RESTRICTED

International Commission for the Northwest Atlantic Fisheries

Serial No. 4011
(D.c.11)

ICNAF Res.Doc. 76/X/125

SPECIAL MEETING OF PANEL A (SEALS) - OCTOBER 1976

The Relationship between Harp Seals and Fish Populations

by

D. E. Sergeant
Environment Canada, Fisheries and Marine Service
Arctic Biological Station
Ste. Anne de Bellevue, Quebec, Canada H9X 3L6

Introduction

This subject has been dealt with exhaustively in a scientific paper (Sergeant, 1973) which is attached as an appendix. The main conclusions were as follows:

1) Harp seals have a very wide food spectrum which comprises especially small, pelagic fish and both pelagic and bottom-living crustaceans. The most important fish eaten in the northwest Atlantic is capelin.

2) Assuming a population of about one million harp seals in the northwest Atlantic, and from knowledge of the quantity of fish eaten by seals in aquaria, annual consumption of capelin was estimated as of the order of half a million metric tons. The major part of this is taken around Newfoundland, but some also at West Greenland. Much smaller quantities are taken of herring, probably because the harp seal lives for a very short period in herring country, and of groundfish.

This paper will deal with necessary revisions of the calculations given in the published paper, consequent on new data. It also gives some new data on foods eaten and reassesses the relation of harp seals and great whales on the one hand, and man on the other, as fish predators.

Critique of the earlier calculation

Boulva (MS, 1975) in an unpublished thesis has criticised the critical assumption of a daily consumption rate of 5% body weight daily. He had studied from the literature the feeding rate of seals in captivity and finds that seals in most aquaria are fed to obesity. He assumes a feeding rate of about 3.0% of body weight per day for an average harbour seal. This would reduce the estimated total consumption of capelin to about 300,000 tons annually.

Actually, Boulva's data shows a consumption of 4.9% of body weight daily for young seals through 3.2% for immatures to 2.6% for adults. This curve should be integrated with the life table to produce a realistic curve of age-specific consumption rates.

Winters (MS, 1975) has taken into account increased total biomass of the seals towards equilibrium population and decreased consumption per animal as such populations are attained, in order to estimate possible consumption by such equilibrium or asymptotic population. He obtains about a 50% increase in consumption between the present population of about one and a quarter million seals to three million.

New data on feeding

Probably by chance, new data has thrown importance on to shrimp *Pandalus borealis*. Fishery officer S. Dudka collected several adult females in the Gulf of St. Lawrence containing this shrimp. Kapel (MS, 1973) mentions the importance of shrimp as well as other crustacea in the stomachs of harp seals from West Greenland. Finally, stomachs of several beaters (0 group harp seals) and 1 year bedlamers taken on the northeast Newfoundland Shelf at 50°30' to 52°N, ca 53°30'W in early April, 1976 contained shrimp, identified as *P. borealis* with a few amphipods in some stomachs but no capelin (although the stomach of one adult female hooded seal taken in the same area contained capelin). Depths exceeded 180 m in the immediate area of capture. Thus, either the shrimp was taken off the bottom, or beaters can dive more deeply than previously supposed. E. J. Sandeman (in litt.) states that *P. borealis* lives at depths exceeding 100 m in this area, may rise off bottom, but does not enter water below about 2°C. The boundary of subzero and deeper warmer water on the N.E. Newfoundland Shelf is at about 100-200 m (Templeman, 1966). No such quantities of *P. borealis* have been found before, euphausiids being a more characteristic food component of beaters. Note however that a variety of decapod shrimps especially *P.*

montagui were the dominant food of harp seals taken at St. Anthony, Newfoundland close to shore in winter 1971 (Sergeant, 1973, Table 1, and p. 20-21).

Discussion

Evidence exists that harp seals in the Newfoundland area in the immediate post-war period (ca 1950) had levelled offin numbers at about 3-4 million. Moulting animals were in poor condition, with thin blubber and much scarring on the males (Sergeant, in press 1976). It is not clear whether population are limited by shortage of food, or by fighting, at such levels. Probably, both factors work together.

At present population levels, about one and a quarter million animals for the western herds, animals are fat and free of scarring at moult and are reproducing at maximal efficiency (Sergeant, MS 1976). This implies that growth is optimal which in turn implies no scarcity of food.

Should the catch of capelin be greatly increased, so that its biomass were significantly reduced, stocks of harp seals could become food-limited. Food limitations would affect harp seals during the winter, when feeding on capelin is heavy, and would likely show as a poor condition at the spring moult (as described above) at lower population levels than hitherto.

Since harp seals are being exploited at a high rate, and will probably within a few years be exploited at the rate of maximal (or optimal sustainable yield, it seems very unlikely that they will be regarded as a competitor of man for the capelin resource. Moreover, at Newfoundland, harp seals feed mainly inshore on capelin and the inshore capelin are not being fished at high levels as compared with the offshore stocks e.g. at the southeast shoal of the Grand Bank.

Winters (MS 1975) calculates the same order of magnitude of consumption of capelin by several species of the great whales (principally fin, minke and humpback whales) in the northwest Atlantic, and these species also consume a good deal of herring (Mitchell, 1975). They are present in good numbers in the northwest Atlantic and are not now being hunted. Their relationship with fishing fleets and shore fishermen merits detailed study. At present, we can discern some trends:

(1) Offshore fleets probably use the presence of whales as one indicator of the presence of capelin shoals.

(2) Many individuals of these three whales species approach the fishing fleets closely and apparently feed on disabled or dead capelin (and other fish) passing through the mesh.

(3) These and other species, most commonly the inshore-moving minke and humpbacks, become meshed in cod traps and other fixed gear and may die, or may pass through, causing damage which has been estimated at ca $250,000 at Newfoundland annually at present. Attempts are being made to reduce this damage by acoustic devices.

Summary

Harp seals are a major predator on capelin and polar cod, but not on herring. Other foods are mainly Crustacea, especially shrimp (including Pandalus borealis but many other species) and Amphipoda.

Consumption of capelin by the western harp seal stock in ICNAF subareas 1 to 4 is re-estimated at about 300,000 tons for the present population, perhaps 430,000 for MSY population. A roughly equivalent amount is estimated for the great whales. The great whales are currently reacting much more closely with man over capelin stocks than are harp seals. This is probably because the major fishing effort and the great whales are offshore, while the harp seals have an inshore distribution where little capelin is taken.

Acknowledgments

Dr. E. J. Sandeman identified the shrimps and gave information on their ecology. Dr. Peter Beamish and Mr. Tom Curran gave the author unpublished information on the behaviour of whales.

References

Boulva, J. MS 1975. The harbour seal, Phoca vitulina concolor in eastern Canada, Ph.D. Thesis, Dalhousie University, Halifax, 1973, 152 p., illus.

Kapel, F. O. MS 1973. Some second-hand reports on the food of harp seals in west Greenland waters. ICES Marine Mammals Committee CM 1973/N:8 Mimeo 7 p.

Mitchell, E. D. 1975. Trophic relationships and competition for food in northwest Atlantic whales. Proc. Can. Soc. Zool., June 2-5, 1974, pp. 123-132. M. D. B. Burt (Ed.), Dept. Biology, Univ. New Brunswick, Fredericton.

Sergeant, D. E. 1973. Feeding, growth and productivity of Northwest Atlantic harp seals (Pagophilus groenlandicus). J. Fish. Res. Board Can. 30: 17-29.

——————— 1976 (in press). History and present status of populations of harp and hooded seals. Biological Conservation.

——————— MS 1976. Studies on harp seals of the western north Atlantic population in 1976. ICNAF Document No. 76/X/124. Serial No. 4010.

Templeman, W. 1966. Marine resources of Newfoundland. Fish. Res. Bd. Canada Bull. 154: 170 p.

Winters, G. H. MS 1975. Review of capelin ecology and estimation of surplus yield from predator dynamics. ICNAF Res. Doc. 75/2, Serial No. 3430, Mimeo, 23 p.

Serial No. 4011
(D.c.11)

ICNAF Res.Doc. 76/X/125
APPENDIX

Feeding, Growth, and Productivity of Northwest Atlantic Harp Seals (*Pagophilus groenlandicus*)

D. E. SERGEANT

Fisheries Research Board of Canada
Arctic Biological Station, Ste. Anne de Bellevue, Que.

SERGEANT, D. E. 1973. Feeding, growth, and productivity of northwest Atlantic harp seals (*Pagophilus groenlandicus*). J. Fish. Res. Board Can. 30: 17–29.

The food of harp seals inhabiting the northwest Atlantic consists chiefly of pelagic fish, especially capelin, *Mallotus villosus*, and pelagic and benthic Crustacea (Euphausiacea, Mysidacea, Amphipoda, Decapoda), with smaller quantities of benthic fish. Feeding has been observed to take place on individual items by suction, and small fish are taken tail first. Feeding is intensive in winter and (by deduction) in summer, less intensive during spring and autumn migration, and in spring during whelping and moult. A weight loss in spring due chiefly to loss in thickness of subcutaneous fat (blubber) is most intensive in adult females as a result of lactation. This loss is made up slowly in summer. The preparturient females are partly segregated in midwinter on what may be the best feeding grounds. During lactation, and immediately following it when they are again segregated from other age-sex groups, adult females tend to feed on decapod Crustacea. In spring, the only time when all age classes are in the same geographic area, there is a stratification of feeding by size of organism and by depth, from chiefly Euphausiacea taken in surface waters by the weaned young, through capelin taken probably at intermediate depths by the immature animals, to herring, cod, and other groundfish taken by the moulting adults to depths of perhaps 150–200 m. Social feeding begins at about 1 year of age with the change from Crustacea to pelagic fish. From knowledge of the rate of feeding, body weights, and reproductive rates, the ecological efficiency of harp seals (i.e. weight of annual increment of population/weight of annual food eaten) is calculated at 0.005, a low figure. Annual weights of food items eaten by the northwest Atlantic population of harp seals are roughly estimated as: all organisms, 2×10^6 metric tons; capelin, 0.5×10^6 tons; and herring, 2×10^4 tons. Predation by harp seals on capelin stocks off eastern Canada occurs only during the winter months when pack ice is present as a resting substrate, the same resource being consumed in the summer months by the great whales (Balaenopteridae).

SERGEANT, D. E. 1973. Feeding, growth, and productivity of northwest Atlantic harp seals (*Pagophilus groenlandicus*). J. Fish. Res. Board Can. 30: 17–29.

La nourriture du phoque du Groenland dans le nord-ouest de l'Atlantique est constituée en majeure partie de poissons pélagiques, surtout le capelan, *Mallotus villosus*, de crustacés pélagiques et benthiques (Euphausiacea, Mysidacea, Amphipoda, Decapoda) et, en quantités moindres, de poissons benthiques. On a vu des phoques saisir des proies individuelles par succion. Les petits poissons sont attrappés la queue la première. Les phoques se nourrissent activement en hiver et aussi (par déduction) en été, à un degré moindre durant les migrations de printemps et d'automne, et durant la mise bas et la mue au printemps. La perte de poids au printemps, causée surtout par l'amincissement de la couche de graisse sous-cutanée, est la plus prononcée chez la femelle adulte, par suite de la lactation. La récupération a lieu lentement au cours de l'été. Il y a ségrégation partielle des femelles gravides avant la parturition à la fin de l'hiver sur ce qui peut être les meilleures aires d'alimentation. Durant la lactation et immédiatement après, alors qu'elles sont de nouveau séparées des mâles et des autres groupes d'âge, les femelles adultes se nourrissent surtout de crustacés décapodes. Au printemps, la seule saison à laquelle toutes les classes d'âge se trouvent dans une même aire, il y a stratification alimentaire selon la taille des proies et la profondeur: dominance d'euphausides capturés à la surface par les jeunes sevrés, capelan probablement mangé par les immatures à des profondeurs intermédiaires, et hareng, morue et autres poissons de fond capturés par les adultes en voie de mue à des profondeurs allant possiblement jusqu'à 150–200 m. L'alimentation sociale commence à l'âge d'un an environ, alors que les poissons pélagiques remplacent les crustacés dans le régime alimentaire. Connaissant le taux d'alimentation, le poids du corps et le taux de reproduction, nous pouvons calculer l'efficacité écologique de l'espèce (poids

Printed in Canada (J2613)

de la croissance annuelle de la population/poids de la nourriture consommée annuellement) et en arriver à une valeur de 0.005, qui est très basse. Le poids des proies consommées annuellement par la population de phoque du Groenland du nord-ouest de l'Atlantique est estimé comme suit: totalité des organismes 2 × 10^6 tonnes métriques, capelan 0.5 × 10^6 tonnes, hareng 2 × 10^4 tonnes. La prédation du phoque du Groenland sur les stocks de capelan de l'est du Canada ne se produit que durant les mois d'hiver, quand il y a des champs de glace solide où le phoque peut se reposer. Les grandes baleines (Balaenoptera) se nourrissent à même cette ressource en été.

Received July 19, 1972

THE population of harp seals inhabiting the western North Atlantic is well-defined morphometrically (Yablokov and Sergeant 1963), while tag recoveries (Sergeant 1965) also show that it is relatively isolated from other populations occurring to the eastward.

The range of the western population extends from the Gulf of St. Lawrence in the south to Smith Sound (77°N) in the north, and from Hudson Bay in the west to Kap Farvel, Greenland, in the east. The population is highly migratory. In summer (June–November) it inhabits mainly the coasts of Davis Strait and Baffin Bay, in winter (December–May) coasts and bordering ice fields of eastern Canada south of Cape Chidley, Labrador (Sergeant 1965). The young are born in early March in the wintering range and are independent about 3 weeks later. The adults and immatures shed their hair coat (moult) in the same region during April.

The foods eaten by harp seals of this population in their winter range have been described briefly by Fisher and Mackenzie (1955), Myers (1959), and, among other topics, by Khuzin (1963). Some attention was paid to the summer foods of these harp seals in west Greenland by Nansen (1925), Dunbar (1949), Vibe (1950), Hansen and Hermann (1953), and Freuchen and Salomonsen (1958). I have added the observations of these authors to new data collected over the period 1952–71 in order to analyze feeding patterns through the year and during growth of the animals. Observations both in aquaria and in nature throw some light on feeding behavior. Analyses of growth and amount of food taken allow a first estimate to be made of the total food intake of the population. Intra- and inter-specific feeding relations are then examined, including those presently occurring with man.

Material and Methods

Most harp seals taken in the water, whether by net, shooting, or hook and line, contain quantities of food remains.

By contrast animals taken on ice usually have empty stomachs. The latter have basked for some hours or days so that digestion is far advanced; only then, as a rule, are they dry and sleepy enough to be taken by stalking and shooting.

The most useful samples for food analysis are therefore of the first type. Our data of this kind are shown in Table 1, of the second kind in Table 2, both referring to seals taken in the wintering range. All available data from the summering range are shown in Table 3. Where two items were found in one stomach each was assigned a frequency of 0.5. No further quantification by volume was attempted.

For experiments in feeding, juvenile harp seals were captured at the icefields near the Magdalen Islands in midMarch 1971, at 2–3 weeks of age, and held in an enclosure, followed at ice-melt by an outdoor pool where they were fed herring and held till midMay. Feeding experiments were performed with isolated animals in plastic tanks at a disused oyster hatchery at Ellerslie, Prince Edward Island. Live, spawning rainbow smelts (*Osmerus mordax*) were captured in neighboring streams and live mysids *Mysis stenolepis* and shrimps *Crago septemspinosus* in the neighboring estuarine waters of Malpeque Bay.

Results

FOODS IN NATURE

Southward migrant seals in Labrador and the northern Gulf of St. Lawrence were sampled from netted catches. The animals were found to be feeding, sometimes lightly and sometimes heavily, on capelin (*Mallotus villosus*), euphausiid Crustacea, and herring.

Wintering animals in the Gulf of St. Lawrence were sampled over two seasons (January–April) near the confluence of the Saguenay River. These samples contained animals of all ages. The animals were shot in the water. Stomachs were nearly always well-filled, chiefly with capelin. Other pelagic fish, decapod and euphausiid Crutacea, and cephalopod Mollusca were occasional. The crustacean species, e.g. *Meganyctiphanes norvegica* and *Pasiphaea tarda*, suggested pelagic feeding.

Another winter sample (also January–April) was collected from the region of St. Anthony, Newfoundland. The animals were netted at coastal sites. Here the food was more variable, and decapod

TABLE 1. Frequency of different foods of harp seals (*Pagophilus groenlandicus*) on the Canadian east coast (seals taken in the water). Some earlier data from Fisher and Mackenzie (1955).

	Fish										Invertebrates									
	Capelin		Herring		Cod		Flatfish		Other		Decapods		Euphaus		Cephalop		Empty		Total	
Locality and date	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Southward migration																				
Nain, Labrador																				
Dec. 13, 1965	1																2		3	
La Tabatière 1950																	100		100	
1951																	100		100	
1952			2														38		40	
1965	6												6				–		12	
	7		2										6				240		255	
Wintering																				
Saguenay–St. Lawrence																				
Jan.–Apr. 1969	88	90.7							1.5[a]	1.5	0.5	0.5	1.5	1.5	0.5	0.5[b]	5	5.3	97	100.0
1971	81	85.2							1.0[c]	1.1	3.5	3.7	3.0	3.2	0.5	0.5[d]	6	6.3	95	100.0
St. Anthony, Nfld.																				
1971	6.5	5.2	1	0.8	1	0.8	1.5	1.2	4[e]	3.2	55	43.6					57	45.2	126	100.0
Twillingate, Nfld.																				
1952	1																		1	
Spring																				
Magdalen Islands[f] Mar.–May 1956			102	54.3	1	0.6	12	6.4	3	1.5[g]			2	1.1			68	36.1	188	100.0
Northward migration																				
Blanc Sablon																				
juv., June 1957	8																		8	
ad. & imm., Apr. 1953	1		12														91		104	

[a]Barracudina *Paralepis rissoi Kroyeri*.
[b]Octopus *Bathypolypus arcticus* (Prosch).
[c]Skate *Raja* sp. indet.
[d]Squid.
[e]Indet.
[f]An independent analysis of data on the same sample reported by Myers (1959).
[g]Redfish *Sebastes marinus*.

TABLE 2. Frequency of different foods of harp seals on the Canadian east coast (seals taken from ice fields). Much of the earlier data is cited from Fisher and Mackenzie (1955).

	Fish										Invertebrates							
	Capelin		Herring		Cod		Flatfish[a]		Other		Decap		Euphaus		Empty		Total	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Juveniles																		
Magdalen Is. Apr.–May 1952											1						1	
N. Gulf, Apr. 6, 1966															6		6	
Front, Apr. 19, 1952	1												1		48		50	
Front Apr. 5–25, 1953													5[b]				5	
Immatures																		
Front Mar. 31, 1953	1																1	
Labrador Mar. 20–30, 1961	1																1	
N. Gulf Apr. 8, 1966															80		80	
Notre Dame Bay, Mar. 23, 1966	1																1	
Adult Males																		
60 m. E. Scatari Apr. 4, 1952					1										99		100	
Labrador Mar. 20–30, 1961 (Khuzin 1963)	1																1	
Front Apr. 6–16, 1954					2		1		1[c]								4	
Adult Females																		
S. Gulf Mar. 8, 1952											2				3		5	
S. Gulf Mar. 6–27, 1954	1		1								2.5[d]		0.5[b]				5	
Front Mar. 14–19, 1953											1		2		2		5	
Front Mar. 1961											4[e]						4	
Notre Dame Bay Mar. 30, 1966	1																1	

[a] *Hippoglossoides platessoides* and *Reinhardtius hippoglossoides*.
[b] *Thysanoessa raschi.*
[c] *Sebastes marinus.*
[d] *Pandalus montagui.*
[e] *Pandalus borealis.*

TABLE 3. Frequency of different foods of harp seals in the arctic.

Locality	Fish		Crustacea			Other	Total No.
	Capelin	Polar Cod[a]	Mysids	Euphausiids	Amphipods		
Frobisher Bay (Dunbar 1949)			1[b]				1
Cumberland Sd. 1967		2.5	1		0.5[c]		4
1969			1.5	2.5[d]	3.0[c]		7
Sleeper Is. Sept. 16, 1958			1[e]				1
Devon Is. Sept. 6, 1965		3					3
Canadian Arctic		5.5	4.5	2.5	3.5		16
Disco Bugt. (Nansen 1925)	++						
Thule (Vibe 1950)		1					1
General (Freuchen & Salomonsen 1958)	+++	+				+	
Godthaab (Dunbar 1959)	+++			++			
West Greenland	+++	+		++		+	

[a]*Boreogadus saida.*
[b]*Mysis oculata, M. mixta.*
[c]*Parathemisto libellula.*
[d]*Thysoanessa inermis, T. raschi.*
[e]*Mysis oculata.*

Crustacea were more frequent than fish. Identifications of the species in a series of 17 stomachs containing well-preserved material were as follows:

	% frequency
Pandalus sp., mostly *P. montagui*	81.5
Eualus fabricii	7.6
Argis dentata	4.2
Spirontocaris spinus	3.4
S. phippsi	1.7
Sclerocrangon boreas	0.8
Lebbeus polaris	0.4
Pasiphaea sp.	0.4
	100.0

These species indicate benthic feeding.

A third, quantitatively useful, sample came from adults at the Magdalen Islands in the southern Gulf of St. Lawrence in spring (March–May). Foods here were mainly fish, among which herring was the most common, and various flatfish (Pleuronectidae).

Last in the samples of Table 1, juvenile seals taken on the northward migration from the Gulf at two or three months of age contained capelin; older seals had mostly empty stomachs with some capelin and more herring.

The less complete data from seals taken on the ice (Table 2) add to coverage in location, time, and age-group. The young seals begin to take their first food in early April. This usually consists of Euphausiidae, particularly of the genus *Thysanoessa*, probably taken close to the floating pack ice, underneath which I have observed and collected specimens at this date. Some capelin is also taken, but this seems to be a much more typical food of the immatures. Lactating adult females at the "whelping patches" eat little but take some decapod Crustacea (especially *Pandalus borealis* and *P. montagui*). Moulting adults on ice east of Newfoundland have been noted as taking Atlantic cod (*Gadus morhua*) and flatfish in addition to capelin. It is also not rare to find the remains of larger, spinier species. In the Gulf of St. Lawrence I have seen the rejected heads of a sea raven (*Hemitripterusa mericanus*) and a shorthorn sculpin (*Myoxocephalus scorpius*) on the ice, the rest having been eaten, while on the ice east of Newfoundland intact redfish (*Sebastes marinus*) are often found on the ice near moulting harp seals.

The massed herds hauling out on the ice fields, especially on sunny days, in April and May seem to forage intermittently. In the northern Gulf of St. Lawrence in April 1966, herds of moulting adults and immatures left the ice fields for several days at a time, presumably to feed. East of Belle Isle in early May 1968, animals sampled from among a herd of adults and immatures had food remains in the hindgut only, indicating recent feeding apparently en masse.

Animals arriving at West Greenland in May–June (Sergeant 1965) feed heavily on capelin, with some euphausiids (Table 3). Hansen and Hermann (1953) write, and I translate:

"At the very time when the capelin concentrate in great shoals at spawning time, the harp seals arrive on migration from their breeding grounds at Newfoundland. The seals ... chase the capelin shoals greedily along the coast and the fjords. It is chiefly capelin which give harp seals their blubber layer in the course of the summer. One can also find capelin in the stomachs of seals during the winter."

The same foods are eaten by the young and immature animals which summer round Disco Island.

It is chiefly adult harp seals which summer in the colder waters of northwest Greenland and the Canadian arctic archipelago. These take arctic cod (*Boreogadus saida*) and various Crustacea including euphausiids, mysids, and the pelagic emphipod *Parathemisto libellula*. All food samples hitherto collected in the arctic from this population are, however, rather small.

Seasonal Changes in Feeding and in Fatness

Seasonal changes in feeding can best be deduced from data on seasonal fatness.

Seasonal fatness is measured either from blubber thickness or condition factor (girth × 100/length), as seen in Fig. 1 and 2. Both measurements show a rapid decrease in adult females during lactation and in both other age classes (immatures and adult males) during the moult, followed by a slow increase through the summer.

Some direct observations are available to support this picture of seasonal changes. Thus, at the Magdalen Islands the percentage of empty stomachs was seen to decrease steadily in both sexes, from March (the season of whelping) to May, indicating an increase in feeding intensity (Table 4). After this date the ice melts and the animals leave the area. The percentage of full stomachs in April and May is surprising in view of the rare examples of animals moulting on ice being found to contain food remains. One reason for the discrepancy is the difference in the nature of the samples discussed above. The real feeding rate must be intermediate between that derived from either sample.

Feeding Behavior

How prey is taken — Juvenile harp seals, fed smelt, shrimps, and mysids, took individual prey, largely by suction, which was audible if the seal's snout surfaced. The fish were swallowed tail-first, which accords with a commonly found position of capelin at the cardiac end of harp seal stomachs examined from the Saguenay area. The teeth were used to grasp only lightly. Nevertheless, large fish (e.g. *H. americanus*) must be bitten or ripped by the teeth.

Where prey is taken — Depth of feeding must at present be deduced from the food organisms ingest-

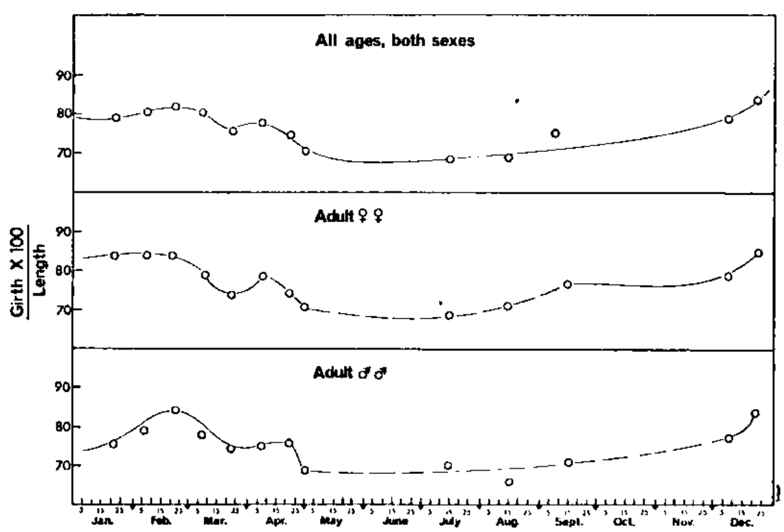

FIG. 1. Condition factor of harp seals through the year. Plotted points represent up to 50 animals.

ed. Templeman (1959, p. 73 and Fig. 43) considered that over the northeast Newfoundland shelf *S. marinus* are found deeper than 120 and, generally, 140 fath (220 and 256 m). I found fresh American plaice (*Hippoglossoides platessoides*) in stomachs of 20 adult harp seals on April 11, 1954, at 49°26'N, 50°05'W over a depth of 150–160 fath (274–293 m), 80–100 km from the nearest shallow water at Baccalieu Bank. These data suggest diving abilities of adult harp seals to as much as 250 m. In the last

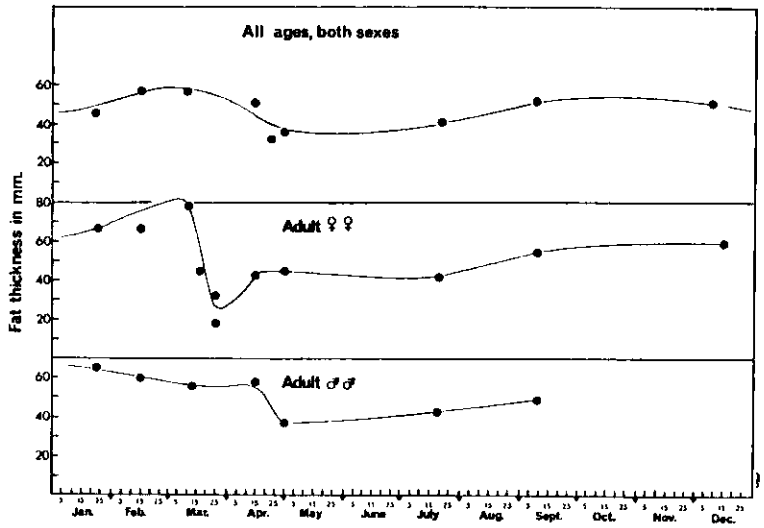

FIG. 2. Fat thickness of harp seals through the year. Plotted points represent up to 50 animals.

TABLE 4. Seasonal changes in feeding intensity of harp seals in spring, as shown by stomach contents of harp seals from the Magdalen Islands collected from March to May, 1956. F = females, M = males.

Time period	% of stomachs containing: Herring	Flatfish	Redfish	Gadidae	Invertebrates	% empty	Total no.
Mar.							
F	19.3	3.4	–	–	2.3	75.0	44
M	28.6	–	–	–	–	71.4	14
Apr. 1–15							
F	47.7	2.3	2.3	2.2	–	45.5	11
M	57.1	28.6	–	–	–	14.3	7
Apr. 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
M	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	1.1	36.1	188

JOURNAL FISHERIES RESEARCH BOARD OF CANADA, VOL. 30, NO. 1, 1973

example stomachs of immature seals were empty suggesting that they could not dive as deeply.

Social Behavior

Juvenile harp seals are solitary or indifferent to other animals through their first spring, summer, and winter, thereafter becoming highly social. This change in behavior correlates well with a shift in feeding from pelagic Crustacea to schooling pelagic fish.

In wintering seals, both in 1969 and 1971, a fine gradient in feeding behavior was seen from the sampling of hunters' returns (Fig. 3). The hunting area stretched 30 km from Escoumins in the east to Tadoussac and the mouth of the Saguenay River in the west. This part of the estuary of the St. Lawrence is known to be an area of intense upwelling (Hachey et al. 1957) and rich production and in winter tends to be clear of ice. Analysis of the 1969 catch showed young immatures concentrated in the eastern sector, adults in the western sector.

Both years' data showed that it was chiefly adult females which concentrated westwards (Fig. 3). It is therefore tempting to suppose that adult pregnant females seek out the richest feeding grounds, and that these are found in the Saguenay region at the western end of the feeding zone near Tadoussac. While detailed knowledge of productivity in this region is still lacking, the intensity of upwelling is greatest near Tadoussac where the shelf rapidly shallows.

Segregation of this kind was found by Wada (1969) in wintering northern fur seals (*Callorhinus ursinus*) off Japan. The adult females were found in deeper waters containing larger food organisms than where the juveniles were concentrated.

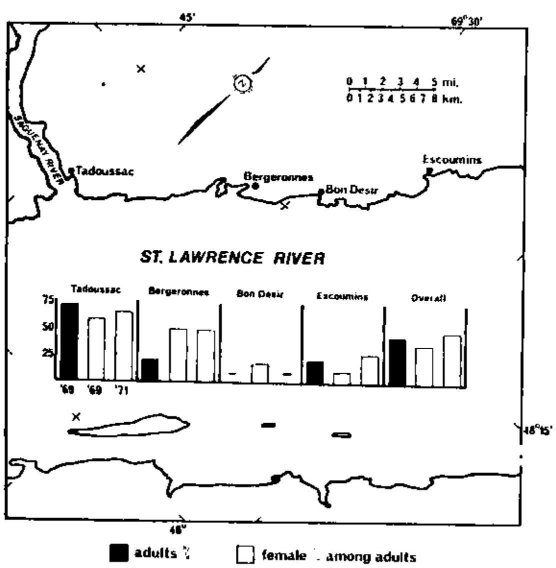

Fig. 3. Differential winter distribution of harp seals in the St. Lawrence estuary. For each locality of capture, dark hatching represents adult percentage, light hatching — percentage of females among adults.

Food Consumption and Growth in Nature and in Captivity

Dr G. C. Ray, while Curator at the New York Aquarium, told the writer that, in his experience, adult seals eat about 5% of their body weight per diem and young seals about 10%. Detailed information for two young harp seals is available from the studies of Geraci (1971) at the Montreal Aquarium. In these studies two control animals were kept for 16 months on an ad libitum diet of smelt and herring supplemented with thiamin. Mean daily rations and weights were recorded each month (Table 5). Seasonal changes in feeding were marked, with maxima in July–November or December, and minima in March, which may indicate retention of a natural feeding cycle. There was no consistent cycle of weight change, however. The daily ration averaged 3.90–3.96 kg or 6.9–8.4% of body weight (mean =

Table 5. Weight gain and food intake of harp seals in captivity (after Geraci 1971).

		Seal no.			
		478		1867	
Month	Age (*months*)	S.wt.[a]	%C[b]	S.wt.	%C
Apr.	1	27	5.9	35	5.7
May	2	27	8.5	36	5.8
June	3	30	7.9	37	6.5
July	4	30	11.7	37	10.8
Aug.	5	32	11.3	41	9.8
Sept.	6	35	9.1	44	7.5
Oct.	7	37	10.5	48	8.8
Nov.	8	50	12.8	61	11.6
Dec.	9	63	10.0	71	5.8
Jan.	10	68	6.3	78	5.4
Feb.	11	72	5.3	79	4.2
Mar.	12	77	3.2	80	3.5
Apr.	13	70	5.1	81	4.4
May	14	68	6.9	81	6.4
June	15	65	11.7	83	7.6
Mean			8.4		6.9

[a]S.wt. = seal weight in kg.
[b]%C = food intake: mean percent of body weight consumed per day.

7.6% for both animals). These results for two immature animals support the general conclusions of Ray.

Highest weights of stomach contents recorded in nature were 1.75 kg for a one-year-old seal of 40-kg estimated body weight; and 4.7 kg for an estimated 100-kg adult — or about 4.7% of body weight in each case. The frequency and duration of feeding episodes in the wild are unknown. In the estuary of the St. Lawrence digested capelin was usually found in the pylorus with fresh capelin filling the rest of the stomach. This circumstance suggested extended periods of feeding.

The captive animals showed higher growth rates than in nature, reaching 65–83 (mean, 74) kg at 1½ years instead of at 3–4 years as in nature (Fig. 4), and appeared obese. Indeed, in one of the two animals, dead after 2¾ years, the condition factor was at the high level of 107. However, its length at 142 cm was also high so that some of the increased growth may have been in carcass weight as well as in fatness. The captive seals, as well as being supplied with abundant food, were confined, leading to less exercise, and were maintained at a higher ambient temperature than in nature. Nevertheless, the suspicion arises that feeding in nature may often be less than optimal. Indirect evidence bearing on this subject is discussed below (p. 26).

Production and Ecological Efficiency

Age determination of harp seals from growth layers in the canine teeth is accurate and allows study of age-specific growth rates (Fig. 4).

Since a good deal of the harp seal's weight is blubber which thickens rapidly in early development and later varies seasonally, the estimate of biomass is rather arbitrary. Production could be estimated starting from the weight of newborn young (about 9 kg), but I shall use as a starting point the mean weight of the weaned young (about 35 kg). Mean weight of adults and immatures in spring is about 100 kg. In harp seals, adults represent about 50% of the total population of adults and immatures just before birth of the year's crop of young. The sexes are equal in numbers, and about 90% of the adult females give birth annually. Annual production is therefore equal to $0.25 \times 0.9 = 0.225$ of the population and annual production (of weaned young) in weight is $0.35 \times 0.225 = 0.07875$ of unit biomass.

Annual food consumption by an immature or adult harp seal is assumed to be 5 kg daily. Allowing for fasting periods in spring this might be maintained for 300 days in the year, giving an annual food consumption of about 1500 kg (1.5 metric tons), or 15 kg for every kg of seal.

Ecological efficiency is defined as yield or organism divided by its food intake (Paloheimo and Dickie 1970). This, for harp seals, is therefore estimated at $0.07875 \times 1/15 = 0.00525$, or about 0.5%. A common value of ecological efficiency at lower trophic levels is about 10%. Harp seals (as perhaps other sea mammals) are therefore inefficient converters of fish flesh. Elephants (*Loxodonta africanus*) have a food conversion efficiency (measured as growth/food consumed i.e. equivalent to the para-

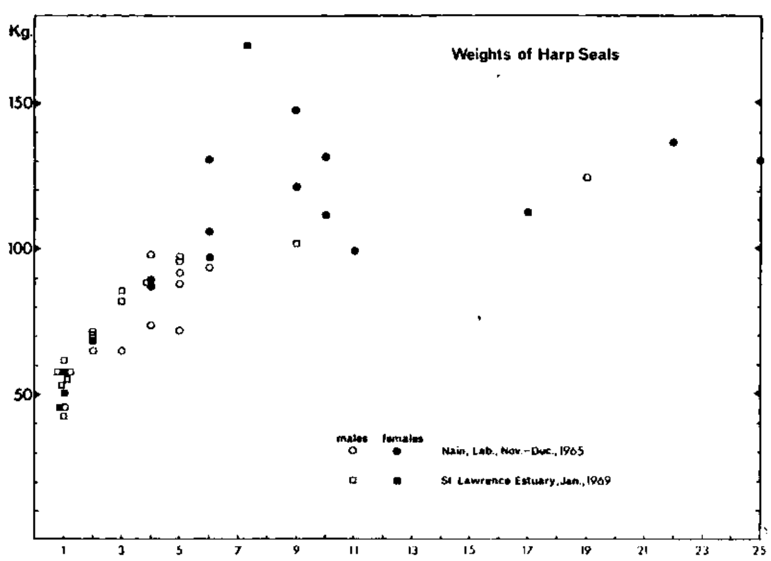

FIG. 4. Age-specific growth in weight of free-living harp seals.

meter measured above) of 0.005, deer (*Odocoileus virginianus*) of 0.012, and cattle (*Bos taurus*) of 0.060 (Petrides et al. 1968).

Discussion

Food Consumption and Intraspecific Relations

How much food is consumed by harp seals? The population in the northwest Atlantic in the late 1960's produced about 300,000 young annually (Sergeant 1971b), necessitating a stock size of about $1\frac{1}{3}$ million animals just before birth of the young. At an annual feeding rate of 1.5 tons per animal, this population would consume about 2 million tons of food per annum.

A very crude estimate of the overall composition of the food is shown in Table 6. This is obtained by summing the number of times each food item was found, each sample yielding one occurrence of any item found in it. According to this analysis, fish constitute some 60% of the food, and capelin alone some 25%.

On this basis, the northwest Atlantic harp seals eat some half million tons of capelin annually. Judging by respective residence times of the seals, they eat most of this (perhaps 0.4 million tons) during the winter in the eastern Canadian region, the remainder in west Greenland waters. This resource is shared with many other predators, such as the balaenopterid whales, as discussed below. For comparison, about 1.5 million tons of capelin were caught by Norway in the northeast Atlantic (Barents Sea, etc.) in 1970, and about 0.2 million tons by Iceland, (O. Dragesund personal communication). The northwest Atlantic fishery has until very recently been negligible — 3574 tons in 1968, for example (Anon 1970).

TABLE 6. Frequencies of different food items found in harp seals.

Fish	No. of occasions		No. of occasions
		Crustacea	
Capelin	16 (26%)	Euphausiids	9
Herring	5	Decapods	7
Cod	4	Mysids	4
Polar cod	4	Amphipods	2
Flatfish	3		
Redfish	2	*Mollusca*	
Skate	1	Cephalopods	2
Barracudina	1		
Indet.	1		
	37 (61%)		24 (39%)

These estimates of food consumption suggest that availability of food could be a limiting factor for harp seals. Indirect evidence comes from studies of age at maturity (Sergeant 1966). As the exploited harp seal populations have decreased in recent decades, age at first maturity has decreased. Since age at first maturity is a function of growth (Laws 1959), growth has improved over this period. There is a strong suspicion that improved growth has resulted from improved nutrition. While I have not been able to demonstrate either improved growth or improved nutrition over the years, I have observed greatly improved condition of moulting animals between the early 1950s and late 1960s with disappearance of cracked skin in adult males at the height of moult in late April. Probably blubber thickness has increased over the same period but the data are not sufficient for critical testing.

If food was, or is, limiting to the population one would look for mechanisms reducing intraspecific competition. These seem to exist in the form of feeding segregation in either the vertical plane (adults diving more deeply) or the horizontal plane (geographical segregation on a greater or lesser scale). In spring all age classes are concentrated in a reduced range and here segregation by depth appears to be most marked with adults alone eating the larger food organisms (herring in the Gulf, groundfish off eastern Newfoundland), with some segregation by area (adults remaining among the ice of the whelping ground, immatures at its southern fringe). On arrival in west Greenland there is a temporary concentration of all age-sex classes on the abundant spawning capelin, but by high summer the adults have dispersed into high arctic waters leaving the young immatures in subarctic waters. This large-scale spatial separation persists into winter when the young immatures delay their migration southward (Sergeant 1965).

The increasing sociality that occurs after the first year may in some way result in more effective feeding on active, pelagic fish species such as herring.

Interspecific Relations

Since the pelagic food resources (decapod Crustacea, capelin, herring, and groundfish) in the eastern Canadian region are resident, why do the harp seals undergo long seasonal migrations? Why do they not feed on the abundant spawning capelin at Newfoundland in early summer as they do at Greenland? So long a migration necessitates heavy expenditures of energy.

Looked at in the present context, one can only say that the harp seal requires both a pelagic food resource and a resting substrate of pack ice, and can only persist where both are present, so that

migrations are forced on it to the degree that seasonal changes occur in ice distribution. As usual, exceptional situations are revealing. Very rarely, young harp seals attempt to summer in the Gulf of St. Lawrence or on the east coast of Newfoundland. Usually, these young animals are associated with Atlantic harbour seals (*Phoca vitulina concolor*). Only two animals are well-documented. A juvenile taken at Escoumins on the north shore of the Gulf of St. Lawrence on June 30, 1969, had plant material in the stomach (the species *Triglochin maritima*, *Glaux maritima*, and possibly a sedge family Cyperaceae) indicating that it had fed around a sandy or salt-marsh coast. Its girth and fat thickness were abnormally low. A tagged juvenile killed at Bay of Islands, Newfoundland, in August 1966 had a carcass weight of 10 kg, about half the normal weight. One cannot distinguish from these data whether abnormally small animals failed to migrate, or whether animals that failed to migrate suffered unusually poor growth, but the latter seems more likely.

This evidence suggests that young harp seals cannot find suitable feeding conditions close to coastal resting sites. The rarity of the episodes demonstrates the accuracy of the north-seeking migratory behavior of young harp seals in spring (Sergeant 1971a), which in turn indicates intense selection over a long period towards the migratory habit.

Viewed over the evolutionary time-span, one may suppose the harp seal with its white-coated pup to have had a long association with ice. It moves southwards into open water only in early winter in search of the rich, boreal stocks of pelagic fish and euphausiids, suggesting a barrier to further southward dispersal.

Species such as fin whale *Balaenoptera physalus* (Jonsgaard 1966) and minke whale *B. acutorostrata* (Sergeant 1963) are major consumers of capelin and euphausiids in the northwest Atlantic. The cold-adapted minke whale migrates north in spring, close behind the migration of the harp seals, and south in the fall, shortly ahead of the seals. Harp seals enter the Newfoundland–Gulf of St. Lawrence area in December and depart in April or May, the great whales departing in November and arriving in May or June.

Several documented episodes of stranding of fin whales by ice on lee shores (Sergeant, et al. 1970) show that selection works against whales that linger in waters liable to be covered with pack ice. In west Greenland, at the period when the harp seals feed on capelin, there is a notable lack of fin whale catches although sperm whales (*Physeter catodon*) were caught in May–June.

Two hypotheses are therefore available to explain the reciprocal distribution of seals and whales feeding on the same capelin resource: (1) each exploits the niche when it can — the seals when there is ice, the whales when there is none — and no competition occurs. Food is not limiting. (2) There is limited competition between them, and collectively they are food-limited, which limits total numbers of each.

If there is drift ice in southwest Greenland in May–June when the seals arrive, having left the Newfoundland capelin stocks, (1) is probably true; if there is no drift ice, (2) is probably true. A study of the Danish Ice Atlas (Det Danske Meteorologiske Institut 1928–) shows that ice is typical in this region, suggesting that (1) is true. Probably the seals haul out on the ice to rest after the long journey across Davis Strait.

A further test will come from intensive human exploitation of capelin expected in the next few years. If food is limiting to the natural predators, they will suffer further food shortage when man is added as a predator and the populations that can be maintained will be lower than hitherto.

TABLE 7. Calculated consumption of herring in the Gulf of St. Lawrence by harp seals, with feeding rates from Table 4.

Month	Supposed population present	Proportion feeding	Individual daily consumption (*kg*)	Days	Tons consumed
Mar.					
2nd half	250,000	0.25	5	15	4687
Apr.					
1st half	200,000	0.50	5	15	7500
2nd half	100,000	0.75	5	15	5625
May					
1st half	50,000	1.00	5	15	3750
Total					21,562

INTERACTION WITH MAN

Turning the last problem around, do harp seals interfere greatly with predation by man or by how much do harp seals reduce the sustainable yields of individual fishery resources to man?

The species of invertebrates eaten by harp seals in the northwest Atlantic are, for the most part, noncommercial. The diversity of decapod Crustacea taken does not indicate much interference with the new and growing human fishery for *Pandalus borealis*. Capelin is not, as yet, fished in large tonnage in the northwest Atlantic. Consumption of herring by harp seals is much less than of capelin. It occurs mainly in the Gulf of St. Lawrence, where about one-third of the harp seal population, or some 450,000 animals, live. Herring is there taken mainly by the adults (about 250,000 animals). Also, during the season of herring feeding at the Magdalen Islands, the animals are gradually moving north as the ice disappears to be replaced as predators of herring by fin and other species of whales. Combining the increasing intensity of feeding in spring with arbitrary rates of emigration between March and May results in an estimated herring consumption by harp seals around the Magdalen Islands of about 20,000 tons (Table 7). This compares with a human fishery in the Gulf of St. Lawrence in 1968 of 100,000 tons (Anon. 1970), which may have overtaxed the stocks since subsequent catches have declined.

The estimate of herring consumption may be too high because, in many years, disappearance of the ice and northward migration of the seal take place a month earlier, by mid-April; in the sampling year (1956), the ice persisted into May near the Magdalen Islands. However, some harp seal herring feeding that cannot be quantified was recorded also in the northern Gulf and this could increase the estimate to a higher level.

Acknowledgments

Hr E. Vangstein, Sandefjord, supplied whaling statistics for West Greenland. In 1965 Dr M. M. R. Freeman sent details of harp seal feeding from Grise Fjord, Ellesmere Island, and Mr H. A. Williamson sent the same from Nain, Labrador. Collections and analyses of stomach contents were made at the Magdalen Islands in 1956 by Mr P. Montreuil who gave access to original data and to unpublished information on feeding of captive harp seals at the Montreal Aquarium in 1971. Dr T. G. Smith collected data in Cumberland Sound, Baffin Island, in 1968, and he and Mr W. Hoek initiated collections in the St. Lawrence estuary in January 1969, which were continued by purchase from hunters. Dr D. E. McAllister, National Museum of Natural Sciences, Ottawa, identified the fishes; Dr M. C. Mercer, Fisheries Research Board Biological Station, St. John's, Nfld., the Cephalopoda; Dr E. H. Grainger, Fisheries Research Board Arctic Biological Station, Ste. Anne de Bellevue, Que., the decapod Crustacea; and Dr D. E. Swales, Macdonald College, Que., the plant material. To all these people I am very grateful.

ANON. 1970. International commission for the Northwest Atlantic Fisheries. Statistical Bulletin 18 for the year 1968. Dartmouth, N.S. 141 p.

DET DANSKE METEOROLOGISKE INSTITUT. 1928. Isforholdene i de Arktiske Have. [Continued (1955-) as Isforholdene i de Grønlandske Farvande.] Charlottenlund.

DUNBAR, M. J. 1949. The Pinnipedia of the arctic and subarctic. Fish. Res. Board Can. Bull. 85: 22 p.

FISHER, H. D., AND B. A. MACKENZIE. 1955. Food habits of seals in the Maritimes. Fish. Res. Board Can. Progr. Rep. Atl. Coast Sta. 61: 5–9.

FREUCHEN, P., AND F. SALOMONSEN. 1958. The arctic year. G. P. Putnam's Sons, New York, N.Y. 438 p.

GERACI, J. R. 1971. Experimental thiamine deficiency in captive harp seals, *Phoca groenlandica*, induced by eating herring, *Clupea harengus*, and smelts, *Osmerus mordax*. Can. J. Zool. 50: 179–195.

HACHEY, H. B., L. LAUZIER, AND W. B. BAILEY. 1957. Oceanographic features of submarine topography. Trans. Roy. Soc. Can. 50(3): 67–81.

HANSEN, P., AND F. HERMANN. 1953. Fisken og Havet ved Grønland. Kobenhavn. 128 p.

JONSGAARD, A. 1966. Biology of the north Atlantic fin whale (*Balaenoptera physalus* L.). Taxonomy, distribution, migration and food. Hvalradets Skr. 49: 62 p.

KHUZIN, R. S. 1963. Materialy po biologii i promyslu grenlandskogo tyulenya (*Pagophilus groenlandicus* Erxl. 1777) i Nyufaundlenda. (Materials on the biology and hunting of the harp seal (*Pagophilus groenlandicus* Erxl. 1777) in Newfoundland.) Tr. PINRO 15: 235–249.

LAWS, R. M. 1959. Accelerated growth in seals with special reference to the Phocidae. Norsk Hvalfangst Tid. 48: 425–452.

MYERS, B. J. 1959. The stomach contents of harp seals (*Phoca groenlandica* Erxleben) from the Magdalen Islands, Quebec. Can. J. Zool. 37: 378.

NANSEN, F. 1925. Hunting and adventure in the north. Duffield and Co., New York, N.Y. 462 p.

PALOHEIMO, J. E., AND L. M. DICKIE. 1970. Production and food supply, p. 499–527. *In* J. H. Steele [ed.] Marine food chains. Oliver & Boyd Ltd., Edinburgh.

PETRIDES, G. A., F. B. GOLLEY, AND I. L. BRISBIN. 1968. Energy flow and secondary productivity, p. 9–20. *In* F. B. Golley and H. L. Buechner [ed.]. A practical guide to the study of the productivity of large herbivores. Int. Biol. Handb. 7. Blackwell Scientific Publications, Oxford.

SERGEANT, D. E. 1963. Minke whales *Balaenoptera acutorostrata* Lacépède, of the western north Atlantic. J. Fish. Res. Board Can. 20: 1489–1504.

1965. Migrations of harp seals *Pagophilus groenlandicus* (Erxleben) in the northwest Atlantic. J. Fish. Res. Board Can. 22: 433–464.

1966. Reproductive rates of harp seals, *Pagophilus groenlandicus* (Erxleben). J. Fish. Res. Board Can. 23: 757–766.

1971a. Migration and orientation in harp seals. Proc. Seventh Annu. Conf. Biol. Sonar Diving Mammals Stanford Res. Inst. 1970: 123–131.

1971b. Calculation of production of harp seals in the western north Atlantic. Int. Comm. Northwest Atl. Fish. Redbook 1971: 157–184. (Mimeogr.)

SERGEANT, D. E., A. W. MANSFIELD, AND B. BECK. 1970. Inshore records of Cetacea for eastern Canada, 1949–68. J. Fish. Res. Board Can. 27: 1903–1915.

TEMPLEMAN, W. 1959. Redfish distribution in the north Atlantic. Fish. Res. Board Can. Bull. 120: 173 p.

VIBE, C. 1950. The marine mammals and the marine fauna in the Thule District (Northwest Greenland) with observations on ice conditions in 1939–41. Medd. Gronland 150(6): 115.

WADA, K. 1969. Migration of northern fur seals along the coast of Sanriku. Bull. Tokai Reg. Fish. Res. Lab. 58: 19–82. (Transl. from Japanese by Fish. Res. Board Can. Transl. Ser. No. 1682, 1971)

YABLOKOV, A. V., AND D. E. SERGEANT. 1963. Izmenchivost' krainologickeskikh priznakov grenlandskogo tiuleniya (*Pagophilus groenlandicus* Erxleben, 1777). (Cranial variation in the harp seal.) Zool. Zh. 42: 1857–1865.