

Growth patterns and food habits of *Baetis rhodani*, *Capnia pygmaea* and *Diura nanseni* in a West Norwegian river

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As a part of weir-pond-ecosystem project, the growth patterns and food habits of *Baetis rhodani* (Ephemeroptera), *Capnia pygmaea* (Plecoptera), and *Diura nanseni* (Plecoptera) were investigated. *B. rhodani* was bivoltine. The winter generation consisted of three cohorts. *C. pygmaea* and *D. nanseni* accomplished their nymphal growth in one year. The predominate food consumed by *B. rhodani* and *C. pygmaea* was detritus. Variations in the diet of these detritivores are discussed in relation to microdistribution and possible competition. The most common prey items of the carnivorous *D. nanseni* were chironomids and nymphs of *B. rhodani* and *C. pygmaea*. Prey shortage is suggested to be the reason for small *D. nanseni* eating detritus.

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1. Introduction

Many rivers in Norway are regulated and their water discharge considerably reduced. In some instances weirs are built along the rivers to maintain the water levels. In 1975 a project, "Terskelprosjektet" ("The Weir Project"), was started with the intention to clarify the biological effects of weirs (Mellquist 1976). Most of the investigation was carried out at a particular weir-pond-ecosystem in the river Ekso in western Norway. The present study is a part of this investigation and concentrates on the food habits and growth patterns of the nymphs of the mayfly *Baetis rhodani* Pictet and the stoneflies *Capnia pygmaea* Zetterstedt and *Diura nanseni* Kempney.

B. rhodani and *C. pygmaea* were both abundant and presumably important members of the benthic animal community. *D. nanseni* was the most common macrobenthic predator. Its carnivorous habits have previously been shown by Brinck (1949). Current literature states that *B. rhodani* is herbivorous and detritivorous (Jones 1950, Brown 1961, Chapman and Demory 1963) and *C. pygmaea* detritivorous (Brinck 1949).

2. Study area

The river Ekso is situated about 100 km NE of Bergen in the Eksingedalen valley, western Norway. The present study was carried out in 1976–77, at Ekse ($60^{\circ}15'N$, $6^{\circ}15'E$), in the subalpine region at 560 m a.s.l.

The terrestrial vegetation along the river banks consists of herbs, shrubs, and the predominating trees *Betula pubescens* Ehrh. and *Salix* spp. The river is about 40 m wide and the water discharge between 0.1 and 14 $m^3 s^{-1}$. The mean water temperature ranges from $0^{\circ}C$ in the winter to $20^{\circ}C$ in the summer (Fig. 1). Ice covers the river from November until May. The electrical conductivity ranges between 10 and 49 $\mu S cm^{-1}$ and the pH between 6.0 and 6.5.

The bottom substrate consists of gravel and small stones interspersed with sand and organic matter (detritus). The aquatic vegetation mostly comprises algae, chiefly diatoms, and only scattered patches of mosses.

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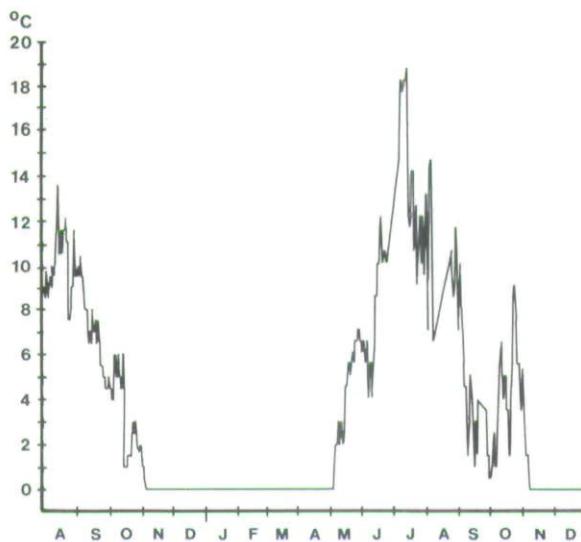


Fig. 1. Daily mean water temperature ($^{\circ}\text{C}$) at Ekse from August 1976 to January 1977.

3. Methods

The nymphs were collected just below the weir, using a kicking technique (Frost et al. 1971), and preserved in 70% ethanol. The collecting net had a mesh-size of 250 μm .

The analyses of growth patterns were based on head width measurements. Time of emergence was estimated from observations of imagines in the field and from the absence or presence of mature nymphs. Because of the large size variations found in *B. rhodani*, four size groups were used:

I	0.10–0.32 mm head width
II	0.34–0.62 "
III	0.64–0.92 "
IV	≥ 0.94 "

The food habits of *B. rhodani* and *C. pygmaea* were analysed using a filtration technique according to Mecom and Cummins (1964) and Coffman et al. (1971). The nymphs were dissected, the food of the foreguts taken out, dispersed in distilled water, and filtered onto a filter with pore-size 0.45 μm and diameter 25 mm (Sartorius Membranfilter with grids). The food was grouped in four categories:

1. Coarse detritus: dead organic matter with a clear cellular structure (including microorganisms).
2. Fine detritus: dead organic matter without visible cellular structure; amorphous (including microorganisms).
3. Diatoms.
4. Other algae.

Every food particle was converted to a common unit defined as the mean area of the smallest size group of food particles. The percentage representation was then calculated.

For small nymphs, (group I of *B. rhodani* and the August and September samples of *C. pygmaea*) a different technique was used. After dissection, the gut contents were squeezed onto a glass slide, cleared in lactic acid, and counted along five randomly chosen transects. Every food particle, except for fine detritus, on the transect was measured and subtracted from an initial assumed fine detritus part of 100%. This technique is less accurate than the filtration technique, but easier and quicker to use, particularly on small nymphs.

For *D. nanseni*, the foregut contents were put on a glass slide, cleared in lactic acid, and the food items identified and counted.

4. Results

4.1. Growth patterns

In September the small nymphs of *B. rhodani* (group I) dominated (Fig. 2). They grew into group II within one month and reached group III in January. The nymphs entered the final group (IV) in April–May and the imagines emerged soon after. This winter-growing generation hatched from eggs in two waves, producing one cohort in September and another in December. The December-cohort remained in group I somewhat longer than the September-cohort; probably due to the lower water temperature. However, the two cohorts subsequently emerged within the same short period of time. In April, when ice still covered the river and no imagines had emerged, small nymphs reappeared. They were presumably a third cohort of the winter generation. However, it soon mixed with the summer generation appearing from about May–June to September.

In general, the growth rate was reduced at lower temperature, but even at 0°C a considerable growth occurred.

The growth pattern of *C. pygmaea* is shown in Fig. 3. There were two periods of rapid growth; one from Au-

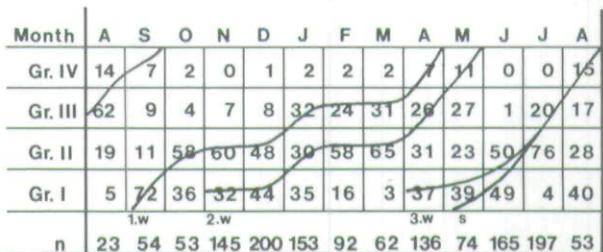


Fig. 2. Percentage composition of size groups, based on head width measurements, of *Baetis rhodani*. Group I consists of the smallest and group IV of the largest individuals. 1.w, 2.w, and 3.w denote the start of the first, second, and third cohort of the winter generation. s denotes the start of the summer generation. n is the sample size.

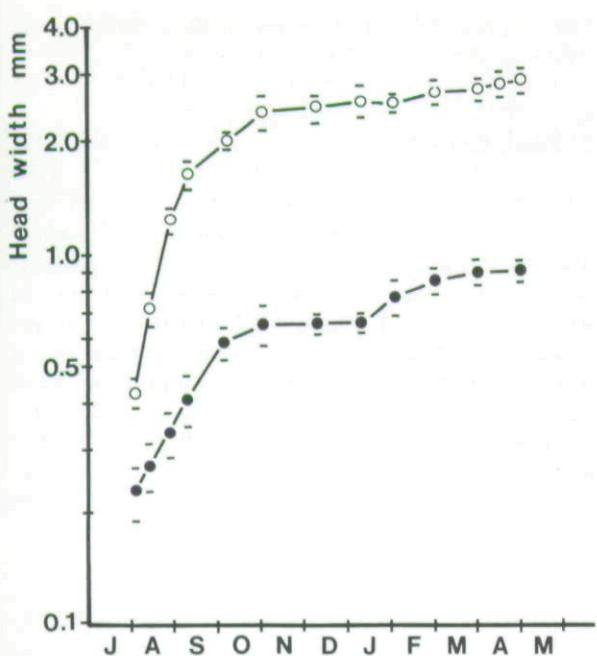


Fig. 3. The head width growth pattern of *Capnia pygmaea* (●) and *Diura nanseni* (○) as mean values \pm SD. Sample size of *C. pygmaea* in August is 21, 29 and 30, whereas the rest range between 50 and 100. Sample size of *D. nanseni* as in Fig. 6.

gust to November and one from February to May. At the end of the latter period the imagines emerged. The growth of the nymphs decreased as the water temperature decreased from August to November, but from February and onwards there was no clear relationship.

The growth pattern of *D. nanseni* is shown in Fig. 3. There was one period of rapid growth from August to November. The emergence of imagines started sometimes in the first two weeks of May and was completed within the 7 June.

Growth rate and water temperature were related. However, growth occurred even at 0°C.

4.2. Food habits

The diet of *B. rhodani* changed as the nymphs passed the successive groups (Fig. 4). In groups I and III the food mostly consisted of fine detritus, less so in group II. The coarse detritus, which was mainly made up of leaves and other terrestrial plant fragments, had its highest proportions (about 5%) in October–November. Diatoms were most common in July, October, and November, when the group II individuals predominated. Other algae showed a similar pattern, but they were less common.

C. pygmaea was clearly detritivorous (Fig. 5). The food mostly consisted of fine detritus. The coarse detritus reached a maximum of 4% and had the same composition as found in *B. rhodani*. The frequency of diatoms was highest in winter; reaching a maximum in

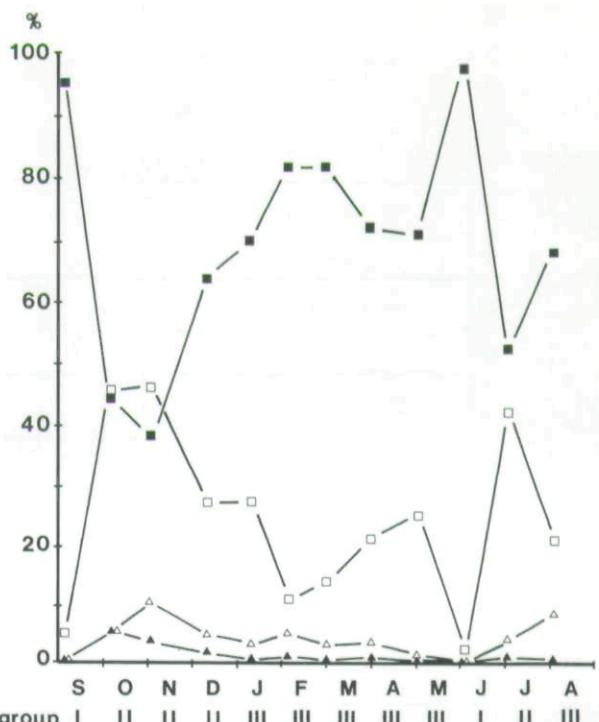


Fig. 4. Percentage composition of food items of *Baetis rhodani*. The examined size group is shown below. Twenty individuals were analysed. ▲ is coarse detritus, ■ fine detritus, □ diatoms, △ other algae.

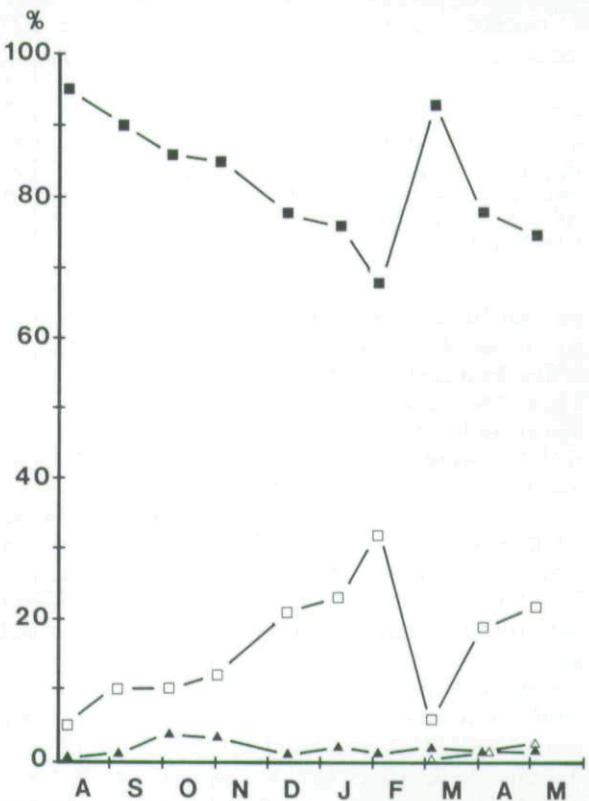


Fig. 5. Percentage composition of food items of *Capnia pygmaea*. Twenty individuals were analysed. ▲ is coarse detritus, ■ fine detritus, □ diatoms, and △ other algae.

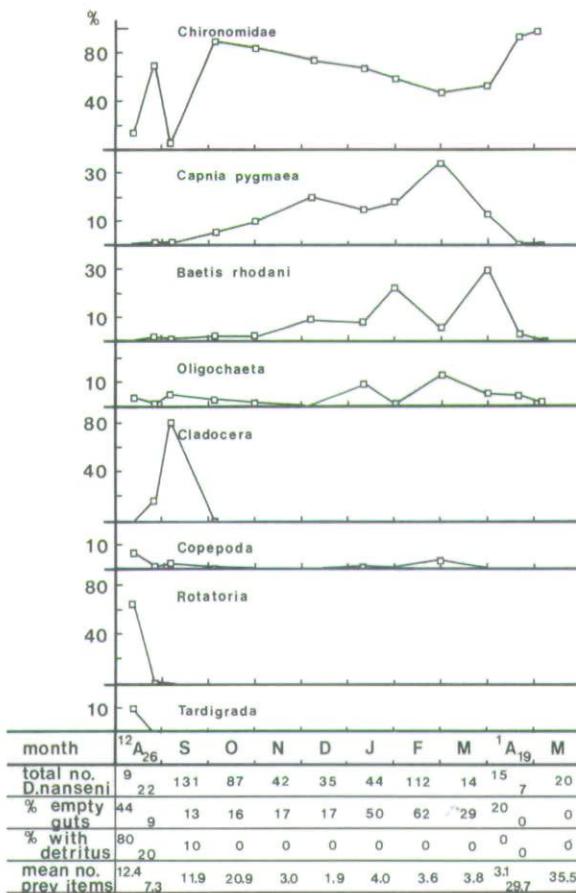


Fig. 6. Percentage composition of prey items of *Diura nanseni*. The lower part presents the numbers examined, those containing detritus (of those containing food), empty guts, and the mean number of prey for each *D. nanseni*. In August and April two samples were taken and the sample-dates are shown in opposite corners. The results on those days have a corresponding position.

February of about 32%. Other algae reached measurable quantities only in April and May.

The food composition of *D. nanseni* is presented in Fig. 6. The frequency of nymphs with empty guts was highest in January and February (50 and 62% respectively). Among the smallest nymphs there was, however, also a large proportion of empty guts.

In nymphs which contained food, about 80% of the smallest contained detritus and half of these had eaten nothing but detritus. Two weeks later only 20% of the nymphs contained detritus and after another two weeks only 10%. In addition to detritus, the early stages had eaten Rotatoria, Tardigrada, Cladocera and Copepoda. During the rest of its nymphal life *D. nanseni* was entirely carnivorous; the most common prey items being chironomids. The numbers of *B. rhodani* and *C. pygmaea* in the diet increased as the winter progressed. Oligochaeta were rarely taken, reaching a maximum in January and March of about 10%. Only traces of other benthic animals were found. The high number of prey in

some months was due to many small animals; mostly chironomids.

5. Discussion

5.1. Growth patterns

In the river Ekso *B. rhodani* has a complex life cycle. There is a continuous overlap between developmental stages as has also previously been recorded for this species (Hynes 1961, Elliott 1967, Larsen 1968, Humpesch 1979). Macan (1970) found two cohorts in the winter generation and the growth pattern described is quite similar to that found in the present study. But small nymphs at Ekse appear in April before the imagines emerge and can not be a part of the summer generation from which, however, it is difficult to discern. In a recent work Humpesch (1979) reveals an even more complicated situation with two or three winter cohorts and one to three summer cohorts of *Baetis lutheir* Müller-Liebenau and *B. rhodani* in Austria.

No hibernating eggs of *B. rhodani* were found by Andersen et al. (1978) in the river Ekso. Nymphs of the third cohort may therefore have been hibernating as nymphs, probably in the hyporheal. The hyporheal may be difficult to sample with ordinary means and some parts of the populations may be present there. The importance of the hyporheal is emphasised by Hynes et al. (1976) and Schwoerbel (1964) pointed out its importance as a habitat for small chironomids, mayflies, and stoneflies.

Other life cycles of *B. rhodani* have been observed (Illies 1952, Bretschko 1965) and the flexibility of the life cycle strategies enables *B. rhodani* to inhabit different water sheds and makes it a widely distributed species (Illies 1978).

Both *C. pygmaea*, *D. nanseni*, and the first cohort of *B. rhodani* have their main growth in the autumn, presumably with temperature as the main factor affecting the growth rates (Lillehammer 1975, Brittain 1976, Humpesch 1979). However, growth also occurred at 0°C, although at rather low rate for *D. nanseni*. *C. pygmaea* started on a second growth period at this temperature and *B. rhodani* also had a considerable growth. This shows that growth in winter is not solely temperature related, but dependent also on other factors.

5.2. Food habits

Because of a steady input of organic matter to the ecosystem (Baekken et al. in press) food quantity presumably does not restrict growth although food quality may. The protein content of the food, often increased by microorganisms (Hynes et al. 1974), is of great importance for growth and may affect life cycle strategies of species (Iversen 1974). Lillehammer (1975) showed that the growth of some stoneflies was positively corre-

lated with temperature. However, in laboratory populations it is difficult to discriminate between the direct effect of temperature and the indirect effect via microbial activity producing high quality food (see also Larsen 1978, Ward and Cummins 1979).

The detritivorous food habits of *B. rhodani* have also been demonstrated by other works (Jones 1950, Brown 1961, Chapman and Demory 1963). As also found by Brinck (1949) *C. pygmaea* was detritivorous. These food habits of two abundant members of benthic consumers stress the importance of allochthonous matter in this ecosystem and is in agreement with the potential energy available to herbivores and detritivores found by Baekken et al. (in press): 1% moss, 8% CPOM on the bottom, 86% CPOM, FPOM, and DOM in the substrate, 4% periphyton upsurface stone, and 1% periphyton downsurface stone – yearly means from a substrate 15 cm deep.

The smallest nymphs of *B. rhodani* (group I) were examined at a time when the primary production was high. Despite this, algae were scarce in the guts. Ulfstrand (1968) pointed out the importance of food distribution in relation to the distribution of animals which implies that food habits reflect the microdistribution. Accordingly, group I seems to be absent from light exposed places. They are presumably to be found beneath stones or deeper in the substrate. Group II obviously moves into more light exposed microhabitats as suggested by the higher algal content in their guts. Group III individual again have less algae in their diet than those from group II which presumably reflects a lower primary production rather than a movement to less light exposed microhabitats.

In relation to primary production, variations in algal content in the diet of *C. pygmaea* are contrary to what would be expected. The guts contain more algae when daylength is shorter. This may be explained by movements within the habitat: *C. pygmaea* stays in its most preferred microhabitat which may at least partly be phototactically controlled. All samples were taken at 1800 hours and thus at different light intensities through the season. At this hour *C. pygmaea* would stay beneath the stones during the lighter times of the year, but stay upon in the dark parts when a limited primary production occurred during the midday. In April and May, however, the high algal content in the food is probably caused by a high availability during an algal bloom.

The nutritive value of diatoms and other algae is uncertain. They may pass the gut undamaged or may contribute significantly to the diet, depending on plant and animal species (Brown 1960). A survey in the river Ekso in December 1977, showed that of ten *C. pygmaea* with algae in rectum, all contained living algae.

D. nansenii is a carnivore. However, as also found for other benthic carnivores, the early stages consumed considerable amounts of detritus (Winterbourn 1974, Crosby 1975, Fuller and Stewart 1977).

The proportions of prey-groups found in the river bed differ from those found in the guts of *D. nansenii*, indicating their different availability (Baekken 1978).

In August much of the river benthos is in pre-adult stages, in the egg stage or in newly hatched stages. The first category consists of relatively large animals unavailable for small *D. nansenii* nymphs. Newly hatched nymphs and the eggs may have a maximum contagious distribution arising from selective oviposition. The egg stage is immobile and does not attract predators by motion. All this may cause a temporal prey shortage making the ubiquitous detritus an alternative food resource (see Siegfried and Knight 1976). Later on, prey become more numerous, the predator distributes more evenly in relation to its prey, and the need for detritus decreases.

5.3. Competition and microdistribution

Morisita's coefficient of food overlap, improved by Horn (1966), may be used as a measure of competition. This coefficient, which range from 0 (no food overlap) to 1 (complete food overlap) was calculated for the two detritivorous species in this study. The individuals used are of comparable size except in August when *B. rhodani* is represented by large nymphs (group III) and *C. pygmaea* by small (see result section). The following results appeared:

Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
0.92	0.79	0.74	0.69	0.89	0.99	0.95	0.98	0.93	1.00

According to this the most serious competition occurred during winter and spring. But there was also a large food overlap the remaining season. The usefulness of such coefficients are discussable, e.g. Fuller and Stewart (1977) object that such comparisons obscure differences that reduce competition for food. That is a sound objection, and as was suggested in the above discussion on food habits, relatively small changes in food composition may involve considerable shifts of microhabitats. Thus, although both *B. rhodani* and *C. pygmaea* are detritivorous, the large size variations of *B. rhodani* nymphs and their different spacing (as suggested by the algal content of their guts) reduce the interaction between stages both within *B. rhodani* and between the two detritivorous species. In addition these species are partly separated in time.

The microdistribution is also an important factor in the predatory-prey relationships and probably accounts for most of the prey frequencies in the guts of carnivorous freshwater invertebrates. These animals are generally known as opportunistic feeders; eating any prey available. The opportunistic nature of *D. nansenii* was demonstrated by its partly detritivorous habits and in September when it exploited the temporary large input of planktic crustaceans (*Bosmina*) which originated in the main waterpower basin some kilometers above.

At last, great emphasis on microdistribution – spacing

of animals – in the partitioning of relatively homogeneous food resources would also seem reasonable from an evolutionary point of view. Apart from the ordinary herbivore, detritivore, and carnivore categories, benthic river animals are considered generalists (Cummins 1973). This lack of food specialisation should be expected to be compensated by a spatial or temporal habitat segregation; the physical environment (substrate) is heterogeneous whereas the food resource is homogeneous.

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