The Bottom Fauna of Lake Lille-Jonsvann, Tröndelag, Norway

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Quantitative bottom fauna investigations covering the littoral and sublittoral zones in the mesotrophic lake Lille-Jonsvann (62°23'N, 10°33'E), Trondheim, are presented. Higher taxa particularly treated are Oligochaeta, Hirudinea, Heteroptera, Trichoptera, Coleoptera, Gastropoda, and Bivalvia (Sphaeriidae). Of the total fauna, the insects represent 62% of the number of specimens and 39% of the biomass in the depth range 0.2–10 m. The corresponding values of the molluscs are 27% and 47%, respectively. The insects and the molluscs are by far the dominating animal groups. Three of the species treated clearly showed migration to deeper water in autumn, and factors affecting the migration are discussed. A correlation between the depth distribution of the caddis larvae and the oviposition procedure of the females is discussed.

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INTRODUCTION

The present investigation on the bottom fauna of lake Lille-Jonsvann, Trondheim, was initiated because of several aspects, but mainly because a thorough knowledge of the bottom fauna of lakes in Norway seemed to be restricted to one lake only, namely, the eutrophic lake Borrevann (J. Ökland 1964). Other investigations dealing with the bottom fauna of lakes have focused on problems concerning fishery-biology, and to a great extent only higher taxa like genera, families, and orders have been dealt with. The sampling has also mostly been concentrated into a short period in the summer months, and as a consequence of fishery-biological problems, most investigations have been carried out in oligotrophic waters.

Preliminary investigations showed that the fauna of Lille-Jonsvann was rich and was thus in contrast to that of oligotrophic lakes. Although the lake is not typically eutrophic, being intermediate to the oligotrophic and eutrophic lake, the fauna must be regarded as rich.

Other factors that made the choice of lake for the investigation easy were, the circumstance that a hydrographical survey covering one year was previously carried out in the lake (Holtan 1961), that lake Store-Jonsvann, which is connected to Lille-Jonsvann, serves as a water reservoir for the city of Trondheim, and also that lake Lille-Jonsvann is protected against severe pollution.

DESCRIPTION OF LAKE LILLE-JONSVANN

Lake Lille-Jonsvann is situated 15–20 km from the centre of the city of Trondheim in the Tröndelag area. The coordinates are lat. 63°23′N and long. 10°33′E of Greenwich (Fig. 1). The altitude above sea level is 149 m, and Lille-Jonsvann is situated in the coniferous region, although with scattered occurrences of nemoral species such as *Tilia cordata* (Sjörs 1963).

The surface area of the lake is 1.55 km², the greatest depth 35.6 m and the medium depth 11.9 m (Holtan 1961).

Lille-Jonsvann is connected to the larger basin of Store-Jonsvann by a narrow 2 m deep canal. The deepest part of the lake is just outside the connection with Store-Jonsvann. With respect to the hydrographic measurements carried out by Holtan (1961), Lille-Jonsvann must be regarded as a mesotrophic lake. Hydrographic measurements carried out close to the connection with Store-Jonsvann and in the deepest part of the lake showed a decrease in oxygen content in the deeper layers of water down to about 75% of full saturation during the stagnation periods (Table I). However, measurements carried out near the outlet in 1958 by the Norwegian Institute for Water Research, showed the oxygen content to be only 10–12% of full saturation during stagnation periods in the deeper layers of water. According to these data, the entrophication is pronounced towards the outlet.

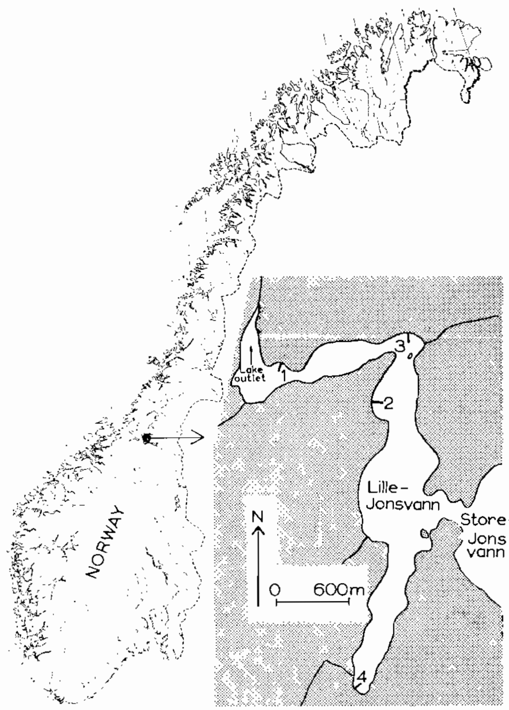


Fig. 1. The situation of the stations investigated in lake Lille-Jonsvann. Station 1 is nearest to the outlet.

Table II (Holtan 1961) shows the minimum, maximum and mean values of the hydrographic conditions during March 1960 and February

Table I. O_2 saturation in Lille-Jonsvann 1960–1961 (after Holtan 1961)

Depth	30 May 1960	23 June 1960	22 July 1960	18 Aug. 1960	15 Sep. 1960	12 Oct. 1960	9 Nov. 1960	3 Jan. 1961	15 Feb. 1961
0	104.2	102.8	101.0	95.0					
1					95.7	90.9	87.5	104.3	105.0
2	103.2	101.4	99.8						
4	104.5	103.5	98.4	95.0	95.5	90.9	87.5	107.9	97.6
8	101.4	101.6	96.2	88.3	85.2	90.9	87.1	90.4	88.9
12	97.8		91.2	85.9	83.6		87.3	89.7	88.3
16	95.6	91.5	90.2	84.0	81.6	82.8	87.3	88.4	87.6
20	96.2						87.3	88.2	86.7
30	94.8	88.9	85.8	84.0	79.0	74.8	87.0	82.4	79.0

1961. The data were obtained from the deepest part of the lake.

The dominating helophytes in Lille-Jonsvann are: *Phragmites communis* Trin., *Scirpus lacustris* L., and *Equisetum fluviatile* L. Among the isoetids and elodeids, the following species may be mentioned: *Isoetes lacustris* L., *Lobelia dortmanna* L., *Myriophyllum alterniflorum* L., and of the nymphaeids: *Potamogeton perfoliatus* L., *Nuphar luteum* (L.) Sm., and *Nymphaea* sp. The macrovegetation penetrates down to a depth of 4 m, and the greatest abundance is found at 2–3 m. Here, especially *Isoetes lacustris, Myriophyllum alterniflorum,* and *Potamogeton perfoliatus* make very dense belts.

The more eutrophic character of Lille-Jonsvann than Store-Jonsvann, which is typically oligotrophic, is to some degree certainly due to the surroundings, which are cultivated fields. The surroundings of Store-Jonsvann are mostly coniferous trees.

During the sampling period in 1967, the greatest water level fluctuation was −0.815 m from zero level; in 1968 it was −1.275 m. This occurred in October both years. When the results were treated, this was not taken into consideration. The depths given refer to the actual depth measured during the different months. This was done because the water level fluctuations are no greater than must be expected in natural waters.

METHODS

Quantitative samples were taken at depths from 0.2 to 15 m with a 200 cm² Ekman grab. At each station at a given depth, 5 samples were collected each time, and thus a bottom area of 0.1 m² was covered. Usually the grab was operated with a wire, but in shallow waters down to 2 m a few samples were collected when the grab was operated by an aluminium rod. When the aluminium rod was not used, the grab was operated with extra loads thus making it heavier and therefore more able to penetrate into the substratum. At a depth of 0.2 m, the grab was also pressed into the substratum by the hands. As the most critical phase for losing animals is when the grab is lifted out of the water, a sieve with a mesh width of 0.5 mm was put under it before lifting.

The bottom material was sifted through a screen with an actual mesh width of 0.5 mm,

Table II. Minimum, maximum and mean values of hydrographic data for Lille-Jonsvann obtained in 1960–1961 (after Holtan 1961)

	pH	$\kappa_{18} =$ n · 10^{-6}	Total hardness mg CaO/l	Cl^-/l mg	Alkalinity ml n/10 · HCl/l	Colour mg Pt/l	Turbidity mg SiO_2/l	$KMnO_4$ mg O_2/l
Minimum values	6.6	50.6	9.7	4.62	2.8	5.0	0.19	1.99
Maximum values	7.3	55.3	12.3	5.76	3.7	23.2	1.53	3.01
Mean values	7.0	53	11.2	5.07	3.2	12.2	0.51	2.44

which was found sufficient for the present study. Screens with smaller mesh give more animals, but at the same time the time spent in sorting increases. All samples were sorted by hand. Sorting was first carried out in white plastic trays, and afterwards in black ones, to control the picking up of small molluscs, chironomid larvae, nematods, and oligochaetes. All material was preserved in 70% alcohol.

Later the animals were counted, but before weighing, they were placed on absorbent paper for one minute to allow preservation fluid to drain off. Because of the great mass of animals in some samples, they were divided into portions small enough to give a 'stable' weight when dried for one minute.

Weighing of Ephemeroptera and the family Sphaeriidae was carried out before the species had been identified. Weighing was carried out with an accuracy of ± 0.1 mg.

The 5 grabs at a given depth were combined in one sample, on the one hand to save time in the field, while on the other, more samples could be taken. It can be a disadvantage to combine grabs into one sample, because some information is lost, e.g. a better knowledge of the variations in number. However, as 4 stations were investigated in 1967 and 3 in 1968, the disadvantage was virtually negligible.

STATIONS INVESTIGATED

Quantitative samples were taken at the stations shown in Fig. 1. In 1967 investigations were carried out at all four stations and in 1968 at stations 2, 3, and 4.

Station 1. The station is situated near the outlet of Lille-Jonsvann, and is fairly well sheltered against wind and wave actions. Dense belts of *Equisetum fluviatile* are very conspicuous. Nymphaeids are present. The site faces south.

Station 2. This station is sited on the western shore in the middle of the lake, and is moderately sheltered. Of the helophytes, *Equisetum fluviatile* dominates, but further towards the south there are dense belts of *Phragmites communis.* Nymphaeids are present, but not so abundantly as at the other stations. Northwards the shore is rocky. At a depth of 2 m, the bottom consists of clay.

Station 3. This was the most exposed station investigated. It faces south, and at the sampling site the shore consists of fine sand and gravel. However, on both sides of the sampling site, the shore consists of rocks. Down to a depth of 1 m, the bottom substratum consists of fine sand and gravel, and no macro-vegetation is present. From this depth on, *Myriophyllum, Isoetes,* and *Lobelia* occur, but there are few above 2 m. Together with *Potamogeton perfoliatus,* these plants make a very dense belt at 2–3 m depth. The macrovegetation stops at nearly 4 m depth. Helophytes are not present, nor are *Nymphaea* spp.

Station 4. This was the most sheltered of the four stations investigated. It is situated at the southern end of the lake. *Equisetum fluviatile* dominates among the helophytes, and outside *E. fluviatile,* there is a dense belt of nymphaeids. *Isoetes, Lobelia,* and *Myriophyllum* do not make such a dense and conspicuous belt as at station 3; this also applies to stations 1 and 2.

SAMPLES TAKEN

The total number of Ekman grab samples taken in 1967 was 290; 280 in 1968. The total area investigated thus covers 11.4 m^2. Table III shows the number of Ekman samples investigated for the different major groups of bottom animals, while Table IV shows the sampling months at the four stations. The values for number and weights per m^2 are based on the number of Ekman samples given in Table III.

Because groups that occurred in small numbers were of particular interest, they were covered by more samples than, e.g., groups such as Chironomidae. This is why the number of samples differs from group to group.

RESULTS AND DISCUSSION

PORIFERA

Porifera were twice found in the samples; at a depth of 2 m at station 1 and 4 m at station 3. Further identification was not carried out.

Table III. The number of Ekman grab samples and the area in m² investigated for the different major groups of bottom animals in Lille-Jonsvann in 1967–1968

	Nematoda		Hirudinea		Gammarus		Oligochaeta Chironomidae Cera-topogonidae		Insecta except Chironomidae Cera-topogonidae		Gastropoda		Sphaeriidae	
Depth in metres	No. Ek-man	Area in m²	No. Ek-man	Area in m²	No. Ek-man	Area in m²	No. Ek-man	Area in m²	No. Ek-man	Area in m²	No. Ek-man	Area in m²	No. Ek-man	Area in m²
0.2	20	0.4	50	1.0	50	1.0	20	0.4	50	1.0	30	0.6	30	0.6
1	30	0.6	85	1.7	85	1.7	30	0.6	85	1.7	55	1.1	40	0.8
2	30	0.6	85	1.7	85	1.7	30	0.6	85	1.7	55	1.1	40	0.8
3	30	0.6	75	1.5	75	1.5	30	0.6	75	1.5	55	1.1	40	0.8
4	30	0.6	80	1.6	80	1.6	30	0.6	80	1.6	55	1.1	40	0.8
5	30	0.6	75	1.5	75	1.5	30	0.6	75	1.5	55	1.1	40	0.8
7	25	0.5	60	1.2	60	1.2	25	0.5	60	1.2	45	0.9	35	0.7
10	25	0.5	55	1.1	55	1.1	25	0.5	55	1.1	40	0.8	30	0.6
15	5	0.1	5	0.1	5	0.1	5	0.1	5	0.1	5	0.1	5	0.1
Sum	195	4.5	570	11.4	570	11.4	195	4.5	570	11.4	395	7.9	300	6.0

NEMATOMORPHA

No species of this group were found in the quantitative samples. However, when dredging at station 3 at a depth of 2–3 m, 2 specimens identified as *Gordius albopunctatus* Müll. were found. The identification was carried out after Heinze (1941).

The worms, one male and one female, were found on 9 July 1970. The length of the female was 19 cm, while the male was 22.5 cm.

NEMATODA

The nematods were not identified to species, and only 35 specimens were collected. They were found in samples from a depth of 1 m down to 15 m. None were found at a depth of 0.2 m. The highest population density occurred at depths of 1 and 2 m, with an average of 20 and 15 individuals per m² weighing 0.03 and 0.01 g, respectively (Table V). The lowest population density occurred at depths between 7 and 10 m, where an average of only 2 individuals per m² weighing about 0.001 g, occurred. Although the samples taken in 1967 and 1968 are treated together, separately they show the same general pattern of benthic distribution. In Borrevann (J. Ökland 1964), the highest population density of Nematoda was found at a depth of 10 m (18 individuals per m² weighing 0.05 g).

Table IV. The sampling months at the four stations investigated

Year	Station 1	Station 2	Station 3	Station 4
1967	June		June	
	Sep.	Sep.	Sep.	Sep.
		Oct.	Oct.	Oct.
1968		July	June	July
		Sep.	Sep.	Sep.
		Oct.	Oct.	

Table V. The average number of individuals and weights of Nematoda per m² in Lille-Jonsvann in 1967–1968

Depth in m	1	2	3	4	5	7	10
Number of ind. per m²	20	15	7	5	5	2	2
Weight in g	0.03	0.01	0.001	0.001	0.001	0.001	0.001

OLIGOCHAETA

The benthic distribution of Oligochaeta is given in Fig. 2. The greatest density was found at depths of 0.2 and 1 m, where on average 1013 and 542 specimens per m² weighing 1.57 and 1.59 g, respectively, occurred. Towards greater depths, the number decreases successively down

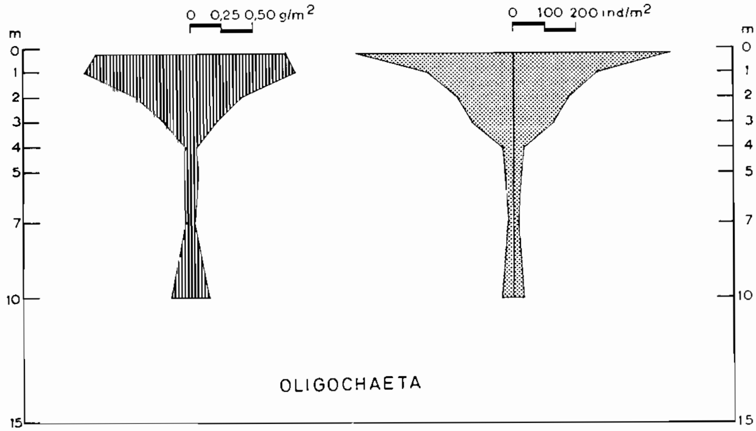


Fig. 2. The weight and number of specimens of Oligochaeta per m².

to 7 m, where the lowest density was found – 34 individuals per m² weighing 0.08 g. At a depth of 10 m, the population density was estimated at 69 individuals per m² weighing 0.31 g.

The following species of Oligochaeta were identified: *Peloscolex ferox* (Eisen), *Stylodrilus heringianus* Claparede, and *Lumbriculus variegatus* (Müller).

Of those identified, *Peloscolex ferox* was the most numerous and occurred down to a depth of 7 m at St. 3, while the greatest depth at St. 1 was 2 m. In Llyn Tegid (Lake Bala) Merionethshire, Dunn (1961) found that *P. ferox* was most abundant in the profundal zone at a depth of 30 m; Humphries (1936) found it at a depth of 60 m in Lake Windermere. Brinckhurst (1964) and Milbrink (1970) stated that *P. ferox* occurred in great numbers in clear oligotrophic waters, and Milbrink (1972) has said that it is a clear water species. Regarding this statement, *P. ferox* also indicates a greater eutrophication of the water towards the outlet of Lille-Jonsvann, which agrees with the hydrographic conditions. *Stylodrilus heringianus* was only found in the upper littoral zone, and this too is a species with its maximum abundance in oligotrophic waters, where it can penetrate into great depths (Milbrink 1969). The abundance of *P. ferox* (and *S. heringianus*) supports the classification that the conditions in Lille-Jonsvann are intermediate between oligotrophic and eutrophic. In a typically oligotrophic lake, e.g. Huddingsvann (Sivertsen 1973) in the Tröndelag area, *P. ferox* was found down to a depth of 22 m, and is more abundant than in Lille-Jonsvann.

In northern Sweden, Piguet (1919) found the oligochaete fauna to be poor when compared with the number of species in each lake. The species most frequently found by Piguet was *P. ferox,* while *L. variegatus* and *S. heringianus* occurred in fewer samples.

HIRUDINEA

The quantitative samples of Hirudinea refer to the species *Glossiphonia complanata* (L.), *Helobdella stagnalis* (L.), and *Theromyzon maculosum* (Rath.) Additionally, *Haemopis sanguisuga* (L.) was taken in qualitative samples.

The benthic distribution of Hirudinea total is shown in Fig. 3. Their greatest weight and density were found at 3 m, where on average 1.01 g and 40 individuals per m² occurred. However, the leeches are fairly abundant down to 5 m. Below this level, there is a sudden drop in the population density, and on average only 3 and 2 individuals per m² were found to occur at the depths of 7 and 10 m, respectively. The average weights at 7 and 10 m were only 0.04 and 0.01 g, respectively.

Theromyzon maculosum

T. maculosum was found once in the quantitative samples. It was taken at a depth of 0.2 m at St. 4. Further, two other records have been made in Lille-Jonsvann, and one in the outflowing rivulet. The two findings from qualita-

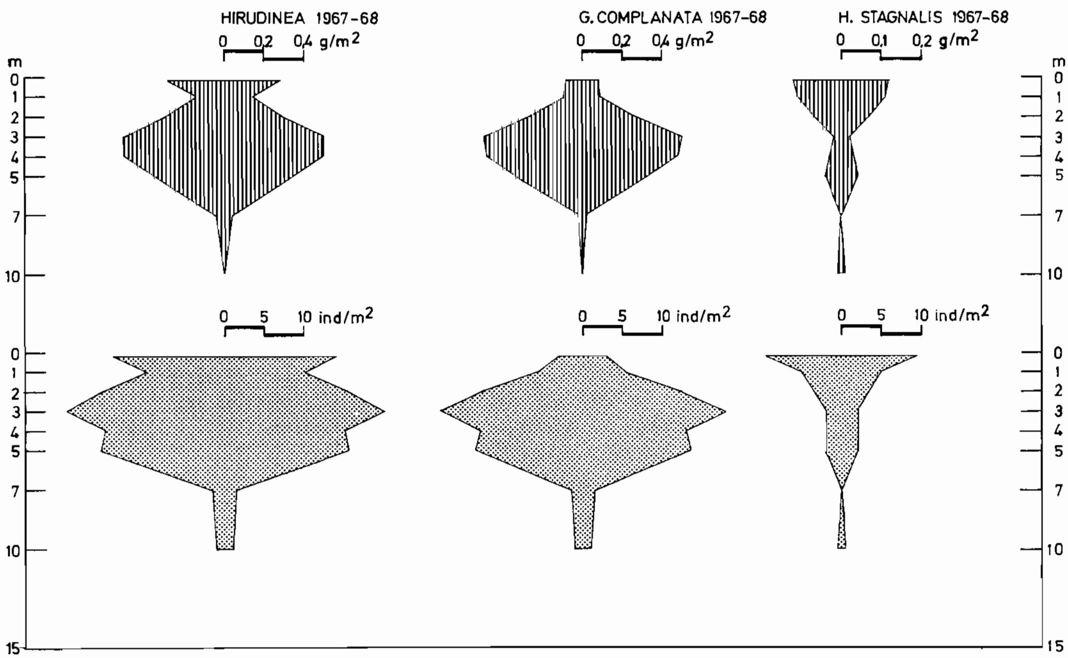


Fig. 3. The weight and average benthic distribution of Hirudinea total, *Glossiphonia complanata* and *Helobdella stagnalis*.

tive samples in the lake were made on stony shores, where the stones were overgrown with algae and the macro-vegetation abundant.

T. maculosum was reported for the first time from Norway by Fjeldså (1971), and Fjeldså (1972) discussed distribution, ecology, and life history. *T. maculosum* probably has an optimum in northern productive hardwater lakes (Fjeldså 1972).

Haemopis sanguisuga

H. sanguisuga was occasionally found during the summer months under stones at the water edge, which seems to be its summer habitat. Mann (1955) stated its winter habitat to be under large stones at depths of 0.5–1 m. Here the leeches congregate under stones. In northern Norway, *H. sanguisuga* was found to be local in the investigated area (Fjeldså 1971).

Glossiphonia complanata

This is the most dominant leech species in Lille-Jonsvann, and the average benthic distribution is shown in Fig. 3.

As we see, the benthic distribution increases as the depth increases down to the 3 m level, where the greatest density, 36 individuals per m^2 weighing 1.00 g, is found. Then there is a slow decrease in the population density down to the 5 m level. Towards greater depths, there is a sudden decrease in the population density, and only 3 and 2 individuals per m^2 were estimated at 7 and 10 m, respectively. This distributional pattern shows that *G. complanata* is connected to the lower littoral zone.

Specimens carrying young were occasionally found in late June, while the greater part of the leeches collected in July were carrying young. However, very young specimens were found throughout the sampling period.

Fig. 4 shows the seasonal variation in the benthic distribution in 1968 at St. 3. In June and September the population is connected to the littoral zone, while in October it has penetrated down to a depth of 7 m. As the abundance was found to be very great at the 2 m level in September and October, it must be expected that most of the young were born at this depth. The

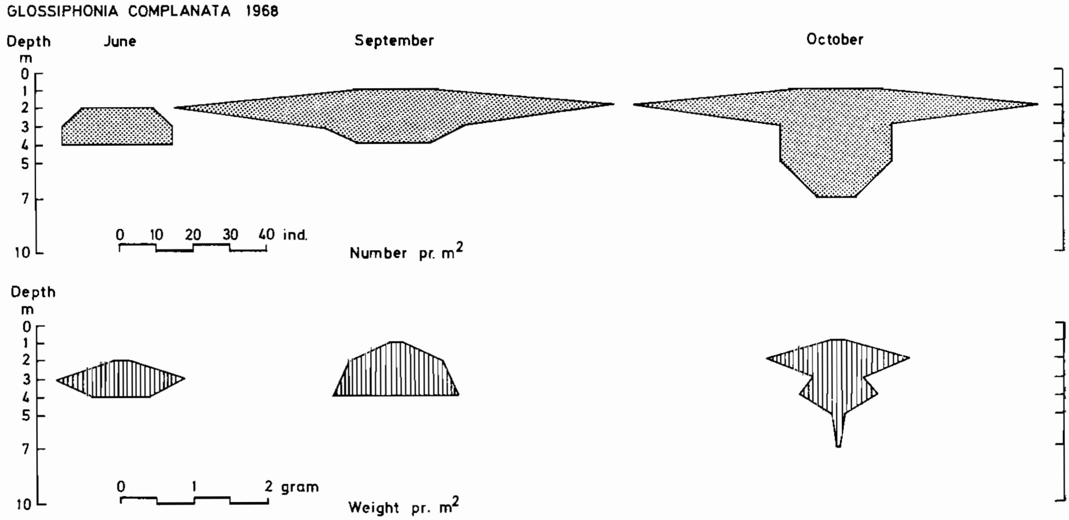


Fig. 4. Seasonal variation in the benthic distribution of *Glossiphonia complanata.*

littoral zone obviously exhibits better conditions for reproduction than other areas, and this causes a great abundance in this area during late summer and autumn. Due to this fact, it must be assumed that migration to deeper water in October is caused by the dense population in the littoral zone.

According to Mann (1955, 1962) and Bennike (1943), *G. complanata* is found in almost every kind of water, and has a great ecological range.

Helobdella stagnalis

H. stagnalis ranges second in number of the dominating species of leeches (Fig. 3 shows the average benthic distribution). As will be seen, this species has a distribution which differs from that of *G. complanata*. The highest density occurs at a depth of 0.2 m, where 19 individuals per m^2 weighing 0.12 g were found. *H. stagnalis* was regularly found down to a depth of 5 m, and only occasionally at greater depths. Only one specimen per m^2 was estimated at 10 m. At a depth of 7 m, none was found.

As Fig. 3 shows, the distribution of *H. stagnalis* is connected to the littoral zone, with the greatest density in the upper littoral. However, *H. stagnalis* was not found in the samples taken on the sandy shore at St. 3. In the June samples, the specimens were carrying eggs, while in July they were carrying young.

According to Mann (1955), *H. stagnalis* is normally the most numerous leech in eutrophic lakes, but it is present in almost every kind of water. Bennicke (1943) found it absent in only one type of freshwater, the sphagnum bogs, and he also found it belonging to the group of leeches that has been taken at the lowest values of bicarbonate content and pH, i.e. as low as corresponding to 1 mg 'CaO'/l and pH 4.0–4.2. Fjeldså (1971) showed *H. stagnalis* to be present in oligotrophic water with only 1 mg Ca^{++}/l.

CRUSTACEA

The group Malacostraca is represented by *Gammarus lacustris* G. O. Sars and *Astacus astacus* L. *A. astacus* was introduced by man, probably in 1932. As far as I know, there is no information on the population density, but I doubt if it is very high. However, as the population has survived for 40 years, *A. astacus* must be considered as a true inhabitant of lake Lille-Jonsvann.

Gammarus lacustris

The average benthic distribution of *G. lacustris* is shown in Fig. 5. It was found at all depths investigated down to 10 m. The greatest density

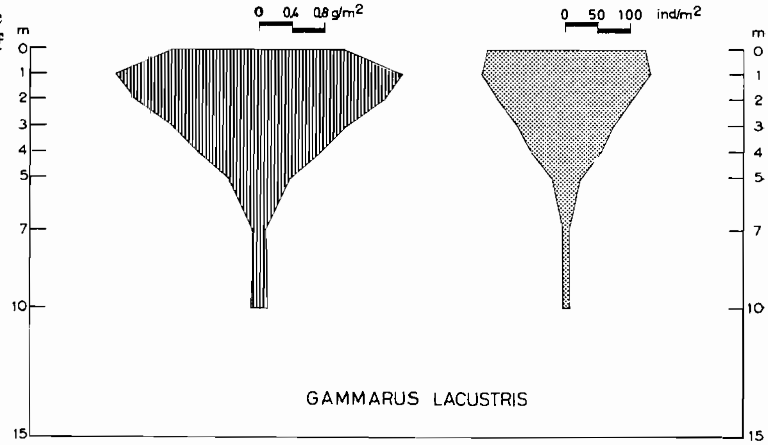


Fig. 5. Weight and average benthic distribution of *Gammarus lacustris.*

occurred at a depth of 1 m, where an average of 259 specimens per m² weighing 3.46 g was estimated. Towards greater depths, the number per m² decreases successively to a depth of 10 m, where on average 9 individuals per m² were found.

ODONATA

Specimens belonging to this group did not occur in the quantitative samples. However, in dredge samples a few nymphs of *Enallagma cyanthigerum* (Charp.) were found in the plant belts at depths of 2–3 m. *E. cyanthigerum* is so far the only species among the dragonflies collected as adult along the shore of Lille-Jonsvann. *E. cyanthigerum* is reported in all counties of Norway, and is regarded as a total form by Tjönneland (1952). It is also reported to be more often found at eutrophic and oligotrophic lakes (Schmidt 1966), than at other localities.

EPHEMEROPTERA

Fig. 6 shows the average benthic distribution of the Ephemeroptera. Their greatest average density occurred at depths of between 0.2 and 1 m, where on average 108 and 98 individuals per m² weighing 0.15 and 0.57 g, respectively, were estimated. They were recorded down to the 5 m level, where only the species *Ephemera vulgata* L. was found. The most abundant species in the samples were *Ephemera vulgata* L., *Leptophlebia vespertina* L. and *Caenis horaria* L.

In Borrevann (J. Ökland 1964), the group was not represented deeper than 4 m, while Humphries (1936) recorded *Caenis* sp. down to 9 m in Lake Windermere.

Of the three most abundant species in Lille-Jonsvann, only two, *E. vulgata* and *C. horaria,* were found to inhabit the eutrophic lake Borrevann (J. Ökland 1964), *L. vespertina* being absent. In the dystrophic lake Gribsö (Berg 1956),

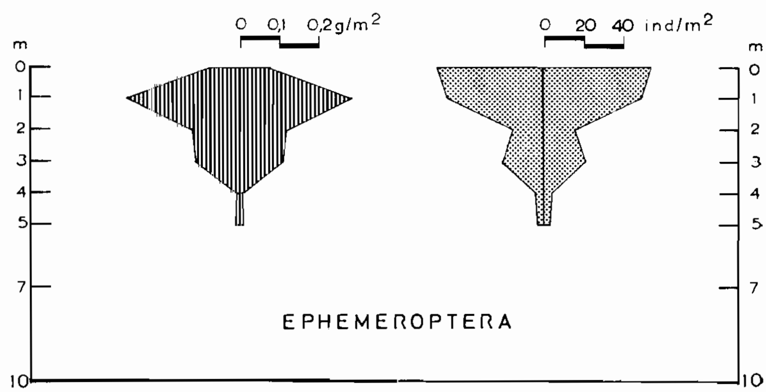


Fig. 6. Weight and average benthic distribution of Ephemeroptera total.

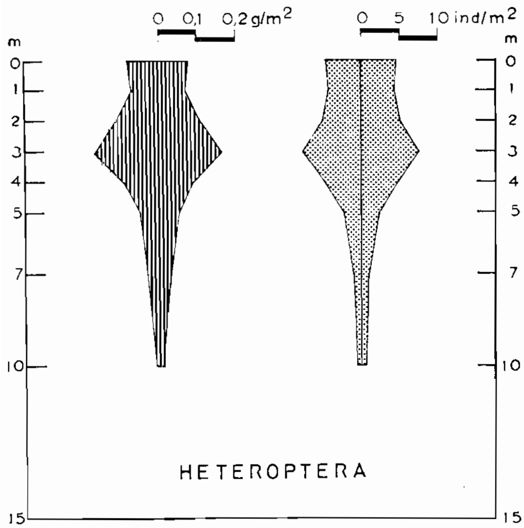


Fig. 7. Weight and average benthic distribution of Heteroptera total.

L. vespertina was present, while it was found only once in the eutrophic Esrom Lake (Berg 1938). Esben-Petersen (1910) suggests that *L. vespertina* probably prefers brown water.

On the sandy substratum at a depth of 0.2 m at St. 3, no ephemerids were found, while they occurred in the samples at this depth at all other stations. In the autumn samples at 0.2 and 1 m at St. 2, *L. vespertina* was more abundant than at the other stations. The nymphs of *E. vulgata* occurred more commonly in the samples at stations 1, 2, and 3, compared with the samples at St. 4.

HETEROPTERA

Only the family Corixidae of Heteroptera was represented in the quantitative samples. Greatest density occurred in the plant belt at a depth of 3 m, where on average 15 specimens weighing 0.33 g per m² were found (Fig. 7). The maximum depth at which specimens were found was 10 m and these were nymphs which were not identified. Regarding the 1967 and 1968 samples totally, the highest frequency occurred at 2, 3, and 4 m.

In the June samples only a few specimens were found; they were more frequent in the autumn samples (September and October). In Fig. 8, the bathymetric distribution of the identified species is shown. The data are based on quantitative and qualitative samples. In the quantitative samples the most dominant species were *Glaenocorisa quadrata* Walley, *Arctocorisa germari* Firb., and *Callocorixa wollastoni* Dong. et Sc. *Cymatia bonsdorffi* Sahlb. and *Sigara distincta* Firb. were collected with only a few specimens which were found at the 0.2 m level. *A. germari* and *C. wollastoni* occurred in the range 0.2 m down to 5 m. *G. quadrata* was not collected in the uppermost littoral zone, but was met with between depths 2 and 7 m. The habitat of *G. quadrata* was found to be in deeper water than that of the other corixids found, and the results agree with Macan (1954). Macan (1954) is of the opinion that the same is also true of *A. germari,* but this species was found at the 0.2 m level in both the quantitative and qualitative samples in Lille-Jonsvann.

In the qualitative samples, taken in a not too dense *Phragmites communis* belt, *S. distincta* was the dominant species, while *C. bonsdorffi, A. germari,* and *C. wollastoni* occurred, but with only a few individuals. According to Macan (1954), *S. distincta* is found most abundant where organic matter has accumulated on the bottom. *C. wollastoni* was found in Britain

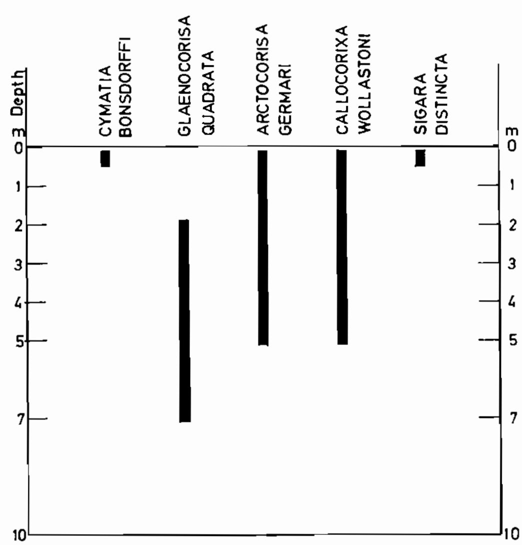
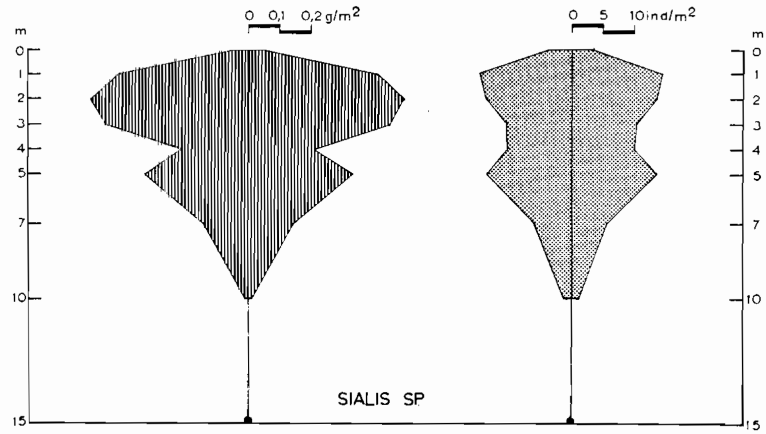


Fig. 8. Bathymetric distribution of the various species of the family Corixidae.

Fig. 9. Weight and average benthic distribution of *Sialis* sp.



(Macan 1954) at high altitudes, a fact which may indicate that the species belongs to more northern areas.

A survey of the species reported from Norway is given by Warloe (1924), whose list includes all the species found in Lille-Jonsvann. Species reported in this study and new to the fauna of Sör-Tröndelag are: *Cymatia bonsdorffi, Glaenocorisa quadrata, Callocorixa wollastoni,* and *Arctocorisa germari.*

MEGALOPTERA

All larval specimens of this group belong to the genus *Sialis,* and are assumed to belong to the species *S. lutaria,* since this species was the only one collected as adult, and with the most intensive flight period in June and July.

The larvae occurred in the samples from a depth of 0.2 m down to 15 m. The highest number of density estimated was between depths 1 and 5 m, where the average number varied from 20 to 29 individuals per m^2, and the average weight between 0.42 and 1.0 g (Fig. 9). At 10 m, the average number per m^2 was only 2 individuals.

The fairly low average number per m^2 at a depth of 0.2 m indicates that the optimum habitat of *S. lutaria* larvae is below the depth of wave action. On the sandy shore at St. 3, *S. lutaria* larvae were not recorded in the samples at 0.2 m. At the other stations, which are more sheltered than St. 3, larvae were found in the samples from 0.2 m also. At 1 m at St. 3, where the wave action must be assumed to be fairly moderate according to the thin layer of mud covering the sandy bottom substratum, larvae occurred. This is also in agreement with the data given by J. Ökland (1964) for lake Borrevann.

TRICHOPTERA

The collections of Trichoptera comprise both larvae and pupae, and identifications of the families Polycentropidae, Sericostomatidae, Phryganeidae, Molannidae, and Leptoceridae have been stressed to species level.

Fig. 10 shows the average benthic distribution of Trichoptera total. The density was fairly uniform at depths of 0.2, 1, and 2 m, where 96, 89, and 97 specimens per m^2, respectively, occurred. Regarding the weight, the highest value (3.75 g per m^2) was estimated at a depth of 0.2 m. This was considerably greater than the weight estimated for the depths of 1 and 2 m, 2.06 and 2.18 g, respectively. The difference in weight between 0.2 and 1–2 m, is certainly due to the collecting of very large specimens of the fam. Limnephilidae, which was most abundant at a depth of 0.2 m.

Larvae of Trichoptera were found down to the 10 m level, where 12 individuals per m^2 weighing 0.06 g were estimated. In lake Borrevann (J. Ökland 1964), the maximum depth to which larvae of Trichoptera penetrated was 6 m, and only specimens of *Ecnomus tenellus* Ramb. were present, while in Esrom Lake, Berg (1938) recorded several species (*Cyrnus flavidus* McLachlan, *Oxyethira flavicornis* Pict. = *O.*

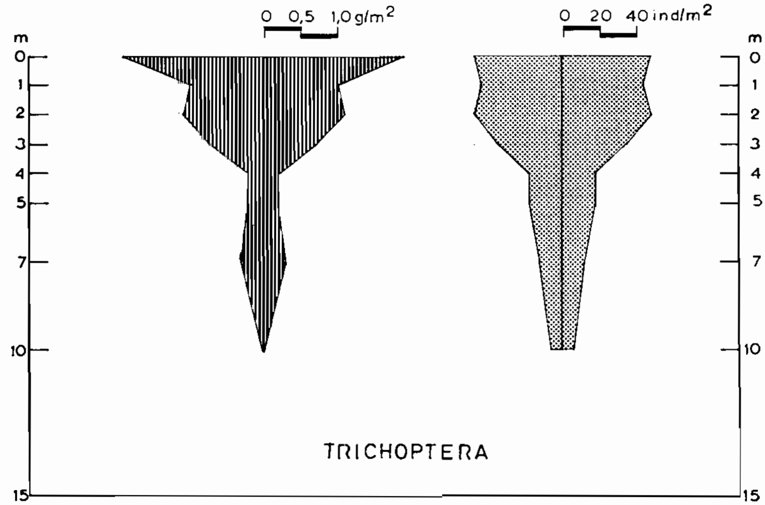


Fig. 10. Weight and average benthic distribution of Trichoptera total.

costalis Curt., and *Athripsodes* sp. = *Leptocerus* sp.) at depths of 10–14 m. The species present at a depth of 10 m in Lille-Jonsvann were *Cyrnus flavidus, Molanna angustata* Curt., *Athripsodes aterrimus* Steph., and *Limnephilus* sp.

In the quantitative collections, the following species, genera, and families were present:

Cyrnus flavidus McLachlan
Polycentropus flavomaculatus Pictet
Holocentropus picicornis Stephens
Phryganea bipunctata (Retzius) = *P. striata* L.
Agrypnia obsoleta (Hagen) = *P. obsoleta* McLachlan
Molanna angustata Curtis
M. albicans (Zetterstedt)
Molannodes tincta (Zetterstedt)
Lepidostoma hirtum (Fabricius)
Athripsodes aterrimus (Stephens)
A. cinereus (Curtis)
A. sp.
Nemotaulius punctatolineatus (Retzius)
Limnephilus rhombicus (Linnaeus)
Limnephilus sp.
Limnephilidae

Species which occurred commonly in the samples were: *Cyrnus flavidus, Molanna angustata, Phryganea bipunctata,* and *Agrypnia obsoleta.* The rest of the species were rarely found.

Fam. Polycentropidae
Three species belonging to this family were identified in the quantitative collections. *Polycentropus flavomaculatus* and *Holocentropus picicornis* occurred rarely at 0.2 m, but they are certainly more abundant on exposed shores than on the stations investigated.

Cyrnus flavidus
C. flavidus is the trichopteran species in greatest abundance, and in spite of findings down to the 10 m level, it was found to be closely allied to the zone of macrovegetation (Fig. 11). The greatest abundance and weight were found at a depth of 2 m, where on average 69 individuals weighing 0.87 g were estimated.

The seasonal variation of the benthic distribution of *C. flavidus* at St. 3 is shown in Fig. 12, which illustrates that very few specimens of *C. flavidus* occurred in the June samples. In September, *C. flavidus* was very common at depths of 1, 2, and 3 m; the same trend was also found in October. The greatest density in September was 78 individuals per m², and in October it was 72 individuals per m². Since the samples taken in September show a great increase in density when compared with the June samples at depths of 1, 2, and 3 m, this is certainly due to the fact that egglaying and hatching of young larvae have been connected to this area.

The larvae were found at greater depths in

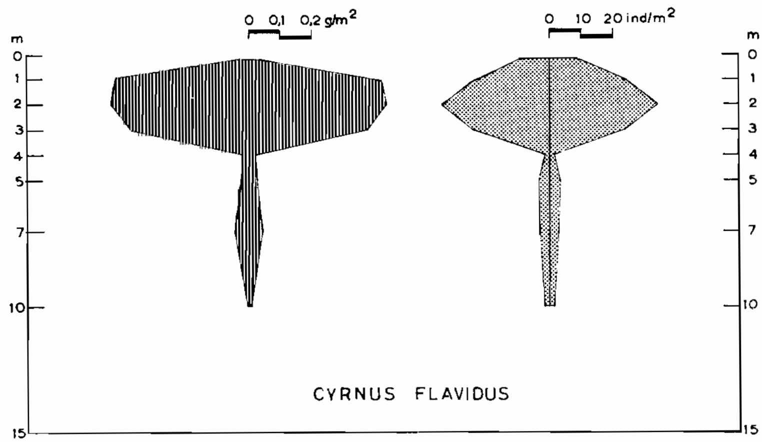


Fig. 11. Weight and average benthic distribution of *Cyrnus flavidus*.

October than in September. In my opinion, this could be because of two factors – a migration to deeper water in the autumn, or a delayed development of eggs and larvae at deeper water. However, since the average weight per larva in October was found to be greatest at depths of 7 and 10 m, a migration must have occurred. As for other aspects, the results from St. 3 are treated because the trend in the results was most clear here.

The life cycle is one year, and the larvae must have a rapid growth in the summer months, because all specimens taken in September were large (10–12 mm in length). The larvae have been feeding on Cladocera and Chironomidae.

Fam. Molannidae

In the fam. Molannidae, 3 species were identified – *Molanna angustata, M. albicans,* and *Molannodes tincta.* Only *M. angustata* was abundant in the samples, while *M. albicans* and *M. tincta* rarely occurred. The latter two species were found only at St. 4. *M. albicans* was collected from depths of 0.2 m down to 5 m, while *M. tincta* was found in the samples at 1 and 2 m. A description of the Norwegian larva of *M. albicans* and notes on its ecology have been given by Solem (1970). The food was found to consist of filamentous algae, Cladocera and larvae of chironomids.

Molanna angustata

Among the Trichoptera, *M. angustata* was second in number with respect to dominance. Fig. 13 shows the average benthic distribution. The species occurred from depths of 0.2 m down to 10 m. The greatest number per m² was found at 4 m, where on average 25 specimens weighing 0.15 g occurred. The greatest weight was found at a depth of 3 m, where 0.30 g and 17 individuals per m² were estimated.

The seasonal variation in the benthic distribution is shown in Fig. 14, which also gives information about the life cycle. Very few specimens were found in the samples taken in June/July, while they were abundant in September and October. Fig. 14 refers to the data from St. 3 in 1968. In September the greatest abundance (99 individuals per m²) occurred at a depth of 7 m, and since it was composed of very

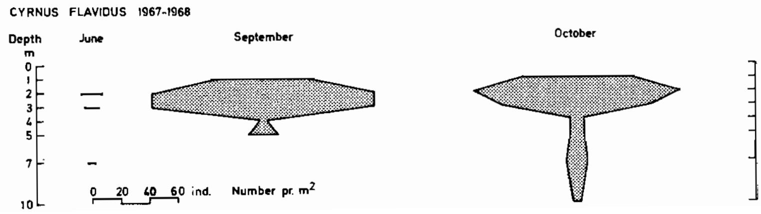


Fig. 12. Seasonal variation in the benthic distribution of *Cyrnus flavidus* at station 3.

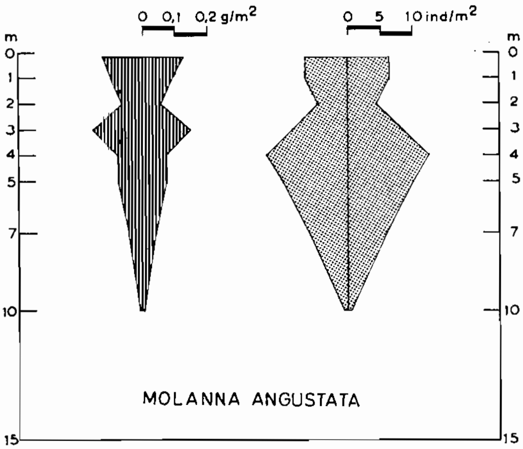


Fig. 13. Weight and average benthic distribution of *Molanna angustata.*

small larvae, the eggs must have been dropped and developed down to this depth. The oviposition and the development of the eggs therefore seems to have occurred over a wide range in the littoral and sublittoral zones. In October the larvae congregated in the transitional area of the littoral/sublittoral zones at a depth of 4 m. Fig. 14 indicates that the life cycle is one year. The gut content of some of the larvae dissected consisted of Cladocera and larvae of chironomids.

Fam. Phryganeidae

The fam. Phryganeidae was represented by two species in the quantitative samples, *Phryganea bipunctata* and *Agrypnia obsoleta.* Additionally *Phryganea grandis* was found in the quantitative samples. Fig. 15 shows the average benthic distribution of *P. bipunctata* and *A. obsoleta.* Considering the caddis species collected, the larvae of *P. bipunctata* and *A. obsoleta* are fairly large, and compared with the collections of *C. flavidus* and *M. angustata,* their abundance is low, but the weight per m² is high.

Phryganea bipunctata

The greatest average density of *P. bipunctata* was found at a depth of 0.2 m, where 5 specimens per m² weighing 0.69 g occurred. The larvae were collected down to 7 m. In the lowland area of Tröndelag, the life cycle of *P. bipunctata* was found to be one year (Solem 1969), and this also includes the population in lake Lille-Jonsvann. The fact that the larvae have a fairly high growth rate in the summer and spend the winter as fullgrown was also found by Bray (1969).

The food of the *P. bipunctata* larvae was found to be diatoms in the first larval stage. Most likely the larvae feed on the epiflora and epifauna on the stones, stems, etc. In the later

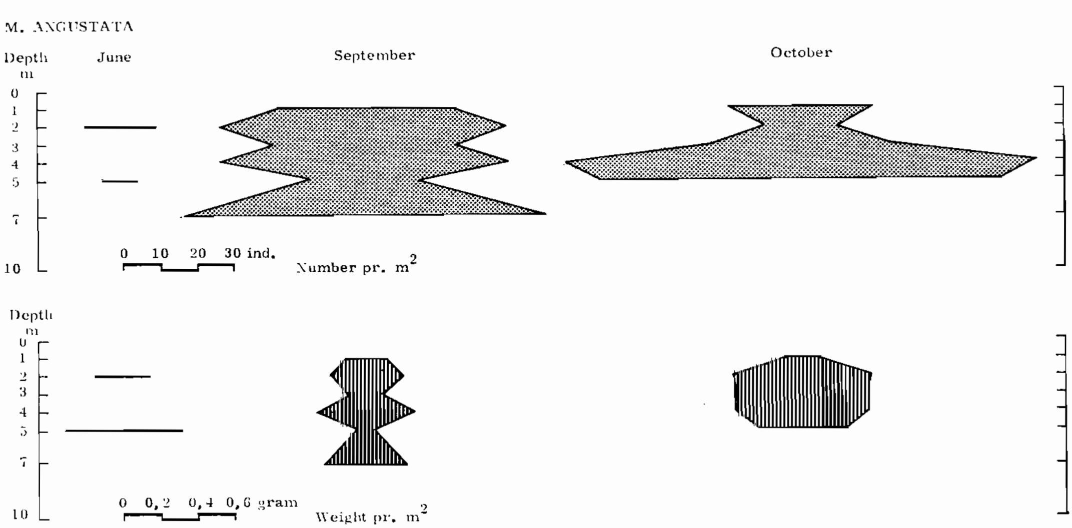
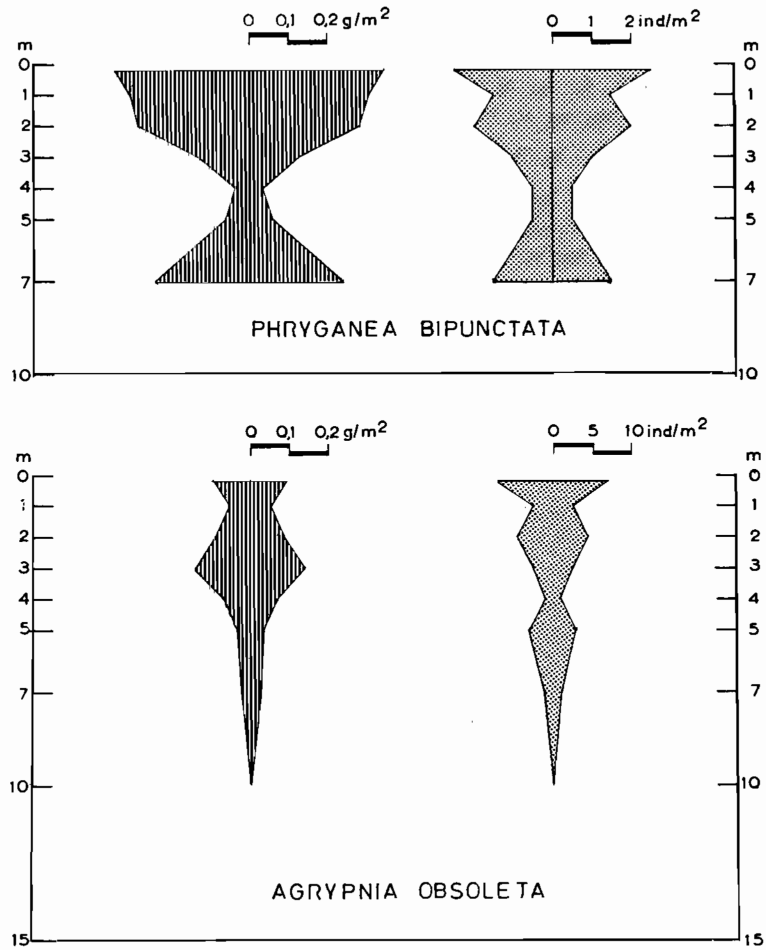


Fig. 14. Seasonal variation in the benthic distribution of *Molanna angustata* at station 3.

Fig. 15. Weight and average benthic distribution of *Phryganea bipunctata* and *Agrypnia obsoleta.*



larval stages, they become more carnivorous and animals found in their stomachs were Hydracarina, Cladocera, Ephemeroptera, Trichoptera, Chironomidae, Gastropoda (?), and Oligochaeta (?). However, fragments of plants also occurred in the stomachs of the larvae investigated.

Agrypnia obsoleta

The greatest abundance of *A. obsoleta* was at a depth of 0.2 m, where 14 individuals per m^2 weighing 0.18 g occurred. However, the greatest weight occurred at a level of 3 m, where on average 5 individuals weighing 0.28 g were estimated. This indicates that the younger larvae inhabit the shallow water, where the eggs were deposited, while the older larvae penetrate to greater depths. The greatest depth at which larvae of *A. obsoleta* occurred was 7 m.

In contrast to *P. bipunctata,* the wintering larvae of *A. obsoleta* were of variable size and represented several stages. The life cycle is one year in the lowland, which includes Lille-Jonsvann, but in the high mountain regions the species has at least a two year cycle (Solem 1969). The food was much the same as that of *P. bipunctata,* but with a greater frequency of Cladocera and lesser plant fragments.

Fam. Leptoceridae

Two species, *Athripsodes aterrimus* and *A. cinereus* were identified from larval specimens, additionally, one specimen of a species probably unknown as larva was collected. The unidenti-

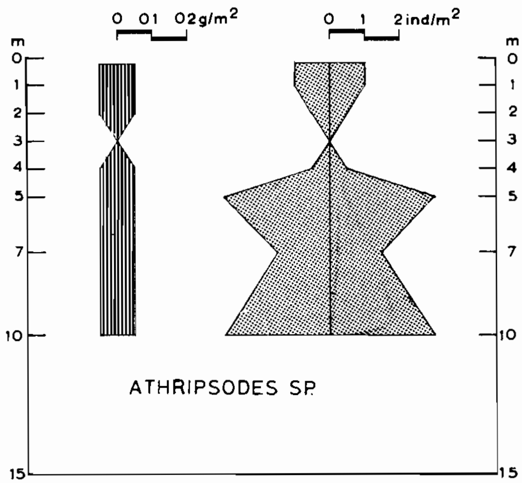


Fig. 16. Weight and average benthic distribution of *Athripsodes* sp.

fied larva certainly belongs to the genus *Athripsodes,* and might perhaps belong to the species *dissimilis.*

The greatest abundance was found at depths of 5 and 10 m, where the estimated number was 6 individuals per m² (Fig. 16). The weight is very low, only about 0.01 g per m².

The greater abundance of leptocerid larvae in deeper than in shallow water may be due to behaviour during the deposition of eggs. As with *M. angustata,* these species drop the eggmasses on the water surface, and because of that the eggmasses may be dropped on deep water.

Fam. Limnephilidae

Only two species of the fam. Limnephilidae have been identified – *Nemotaulius punctatolineatus* and *Limnephilus rhombicus.* However, most of the material remains unidentified. The collecting of adults showed that many species found are poorly known or even unknown in the larval stage, and because of that, identification of the Limnephilidae material has not been stressed. Fig. 17 shows the average benthic distribution of the family, and the limnephilids have their greatest abundance in shallow water. The greatest number per m² occurred at a depth of 0.2 m, where 38 individuals weighing 1.08 g were found. Towards greater depths, the number per m² decreases rapidly, but specimens were found down to a depth of 10 m. In the single sample at 15 m, no members of the fam. Limnephilidae occurred.

With respect to the stations investigated, the fam. Limnephilidae was more frequently found at the stations sheltered against wind and with abundant helophytes. At the wind-exposed station 3, specimens were found only occasionally.

In Borrevann, J. Ökland (1964) did not find members of the fam. Limnephilidae deeper than half a meter, while in Lille-Jonsvann they occurred down to a depth of 10 m.

Fam. Lepidostomatidae

The fam. Lepidostomatidae was represented by

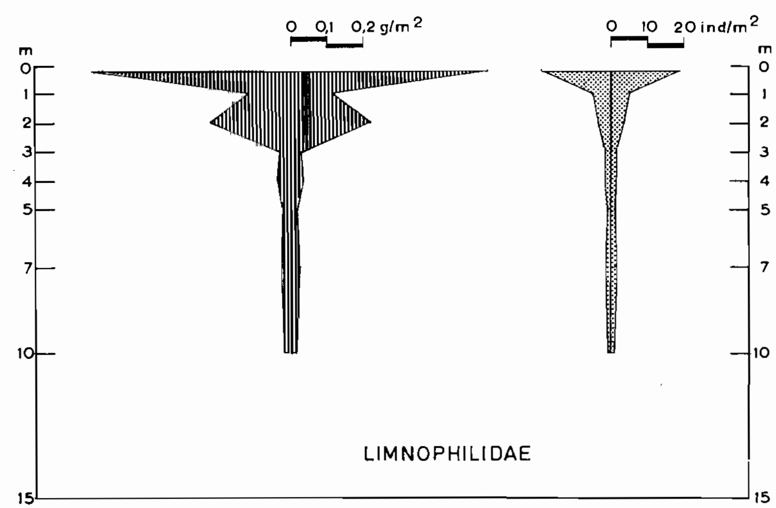


Fig. 17. Weight and average benthic distribution of the family Limnephilidae.

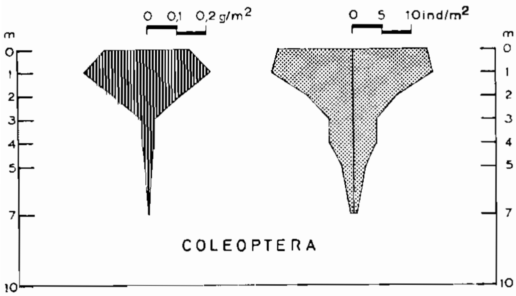


Fig. 18. Weight and average benthic distribution of Coleoptera.

the species *Lepidostoma hirtum*, which was found in a couple of samples at station 3. The specimens were found at a depth of 1 m.

COLEOPTERA

The samples of Coleoptera comprise larvae, pupae, and adults. They occurred in the samples from 0.2 m down to 7 m. Fig. 18 shows their greatest density to be at depths down to 2 m. The highest abundance was at 1 m, where 27 individuals per m^2 weighing 0.43 g were estimated. Towards greater depths, the average number and weight per m^2 decreased, and below 7 m, no individuals were collected. Table VI gives a species list of water beetles, and the sites at which they were collected.

Table VI. The species of water beetles found in the quantitative samples, and the stations at which they occurred

	Stations 1	2	3	4
Fam. Haliplidae				
Haliplus fulvus F.				×
Fam. Dytiscidae				
Hygrotus quinquelineatus Zett.	×			×
Hydroporus palustris L.				×
Deronectes depressus F.			×	×
Deronectes multilineatus Flkstr.	×		×	×
Deronectes rivalis Gyll.			×	
Platambus maculatus L.	×			
Fam. Gyrinidae				
Gyrinus opacus Sahlb.				×
Gyrinus sp. larvae	×	×		
Fam. Chrysomelidae				
Macroplea appendiculata Panz.	×		×	
Donacia clavipes Fabr.	×			
Donacia versicolorea Brahm				×
Donacia/Macroplea spp. larvae	×		×	×

Fam. Haliplidae

The species *Haliplus fulvus* F., which was the only one collected, was found in the sample at a depth of 0.2 m at station 4.

Fam. Dytiscidae

The family was represented by six species, belonging to four genera. The bathymetric distribution is given in Fig. 19, which shows that only *Deronectes depressus* F., *D. multilineatus* Falk and *D. rivalis* Gyll. occurred below a depth of 1 m. These were also the only species found at station 3, the most exposed station and the only one without helophytes. This may indicate that *Hygrotus quinquelineatus* Zett., *Platambus maculatus* L., and *Hydroporus palustris* L. prefer more sheltered conditions than the *Deronectes* species. One species, *Deronectes multilineatus,* occurred at three stations.

According to Lindroth (1960), all species of water beetles mentioned are known to belong to the fauna of the inner part of Sör-Tröndelag (= STi after Strand (1943)). Curiously enough, no water beetles, except 2 larvae of *Gyrinus* sp., were collected at station 2.

Regarding the finding of the fam. Gyrinidae, Haloplidae, and Dytiscidae, most species and genera were found at station 4, indicating that sheltered conditions favour a more varied fauna.

Fam. Gyrinidae

Only one species, *Gyrinus opacus* Sahlb., occurred in the quantitative samples. Adult gyrinids were frequently seen in great numbers, scattering along the water surface. Five larvae were collected, but were not identified. The larvae were collected at stations 1 and 2, at depths of 3 and 1 m, respectively.

Fam. Chrysomelidae

Larvae and pupae belonging to the genera *Donacia* and *Macroplea* (Haemonia) occurred in the samples at depths of 0.2, 1, and 2 m. They were most frequently found in the samples at a depth of 1 m. As will be seen from Figs. 18

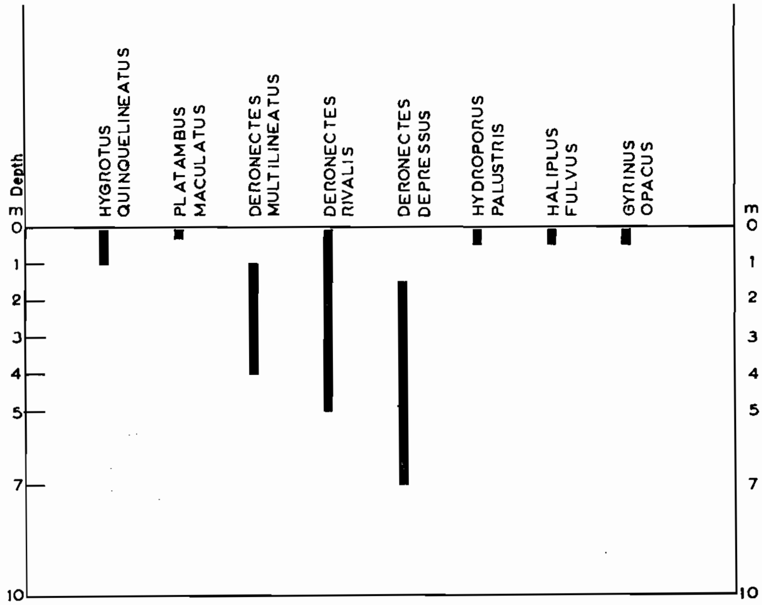


Fig. 19. Bathymetric distribution of Coleoptera.

and 20, most of the Coleoptera collected down to the 2 m level was due to the *Donacia* spp. and *Macroplea* sp. The greatest average number was at a depth of 1 m, where 18 individuals per m² weighing 0.37 g were found. Pupae were present in the June, July, and September samples.

Table VI shows that three species, *Macroplea appendiculata* Panz., *Donacia clavipes* F. and *D. versicolorea* Br., were identified. Identification was made using adults taken from cocoons.

In July 1970, some qualitative investigations were made at station 3, and adults of *M. appendiculata* were collected in the belt of *Potamogeton perfoliatus* at a depth of 2–3 m. In Målsjöen, Klæbu, cocoons were attached to *P. natans*, and Solem (1972) reports that freeliving adults of *M. appendiculata* occurred from the beginning of June and throughout July. *M. appendiculata* is so far only reported from the lakes Lille-Jonsvann and Målsjöen, Tröndelag, in Norway.

DIPTERA

The average benthic distribution of Diptera is shown in Fig. 21. Their maximum abundance was found to be in the littoral zone at a depth of 3 m, where on average 3249 specimens per m² weighing 7.48 g were found. This represents the greatest abundance and weight found among the Insecta. Diptera was found at all depths investigated. The estimated number and weight per m² at a depth of 15 m must be regarded with caution, because the estimation is based on 5 Ekman grabs (one sample) only. The identification of Diptera has been carried out to the family level only.

Fam. Chironomidae

The Diptera material almost entirely belongs to the fam. Chironomidae, the benthic distribution of which will be almost identical to that in Fig. 21. The numbers per m² are reduced by about 100–110 specimens (at a depth of 2 m) or less.

Fam. Ceratopogonidae

Larvae belonging to the fam. Ceratopogonidae were found in the samples from depths of 1 m

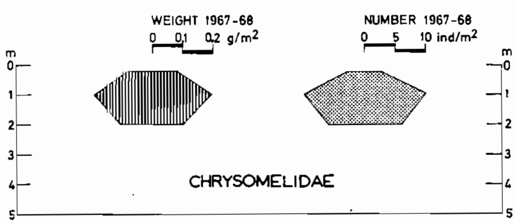


Fig. 20. Weight and average benthic distribution of Chrysomelidae.

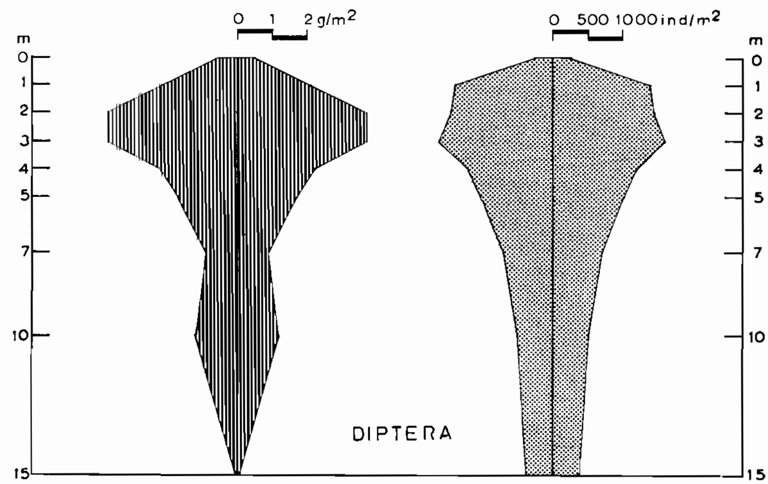


Fig. 21. Weight and average benthic distribution of Diptera.

down to 10 m. Their maximum abundance was at 2 m, where on average 105 specimens per m² weighing 0.06 g occurred (Fig. 22). Towards greater depths, the density decreased steadily, and at the 10 m level, the average number per m² was estimated as 7 individuals weighing only 0.005 g.

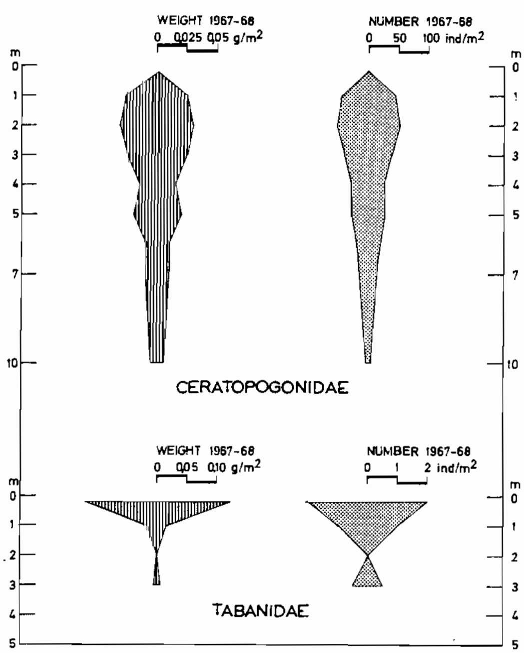


Fig. 22. Weight and average benthic distribution of Ceratopogonidae and Tabanidae.

Fam. Tabanidae

Species belonging to the fam. Tabanidae occasionally occurred in the samples down to a depth of 3 m. They were met with at the sheltered stations 1, 2, and 4. No finding was made at the wind-exposed station 3. The total number of specimens collected was 8. At 0.2 m, the estimated number per m² was 4 individuals weighing 0.24 g. This number was reduced to 2 individuals per m² weighing 0.03 g at a depth of 1 m (Fig. 22).

HYDRACARINA

Hydracarina was treated in the qualitative way only, and in part the material was identified after Koenike (1909). Identification was only stressed to the genus level, except for one species – *Limnochares aquatica* (L.). The material belongs to 6 genera, *Lebertia, Mideopsis, Piona, Arrhenurus, Hydracna,* and *Oxus.* All except *Hydracna* were found to occur down to 10 m. *Hydracna* was found only at 4 m. According to Viets (1967), species within all genera mentioned and *Limnochares aquatica* are known from Norway.

GASTROPODA

The average benthic distribution of the gastropods is shown in Fig. 23, and they were found from 0.2 m down to 10 m. The greatest density occurred in the macrovegetation at depths of 2

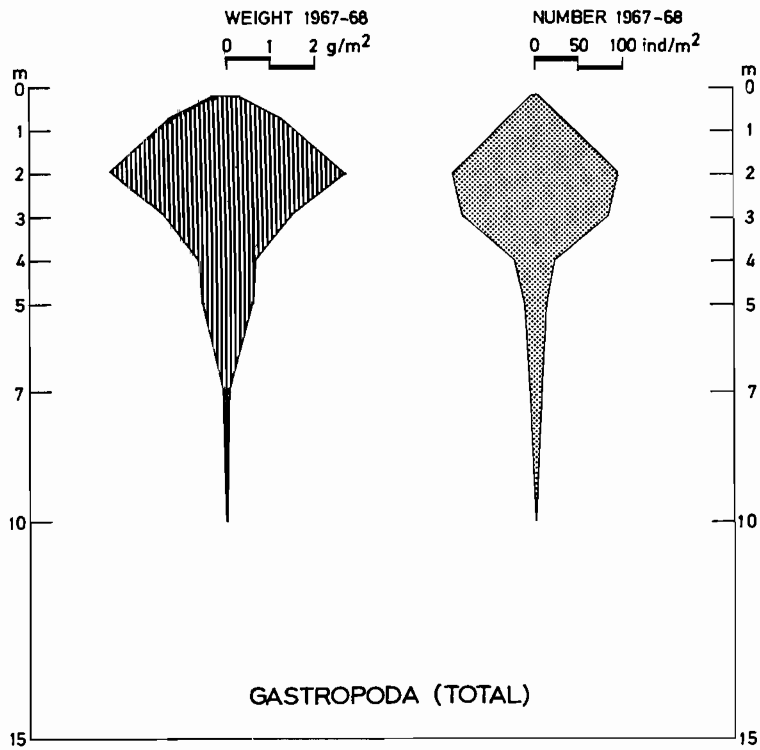


Fig. 23. Weight and average benthic distribution of Gastropoda.

m and 3 m. Here, the estimated density was 193 and 171 individuals per m^2, respectively, and the corresponding weights, 5.53 and 2.94 g. At the lower limit of the macrovegetation, between depths of 3 and 4 m, there was a sudden decrease in the gastropod density. At the 4 m level, 45 specimens per m^2 occurred, and towards greater depths, the density successively decreased.

The species identified in the gastropod collection from Lille-Jonsvann were: *Lymnaea peregra* (Müll.), *Gyraulus acronicus* (Fèrussac), and *Bathyomphalus contortus* (L.). According to Boycott (1936), Hubendick (1949), and J. Ökland (1969), all three species are widely distributed and seem to have great ecological ranges. According to J. Ökland (1969) they are distributed throughout Norway or at least in most parts of the country.

The most dominating gastropod in Lille-Jonsvann, *Gyraulus acronicus*, made up about 74% of the gastropods. The second in number of dominance was *L. peregra* making 23%, while *B. contortus* represented about 3% of the gastropod fauna.

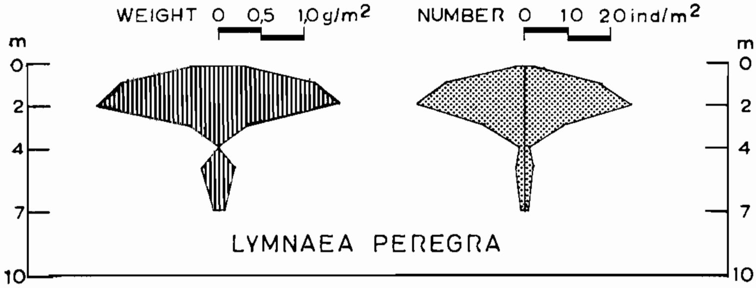
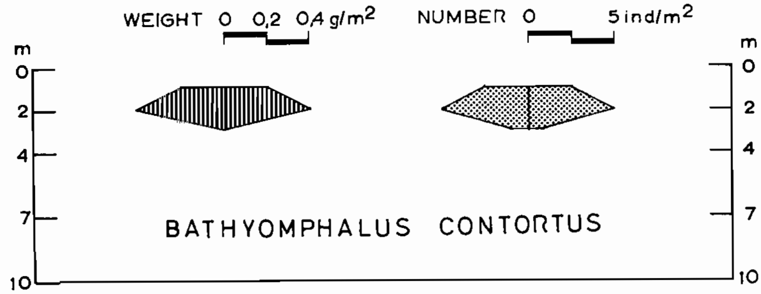


Fig. 24. Weight and average benthic distribution of *Lymnaea peregra*.

Fig. 25. Weight and average benthic distribution of *Bathyomphalus contortus.*



Lymnaea peregra

L. peregra occurred at all the stations investigated, and the benthic distribution ranged from a depth of 0.2 m down to 7 m. The highest population density was found at 2 m, where 50 individuals per m² weighing 2.82 g occurred. Among the gastropods, this was the highest average weight per m² observed. As mentioned earlier for several other species, neither was *L. peregra* found on the sandy shore at the water line at station 3, but observations were made on the stony shore on both sides of the station (3). Although the estimated numbers of *L. peregra* per m² were low (4–7 individuals per m²) in lake Borrevann (J. Ökland 1964), the highest densities occurred at nearly the same depth levels in both Borrevann and Lille-Jonsvann, 1.5 m and 2 m, respectively. The average benthic distribution in Fig. 24 shows that *L. peregra* penetrates down to a depth of 7 m. But this occurred only at station 3, which is the most wind-exposed station. At station 2, the second most exposed, *L. peregra* was found down to 5 m. At the other two stations, 1 and 4, which are the most sheltered, the species did not occur below 3 m. In Borrevann the greatest depth distribution was down to the 2 m level (J. Ökland 1964). With respect to seasonal variation in the benthic distribution, this was seen only from the samples at station 3. Like several other species, *L. peregra* also seems to have a tendency to migrate to deeper water in autumn. J. Ökland (1969) reported *L. peregra* as having a preference for lakes and slow running rivers and rich vegetation both quantitatively and qualitatively, but the species is more or less indifferent to low or high values for total hardness ('CaO'/l).

Bathyomphalus contortus

The species occurred only in the samples at station 3. The average benthic distribution is given in Fig. 25, and shows the distribution to be restricted to depths of 1, 2, and 3 m. It did not occur on the sandy bottom at 0.2 m. The highest population density was at a depth of 2 m, where on average 10 individuals per m² weighing 0.68 g occurred.

The benthic distribution in Borrevann was restricted to less than half a meter (J. Ökland 1964), and here there was a tendency for *B. contortus* to occur with higher population density in sheltered conditions and abundant macrovegetation, but the species was usually found in small numbers. The average quantity in Borrevann was 20 individuals per m². *B. contortus* has a slight preference for lakes, a high preference for rich macrovegetation, both quantitatively and qualitatively, and also a high preference for high values of total hardness in the water (J. Ökland 1969).

Gyraulus acronicus

G. acronicus was the most abundant gastropod; the benthic distribution is shown in Fig. 26. The species occurred at depths from 0.2 m down to 10 m. The greatest population density was found in the dense submerged vegetation belt at 2 and 3 m depth, where on average 133 and 151 individuals per m² weighing 2.63 and 2.29 g, respectively, occurred. Below the 3 m level and down to 10 m, the number and weight per m² successively decreased.

Fig. 27, which is based on the weights of 403 specimens, gives further information about the benthic distribution. In the June samples in both years, *G. acronicus* was found in the plant belt

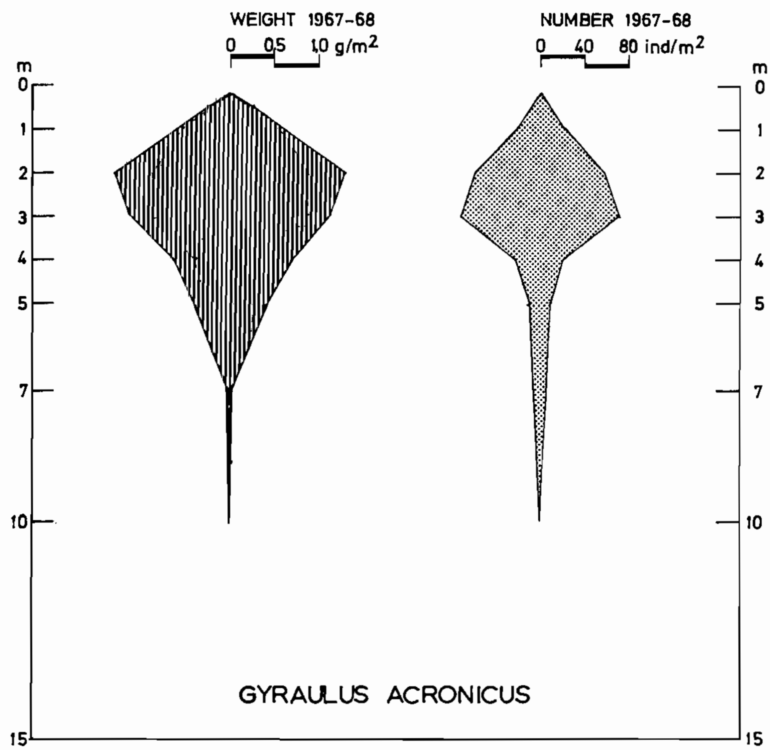


Fig. 26. Weight and average benthic distribution of *Gyraulus acronicus*.

only down to a depth of 4 m. In 1967, the maximum depth of *G. acronicus* in September and October was 5 and 7 m, respectively; the corresponding values in the same months in 1968 were 7 and 10 m. The seasonal variation in the benthic distribution may be due to two factors, migration or delayed hatching of young in the deeper areas, when compared with the shallower areas in the lake. But the main trend in Fig. 27 is an increase in weight per specimen with increasing depth. In other words, the greatest and thus the oldest specimens were caught in the deepest areas, thus indicating that the seasonal variation is due to migration. The same data indicates that reproduction is confined to shallow water, and occurs in the vegetation belt down to a depth of about 4 m.

In Borrevann (J. Ökland 1964), the depth distribution of *G. acronicus* was restricted to the upper half meter, but the species was not represented in the quantitative samples. In the same paper J. Ökland also mentions that *G. acronicus* is often confused with *G. albus*. According to J. Ökland (1969), *G. acronicus* has a slight preference for lakes and slow flowing rivers and for quantitatively rich macrovegetation, but is not particularly affected by low or high values of total hardness.

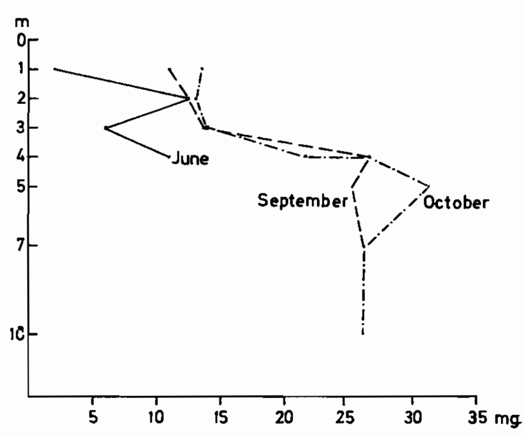


Fig. 27. The average weight per specimen of *Gyraulus acronicus* at different depths. Both years are treated together.

Table VII. Frequency as number of samples in which the Sphaeriidae species occurred, and notes on the abundance. 50 samples total

Species	Frequency	Abundance
Pisidium casertanum	12	locally abundant
Pisidium conventus	5	
Pisidium hibernicum	30	locally abundant
Pisidium lilljeborgi	39	quantitative dominant
Pisidium nitidum	36	not abundant
Pisidium nilium	2	
Pisidium obtusale	4	
Pisidium subtruncatum	23	locally abundant
Sphaerium nitidum	29	locally abundant

BIVALVIA

Of Bivalvia, only the family Sphaeriidae was found to be present in Lille-Jonsvann, and it was represented by 9 species. Of the genus *Sphaerium,* only *Sphaerium nitidum* Clessin occurred, while 8 species of *Pisidium* were identified. These were *P. lilljeborgi* Clessin, *P. casertanum* (Poli), *P. hibernicum* Westerlund, *P. subtruncatum* Malm, *P. nitidum* Jenyns, *P. conventus* Clessin, *P. milium* Held, and *P. obtusale* (Lemarck). According to Kuiper (1963), these are the only species of *Pisidium* found in the boreal zone. For distribution of the species in Norway, I refer the reader to J. Ökland (1964) and K. A. Ökland (1971).

Table VII shows the frequency as the number of samples in which the different species occurred, and notes on the abundance are given. The average number per m² of the most abundant species is given in Fig. 28. Fig. 29 shows the average number per m² of the gen. *Pisidium* and the fam. Sphaeriidae. Figs. 28 and 29 are based on the samples taken at stations 1, 2, and 3 in 1967. In the samples from St. 4, the species have only been regarded as abundant, common or rare.

Sphaerium nitidum

Locally abundant and recorded from depths of 1 m down to 10 m, *S. nitidum* occurred at all the stations investigated. It was abundant at stations 3 and 4, but was scarce at 1 and 2, where between 2 and 4 m depth the submerged

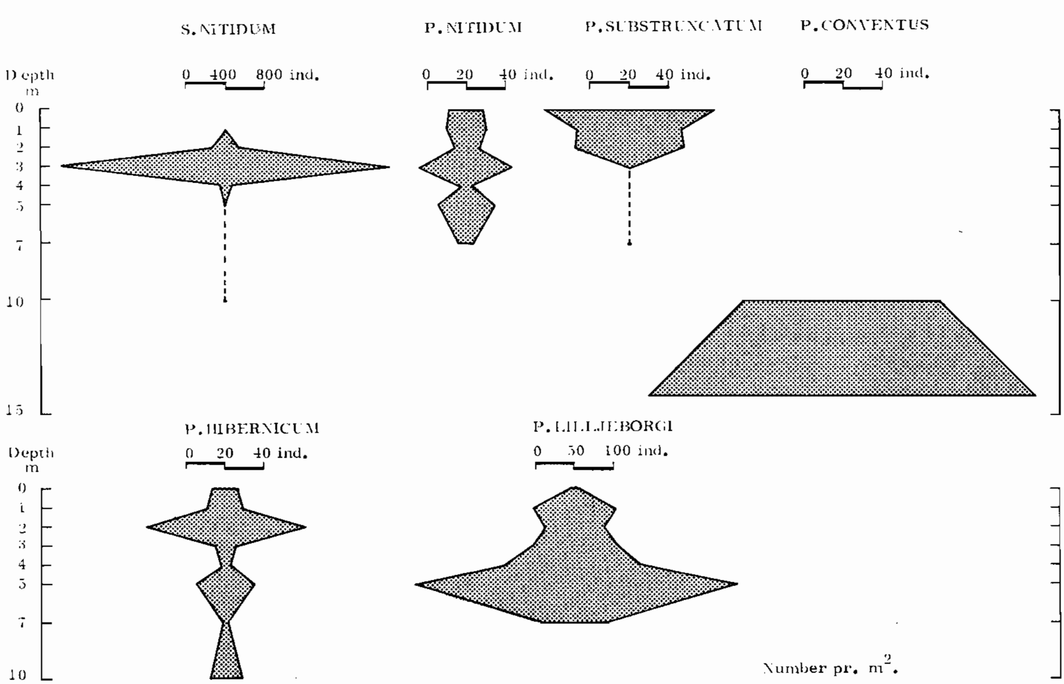


Fig. 28. The benthic distribution of the most common species of the family Sphaeriidae. Data from stations 1, 2, and 3 in 1971 only.

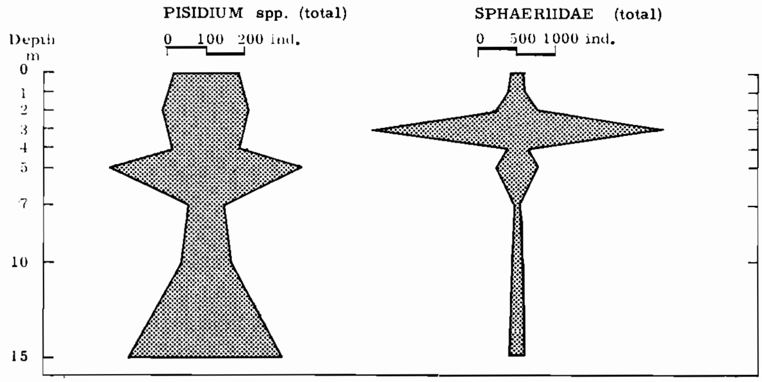


Fig. 29. The benthic distribution of *Pisidium* spp. and the family Sphaeriidae total.

plant belt is less conspicuous than at the other two stations.

The maximum average density was found at station 3 at a depth of 3 m (Fig. 30), where on average 5530 individuals per m² occurred. But when stations 1, 2, and 3 (Fig. 28) are combined, the average number only amounts to 3350 individuals per m². The species was found to be very closely allied with the macrovegetation. *S. nitidum* clings to the submerged vegetation, and at station 3, where it was most numerous, it almost covered the *Isoetes* specimens that occurred in the bottom samples. Although it did not cover the *Potamogeton perfoliatus* in the same way, it was observed to be very numerous on these plants too.

Juvenile specimens of *S. nitidum* were found in the samples from June and October. *S. nitidum* is regarded as subarctic and cold stenotherm (K. A. Ökland 1971).

Pisidium lilljeborgi

This was the quantitatively dominant species in the lake and was recorded at all four stations. It occurred from 0.2 m down to 7 m. The highest density was below the macrovegetation in the sublittoral zone at a depth of 5 m, where on average 422 individuals per m² were estimated (Fig. 28). The benthic distribution of *P. lilljeborgi* at stations 1 and 2 increased steadily down to 5 m and then decreased. The benthic distribution of *P. lilljeborgi* at St. 3 is shown in Fig. 30. It shows a decrease of individuals per m² from 1 m down to 3 m. The number per m² then increases down to 5 m, and towards greater depths, decreases again. This peculiar distribution is caused I think by *Sphaerium nitidum,* which at a depth of 3 m reaches the number of 5530 individuals per m², and thus actually suppresses *P. lilljeborgi* from this depth. Since *P. lilljeborgi* was common at this depth at stations 1, 2, and 4, while *S. nitidum* was not so abundant at these stations as at station 3, the explanation seems likely.

Boycott (1936) reported that *P. lilljeborgi* liked clear gritty sand or silt, and not mud. Further, *P. lilljeborgi* is characteristic of mountain lakes, and has a greater frequency in soft water than in hard water. Boycott (1936) assumed that this is determined by the nature of the bottom rather than of the water. In this regard it must be mentioned that J. Ökland (1964) did not report the species to be present in the eutrophic lake Borrevann, while investigations

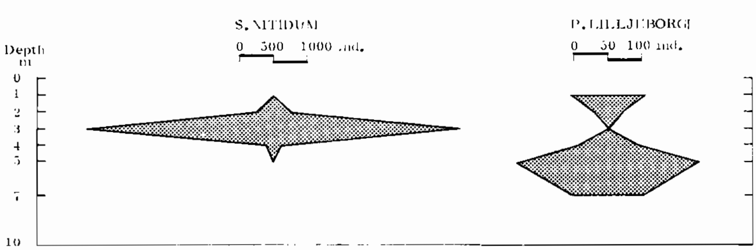


Fig. 30. The benthic distribution of *Sphaerium nitidum* and *Pisidium lilljeborgi* at station 3. Basic data from 1967 only.

of several oligotrophic lakes in the Tröndelag area have shown *P. lilljeborgi* to be present (unpublished data from E. Sivertsen). In lakes Ankarvattnet and Blåsjöen, northern Sweden, Grimås (1961) reported that *P. lilljeborgi* was restricted to the littoral zone.

Pisidium casertanum

P. casertanum is locally abundant and was found to be present at stations 1, 2, and 4, but it did not occur in the samples at station 3. Collections of the species in Lille-Jonsvann were made between depths of 2 and 7 m, with the greatest frequency at 5 and 7 m. According to the data from station 4, *P. casertanum* was most abundant there, where it occurred in every sample from 2 m down to 7 m. At St. 4, *P. casertanum* was characterized as rare at 2 and 3 m, common at 4 m, 3 specimens occurred at 5 m, and more than 130 at 7 m. At stations 1 and 2, only one specimen at 5 and 7 m, respectively, was found. These findings indicate that *P. casertanum* belongs to the lower littoral/sublittoral zone in Lille-Jonsvann. Maximum depth in Borrevann was 6 m, and it occurred frequently in the samples in the depth region 1.5–3 m (J. Ökland 1964). Boycott (1936) found that *P. casertanum* inhabits all kinds of habitats.

Pisidium hibernicum

P. hibernicum is locally abundant, and was found at all stations except St. 3. It occurred at all depths investigated between 0.2 and 10 m, and its greatest density was at St. 4. The average numbers per m² (shown in Fig. 28) are estimated from the samples taken at stations 1, 2, and 3. The species must be regarded as belonging to the littoral fauna. The greatest average number per m² was found at a depth of 2 m, where 82 specimens per m² were found. Boycott (1936) mentions that *P. hibernicum* inhabits lakes, canals, rivers, and streams. The species did not occur in Borrevann (J. Ökland 1964).

Pisidium subtruncatum

P. subtruncatum is regarded as locally abundant, but was found at all the stations investigated. The occurrence was from a depth of 0.2 m down to 7 m (Fig. 28). Maximum density was found to be at a level of 0.2 m, where on average 88 individuals per m² were present. There was a slight decrease in the average number per m² down to 2 m (56 individuals per m²). Between depths of 2 and 3 m there was a great drop in number, only 2 individuals per m² were found to occur at the 3 m level. At greater depths, the same low number per m² was found to occur. In Borrevann, most of the specimens were found in the depth region 1.5–3 m (J. Ökland 1964).

Boycott (1936) stated that *P. subtruncatum* inhabits rivers, canals, lakes, draining ditches, and ponds.

In Lille-Jonsvann, this species belongs to the littoral fauna with its greatest density above the submerged plant belt.

Pisidium nitidum

P. nitidum is not abundant. It occurred in the samples from all stations. Fig. 28 shows the average benthic distribution, and it was found from depths of 0.2 m down to 7 m. It occurred most frequently in the samples from stations 1 and 4. The maximum average density (48 specimens per m²) was at the 3 m level. It did not occur at the 3 m level at St. 3, where *P. nitidum*, like *P. lilljeborgi*, is assumed to be suppressed by *S. nitidum*. *P. nitidum* is found to belong to the littoral and upper sublittoral zones. J. Ökland (1964) stated that *P. nitidum* was one of the dominating species in Borrevann, where its maximum depth was 3 m. In Britain, *P. nitidum* is found in ponds, rivers, canals, tarns, but not in bad water (Boycott 1936).

Pisidium conventus

P. conventus was found at depths of 10 and 15 m. Only one sample (5 Ekman grabs) was taken at 15 m, and the number per m² at this depth (Fig. 18) must be regarded with caution. The species is known to penetrate into deep water, and is probably abundant below 10 m in Lille-Jonsvann. On the European continent, *P. conventus* is very often followed by *P. personatum* (Kuiper in litt.). In Britain, *P. conventus* inhabits mountain tarns, mostly high and cold, and it has been dredged from 400 ft. in L. Ness (Boycott 1936). Valle (1927) stated *P. conventus* to be cold stenotherm. The species was not recorded in Borrevann (J. Ökland 1964). In lakes Ankarvattnet and Blåsjöen, northern Sweden, Grimås (1961) found *P. conventus* to be present from the uppermost littoral zone down to the greatest depths (about 32 m).

Pisidium milium

The species was only found at St. 1 at 0.2 m depth. In the sample from July 1967, 3 specimens were found, and 18 specimens in the sample from September the same year. Since it occurred only at this station, it must be regarded as very local in Lille-Jonsvann. In Borrevann, J. Ökland (1964) found *P. milium* above a depth of 0.5 m, but only one specimen was collected.

Boycott (1936) mentioned that *P. milium* can be found in ponds, rivers, canals, and tarns.

Pisidium obtusale

The species was only recorded at stations 1 and 4, the two most eutrophic and sheltered ones, where it was found in samples from the 0.2 and 1 m levels. *P. obtusale* was only found once at station 1, and only 3 specimens were collected. At St. 4, 6 specimens were found at 0.2 m, and at the 1 m level it was regarded as common. In Borrevann, J. Ökland (1964) found its maximum depth to be about 0.5 m. *P. obtusale* is known from small ponds, stagnant waters, but not usual in running water (Boycott 1936).

Remarks on the fam. Sphaeriidae

It is found (Figs. 28, 29, and 30) that the species of the fam. Sphaeriidae occupy different levels of the littoral and sublittoral zones, and according to the notes given of the different species, they also seem to prefer quite different habitats.

According to the notes given on the benthic distribution, the species may be classified as follows: Upper littoral species; *Pisidium obtusale, P. milium,* and *P. subtruncatum.* Medium and lower littoral species; *Sphaerium nitidum, P. hibernicum,* and *P. nitidum.* Upper sublittoral; *P. casertanum* and *P. lilljeborgi.* Lower sublittoral (and also probably profundal); *P. conventus.*

The benthic distribution of the species and their abundance at the different stations also give some information about the competition between the different species. This is particularly so with regard to the conditions at St. 3 where *Sphaerium nitidum* seems to occupy all the available niches at a level of 3 m, and *P. lilljeborgi, P. nitidum,* and *P. subtruncatum* seem to be suppressed by competition at this particular depth level.

GENERAL DISCUSSION

COMPOSITION OF THE BOTTOM FAUNA

Since the investigation covered two years, I was given the opportunity to study the variation in the fauna for two successive years. This is shown in Figs. 31 and 32.

Due to the fact that such a comparison was not the intention at the outset, the samples taken at a depth of 0.2 m can not be compared for the two years. The percentage composition of the fauna at 0.2 m is therefore based only on the 1967 samples. However, from the figures, we see that there are relatively small differences between the 1967 and the 1968 samples. Therefore, the figures from 1967 at the 0.2 m level may be expected to be fairly representative, although this is the depth where we may expect the variation to be greatest.

First I will compare the numbers of individuals of the total fauna for the two successive years (Fig. 31).

At the 0.2 m level, the dominating groups are oligochaetes and insects, which together amount to about 70% of the total fauna (oligochaetes 40%, insects 30%). That the oligochaetes should be the most dominating group at this depth was somewhat unexpected, but the samples taken on the sandy substratum at St. 3 consisted almost entirely of oligochaeta. In deeper water, the oligochaetes represent only about 10% or less of the total bottom fauna.

The insects, on the other hand, show a reverse curve. With increasing depth, their part of

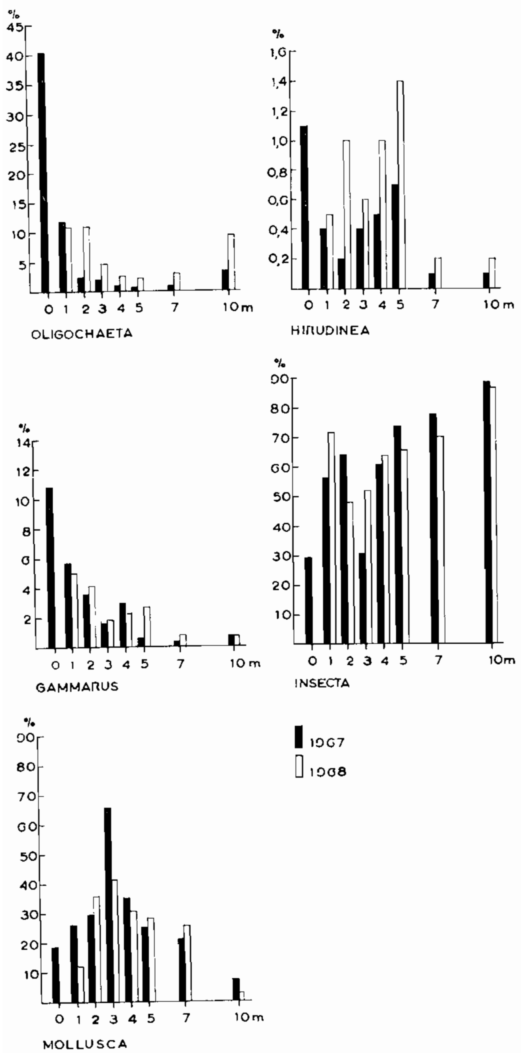


Fig. 31. The percentage composition of the different major groups, based on numbers.

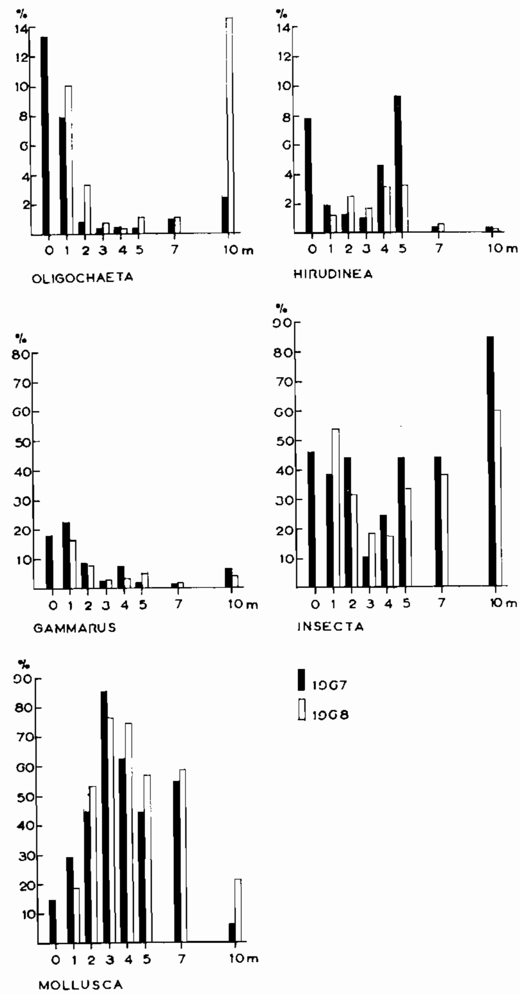


Fig. 32. The percentage composition of the different major groups, based on weights.

the bottom fauna becomes greater. They represent more than 50–60% at all depths, except at the 3 m level, where the average per cent combined for the two years is about 40 (in 1967, 30%; in 1968, 51%). At a depth of 10 m, the fauna consists of nearly 90% insects.

With respect to the number of individuals, the group that comes next to the insects is the molluscs. In the depth range 0.2–7 m, their part of the fauna is in the order of 20–50%, combined for 1967 and 1968. The highest abundance was at the 3 m level, where in 1967 the molluscs amounted to 65% and in 1968 to 41%. Except at the 3 m level, the percentage variation of the molluscs for the two years is within the range of approximately 10%, while it is 24% at a depth of 3 m. This great variation is certainly caused by the species *Sphaerium nitidum,* which at this depth completely dominated the mollusc fauna, and was also found to be locally dominant.

The Crustacea, represented by *Gammarus lacustris,* is not a dominant group, but at the 0.2 m level, they amount to 11%. Towards deeper

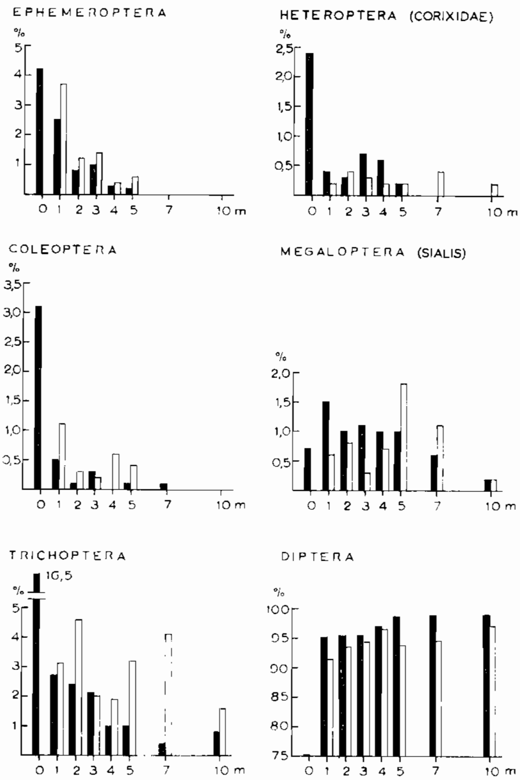


Fig. 33. The percentage composition of the major groups of insects, based on the numbers and on the insects only.

water their part of the fauna decreases steadily to below 1% at depths of 7 and 10 m.

The last group which comes into consideration in these aspects is the Hirudinea, but they make up a very small part of the fauna. On average they represent less than 1% of the bottom fauna.

As to the weights of the bottom fauna, there are two important groups – the insects and the molluscs (Fig. 32). With the exception of the oligochaeta at 0.2 and 10 m, and *Gammarus* at 0.2 and 1 m, none of the Oligochaeta, Hirudinea, and *Gammarus* amount to more than 10% of the total weight of the bottom fauna. *G. lacustris* has been found to constitute more than 40% of the weight of the bottom fauna at certain depths in lake Helin, situated in the mountainous part of central Norway (K. A. Ökland 1969).

Except at 3, 4, and 10 m, the insects comprise 30–50% of the total biomass. At depths of 0.2 and 1 m, the insects are responsible for 40–50% of the total weight. In the depth range of 2–7 m, the molluscs have the greatest percentage of the total weight; the range is about 45 to 85%. However, at a depth of 10 m, the insects amount to about 70% (85% in 1967, 60% in 1968).

When studying the composition of the insect fauna only (Fig. 33), we find that two taxa, Trichoptera and Diptera, are the most important ones. With respect to the number per m², Diptera dominate with more than 90% at all depths investigated, except at 0.2 m, where they represent about 75%. The caddis larvae (Trichoptera) were most numerous at a depth of 0.2 m, where they represented 16.5%. At all other depths they made up less than 5%. Of the other taxa, Ephemeroptera were found to constitute about 4% at the 0.2 m level, and at other depths, 3% or less. All other taxa, Heteroptera (Corixidae), Megaloptera *(Sialis)*, and Coleoptera, represented 3% or less of the total insect fauna.

A similar trend is also found for the weights, but the dominance of Diptera is not so conspicuous as the numbers. At a 0.2 m level, the Diptera represent about 18%, the percentage increasing successively to about 90% at the 10 m level. At the 0.2 m level, Trichoptera is the major taxon representing about 67% of the weight of insects. At a depth of 1 m their part is 20–25%, the percentage decreasing to 8–9% at the 5 m level, and at greater depths less than 1%. In the depth range 1 to 7 m, Megaloptera *(Sialis)* make out nearly the same percentage weight of the insects at all depths in question, and no decreasing tendency in the values appears above the 7 m level. The Heteroptera (Corixidae) have their greatest part of the insect biomass at the 4 m level, the transitional zone between the littoral and sublittoral zones. The taxa Megaloptera *(Sialis)*, Ephemeroptera, Coleoptera, and Heteroptera (Corixidae), each represents a maximum 17% at a given depth of the insect biomass, but usually 10% or less.

The greatest percentage variation in the composition of the insects for the two years was 27%, but in general, the variations were of the order 10% or less.

The average composition of the total fauna in

Table VIII. Mean percentage composition of the major groups of the bottom fauna in the depth range of 0.2–10 m

	Oligochaeta	Hirudinea	Crustacea (*Gammarus lacustris*)	Insecta	Mollusca	Total %
Number %	7	1	3	62	27	100
Standing crop %	4	3	7	39	47	100

the depth range 0.2–10 m is presented in Table VIII. As to the number, the insects amounted to about 62% and the molluscs to about 27%, which in total outnumbered the other groups (each represented by 7% or less). The percentage values of the biomass showed that the molluscs made up 47% and the insects 39%. And, like that of the number, the molluscs and the insects are by far the most dominating groups. Oligochaeta, Hirudinea, and Crustacea (*Gammarus lacustris*) represent from 3 to 7% only.

Regarding the number per m², only two taxa – Oligochaeta and Chironomidae – dominated at all depths in Huddingsvann (Sivertsen 1973). In Lille-Jonsvann, four taxa – Oligochaeta, Trichoptera, Diptera (mostly Chironomidae), and Mollusca (mostly Sphaeriidae) – are regarded as dominant, and J. Ökland (1964) mentioned Ephemeroptera, Trichoptera, Gastropoda, Oligochaeta, and Chironomidae as being the most important groups at different levels in the littoral and sublittoral zones of Borrevann. *Anodonta* is not included in the data quoted from Borrevann.

VERTICAL ZONATION OF THE TOTAL FAUNA

Fig. 34 gives the estimated average weights and numbers per m² of the total fauna, the molluscs only, and the total fauna when excluding the molluscs. The weight and number per m² are estimated from the actual numbers of the total fauna in each sampling, and may therefore differ a little from the numbers estimated for the different groups when these data are summarized.

In general, the highest weight and number per m² occur in the littoral zone, with a maximum at the 3 m level, where 76.4 g and 8461 specimens per m² were found. The lowest values of the weight and number per m² in the littoral zone were estimated at the 0.2 m level.

The arithmetic mean weight and number per m² of the total fauna in the littoral zone are 32.5 g and 5314 individuals, while figures for the sublittoral are 7.6 g and 2042 individuals. Both the biomass and the number per m² are considerably higher in the littoral zone than in the sublittoral. Factors affecting this, and which have been discussed by several authors, e.g. Berg (1938), Berg & Petersen (1956), and J. Ökland (1964), are, that the littoral zone is the producer of nutrients, that macrovegetation is found here and, that oxygen and other physico-chemical factors are nearly always within the range tolerated by most animals. The littoral zone is also much more heterogeneous than the deeper parts of a lake, and provides more varied food elements, better hiding places, and several more niches. Because of the factors mentioned and others, it must be expected that the littoral zone is inhabited by more specimens and species than the sublittoral and profundal, which compared with the littoral zone, have a more monotonous substratum and food. In the profundal zone, the oxygen and other physico-chemical factors may also be limiting factors during periods of the year.

The great variations between the maximum and minimum weight and number per m² in the littoral zone are almost entirely due to the molluscs (Fig. 34). The weight of Mollusca per m² varies from 0.9 g to 62.3 g, and the number per m² from 234 to 4596. When excluding the molluscs, the range in weight per m² is only between 7.5 and 14.9 g, and that of the number per m², 2276–4646.

As pointed out by J. Ökland (1964), it is often very difficult to carry out an exact comparison between the bottom fauna in different

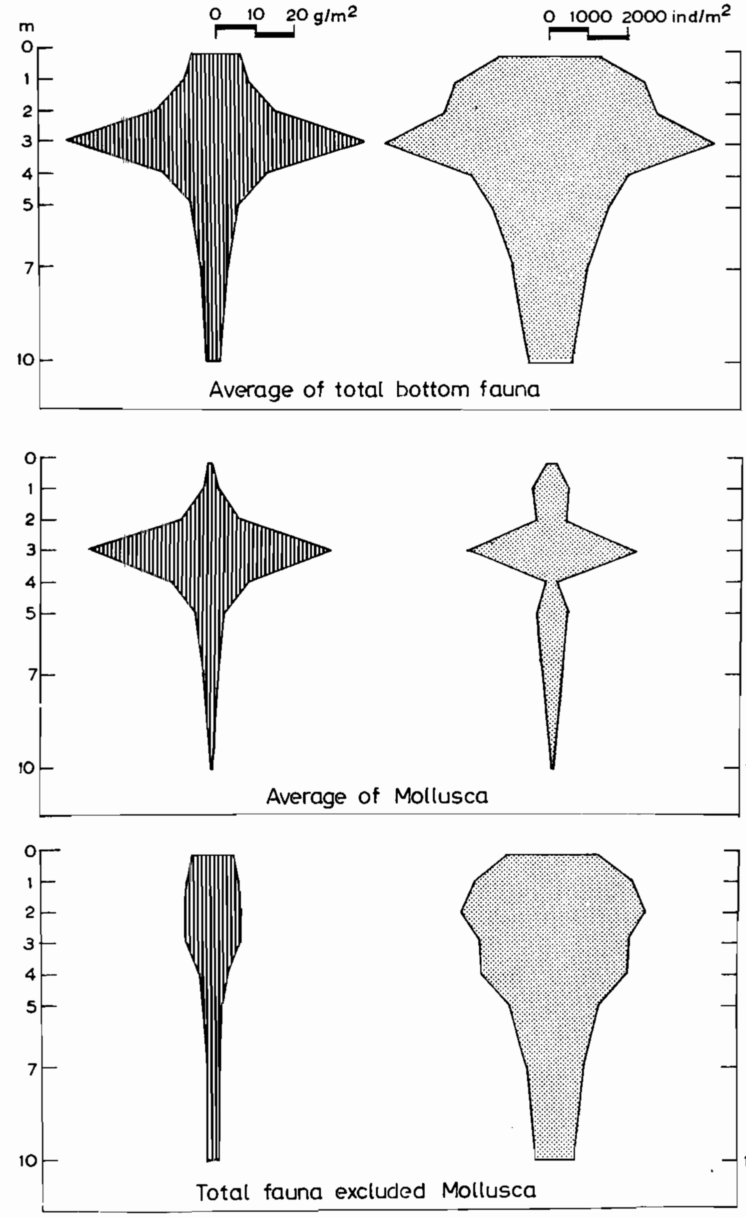


Fig. 34. The average weight and number per m² of the total fauna in 1967–1968, the same for Mollusca total, and that of the total fauna excluding the Mollusca.

lakes because of the different kinds of sampling techniques, different numbers of samples collected, different distribution in space and time for the sampling, etc. But in spite of that, there are several differences which are so clear that they cannot just be caused by the differences mentioned above. I will therefore compare the data obtained in this study with that from other Norwegian investigations.

A review of Norwegian investigations on the bottom fauna of 42 lakes was given by J. Økland (1963, 1964), in which he showed that in 13 lakes that may be regarded as having been fairly well investigated, the arithmetic average weights are as follows: 5.0 g per m² in the zone 0–5 m, 3.5 g per m² in the zone 5–10 m, and 2.2 g per m² in the zone below 10 m. All of these 13 lakes are classified as primarily oligotrophic and so also are all the others except one, Haugatjern, which is of the eutrophic lake type. The average weights per m² found for the 13 oligotrophic lakes correspond well with data obtained from several oligotrophic lakes in the Tröndelag area (unpublished data from E. Sivertsen and J. W. Jensen). When including Borrevann, the bottom fauna of two eutrophic lakes in Norway have been investigated, and, compared with the oligotrophic lake type, the number of specimens and weights per m² are high in the eutrophic lakes. When comparing the bottom fauna of Lille-Jonsvann with that of other Norwegian lakes, it would seem natural to compare it with Haugatjern and Borrevann, although Lille-Jonsvann is not a typical eutrophic lake, it is intermediate between the oligotrophic and eutrophic state. Because the data in the present study only concern the littoral and sublittoral zones, a comparison can only be made with these zones in Borrevann and Haugatjern. In Borrevann, the average weight per m² in the littoral zone is 365 g, including *Anodonta piscinalis.* If *Anodonta* is excluded from the data, only 25 g per m² was found. As for Haugatjern, the average weight per m² in the region 0–5 m is 87.5 g, while in the littoral zone (0–4 m) of Lille-Jonsvann, an arithmetic average of 32.5 g (Table VIII) was estimated. These data show that the bottom fauna of the lakes Borrevann, Haugatjern, and Lille-Jonsvann, has a considerably higher standing crop than the typically oligotrophic lakes.

In Borrevann, J. Ökland (1964) found the fauna to a large extent dominated by Mollusca. This is also true for lake Lille-Jonsvann. The most important family of Mollusca in Borrevann is Unionidae, while in Lille-Jonsvann it is Sphaeriidae, and the species in question are *Anodonta piscinalis* and *Sphaerium nitidum,* respectively.

The gastropods in Borrevann are represented by 12 species, while there were only 3 found in Lille-Jonsvann. While the highest density of gastropods in Lille-Jonsvann was about 200 individuals per m², it was about 4000 individuals per m² in Borrevann. In both lakes, the greatest abundance of gastropods was at the middle depth of the littoral zone, 1.5 m in Borrevann and 2 m in Lille-Jonsvann. In the same way as the gastropods dominated the mollusc fauna of Borrevann, the sphaeriids dominated the bottom fauna in lake Lille-Jonsvann.

If we exclude *Anodonta piscinalis* the Bivalvia (Sphaeriidae) is poorly represented in the eutrophic lake Borrevann, while the sphaeriids are the most dominating group in Lille-Jonsvann. In the quantitative data of productive hardwater lakes in northern Norway (Fjeldså 1972), a similar feature to that obtained in Lille-Jonsvann appears. In 3 of the 4 lakes, from which data are available, the *Pisidium* spp. outnumbers the other groups. For the fourth lake, no quantitative data are given.

In spite of the few quantitative investigations in more productive or more eutrophic lakes in Norway, the sphaeriids seem to make up the most important part of the bottom fauna in more northern latitudes in Norway, at least with regard to number, but possibly also with respect to weight.

VERTICAL SEASONAL VARIATION AND FACTORS AFFECTING THE VERTICAL ZONATION

Obviously, several factors affect the vertical zonation, but in this chapter I will deal with two factors only, first the vertical seasonal variation in the benthic distribution, and thereafter the behaviour of the insects during egg-laying.

In lake Lille-Jonsvann, the vertical seasonal variation in the benthic distribution of species seems to be caused by migration, and Berg (1938) gives a review of the factors that have been taken into consideration when discussing migration of the bottom fauna in lakes. The factors which have been thought to have the greatest effect are temperature and oxygen.

In the present study, some species clearly indicated a migration towards deeper water in autumn. The upward migration, if any, has occurred earlier in the spring than the first sample taken, and therefore, there is no evidence in the material of an upward migration.

However, as to the downward migration, the species that clearly show a descendence to deeper water are: *Glossiphonia complanata* (Fig. 4), *Cyrnus flavidus* (Fig. 12), and *Gyraulus acronicus* (Fig. 27). Another species, which also descends from shallow to deeper water, is the larvae of *Sialis lutaria,* but due to its life cycle (about 2 years), this is not shown in any figure. There is also a slight indication that the larvae of *Agrypnia obsoleta* and the snail *Lymnaea peregra* descend to deeper water, and that the descendence is caused by the same factors that will be discussed below.

As to the factors affecting a downward migration reviewed by Berg (1938), it is very difficult to find a good correlation between the descendence and the curves of temperature and oxygen. In the range 0.2–10 m of depth, we must regard the values obtained by Holtan (1961) to be fairly representative, because of the fairly stable water level of the lake.

Since it is difficult to find any good correlation between downward migration and temperature – oxygen (cf. also Berg 1938), we must look for other important factors. From Figs. 4, 12, and 27, it is clear that the main hatching of young occurs in a restricted area in the littoral zone. Because of that, the population will be very dense here, and as the young grow, they migrate to areas less densely populated, e.g. downwards to deeper water. As for *G. acronicus,* Fig. 27 indicates that the greatest specimens descend. The same tendency also appears for *C. flavidus.* A migration from densely populated shallow water areas to less densely populated areas in deeper water was also found by Swanson (1967), who studied *Hexagenia* nymphs (Ephemeroptera). As Berg (1938) points out, it can hardly be doubted that the downward migration in the autumn is of great value in a nutritional respect by removing individuals from the shallow water, where they are hatched, and dispersing them over larger areas.

According to the data in the present study and that presented by Berg (1938) and Swanson (1967), the most plausible explanation of the problem of downward migration seems to be that populations disperse from the area of reproduction to areas less densely populated where they find suitable nutritional conditions. A contribution to the nutritional aspect in the problem of downward migration is that the leech *Glossiphonia complanata* in both years descended to deeper water later in the autumn than the snail *Gyraulus acronicus* (Figs. 4, 27). According to Autrum (1958) and Mann (1964), *G. complanata* feeds on snails.

As for the constant water inhabitants – *G. complanata* and *G. acronicus* – the upward migration, if it occurs, may be due to a searching for optimum conditions of reproduction. The upward migration may be caused by temperature, but light is also a factor that must be taken into consideration. Besides temperature, light is important as a stimulus for the locomotoric activity of animals. And, increasing light intensity or increasing day length may be the signal for an upward migration. As one factor seldom acts alone, a combination of both the temperature and the light is very likely in this present question.

Another factor which may be of importance to the benthic distribution, at least among the insects, is their behaviour during egg-laying. Here the behaviour of caddis flies (Trichoptera) in particular will be treated. In lotic systems it has been suggested that some species, due to their behaviour, require certain topographical conditions for depositing the eggs (Macan 1961, Elliott 1969), and if this is also the case in lentic systems, behaviour during the deposition of eggs will affect the benthic distribution (Solem 1971).

To explain more clearly this theory, I will give some examples of the procedure during the deposition of eggs, and correlate the behaviour with the distribution found in the littoral and sublittoral zones. A species like *Agrypnia obsoleta* is found to go down in the water along the stems of plants, stones, etc. to deposit their eggs on the bottom of the lake, or may fasten the eggs to floating leaves of water plants (Ulmer 1903, Silfenius 1906, Solem 1969). Several species within the genera *Limnephilus* attach the eggmasses on leaves or stems of plants just above the water surface (Silfenius 1906, Novak & Schnal 1963, Wiggins 1973). This concerns species like *Limnephilus stigma* Curtis, *L. rhombicus* (L.), *L. extricatus* McLach., *L. fuscinervis* (Zett.), *Glyphotaelius pellucidus* (Retz.), *Nemo-*

taulius punctatolineatus (Retz.), which all are identified in the adult collections from Lille-Jonsvann. Due to this behavioural pattern during the oviposition, the larvae of *A. obsoleta* and *Limnephilus* spp. are more likely to be found in the littoral zone than in other areas of the lake. This was also found in this present study (Figs. 15 and 17), and regarding the depth distribution of the Limnephilidae cf. also J. Ökland (1964). Likewise it must also be noted that specimens of the fam. Limnephilidae were more frequently found at stations 1, 2, and 4, which have abundant helophytes, while specimens were only occasionally found at station 3, where the helophytes are lacking.

Species with different behaviour at the oviposition than those mentioned above are found in the genera *Molanna* and *Athripsodes.* As for *Molanna angustata* and several species in the gen. *Athripsodes,* they fly out from the shore and drop the eggmasses on the water surface (Silfenius 1906, Solem unpublished). In this way they may go a longer distance from the shore and thus drop the eggs on deeper water. The species in the genera *Athripsodes* were also more frequently found below the littoral zone (Fig. 16) (cf. also Berg 1938, J. Ökland 1964), and the highest density of *M. angustata* was found at a depth of 4 m, at the transitional area of the littoral/sublittoral zones.

In the examples given, there is a fairly good correlation between the behaviour at the oviposition and the benthic distribution of the larvae of the different caddis fly species. When considering the species treated, a similar benthic distribution occurred in the eutrophic lakes Esrom, Denmark, and Borrevann (Berg 1938, J. Ökland 1964).

Certainly, several factors may affect the vertical zonation of animals in lakes, and the one nearest to the limits of tolerance will be the one which is the most important. However, when nutritional conditions are good, temperature, oxygen, physico-chemical factors, etc., are within the limits of tolerance, the behaviour at oviposition of some species seems to affect the benthic distribution of the larvae.

SUMMARY

Bottom fauna investigations from the mesotrophic lake Lille-Jonsvann (63°23′N, 10°33′E), just outside Trondheim, are presented. The sampling was mainly carried out with an Ekman grab, but some qualitative sampling is included. The quantitative samples were taken at depths of 0.2, 1, 2, 3, 4, 5, 7, and 10 m, this depth range covering the littoral and sublittoral zones. Additionally, one single sample (5 Ekman grabs) was taken at a depth of 15 m. The samples were taken in June, July, September, and October in the years 1967 and 1968, and each year 4 and 3 stations, respectively, were investigated.

The fauna was found to be rich both in quantity and quality, and to be dominated by two groups of animals. The two dominant groups were Insecta and Mollusca, and with regard to number, they represented 63% and 27%, respectively, of the total fauna. Among the rest of the major groups, the Oligochaeta amounted to 7%, while Crustacea and Hirudinea made up 3% or less.

Of the biomass, the Mollusca represented 47% and the Insecta 39%; each of the other major groups less than 7%.

Bivalvia was the most abundant group of Mollusca. Only the fam. Sphaeriidae represented by 9 species was present, and the quantitatively dominant species was *Pisidium lilljeborgi.* The northern and cold stenotherm *Sphaerium nitidum* was locally abundant and at certain sites and depths a maximum average density of 5530 individuals per m² was estimated.

Three species of gastropods were identified, and regarding the number per m², *Gyraulus acronicus* was the most dominant, making up 74% of the gastropods.

The insects were dominated by Diptera, of which the entire material almost completely belonged to the fam. Chironomidae. Other taxa among the insects represented in general 10% or less, except the Trichoptera at a depth of 0.2 m.

Among the Oligochaeta, the species *Peloscolex ferox, Stylodrilus heringianus,* and *Lum-*

briculus variegatus were identified. The first two mentioned are regarded as clear water (oligotrophic lakes) species, and were found only down to a depth of 7 m. However, at station 1, *P. ferox* only penetrated down to 2 m. This is an indication that the process of eutrophication is more pronounced in this part of the lake than, e.g., at station 3.

Values for the arithmetic mean weight and number per m^2 of the total fauna in the littoral zone (0–4 m) are 32.5 g and 5314 individuals, while those of the sublittoral (5–10 m) are 7.6 g and 2042 individuals per m^2. Maximum weight and number per m^2 occurred at the level of 3 m, where 76.4 g and 8461 individuals per m^2 were found.

Three of the species treated – *Glossiphonia complanata* (Hirudinea), *Cyrnus flavidus* (Trichoptera), and *Gyraulus acronicus* (Gastropoda) – clearly showed a seasonal variation in their benthic distribution. For all three species, the hatching of young occurred in a very restricted area in the littoral zone, and the individuals migrated to areas less densely populated and where suitable food could be found in late summer and autumn.

A correlation between the depth distribution of the caddis larvae and the behaviour of the females at the oviposition was also found. Larvae of species that drop eggmasses randomly on the water surface are more frequently found in deeper water than the larvae of species that deposit the eggs in the vegetation belt, in which the eggs are fastened to the plants or attached to the bottom substratum.

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