

The diet of the Saimaa ringed seal *Phoca hispida saimensis*

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The diet of the Saimaa ringed seal *Phoca hispida saimensis* Nordquist, 1899 was studied by the analysis of stomach contents and by feeding trials with a captive seal. Nine prey species were found in the stomachs, the most important being small schooling fish species: perch *Perca fluviatilis*, roach *Rutilus rutilus*, vendace *Coregonus albula*, smelt *Osmerus eperlanus* and ruff *Acerina cernua*. The importance of crustaceans in the diet of the ringed seal in Lake Saimaa is insignificant. Length of the intestinal tract of the Saimaa ringed seal is relatively shorter than those of marine ringed seals. In cafeteria tests on one captive seal the preferred fish species were vendace and smelt. The captive seal displayed clear seasonal variation in feeding activity. The consumption of fish was lowest in springtime and highest in autumn and winter.

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Introduction

The Saimaa ringed seal *Phoca hispida saimensis* Nordquist, 1899 is a subspecies of the ringed seal *Phoca hispida* Schreber, 1775. This subspecies has been living in freshwater Lake Saimaa in eastern Finland, separated from other ringed seals, for over 8 000 years. Nowadays it differs morphologically from the other subspecies; the Ladoga ringed seal *P. h. ladogensis* Nordquist, 1899 and the Baltic ringed seal *P. h. botnica* Gmelin, 1785 (Hyvärinen and Nieminen 1990). The present population of the endangered Saimaa ringed seal includes only about 200–220 animals.

The Saimaa ringed seal is adapted to living in very different conditions from those of the other subspecies. The average depth of Lake Saimaa is 17 m (Max 85 m) and it is 194 km long and 138 km wide. Its total surface area is 4 460 km². Lake Saimaa has a comparatively long shoreline of almost 15 000 km. The habitat is made even more labyrinthine by its islands, ca 14 000. Permanent ice usually persists from November until the beginning of May. The lake is inhabited by 35 fish species (Toivonen 1985) and seven species of macrocrustaceans (Bagge 1992).

The behaviour of the Saimaa ringed seal has been studied by radiotagging. Telemetry studies have shown that adult Saimaa ringed seals are very good divers

and also live in a small area compared with marine ringed seals (Hyvärinen *et al.* 1995). In addition, large differences were found in the fat-soluble vitamin and fatty acid compositions of the tissues of the Saimaa ringed seal compared with those of marine ringed seals due to different amounts supplied in freshwater as opposed to marine food webs (Käkelä *et al.* 1995, 1997, Käkelä and Hyvärinen 1997). However, no records have been published concerning the diet of the Saimaa ringed seal.

The diet of ringed seals in the Arctic Ocean, varies markedly depending on season and geographical location. Fishes of the cod family (Gadidae), pelagic amphipods, euphausiids, shrimps and other crustaceans make up the bulk of the diet (Lowry *et al.* 1978, 1980, Gjertz and Lydersen 1986, Smith 1987, Lydersen *et al.* 1989, Weslawski *et al.* 1994). McLaren (1958) reported that 72 prey species were found in the stomachs of ringed seals from eastern Canada. In general, only sparse information has previously been available on the diet of freshwater seals (Power and Gregoire 1978, Tormosov and Filatov 1979, Yablokov 1985).

Thus the aims of the present study were (1) to provide information about the diet of the Saimaa ringed seal in nature, (2) to measure the length of the intestine of the Saimaa ringed seal, (3) to determine what are the preferred prey species of the captive Saimaa ringed seal and (4) to measure seasonal changes in its food consumption in captivity.

Material and methods

Diet analysis was based on stomach contents, which were removed from Saimaa seals that had been found recently dead. Morphometric data were obtained and the stomach contents were stored in 70% ethyl alcohol. In addition, the sex and age of each seal as well as the cause of death was recorded. Most of these seals were young, and had died by entanglement in fishing gear.

We analysed 43 stomach contents from seals younger than 1 year old and 20 from yearling or older seals. Among them, 51 stomachs contained food and identifiable prey remains. The food remains in the stomachs consisted mainly of slowly digestible hard parts of the seal's prey. Therefore, the wet weights of individual stomach contents are not given. Fish were assigned to species by the identification of undigested specimens, sagittal otoliths or diagnostic bones. Preys were identified to the lowest possible taxon using a stereo microscope and reference collection of Finnish freshwater fish species and published guides (Wheeler 1978, Härkönen 1986). Undigested fish were measured and weighed.

In addition, we measured the intestinal tract from the beginning of the small intestine to the end of the rectum of 20 newly born, 34 under 1 year and 16 yearling or adult Saimaa seals of both sexes. Length of the intestines was compared to the standard body length of seals (measured from nose to anus).

Food consumption of the Saimaa ringed seal was studied by observing a captive seal. One adult male was housed in a small oligotrophic lake (0.4 km², length of 1.7 km and Max depth of 32 m) in 1986–1990 (see Hyvärinen *et al.* 1995). The seal was fed mostly with vendace *Coregonus albula* and smelt *Osmerus eperlanus* every second or third day in winter and daily in summertime. Feeding time was at noon and the fish were kept in the water in metal threads until the next feeding time. About 2.5–4.5 kg fish were available per day. The offered amount of fish was higher than the amount eaten per day. Vitamins were added to food for preventing the shortage of vitamins and selenium for lowering the methyl mercury concentration in the tissues of the seal (see Hyvärinen *et al.* 1998). The seal's food consumption was monitored in 1987–1989. Although, there were also some fish in the lake and the seal might have captured some of its own food, we supposed that the use of offered fish indicates the changes in food consumption of the seal.

Three cafeteria tests were made in 1987–88 using the seal in captivity. During a cafeteria test we offered the seal nine fish species: vendace, smelt, whitefish *Coregonus lavaretus*, pike perch *Stizostedion lucioperca*, perch *Perca fluviatilis*, roach *Rutilus rutilus*, trout *Salmo trutta*, pike *Esox lucius* and burbot *Lota lota*. Prey lengths and masses varied among the cafeteria tests. The average weights of the prey fish species are given in Table 2. Fish attached to strings were served underwater. The distance between strings was about half a metre. About 2.7 to 3.5 kg of fish were available at the same time daily in the cafeteria test. Duration of the test was five days and fish were available two hours a day from 12 00 h to 14 00 h. Consumption of the different fish species was determined.

Results

Analysis of the stomach contents indicates that fish constituted the bulk of the diet whereas crustaceans, the only other taxa represented, occurred only in one sample (Table 1). Among the identified prey species perch (found in 26.1 % of stomachs), roach (20.5%), vendace (14.8%), smelt (14.8%) and ruff *Acerina cernua* (13.6%) were the most important prey species. Typically, there were 1 to 4 fish species in the stomach. The mean standard length of the fish represented in the sample was 9.0 cm (SE = 0.30; $n = 158$) and the Max length, 21 cm. The mean weight was 10.72 g (SE = 1.28; $n = 78$) and the Max weight, 56 g. Some other small particles (iron nail, pebbles, sand, wooden sticks, plants, pieces of bark) were also found in 14 stomachs.

Table 1. Number of Saimaa ringed seal stomachs ($n = 51$) containing specified prey.

Prey	No. of stomachs
Perch <i>Perca fluviatilis</i>	23
Roach <i>Rutilus rutilus</i>	18
Vendace <i>Coregonus albula</i>	13
Smelt <i>Osmerus eperlanus</i>	13
Ruff <i>Acerina cernua</i>	12
Nine-spined stickleback <i>Pungitius pungitius</i>	5
Bleak <i>Alburnus alburnus</i>	1
Burbot <i>Lota lota</i>	2
Unidentified fish	24
Opossum shrimp <i>Mysis relicta</i>	1

Table 2. Standard body length and intestinal tract (from the beginning of the small intestine to the end of rectum) length of Saimaa ringed seals in different age classes.

Age	n	Standard body length	Intestine length (cm)	Intestine length/ Standard body length
		(cm) $\bar{x} \pm SE$	$\bar{x} \pm SE$	$\bar{x} \pm SE$
Newborn	20	57.8 \pm 0.9	615.8 \pm 28.8	10.6 \pm 0.4
< 1 year	34	86.3 \pm 1.7	1002.0 \pm 33.1	11.6 \pm 0.3
\geq 1 year	16	117.1 \pm 3.8	1229.2 \pm 60.1	10.5 \pm 0.5
All age classes	70	84.0 \pm 2.7	933.8 \pm 34.2	11.1 \pm 0.2

Table 3. Percentage of the offered fish species consumed by the captive Saimaa ringed seal in cafeteria tests.

Fish species	Mean weight	Cafeteria test		
		July 1987 % eaten	August 1987 % eaten	February 1988 % eaten
Vendace	28	58	98.9	35.7
Smelt	7	65.8	79.1	4.6
Whitefish	197	0	20.2	40.3
Salmon	165	0	13.2	0
Roach	25	1.5	0	0
Perch	45	0	0	0
Pike	650	0	0	0
Pike Perch	318	0	0	0
Burbot	295	0	0	0

The mean length of the intestinal tract was about 11 times the standard body length of the Saimaa ringed seal (Table 2). There were no significant sex related differences in the length of the intestinal tract.

The mean, daily offered, fish consumption of the captive seal was 2.2 kg, and the feeding rate varied seasonally (Fig. 1). Food consumption was lowest in May and June and increased after midsummer, reaching a peak in autumn and winter. In the cafeteria tests vendace and smelt were the most preferred food items (Table 3).

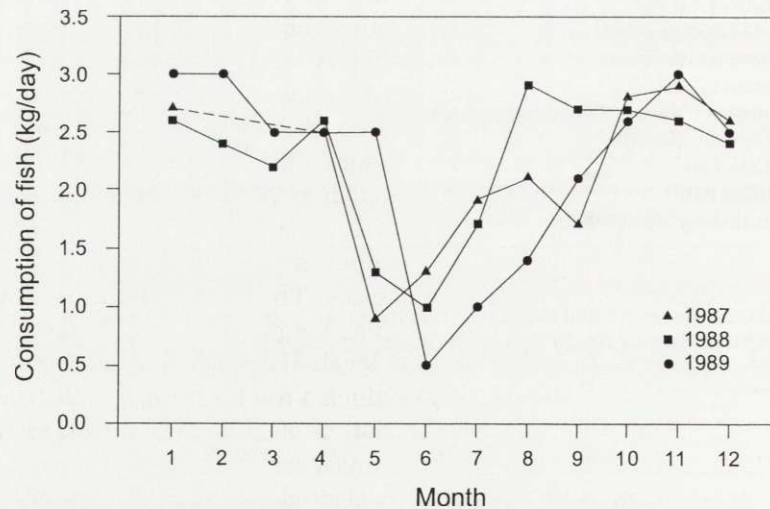


Fig. 1. Mean daily intake of offered fish for each month in 1987–1989 by a male Saimaa ringed seal living in seminatural conditions in a small lake (In February and March 1987 consumption of fish was not measured quantitatively)

Discussion

According to analysis of the stomach contents, small schooling fish were the main prey of the Saimaa ringed seal. Perch, roach, vendace, smelt and ruff represented about 90% of the prey identified in the stomachs. These preys also represent the most abundant and available fish species in Lake Saimaa (Toivonen 1985). Like other ringed seals, the Saimaa seal is an opportunistic feeder within some groups of prey. Ringed seals rarely prey upon more than 10–15 species, and 2–4 of these are the main prey species (Söderberg 1975, Lowry *et al.* 1980, Smith 1987, Weslawski *et al.* 1994). According to Tormosov and Filatov (1979) even though there are 48 fish species in Lake Ladoga, ringed seals generally eat about 10 fish species.

The size of the fish ingested by the Saimaa ringed seal agrees well with those reported for the ringed seal in other localities in the Arctic. Fish eaten by ringed seals are usually small: 5–10 cm long, seldom exceeding 20 cm (McLaren 1958, Lowry *et al.* 1980, Gjertz and Lydersen 1986, Smith 1987, Lydersen *et al.* 1989, Weslawski *et al.* 1994). Prey size might be one of the most important reasons for the ringed seal's choice of food. In cafeteria tests, the seal studied usually chose the smallest prey species; among these the preferred species were vendace and smelt. Occasionally, however, the seal ate larger fish species such as whitefish and salmon in our cafeteria tests.

It has long been supposed that vendace and smelt might be the predominant and most important prey of the Saimaa ringed seal (eg Hyvärinen *et al.* 1984). This was partly supported in cafeteria tests in the present study. Yablokov (1985) also found that vendace and smelt are among the main prey species of the Ladoga ringed seal. However, perch and roach were the most frequent fish in the stomach contents analysed here. This may be explained by two hypothesis: (1) our material consists mainly of young seals, whose feeding habits might differ from those of adults. According to telemetry studies a recently weaned pup spends more time in shallow waters near the pupping area (M. Kunnasranta, H. Hyvärinen and J. T. Koskela, unpubl.). In addition, perch and roach typically live in these shallow waters. In contrast, adult seals seem to forage mainly in deeper offshore waters, which are inhabited by pelagic fish species such as vendace and smelt. And (2) the population density of vendace has been low for the last ten years in Lake Saimaa (Jurvelius *et al.* 1992) and the seals may compensate for the shortage of vendace by preying more intensively on other fish species. This last hypothesis agrees with heavy-metal studies, which show that Saimaa ringed seals might have started to use other fish species from higher trophic levels (Hyvärinen *et al.* 1998).

It is noteworthy that the stomachs contained a number of fish otoliths which we could not identify. One reason for the erosion of otoliths in many stomachs is the quick and effective digestion system of the ringed seal. According to Parsons (1977), the digestive tract of the ringed seal can be cleared within 6–8 hours of feeding.

The length of intestines of pinnipeds is long as compared with other carnivores (Helm 1984). For example the small intestine of the Harbour seal *Phoca vitulina richardsi* is nearly 16 times the body length and those of the Elephant seal

Mirounga angustirostris is about 25 times the body length (Helm 1983). There is, however little data regarding the length of the intestines of ringed seals. According to Frost and Lowry (1981), the length of the small intestine of the Arctic ringed seal ($n = 12$) is 13.8 times the standard length of the animal. Evidently the Saimaa ringed seal has a shorter intestinal tract than marine ringed seals. According to the present study, the length of the Saimaa ringed seal's whole intestine is about 11 times the standard length of the animal. The Saimaa ringed seal seems to feed almost exclusively on fish and a shorter intestine tract might be related to the seal's restricted diet.

The present study shows that compared with marine ringed seals, crustaceans are of minor importance as prey for the Saimaa ringed seal. Crustaceans are an important part of the ringed seal's diet in the Arctic and in the Baltic Sea (McLaren 1958, Söderberg 1975, Lowry *et al.* 1978, 1980, Smith 1987), especially among young animals (Lowry and Frost 1981). Crustaceans, however, were only represented in one ringed seal's stomach content from Lake Saimaa. The Opossum shrimp *Mysis relicta* is a pelagic species that occurs in deeper waters. Among the seven species of macroscopic crustaceans in Lake Saimaa, this is the only species living in densities high enough for the economical feeding of seals. In general crustaceans densities are very low in lakes compared with those in the sea and fish is the predominant prey also for other phocic seals living in freshwater lakes (Tormosov and Filatov 1979, Yablokov 1985). This is in accordance with the negligible amounts of long-chain monounsaturated fatty acids found in the tissues of ringed seals from Lake Saimaa and Lake Ladoga. These fatty acids, which originate from crustacean wax esters are abundant in the tissues of marine seals (Käkelä *et al.* 1993, Käkelä and Hyvärinen 1997).

There is only sparse information available on the total fish consumption of adult ringed seals. According to Söderberg (1975), the daily need of the Baltic ringed seal for fish (based on an average body weight) is estimated to be about 3.5 kg. The Baltic ringed seal is the largest of the subspecies (mean weight about 90 kg, Helle 1979) and the daily food intake in the smaller Saimaa ringed seal (mean weight about 60 kg, Sipilä *et al.* 1996) must be lower. The results from our study of the captive Saimaa ringed seal showed that the mean consumption of offered fish per day was 2.2 kg (about 800 kg annually). In addition, the seal might have caught wild fish from the lake. The fish production in this kind of oligotrophic lake in Finland is 5–10 kg/ha (Toivonen 1972) and according to this, the fish production in our lake was about 200–400 kg per year. Thus, total fish consumption of the captive Saimaa seal was at least the measured 800 kg, but not over 1200 kg annually.

Although, the seal may have eaten some fish from the lake, we suggest that the amount of offered fish consumed is a good indicator of seasonal changes in total food consumption. Seasonal changes in food intake in ringed seals have been suggested in several previous studies (eg McLaren 1958, Lowry *et al.* 1980, Smith 1987, Ryg *et al.* 1990). Our study on the captive seal in seminatural conditions shows that Saimaa ringed seals exhibit a clear seasonal feeding cycle. The seal's consumption of the offered fish in springtime diminished and every year it also had

short total fasting periods. The low food-intake periods were almost at the same time in spring (May–June) in different years. In 1989, however, the low food-intake period occurred a month later. This later starting fasting period was also seen in the body weight of the seal. The seal weighed 70 kg at the beginning of July 1989, whereas in July of the previous year it had been 10 kg lighter. It is known that ringed seals usually lose weight in springtime. The weight loss is associated with the haul-out periods of the moulting seals, and changes in body mass are due mainly to changes in body fat (Ryg *et al.* 1990). The decreases in body weight of the ringed seal observed in earlier studies in spring time (eg Ryg *et al.* 1990), fit well with simultaneous fasting periods of our captive seal. In addition, radiotelemetry studies have also shown that during spring and early summer Saimaa ringed seals spend much more of their time hauling out than they do in late summer (Hyvärinen *et al.* 1995). After moulting, seals start to increase the amount of blubber by resuming feeding in early summer (McLaren 1958). In the present study the seal started to eat more actively after June, and eating was most intensive between August and November. These findings are contrary to those of Parsons (1977), who found that captive ringed seals consumed constant amounts of food throughout the year.

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References

- Bagge P. 1992. The macrocrustaceans (Branchiura and Peracarida) in Lake Saimaa. [In: Saimaa seminaari 1992 Tutkimus Saimaalla. M. Viljanen and S. Ollikainen, eds]. Publications of Karelian Institution, University of Joensuu, Joensuu: 103: 117–128. [In Finnish with English summary]
- Frost K. J. and Lowry F. L. 1981. Ringed, Baikal and Caspian seals. [In: Handbook of marine mammals Vol. 2. S. H. Ridgway and R. J. Harrison, eds]. Academic Press, London: 29–53.
- Gjertz I. and Lydersen C. 1986. The ringed seal (*Phoca hispida*) spring diet in northwestern Spitsbergen, Svalbard. *Polar Research* 4: 53–56.
- Helle E. 1979. Growth and size of the ringed seal *Phoca (Pusa) hispida* Schreber in the Bothnian Bay, Baltic. *Zeitschrift für Säugetierkunde* 44: 208–220.
- Helm R. G. 1983. Intestinal length of three California pinniped species. *Journal of Zoology*, London 199: 297–304.
- Helm R. G. 1984. Rate of digestion in three species of pinnipeds. *Canadian Journal of Zoology* 62: 1751–1756.
- Hyvärinen H., Hämäläinen E. and Kunnasranta M. 1995. Diving behavior of the Saimaa ringed seal (*Phoca hispida saimensis* Nordq.). *Marine Mammal Science* 11(3): 324–334.
- Hyvärinen H. and Nieminen M. 1990. Differentiation of the ringed seal in the Baltic Sea, Lake Ladoga and Lake Saimaa. *Finnish Game Research* 47: 21–27.
- Hyvärinen H., Sipilä T., Kunnasranta M. and Koskela J. T. 1998. Mercury pollution and the Saimaa ringed seal (*Phoca hispida saimensis*). *Marine Pollution Bulletin* 36 (1): 76–81.
- Hyvärinen H., Sipilä T. and Tyni P. 1984. Saimaannorpan biologiaa. [In: Saimaannorppa. P. Becker, ed]. Forssan Kirjapaino Oy, Forssa 58–75. [In Finnish with English summary]
- Härkönen T. 1986. Guide to the otoliths of the bony fishes of the northeastern Atlantic. Danbiu ApS. Biological Consultants, Denmark: 1–255.
- Jurvelius J., Salmi P. and Auvinen H. 1992. The effect of fluctuation vendace [*Coregonus albula* (L.)] stocks on professional fishery. [In: Saimaa seminaari 1992 Tutkimus Saimaalla. M. Viljanen and S.

- Ollikainen, eds]. Publications of Karelian Institution, University of Joensuu, Joensuu: 103: 239–248. [In Finnish with English summary]
- Käkelä R., Ackman R. G. and Hyvärinen H. 1995. Very long chain polyunsaturated fatty acids in the blubber of ringed seals (*Phoca hispida* sp.) from Lake Saimaa, Lake Ladoga, the Baltic Sea and Spitsbergen. *Lipids* 30: 725–731
- Käkelä R. and Hyvärinen H. 1997. Fatty acid compositions and vitamin A and E status of endangered freshwater ringed seals (from Finland and western Russia) differ from those of marine seals. *Recent Research Developments in Lipids Research* 1: 1–7.
- Käkelä R., Hyvärinen H. and Käkelä A. 1997. Vitamins A₁ (Retinol), A₂ (3,4-Didehydroretinol) and E (α -Tocopherol) in the liver and blubber of lacustrine and marine ringed seals. *Comparative Biochemistry and Physiology* 116B: 27–33.
- Käkelä R., Hyvärinen H. and Vainiotalo P. 1993. Fatty acid composition in liver and blubber of the Saimaa ringed seal (*Phoca hispida saimensis*) compared with that of the ringed seal (*Phoca hispida botnica*) and grey seal (*Halichoerus grypus*) from the Baltic. *Comparative Biochemistry and Physiology* 105B: 553–565.
- Lowry L. F. and Frost K. J. 1981. Feeding and trophic relationships of phocid seals and walruses in the eastern Bering Sea. [In: The eastern Bering Sea shelf: oceanography and resources. D. W. Hood and J. A. Calder, eds]. Office of Marine Pollution Assessment, NOAA 2: 813–824.
- Lowry L. F., Frost K. J. and Burns J. J. 1978. Food of ringed seals and Bowhead whales near Point Barrow, Alaska. *Canadian Field-Naturalist* 92 (1): 67–70.
- Lowry L. F., Frost K. J. and Burns J. J. 1980. Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 2254–2261.
- Lydersen C., Gjertz I. and Weslawski J. M. 1989. Stomach contents of autumn-feeding marine vertebrates from Hornsund, Svalbard. *Polar Record* 25 (153): 107–114.
- McLaren I. A. 1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic. *Bulletin of the Fisheries Research Board of Canada* 118: 1–97.
- Parsons J. L. 1977. Metabolic studies on ringed seals (*Phoca hispida*). M Sc thesis, University of Guelph, Ontario: 1–82.
- Power G. and Gregoire J. 1978. Predation by freshwater seals on the fish community of Lower Seal Lake, Quebec. *Journal of Fisheries Research Board of Canada* 35: 844–850.
- Ryg M., Smith T. G. and Øritsland N. A. 1990. Seasonal changes in body mass and body composition of ringed seals (*Phoca hispida*) on Svalbard. *Canadian Journal of Zoology* 68: 470–475.
- Sipilä T., Medvedev N. V. and Hyvärinen H. 1996. The Ladoga seal (*Phoca hispida ladogensis* Nordq.). *Hydrobiologia* 322: 193–198.
- Smith T. G. 1987. The Ringed Seal, *Phoca hispida*, of the Canadian Western Arctic. *Canadian Bulletin of Fisheries and Aquatic Sciences* 216: 1–81.
- Söderberg S. 1975. Feeding habits and commercial damage of seals in the Baltic. *National Swedish Environment Protection Board* 591: 66–75.
- Toivonen J. 1972. The fish fauna and limnology of large oligotrophic glacial lakes in Europe. *Journal of Fisheries Research Board of Canada* 29: 629–637.
- Toivonen J. 1985. The fish fauna and the fisheries in the Lake Saimaa. [In: Saimaa seminaari 1985 Saimaan nykytila. M. Viljanen, ed]. Publications of Karelian Institution, University of Joensuu, Joensuu: 71: 193–201. [In Finnish with English summary]
- Tormosov D. D. and Filatov I. J. 1979. Ladozhskaya nerpaob'ekt issledovaniya. *Priroda* 3: 103–107. [In Russian]
- Weslawski J. M., Ryg M., Smith T. G. and Øritsland N. A. 1994. Diet of ringed seals in a fjord of west Svalbard. *Arctic* 47: 109–114.
- Wheeler A. 1978. Key to the fishes of northern Europe. Frederic Warne Publications, London: 1–380.
- Yablokov A. 1985. Marine mammal – Fishery interactions in the Baikal and Ladoga Lakes and in the Caspian and White Seas. [In: Marine Mammals and Fisheries. J. R. Beddington, R. J. H. Beverton and D. M. Lavigne, eds]. George Allen & Unwin Publishers, London: 106–110.