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The Ice Lover: Biology of the Harp Seal (*Phoca groenlandica*)

K. Ronald and J. L. Dougan

The exploitation of other animals by man has often proceeded undeterred by any knowledge of the exploited species' biology and ecology. Biological investigations now provide us with a more rational base for the exploitative and nonexploitative use of some species. In the case of certain marine species, it is now recognized that modification of certain environmental conditions affecting their habitat may also have a direct effect on ourselves. In this article we review the biology of one such species, the harp seal (*Phoca groenlandica*).

Migration of the Harp Seal

In the late summer, a slow gathering together and movement of harp seals begins in the high Arctic. The summering grounds are abandoned to the slowly encroaching Arctic ice, as the seals move south toward winter or spring breeding grounds. Estimates provided by the scientific community during the

last decade suggest a world population of some 2.25 million to 3 million harp seals, divided among three separate breeding stocks (Fig. 1). In the Northeast Atlantic, 500,000 (1) to 800,000 (2) harp seals arrive each year in the White Sea (the East Ice) to breed and an estimated 100,000 to 150,000 (3) gather annually at breeding grounds in the Greenland Sea (the West Ice) between Jan Mayen and Svalbard. The harp seals in the Northwest Atlantic combine to form the largest stock, estimated variously to include fewer than 1 million (4) to 1.57 million (3) seals aged 1 year and older, producing some 250,000 (5) (1977 estimate) to 400,000 pups annually. Recent information suggests that these estimates may be somewhat low.

The differences between the estimates are associated with the lack of a solid data base. Critical to the attainment of a data base are accurate values for natural mortality rates and reproductive potential. Because estimates of natural mortality have varied (for animals 1 year and

older, from 8 to 14 percent per year) a compromise figure of 10 percent now is being used (6). This will require further substantiation either by tagging and recapturing methods or by aerial censusing techniques. Attempts are currently being made to evaluate reproductive rates by studying seals killed by hunters and calculating percentages of successful fertilizations and subsequent implantations. Other variables are also integral in accurate population determination, such as density-dependent changes in maturation rates. As the scientific activity supporting the management strategies for the seal herds continues to increase, so presumably will the availability of more precise data on which to base population estimates.

Most of the Northwest Atlantic harp seals congregate to breed on the ice off the east coast of Newfoundland-Labrador (the Front). The remainder, the Gulf herd, gather to whelp near the Magdalen Islands in the Gulf of St. Lawrence. The genetic similarity between the harp seals at the Front and at the Gulf suggests that interbreeding occurs between these groups (7), and management in the Northwest Atlantic is currently based on the existence of one interbreeding stock. There is some suggestion, however, based on analyses of biocide residues in seal carcasses, that two units may exist, separated at least with regard to feeding habits (8, 9). Certainty as to whether

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there is one stock or two (and if there is one, knowledge of the extent to which interbreeding occurs) is obviously vital to good management; for example, the effect of over-hunting in one breeding area will vary depending on whether or not there may be compensatory movement of animals from the other area.

In their full migration harp seals travel up to 5000 kilometers, and during all of this period they may be hunted. As they move south, migrating harp seals penetrate the waters of the Gulf and the Front between late November and early January. Females reach the breeding grounds at the Gulf by mid-February, at the Front by early March, and begin to move onto the ice (haul-out) before whelping. The formation of gregarious whelping "patches" continues for some 2 to 3 weeks. Should suitable ice be absent (as was the case in 1969 and 1981) the females appear to be able to delay parturition; however, the absence of ice platforms obviously does impose a burden on herd survival. Such natural catastrophes are doubly significant in a year during which hunters may have killed more than the total allowable catch (as in 1981, for example).

Growth and Development

The parturient female characteristically displays no behavioral changes as the time of delivery approaches. Birth is rapid on the drifting ice floes: deliveries lasting just 15 to 40 seconds have been observed (10). The umbilical cord usually breaks during or immediately after parturition (10). In three harp seal births observed in the wild by biologists, the placenta had not been expelled by 15 minutes postpartum (10), but discharge of the placenta has been estimated to occur within 30 minutes (11).

At birth the harp seal neonate must contend with extensive thermal shock. Thrust from a uterine temperature of +37°C into an air temperature of -15° to +5°C, often combined with high wind chill, the pup now lacks the ample insulative layer of subcutaneous blubber that will later develop, and its coat is damp, offering little insulation. The onset of shivering within 1 hour after birth is reported to allow the pup to retain body core temperature through rapid internal heat generation, and to dry its wet coat (12). The neonate apparently tolerates deep body core temperatures within a range of 35° to 41°C (13). The pup is likely to be able to maintain homeothermia in dry cold, but if rain and sleet

prevail it has been suggested that pup mortality rates may increase (12).

Visible shivering apparently ceases when the coat is dry, probably within 3 to 4 hours (12). Stores of glycogen and triglyceride in liver and skeletal muscle, low at birth, are further depleted. Until the pup can acquire total energy needs from food, it must generate body heat primarily through nonshivering thermogenesis, an aerobic process using mitochondria in thermogenic adipose tissue. Such tissue is found subcutaneously in a layer along the back, and internally around venous plexuses in the neck, on the pericardium, and on the kidneys and the abdominal walls. Use of the subcuta-

neous deposits continues for the first 3 days or so after birth, by the end of which time a blubber layer has formed (12) (Fig. 2).

male's apparent inability to recognize her offspring at a distance. Human handling of a pup does not appear to result in its subsequent rejection by the mother as long as this is neither prolonged nor repeated, and that the pup is not moved away from the immediate area. Knowledge of this kind is vital to an assessment of the effects of pup disturbance due to human encounters (for example, with tourists, biologists, conservationists) or during annual hunting (18).

Suckling commences within 2 hours after birth. The water content of harp seal milk decreases during lactation. The fat content is approximately 25 percent at the start of lactation and increases to

Summary. The number of harp seals, *Phoca groenlandica* (Erxleben 1777) may now range from 2.25 million to 3 million. The total population is divided among three separate breeding stocks in the White Sea, the Greenland Sea, and the Northwest Atlantic. The continued exploitation of the Northwest Atlantic stock has caused controversy, primarily because of public concern for the fate of the newborn "whitecoat." The harp seal's life-cycle is marked by a progression from on-ice birth to in-water mating and subsequent on-ice molt. An extensive migration follows, taking these animals northward to high Arctic summering grounds and southward in an autumnal return migration to the breeding grounds. Harp seals are efficient divers and possess well-developed microsensory perceptions associated with anatomical adaptation to their environment. The relation between our understanding of the basic biology of the species and the confrontation that occurs between these mammals and man is considered with respect to our technological invasion of the North, the regulated commercial kill, and the slow movement toward multispecies management. Sound decisions regarding the exploitation of this species can only be made with a knowledge of its biology.

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Solar heating may provide a needed source of external energy to the newborn harp seal, particularly during the first few days after birth. Significant amounts of solar radiation pass through the white lanugo coat of the neonate and are absorbed as heat (14-16). Pups appear to be able to alleviate hyperthermia by seeking shade or exposing their flippers (a major source of heat dissipation) to the air. Should these methods prove inadequate, thermoregulation can be achieved by entry into the water (13).

The pup is "nosed" by its mother shortly after birth, apparently to ensure its later identification. Pups sometimes approach females other than their mothers to be suckled, but are rejected (17). Observations at whelping patches indicate that harp seal cows use a combination of sound, sight, and smell at close range to locate their pups. Reliance on spatial memory is hampered by a constantly changing landscape and the fe-

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40 percent at the time of weaning (19); cow's milk, in comparison, contains some 5 percent fat (20). The pup gains about 2.5 kilograms per day during the nursing period (usually 9 days); most of this weight increase (1.9 kilograms per day) is in the blubber layer, the remainder is in the body core (21). The growth rate of the nursing pup appears to remain constant, despite the ingestion of increasingly fat-rich milk. It has been suggested that the frequency of suckling declines as lactation progresses, thereby leaving the total daily energy intake from milk constant (19).

In neonatal gray (*Halichoerus grypus*) and harbor (*Phoca vitulina*) seals, a notably large thyroid has been reported (22). Although harp seal pups face considerable thermal stress at birth, this calorigenic gland appeared relatively inactive in all but one of several neonatal and adult harp seals examined. Despite this, serum thyroxine and triiodothyronine concentrations were higher in neonates than adults. These hormones may be obtained in part from milk, and the high neonatal levels may be due to a new-

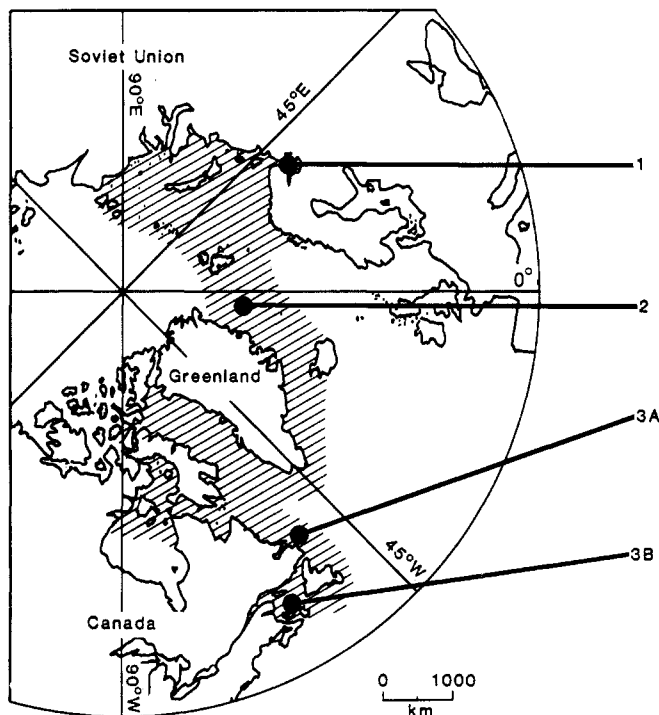


Fig. 1. The distribution and breeding grounds of the harp seal. The breeding stocks are located in 1, the White Sea; 2, the Greenland Sea; and 3, the Northwest Atlantic, where there is (A) the Front herd and (B) the Gulf herd.

born's need for increased growth and developmental hormones (23).

The pup may also ingest while suckling a percentage of the mother's total organochlorine load (9, 24). Mean total concentrations of 1.45 ± 1.21 milligrams of DDT per kilogram of body weight, and mean concentrations of 1.17 ± 0.82 milligrams of polychlorinated biphenyls (PCB's) per kilogram have been identified in the blubber of pups at the Gulf and at the Front (9). Seals accumulate these lipophilic substances by virtue of their position near the top of the food chain and their large blubber mass (9, 25). Although the organochlorine levels carried by harp seals are lower than those borne by some other pinniped species in Northwest Atlantic and European waters (26), ingestion of both DDT and PCB's in particular by Northwest Atlantic harp seals may be considerable, especially in the southern breeding grounds which are close to agricultural and industrial activities. Adult males at the Gulf carried mean total DDT concentrations of 10.2 ± 7.10 milligrams per kilogram and mean PCB concentrations of 8.21 ± 4.83 milligrams per kilogram (9).

During lactation, the female apparently eats little or not at all, relying largely on crucial energy stores acquired en route to the breeding grounds (27). The decreasing percentage of water in milk as lactation progresses may help her maintain internal water balance during the nursing period (19).

Pups are weaned in their second week. Abruptly cut off their source of energy-rich milk, they fast, and rely primarily on

accumulated energy stores. At the time of weaning a marked increase in total carbohydrate stores in the liver of harp seal pups has been observed, possibly resulting from the transformation of protein from muscle tissue into carbohydrates. Stored energy initially appears to be taken from the body core rather than from the sculp (subcutaneous skin and blubber layer). Large energy losses from the vital insulative sculp are thereby prevented, in preparation for the insulatory demands of the aquatic environment that the pup will soon be entering. During most of the fasting period, the pup may be viewed as a relatively lean animal surrounded by a vital and effective layer of insulation, rather than as an animal with fat reserves (28).

It is during this postweaning period that pups molt. The whitecoat of the newborn starts to loosen before weaning, revealing a darker coat beneath. A young harp seal at weaning has been described as a graycoat (21). Some 12 to 15 days after birth the shedding of loose hairs begins (21). During this stage, while their coats are molted in patches, pups are aptly known as "raggedy jackets." When this molt is completed, the pelage is light gray with dark patches. The pups are now called beaters, and their new coats will remain until molted the following spring. To the sealer, the intermediate raggedy-jacket pelt is of less value than the whitecoat or beater. The selective take of pelts at various developmental stages is part of the commercial hunt strategy to provide maximum profit.

Pups usually make no attempt to enter the water until the molt is completed. Beaters may then enter the water in search of food or as a means of cooling themselves, but they are often literally tipped in as the shifting ice breaks beneath them.

In captivity, 1-week-old harp seals have been force-fed with fish (29). In the wild, fully molted beaters may begin to feed at 4 weeks of age, but they are still reliant on internal energy stores. Once independent feeding is mastered, however, the beater will replenish depleted energy stores through a diet consisting largely of pelagic crustaceans (30). It has been suggested that management of harp seals should take into consideration a possible increase in mortality rates among beaters at this time, when they endure the stresses inherent in weaning and molting and attempt to attain self-sufficiency in a new, aquatic environment (21).

Reproduction

Copulation seems most likely to occur during the latter half of March as lactation ends and the pups are weaned. The approach of the mating season is signaled by males congregating in the water adjacent to the females, who usually remain on the ice. The males now appear to engage in underwater displays involving vocalizations accompanied by streams of air bubbles and pawing movements with the fore-flippers (31). Males may haul-out and approach females on the ice; however, it appears that females attempt to repel on-land advances. Copulation usually takes place in the water (31).

Recordings have been made at the Gulf of up to 16 types of underwater harp seal calls (32). The peak number of high-frequency calls occurred during mid-March; a time apparently coinciding with maximum courtship behavior (33). Undisturbed, the animals vocalized throughout the day and night; however, the arrival of a vessel (such as an ice breaker) was followed by a marked decline in vocal activity, perhaps as the seals moved away from the area or modified their normal behavior. Phocids may only vocalize during the breeding season. A vessel coming within 2 kilometers emitted enough noise to effectively drown out the seals' calls, severely inhibiting communication. The continued infiltration of loud vessels into the waters adjacent to the whelping patches may place the future well-being of these animals in jeopardy. This noise may not

only cause altered behavior of the seals, but also, as a result of the seals' movement to unknown areas, lead to inaccurate population estimates on which subsequent management decisions may be made. The acoustic pollution may also interfere with a communication process essential to reproduction (34).

Adult females normally ovulate once a year, with ovulation occurring in alternate ovaries each breeding season. Ovulation and copulation occur each spring but implantation of the fertilized blastocyst is delayed about 2 to 3 months after the time of fertilization (35). The fetus then develops for about 8 months. A gestation period of approximately 11.5 months ensures that parturition, lactation, and copulation will all be accomplished during one season each year.

Between 1952 and the early 1970's, heavy commercial exploitation led to the decline of the Northwest Atlantic harp seal population by about 50 percent (36). The mean age of sexual maturity for female harp seals, which is thought to be density-dependent (37), declined from 6.2 years in 1952 to 4.5 years in 1979 (38). Female fertility rates are said to have increased from 85 to 94 percent during the same period (38). Although the Northwest Atlantic harp seal population is thought to have increased following the introduction of seal catch quotas in 1971, an increase in mean age at maturity is not yet apparent (38).

The Adult Harp Seal

Once the mating season has ended, the harp seals move to more northerly ice in preparation for the annual molt (Fig. 3), leaving the newly weaned pups at the breeding grounds. Harp seals group together in their thousands to molt, in denser aggregations than those formed previously for whelping and mating (30). Molting is believed to be a time of fasting; however, adult females apparently do eat after mating, "feeding heavily for some weeks" to replenish lost energy stores (30). Immature males (age 0 to 5 years) and adult males may arrive at the molting grounds before the arrival of the adult females (39).

During a molting period of approximately 2 weeks, the 1-year-old beaters shed their pelage and gain the spotted markings of bedlamers. Over successive annual molts, a faint harp outline will begin to appear among the bedlamer markings. This intermediate "spotted-harp" coat appears among males from 4 to 7 years of age (40) and is usually shed by age 8 to 9 years (35) to reveal the

mature pelage, that is, a dark harp pattern on a silver-gray undercoat. A few males become very dark prior to maturation and are called sooties. The females may occasionally keep their bedlamer coats until they are 14 years old and not shed their intermediate markings until age 20 years (40). Some females never acquire the mature coat, which is generally lighter in coloration in females than in males and may be broken or spotted in appearance (41).

After molting, harp seals leave the drifting Atlantic ice and move north along the east coast of Canada toward their Arctic summering grounds, spending the summer in the open water and

among the ice floes of the Eastern Canadian Arctic or along the west coast of Greenland (30, 39). Few young-of-the-year appear to summer in the waters of the Canadian Arctic archipelago. Recovery of tagged or branded harp seals indicates that most of the current year class migrate from the breeding grounds of the Northwest Atlantic toward the Southwest Greenland coast (39).

Each summer some 10,000 harp seals are taken in Canadian Arctic waters and off the West Greenland coast by aboriginal hunters. A significant and possibly equal number of seals are lost as a result of sinkage after they are wounded by hunters.



Fig. 2. A newborn harp seal. [Photograph courtesy of D. M. Lavigne]



Fig. 3. A group of adult harp seals on ice at the Gulf. [Photograph courtesy of W. King]

Thermoregulation, Energetics, and the Pursuit of Prey

Harp seals are believed to feed opportunistically and at several trophic levels (42, 43). At the summer feeding grounds they apparently feed to a large extent on polar cod (*Boreogadus saida*). Toward the more southerly latitudes and at the breeding grounds, capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus*), and other pelagic fish and crustaceans are thought to form the mainstay of the diet (27). During the summer, the young-of-the-year apparently continue to feed on crustaceans.

As food is usually swallowed whole, taste is not believed to play a major role in its selection. Observation of feeding behavior, however, indicates that harp seals do discriminate between foodstuff in the mouth, accepting some but rejecting others (44). Food is digested quickly, which may allow rapid feeding during those times when abundant prey is available. Preliminary investigations with captive harp seals reveal that the efficiency of harp seal digestion may relate slightly more to frequency of feeding than to the total volume of food ingested (45).

The harp seal must seek its prey within the water. Although not usually considered to be a very deep diver, the harp seal will commonly submerge to the 100-meter level and dives to a depth of 250 meters have been reported (30). A major portion of the harp seal's metabolic energy is thought to be used for locomotion.

Studies of captive animals within an aquatic flume enabled estimates to be made of the extent of this energy loss. A 100-kilogram harp seal used approximately 0.42 calorie per gram per kilometer to swim 1.0 meters per second. This is within the range of estimates obtained previously by means of models or hydrodynamic analysis (0.34 to 0.46 calorie per gram per kilometer) (46).

In water, these aquatic mammals appear to have a wide thermoneutral zone, extending through at least 28°C. Within this range (1.8° to 28.2°C), water temperature does not seem to have any significant effect on body core temperature, diving pattern, or respiration. Thermal equilibrium is apparently maintained through controlled heat loss rather than by an increase in basal metabolic rate; in fact, the basal metabolic rate of these mammals is comparable to that of terrestrial mammals of similar size. In water, heat loss is seemingly governed by internal conduction rather than by external

convection (47). The young harp seal minimizes cooling of the central body core by warming the returning blood supply through venous plexuses, which are embedded in brown adipose tissue (48). This brown adipose tissue-venous plexus complex functions as a high-efficiency tubular heat exchanger which warms the venous return (49).

Adequate vision both above water and below, in light and in near-darkness, is of obvious importance to the seal or to any species moving actively at night and in two media. The harp seal is well-adapted to cope with the visual confines of its environment. It is believed to possess a duplex retina, shifting from cone to rod vision as light decreases and vice versa as greater illumination returns (50). The presence of both photoreceptor types within the harp seal retina has limited anatomical support (51); physiological investigations (including critical flicker frequency response, dark adaptation, and the presence of a Purkinje shift) are more conclusive (50).

In temperate and polar seas, the spectral region of greatest intensity is in the greener wavelengths, while in tropical oceans it is shifted toward the blue. Correspondingly, the rod visual pigment of the harp seal is more sensitive to green (50).

Other adaptations to underwater vision include a highly developed retinal reflective layer (tapetum lucidum); possession of a large spherical lens, much like that of the fish; and a rod-dominated retina (15). The spectral distribution of rod visual pigments tends to correlate with the underwater spectral distribution of radiant energy, theoretically allowing the harp seal to distinguish prey in the water, silhouetted against the surface light (50).

In dim light, in air, an inherent corneal astigmatism and large lens render the harp seal myopic. Pupil size varies with ambient light intensity, closing to a narrow vertical slit in bright light (52). This narrowing increases depth of focus and protects the retina to some extent from prolonged exposure to harsh light, such as the sun on ice and snow.

This, then, is the harp seal; a highly evolved species more than adequately equipped to cope with what to man is an inhospitable environment. Yet this is an environment man occupies and desires to overcome technologically. The challenges that increasing human activities may present to the future survival of the harp seal will probably be far greater than those presented to it by nature.

Management

Canadian management of the Northwest Atlantic harp seal embraces a policy permitting these animals to be taken each year for commercial purposes by licensed hunters in a regulated hunt. Fervent opposition to this annual hunt arises each year on both a national and an international scale, and is met by the equally fierce desire of the sealers to protect not only their livelihood but what they regard as their heritage, by ensuring the hunt's continuation.

Controversy in the media and from many environmental groups usually centers around the fate of the white-coated newborn, which possesses both undeniable emotional appeal and a valuable pelt. Each side continues in a bitter and emotional struggle. The media are the battleground, carefully selected "facts" are the weapons, and public support is the prize. The end result is a situation which is often difficult to view objectively, but the decisions made must owe more to reason than to passion if the species itself is not to become the ultimate loser.

It has been said that this species has been studied so much in the past few years that "more is known about Northwest Atlantic harp seals *Pagophilus groenlandicus* than about most exploited marine mammal stocks" (7). Over the past decade, there has been a gradual modification in the methods used by biologists to manage, protect, and conserve the stocks. In making decisions governing annual quotas, there is a movement (in theory, if not altogether in practice) away from the single species oriented concept of maximum sustainable yield toward a more holistic and multispecific approach. The latter view encompasses consideration of resulting risk to other species, and multifactorial impingements which may come to bear on the species in question from man and the environment.

The total allowable catch for harp seals is revised annually by the Canadian government on the basis of the best available population estimates of herd size and condition. With the use of ultraviolet light, white-coated pups previously indistinct in aerial surveys become dark and distinguishable silhouettes on the ice (14, 15). Although this method may be unreliable in adverse weather conditions, under good conditions it matches the tagging and recapturing technique in accuracy. Techniques for determining population sizes are therefore available, but these should be put to

use more regularly, for example, in the case of aerial surveys with ultraviolet light, as often as quadrennially. The last partial aerial survey was in 1977 (5).

Final consideration of the hunting of seals can be brought down to four basic concepts. (i) If we kill seals, do sufficient numbers survive to allow the population to remain stable or to increase? At present, it appears that sufficient numbers do survive; however, the vagaries of "paper seal" management are such that many safety factors must be cautiously applied to overcome the possibility of herd reduction. An increasing herd would probably regulate itself, long before it would offer competition to man for food resources. (ii) If we kill seals in a stable population, is it done humanely? In the Northwest Atlantic 170,000 highly evolved and aesthetically attractive animals are killed annually in an open-air commercial hunt. This is regarded by many as a massacre; others believe the killing methods to be humane—or no less humane than those used daily in slaughter houses. To those opposed to the hunt, is the continuation of both operations therefore equally reprehensible? (iii) If one kills seals from a stable population and as humanely as possible, how does one ensure that the resource is well used? At present, sealing brings a gross return of some \$5 million to Canada. Although some sealers may gain as much as \$3000 per season, others lose money. Recently, attempts have been made to bring the more profitable tertiary processing of pelts to the areas where the seals are killed. At present, Canada is distributing this resource to other countries for small return. (iv) One last concept concerns the emotional response evoked in humans by the killing of seals. If we were to classify animals according to the response each evoked and treat them accordingly, the seal would presumably be a worthy "type A" animal and hunting them would be prohibited. A cockroach, in contrast, would presumably be a "type Z" animal and could be ground under heel with impunity. The classification of species in this manner is, of course, biologically insupportable, and the seal hunt, which is based primar-

ily on the exploitative needs of man, will probably continue. Thus a sound biological base is essential to the proper management of this species.

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