Food and feeding of diving ducks breeding at Lake Mývatn, Iceland

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The food and feeding habits of diving ducks breeding at Lake Mývatn in northeastern Iceland were studied. About 1,280 fishing-net casualties (adults and young) of *Aythya marila, A. fuligula, Bucephala islandica, Clangula hyemalis, Melanitta nigra,* and *Mergus serrator* were examined to determine the composition of their diets on the basis of oesophagus contents. *M. serrator* had been feeding almost exclusively on sticklebacks *Gasterosteus aculeatus.* The other five species overlapped considerably in their food habits and the adults had been feeding chiefly on chironomid larvae (Diptera, Chironomidae) which constituted the bulk of the benthic animal food resources of the lake. Although incompletely segregated in terms of food the five species differed slightly (though statistically significant) from each other with respect to dietary composition. *A. fuligula* and *B. islandica* took more Molluscs (*Lymnaea* spp.) than *A. marila* and especially *C. hyemalis* and *M. nigra.* The two latter species and *A. marila* were feeding extensively on crustaceans (Cladocera). The two *Aythya* species had eaten relatively more seeds than the others. Some of the differences between the species could be associated with differences in preferences for feeding habitats and selection of feeding areas. Differences in the composition of the diet between the sexes were observed in all species except *M. serrator.* Seasonal and annual changes in the composition of the diets were associated with differences in the abundance and availability of food. Ducklings of the diving ducks also subsisted chiefly on chironomids (adults and larvae) but as with the adults there were some specific differences.

Fourteen species of ducks breed at Lake Mývatn in northeastern Iceland (65°35′ N, 17°00′W). There are six species of surface feeders (genus *Anas*), which subsist mainly on plant food, and eight species of diving ducks (genera *Aythya, Bucephala, Clangula, Melanitta,* and *Mergus*), feeding predominantly on animal food obtained by diving. The purpose of this study was to evaluate differences in the composition of diet and feeding habitat between the Scaup *Aythya marila,* Tufted Duck *Aythya fuligula,* Barrow's Goldeneye *Bucephala islandica,* Long-tailed Duck *Clangula hyemalis,* Common Scoter *Melanitta nigra,* and Red-breasted Merganser *Mergus serrator.*

This paper is a part of a long-term study initiated in 1960; most of the data on the food ecology of the ducks were collected in 1968—1970.

Study area

Mývatn is the third largest lake (38 km²) in Iceland and quite shallow (mostly less than 4 m in depth). It is considered to be one of the most productive lakes in Iceland (STEFÁNSSON 1970) and supports many breeding ducks. In 1965—1970 the total size of the duck populations varied between about 13,000

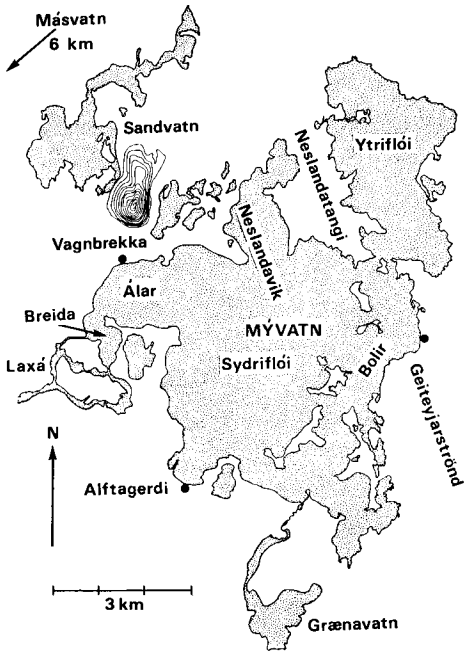

FIGURE 1. Lake Mývatn with the names of localities mentioned in the text. Black circles indicate farms referred to.

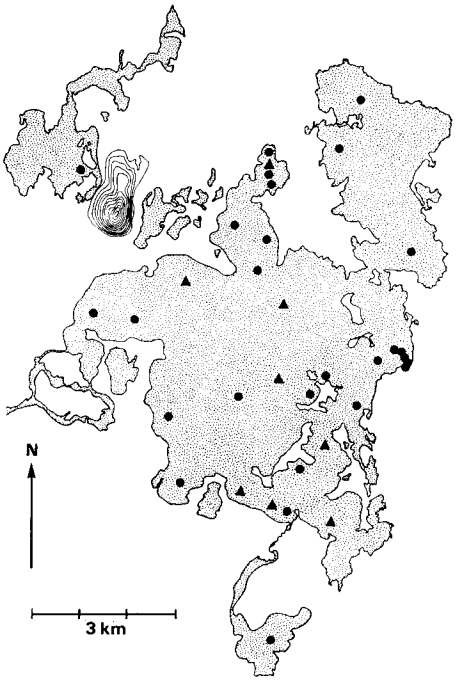

FIGURE 2. Benthic sampling stations used in 1970. Black triangles indicate sampling stations used in 1968—1970.

and 18,000 pairs of which the six above-mentioned diving duck species made up about 10,000 to 15,000 pairs (BENGTSON in press).

The benthic communities of Mývatn are relatively simple and larvae and pupae of several species of chironomids (Diptera, Chironomidae), molluscs (*Lymnaea* spp. and *Pisidium* spp.), and algae (*Cladophora* spp. and *Nostoc* spp.) dominate. The subaquatic macrovegetation is patchy and comprises milfoils (*Myriophyllum spicatum* and *M. alterniflorum*) and pondweeds (*Potamogeton perfoliatus* and *P. filiformis*).

Zooplankton, mainly *Daphnia longispina* (Cladocera), occur chiefly in the central parts of Sydriflói (see Figure 1) and in Neslandavik (where there are several additional species). Three species of fish occur in Mývatn: Char *Salvelinus alpinus,* Trout *Salmo trutta,* and Three-spined Stickleback *Gasterosteus aculeatus,* all of which are common.

Material and methods

In 1968—1970 about 1,280 fishing-net casualties were obtained from all parts of the lake: Scaup, 209 adult and 250 ducklings, Tufted Duck, 72 and 135, Barrow's Goldeneye, 48 and 34, Long-tailed Duck, 105 and 33, Common Scoter, 93 and 157, and Red-breasted Merganser, 64 and 79. Since practically all the birds obtained were drowned during feeding activities many of them were filled with food. The composition of the diet, which is entirely based on analyses of the oesophagus contents, is given as per cent by wet weight, calculated by converting the number of individual food items to grams wet weight (BENGTSON in press), and as constancy (per cent by occurrence). Mollusc weights include the shells. Plant food, other than seeds and *Nostoc* spp., was frequently found in the oesophagus but could not be weighed. However, this was not considered a serious bias because it rarely exceeded one per cent of the total oesophagus content. By using oesophagus contents and calculating weights from the number of individual food items it is thought that biases resulting from different rates of digestion of food were reduced; although some small or soft-bodied organisms (e.g. oligochaetes) may have been missed. Per cent by weight and constancy may, and often do, complement each other (DIRSCHL 1969) so that, for instance,

a food item that comprises a relatively small portion of the diet by weight may in fact be eaten quite frequently (e.g. adult insects) and a food item that is relatively seldom taken may by weight constitute a relatively large proportion of the total diet (e.g. eggs of and adult sticklebacks).

In 1968, 1969, and 1970 benthic samples were taken at 8, 19, and 33 localities in Mývatn, respectively (Figure 2). Sampling procedures and results are described elsewhere (BENGTSON in press). For comparison benthic samples were taken in 1970 in the smaller lakes Graenavatn, Sandvatn, and Másvatn (Figure 1). No quantitative data on the abundance of plankton, vegetation, or fish are available.

Five feeding habitats were distinguished: (1) potholes which are common west and east of the lake, (2) shallow waters close to the shore and with abundant aquatic reeds (chiefly sedges *Carex* spp.) which are restricted to a few places only, (3) shallow waters close to the shore and with little or no reeds, (4) deeper open waters which comprise the largest area, and (5) running waters (chiefly the river Laxá). The habitats are not equal in size and number (3) and (4) are the largest and where usually most ducks are to be seen. For each of the habitats the mean density of each species of duck was determined. The five mean values obtained were then added for each species and the per cent of the total was calculated for each habitat. These percentages are taken to indicate feeding habitat preferences.

Food resources

The results of the benthic samplings in 1968—1970 are given by BENGTSON (in press) and for the end of July and first week of August in 1970 in Table 1. In 1970 (when the largest number of samples were taken) there were no great differences in the abundance of chironomid larvae between the subdivisions of the lake, except for Ytriflói which on the whole has a quantitatively poorer benthic animal community than other parts. Molluscs were found everywhere, although *Lymnaea* was found in highest abundance close to the shores and in Mývatn not deeper than 3 m (in Másvatn at a depth of 8—9 m). Other groups of bottom living animals that were of little or no importance as food for the ducks were oligochaetes which were abundant, caddis flies (Trichoptera) which were common especially in parts of Bolir, and leeches (Hirudinae) which were found in highest density in Álar.

Seasonal changes in the abundance were found in the chironomid larvae which increased from early June to early August. Each summer there are usually two to four major hatching peaks of chironomids starting at the end of May or beginning of June. During and immediately after such peaks there are numerous adult insects and pupal cases floating on the water and accumulating along drift lines of the shores. Observations also suggest that there is an increase in the abundance of Cladocera in July and August.

TABLE 1. Local differences in the abundance (individuals/m²) of benthic animals in the Mývatn area at the end of July and first week of August 1970.

Sub-area	No. of localities	Mean depth (m)	Chironomidae (larvae)	*Lymnaea* spp.	*Pisidium* spp.
Ytriflói	3	1.1	329	0	13
Bolir (northern)	9	2.5	1,755	181	193
Bolir (southern)	6	2.0	777	35	119
Sydriflói	5	2.7	2,332	0	205
Álar	3	2.4	1,149	105	9
Neslandavik (southern)	3	2.6	895	0	88
Neslandavik (northern)	4	1.5	1,935	20	86
Graenavatn	1	1.0	5,369	421	26
Sandvatn	1	1.6	10,002	0	316
Másvatn	1	8—9	1,290	132	1,026

Annual variations in the abundance of benthic animals were also recorded. In 1970 the abundance of chironomid larvae was significantly lower than in 1968 and 1969 and in July 1970 the abundance of *Lymnaea* and *Pisidium* was also significantly lower than at the corresponding times in 1968 and 1969 (BENGTSON in press).

Some kinds of potential duck food could not be quantified including eggs of sticklebacks which are found in abundance in shallow waters early in the summer, adult sticklebacks which are common and some are usually also to be found dead along drift lines of the shores where also much *Nostoc* is washed ashore.

Major feeding areas

From May to mid-June the duck pairs are dispersed all over the study area and there are no dense aggregations of ducks until in the later part of June. In July and August large flocks of moulting diving ducks feed in Mývatn. The largest numbers are usually found in Álar, southern parts of Neslandavik, and especially in the central parts of Sydriflói. These concentrations of ducks include most of the Scaup, Long-tailed Duck, Common Scoter (only females since the males depart from the breeding grounds at the end of June), and some Tufted Duck. The latter species is, however, relatively more numerous around the large islands in Bolir, in the potholes on Neslandatangi, and along the eastern and southern shores of the lake. Flocks of feeding Barrow's Goldeneye are most often found in the southern parts of Sydriflói, eastern Álar, on Breida, and along Laxá. The Red-breasted Merganser feeds in all parts of the lake but especially in shallow waters along the eastern shores.

Food and feeding of the different species

For each species investigated the results of the study are presented in the following order:

Feeding habitat preference (Table 2).
Composition of the diets of males and females (Table 3).
Seasonal changes in the composition of the diet (Table 5).
Annual variations in the composition of the diet (Table 6).
Composition of the diets of ducklings of different ages (Table 7).

Aythya marila

The Scaup preferred to feed on relatively deep offshore waters and this was also the kind of places where most birds were usually seen (e.g. in the central parts of Sydriflói).

The males had eaten mainly chironomid larvae and some fish-eggs and molluscs. Chironomid larvae and molluscs (chiefly *Lymnaea*) were important also to the females which had also taken more fish-eggs, sticklebacks, and seeds than the males. Most of the seeds eaten were *Carex* spp. (Table 4).

The importance of chironomid larvae increased with advancing season. Fish-eggs and molluscs were mostly eaten early in the summer and Cladocera in July and August. Seeds were relatively more important in May and June than later in the summer.

In 1970, when chironomid larvae were relatively scarce, molluscs, sticklebacks, and seeds were eaten relatively more frequently than in preceding years. Fish-eggs were relatively important in 1968 and 1970 but absent from the samples in 1969. The opposite was true of Cladocera.

The ducklings take more food from the surface than the adults. Newly hatched and small ducklings fed mainly on chironomid larvae and seeds, al-

TABLE 2. Feeding habitats of diving ducks in the Mývatn area. The figures (percentages) refer to indices of preference (see the text).

Feeding habitat		Potholes	Lake			Running water
			Near shore	Near shore	Offshore	
Shore-line aquatic vegetation		Plenty	Some	Sparse or none	None	Little
Approximate depth (m)		0.5—2.0	1.5	1.5—2.0	1.5—3.5	0.5—1.5
Species	No. of individuals recorded	Preference (percentage)				
A. marila	39,112	8	10	21	54	7
A. fuligula	31,514	18	29	20	28	5
B. islandica	11,536	1	5	36	19	39
C. hyemalis	6,319	8	11	21	50	10
M. nigra	6,015	13	7	18	60	2
M. serrator	5,992	5	35	39	15	6

though they also took some Cladocera and adult insects (chironomids) that were floating on the water or sitting on vegetation. As the young grew larger seeds and adult insects became less important and more Cladocera, molluscs (chiefly *Lymnaea*), and chironomid larvae were taken. Ducklings less than two weeks old had eaten mostly seeds of *Carex* spp. and older ducklings relatively more *Hippuris* and *Batrachium* (Table 8).

Aythya fuligula

The Tufted Duck favoured all types of feeding habitat except running water, and did not show any strong preference.

There was no significant difference in the composition of the diet between the sexes in terms of per cent by weight ($\chi^2_{(8)} = 5.22$; $0.80 > P > 0.70$). Molluscs (chiefly *Lymnaea*), chironomid larvae and to some extent fish-eggs (especially by weight) were the most important food items. Only the males had eaten Cladocera. Seeds were often eaten by both sexes; mainly *Hippuris* and some *Potamogeton* spp. (Table 4).

No marked seasonal changes in the diet were observed. The decrease in the proportions of chironomid larvae and *Lymnaea* in July are probably due to the relatively small sample and the large amout of sticklebacks eaten. Fish-eggs were only taken early, and Cladocera late, in the summer.

Chironomid larvae were, by constancy, the most important food in all years but, by weight, fish-eggs dominated the diet in all three years and in 1969 also *Lymnaea* constituted a large portion. No sticklebacks were recorded in 1969.

As in the previous species the ducklings take more food from the surface than the adults. Newly hatched and small ducklings fed almost entirely on seeds and adult insects. When the young were about small to half-grown they switched to *Lymnaea,* and chironomid larvae also became important. Most of the seeds eaten by less than two weeks old ducklings were *Carex* spp. whereas older ducklings took mainly *Potamogeton* spp. and *Batrachium* (Table 8).

TABLE 3. The composition of the diets of the sexes of diving ducks in Mývatn in terms of constancy (c, per cent by occurrence) and per cent by wet weight (w). Symbols: + less than 0.1 %, ++ 0.1—0.5 %, and — no traces.

		Chironomid larvae		*Lymnaea* spp.		*Pisidium* spp.		Cladocera		*Gasterosteus aculeatus*		Fish-eggs		Misc. animal food		Seeds		*Nostoc* spp.		Misc. plant food	
	(*n*)	c	w	c	w	c	w	c	w	c	w	c	w	c	w	c	w	c	w	c	w
A. marila																					
♀♀	(119)	54	17	42	10	29	1	25	2	22	10	19	55	7	+	24	5	2	+	86	+
♂♂	(90)	78	73	13	4	20	1	4	1	—	—	9	21	4	+	11	++	2	+	93	+
A. fuligula																					
♀♀	(32)	38	26	63	22	31	++	—	—	31	6	13	45	6	+	31	++	13	+	31	+
♂♂	(40)	80	13	35	18	10	++	10	1	10	3	20	64	5	+	45	1	—	—	70	+
B. islandica																					
♀♀	(24)	75	38	25	33	—	—	—	—	—	—	8	11	17	18	17	+	—	—	92	+
♂♂	(24)	42	7	33	1	—	—	8	+	8	+	17	92	—	—	8	+	17	+	75	+
C. hyemalis																					
♀♀	(52)	81	86	—	—	4	+	19	4	4	4	4	7	4	+	4	+	4	+	85	+
♂♂	(53)	74	62	4	++	—	—	—	—	7	2	11	35	4	+	7	+	—	—	82	+
M. nigra																					
♀♀	(81)	83	64	5	10	7	5	2	1	—	—	2	16	5	+	17	4	2	+	98	+
♂♂	(12)	33	9	—	—	—	—	33	3	—	—	33	86	33	+	17	3	—	—	33	+
M. serrator																					
♀♀	(32)	19	1	6	+	—	—	—	—	81	99	—	—	19	+	19	+	—	—	31	+
♂♂	(32)	—	—	—	—	25	++	—	—	88	93	6	7	—	—	19	++	—	—	13	+

TABLE 4. Composition (per cent of total) of seeds found in oesophagus analyses of adult diving ducks from Mývatn.

Species	*A. marila*	*A. fuligula*	*B. islandica*	*C. hyemalis*	*M. nigra*	*M. serrator*
Carex spp.	24	10	25	13	19	—
Potamogeton spp.	16	24	60	25	43	—
Hippuris vulgaris	15	49	10	50	12	100
Batrachium trichophyllum	7	10	—	—	12	—
Menyanthes trifoliata	—	2	—	—	—	—
Empetrum spp.	2	—	—	—	12	—
Graminae	2	—	—	—	—	—
Unidentified	34	5	5	13	—	—
Total no. of seeds	124	82	20	16	32	10

Bucephala islandica

Barrow's Goldeneye preferred to feed in running water and was usually common on the river Laxá but also frequented not too deep waters close to shores with sparse or no vegetation.

The females had mostly eaten chironomid larvae and *Lymnaea*. It should also be noted that almost everything listed under the heading of miscellaneous animal food (Table 3) consisted of larvae of simuliids (Diptera, Simuliidae) which were found in some birds obtained near the outflow and upper reaches of the river Laxá. The males had been feeding on fish-eggs, chironomid larvae, and *Lymnaea*. Most of the seeds taken were *Potamogeton* spp. (Table 4). Seasonal changes in the diet were restricted to *Lymnaea* being slightly less important in late summer and a possible increase in the utilization of chironomid larvae with advancing season. Fish-eggs were only eaten in June and July.

As to annual variations the samples were relatively small in 1968 and 1969 but it appears that chironomid larvae were less important in 1970 when relatively more fish-eggs were eaten.

Newly hatched and small ducklings subsisted chiefly on *Lymnaea* and some chironomid larvae and adults. As the young grew older the importance of chironomid larvae increased and comprised nearly the entire diet of large and full-grown young. Seeds were not important to young Barrow's Goldeneye.

Clangula hyemalis

The Long-tailed Duck preferred to feed on relatively deep offshore waters and most birds were seen in the central parts of the lake.

Both males and females fed predominantly on chironomid larvae and there was no significant difference in the composition of the diet by weight between the sexes ($\chi^2_{(8)} = 14.82$; $0.10 > P > 0.05$). The males, however, had eaten more fish-eggs than the females and only the latter had been feeding on Cladocera.

The importance of chironomid larvae as food increased towards the end of the summer. Fish-eggs were relatively important only in June and July and Cladocera in August.

Chironomid larvae was the main food in all years, although not in terms of per cent by weight in 1970 when large quantities of fish-eggs were taken. In 1969 the Long-tailed Duck fed relatively more on Cladocera than in the other years and sticklebacks were eaten only in 1970.

Newly hatched to half-grown ducklings were feeding almost exclusively on Cla-

TABLE 5. Seasonal changes in the composition of the diets of adult diving ducks in Mývatn in terms of constancy (c) and per cent by wet weight (w) Symbols as in Table 3.

		Chironomid larvae		*Lymnaea* spp.		*Pisidium* spp.		Cladocera		*Gasteros-teus aculeatus*		Fish-eggs		Misc. animal food		Seeds		*Nostoc* spp.		Misc. plant food	
	(*n*)	c	w	c	w	c	w	c	w	c	w	c	w	c	w	c	w	c	w	c	w
A. marila																					
May	(4)	100	95	—	—	—	—	—	—	—	—	—	—	—	—	100	5	—	—	100	+
June	(30)	33	5	53	10	67	2	7	1	7	2	40	66	13	+	27	15	7	+	93	+
July	(65)	40	11	52	10	43	1	15	1	37	14	28	64	3	++	22	++	3	+	80	+
August	(85)	84	92	12	4	5	1	22	3	—	—	—	—	7	++	12	++	—	—	96	+
September	(24)	100	99	—	—	—	—	8	+	—	—	—	—	8	+	8	+	—	—	92	+
A. fuligula																					
June	(6)	67	10	67	42	67	+	—	—	—	—	67	48	—	—	67	+	—	—	67	+
July	(20)	40	16	40	16	20	+	—	—	70	33	40	36	20	+	50	+	—	—	30	+
August	(31)	65	38	39	54	13	+	7	2	—	—	—	—	—	—	19	4	7	+	52	+
September	(15)	80	16	67	80	13	2	13	+	—	—	—	—	—	—	53	2	—	—	80	+
B. islandica																					
June	(10)	60	13	40	17	—	—	—	—	—	—	20	27	20	44[1]	—	—	20	+	80	+
July	(18)	22	+	33	1	—	—	11	+	—	—	22	99	—	—	—	—	11	+	89	+
August	(18)	78	93	11	7	—	—	—	—	11	+	—	—	—	—	22	+	—	—	89	+
C. hyemalis																					
June	(4)	50	8	50	7	—	—	—	—	—	—	50	85	—	—	—	—	—	—	100	+
July	(55)	80	74	4	+	4	+	7	1	11	6	11	19	4	+	7	+	4	+	76	+
August	(30)	80	96	—	—	—	—	20	4	—	—	—	—	7	+	7	+	—	—	93	+
September	(16)	100	100	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	88	+
M. nigra																					
June	(12)	67	38	—	—	—	—	17	4	—	—	—	—	17	+	33	58	—	—	67	+
July	(33)	73	35	12	12	12	6	6	+	—	—	18	47	18	+	18	+	—	—	97	+
August	(10)	100	94	—	—	20	+	20	6	—	—	—	—	—	—	20	+	—	—	100	+
September	(38)	100	100	—	—	—	—	—	—	—	—	—	—	—	—	11	+	—	—	100	+

[1] Simuliid larvae.

TABLE 6. Differences between years in the composition of the diets of adult diving ducks in Mývatn in terms of constancy (c) and per cent by wet weight (w). Symbols as in Table 3.

		Chironomid larvae		*Lymnaea* spp.		*Pisidium* spp.		Cladocera		*Gasterosteus aculeatus*		Fish-eggs		Misc. animal food		Seeds		*Nostoc* spp.		Misc. plant food	
	(*n*)	c	w	c	w	c	w	c	w	c	w	c	w	c	w	c	w	c	w	c	w
A. marila																					
1968	(75)	72	30	35	7	24	1	5	1	8	3	24	58	—	—	16	+	—	—	91	+
1969	(70)	83	69	11	11	11	1	29	4	3	13	—	—	11	1	17	+	—	—	89	+
1970	(64)	34	10	44	13	41	2	16	3	28	18	19	35	6	+	22	20	3	+	94	+
A. fuligula																					
1968	(8)	100	3	50	4	25	+	—	—	50	11	50	83	25	+	25	+	—	—	100	+
1969	(44)	64	12	50	35	14	1	9	1	—	—	5	49	5	1	40	1	5	+	55	+
1970	(20)	50	21	40	3	30	1	—	—	50	11	30	64	—	—	40	+	—	—	50	+
B. islandica																					
1968	(13)	92	63	54	++	—	—	—	—	—	—	8	5	23	32	31	+	—	—	100	+
1969	(4)	50	20	100	77	—	—	—	—	—	—	—	—	25	+	25	4	100	+	50	+
1970	(31)	55	1	39	10	—	—	7	+	7	+	19	89	—	—	3	+	—	—	87	+
C. hyemalis																					
1968	(28)	86	88	7	+	—	—	—	—	—	—	14	12	—	—	7	+	—	—	93	+
1969	(35)	80	93	—	—	—	—	23	7	—	—	—	—	11	+	6	+	11	+	91	+
1970	(42)	71	39	—	—	5	+	5	1	14	9	10	51	—	—	—	—	5	+	86	+
M. nigra																					
1968	(12)	50	24	17	1	17	+	17	+	—	—	33	75	17	+	17	+	—	—	83	+
1969	(59)	85	70	3	12	7	7	3	1	—	—	3	10	3	+	17	++	—	—	100	+
1970	(22)	73	29	—	—	—	—	9	2	—	—	18	44	18	+	9	25	9	+	82	+
M. serrator																					
1968	(6)	33	+	—	—	—	—	—	—	100	100	—	—	33	+	—	—	—	—	—	—
1969	(16)	25	1	13	++	—	—	—	—	63	99	—	—	13	+	38	++	—	—	50	+
1970	(42)	—	—	—	—	19	++	—	—	91	94	5	6	5	+	14	++	—	—	14	+

		Chironomid larvae		*Lymnaea* spp.		*Pisidium* spp.		Cladocera		*Gasterosteus aculeatus*		Fish-eggs		Misc. animal food		Seeds		*Nostoc* spp.		Misc. plant food	
	(*n*)	c	w	c	w	c	w	c	w	c	w	c	w	c	w	c	w	c	w	c	w
A. marila																					
nh	(28)	36	46	—	—	—	—	21	8	—	—	—	—	64	8	86	39	—	—	57	+
s	(63)	3	+	—	—	—	—	3	7	—	—	—	—	19	7	89	86	10	+	48	+
shg	(28)	43	36	43	25	7	+	14	32	—	—	—	—	57	7	14	+	7	+	29	+
hg	(44)	50	62	36	27	18	6	—	—	—	—	—	—	27	1	14	4	27	+	55	+
hgl	(29)	41	39	14	61	14	+	—	—	—	—	—	—	—	—	35	+	7	+	62	+
l	(26)	79	72	29	22	36	3	7	3	—	—	—	—	36	+	14	+	—	—	93	+
fg	(32)	100	70	13	12	31	18	13	1	—	—	6	+	6	+	38	+	6	+	88	+
A. fuligula																					
nh	(33)	—	—	—	—	—	—	—	—	—	—	—	—	30	4	97	96	—	—	36	+
s	(41)	—	—	—	—	—	—	5	6	—	—	—	—	34	6	83	83	5	6	34	+
shg	(6)	—	—	33	97	—	—	—	—	—	—	—	—	33	3	—	—	33	+	—	—
hg	(20)	30	21	60	77	—	—	10	1	—	—	—	—	20	+	10	1	—	—	30	+
hgl	(6)	66	29	66	71	33	+	—	—	—	—	—	—	—	—	33	+	33	+	33	+
l	(17)	82	43	35	48	12	+	—	—	12	5	—	—	24	+	35	2	24	2	47	+
fg	(12)	83	20	83	80	33	+	—	—	—	—	—	—	—	—	33	+	17	+	67	+
B. islandica																					
nh-shg	(14)	71	22	57	67	—	—	—	—	—	—	—	—	100	11	14	+	—	—	14	+
hg-hgl	(10)	80	60	20	20	—	—	—	—	—	—	—	—	100	20	—	—	—	—	40	+
l-fg	(10)	100	94	—	—	—	—	—	—	—	—	—	—	—	—	20	+	20	6	60	+
C. hyemalis																					
nh-shg	(6)	50	+	—	—	—	—	100	100	—	—	—	—	—	—	—	—	—	—	100	+
hg-hgl	(15)	60	90	—	—	20	+	40	7	—	—	—	—	20	2	40	+	—	—	40	+
l-fg	(12)	50	87	—	—	—	—	25	3	25	10	—	—	—	—	—	—	25	+	50	+
M. nigra																					
nh	(6)	—	—	—	—	—	—	—	—	—	—	—	—	67	+	100	100	—	—	67	+
s	(10)	—	—	—	—	—	—	—	—	—	—	—	—	20	+	80	100	—	—	100	+
shg	(12)	67	77	—	—	—	—	33	19	—	—	—	—	17	4	—	—	17	+	67	+
hg	(51)	59	81	4	+	4	+	31	14	4	3	—	—	12	+	51	1	12	2	71	+
hgl	(45)	76	82	9	+	18	1	44	18	4	+	—	—	22	+	18	+	4	+	93	+
l	(25)	88	97	—	—	—	—	24	3	—	—	8	+	8	+	8	+	—	—	96	+
fg	(8)	100	100	—	—	—	—	25	+	—	—	—	—	—	—	—	—	—	—	25	+

TABLE 8. Composition (per cent of total) of seeds found in oesophagus analyses of ducklings of diving ducks from Mývatn. + indicates less than 0.5 %.

	Smaller ducklings[1]				Larger ducklings[2]			
	A. marila	*A. fuligula*	*M. nigra*	*M. serrator*	*A. marila*	*A. fuligula*	*M. nigra*	*M. serrator*
Carex spp.	56	76	28	47	—	—	4	—
Potamogeton spp.	10	3	51	19	3	43	7	—
Hippuris vulgaris	18	10	5	5	42	22	11	—
Batrachium trichophyllum	5	1	—	—	52	35	67	—
Menyanthes trifoliata	3	5	—	5	—	—	—	—
Sparganium angustifolium	—	1	—	—	—	—	—	—
Scirpus spp.	1	3	—	2	—	—	—	—
Comarum palustre	+	—	2	3	—	—	—	—
Polygonum viviparum	—	—	—	2	—	—	—	—
Empetrum spp.	5	1	8	6	3	—	4	—
Betula pubescens	—	+	—	—	—	—	—	—
Unidentified	2	1	6	11	—	—	7	—
Total no. of seeds	662	1,760	122	132	58	28	54	—

[1] Less than two weeks old. [2] More than two weeks old.

docera. When the young were half-grown and larger chironomid larvae became the main food, although some Cladocera were also taken. Only a few molluscs (*Pisidium*) were eaten and seeds were not important.

Melanitta nigra

The Common Scoter preferred open and relatively deep waters and like the Scaup and Long-tailed Duck most of the birds were usually seen feeding in the central parts of the lake.

The females fed mainly on chironomid larvae but also took some fish-eggs, molluscs (*Lymnaea*), and seeds. Only a small sample of males was available for analyses and they had eaten mainly fish-eggs and some chironomid larvae, Cladocera, and seeds. The dominant type of seeds was *Potamogeton* spp. (Table 4).

Chironomid larvae and Cladocera increased in importance with advancing season. Seeds were mostly eaten early in the summer and molluscs and fish-eggs in July.

In all three years chironomid larvae were eaten extensively although in 1968 and 1970 they were exceeded by fish-eggs in terms of weight. No molluscs were recorded in the samples from 1970 but relatively large quantities of seeds.

Ducklings less than half-grown had mainly been feeding on adult insects and seeds (chiefly *Potamogeton* spp.; Table 8) but thereafter chironomid larvae and some Cladocera became the most important food items. Ducklings more than two weeks old were eating relatively more seeds of *Batrachium* than smaller ducklings (Table 8).

TABLE 7. ← The composition of the diets of diving duck ducklings in Mývatn in terms of constancy (c) and per cent by wet weight (w). The age-classes of ducklings are abbreviated as follows: newly hatched (nh), small (s), small to half-grown (shg), half-grown (hg), half-grown to large (hgl), large (l), and full-grown (fg); all referring to the size of the duckling in relation to the size of an adult of the same species. Symbols as in Table 3.

TABLE 9. Comparison between composition of benthic samples and oesophagus contents of diving ducks caught at the sampling localities within three days of the sampling. Figures are weight percentages. + indicates less than 0.5 %.

Area/species	*n*	Chironomid larvae	*Lymnaea*	*Pisidium*	Cladocera	Fish-eggs	Seeds	Others
Geiteyjarströnd (July 21, 1969)	4	73	20	6	—	—	2	+
A. marila (ad.)	2	73	26	1	—	—	—	+
A. marila (hg)	4	69	24	—	—	—	2	5
A. fuligula (hg)	5	—	100	+	—	—	+	—
B. islandica (shg)	7	37	50	—	—	—	3	10
C. hyemalis (hg)	1	25	—	—	—	—	—	75[1]
Alftagerdi (July 26, 1970)	16	79	—	13	+	—	—	8
A. marila (ad.)	5	72	—	28	—	—	—	—
A. fuligula (ad.)	1	100	—	—	—	—	—	—
B. islandica (ad.)	2	88	—	—	12	—	—	+
C. hyemalis (ad.)	6	100	—	—	—	—	—	—
Vagnbrekka (August 2-3, 1970)	16	36	37	3	+	—	—	24[2]
A. marila (ad.)	7	20	27	3	44	5	—	—
A. fuligula (ad.)	2	—	10	+	—	89	—	+
B. islandica (ad.)	6	—	1	—	—	99	—	—
C. hyemalis (ad.)	5	19	—	1	9	71	—	—

[1] Sticklebacks. [2] Trichoptera, Hirudinae, and Oligochaeta.

Mergus serrator

The Red-breasted Merganser preferred relatively shallow waters close to the shores for feeding.

Both sexes were feeding predominantly on sticklebacks. No seasonal or annual variations in the composition of the diet were found.

Newly hatched and small ducklings (a total of 65 young) had mainly eaten sticklebacks (constancy 63 per cent and by weight 84 per cent) but also some adult insects (94 and 8 per cent) and seeds (72 and 7 per cent); mainly of *Carex* spp. (Table 8). Five half-grown young had eaten sticklebacks exclusively and 9 large and full-grown young sticklebacks (100 and 96 per cent), Cladocera (3 per cent by weight), and traces of adult insects, chironomid larvae, and some plant matter.

Composition of the diet in relation to abundance and availability

There are several interrelated factors that may determine or at least affect the composition of the diets of the ducks. The birds may be restricted anatomically or in their diving abilities to certain types of food or their diets may simply reflect the abundance and/or availability of the different food items in a certain area and at a certain time.

In Table 9 the oesophagus contents of diving ducks obtained from near the farms Geiteyjarströnd, Alftagerdi, and Vagnbrekka (Figure 1) are compared with benthic samples of the food resources in the same places and on the same days (end of July and early August) that the ducks were caught. The comparisons are biased in the respect that benthic sampling does not give reliable

TABLE 10. The composition of the diets (in per cent by wet weight) of adult diving ducks caught in the same places and within the same limited period of time (3—5 days) in Mývatn. Figures in brackets refer to number of ducks (= constancy). Symbols as in Table 3.

Case and species		*n*	Chironomid larvae	*Lymnaea* spp.	*Pisidium* spp.	Cladocera	*Gasterosteus aculeatus*	Fish-eggs	Misc. animal food	Seeds
I: Neslandavik, July 1969										
C. hyemalis	♀♀	5	98 (4)	—	—	2 (2)	—	—	+ (1)	++ (1)
M. nigra	♀♀	8	97 (7)	—	—	2 (1)	—	—	—	1 (2)
II: Álar, August 1969										
A. marila	♂♂	5	66 (4)	—	—	34 (1)	—	—	—	—
„	♀♀	12	75 (12)	1 (1)	—	24 (9)	—	—	+ (2)	—
A. fuligula	♂♂	9	30 (7)	63 (3)	—	5 (2)	—	—	—	2 (3)
C. hyemalis	♂♂	5	100 (5)	—	—	—	—	—	+ (1)	+ (1)
„	♀♀	3	41 (3)	—	—	59 (2)	—	—	—	—
III: Álar, July 1970										
A. marila	♀♀	9	2 (2)	9 (5)	1 (3)	1 (1)	15 (3)	73 (4)	+ (1)	+ (1)
C. hyemalis	♀♀	4	12 (2)	—	+ (1)	7 (1)	31 (1)	50 (1)	—	—
IV: Álar, July 1968										
A. marila	♂♂	15	100 (14)	—	—	—	—	—	—	++ (2)
C. hyemalis	♂♂	7	100 (7)	—	—	—	—	—	—	—
V: Sydriflói, July 1970										
A. marila	♂♂	3	100 (3)	—	—	—	—	—	—	—
„	♀♀	5	71 (3)	6 (1)	1 (2)	22 (1)	+ (1)	—	—	—
A. fuligula	♂♂	2	100 (2)	—	—	—	—	—	—	—
B. islandica	♂♂	6	2 (3)	—	—	+ (1)	+ (1)	98 (1)	—	++ (1)
„	♀♀	3	100 (3)	—	—	—	—	—	—	—
C. hyemalis	♂♂	6	100 (6)	—	—	—	—	—	—	—
„	♀♀	4	100 (4)	—	—	—	—	—	—	—
M. nigra	♀♀	3	100 (3)	—	—	—	—	—	—	—
VI: Bolir (southern), July 1968										
A. marila	♀♀	7	+ (1)	29 (6)	4 (4)	2 (1)	12 (2)	53 (5)	—	+ (1)
A. fuligula	♀♀	2	1 (2)	5 (2)	++ (1)	—	10 (1)	84 (1)	—	+ (1)
VII: Bolir (southern), August 1969										
A. marila	♀♀	2	88 (1)	12 (1)	++ (1)	—	—	—	—	—
A. fuligula	♀♀	5	32 (4)	64 (3)	2 (1)	—	—	—	—	2 (2)
VIII: Bolir (northern), September 1969										
A. marila	♀♀	6	100 (6)	—	—	—	—	—	—	+ (1)
C. hyemalis	♀♀	5	100 (5)	—	—	—	—	—	—	—
M. nigra	♀♀	18	100 (17)	—	—	—	—	—	—	++ (1)

information on the amount of favoured duck food such as fish-eggs, Cladocera, aquatic vegetation, and adult insects that is available to the ducks. In most of the cases in Table 9 the diet of the ducks closely agrees with the composition of the benthic food resources although in a few cases, for instance in young of the Tufted Duck and Barrow's Goldeneye at Geiteyjarströnd, *Lymnaea* seems to be a preferred food item.

In another attempt to analyse the effects of the available food resources on the composition of the diets of adult

diving ducks birds caught in more or less exactly the same spot and within 3—5 days were compared with each other. Eight such samples (I—VIII) involving 2 to 5 species in each case are presented in Table 10. The results strongly suggest that all species feeding in a certain area often take the same kind of food which is usually abundant in that particular area and that particular time (e.g. chironomid larvae and Cladocera).

Thus, the diving ducks often feed on what is abundant and easily available i.e. they are to some extent opportunists. Seasonal changes and annual variations in the composition of the diets are possibly to a large extent determined or modified by variations in the availability of the different food items. For instance, fish-eggs are almost entirely eaten early and Cladocera later in the summer when they are most abundant and the proportion of chironomid larvae in the diet usually increases as the season advances. Opportunistic feeding is commonly seen when there is a peak in the hatching of chironomid larvae and most of the ducks eat almost entirely adult chironomids and pupal cases that are floating on the surface of the water. When the ducklings are relatively small, adult insects, seeds, and Cladocera are abundant and are presumably easy to obtain compared with benthic organisms (chironamid larvae and molluscs) which often constitute the bulk of the food of older young.

Segregation between the species

The surface feeding species (*Anas* spp.) are segregated from the diving ducks by eating chiefly plant food (unpublished data) whereas the diving ducks at Mývatn (except small ducklings) feed almost entirely on animal food. The general food habits of the diving ducks are outlined in Table 11. The Red-breasted Merganser is segregated from the rest by feeding almost exclusively on sticklebacks. The other five species overlap considerably with respect to the kinds of food they eat; all depend chiefly on chironomid larvae which are usually "superabundant". Fish-eggs (of sticklebacks) are by weight important to the five above-mentioned species although relatively few individuals feed on them. The Tufted Duck and Barrow's Goldeneye take more *Lymnaea* than the others. At least at certain times and in certain parts of the lake the Long-tailed Duck, Common Scoter, and Scaup feed extensively on Cladocera. Sticklebacks are taken especially by the Scaup, Tufted Duck, and Long-tailed Duck. The Scaup and Tufted Duck eat relatively more seeds than the others.

Between all six species there are statistically significant differences (at a 5 % probability level or less; using chi-square tests) in the composition of the diets of adult ducks except between the Tufted Duck and Barrow's Goldeneye in terms of per cent by weight ($\chi^2_{(8)} = 14.74$; $0.10 > P > 0.05$). At sea in winter all species discussed above, except the Red-breasted Merganser, feed chiefly on molluscs and are ecologically segregated by differences in food-species, size of prey, and feeding sites (MADSEN 1954). According to the principles of coexistence and competitive exclusion of congeneric species, basically known as "Gause's hypothesis" (referring to the work of GAUSE 1934), coexisting species differ in their ecology with respect to environmental resources which are utilized in common but are in short supply and thereby limit the number of individuals (see LACK 1954, 1971). The great abundance of food has always been considered the major factor responsible for the large number of ducks in the Mývatn area and the statistically significant differences in the food habits between the diving duck species there-

TABLE 11. General food habits and feeding habitat preferences of the adult diving ducks breeding at Mývatn.

Species	Main food items	Other food items	Feeding habitat preferences
A. marila	Chironomid larvae Fish-eggs	*Lymnaea* Cladocera Sticklebacks	Out on the lake on relatively deep waters
A. fuligula	Chironomid larvae *Lymnaea* Fish-eggs	Sticklebacks Seeds	In a variety of habitats
B. islandica	Chironomid larvae *Lymnaea* Fish-eggs		Running waters and out on the lake in shallow waters
C. hyemalis	Chironomid larvae	Fish-eggs Cladocera Sticklebacks	Out on the lake on relatively deep waters
M. nigra	Chironomid larvae	Fish-eggs Molluscs Cladocera Seeds	As above
M. serrator	Sticklebacks		In relatively shallow waters

fore suggest that food at least at one time limited their numbers. During the last few decades the diving duck populations have, however, decreased markedly (BENGTSON in press), but it is not known if the food supply has also changed.

In all species, except the Red-breasted Merganser, there are significant differences in the composition of the diet between the sexes. Apart from the work of BARTONEK & HICKEY (1969), such differences have rarely been demonstrated for ducks although the sexes often differ in body-size and in size and structure of the bill. The differences observed at Mývatn cannot conceivably be attributed to differences in places or seasons of capture of the male and female samples. The differences in diet of the sexes on the breeding grounds are possibly also associated with the females' need for highly nutrional food at the time of egg-laying.

There are certain differences also in the food habits of the ducklings of the different species. The young of all species, except the fish-eating Red-breasted Merganser, feed predominantly on chironomids (larvae and adults) but the Scaup, Barrow's Goldeneye and especially the Tufted Duck also take a considerable amount of *Lymnaea* and the Scaup, Long-tailed Duck, and Common Scoter eat more Cladocera than the others. Seeds are unimportant to the ducklings of the Long-tailed Duck and Barrow's Goldeneye.

In Table 11 some relationships between the food habits and the feeding habitat preferences can be seen. For instance, the Tufted Duck and Barrow's Goldeneye often feed in relatively shallow waters close to the shores where *Lymnaea* is most abundant; the Scaup, Long-tailed Duck, and Common Scoter often eat Cladocera which are abundant offshore, and the Tufted Duck and Common Scoter (although not the Scaup) show a relatively strong preference for potholes where aquatic vegetation (i.e. seeds) is abundant. Preferences for certain feeding habitats and the location of large flocks of feeding diving ducks

in Mývatn are, however, not entirely associated with food but are also determined by several other closely interrelated factors such as protection against predators, weather (chiefly wind), disturbance by man, tradition, and interspecific relationships (see SZIJJ 1965).

In conclusion it seems that the diving duck species at Mývatn, except the fish-eating Red-breasted Merganser, effectively eat the same kind of food (of which chironomid larvae are often "superabundant") although there are small statistical differences between the species with respect to the composition of the diet which is closely associated with the selection of feeding habitat and feeding areas.

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Selostus: **Sukeltajasorsien ravinnosta ja ruokailusta Mývatn-järvellä Islannissa.**

Sukeltajasorsien ravintoa ja ruokailukäyttäytymistä tutkittiin Koillis-Islannissa sijaitsevalla Mývatn-järvellä (65°35'N, 17°00'W). Noin 1280 kalaverkkoihin kuolleelta (sekä vanhoja lintuja että poikasia) lapasotkalta, tukkasotkalta, Islannin telkältä, allilta, mustalinnulta ja tukkakoskelolta selvitettiin ravinnon koostumus ruokatorven sisällön perusteella.

Tukkakoskelot olivat syöneet lähes pelkästään kolmipiikkejä *Gasterosteus aculeatus*. Muilla viidellä lajilla ravinnon koostumus oli melko yhdenmukainen: aikuisten ravinnon pääosana olivat surviaissääskien toukat (Diptera, Chironomidae), jotka muodostivat tärkeimmän osan järven benthoksen eläinravintovaroista.

Vaikka lajien välillä ei ravinnon koostumuksessa ollut kvalitatiivisia eroja, oli eri ravintokohteitten suhteellisissa osuuksissa pieniä, mutta tilastollisesti merkitseviä eroja. Niinpä tukkasotka ja Islannin telkkä söivät enemmän nilviäisiä (*Lymnaea* spp.) kuin lapasotka ja erityisesti alli ja mustalintu. Lapasotka, alli ja mustalintu söivät huomattavasti äyriäisiä. Sotkat olivat syöneet suhteellisesti enemmän kasvisravintoa kuin muut mainitut lajit.

Lajien välillä ilmeni eroja ruokailualueiden valinnassa, johon havaitut ravinnonkoostumuksen erot voitiin osaksi yhdistää. Tukkakoskeloa lukuunottamatta ilmeni kaikilla lajeilla sukupuolien välisiä eroja ravinnon koostumuksessa. Vuodenaikaiset ja vuosien väliset vaihtelut ravinnon koostumuksessa johtuivat tarjolla olevien ravintoeläinten kannanvaihteluista.

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