Seasonal variations in the diet of the brown trout *(Salmo trutta* L.*)* in a Norwegian mountain lake compared with the variations in the plankton and bottom fauna

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The seasonal variations in the plankton fauna, the bottom fauna, and the feeding habits of the brown trout *(Salmo trutta* L.) in Lake Dalsvatn, an oligotrophic mountain lake of 52 ha in central Norway, were studied in the period October 1970 to October 1971. Bottom food dominated the diet, plankton food being important especially for smaller trout in autumn and winter. Surface food was eaten in the ice-free season. The bottom fauna consisted mainly of Oligochaeta, Hirudinea, Chironomidae, Trichoptera, Ephemeroptera, and Gastropoda. Of these groups the insect larvae, especially Trichoptera, were important as trout food. The plankton fauna was dominated by *Bosmina longispina,* but *Daphnia galeata* was the most important prey of the trout.

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INTRODUCTION

The seasonal variations in the plankton fauna, the bottom fauna, and the feeding habits of brown trout *(Salmo trutta* L.) in Lake Dalsvatn were studied in the period October 1970 to October 1971.

In previous investigations trout have been shown to feed upon what is available, with little or no selection (Nilsson 1955, Ball 1961, Graham & Jones 1962). Hunt & Jones (1972) found in their investigations in Llyn Alaw that approximately 90% of the bottom fauna was not available to the trout. The purpose of this investigation was to study the seasonal variations in the diet of the brown trout compared with the variations in the plankton and bottom fauna.

THE STUDY AREA

Lake Dalsvatn is situated at an elevation of 582 m above sea level in the southern part of Trollheimen, central Norway (62°40′N, 9° 15′E). The lake is formed by quaternary deposits and the drainage area (11 km^2) consists of high mountains, birch forest, and some bog areas. The area of the lake is 52 ha. The greatest depth is 9 m.

In the summer the water temperature reached 10–15°C. A distinct stratification was never established; even at midsummer homothermal conditions were sometimes recorded. Lake Dalsvatn is an oligotrophic and oligohumic lake with rather soft water. For further details see Johnsen (1973).

MATERIAL AND METHODS

Zooplankton samples were taken by vertical hauls with a net 29 cm in diameter and mesh size 250 μm from the same place and from the same depth (7 m) each time. One to three hauls were taken each month. Totally 19 hauls were taken. Small animals, as for example the first copepodite stages of *Cyclops scutifer* Sars, will pass through the net. The data for this species are therefore uncertain. The results are, however, supposed

to give a general view of the occurrence of planktonic crustaceans that were of such a size that the fish were interested in them as food objects. Bottom fauna samples were taken with an Ekman bottom sampler covering an area of 0.02 m^2. The samples were taken at the same station each time from 2, 3, 4, 5, 6 and 7 m depth. Five samples were taken from each depth once or twice a month. During the investigation period 370 samples were taken. The bottom material was sieved through a net with mesh size 0.5 mm, and the animals were sorted alive.

During the winter the fish samples were taken once every third week. During the summer, material was collected twice a month. All the fish were caught by using bottom nets of varying mesh sizes. A total of 1112 fish were caught and 967 stomachs were examined.

In the laboratory the material from each stomach including the oesophagus was examined separately, and the contents were identified and sorted into five main groups: bottom food, plankton food, surface food, plant remains, and fish and spawn. A similar grouping was used by Nilsson (1955) and Klemetsen (1968).

To compare the main food categories and the main groups within bottom food, the volumetric method of Nilsson (1955) was used. The percentage of every food item was estimated for every stomach. The figures obtained were summed up and divided by the number of stomachs investigated. This method expresses the average dietary state of the population at a certain time and is marked "volume %" in the figures.

To compare the different species within plankton food, the percentage frequency method was used (Hynes 1950). The presence of the different food objects was noted and calculated as a percentage of the stomachs investigated. This method is marked "frequency %" in the figures.

The material was not treated statistically.

RESULTS AND DISCUSSION

Most papers dealing with the food of brown trout conclude that the species is mainly a bottom feeding fish (cf. Kennedy & Fitzmaurice 1971, Hunt & Jones 1972). The seasonal variations in the feeding habits of trout seem to depend on seasonal variations in the fauna itself (Nilsson 1955). This means that the fish usually feed on what is common and available at the time. The term 'available' means that an animal is visible to the fish, and of suitable size and taste to be eaten by the fish (Nilsson op. cit.).

The bottom fauna and the bottom food

The total biomass of macrobenthos was found to be about 3.8 g/m^2 (wet weight) on the average in the depth interval 0–5 m and 3.1 g/m^2 in the deeper part. These values are of the same order of magnitude as found in many Norwegian mountain lakes (Økland 1963, Sivertsen 1974). Fig. 1 shows the occurrence of the most important fauna groups in the bottom samples and in the stomach samples throughout the year.

Chironomidae were the dominating group in the bottom samples, with a mean density throughout the year of 1440 ind./m^2, which is 65% of the total number of animals collected from the bottom fauna. They were found in considerable numbers at all depths. Chironominae and Orthocladiinae were the most abundant subfamilies.

Chironomidae larvae were a quite important part of the diet of the trout in the period February – April. Larvae of Chironominae were the most important. They are usually hidden in the bottom mud, and are therefore less available to the fish. Some stomachs were filled with Tanypodinae larvae, which are free-swimming predators (Sæther 1968) and therefore easily accessible to fish.

Oligochaeta represented 22% of the total number of individuals in the bottom fauna, averaging 480 ind./m^2. *Peloscolex ferox* Eisen was the most abundant species (60% of the Oligochaeta) which confirms the oligotrophic and clear-water character of the lake (Milbrinck 1972). Other species identified were *Lumbriculus variegatus* Müller, *Stylodrilus heringianus* Clap., and *Eiseniella tetraedra* Sav.

Oligochaeta are not usually available to trout because of their hidden life in the bottom sediments (Frost 1945, Frost & Smyly 1952, Nilsson 1955, Grimås 1963). Also in the present investigation Oligochaeta were very common in the bottom samples and rare in

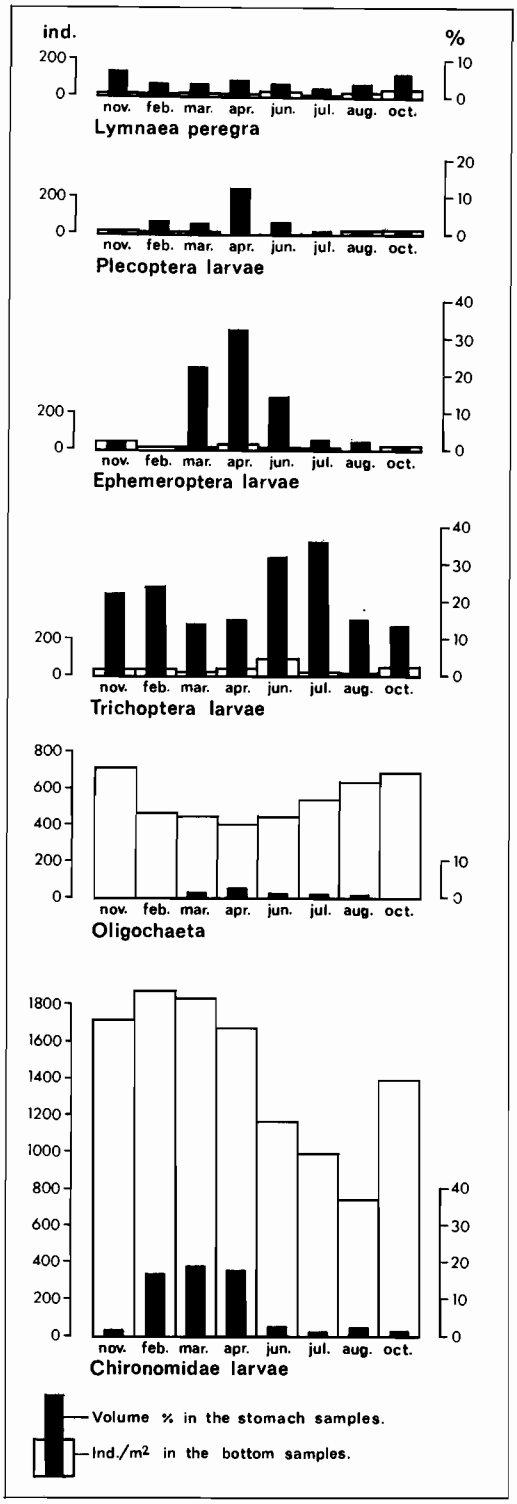

Fig. 1. The occurrence of the most important bottom fauna groups in the stomach samples (volume %) compared with their occurrence in the bottom samples (ind./m²) in the period November 1970 – October 1971.

the stomach samples. The species *Eiseniella tetraedra* was found in great numbers in two fish stomachs in May during the period of the ice breaking up. This species usually occurs along shores, following the movements of the water line (Julin 1949). In connection with the increasing water level during the thawing, it became available to the trout. Aarefjord et al. (1973), who investigated the stomach contents of trout from 8 lakes in Scandinavia, concluded that *E. tetraedra* was the only limnetic oligochaete species recorded in the stomach contents of brown trout.

Hirudinea was the third most numerous group (115 ind./m² – 5% of the total). *Helobdella stagnalis* L. represented 95% of the leeches, *Glossiphonia complanata* L. the rest (Sivertsen 1975).

Hirudinea was little utilized as fish food. This was also shown by Hunt & Jones (1972).

The remaining 8% of the bottom fauna consisted of several groups of insect larvae, Gastropoda, Bivalvia, and Hydracarina.

Trichoptera larvae and pupae were the dominating group in the bottom food of the fish. *Mystacides azurea* and *Oxyethira flavicornis* were the most common trichopteran species in the bottom samples, and the same two species were most important in the food of the trout.

Ephemeroptera and Plecoptera larvae were also important in the bottom food, especially in winter and spring. *Leptophlebia* and *Nemoura* were the most common genera in both stomach samples and bottom samples.

Leptophlebia spp. are usually described as swimming larvae (Økland 1964) and therefore available to the fish. Their greatest occurrence in the bottom fauna was in November, but at that time the larvae were small and assumed to be less available as food for the trout. According to Brittain (1972), the larvae increase their activity in connection with accelerated growth before hatching. In Lake Dalsvatn this seems to have taken place in March and April, and the larvae then became attractive as fish food. In June the larvae were still common in the stomach

samples in spite of their disappearance from the bottom samples. This may be due to the fact that the larvae at this time were occurring at less than 1 m depth. In this region no bottom samples were taken. *Nemoura* spp. were also most common in the stomach samples in late winter and spring. Another plecopteran species, *Taeniopteryx nebulosa* L., was commonly found in the stomachs in April at the time of the ice breaking up. At the same time great numbers of larvae and imagines of this species were found crawling on the snow.

Lymnaea peregra was most common in the stomach samples in spring and autumn corresponding to its greatest seasonal occurrence in the bottom samples.

Hydracarina were common in the bottom samples and rare in the stomach samples. This may be due to their small size. Egglishaw (1967) reported that salmon in aquaria often caught swimming Hydracarina, but spit them out at once.

With exception of the Chironomidae that in periods were of a certain interest as fish food, the trout was mainly seeking its bottom food among the animals that made up 8% of the total bottom fauna.

The plankton food

The brown trout cannot filtrate plankton organisms from the water. It must catch the animals one by one, and must therefore spend much time and energy to fill its stomach with planktonic crustaceans (Frost & Brown 1967). It is therefore natural that the fish prefers the largest species like *Daphnia galeata* and *Holopedium gibberum* Zaddach (Fig. 2). *B. longispina,* which dominated the plankton samples most of the year, was to a little degree utilized by the brown trout as food. Southern (1935) found the same in Lough Dergh.

Cyclops scutifer was also common in the plankton samples, but like *B. longispina* not utilized by the fish. Jensen (1972) found in Lake Holden, central Norway, that the

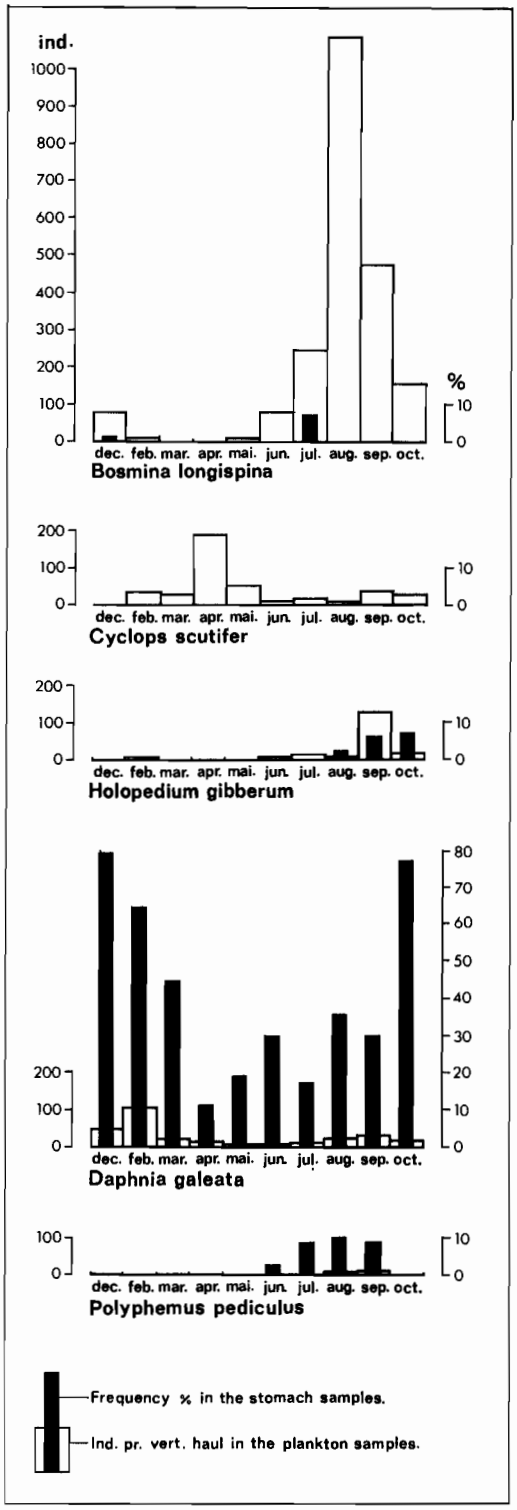

Fig. 2. The occurrence of the most important species of planktonic crustaceans in the stomach samples (frequency %) compared with their occurrence in the plankton samples (ind./vertical haul) in the period December 1970 – October 1971.

plankton fauna consisted mainly of *C. scutifer* (82%). In spite of this it was not found in the stomachs of the trout, and the trout in Lake Holden had other planktonic crustaceans as its most important food at that time. Southern (1932, 1935) and Nilsson (1955) reported that *Cyclops* spp. were only to a little extent eaten by the trout even when they were occurring in great numbers in the water masses. Aass (1973) concluded that Copepoda are normally not utilized to a great extent by the trout.

The surface food

Norlin (1967) compared the biomass of bottom animals in impounded mountain lakes and the biomass of surface animals and found that the biomass of bottom animals generally was 1000 times greater than the biomass of surface animals. A comparison of the importance of the two groups as fish food showed that in Lake Blåsjön the bottom animals were only 8 times as frequent in the stomachs as surface animals. Norlin (op. cit.) concluded that the surface animals are available to the fish to a much higher degree because they lack the opportunities for hiding and escaping that bottom animals have. Instead they are clearly seen against the sky. The activity of the insects depends largely on the weather. Allen (1938) stated that in Lake Windemere the surface animals were eaten by the trout as early as in April in years with good weather. In years with bad weather they were not important as fish food until June. In Lake Dalsvatn the surface animals were important in the trout stomachs in periods with high air temperature and/or little precipitation. In periods with low air temperature and/or much precipitation they were sparse in the trout stomachs.

Among the ephemeropterans the greatest numbers of the species *Leptophlebia marginata* L. and *Leptophlebia vespertina* L. hatched during June. Imagines were, however, not found in the stomach samples. Grimeland (1966) found that *L. vespertina* was swarming at a certain distance from the lake, and if there was wind it hid among the vegetation on the ground. This species will therefore probably not be easily brought to the water surface. The same cause may explain the lack of imagines of the trichopterans *M. azurea* and *O. flavicornis* in the stomach samples in spite of their great importance in the stomach content as larvae and pupae.

The seasonal variations in the diet of the trout

The results of stomach analyses of brown trout from Lake Dalsvatn from October 1970 to October 1971 are presented in Fig. 3. The food categories "fish and spawn" and "plant remains" were of little importance.

The present investigation showed that the trout in Lake Dalsvatn was mainly bottom feeding, but there were seasonal variations in the diet corresponding to seasonal variations in the prey fauna. On which food item the trout is feeding at a certain time depends on the availability of the different food categories at that time. Comparing the three main food categories bottom food, plankton food,

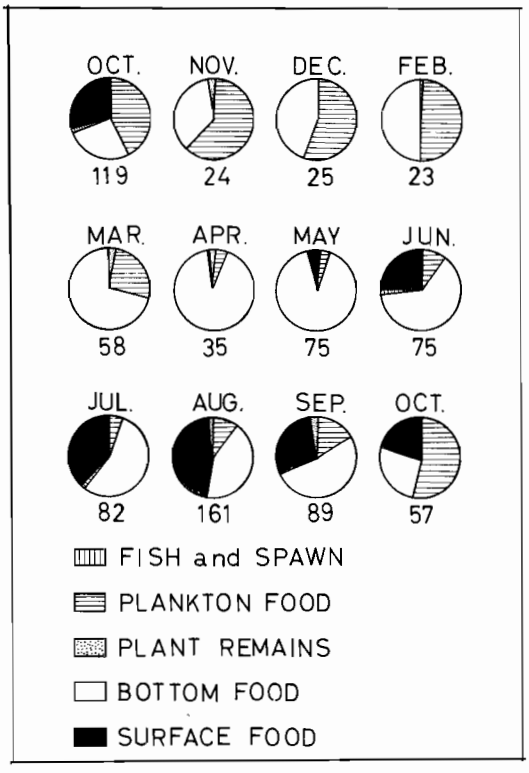

Fig. 3. The occurrence of the main food categories (volume %) in the stomach samples in the period October 1970 – October 1971. The figures give the number of stomach samples investigated each month.

and surface food in Lake Dalsvatn, surface animals are the most available, plankton animals the least. Surface animals are large, easy to see and to catch. Planktonic crustaceans are small and hard to see. This means that in summer, when all three food categories are present, the trout will prefer surface animals because they are easy to get to. In Lake Dalsvatn the diet of the trout in summer alternated between surface food and bottom food. In periods with nice weather, that is when surface animals were present, the stomachs of the trout were filled with them. On the other hand, in periods with bad weather the trout had to feed on bottom animals. In late autumn and early winter the supply of surface animals was small. At the same time the new generation of insect larvae was little available to the fish because of their small size. In autumn and early winter the trout therefore had to feed on planktonic crustaceans, and the largest specimens were chosen. In late winter and spring the insect larvae increased both their size and their activity and became available to the trout. The trout was feeding mainly on these until they hatched in the summer and the surface food again became available.

The main food categories and the fish size

The fish were divided into five length groups, and the data on stomach contents for the whole year were added (Fig. 4). With exception of the smallest fish the figure shows the decrease of the planktonic crustacean fraction of the stomach contents with increasing fish size. (The smallest fish were mainly caught during the summer when the plankton in general had little importance as fish food.) Both surface animals and bottom animals increased their importance with increasing fish size. The largest fish had eaten bottom and surface food almost exclusively. Only two fish-feeding brown trout were found. They were both large fish, 320 g and 1,300 g.

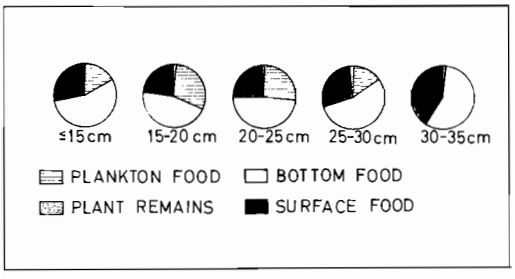

Fig. 4. The occurrence of the main food categories (volume %) in the stomach samples of fish of different length groups. The figure is based on the total number of stomach samples for the whole year.

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