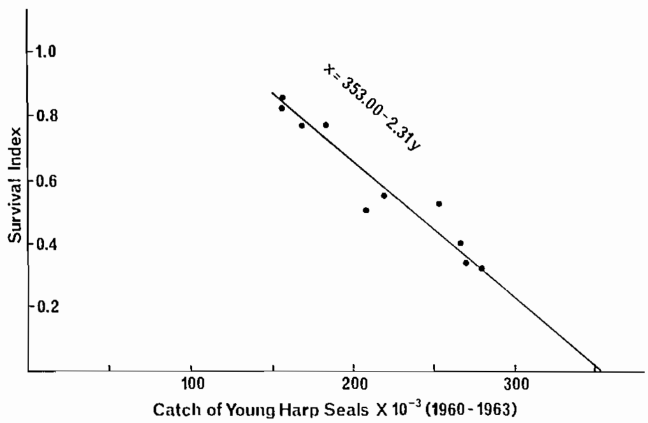


FIG. 84. Index of survival of western Atlantic age-classes plotted against catch of young, 1960 to 1969 (from Sergeant 1971).

estimates. However with the large scale marking of pups, a collection is slowly being obtained of known-age teeth, the real age of which can in the future be compared against the age read from growth layers.

Results of all these attempts to measure production are summarised in Table 43 and Fig. 86. Least weight can be given to Fisher's extrapolated aerial estimates in 1950–51, considering the lack of other methods available to check them; yet there was independent evidence of high density of animals at the time (p. 119 et seq.). Three independent methods (all done except aerial survey) are in good agreement in the mid 1960's. The results of

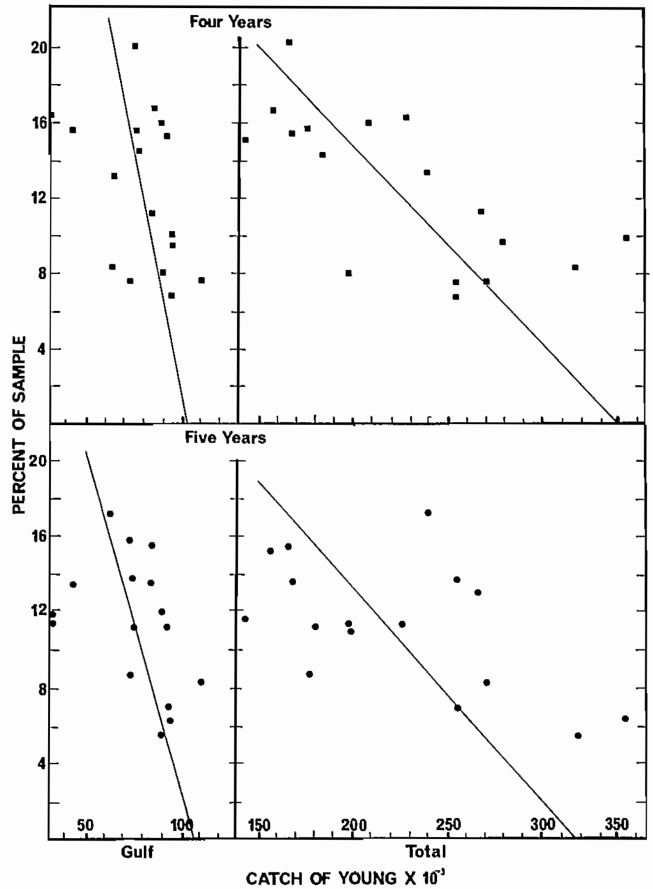


FIG. 85. La Tabatière netted samples at 4 and 5 yr (1950 to 1966). Age class strength (as % total seals) plotted against total catch and Gulf catch of young.

the combined aerial photo surveys of 1975–77 were probably rather incomplete. The increasing level of production believed to occur in the mid 1980's leads us to expect density-dependent effects on the population, but none were delectable in female reproductive rate up to 1987 (p. 119).

5. Historical Studies: Catch and Effort Analysis of Maximum Sustainable Yield

What is the maximum sustainable yield from the population of the northwest Atlantic? A rough estimate can be gained from a study of the mid-nineteenth and mid-twentieth century fisheries.

In the decade of the 1840's, the total mean catch reached its all-time greatest ever level of about 485 000 seals (Fig. 76). We need to refine these figures into catches of young harp seals. I assume that the early Newfoundland fishery caught mainly pups. There seems to be no historical evidence for the type of catch in the first half of the 19th century, and it is generally assumed that the late 19th century catch mainly of whitecoats represented the historic pattern. Any other catch on the ice would have required firearms, which have never been widely used at the fishery, but only in the hands of

TABLE 43. Summary of findings on production of Northwest Atlantic harp seals.

Year	Technique	Gulf	Front	Total
1950–51	Aerial photo survey	348 000	381 000	729 000
1959–60	Aerial photo survey	102 500	214 000	316 500
1975–77	Aerial photo survey	(117 469)[a]	200 000	(317 460)[a]
1964–66	Capture–recapture tagging	127 336	188 913	316 000
1978–80	Capture–recapture tagging			497 500
1983	Aerial photo survey	—	295 000	(468 000)[a]
1983	Capture–recapture tagging		(336 420)[a]	534 000
1967	Maximum catch			~ 300 000
1958		110 000		320 000–350 000
1960–69	Catch and survival			350 000

[a]Scaled up or down by ratio Gulf/Front of (63/37) of whelpers.

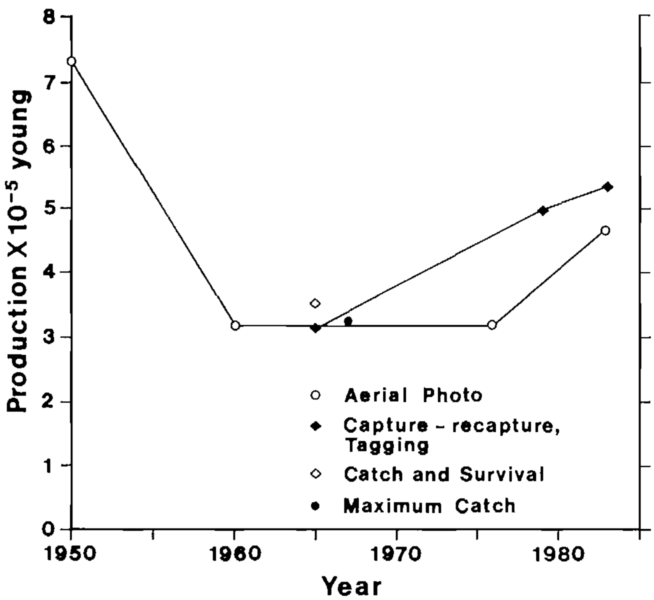


FIG. 86. Summary of estimates of production of harp seals at Newfoundland, over time, by various methods.

marksmen or officers.[21] Moreover, intensive killing of adult females at the whelping patches is only possible if the patches are entered soon after whelping, which (except on a chance basis) requires efficient ice-breaking vessels.

I suppose that second and third trips were about as frequent then for Newfoundland ships as they were in the late 1940's and early 1950's, when small wooden ships were again used, and detailed statistics are available. Then, catches of young seals were about 70% of the total (72% in 1945–54). Secondly, I suppose that hooded seals represented a small part of the total; in 1895 to 1914, they were 6.5%. The catch of young harp seals would on this basis have been about 485 000 × 0.7 × 0.935 or some 317 000. A further reduction is necessary for the number of adult females taken at the whelping patches when no protection for them is given. I estimated this at 10% of pups from a patch at the Front in 1953, before controls were applied. However this figure is very sensitive to starting date of hunting or date of arrival of ships among whelping seals, because the mothers leave the pups after 10 d. I will use 5%, which reduces the catch figure of young still further to 300 000. This level of catch slowly reduced the population. Therefore, a level of 300 000 young seals was greater than the maximum sustainable yield, but since the subsequent decline was slow, not very much greater than it.

We may also conclude that the mean level of 220 000 young seals caught in the period 1945–71, which followed a period of negligible sealing, was also excessive, since it reduced the population rather rapidly. The difference in the figures arrived at is doubtless due to the fact that since 1945 the catch of harp seals older than young was very great, especially prior to 1961 when there was no closing date, whereas in the 19th century it is doubtful if the Newfoundland fishery took many moulting old seals, as explained above. We arrive at a maximum sustainable yield of approximately 200 000–250 000 if catches of seals older than young are kept low.

A much more detailed analysis of the 19th and 20th century fishery has been carried out by Barchard (1978) and represents the ultimate that can be achieved from historical data using modern manipulation of statistics and technique of analysis of catch and effort. Barchard first took pains to assemble all catch and effort data and found sufficiently reliable figures for catch and number of ships beginning in 1798. The fishery shifted from sail to steam beginning in 1863 and from steam to motor vessels in 1945. It was necessary to calculate efficiencies of sailing ships versus steam sealers in order to estimate effort. Barchard looked at a number of possible measures of effort: vessel tonnage, vessel horsepower, number of men and time spent sealing; and modifying factors of ice and weather. Tonnage and weather-corrected ship-season as ideal measures could not be used for the full time period, since tonnage and weather were unknown before 1863, so that the number of ships hunting in any season was used as the single best available measure of effort. From comparisons of catch per season by the sailing ship and steam ship fleets, the increase in efficiency from sail to steam was calculated as 5.63 times; there was no evidence of any significant change in efficiency between steam and motor-driven fleets.

Figures of catch and calculated indices of effort were smoothed. There exist a number of methods of calculating population when a long time series of catch and effort data are available; all assume that catch per unit of

[21] Carroll's figures for 1872 (see p. 95) give 1 gun per 15 men, about the same as the recent ratio.

effort (CUE) is proportional to population size. Barchard employs five such methods, and gives most weight to the three of them which are biologically more sophisticated in taking into account recruitment and natural mortality (Chapman's, Least Squares, and Allen's *M* and *R* estimates). His analysis shows that stock sizes slowly declined through the 2nd half of the 19th century, at a mean level of population of about 2 million seals of all ages, equivalent to an annual production of about 400 000 pups.

In the period 1819–71 effort was high and catch per unit effort low, indicating competition between ships. This inefficiency was somewhat reduced between 1872 and 1914, and greatly reduced between 1915 and 1945. This accords with what we know about the rationalisation of the sealing fleet in St. John's, sinking of ships during the 1914–18 war and the effect of ensuing economic depressions which reduced demand for seal oil (p. 96). These last factors allowed stocks to recover to near-maximum capacity by 1945.

Barchard's best estimate of maximum sustainable yield was 243 632 seals for an equivalent total population of 2.1×10^6 seals and an equilibrium population (before fishing had begun) of 4.1×10^6 seals. He assumes a catch of 81% young, 11% immatures and 8% adults for the traditional Newfoundland fishery but ignores hooded seals.

Figure 87 shows Barchard's exponentially smoothed catch for the nearly two centuries-long period. The steady decline in catches between the mid nineteenth century and the 1920's–1930's is well shown. It is always surprising to realise that the biggest catches were taken before sail gave place to steam. Figure 88, also from Barchard, shows the estimated effort, in numbers of ships, corrected for increasing efficiency of steam and motor (assumed to be equivalent) over sail. The high effort reached by about 1850 is then seen clearly, as well as the increase in the second half of the twentieth century.

6. Sequential Population Analysis

This method, pioneered by fish biologists, uses catch-at-age data when good effort data are not available to estimate fish population mortalities. The form known as *cohort analysis* assumes that natural and fishing mortality occur seasonally (discretely). Cohort size within an age group is assumed to depend on cohort size within the age-group the year after, and the equation is used to calculate the population size in the initial year from the final year's population. The process is therefore a simulation of population history backwards in time. A starting (= final) value for age-specific hunting mortality *F* is required.

Lett and Benjaminsen (1977) used this approach utilising all available data on age composition, data which had been obtained sporadically since 1952 and more intensively since 1960, for harp seals of the northwest Atlantic, and on catch levels, so that catch could be made age-specific through this period. The resulting estimates showed a decline of 55% in population between 1952 and 1968 which fits well with knowledge from aerial photography and marking and recapture.

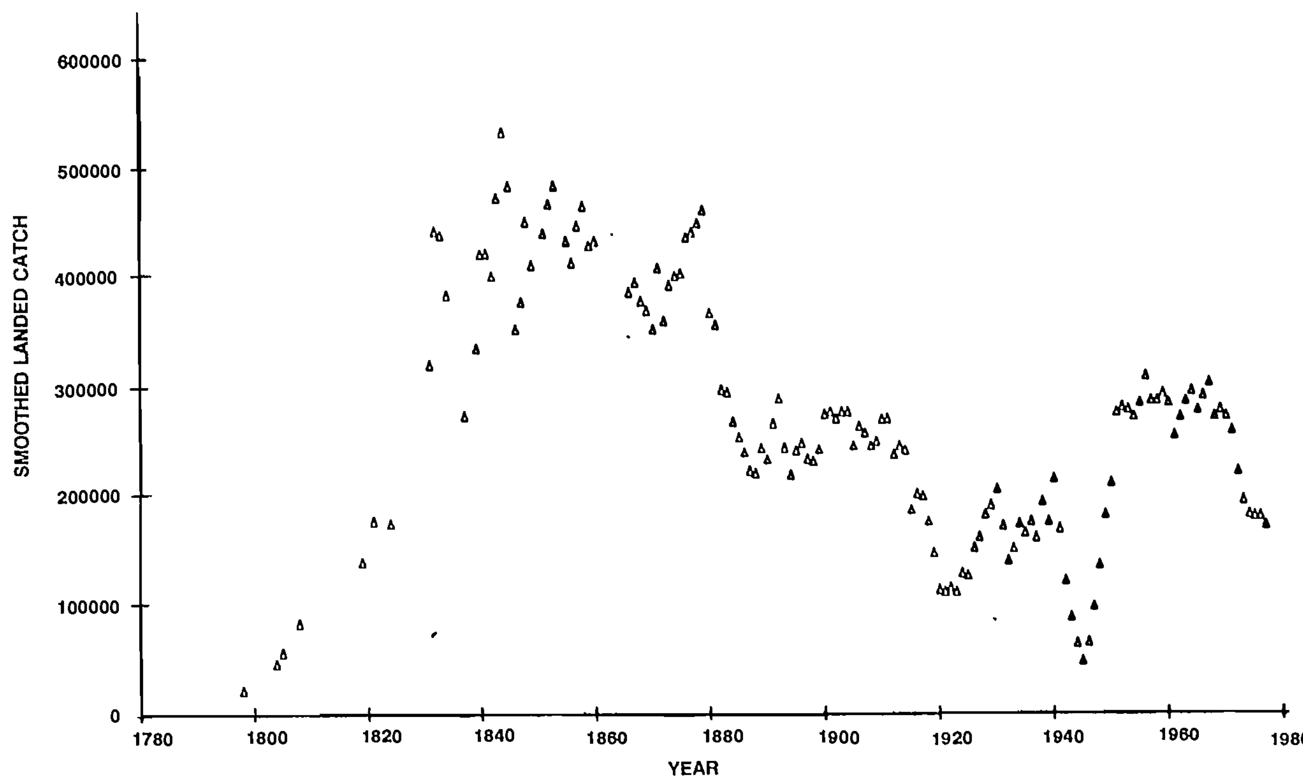


FIG. 87. Exponentially smoothed landed catch at Newfoundland, 1798 to 1977 (Barchard 1978, fig. 7).

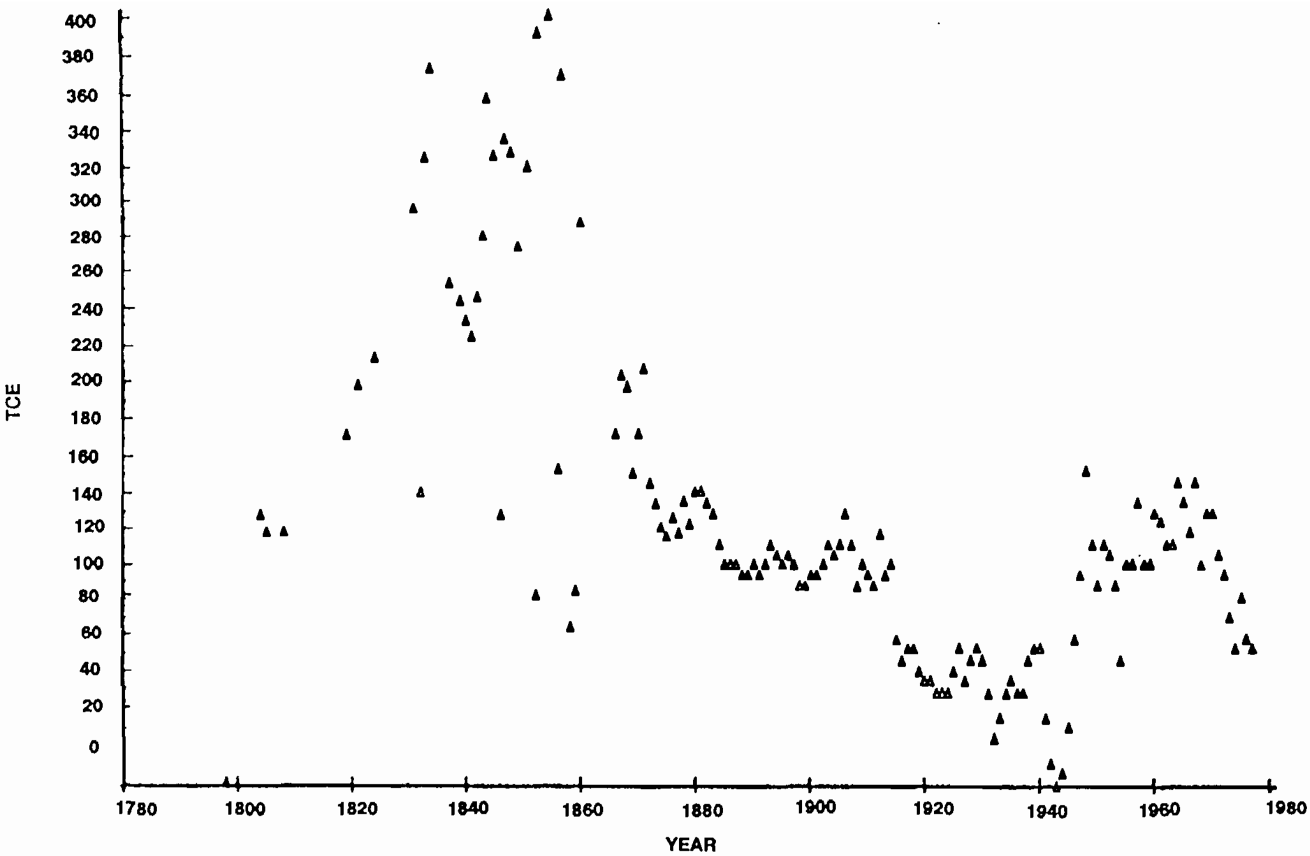


FIG. 88. Technology-corrected effort (fishing capacity) at Newfoundland (Barchard 1978, fig. 2b).

Lett and Benjaminsen took into account that, as the population had declined, fertility had increased mainly due to a rise in mean age at first sexual maturity of females (Bowen et al. 1981), but assumed a constant natural mortality rate. The population size at its maximal point was calculated to be 3.7 million, but was only 2.3 million in 1952, i.e. the population during the second war had not reached equilibrium level. Maximal pup production was about 800 000, and the maximal sustainable yield was about 200 000 pups and 40 000 older animals from a breeding population of 375 000 females and total 1-plus-year seal population of 1.6 million. These last figures are rather close to Barchard's derived from historic sources.

Lett et al. (1981) re-estimated total pup production as 290 000 in 1972, 310 000 in 1975 and 320 000 in 1977, while production in the Gulf was estimated at 90 000 in 1971, 89 000 in 1975 and 93 000 in 1977. Their revised model introduced density-dependent pup mortality as a third feedback control (see p. 102). However, with the three controls, the stock/recruitment model still does not have a descending right limb, i.e. pup production still increases slowly.

A number of other authors (Table 44) examined retrospectively the state of the western harp seal population during the period of heavy exploitation between the early 1950's and early 1970's. All these analyses were made after protection by quota had been achieved in 1972, and were designed to estimate what was happening to the population after such protection. (They were also, often and importantly, examining methodology and attempting to improve it.) Yet, among the later (1983 –) of such studies, only those of Roff and Bowen (1983, 1986) took into account later estimates of production in order to constrain the output of their models within these known (or at least estimated) levels. These were the capture–recapture estimates of 1978–80 (Bowen and Sergeant 1983) and of 1983 (Bowen and Sergeant 1985). Roff and Bowen's (1983) simulations of history of pup production and of total (1 + yr) population are shown in Fig. 90a. Analyses by Ugland (1985) and Cooke (1986) merely reexamine population history during the period 1950's–late 1960's and results of their simulations are summarised in Table 44. All these authors base themselves largely on published age frequencies, and all are critical of the survival index method. Roff and Bowen (1983, 1986) therefore use a maximum likelihood method, while Ugland (1985) describes a least squares method. Cooke (1986) simulates results of the survival index method and shows that it ceases to reflect real trends over time periods exceeding 20 yr.

Discussion

Doubleday and Bowen (1980) criticized the survival index method, believing that it may bias estimates of pup production upward by as much as 10%, that errors in age determination may also bias estimates of natural

TABLE 44. Estimates of vital statistics for western harp seals by different authors (M = natural mortality of adults, M_0 of young).

Authors	M	M_0	Pup production in:			Estimated MSY	
			early 1950's	late 1960's	1980's	Field	Stock
Allen 1975	0.08		450 000	325 000	see paper	250 000	470 000 pups ?? 2 × 10^6
Lett and Benjaminsen 1977	0.114			420 000	—	240 000	1.6 × 10^6
Lett et al. 1981		0.2 0.1–0.15				230 000 215 000	2.5 × 10^6 1.4 × 10^6
Barchard 1978						243 632	2.1 × 10^6
Winters 1978	0.10		500 000	365 000	Incr. at 3% p.a.	290 000	1.8 × 10^6
Roff and Bowen 1983		0.075 = M 0.0725 = 3M		370 000 380 000	480 000 in 1980	Replacement 300 000	
Ugland 1985	0.105			400 000	390 000 (1980)	—	
Cooke 1986			500 000	400 000	—	—	
Roff and Bowen 1986				370 000 to 400 000	534 000 in 1983	200 000 to 350 000	

mortality by the same figure (up or down?) and overestimate mean age at first maturity. Bias can be removed, but variance of the estimate then increases.

Roff and Bowen (1983) stress that there are high variances for all existing population estimates.

In view of all the uncertainties in population modelling, is there an empirical method which will enable us to assess the state of the population? The 1972 quota, having almost halved the catch of young (Fig. 89), greatly increased their survival, and the abundance of animals of year-classes beginning with that of 1972 is evident from all later compilations of age-frequency (Fig. 91). Most striking was the beginning of a catch of immature seals by small craft and long-liners in Notre Dame Bay, beginning in about 1973, which went on to take 20 000 animals a year. Evidently, prior to 1972, there was no predictable escapement of young seals growing into bedlamers which could allow the existence of such a fishery. The composition of this catch became similar to that formerly taken as moulting seals by the larger ships, a catch which almost disappeared with the guarantee of good catches of young by each ship. The small-craft catch therefore replaced the moulting catch, and since the seals were now taken in February rather than when moulting in April, their pelts were of better quality.

But this increased survival of pups and of adult females does not guarantee that the population is increasing, which is a matter of quantitative dynamics. There seems to be one set of data which shows clearly the recent history of the population: the catch at West Greenland (Kapel 1986). Since much of this catch is of 0 and 1 group seals (p. 48) it is an index of the escapement from the Newfoundland catch of young; moreover, the effect of improved recruitment plus escapement is rather soon

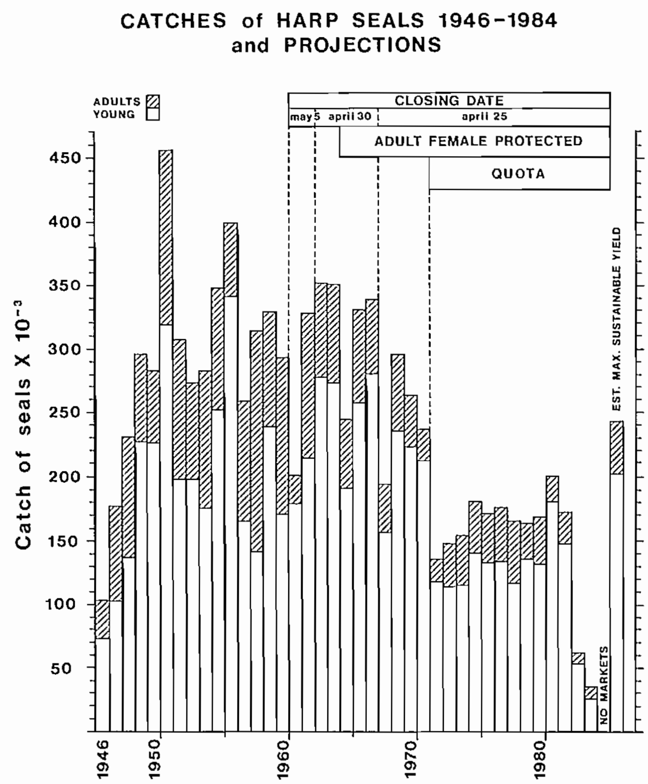


FIG. 89. Catches of young and old seals at Newfoundland before and after the 1972 quota.

shown. If catches at West Greenland are plotted against time (Fig. 92) they are seen to have declined from about 20 000 in the early 1950's to a low point of about 5 000 in the early 1970's, after which a rise begins and catches increase to about 18 000 by 1983. The first half of these changes exactly parallels what we believe to have happened in the history of depletion (Lavigne 1979; Lavigne and Kovacs 1988). Therefore, the second half of the change likely indicates that protection during and subsequent to 1972 was indeed effective protection. Admittedly, we do not know in detail what changes of effort have occurred in West Greenland. The numbers of fishermen do not seem to have changed very much. Aarsberetning *Grønland* (Anon. Denmark 1986 and previous issues) gives 4 000 people, of which 1 000 hunters, in 1968, and 2 500 hunters and families in 1983). Moreover, improvements in mobility, such as given by larger boats and engines, have likely been offset by increased distance of hunters from hunting grounds, people having moved to larger centres. These results seem to fit the forecast of Lett and Benjaminsen (1977, fig. 11, here reproduced as Fig. 93) that with a catch of 170 000 young seals and low adult catch the population would rise slowly. This is close to the levels of catch that have occurred under the quota (Fig. 89). They also fit well the probable trend of increased production and population modelled by Roff and Bowen (1983), as shown in Fig. 90.

All authors who estimate it seem to agree well on the maximum sustainable yield that can be obtained from the northwest Atlantic population of harp seals (Table 44);

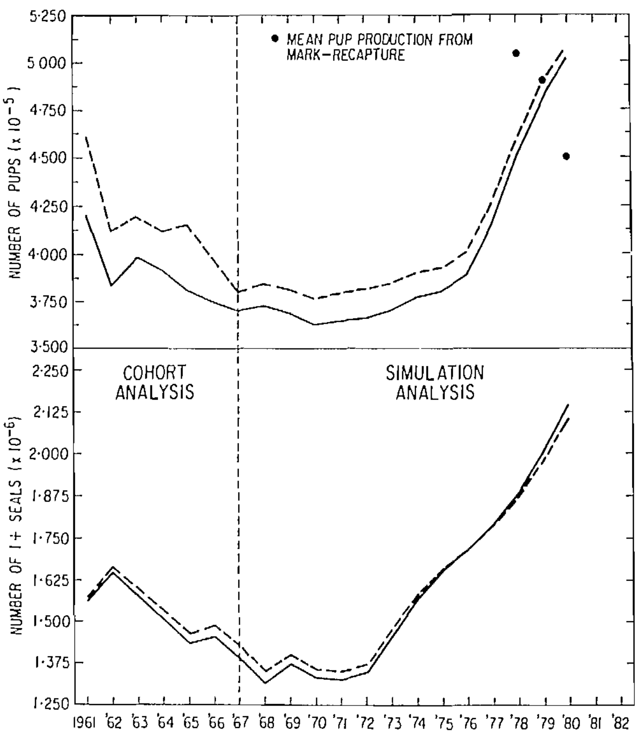


FIG. 90. Estimates of 1 + population (millions) and pup production (hundred thousands) from 1961 to 1980 using the most likely estimates of M and 1967 pup production. (—) $M_0 = M$, (. . .) $M_0 = 3M$ (Roff and Bowen 1983, fig. 2).

about 240 000 seals, taken as 200 000 young and 40 000 older animals, presumably bedlamers and adult males (to fit a spread of types of sealing). These would come from a population of about 2 million animals including young of the year.

Results, Other Areas

1. Jan Mayen

At Jan Mayen, far from inhabited regions with airfields[22], and having extremely bad weather in March and April, aerial survey has not proved possible in the past for harp seals.

Øritsland (1976) discusses exploitation since 1948. In that year catches reached 60 000 but declined to about 20 000 seals per year in the late 1960's. A quota was applied of 15 000 pups with no older seals in 1971 (Fig. 69). In 1976 it was increased to 16 500 pups. The equilibrium yield was estimated in 1971 at 14 000 pups (Ulltang and Øritsland 1971). The excess of quota over estimated yield was explained by the fact that each ship had its quota, not transferable to other ships, so that the full quota was never reached; the average catch for 1971 to 1976 was 11 953 pups. It was assumed that this saving over quota allowed a slow increase of population. Quotas were increased steadily up to 21 000 in 1980 but catches from 1976 to 1980 averaged only 14 980 (Øritsland in litt., 20-I-1981) in spite of an average quota of 18 800 during this time period. Moreover the number of Norwegian ships simultaneously declined from 15 to 9. Therefore, either production was declining in 1971–80, estimates of production having been too high, or economic conditions had reduced the profitability of hunting harp seals. Wiig (1988c) gives a preliminary estimate made in 1988, based on age sampling and tag recoveries, of about 40 000 pups and a stock size of about 200 000 for 1980. Further protection followed. A recent informal estimate from Norway of the size of this population is "over 350 000 seals" (O. Grahls-Nielsen in *Bergens Tidende*, 17 Dec. 1987) which seems reasonable, particularly since the author estimates the White Sea herd as "well over a million" which agrees with other sources (p. 92).

2. White Sea

On p. 103 I discussed production estimates for the White Sea population from the late 1920's up to the ban on ship killing and quota of 1965, from results of aerial surveys of adults and of young, and later also of studies of age and sex composition. These study methods have continued to be used (Anon. USSR, 1969 to 1979).

Benjaminsen (1979) used a survival index to calculate the history of this population from 1962 to 1965, using Norwegian age samples of moulters collected in the

[22] There is now one at Angmagssalik, S.E. Greenland.

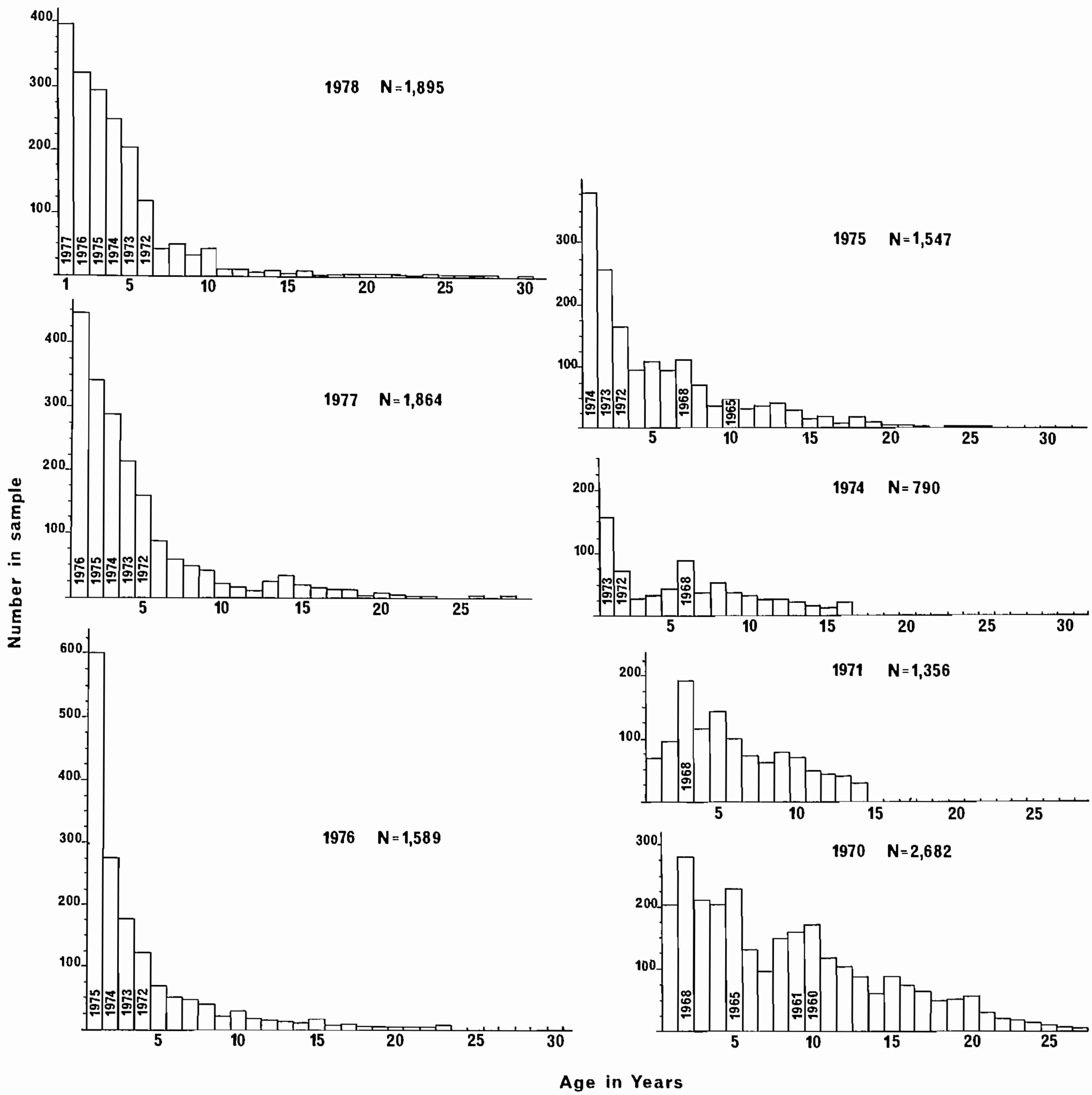


FIG. 91. Combined annual age frequencies from samples at Newfoundland, before and after the 1972 quota. Only the 1968 age class was outstanding before the quota; but all age classes thereafter.

southeast Barents Sea from 1964 to 1972. He then projected the population forward to 1978 using standard figures of age at sexual maturity, pregnancy rate and natural mortality used for other populations (Lett and Benjaminsen 1977). A low point of 98 000 pups was calculated for production in 1965. The median of Benjaminsen's estimates shows a steady increase to a production of about 160 000 in 1978, a rate of increase of about 5% per year. The figures are about 50% in excess of Soviet counts of whelping females on the ice — the low bound of their estimates increases from 74 000 in 1965 to 91 000 in 1978 — probably because some females are always missed in the water. These results were confirmed by Borodin (1978) who estimated that a maximal production would be achieved of about 2.4×10^5 pups in 1980–82. The population does indeed seem to have stabilised (Yablokov and Nazarenko 1986) since the age distribution of whelping females now contains many animals up to 30 yr of age (Fig. 94) and the mean age of entry to the whelping adult females has moved up from 4 to 6–7 yr (Table 45), a change which was already marked after 10 yr of protection.

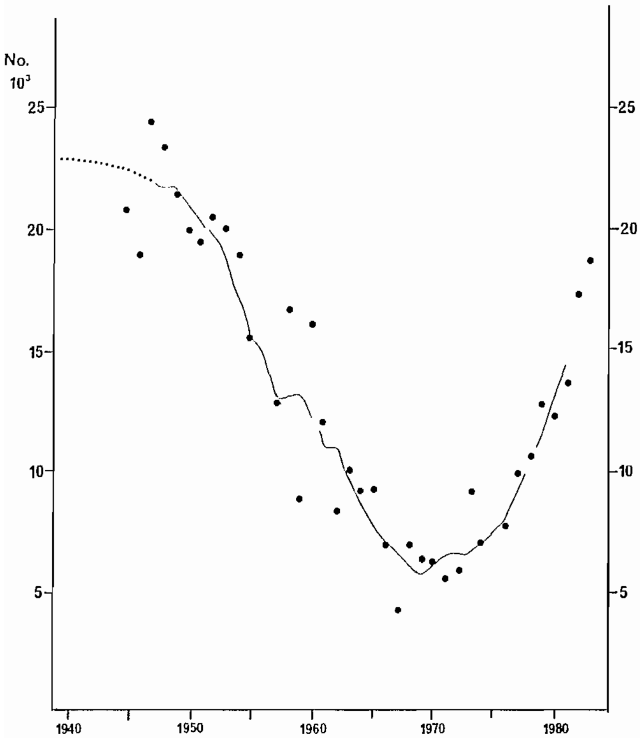


FIG. 92. Catches at West Greenland, 1945 to 1983 (from Kapel 1986). The continuous line joins 5-yr running mean figures.

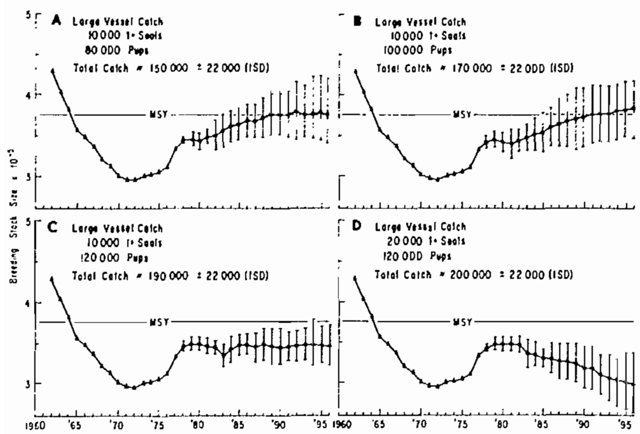


FIG. 93. Projected breeding stock of the northwest Atlantic harp seal in relation to varying management strategies. Confidence limits are shown. Lett and Benjaminsen 1977, fig. 11. Catches following the 1972 quota approximated projection B.

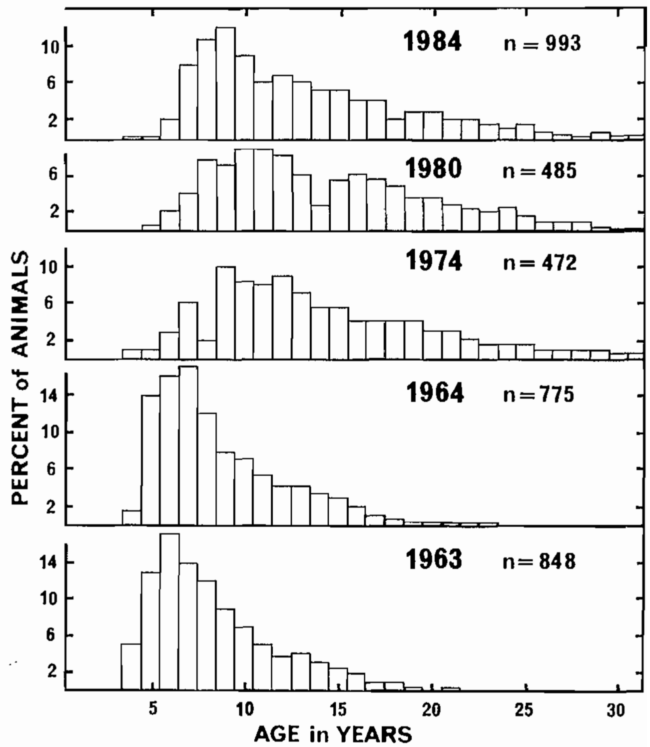


FIG. 94. Changes in age-composition of whelping adult female harp seals in the White Sea, 1963–84 (after Nazarenko and Yablokov 1986).

TABLE 45. Mean age of sexual maturity of female harp seals, calculated by the method of DeMaster (1978). (Data from Fig. 94 and 96.)

Years after protection	White Sea	Newfoundland	
−1	3.94 (1963)		
0	4.13 (1964)		
5			
			4.50 (1978)
10	5.70 (1974)	4.55 (4.1–5.05)	4.95 (1982)
			4.50 (1987)
15	6.95 (1980)		
20	6.17 (1984		

A production of this size implies a total population, excluding pups, of about 1 million animals.

Whatever the cause of these recent density-dependent changes — climatic cooling or shortage of food or both — they occurred at an unexpectedly low population size, compared with population estimates for this herd made for 1928–30. Thus, Borodin (1978) using virtual population analysis back-calculated that the size of the stock in 1930 was some 2.6×10^6 animals[23]. This agrees well with 3 to 3.5×10^6 by aerial survey in 1928 (p. 103) and heavy catching between the two dates. There are about 2.5×10^5 pups produced now as compared with about 5×10^5 in 1928–30. Therefore, the carrying capacity of the White Sea for harp seals has greatly decreased between the late 1920's and the present time.

[23] Unfortunately Borodin's 1928 paper is a summary only, so that his results cannot be checked.

Chapter IX. Natural Regulation of Harp Seal Populations

Summary

Predation by polar bears, killer whales and Greenland sharks occurs on harp seals but usually appears negligible, as do parasitism and disease associated with high numbers, at least in populations observed to date. Thus population size must be regulated primarily by food or space or both.

Severe shortage of ice has been shown to increase pup mortality. It occurs about once per decade at whelping time in the marginal habitat of the Gulf of St. Lawrence, when the resulting deaths of pups may reach high levels relative to production. Rafting of ice against land during lactation or after weaning, when some whitecoats and attendant females or beaters can be crushed, occurs with some frequency at the Front and in the White Sea, but does not seem to cause high levels of mortality relative to production.

Although shortage of capelin as food for wintering pregnant females and young seals has been demonstrated to occur in the Gulf of St. Lawrence, there is as yet no unequivocal evidence that such food shortage results in increased mortality of young. Under these conditions, females continue to transfer normal amounts of body reserves to their young during lactation, and apparently avoid risk of their own decreased viability by the normal process of a short, intensive feeding period immediately after weaning and mating.

The evidence to date, therefore, is that population regulation is achieved first and foremost by reduction in reproductive rate, though this may be because a change in age at maturity of the females is easier to detect than, for example, a greater mortality of pups at higher levels of production.

Introduction

Populations of large animals, first reduced and then left alone by man, do not rise indefinitely. Sooner or later the rate of increase levels off and the population reaches a plateau with (small) oscillations. The whole process from scarcity to the level of abundance, set by the environment's "carrying capacity", goes in the form of a flat, forward-titled S-shaped or *logistic* curve. At first the rate of increase is slow because the species is rare and contacts are few. It then quickens as the species multiplies by compound interest. Finally it slows due to various problems associated with density.

This is a difficult subject to study in any natural population of large mammals, partly because possible factors are many and episodes e.g. of die-off or disease, are sporadic. That is, one must be at the right place at the right time to observe them. This will be a rare chance with a pelagic seal species. With harp seals, practical difficulties are compounded by the fact that all populations were reduced when investigations began during the 20th century, with the possible exception of the Newfoundland population when research was just beginning in the 1950's. Only the White Sea and probably the Newfoundland populations during the last decade or two have been abundant enough and increasing rapidly enough for studies of natural regulation to be fruitful.

Predation

Predators, other than man, seem remarkably unimportant for harp seals. Three, however, can be listed: polar bears *Thalarctos maritimus* L., killer whales *Orcinus orca* L. and Greenland sharks *Somniosus microcephalus* (Bloch and Schneider). I have once seen polar bears and once killer whales at the Front ice, and once obtained evidence of Greenland shark predation. Though rare, such episodes are of interest.

Polar Bears

On March 11, 1966, M/V *Theron* was en route from the Gulf to the Front, passing through loose ice in a heavy easterly swell off the coast of southern Labrador. On one string of ice we came across a bear with two half-grown cubs, pressing on into the (north) wind and ignoring the ship. The reason, soon seen, was a scattered patch of harp seals with well-grown whitecoats. The patch was too small for the ship to stop (the main patch was further north) so we didn't see the outcome. Most later observers have reported small numbers of polar bears at the Front ice and some predation on harp seal pups (W.D. Bowen, in litt.).

The relative rarity of bears offshore on the Front must mean that they normally prey on something close to the coast — ringed seals in all probability — and are only tempted out by the harps if these are initially close to shore. As to the probable origin and fate of such bears, Dr. C.R. Harington wrote, in a letter of October 3, 1966:

> "The source area for the bears in question is (unknown), but I think they are most likely derived from the eastern coast of Baffin Island, where the species is abundant, and where the powerful Canadian Current, which washes the Labrador coast, passes. Hudson Strait, southwest Greenland and the Labrador coast are relatively poor source areas for polar bears, as far as I know. Males, and mothers with cubs in their second year, sometimes hunt near the fast ice margin off eastern Baffin Island in winter and could be carried south on the pack ice. Yet such early occurrences of polar bears near Belle Isle seem remarkable. A number of polar bears have been recorded along the north shore of the Gulf of St. Lawrence; some far inland. Keeping in mind that polar bears are labile in their feeding habits and can survive long periods with little food, some may return to the north, but nothing certain is known of this. One adult female polar bear was shot near Lac St. Jean, Québec, in the summer, and I suspect it could have worked its way there from the north shore of the Gulf".

As recorded by Nansen (p. 57) predation by polar bears is rather common on harp and hooded seals at Jan Mayen. We have also met it among hooded seals which form up in Davis Strait in March at about 64°N (Sergeant 1974). The ice-edge trends seawards from here towards Resolution Island, and the hooded seals drift southward or are displaced westward by easterly winds. Polar bears were observed along this pack ice edge in every survey in March and April over 3 years (MacLaren Marex 1979 a,c).

Killer Whales

On March 14, 1970 our photographic survey plane was searching the Front ice northeast of Belle Isle. The ice was unusually broken up in this region, presumably by heavy swells. Circling, we watched three killer whales surfacing in a lead only a few miles outside (east) of a patch of some hundreds of harp seals.

Sharks

A beater pelt taken at L'Anse au Loup, Strait of Belle Isle, in April 1964 was sent to us by Mr. J. Grieve of Bowring Brothers Limited, St. John's, Newfoundland. It bore an oval scar about 15 × 19 cm in diameter, and along the edge of the scar, points could be seen at regular intervals. The scar could be guessed as that resulting from the bite of a shark, presumably the cold-water Greenland shark *Somniosus microcephalus*.

Parasites

Parasitic roundworms are common in the stomach and intestine of harp seals (Myers 1957 and see p. 127). So far no evidence of death of seals due to high infections has been found in the wild. However, Wilson and Stockdale (1970) examined an adult female which died in captivity and found high infestations of *Contracaecum* sp. from oesophagus to rectum, with lesions and haemorrhaging. In 11 other captive specimens of unstated age no such infestations were seen, and deaths were presumably due to other causes.

Dr. T.G. Smith collected a large number of seal lice *Echinophthirius horridus* from the neck and back region of a 1-yr-old male harp seal on September 25, 1969 in Cumberland Sound, Baffin I. Such heavy infestations are rarely seen.

Shortage of Space and Climatic Change

Harp seals usually have suitable ice in excess of their needs for whelping. However in some years there is a shortage of ice either before whelping, which restricts whelping (p. 38–40) or after whelping, which can result in large-scale mortality of young due to ice-rafting (p. 81–82). Thus the environment itself varies from year to year and can limit either production or survival of young. In 1981, with almost no ice in the Gulf, mortality of at least several hundred young and tens of adults was seen on the north shore beaches of Prince Edward Island (Dr. J. Geraci, in litt., 8-VI-81). The young proved to have died "of starvation, associated with premature weaning or abandonment, and of cold-temperature stress resulting from an inadequate blubber layer at the time they entered the water". (Geraci, op. cit.). A few adult females were examined, one pregnant with a full-term foetus, but the causes of death of these were unknown due to their decomposition. The 1981 year-class from the Gulf, sampled in winter 1984–85 in the estuary of the St. Lawrence, proved to be extremely small (Fig. 30), apparently due to a combination of the poor ice and a relatively high catch (Table 49).

Sergeant (1982) found that ice conditions affected whelping patterns markedly in the Gulf of St. Lawrence in 1953, 1969 and 1981, or about one year in ten. In 1969 at least, ice conditions at the Front and in the Strait of Belle Isle were light also and would have allowed adult females which had not whelped in the Gulf to search northward for ice; some may have done so (p. 56). If the environment of the Labrador Current has no long-term change, only these annual variations occurring, the ice mass suitable for whelping is on average constant. A growing population of harp seals will then, by degrees, find more seasons when the amount of suitable ice is limited.

Excellent ice charts have been available in spring for the eastern Canadian seaboard, designed for shipping, and it is possible to categorise the type of ice used by harp seals for whelping (Fig. 127). This is medium winter ice in late February with 6 to 8/10 ice cover, i.e. it must be strong enough but have enough open leads for the seals to penetrate it. With this information, it should be possible to map the extent of suitable whelping ice each winter. Unfortunately, the Canadian government ceased publication of the summaries of ice conditions after 1971 (Environment Canada 1974), and later information must be obtained from archived ice charts as we have done above.

Food Limitation for Young Seals

In 1978 we marked large numbers of young harp seals in the Gulf and at the Front ice and found that the Gulf young but not adults were delayed in migrating northward, summering mostly in the Gulf till as late as August (Table 46). The Front young went on to West Greenland by June in the usual way. In 1979 and 1980 both groups migrated normally.

The delayed migration of the Gulf young in 1978 could be interpreted in various ways, one of which could be to assume that the animals did not initially have food reserves adequate for the longer migration. Stewart and Lavigne (1984) studied body condition of adult females in the Gulf in 1976, and of adult females and pups in 1978 to 1980. They showed that compared with 1976, adult females in the 3 later years had lower body reserves at the onset of lactation. These could have been transmitted to pups as a lower body size, with lower food reserves, although 1976 controls are lacking for pups. The period of decline of female body condition correlates well with a reduction in the stock of food capelin in the northwest Atlantic, particularly on the northeast Newfoundland Shelf (ICNAF 2J and 3K) though the capelin of the

TABLE 46. Abnormal migration of harp seals from the Gulf and typical migration from the Front in 1978. Table shows recoveries from each ICNAF (NAFO) area (see Fig. 7) by months of seals tagged in the Gulf (N = 4 378) and at the Front (N = 5 000) in March, 1978, with 1979 for comparison.

Tagging	2 & 3 Front					4 Gulf					
Recoveries	0	1	2	3	4	0	1	2	3	4	5
1978											
March			16	3					12	227	
April			6	15					3	12	
May			2	39					4	5	
June		10		2			1		1	16	1
July		7		1			2		2	5	
August		7					1			2	
September	1	3				1	3				
October		2									
November		2		2			2		1	1	
December		5		1	2		1			1	
1979											
January		4		1	2				2		
February		5		6			1		11	1	
March		2	1	46			1		37	3	
April			4	33	8				16	12	
May			1	18	6				5	4	
June				1	1		1	1		1	
Subtotal	1	47	30	168	19		13	1	94	290	1
Totals			265						400		
Totals Jan.-May/79			137						93		

TABLE 47. Recovery rates of tags from seals at wintering ice fields after 1 yr (from Bowen and Sergeant 1983).

	Gulf		Front	
Year	Number effectively tagged	Recoveries (and rate)	Number effectively tagged	Recoveries (and rate)
1978	4 170	90 (0.022)	4 984	124 (0.024)
1979	2 574	76 (0.030)	2 365	42 (0.018)
1980	3 601	49 (0.014)	1 902	15 (0.008)
Sum	10 345	215 (0.020)	9 251	181 (0.019)

St. Lawrence estuary were likely not affected (Fortier et al. 1987). The former stock was especially low in 1978-80 (Fig. 95) and shortage of capelin could have affected the migrating Gulf seals.

Because of the marking of cohorts of pups in the Gulf and at the Front of 1978 to 1980, it is possible to follow the survival rate of this 1978 Gulf cohort in relation to that of the 5 other marked cohorts (Gulf in 1979 and 1980, and the Front-born young in 1978 through 1980) by examining the recovery rate in later years, e.g. when the animals were taken on the wintering ice field at age 1 year (Table 95). These data show that there was no significant difference in mortality in the first year between the 1978 Gulf and Front cohorts, nor between the 1978 Gulf cohort and the mean for 3 years of Gulf animals. Therefore the short or delayed migration of the 1978 Gulf cohort, while perhaps a direct response to shortage of food resources of their mothers, does not seem to have landed the animals in a summering area with a shortage of food available to them, at least, not as compared with the other 5 cohorts in 1978–80. Comparison with earlier years is not possible because no tagging was then done

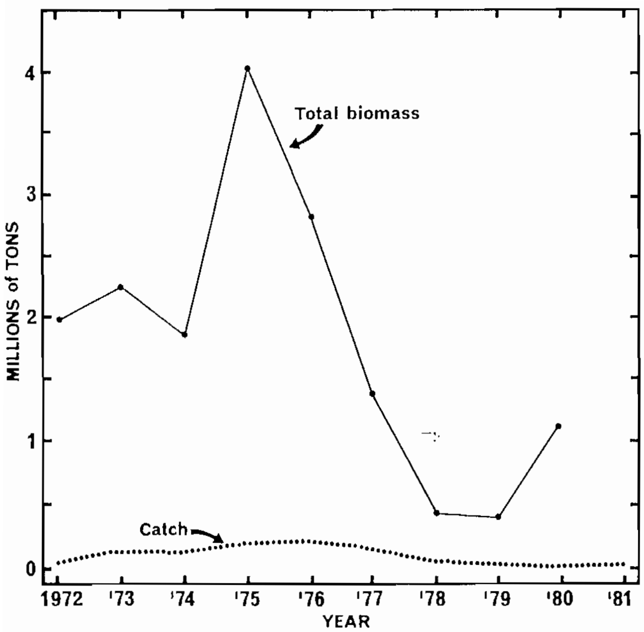


FIG. 95. Estimated capelin biomass (age 2 +, 1972–80) and annual catches, 1972–81), for ICNAF subdivision 2J3K (northeast Newfoundland - southeast-Labrador) capelin stock (from Leggett et al. 1984, fig. 5).

in both areas with the same type of tag in both areas.

Is there any other evidence bearing on the viability of age classes 1978–80? Studies of age frequencies of harp seals in succeeding years might be expected to demonstrate the mortality rates of these age classes. Such age-samples exist for Gulf-born animals (Fig. 30). Indeed, age classes 1978–80 are weakly represented as compared with those of 1975–77 (Table 48). Unfortunately, catch figures (Table 49) show that in 1978–80 there was a shift of hunting success from Front to Gulf, increasing Gulf catches of young, so that the reduced strength of surviving year-classes 1978–80 must be first and foremost attributed to higher mortality at human hands, with any effect of natural mortality masked.

TABLE 48. Dominant year classes of harp seals in the Gulf of St. Lawrence, from winter samples taken at or near Escoumins, Québec. (Data from Fig. 30.)

Year of sampling	Dominant year-class(es)
1969	1968
1970	1967
1971	1968
1978	1975
1979	1977
1980	1977
1981	1976
1982	1976
1983	1976 & 1977
1984	1979
1985	1982
1986	Data inadequate
1987	1986

TABLE 49. Catches of young seals (whitecoats and beaters) by ICNAF subarea (4 = Gulf, 2–3 = Front) from 1972 to 1983.

Year	Catch × 10^{-3} animals		
	Gulf	Front	Total
1972	5.0	111.8	116.8
1973	10.7	87.7	98.3
1974	16.3	98.5	114.8
1975	7.4	133.2	140.6
1976	11.6	120.5	132.1
1977	14.5	112.5	127.0
1978	39.6	76.6	116.2
1979	41.3	91.2	132.5
1980	35.2	97.2	132.4
1981	48.8[a]	129.6	178.4
1982	41.2	104.1	145.3
1983	14.0	42.5	56.5

[a]Also many drowned pups (p. 00).

Because of the major and unprecedented downturn in capelin abundance which occurred in ICNAF subareas 2J and 3K in 1976–1980 (Fig. 95), it is important to study a series of age-classes of Front harp seals over the same period. Published data (Bowen 1982) are available up to year-class 1979 but do not show any clear results (Table 50). It therefore remains unclear whether poorly-fed cohorts of young harp seals suffer greater mortality than usual, or not. Since the evidence to date is negative it may be that they can make up early deficient feeding later in other areas, perhaps with foods other than capelin.

The Young During the Rest of the Year

We have observations from the Front on young about 1-1.5 months old which have completed their moult but remain caught inside the ice by easterly winds (see p. 00). Under these conditions the young move toward the ice edge, often on top of the ice, and concentrate at the edge. Here they might very well compete for limited food resources. A more typical pattern is for the ice of the White Bay triangle to be drifted southward when east winds abate, reaching south to Bonavista, Trinity and Conception bays. Then the ice margin, with beaters feeding along it, becomes much more stretched out.

Once the beaters migrate northward, we have very little information on their way of life, though first-hand investigations in northwest Greenland in their areas of concentration would seem very well worth while. In general, one can imagine that as the number of young increases, so their density increases in the preferred spring, summer and winter feeding areas, and therefore their interaction increases. To measure the effects of this, one would need to study systematically their weight and condition in such areas. J. Hanks (1981) has suggested a number of tests of anatomical and physiological condition of mammals which could be used to test "population resilience". These include: deposited fat reserves, adrenocortical condition, various measures of blood chemistry and haematology and body growth.

TABLE 50. Strength of year-class of Front harp seals at 1 yr of age, from two different samples (Data in Bowen 1982, appendix, table A.)

Year-Class	Long-liner catch in White Bay: Sample size N_T	Number at 1 yr N	N_1/N_T	Net catch in White Bay[a]: Sample size N_T	Number at 1 yr N_1	N_1/N_T	Abundance of Front capelin
1972	—	—	—	312	6	0.02	+
1973	278	152	0.55	303	8	0.03	+
1974	374	201	0.54	780	177	0.23	+
1975	366	188	0.51	459	115	0.25	+ +
1976	422	117	0.28	541	92	0.17	+
1977	529	228	0.43	476	116	0.24	–
1978	204	113	0.55	872	142	0.16	– –
1979	827	382	0.46	411	35	0.09	– –

[a]With some animals from Labrador net catch in 1974 to 1976.

TABLE 51. Median age at first reproduction of harp seal females in the Gulf of St. Lawrence, by the method of DeMaster (1978). Animals collected annually in the estuary, December to February, and age back-calculated to age of fertilization in previous March. (Full data in Appendix 1.)

Year of collection	Sample size of females: Immature	Mature	Total	Median age and variance of sexual maturity: $\bar{X}$	$v(x)$	95% C.L.
1969 & 1971[a]	21	16	37	> 4, < 7[a]	—	—
1978	21	6	27	4.50	0.59	±1.51
1979	41	21	62	4.40	0.38	±1.21
1980	52	40	92	4.40	0.33	±1.12
1981	43	43	68	4.16	0.50	±1.39
1982	40	38	78	4.97	0.87	±1.82
1983	16	46	62	4.38	0.24	±0.96
1984	45	55	100	4.83	0.27	±1.02
1985	44	72	116	4.97	0.53	±1.43
1986[a]	8	11	19	> 3, < 5[a]	—	—
1987	46	32	78	4.50	?	?
1978–1986				4.57	0.058	±.470

[a]Data inadequate among critical age-groups, 3–6.

Reproductive Rate of Adults

Females

In female harp seals, a change in first age of reproduction appears to have occurred progressively between the early 1950's and the late 1960's, with the median age shifting downward by about a year (Bowen et al. 1981). Since this took place during a period of population decline, it may have been density-dependent. A change in reproductive rate of seals can be associated with a change in growth rate (Laws 1959). Innes et al. (1981) claim to have found such a change comparing growth of harp seals in the early 1950's with that in the early 1970's. The early data they used was mine, given to Dr. Laws, and the animals were aged by pelage up to 7 yr, and all dark females assumed to be older. The analysis probably therefore gives a low asymptotic length. The change nevertheless is probably real. The indirect method of examining reproductive rate is simpler but has a lag of 5 yr to it between birth and average first reproduction.

During 1969, 1971 and from 1978 to 1987, winter samples of females in late pregnancy were collected by hunters in the St. Lawrence estuary and the reproductive rate studied (Table 51, Fig. 96). Sample size was inadequate for determining the critical ages of maturation in 1969, 1971 (or these 2 yr combined) and 1986. The analysis for 1978 through 1987 does not show any significant change in median age of sexual maturity of females, which lay at 4.57 ± 0.47 for the whole sample. This is the same value as found for 1979 by Bowen et al. (1981). Fertility rate of females (Table 52) also remained at the same level of 0.95 reported by Bowen et al. 1981. There is thus no clear evidence yet of a density-dependent slowing of female reproductive rate in the present northwest Atlantic herds. However, as described above (p. 113, Fig. 94), in the White Sea such density-dependence developed within 10 yr after protection, and it is probable here that food resources became limiting due to heavy fishing of the resource base, especially capelin.

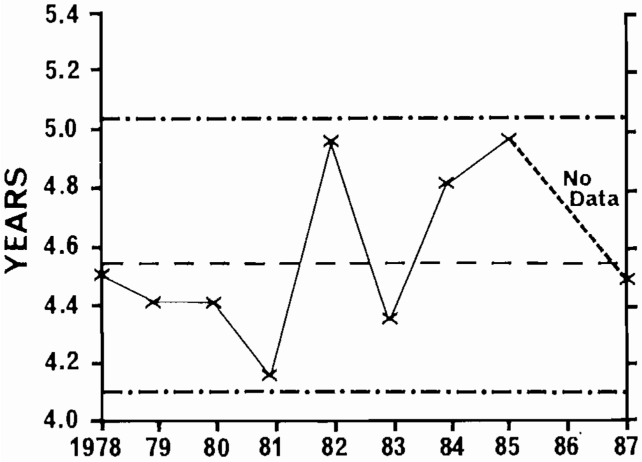


FIG. 96. Harp seals. Variations in mean age of female reproductive rate in the Gulf of Saint-Lawrence, 1978 to 1987 with overall mean (— —) and its 95% confidence limits (· — ·).

TABLE 52. Fecundity in late-term pregnancy, estuary and Gulf of St. Lawrence.

Years	Mature pregnant	Mature non pregnant	Total	% Pregnant
(a) *La Tabatière, northern Gulf*				
1978	35	3	38	
1982	19	3	22	
Subtotal	54	6	60	0.90
(b) *Les Escoumins, estuary*				
1969–78	20	3	23	0.87
1979–82	103	5	108	0.95
1983–86	137	7	144	0.95
Subtotal	260	15	275	0.95
(c) *Combined*				
1969–78	55	6	61	0.902
1979–82	122	8	130	0.938
1983–86	137	7	144	0.951
Total	314	21	335	0.937

Males

Reproductive maturation (as defined by a mean testis weight of 125 g or more) occurred 2 years later in the northwest Atlantic in 1952-57 than for males of the White Sea herd in 1958-64 (Table 3). In 1971, the mean age for the northwest Atlantic, based on less reliable data, was about 6 yr (Sergeant 1973b). (It could be argued that a difference existed in methods of age determination, but highest reproductive rates for females were much more similar in the two areas (Fig. 16), arguing for comparable aging techniques, so a real difference seems more probable). One can deduce, first, that there is density dependence in male reproductive rate; and second, that the Northwest Atlantic males were not reduced in numbers so strongly as in the White Sea.

Another feature seen in males which appears to have varied in time is wounding in the neck region, apparently due to fights between males during the season of mating. I observed these wounds among moulting males at the Front on April 16, 1953, but failed to find them from comparable samples on April 28–30, 1968 when I judged the adult males also to be in much better external condition. R.E.A. Stewart (1983), however, observed and photographed neck wounds in males in the Gulf in late March 1976 to 1980. This sequence could suggest a reduction of population of the males from 1953 to 1968 leading to reduced density at the whelping patches and reduced fighting, and an increased population with increased fighting in the late 1970's.

If this interpretation is valid, then male maturation rate is slowed at high density more readily than that of females, with concomitant changes in the degree of fighting. Such differences might be expected in a polygynous species. However, the whole data base for male harp seals is much weaker than that for females. Detailed studies using histological studies of the testis were done only by Fisher (1954).

Discussion

Knowledge from Other Species

What density-dependent factors are known in other species of seals? In the north Pacific fur seal *Callorhinus ursinus* L. the population was allowed to grow from scarcity to abundance between 1910 and 1950. The species is colonial and breeds on only a few islands, having colonized or recolonized some new ones recently (Peterson and LeBœuf 1969). Lactation lasts through the summer 4 months during which time the young remain on the beaches (Gentry and Holt 1986). At peak abundance in the 1960's the crowded pups suffered from parasitism, disease and malnutrition (Baker et al. 1970). Much mortality was caused by a parasitic hookworm *Uncinaria lucasi*, the eggs of which are transmitted from the seals' faeces to the beach sand and back to the pups the next season (Olsen 1958). Olsen wrote "Hookworms. . . doubtless will stand high among the factors leading to death of many pups. Others. . . are starvation, suffocation in storms and trampling by bulls. Others, so far unrecognizable, might be bacterial and viral diseases, exposure to chilling rains, crowding, congenital deficiencies, and possible overeating when the cows return to the rookeries after a prolonged period of foraging at sea". It was suggested that animals weakened by some of these factors might be more susceptible to mortality at sea, especially during storms in winter (Scheffer 1950b). Lowered growth due to crowding or malnutrition also results at high population densities (Scheffer 1955) and affects maturation rate so that females from crowded populations mature at later ages than females from growing populations, and the birth rate is lowered (Chapman 1964).

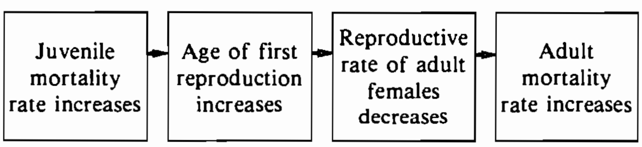
Geraci, St. Aubin and Barber (1982) examined a mass die-off of harbour seals *Phoca vitulina* that occurred on the New England coast between December 1979 and October 1980, and affected mostly animals less than

3 years of age. Deaths were found to be caused by acute pneumonia associated with an influenza virus found in other mammals and in birds. A mycoplasma was also found in the respiratory tract of affected animals. No parasites were associated and the investigators believed the disease was brought about by high seal density and environmental conditions such as warm temperatures. Mortalities of other seals with a similar aetiology were documented including one found in the ice-breeding crabeater seal *Lobodon carcinophagus* by Laws and Taylor (1957). This last finding had been detected close to shore in Graham Land, Antarctica, showing that such infections do occur in ice-living pelagic seals, where they must be more difficult to detect than in seals coming to shore.

Opportunities for mass infection in harp seals could occur especially in the aggregations which occur for a short time each year at whelping and at moult. Especially at moult the animals are in low condition and could be subject to stress and disease. The same must be true for parasitic infections. Geraci et al. (1981) showed that the Anopluran seal louse *Echinophthirius horridus* can serve as intermediate host transmitting the microfilarian Nematode *Dipetalonema spirocauda*, the heartworm of seals, in *Phoca vitulina*. The same louse occurs in harp seals (Mohr 1952) — indeed a specimen from the Magdalen Islands in spring, 1980 was sent to me for identification, coming from the pelt of a beater (moulted juvenile) harp seal. Nevertheless, incidence of this louse in harp seals in the northwest Atlantic has been rare to date except in occasional young or immature animals, (p. 116).

Theory

Siniff et al. (1978) theorised that density-dependent mechanisms probably come into play in the following sequence as a (seal) population increases towards its asymptotic value, following relaxation of catching:



— the first factor being assumed to be the most significant, and so on, on the grounds that in long-lived animals with low reproductive rates. . . "security of the fully adult population is the key to persistence". "Reproductive success in adult females is closely correlated with physical condition and thus, very likely, declines just before conditions reach the point where adult survival declines. It is fairly well established that immatures (juveniles) are most vulnerable to unusual severe environmental conditions, and are the first to suffer as high population levels are approached. It is also likely that reduction in growth rates ensue from the factors that lead to increased juvenile mortality, so that the age of first breeding is delayed".

Application to Harp Seals

The main surprise resulting from our analysis of factors controlling populations of harp seals is that a density-dependent change in age at first reproduction has proved so readily detectable, while a density-dependent mortality of young has not. But at least density-dependent change in growth in early life must be invoked to account for the flexibility in age at first maturity.

Fowler (1987) after a thorough review of density-dependence in populations of large mammals concluded that "food and food resources seem to be the main factor behind the expression of density-dependence in large mammals". Also that "populations exhibit most population regulation at levels close to the carrying capacity". Possibly we have not reached the levels of population of harp seals, nor reduction of their food resources, in the northwest Atlantic that would enable us to observe changes. Yet in the Barents Sea, population regulation due to food limitation seems already to have occurred.

Chapter X. The Importance of Harp Seals to Man

Summary

On North Atlantic coasts with seasonal pack ice, harp and hooded seals provide income at a season when fishing cannot be practised. Such coasts include those of northern Newfoundland and southern Labrador, most of the Gulf of St. Lawrence, and the White Sea. In summer, harp seals supplement ringed seals for Greenlanders and the Canadian arctic Inuit.

The fishery for harp and hooded seals in the northwest Atlantic in 1979 had a gross landed value of about $5.3 million plus a value to primary processors of $4.1 million, or about $9.4 million in all. This value approached the MSY value to be expected from the resource. It is about $1.3 per kg of seal killed.

About 10 000 men were usually involved as actual or potential sealers in any one year in eastern Canada in the mid-1970's. Of these, about 80% lived in Newfoundland or Labrador, 20% in Quebec and a few in Nova Scotia or Prince Edward Island. Adding Inuit and Greenlandic seal hunters gives a total of about 20 000 men in the Northwest Atlantic.

A heavy human fishery on capelin in the Barents Sea through the 1970's–1980's reduced this fish stock to low levels by 1986 when the fishery was closed. The probable effects on White Sea harp seals of capelin scarcity included reduced population growth rate and a major emigration. A major natural reduction in capelin stocks at Newfoundland in 1978–80 had some effects on harp seal physiology and behaviour but not on recruitment or mortality. Harp seals will not likely be perceived as a competitor with man for capelin in the Newfoundland fishing area, so long as capelin catches continue to be restricted. Harp seals are a minor carrier of the codworm parasite which infests fish flesh.

Living with Ice

The Gulf Stream and its northern component, the North Atlantic Drift, because of the Coriolis force, bathe the shores of the eastern North Atlantic, giving extraordinarily anomalous positive sea temperatures to Norway (Fig. 97). The Labrador current on the other side of the North Atlantic brings an extraordinarily subarctic marine climate to eastern Canada. This latter fact, unknown or ignored by early European explorers, led to their high death rate (most commonly, from scurvy) on overwintering expeditions, from Champlain and Jens Munk up to the whaling voyages to Davis Strait of the mid-nineteenth century.

The asymmetry leads to such facts as that the western Barents Sea (to 71°30′N) is ice free at all months, whereas ice from the Gulf of St. Lawrence sometimes reaches Sable Island, off Nova Scotia at 47°N in April or May; that the ice of the Gulf of St. Lawrence at 49°N has about the same annual duration and thickness (50 cm) as that in the White Sea at 67°N; and that the important small forage fish capelin, *Mallotus villosus*, spawns abundantly

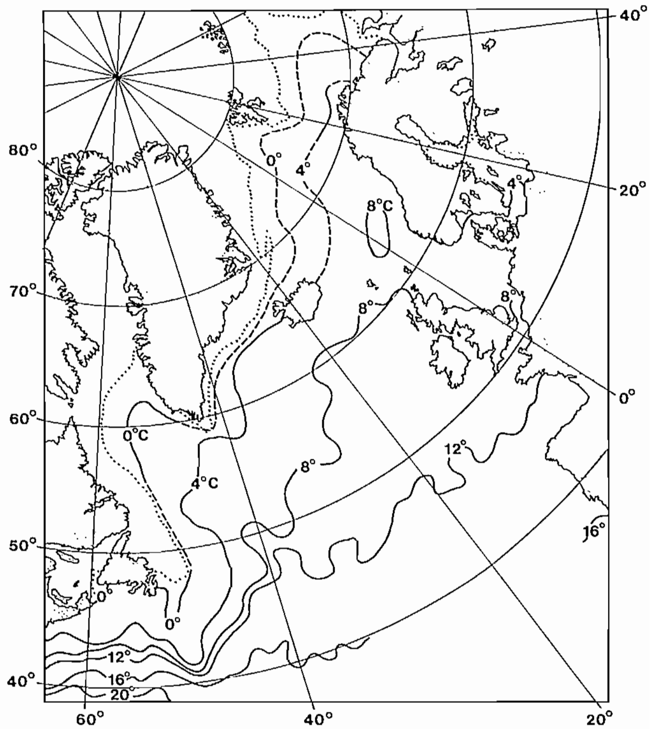


FIG. 97. Surface sea temperatures in the north Atlantic in January (from Anon. U.K., 1974). Dotted line is ice edge.

around Newfoundland and in the Gulf of St. Lawrence (49°–53°N) in May–July but in northernmost Norway (70°30′N) in February–March.

The settlers in northeastern Newfoundland and the marine coasts of Quebec in the late eighteenth century had no way of passing the winter (December–May) productively since ice blocked fishing, and so spent it in idleness, enlivened with feasting and merriment, as far as their meagre resources allowed. They then discovered the seals close to their shores, and exploited them with the methods I have described in Ch. VII, including boats which gradually increased in size and range. They thereby found a resource which occupied their winters and increased their incomes. Now that the seal trade has declined, the winter is again a period of idleness.

It is possible, but not very probable, that industry will come to these areas. Some (e.g. the north shore of Quebec) have abundant potential hydroelectric power, others (including Newfoundland and the Magdalen Islands) do not. An ice season works against cheap and efficient winter shipping, although northern Newfoundland now has a good road system. Offshore oil seems likely to benefit first the Avalon Peninsula which can supply an ice-free oil patch such as the northern Grand Bank where lies Hibernia, its first potential oil field.

I conclude that the ice-dogged areas will not gain much industry; economically they will need the seal fishery for a long time to come. Human populations in these areas have about doubled in the period 1950 to 1980, as elsewhere in Atlantic Canada. Unemployment in Newfoundland is about 20%, well above the national average, currently near 10%.

It is not yet possible to see how the sealing industry can be rehabilitated, except to be fairly certain that the market for whitecoat fur will not reappear. I have argued (Ch. IX) that in the past, hunting for young seals has proved the most long-lived of the varied approaches to seal hunting, and that comparison with the hunting of other large mammals, as well as experience, supports the idea that this is the most rational type of exploitation. We are therefore left with the possibility of exploitation of beaters, animals aged from 1 month to 1 year. The addition of perhaps 20% of bedlamers and adult males is not excluded, but the catch of adult females should be minimised. This mix should give the largest sustainable yield, and if the value of the furs is about equal at all ages (which has been the case) it will give also the greatest value. Such a mix, for instance, allows the take of bedlamers in February and March, and young seals in April, at Newfoundland, a 3 month season. Labrador takes beaters in May; West Greenland from June through December. The Magdalen Islands and North Shore also gain an early spring catch from small vessels. Net fisheries are more destructive but might be permitted for certain communities on Labrador and the North Shore of Quebec which can earn a concentrated income from a relatively small catch.

The criterion of humane killing is also important. Beaters can be clubbed or taken with rifles at short range on the ice, leaving few wounded. The older the seal, the more wary it becomes and so the more readily it enters the water. Many animals shot will then be wounded. Concentrating on beaters is more humane.

At its highest point, what was the industry worth to the fishermen? And how many men were involved?

Production, Yield and Value

Let us assume a sustainable yield in the northwest Atlantic of about 230 000 young seals and an annual market for their pelts of 180 000 fast-furred whitecoats and 50 000 beaters. The respective weights of these animals are 16 and 30 kg. If the value of each category of pelt is about $30 (Dunn 1977 for 1976 prices), then the value of a sustained catch of harp seals works out at $6.9 million to primary producers for a potential yield of seal, if fully-utilised, of 4.4 million kg. That is, the landed value of harp seals is about $1.6 per kg of body weight.

Dunn (1977) provided the first economic analysis for the modern Canadian seal fishery. The structure of the industry changed little after this time. An updated estimate of value of this fishery in 1979 (Anon. Canada. 1980) was a landed value to fishermen of $5.3 million, plus a value to first stage processors of $4 million, or about $9.3 million in all. In 1982 the first stage value was estimated at $3.2 million (less government costs of research, surveillance, and management of ca. $0.7 million) (Anon. Canada. 1986), but by then it was already in decline. The only estimate of value to secondary processing in Norway is that of Scheffer (1970) who cites an estimate from G.C. Rieber and Co., the major fur dresser of seal skins, of $5 million annually for dressed furs and oil, which must include receipts from all harp and hooded seals stocks since their pelts can scarcely be separated as to source. This figure must have increased later due to higher prices even though the total yield decreased after that date.

Traditional products of harp seals were fur and leather, oil and meat. The boycott of whitecoat furs in Europe since 1985 has forced a re-evaluation of the hunt for lack of markets. Leather, including the slipper trade with fur on, results in some very beautiful products when good designs are used. This allows marketing of leather with fur on from beaters and older animals in Europe. However U.S. law, under the *Marine Mammal Act*, has since 1972 prevented the importation of juvenile seals under the age of 8 months: a law designed to allow importation of juvenile pelts, e.g. of South African fur seals for the company processing the Alaskan fur seals, but to prohibit the import of juvenile hair seals, which grow much faster. Thus Canadian producers cannot export to the USA products made from beater harp seals and silver jar seals (juvenile ringed seals).

Seal oil still presumably retains its value, subject to market fluctuations affecting price.

Meat has not previously been used more than locally, although there has been considerable trade in it within Newfoundland since the development of a road system as far as the Great Northern Peninsula during the 1960's. The meat of whitecoats was never much used, only the flippers being taken (a delicacy in Newfoundland — see Appendix II) and some livers for cooking on board. The rest of the carcass is too small to be worth using. However, with beaters, far more meat is obtainable than with whitecoats.

A recent development in Norway has been the use of seal carcasses, added to fish wastes, as a source of protein for salmon and other fish aquaculture.

Thus, during a period of decline in use of whitecoat furs, we might see a utilization of beater and older pelts for fur or leather, with hair on or off, and oil and meat for human and animal consumption.

This kind of trend seems to be occurring. Statistics of catch for 1986 (the most recent available at time of writing in early 1990 — NAFO 1989) show a total catch in the Northwest Atlantic, excluding West Greenland, of 25 888 harp seals. All these were taken by Canada and far more by landsmen (77%) than by small vessels. Of the 21 738 young seals taken, 99.3% were classified as beaters, the remainder as ragged-jackets. Value of this catch is given in unpublished catch figures for Newfoundland (Anon. Canada. 1987) as about $15 per pelt or about $390,000 for the whole catch. Thus, the landed value had been reduced to about a tenth of its value a decade earlier.

Effort

Dunn (1977) gives effort for the year of his analysis, 1976, in eastern Canada and Anon. Canada (1980) updates this record for 1979 (Table 53). Effort was

TABLE 53. Participation in Canadian Seal Fishery (licenses issued), 1976 and 1979 (from Dunn 1977; Anon. 1980).

Area	Newfoundland–Labrador		Quebec		Nova Scotia		Total	
	1976	1979	1976	1979	1976	1979	1976	1979
Landsmen	7 819	10 274	1 767	2 817	78	63	8 649	13 154
Small vessels	199	—	2	—	2	—	203	231
Large vessels	4	—	—	—	3	—	7	9

divided into landsmen, operators of small vessels 35 to 65 ft (10–20 m) in length, and operators of large vessels, exceeding 65 ft. Table 53 shows the numbers of men in each category, totalling some 10 000 in all. By far the greatest number of men worked as landsmen, but only for short periods — 6 wk on average, and those who took out licenses might not use them since the arrival of seals at any locality is unpredictable. Thus, the rate of participation was only 56% in 1976, and lower for the Magdalen Islanders than for Newfoundland because the arrival of seals at the Magdalen Is. is particularly chancy. A feature of the 1970's was the revival of a small ship fishery. Longliners used in summer for the cod fishery filled this role, especially in northeast Newfoundland (Table 53) and had a crew of about 5 (3–10) men; large vessels were at the same time crewed by 27 men on average. Dunn showed that the revenue per pelt landed was about the same for small and large vessels. Although the large vessels could get to the seals more easily, their use for the rest of the year might not be so profitable. Landsmen on the other hand had a low rate of returns. All methods of hunting probably have their place. Table 53 shows that all three showed increased participation between 1976 and 1979, probably because the economy had shown a downturn in ways of making a living other than fishing during this period. We might have expected a continued pressure on the seals, as on other fishery resources. Yet it was good management since 1972 which allowed this diversity of hunting; from the late 1940's to 1972, the seal fishery from small craft did not exist, since there was no guaranteed escapement of young seals from the large vessels, nor of bedlamers in subsequent years, which would have allowed its existence.

Figure 98 shows where this effort came from in one year, 1966. It is based on tag recoveries. Since the finder of the tag was asked to indicate whether or not he took the tag when on board a ship, the figure shows the distribution of sealers between communities which took seals locally, and those which sent men to sea on large sealing ships. In ice-bound areas men hunted locally; in areas with open water (in March) they went on board sealing ships. After the quota of 1972, there were fewer large ships, and more men hunted locally in boats up to the size of long-liners.

During this period Bowen (1979) and Bowen and Sergeant (1983) reported on sampling of sealing communities in Newfoundland in order to assess retention of

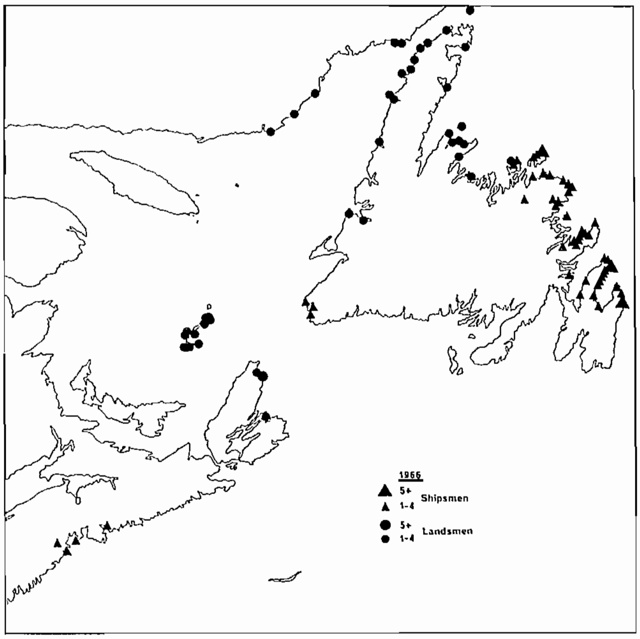


FIG. 98. Distribution of men between communities catching seals locally and those sending men on large vessels, from tag returns in 1966. Numbers of returned tags shown.

tags by sealers. These were sampled from among the majority of Newfoundland sealing communities. They extended from Bonavista Bay northwards in high density through Notre Dame Bay and at the northeast end of the Great Northern Peninsula, and south to Bonne Bay on the west coast.

There are no figures for seal-catching effort in arctic Canada but since virtually all Inuit (and few Indians) catch seals, and the Inuit in arctic Canada now number some 20 000 (16 000 in the Northwest Territories in 1981) (Anon. Canada. 1984 with additions for arctic Quebec and Labrador), the number of full-time or part-time hunters can scarcely exceed 5 000. In Greenland the number of full-time hunters is given by the Greenland Department (Anon. Denmark. 1986) as 2 500 "where hunting is the only or most important source of income". This is a small proportion of the 53 406 people in Greenland, estimated as of January 1986, but the larger southwestern settlements now all depend for their economy on fishing, and there hunting is now a part-time, leisure pursuit. In arctic Canada no fishing except for arctic char and lake trout (*Salvelinus alpinus* and *S. namaycush*) is possible on a commercial scale.[24]

In sum, the number of potential seal hunters in the northwest Atlantic is some 17 500 to 20 000 men.

Harp Seals and Other Fisheries

a) Human Effects on Seals

Harp seals are a major potential competitor with man for primary fish resources, especially capelin and shrimp (*Pandalus borealis*) and to a lesser extent herring (ch. V). They probably take about as much capelin as the great whale species combined in the northwest Atlantic — an estimated 125 000 t, according to Winters and Carscadden (1978) or 500 000 t (Sergeant 1973a) at Newfoundland and west Greenland. Lavigne et al. (1985) using an energetic approach did not refine this estimate though they regarded my (1973a) estimate of 500 000 t of capelin as too high. Using their table 19.7, and assuming that harp seals of all ages eat 60% fish, of which 40% is capelin, I calculate that 2 million harp seals would eat 400 000 t of capelin per year. As we have seen, shortage of food developed for harp seals in the Gulf of St. Lawrence in 1978–80 during a major natural decline of capelin stocks. Humpback whales *Megaptera novaeangliae* showed strong evidence of shortage of capelin as food at northeast Newfoundland in 1978–80 (Whitehead 1986) and, among seabirds, puffins *Fratercula arctica*, which feed their young on capelin close to shore at Newfoundland, failed to raise young in at least 1981 (but were successful in 1982–84) (Evans and Nettleship 1985).

A much more profound change occurred to capelin stocks in the Barents Sea in the 1970's–1980's due to heavy fishing by both Norway and the Soviet Union. Catches of capelin reached 2.64 × 10^6t in 1977 (Fig. 99) and the fishery was closed in 1986 after the estimate of remaining stock size was a mere 120 × 10^3t (Luka and Mukhin 1989). The reduction of capelin stock size reduced cod feeding and cod growth in the Barents Sea in 1986 (Mehl 1989).

As discussed above (p. 59–60) the White Sea herd of harp seals was the main source for the big invasion along the Norwegian coast in 1987, and it seems very likely that a marked reduction of capelin stock size in the Barents Sea after very heavy catching (Fig. 99) played a strong role in both the westward movement of young seals in the late 1970's to Finmark and the big invasion itself, as well as an early approach to the seal population's asymptote (Fig. 94). If this explanation is correct, we have one of the most clear-cut examples to date of the effect of exploitation of a low-level trophic resource upon the level of asymptotic population and the migratory behaviour of a higher trophic level marine carnivore.

However, it is necessary to explain the comparable invation of 1902–03 which occurred before heavy exploitation had taken place on any fisheries resource in the Barents Sea, whether capelin, cod, or harp seals. Could there have been a natural failure of capelin spawning in this cold period? It seems likely. Tønnessen and Johnsen (1982) in their history of north Norwegian whaling record that "fishing in the Varanger area failed disastrously in 1901–3. . . . At the same time seals in inexplicably large numbers descended on this coast, wreaking havoc on the fishing grounds". (There has always been a tendency to see the sea mammals as cause of fishing failure, rather than as a predator species disrupted, like the cod, by absence of their prey fish.)

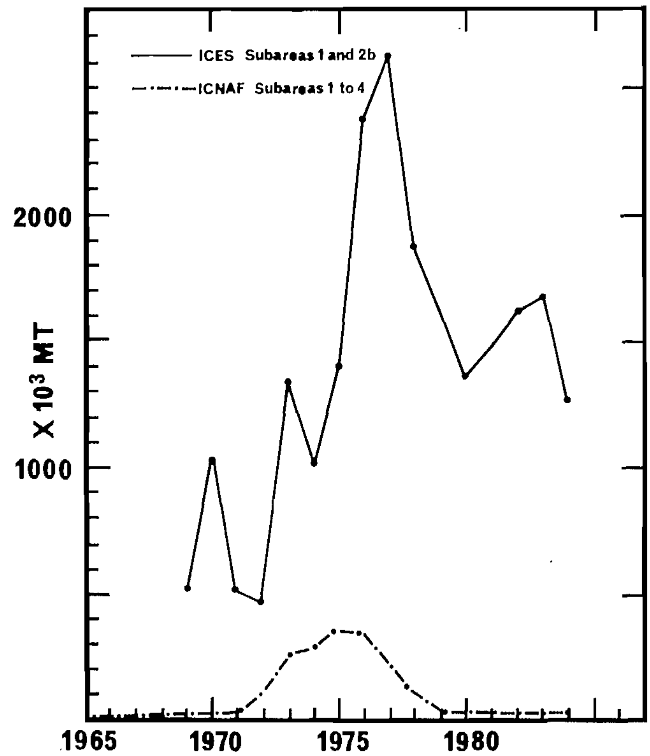


FIG. 99. Nominal catches of capelin *Mallotus villosus)* in the Barents Sea and at Spitsbergen/Bear I. (ICES subareas 1 and 26) and in the northwest Atlantic (ICNAF subareas 1 to 4) compared (from ICES and NAFO catch statistics 1984).

b) The Seals' Effects on Humans

Capelin now provide a relatively minor fishery at Newfoundland, the catch having been controlled since 1978. [Catch figures for 1986 were about 84 000 t, all taken in NAFO sub-areas 2J south to 3PS (Fig. 7) and practically all by Canadian fishermen. (NAFO 1989)]. Harp seals are not therefore likely to be perceived as a competitor with man for this resource in Canada. Shrimp (*Pandalus borealis*) is fished relatively intensely and it is possible that harp seals could be perceived as a competitor for this resource. However, in general harp seals hunt low on the food chain and also during the ice season when human fisheries are halted, and their perceived competition with man should be slight. Yet fishermen do not readily separate one species of seal from another, and

[24] In recent years Greenland halibut *Reinhardtius hippoglossoides* has been fished by handline through the ice of Cumberland Sound for the gourmet trade.

perceived interactions of mankind with grey seals, which include predation of fish in nets and the codworm parasite (see below) will always result in some blame being attributed to harp seals. In Norway, the seal invasions have proved very costly to the fishermen in destroyed gear and the government in these years annually paid several million dollars equivalent of compensation to them for entrapped seals. Since at least 1988 up to 10 000 harp seals have been entrapped in fishing gear at Newfoundland (Lien et al. 1988). However at Newfoundland a residual harp seal fishery remains and possibly these animals are utilised. Moreover, a government subsidy for seal pelts (ca $15.00 per pelt) remains, so that the net result is not unlike that in Norway.

Codworm

The effect of harp seals on man that remains to be considered is the importance of harp seals as vectors of the cod- or sealworm *Pseudoterranova* (*Porrocaecum*) *decipiens*. This is a parasitic nematode for which seals are the final host. The adult worm, found in the stomach and intestinal tract of seals, sheds eggs to the sea. The course of the early life history of the parasite is not clearly known (Scott 1955) but the primary hosts may be mysid (Myers 1960; Scott and Black 1960), or isopod (Bjørge 1979) Crustacea. The older larval nematodes encyst in the muscles of fish of various species such as rainbow smelts (*Osmerus mordax*). Larger fish such as cod may eat the smelts (Scott 1954), or perhaps infected invertebrates, and the larvae encyst or re-encyst in the muscles of the cod. Such wormy cod, although no health hazard to man, because the life cycle does not go to completion in man, are a nuisance to the fish trade and the worms must be removed from the fillets by expensive candling at light tables. This process costs the eastern Canadian fishing industry several million dollars annually and the price of wormy cod to fishermen is reduced.

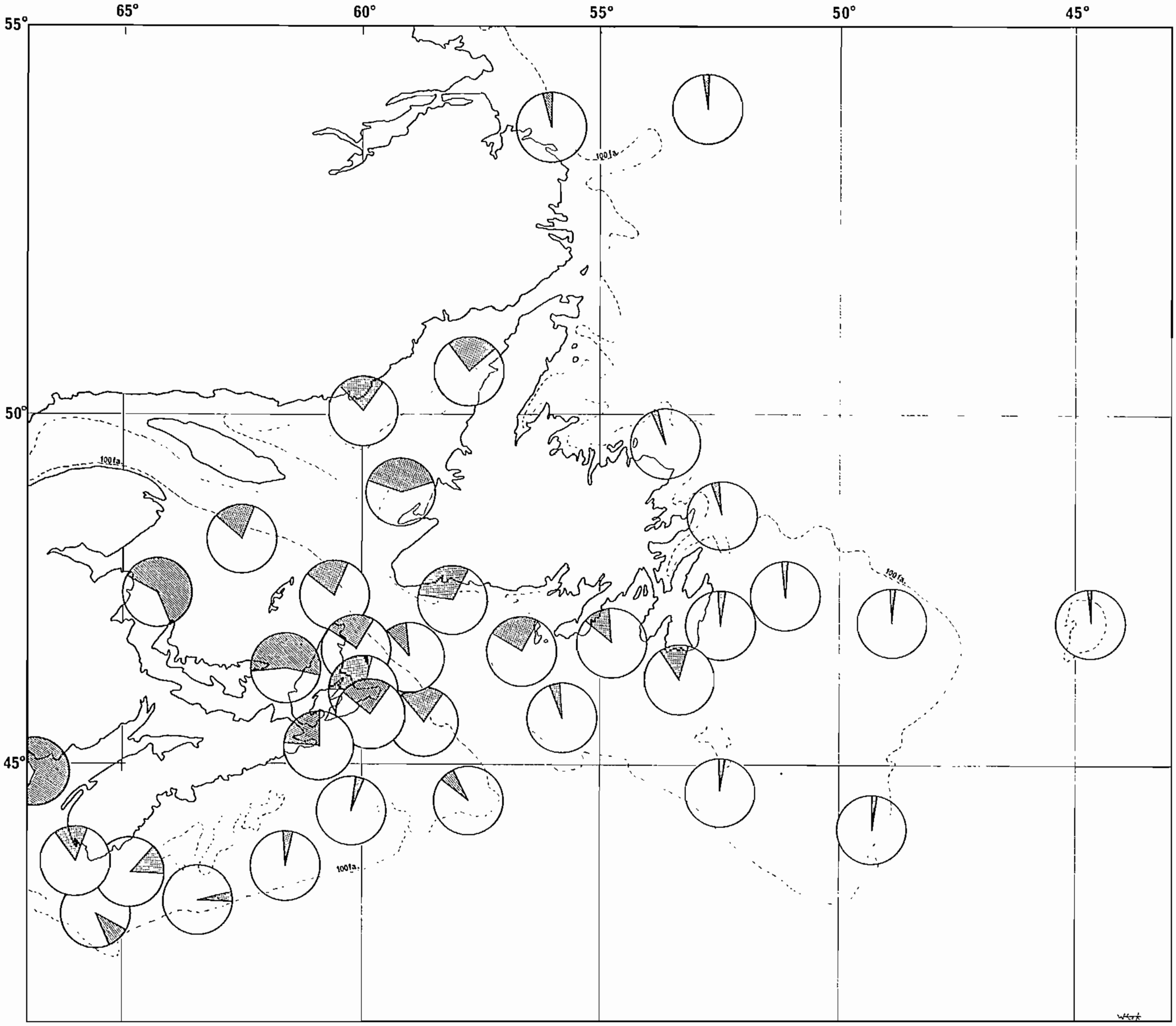


FIG. 100. Percentage of cod fillets containing sealworm parasite *(Pseudoterranova decipiens)* in the 1950's. Data taken from Templeman et al. (1957) and Scott and Martin (1957, 1959).

The distribution of codworm in eastern Canadian waters follows a pattern of highest infection of cod (and some flatfish species) in the enclosed waters of the Gulf of St. Lawrence, especially its southern coasts, around Cape Breton Island and on the southern Newfoundland coast and in offshore waters of the Nova Scotia banks (Fig. 100, 101). This distribution agrees well with the distribution of harbour and grey seals, except that the infection rate in cod decreases northward toward Labrador where the harbour seal is still common, perhaps due to low sea temperatures or absence of another key species in the parasite's life history.

Since seals are virtually the only final hosts of codworm (Scott and Fisher 1958a, b), the parasite could theoretically be eliminated by eradication of all seals. Grey and harbour seals are heavily parasitised in parts of eastern Canada, particularly grey seals which reach a large size and so contain more worms (Scott and Fisher 1958a). The numbers of harbour seals were earlier controlled by a bounty and their numbers decreased (Boulva and McLaren 1979) after which the bounty was transferred to the grey seal. Adult and young grey seals were also culled at some whelping sites during the 1970's and 1980's. In spite of this the numbers of grey seals greatly increased from 1952 to 1985, to a current total of some 70 000 animals (Mansfield 1988).

Harp seals shelter a much lower number of codworm nematodes than these two species of seals, and do not contain the parasite at all where their food is capelin and Crustacea. However, in the southern Gulf of St. Lawrence, harp seals contain codworm and their numbers during the winter months are so large that they could, theoretically, be important transmitters of worm eggs. There is no agreed opinion about the real importance of harp seals as hosts, but the balance of opinion is that they are not major hosts, mainly because the incidence of worms in harp seal stomachs is low and short lived (mainly in April and May, around the Magdalen Is.), and because they have migrated north in the warmwater months when most infection of fish must occur. At the present time the grey seal is doubtless the most important vector. Codworm increased greatly in the 1970's–1980's on the Nova Scotian banks around Sable Island (McClelland et al. 1985) Fig. 101, where at the same time the number of grey seal pups increased about 20-fold from a few hundred to 6 000 (Mansfield and Beck 1977; Mansfield 1988).

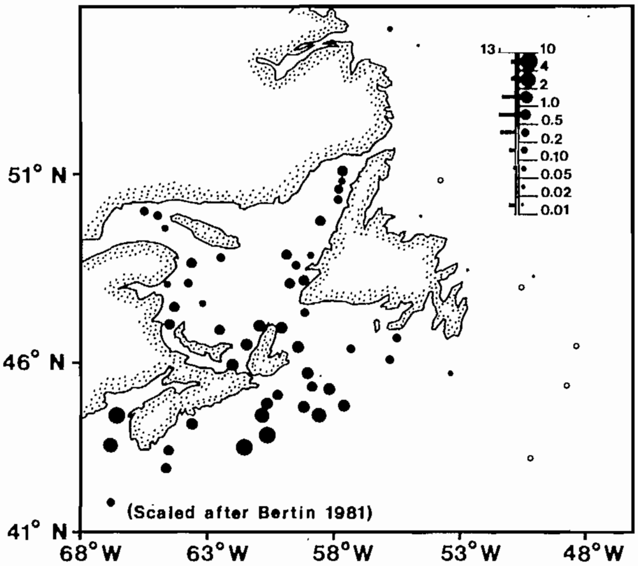


FIG. 101. Geographical distribution of sealworm *(Pseudoterranova decipiens)* in fillets of American plaice (*Hippoglossoides platessoides)* from McClelland et al. (1985). Diameters of symbols scaled after nematode abundances; frequency distribution of fish by nematode abundance also indicated on scale. Open circles — sealworm not detected. (The distribution in cod in 1980–84 was extremely similar but samples were fewer.) For comparison with the 1950's.

Harp seals do contain a lot of adults of another nematode in their stomachs, *Contracaecum osculatum*. This parasite is transmitted from fish such as capelin where it lives in the body cavity and does not become a nuisance to man.

Chapter XI. Pollution and Harp Seals

Summary

Severe fouling of a large number of young harp seals by Bunker "C" oil did not impair their immediate survival or migration, but later mortality probably increased.

DDT residues in the subcutaneous fat of seals increase with length of the seals' residence time in presumably contaminated coastal waters of eastern Canada, being higher in older than younger seals, and higher in resident east coast than in migratory species and lowest in arctic species. Harp seals are in the intermediate category.

Mercury levels were much higher in the livers of harbour, grey and hood seals than in those harp seals. All these other species eat fish and cephalopods higher in the food chain than the Crustacea and pelagic fish eaten by harp seals. Since the migratory hooded seals have as high mercury levels as the resident harbour and grey, the source of mercury is not local and presumably this marine mercury is of natural, not man-made, origin.

Oil Contamination

Ice conditions in the Gulf of St. Lawrence during early March of 1969 were abnormal in that drift ice was nearly confined to Northumberland Strait and the immediate coast of Prince Edward Island. Harp seals were forced to whelp close to shore or to move elsewhere (see p. 56.

On January 30, 1969 a valve on an oil tank ruptured in intense cold at Cape Tormentine, New Brunswick and 4 000 gallons of Bunker "C" oil escaped into the water of Northumberland Strait. This spill later resulted in the severe fouling of the skin and hair of a large number of harp seals.

Observations on the behaviour of the oiled seals were made from helicopters and on the ice by Fishery Officer S. Dudka. Mr. B. Beck of the Arctic Biological Station assisted by fishery officers, tagged 1 556 young harp seals around Prince Edward Island on March 19 and 21. These seals had not yet entered the water.

The following are extracts from Mr. Dudka's reports to the Regional Director, Department of Fisheries Halifax. Locations are shown in Fig. 54.

"The first indication of oil noticed was on or about March 9 off St. Chrysostom, P.E.I., when newly-(born) whitecoat seals were observed being covered with an oil-like substance after being scared into the water by our helicopters".

"On March 18 it was observed that two adult seals off Egmont Bay, P.E.I., had oil on them. On March 19 (at St. Peter's Bay) a pup was observed swimming and when he came back on the ice was observed saturated with oil. I killed him and took part of the pelt and turned it over to the District Protection Officer. . . for further examination".

"On March 25. . . we saw several pups that could not be identified, they looked like walrus. On further examination when we dropped down with our helicopter, a whitecoat scared into the water re-appeared in a few minutes. He was as if tarred and feathered and a thick khaki-like substance was on his pelt. Several of the whitecoats were like this. We surveyed for approximately four square miles and noticed that the ice was black underneath".

"The following day, some of these seals were examined and on their bodies we noticed that there was a sticky substance like glue or spruce gum. This was approximately twelve to fifteen miles north of St. Peters, P.E.I.".

"From about March 27 on. . . almost all the whitecoats were covered with oil. . .".

"On April 1st, flying from a fixed wing aircraft, the same body of seals were approximately five to fifteen miles south of Amherst Island, Magdalen Islands. The ice at this time appeared to be all black. All the seals, approximately 10,000 to 15,000 pups and adults, seemed to be covered with oil, and hardly identifiable as to species. The aircraft seemed to have no effect on them, they showed no fear".

"At no time was an oil slick noticed on the surface of the water. This oil-like substance was approximately one foot beneath the surface of the water, and unless one was there, one would never know that the oil. . . was present".

The location of the oil fouling is thus located as Northumberland Strait, with oily water, ice and seals drifting out therefrom.

Subsequently, large numbers of reports of contaminated young seals (Fig. 102) came from the northernmost part of the Gulf of St. Lawrence and Strait of Belle Isle.

Mr. H.V.E. Smith, Assistant Director of Fisheries for the Newfoundland region, Department of Fisheries, for instance wrote on May 20, 1969:

"In the Straits of Belle Isle. . . hundreds of seals, mostly young, were killed by hunters and seen on icefloes, completely coated with oil. Some of the young seals were so completely saturated that they would not leave the icefloes when approached. Flippers were stuck to the skin and reports indicated that the seals could not swim. There were a few reports of dead seals, but whether or not death resulted from the oil is difficult to say".

FIG. 102. An oiled, juvenile harp seal from western Newfoundland, April 1969 (photo by Fishery Officer).

Mr. R.E. Warner reported that some seals ingested some oil, which caused lesions in the stomach.

The seals in the northern Gulf can be shown to have come from the southern Gulf by two pieces of evidence. First, from the 1 556 young seals tagged in the southern area, tagged seals began to appear in the northern Gulf in April (Fig. 62). Many of these were fouled by oil. Secondly, samples of oil from seal skins taken in the Strait of Belle Isle were examined and analysed by Drs. P.M. Jangaard and R.G. Ackman of the Fisheries Research Board's Technological Laboratory, Halifax, Nova Scotia, and identified as "a thermally cracked petroleum product such as bunker fuel "C". (Memo by these authors to Dr. D.R. Idler dated May 15, 1969). There were no other known sites of oil release.

Of the 1 556 tagged seals, 264 or 17% were recovered in their first spring mostly by fishermen from small craft or alongshore. Most of these were taken in the period April 10 to 25 when the animals were 4–6 weeks old and had become fully moulted "beaters".

As we have seen (p. 38) the normal behaviour of young harp seals, born on the pack ice around the Magdalen Shallows, is first to drift passively towards or around Cape Breton Island, until this ice disintegrates, then to swim actively northward to the Strait of Belle Isle, where they haul up on the ice which usually blocks it at this time. When this ice in its turn melts, they pass northwards towards the summering grounds in West Greenland.

In 1969, very light ice conditions in the southern Gulf were probably responsible for the very few recoveries from Cape Breton Island and the Magdalen Islands, and heavy ice in the Strait of Belle Isle, for the great number from that region. Moreover, a number of animals, again including both oiled and unoiled animals, after clearing the Strait of Belle Isle drifted south again to the coasts of northeast Newfoundland (Fig. 62). This is quite normal behaviour, seen also in April 1968.

The migratory behaviour of the oiled seals was therefore normal. What is remarkable is that so many remained active although heavily contaminated, and as reported, scarcely able to move their flippers. Several factors would have allowed their long survival. Firstly, the young seal normally takes no food after weaning at the ice surface in mid-March until some date early in April, therefore, any impairment of feeding was no immediate problem. Secondly, long before the time of weaning, the blubber layer has taken over the task of thermo-regulation from the skin (Davydov and Makarova 1965). Therefore, heavy contamination of the pelt when the weaned young first entered the water had little effect on its heat balance and did not cause emaciation due to starvation. Only if and when the oil fouling has been so severe that the young animal cannot feed, and exhausts its early fat layer; or if it ingests oil and is poisoned, would heavy mortality be likely to occur.

How many seals were born in the southern Gulf and how many of these became soiled? With such an estimate one might be able to estimate subsequent mortality from a reduced survival as deduced from tag recovery rates as compared with previous years.

On March 20, a careful survey by Fishery Officer Dudka and Mr. B. Beck, at six previous whelping sites in Northumberland Strait and the north side of Prince Edward Island, gave an estimate of 6 600 surviving young following a quota fishery (reduced in 1969 because of the abnormally thin ice conditions) of 32 000. An estimated 6 000 of these young were located on the north side of Prince Edward Island, major catching activity having been in Northumberland Strait.

The recorded catch of beaters from the Gulf of St. Lawrence in 1969 was 7 258. This means that, either the production estimate above was a gross underestimate, or that other whelping took place further north in the Gulf from which the catching partly came. Since secondary whelping often takes place in the northern Gulf, the second seems more likely.

The two major processors of pelts responded to enquiries addressed to them about the number of oil-fouled pelts received. These totalled about 2 000 lightly or heavily fouled. They reported that many additional heavily fouled pelts were discarded by fishermen and not marketed at all. Claimants of tag rewards from 38 or 15% of 259 tagged young seals, reporting directly, spoke of pelts fouled with oil. This is certainly an underestimate since some claimants would not have troubled to mention it. The estimate of fouled pelts was therefore in the region of 30% of animals escaping from the southern Gulf, or 27% of all beaters taken.

In order to estimate subsequent mortality of oiled escapees from the hunt in the northern Gulf and Strait of Belle Isle, I compare subsequent recoveries of seals tagged in the Gulf in 1969 with those in 1966 and 1968 (Table 54). In the 1960's, metal tags were used and were attached through the tail of the seal pup. There had been a change of tag type in 1969, and recaptures show the

TABLE 54. Recovery rates of young seals tagged in the Gulf. In 1969 they were subject to oiling.

Year of Tagging	Type of tags	Escapement after first spring[a]	Recaptures second spring	Kill of 1 yr animals	Recovery rate (%)	
					Direct	Adjusted up
1966	Disc	1 229	30	56 606	2.4	2.4
1968	Disc	1 123	30	55 472	2.6	2.6
1969	Small strap	1 283	17	40 064	1.3	1.9

[a]Number tagged less known recaptures.

TABLE 55. Pesticide residues (ppm) in seal blubber (from Holden 1969) R resident, M migratory and A arctic seals; and in harp seal milk (Cook and Baker 1969).

	Locality	Year	Species	Age	Sex	Dieldrin	DDE	TDE	DDT	No. Animals
R	Sable I.	1968	Grey	ad.	M	0.1	55.0	10.3	40.0	2
		1968	Grey	ad.	F	0.1	7.5	1.3	9.6	9
	Basque I.	1968	Grey	ad.	M, F	0.1	21.0	3.7	24.0	3
	Cabot Strait	1967	Grey	juv.	M	0.1	11.8	1.4	10.6	2
			Grey	juv.	F	0.1	3.4	0.5	3.7	2
	Sable I.	1968	Grey	pups	—	0.1	4.8	0.7	4.8	5
	Basque I.	1968	Grey	pups	—	0.1	5.5	0.5	5.2	2
	Sable I.	1968	Harbour	ad?	M	0.1	11.0	2.8	15.0	1
M	Magdalen Is.	1967	Harp	ad, pup	—	0.1	1.2	0.1	0.4	2
	Cabot Strait	1967	Harp	juv.	—	0.1	2.7	0.5	2.4	2
		1968	Hood	ad?	M, F	0.1	3.6	1.1	5.7	2
A	Baffin I.	1967	Ringed	ad?	M	0.1	1.3	0.3	1.7	3
				ad?	F	0.1	0.3	0.1	0.5	6
				juv.	—	0.1	0.3	0.1	0.4	2
						Rhothane				
	Magdalen Is.	1968	Harp (Milk)	ad.	F	0.1	0.5	—	0.6	1

1969 tags to have persisted much longer than the type used in 1968 or 1966 — up to 12 yr instead of 3 yr. Nevertheless, 1-yr return rates of tags were about 25% lower after 1969 than after 1966 and 1968, indicating a corresponding increase in mortality after weaning and early migration in 1969. However, this could have been in part due to other factors besides oiling, such as the small amount of whelping ice in 1969.

Organochlorines

Holden and Marsden (1967, and Holden 1969) studied the amounts of DDT and its derivatives (DDE, TDE) accumulated in the blubber (subcutaneous fat) of seals, from among other areas along the east and arctic coasts of Canada. Dieldrin was a very unimportant pesticide in this area, as compared with British coasts.

If the seals are arranged in order of time of residence in the Canadian east coast area (Table 55) it is easy to see that the resident species — grey and harbour seals — accumulate much residue in their blubber, the migratory species — harp and hood seals — smaller amounts, and the arctic ringed seals, the least pesticides. Probably, the metabolites in the resident species accumulate in a linear manner with age, but this analysis has not yet been done. Dr. A.W. Mansfield draws my attention to the fact that grey seals from offshore Sable Island accumulate as much pesticide as those closer to the mainland. These grey seals however travel a lot as young, frequently entering the Gulf of St. Lawrence. The expected chief source of contamination is the estuary of the Miramichi River, New Brunswick, frequented by grey seals in the summer months. Much DDT was sprayed over the watershed of the Miramichi in an attempt to control spruce budwrom and passed into the river killing aquatic insects and young salmon (Kerswill 1967). While dilution must have occurred in the estuary and Gulf of St. Lawrence, yet the seals must have picked up and concentrated the residues through the food chain of Crustacea or fish.

Addison et al. (1973) studied levels of DDT metabolites, PCB's and dieldrin in harp seals from the St. Lawrence estuary collected in 1971. Total DDT and metabolites ranged from 3.1 to 22.6 ppm, PCB's from 2 to 22 ppm, dieldrin from 0.1 to 0.3 ppm of blubber lipids. The first two increased with age. Addison, Brodie, Zinck and Sergeant (1984) analysed a second sample from the same source collected in 1982. In the 11-yr interval, DDT grouped levels declined considerably and PCB's slightly.

Mercury

More recently mercury has been shown to accumulate in the liver of seals (Armstrong and Sergeant 1973). The resident grey and harbour seals pick up more mercury than harp seals. However hooded seals pick up as much mercury as the resident species, in spite of their short residence time in the Gulf of St. Lawrence. Grey, harbour and hooded seals eat large fish species and cephalopods, harp seals — small fish and Crustacea, and mercury accumulated through the food chains upwards. Therefore, accumulation of mercury is correlated with the level in the food chain of the food eaten by the seals, and not with their residence time in waters close to industrial

Canada. Indeed it is highly unlikely that this mercury is of industrial origin, even though some has been released by industry in the Saguenay river extending into the St. Lawrence estuary (Loring 1975). Comparisons of mercury levels in harp seals from the St. Lawrence estuary in 1971 and again in 1979 showed no change (Sergeant 1980).

Clearly a pelagic species like the harp seal receives much less pollution from heavy metals and pesticides than a coastal resident seal. Even harp seals wintering for up to 6 months in the St. Lawrence estuary live in a region of intense upwelling and mixing with small volumes of freshwater of cold, oceanic water from depth (Dickie and Trites 1983).

Chapter XII. Prospect

Hunting

The great outcry that arose against hunting young harp seals, which began in 1964 and concluded in 1984 with the disappearance of the European markets, had 3 elements: (1) the affront to aesthetics provided by the killing of suckling whitecoats with a club (2) charges of the cruelty of clubbing and (3) charges of overkill of the seal population, the outcry being focussed on the western seal population. The second objection was overcome with the development of an improved club, and better care in bleeding and skinning. The third was overcome with the suite of protective regulations culminating in the 1972 quota. Even allowing for the slow marshalling of evidence on the effectiveness of protection, doubts on the third item have never been allayed, partly because the anti-sealing alliance aimed at total elimination of the hunt and partly because of the climate of the times, which saw all wild populations of animals as threatened by human expansion. At any rate, loss of the essential European market for furs crippled the hunt. The first objection remains, however, a fundamental emotional one against future taking of whitecoats. I conclude that any future hunt must be based on the category of beater (moulted) young or older animals. Any category older than beater, and some beaters too, have to be taken by shooting. Here there is loss due to wounding, when shot and wounded seals escape into the water, something that always occurred with the shooting of moulting seals (with a loss rate that depended on the skill of the marksmen). The beater category therefore remains the prime candidate for an acceptable hunt. Beaters can best be taken by small craft and longliners in February, April and May, as well as at Greenland from June to December.

There remains also the possibility of using the method developed in the White Sea (p. 92) where helicopters carrying platforms pick up loose-haired, nearly-weaned whitecoats and transport them to shore stations (enclosures) where they are allowed to moult, then killed as full beaters under controlled conditions. Use of such a pattern in Canada for cost reasons would require good prices for beater pelts, and rather short distances from site of enclosure to temporary site of the drifting patch, which at the Magdalen Is. usually begins at 30–50 miles (55–70 km) but can soon increase.

Tourism

Viewing the seals from helicopters began at the Magdalen Is. in 1974 and has more recently been carried out from Prince Edward Island. In 1989, about 700 people took helicopter rides to see or photograph harp seals at the Gulf ice fields. It employs some guides but the main benefit (as with all animal viewing) goes to the operators, the local hotels and motels and the airlines. There are few economies of scale since greater numbers of people require more helicopters. When hooded seals are included in the Gulf of St. Lawrence, the season lasts from March 1st to about 24th. Seals at the Front are too far from land for one to expect expansion of the trade beyond the Gulf. Standards and costs of equipping ships in Canada for passengers are high enough that helicopters will likely continue to be the mode of travel to the ice.

Envoi

For the integrity of the western population of harp seals, there are no immediate problems. The catching of capelin was controlled by the Canadian 200 mile fishing limit in 1978. About 100 000 t are now (1990) taken annually for local use, for meal and oil production, and for sale of the roe to Japan. This compares with about 360 000 t at the peak of the east European offshore fishery off northeast Newfoundland and on the Grand Bank in 1976 (NAFO, Statistical Bulletins) 26 (1976) and 33 (1983). Current low fuel oil prices (as I write in early 1990) have meant a virtual end to oil exploration in the arctic, and very little continuing offshore exploration at Newfoundland. However in the long term, the integrity of the seal population is most threatened by the prospect of repeated oil spills from deep oil drilling in Lancaster Sound or elsewhere in the eastern arctic, and from the carriage of oil through the Northwest Passage, because of the expected effects on the under-ice ecosystem leading to polar cod, and the direct fouling of seals by floating oil (Johnson 1983). In spring 1988, about 10 700 harp seals were taken as incidental catch in gill nets on the west coast of Newfoundland (Lien et al. 1988). While this is regrettable, doubtless some of the animals are used for meat or pelts. This level of catch is not likely to more than slow population increase of the seals.

The White Sea–Barents Sea harp seal population by contrast appears to have been affected seriously by heavy fishing on its capelin food base. Even when the capelin stock is restored, it may be that a certain level of hunting of harp seals in the Barents or White seas will be necessary to prevent the seals becoming at least an occasional and possibly frequent burden to the Norwegian coastal fishermen in winter. One would deduce this from the frequency of wintering of harp seals in the Varanger fjord in recent years of high seal population, and the 1903 seal invasion that occurred with a high seal population and cool climate.

In general, fishermen must receive an income from the seals or else the seals will be a burden to them. I do not believe that seal viewing can be widespread enough to give the necessary benefits, but that some seal hunting with the production of furs, leather, oil and meat will be needed as well, perhaps separated geographically from seal viewing.

Moreover, some revenues are needed to maintain the impetus and funding for further research — especially research on populations, which appears to be dying away at present. Future research needs to be better coordinated between the former sealing nations of the North

Atlantic — Canada, Denmark speaking for Greenland, Norway and the USSR. For instance, better knowledge about the relationships between the three major seal stocks needs simultaneous marking, coupled with observations at the ice 5 years later to detect marked females. The needed coordination can be carried out by international organisations of which sealing nations in the North Atlantic are members; the International Council for the Exploration of the Sea has recently shown initiative in this regard (ICES 1987).

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Appendix I. Details of Female Reproductive Rates, Gulf of St. Lawrence

Age (yr)	*n*	Immature	Pregnant	Mature non pregnant	Fraction mature
			1969–1971		
1		6			
2		4			
3		7			
4		2			
5		1			
6		1	1		0.50
7			1		1.00
8			1		
9					
10			3	1	
11			2		
12			1		
13			2		
14			1		
15+			2	1	
Total	37	21	14	2	
			1978		
1					
2		6			
3		5			
4		7			
5		2	2		0.5
6			2		1.0
7		1	1		
8			1		
9					
10					
11					
12					
13					
14					
15+					
Total	27	21	6		
			1979		
1		5			
2		9			
3		15			
4	11	9	2		0.18
5		3	3		0.50
6			2		1.00
7			5		
8			2		
9			2		
10			1		
11			1		
12			1		
13					
14			1		
15+			1		
Total	62	41	21		

Appendix I. *(Continued)*

Age (yr)	*n*	Immature	Pregnant	Mature non pregnant	Fraction mature
			1980		
1		4			
2		5			
3		19			
4		15			
5		9	2	3	0.36
6			12		1.00
7			8		
8			3		
9			1		
10			2		
11			2		
12			1	1	
13					
14			1		
15+			4		
Total	92	52	36	4	
			1981		
1		1			
2		10			
3		12			
4		11	2		0.15
5		8	18		0.69
6			7		1.00
7			8		
8		1	2		
9					
10			1		
11					
12			1		
13					
14			1		
15+			3		
Total	68	43	43		
			1982		
1		4			
2		6			
3		9			
4		10			
5		8	2		0.20
6		3	15		0.83
7			10		1.00
8			3		
9			4		
10			3		
11					
12					
13		1			
14					
15+				1	
Total	78	40	37	1	

Appendix I. *(Continued)*

Age (yr)	*n*	Immature	Pregnant	Mature non pregnant	Fraction mature
			1983		
1		5			
2		4			
3		1			
4					
5		2	5		0.71
6		1	10		0.91
7			9		1.00
8			10		
9			5		
10			2		
11			3		
12			1		
13		1			
14			1		
15+					
Total	62	16	46		
			1984		
1		3			
2		14			
3		4			
4		8	1		0.11
5		6	5		0.45
6		3	9		0.75
7		1	11	1	0.92
8			7		1.00
9		2	9		
10			4		
11		1	1	1	
12		1	2		
13			1		
14					
15+		2	3		
Total	100	45	53	2	
			1985		
1		3			
2		5			
3		14			
4		5	1		0.17
5		5	3		0.38
6		4	12		0.75
7		4	17		0.81
8		1	11		0.92
9			14		1.00
10		3	3		0.50
11			2		
12			4		
13		1	2		
14					
15+			3		
Total	116	44	72		

Appendix I. *(Continued)*

Age (yr)	*n*	Inmature	Pregnant	Mature non pregnant	Fraction mature
			1986		
1	4	4			
2	1	1			
3					
4	3	3			0.00
5					
6	3		3		1.00
7	5		5		
8					
9	2		2		
10					
11					
12					
13					
14			1		
15+					
Total	19	8	11		
			1987		
1	5	5			
2	19	19			
3	15	15			
4	4	4			
5	7	2	5		0.71
6	5	1	4		0.80
7	8		8		1.00
8	2		2		
9	7		7		
10					
11	2		2		
12	2		2		
13	1		1		
14	1		1		
15+					
Total	78	46	32		

Appendix II. Some Seal Recipes

These were given to the author on board M/V *Algerine* in the spring of 1953 by chief cook Leo Hurley, and I labelled them at the time "World Copyright" and "Top Secret". However, since the firm of Bowring Brothers Ltd. subsequently gave up sealing, it is felt that these recipes should be made more widely available. The large quantities sometimes specified reflect Mr. Hurley's experience in cooking for a sealing wardroom and should be scaled down as needed.

Seal Liver Pie
(for 25 persons)

7 lb liver from young harp or hood or bedlamer harp
1 lb onions
½ lb minced hambutt pork
½ oz savory
pepper and salt to taste
Ingredients for plain pastry:
  ca 3 lb flour
  1 lb shortening or butter
  ½ tsp. salt
Mince liver coarsely and mix all other ingredients.
For gravy, fry small piece of liver and onion.

Seal Sausage

9½ lb choice seal meat
½ lb fatback pork or ham
1 lb onions

Stuffing

  2 oz savory
  ¼ oz mixed spice
  2 lb meat seasoning
  4 lb soaked bread
  ½ oz pepper
  ½ oz salt
  1 ptg. (½ oz) gelatine

Mince the meat with pork and onions. Add water for right consistency to stuff. To stuff, use small sausage skins (keep these in pickle till ready to use).
For stuffing, use gadget drawn (Fig. 103) or some such.
Tie between sausages with gut.

Seal Pudding

As above, but no meat seasoning nor spice, and:
  4 lb meat
  4 lb bread, soaked
  1 lb flour
  Parboil seal meat
  Dice pork and meat, chop onions
  Stuff ingredients in cloth bag very tightly and boil for 3½ hours.

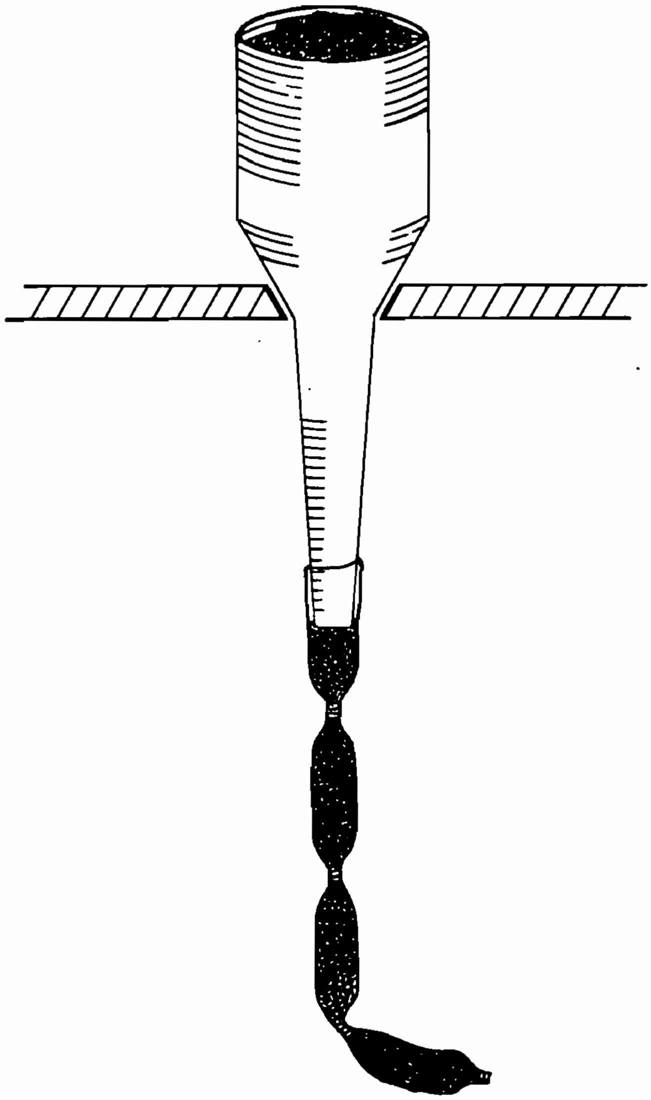

FIG. 103. Sausage stuffer, Mark I.

Seal Flipper Pie
1 Pie — 2 flippers

One person will eat 1/2 to 1 flipper. Flipper may be gamy, but is best coming from the ice (when it may be pale) or from refrigeration, or using the uncut flipper left attached to the pelt [in Newfoundland sealing usage — author]. Young harp flippers are best, and young hood or bedlamer harp flippers are good. The latter are a little larger.
  Clean off all the fat, soak in vinegar and water.
  Add onion, fatback pork, pepper and salt.
  Bake in over for 20 minutes at 375° F.
  Put on pastry. Bake again for 15-20 minutes.
Serve with mixed vegetables as desired.

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