Verh. Internat. Verein. Limnol.	27	1–5	Stuttgart, September 2001

Growth of macroinvertebrates in regulated and free-flowing northern Swedish rivers

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Introduction

Sweden, as well as most other northerly countries in the world, relies on dams to meet the seasonal and daily variations in the need of electricity. These dams store a large amount of the annual precipitation, and release it quickly through hydroelectric power plants to match peak power demands. Unlike other renewable energy sources only hydroelectric systems have the capacity to satisfy these differential needs. However, the rapid water-level fluctuations in rivers and the displacement of water in time and space cause many undesirable environmental effects. The alteration of the hydrograph, as well as the natural hydraulic features of river systems, also bring about changes in the prevalent temperature regime with the risk of distorting life history features of aquatic organisms (Raddum & Fjellheim 1993) or shifting the composition of communities by disfavouring some of the original inhabitants that become competitively inferior compared to other species (Brittain & Saltveit 1989).

In regulated Swedish rivers, the total weekly discharge is typically more or less constant over the year but the flow may fluctuate over the day. Natural rivers, on the other hand, have pronounced spring peaks in discharge coinciding with snow-melt, and a more or less uniform decrease in flow until the end of the winter. These patterns mean that the free-flowing rivers rapidly warm up during the declining summer flow but also more rapidly cool down in the autumn compared to the regulated rivers, where the reservoirs accumulate heat and tend to level out the temperature fluctuations to some extent.

Given the above temperature conditions, one would expect that aquatic insect species that have their main growth period in the colder half of the year, would mature earlier in regulated compared to unregulated rivers, and that the reverse pattern would apply to species that hatch from eggs in spring and reach maturity in the summer. To test this hypothesis, I selected a few representative species that are particularly well known in terms of life histories and that were found in both the Luleälven River (regulated) and in the Kalixälven River (unregulated), both situated in the northernmost part of the country.

The mayflies *Heptagenia fuscogrisea* (Retzius) and *Ephemerella mucronata* Bengtsson have univoltine life cycles. They hatch from eggs at the end of the summer and emerge as adults at the beginning of the next summer. The main growth of larvae is in the autumn and in the spring (Bengtsson 1981, Söderström 1991). Two other mayflies, viz. *H. (Nixe) joernensis* (Bengtsson) and *E. ignita* (Poda), also complete a generation in 1 year, but these species are only found as larvae in the summer in the cold temperate parts of Europe (e.g. Arnekleiv 1985, Pleskot 1958, respectively). In addition to these insects, I studied a holoaquatic gastropod, *Gyraulus acronicus* (Férussac). Its life-cycle in northern Sweden is described by Olsson (1988).

Study area

The Luleälven River is about 450 km long, the total catchment covering 25,238 km^2. The regulated main-stem is fed by four major reservoirs followed by a series of river impoundments extending almost to the mouth. The present study was conducted in one of the lowermost impoundments formed by the Vittjärv Dam and power station. The total length of this impoundment amounts to 75 km. A total of seven localities, evenly distributed between the uppermost tailwater from the Laxede power station, and the lowermost inlet to the Vittjärv power station, were sampled. Whereas the uppermost and lowermost parts of the impoundment are steep and deep, the typical cross-section of the channel consists of comparatively shallow soft-bottoms bordering a deep (>10 m) cleft with a substrate mainly consisting of clay (Fig. 1). The total water level variations are less than 0.5 m, which is rather small compared to most other Swedish river impoundments. Total width is between 200 and 500 m.

The Kalixälven River drains a catchment of

0368-0770/01/0027-01 $ 1.25

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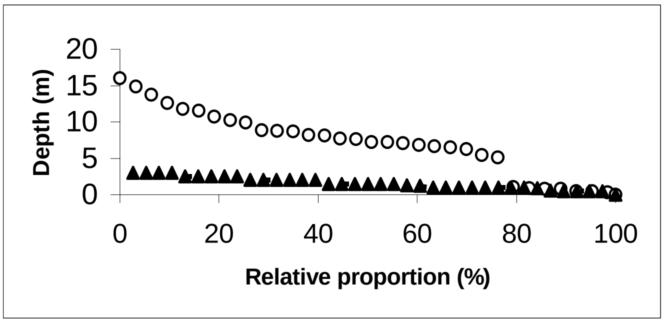

Fig. 1. Typical distribution of different depths (m) in the Luleälven (circles) and Kalixälven (triangles) Rivers.

23,645 km^2. Its total length is about 455 km from the mountains to the mouth and it is characterised by long reaches with slowly flowing water on sandy bottoms interrupted by comparatively short rapids on stony substrate. The water depth is mainly shallow (Fig. 1), although the seasonal fluctuations amount to more than 3 m. The width varies between 100 and 400 m. The three sampling stations covered riffle as well as pool habitats and were located downstream of the Överkalix village.

Material and methods

Individuals of the above mentioned species were sampled at the beginning of October 1985, a few weeks before ice-covering and at spring thaw at the end of May 1986. The last mentioned sampling date represented the end of the larval growth period of the hibernal species. Additional samples were taken at the beginning of July 1986, immediately prior to the maturation of the larvae of the aestival species. Although this scattered sampling is insufficient to accurately describe the growth pattern of species, it was (consequently) sufficient for the comparisons made in the present study.

Samples were taken by a handnet (mesh size 0.1 mm) down to a depth of about 1.2 m and by an Ekman grab at greater depths. They were immediately preserved in formaldehyde for later sorting and analyses in the laboratory. Each sample was kept separate from the others during the whole procedure and only individuals from the same locality have been used for biometric measurements. The distance between the outer rim of the eyes of the larvae was measured to the nearest 0.02 mm under a microscope fitted with an eye-piece. *G. acronicus* ceased to grow in the winter. The shells that were used for size estimates started to increase in width at the beginning of the summer. Since it was easy to distinguish between recently formed and old parts of the shell, I could quantify the individual growth in specimens of this particular species.

Data on temperatures (Table 1) and discharge (Table 2) were obtained from the Swedish Meteorological and Hydrological Institute (SMHI) and are derived from continuous measurements made in close proximity to the study areas in the two rivers.

Results and discussion

The annual total number of degree-days differed very little between the two rivers (Table 1). As expected, the comparatively large water body in the regulated river and its accumulated heat extended the warm period into the autumn. On the other hand, this water volume took a longer time to warm up so that the average temperature in the summer was comparatively low in the regulated Luleälven River. The fact that the two aestival species, i.e. *H. joernensis* and *E. ignita*, grew significantly faster in the Kalixälven River (Table 3) seems to reflect this difference. It may also be the reason why the two hibernal species (*H. fuscogrisea* and *E. mucronata*) appeared to be better off in terms of size in this river in the autumn. It also seems logical that this difference in size between the two populations of *E. mucronata* had levelled out by the end of the following spring since the accumulated number of degree-days, as measured from October–May, was slightly larger in the regulated river (208 and 185 in the Luleälven and Kalixälven Rivers, respectively). However, it does not explain the observation that the

Table 1. Monthly and annual number of degree-days in the regulated (a) Luleälven and in the unregulated (b) Kalixälven Rivers in 1985 and 1986 (compilations based on data obtained from the Swedish Meteorological and Hydrological Institute, SMHI).

Period	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
(a)													
1985	0	0	0	0.1	105	342	490	459	312	124	4.5	0	1838
1986	0	0.1	0.6	0.9	78	381	474	440	273	130	21	0.6	1795
Mean (1971–1986)	0.4	0.4	0.5	0.7	109	345	487	466	310	140	11	0.5	1871
(b)													
1985	1.2	1.7	2.2	2.4	34	351	527	468	270	68	1.8	1.6	1729
1986	1.6	1.1	1.9	3	105	441	512	419	228	71	9	1.2	1794
Mean (1971–1986)	1.2	1.2	1.5	2.1	98	384	526	462	274	76	2.2	1.2	1830

Table 2. Mean monthly and annual average discharge ($m^3 s^{-1}$) in the regulated (a) Luleälven and the unregulated (b) Kalixälven Rivers in 1985 and 1986 (data obtained from SMHI).

Period	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
(a)													
1985	699	721	559	549	529	411	451	554	670	343	447	586	542
1986	649	590	463	508	544	528	496	471	477	345	240	393	475
Mean (1961–1990)	450	437	413	378	530	581	533	586	530	459	439	444	482
(b)													
1985	59	46	39	42	450	622	399	585	664	383	237	122	305
1986	93	74	59	61	1021	562	330	296	231	179	195	95	268
Mean (1937–1990)	76	62	54	76	684	678	487	389	327	259	149	99	280

average *H. fuscogrisea* larva in the regulated river was considerably larger than its conspecific in the unregulated river at the end of spring. In order to interpret this observation one probably has to consider the habitat selected by *H. fuscogrisea*.

In the regulated river, truly lotic habitats are mainly confined to the inlet and outlet parts of the river impoundment. The prevalence of the different mayfly species in these sections, expressed as a per cent of the total number of individuals of the species sampled in the entire impoundment, was: *H. joernensis* (100%) > *E. mucronata* (98%) > *E. ignita* (96%) > *H. fuscogrisea* (3%). It is obvious that *H. fuscogrisea* is the least rheophilic of the four species. Because of the more or less constant water level in the impoundment, *H. fuscogrisea* could thrive among the near-shore macrophytes for most of the year. There, the current is minimal and the shallow water probably warms up rapidly in the spring. This assumption is supported by data on the size of larvae obtained in June from different depths, i.e. 2.31 ± 0.28 (n = 50) at 0–0.2 m, and 1.92 ± 0.28 (n = 37) at ≥1 m, respectively. However, it is probable that these larvae are also guided by the presence of particular kinds of periphyton algae that are used as food. Thus, two other species of mayflies, *Parameletus* spp., are adapted to make use of the temporary but plentiful food and high temperature on river floodplains in northern Sweden (Söderström 1988). The rheophilic scrapers, represented by the three remaining mayfly species, on the other hand, probably make use of epilithic food that is confined to substrates swept by current where the temperature is lower.

G. acronicus was also mainly found on shallow bottoms (<1 m). This species seems to be

Table 3. Size (eye width in mm) of mayfly larvae in Luleälven (regulated) and Kalixälven (unregulated) rivers in 1985 and 1986. Figures denote mean ± S.D, and number (n) of measured specimens. Probabilities (P) calculated according to Student's two-tailed t-test.

	Luleälven	Kalixälven	Luleälven	Kalixälven	Luleälven	Kalixälven
	1985–10–09	1985–10–10	1986–05–30	1986–06–01	1986–07–09	1986–07–10
Heptagenia fuscogrisea	1.30±0.23 n = 74	1.48±0.19 n = 7 (P = 0.041)	2.03±0.25 n = 213	1.69±0.25 n = 199 (P < 0.001)	emerged	emerged
H. joernensis	–	–	–	–	1.05±0.21 n = 32	1.44±0.20 n = 67 (P < 0.001)
Ephemerella mucronata	0.59±0.11 n = 163	0.62±0.09 n = 136 (P = 0.006)	0.99±0.18 n = 51	0.99±0.19 n = 60 (P = 0.96)	emerged	emerged
E. ignita	–	–	–	–	0.75±0.12 n = 24	0.98±0.18 n = 22 (P < 0.001)

rather stationary in northern Sweden and has the capacity to adapt physiologically to freezing (Olsson 1984). Shells of specimens found at the end of May showed no signs of growth increment, but the diameter increased by an average of 100% the following month. Obviously, the temperature threshold for growth is higher in this species than in *H. fuscogrisea*. In contrast to *H. fuscogrisea*, there were no significant differences in growth between the two populations (ANCOVA model; Fisher's F = 2.59; P = 0.11; Fig. 2). The reason for this might be that the temperature close to the shore had levelled out in the two rivers by the end of spring.

The direct alterations of the water temperature following the regulation of the Luleälven River, presupposing that it would naturally have resumed that in the Kalixälven River, are evidently small compared to those induced by the changes in channel morphology. Consequently, distortions of growth patterns were larger than anticipated from differences of average temperatures alone. It seems that truly lotic species that have their main growth in the summer were disfavoured, whereas lentic species

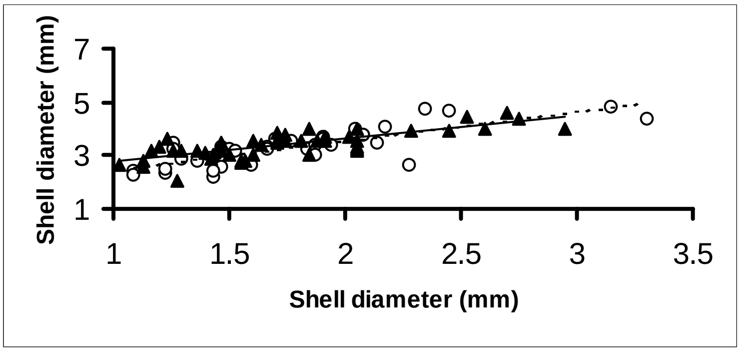

Fig. 2. Size of the snail *G. acronicus* in July (vertical axis) versus May (horizontal axis). Triangles and continuous line represent specimens collected in the unregulated Kalixälven River ($y = 0.84x + 1.95$; $r = 0.76$; $n = 49$); circles and dotted lines those from the regulated Luleälven River ($y = 1.09x + 1.37$; $r = 0.80$; $n = 35$).

that are able to grow at low temperatures were favoured as a result of the regulation of this river. Since reservoir operation in northern Sweden, as well as in other parts of the world with similar climatic conditions, is rather uniform (i.e. water withdrawal during spring runoff and increased release during the cold season) one should expect these alterations to be rather common. Thus, PERRY et al. (1986) observed similar changes in the growth of aquatic insect larvae in regulated streams of the US Rocky Mountains.

BRITTAIN & SALTVEIT (1989), compiling literature data on the impact of river regulation on life cycles of mayflies, conclude that species with short and flexible life cycles have the best prospects of coping with adverse conditions caused by reservoir operation. Although it seems clear that basic life history strategies play a role in a species' ability to withstand river regulation, it remains to be evaluated whether seasonality (i.e. the temporal distribution of life stages during the year) or longevity (i.e. duration of the immature stage) constitute its most important component in this respect.

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