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INCREASED GROWTH AND DISTRIBUTION OF *Ephemerella aurivillii* (EPHEMEROPTERA) AFTER HYDROPOWER REGULATION OF THE AURLAND CATCHMENT IN WESTERN NORWAY

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ABSTRACT

The Aurland watershed has been regulated for hydropower since the establishment of a series of power plants during the period 1970–1983. This resulted in a strong reduction of the flow in the river Vassbygdelvi, the inlet river to lake Vassbygdvatn. In the downstream river Aurland, the flow has varied, but from 2000 the intention has been to simulate pre-regulation winter flow as far as possible. The temperature in the river Vassbygdelvi has increased from about 1500 degree-days per year before regulation to above 2000 degree-days after regulation. In the river Aurland the thermal regime, expressed as degree-days per year, was more or less unchanged, but a small reduction in the summer temperature and a corresponding increase during other periods was observed. The mayfly *Ephemerella aurivillii* (Bengtsson) was not recorded in Vassbygdelvi prior to regulation, but became abundant in the river after. Full-grown larvae were recorded 1–2 months earlier in the river Vassbygdelvi than in the river Aurland after regulation. *E. aurivillii* has a 1-year life cycle with imagos present in June–August. Young larvae occurred from June to early September. It is concluded that larvae of *E. aurivillii* could not complete their life cycle within 1 year before regulation in the river Vassbygdelvi, due to low temperature. The study demonstrates how temperature can regulate the distribution of a species with a strict 1-year life cycle. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: river regulation; *Ephemerella aurivilli* (Bengtsson); temperature; life cycle

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INTRODUCTION

In the Aurland watershed a series of power plants were established during the period 1970–1983. In connection with this, biological investigations of the river were carried out before, during the construction period and after the regulation was finished (Larsen, 1968; Raddum, 1978; Raddum *et al*., 1991; Raddum and Fjellheim, 1993; Raddum *et al*., 2005). The main physical effects of the regulation were reduced flow in streams below dams, while flow increased below power plants. Other changes were increased temperature in stretches with reduced flow and decreased temperature below power plants fed by hypolimnetic water (Tvede, 1994). For the present study, the power plants Aurland I and Vangen (Figure 1) are of importance. The first one reduced the amount of cold water coming into the river Vassbygdelvi from the high mountain area by 80% (Faugli, 1994). The Vangen power plant makes it possible to reduce the discharge in the river Aurland (outlet river of Vassbygdvatn) in order to simulate pre-regulation flow conditions (approximately $3\,m^3\,s^{-1}$) for longer periods during winter.

The river Vassbygdelvi hosts populations of anadromous brown trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.). The minimum flow is set to $2.5\,m^3\,s^{-1}$ from 1 July to 15 September (Tvede, 1994). No requirements exist for the rest of the year. To mitigate periods with almost no surface water in the river, especially during winter and improve the conditions for fish and fisheries, the power company voluntarily decided to release $0.3\,m^3\,s^{-1}$ of water from the middle of the 1990s to maintain a minimum flow. Weir building, some ‘cleaning up’ of the river and changes in the operation scheme of the power plants have also been carried out from 2003; see Hellen *et al*. (2005).

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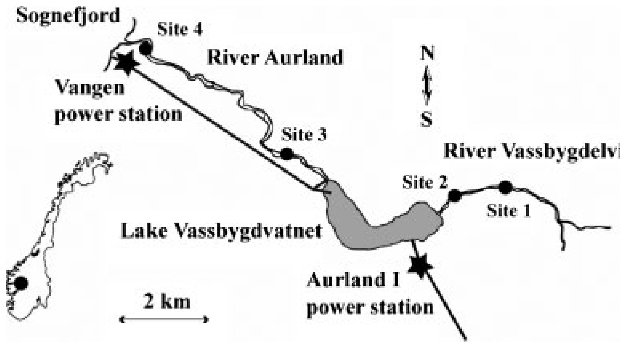

Figure 1. Map of the lower part of the river Aurland watershed showing the investigated sites and the Vangen and Aurland I power plants

Temperature and flow regime are regarded as the most important factors regulating the life cycle, species composition and distribution of mayflies (Brittain and Saltveit, 1989). The present study focusses on regulation effects on the mayfly *Ephemerella aurivillii* (Bengtsson). The species has a 1-year life cycle in Western Norway and we have mostly recorded this species in lower parts of watersheds situated in the middle and inner parts of the fjord systems of the region. In the Aurland watershed, *E. aurivillii* was not found in the river Vassbygdelvi before regulation, but was recorded scarcely in groundwater-dominated tributaries above lake Vassbygdvatn (Larsen, 1968). In this study, we wanted to investigate the effect of temperature on growth of larvae, possible changes in the life cycle and changes in the distribution of *E. aurivillii*. This was addressed by comparing results from 1966/1967, prior to regulation (Larsen, 1968), with data collected in 2002/2003.

STUDY AREA

The Aurland watershed (773 km^2) is situated in the inner part of the Sognefjord, Western Norway. A large part of the catchments area consists of a mountain plateau located at elevations between 1300 and 1500 m.a.s.l. Glaciers are present and cover about 10.5 km^2 of the watershed (Faugli, 1994). Today, five power plants operate in the Aurland watershed and the watershed is considered severely regulated (Faugli, 1994). The power plant Aurland I (Figure 1) is fed by a reservoir 930 m.a.s.l., receiving water from catchments at higher elevations. This transfer of water reduces the discharge of river Vassbygdelvi by 80%. The unregulated catchments below the dam mostly consist of steep mountainsides with very low retention of water. The runoff from these catchments is surface water, causing quick fluctuations in the discharge of the river Vassbygdelvi during the snow-free season. Spring floods can be as high as 38 m^3 s^{-1} (Hellen *et al*., 2005), but of shorter duration compared with the pre-regulated situation. Mean flow of the river Vassbygdelvi for 2003 and 2004 was 2.8 and 3.2 m^3 s^{-1}, respectively. The flow can, however, be very low during dry periods in winter. To avoid drying up of the river the power company voluntarily releases 0.3 m^3 s^{-1} of water as a minimum flow.

Lack of water from melting snow and ice from the mountain plateau enhances the water temperature in the river. Low input of surface water increase the fraction of groundwater in the lowest part of the river Vassbygdelvi. The groundwater maintains a higher temperature during winter and increases the temperature significantly in the coldest periods (Fjellheim and Raddum, 2006). The fraction of cold groundwater is reduced during summer and the cooling effect is less apparent.

The Vangen power plant, situated close to the sea, is fed by water from Vassbygdvatn and receives deep release from Aurland I and surface water from the river Vassbygdelvi (Figure 1). The cold water from the Aurland I entering the lake Vassbygdvatn can bypass the river Aurland and be directed through Vangen power plant. This makes it possible to simulate pre-regulation flow for longer periods in the river Aurland, especially during winter (approximately 3 m^3 s^{-1}). During summer, flow in the river Aurland is adjusted for fish and fisheries, and balanced between optimal water flow for fish running and temperature for fishing. For the period 1989–2002 the mean flow in river Aurland has been 17.6 m^3 s^{-1}, varying between 13 and 22 m^3 s^{-1}. During the period October–April mean flow

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per month has been in the range of 3.5–4 $m^3 s^{-1}$. Similarly the flow from May to August has been in the range of 33–46 $m^3 s^{-1}$ per month. In September, the discharge is gradually reduced to low flow (Hellen *et al*., 2005).

The substratum of the rivers Vassbygdelvi and Aurland consist of boulders and stones with smaller stones and gravel in between. However, per cent composition of stone sizes is not measured. Patches of mosses are also present. Reduction of the flow has probably increased sedimentation of fine and coarse organic material, favouring smaller invertebrates (Baekken *et al*., 1984; Brusven, 1984; Raddum and Fjellheim, 1993).

METHODS

Temperature

Water temperatures were measured every fourth hour using a Minilog (Wemco) reporting an accuracy of 0.1°C in the river Vassbygdelvi at Belle bro, site 1, and in the river Aurland at Onstad, site 4 (Figure 1). The outputs were pooled into a mean daily temperature. Degree-days accumulation was calculated by summarizing the mean daily temperature for the period of interest.

Sampling and tests

Qualitative benthic kick samples (Frost *et al*., 1971) were collected every month from June 2002 to December 2003 usually in the first week. Two sites were sampled in the river Vassbygdelvi, site 1, and the inlet to lake Vassbygdvatn, site 2. In the river Aurland the corresponding sites were downstream lake Vassbygdvatn, site 3 and Onstad, site 4, see (Figure 1). The sampling was performed on 6–10 different habitats at each site and pooled into one sample. The sampling net had a mesh size of 250 μm. Sorting of the samples was done beneath a binocular according to the following procedure: first large Ephemeroptera larvae were removed from the sample. Then the sample mass was divided into subsamples of 1/16. One of these subsamples was fully sorted. All larvae recorded from the sorting were counted and measured to the nearest 1/10 mm using an ocular measuring grid. Different statistical tests were evaluated for testing growth of larvae at different sites. We found that the non-parametric Wilcoxon Sum Rank Test (two-tailed) (Crawley, 2002) was suited for the material. Differences in growth of *E. aurivillii* between sites were tested across all sampling dates in 2002/2003.

RESULTS

Temperature before and after regulation

The temperature at sites 1 and 4 was very similar during winter, spring and early summer in 2003 (Figure 2). The drop in temperature in the middle of July at site 4 was caused by increased release of water from the lake Vassbygdvatn (power plant Aurland I) to meet the flow demand for fishing. During late fall the temperature in the river Aurland was slightly above the temperature in the river Vassbygdelvi.

Degree-days accumulation for sites 1 and 3 in 1966/1967 (from Larsen, 1968) and 2003 (from Hellen *et al*., 2005) and our investigation is shown in Figure 3. At site 1 the number of degree-days before regulation was measured to about 1500, while the numbers had increased to 2050 in 2003, an increase of about 500 degree-days. The corresponding values at site 3 were 1890 and 1870, before and after regulation. The number of degree-days at the different sites during 2002/2003 is shown in Figure 4a, b. The warmest sites were 2 and 1 in 2002 with 2360 and 2139 degree-days, respectively. Site 3 was coldest with 1817, while site 4 had 2000 degree-days.

Growth of E. aurivillii

The length of larvae at the different sites during the growing period is shown in Figure 5a–c. In the river Vassbygdelvi the latest date with full-grown larvae was the first week of June. In the river Aurland such larvae were present until the first week of August at site 3.

The growth of larvae in 1966/1967 at a site between our sites 3 and 4 (from Larsen 1968) is compared with the growth at site 4 during 2002/2003 (Figure 5c). Full-grown larvae were present in July both before and after

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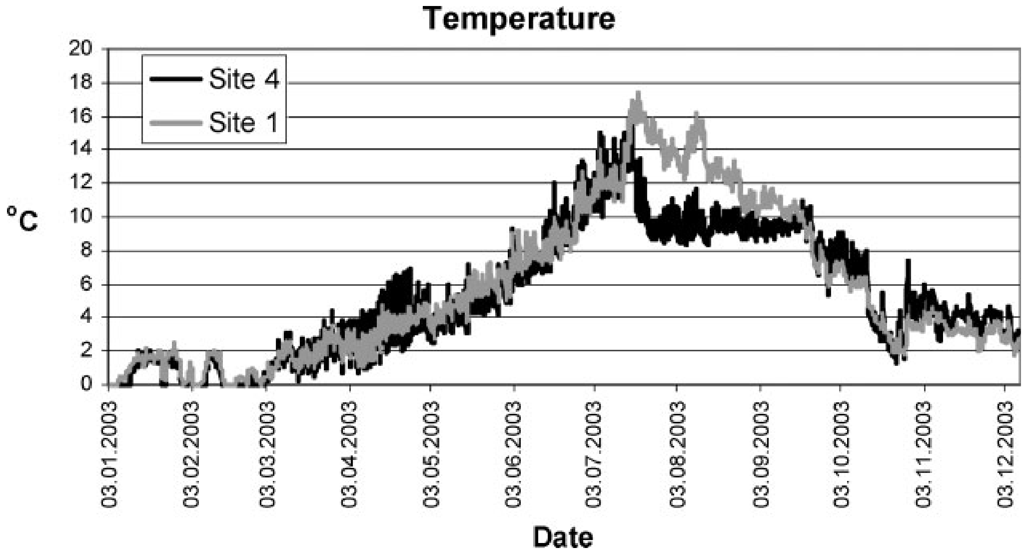

Figure 2. Temperature at sites 1 and 4 measured every fourth hour during 2003

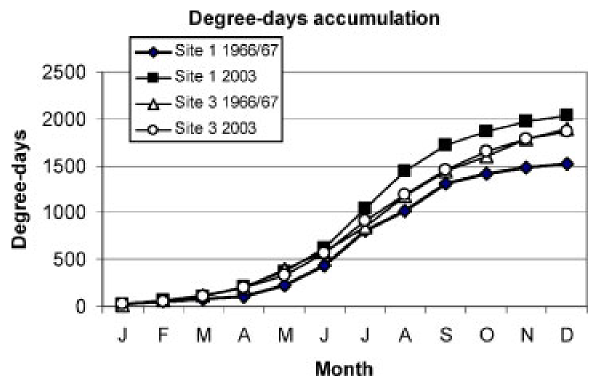

Figure 3. Degree-days accumulation at sites 1 and 3 before regulation, 1966/1967, after Larsen (1968) and after regulation, 2003. This figure is available in colour online at www.interscience.wiley.com/journal/rra

regulation. Newly hatched larvae occurred in September both in 1966/1967 and 2002/2003. The growth was faster during the fall 2002 than in the fall 1966 and slightly larger individuals were noted before emergence in 2002/2003 than in 1966/1967. However, emergences, hatching of new larvae and life cycle pattern in general seem to be similar before and after regulation. Due to lack of raw data from 1966/1967 the similarity could not be tested for the two periods. The differences between 1966/1967 and 2002/2003 were principally small and we conclude that the results from before and after regulation are comparable and that the life cycle was similar in both periods.

In Table I, the size of larvae of *E. aurivillii* is compared and tested for each site after regulation. The test is significant if the differences of larval size are larger than random expectations. The fraction in the table shows the number of significant tests/number of total tests. The tests were performed for every month. The numbers below the dividing line shows the part of significant differences. The differences between sites 1 and 2 and between 3 and 4 were small. On the other hand, most of the tests comparing the sites in the river Vassbygdelvi with the sites in the river Aurland, were significant different. This indicates that the size of the larvae in the two rivers were different in most of the time.

The size/growth of larvae compared with degree-days accumulation was very similar in the river Vassbygdelvi and Aurland (Figure 6a, b). The growth is strictly linear with the numbers of degree-days. The growth regression

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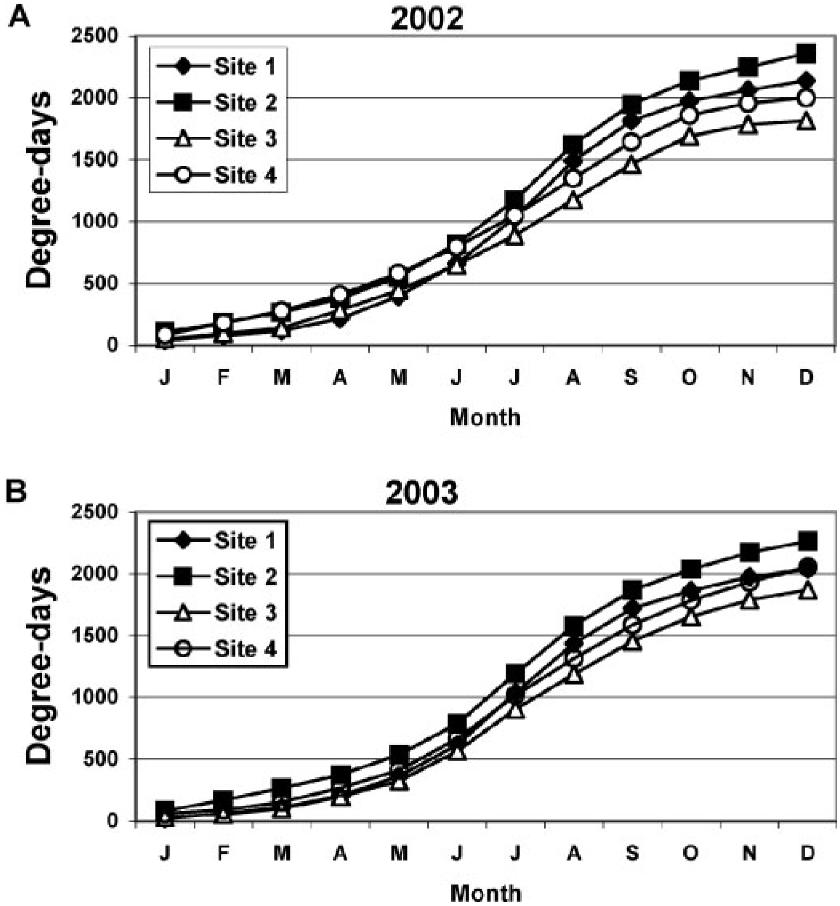

Figure 4. Degree-days accumulation at the investigated sites during (A) 2002 and (B) 2003

lines for the four sites, based on the equation calculated for each of the sites were all in parallel (Figure 6c). Recorded degree-day accumulation for full-grown larvae at sites 1 and 2 was 1499 and 1735, respectively, in the first week of June 2003. Corresponding mean larval length was at that time 10.3 and 11.5 mm. At sites 3 and 4 the growth was 1 or 2 months delayed. The degree-day accumulation for these larvae was more difficult to assess due to the longer period with full-grown individuals present, but the range of degree-days was estimated to be 1500–1600. It was found that *E. aurivillii* had more or less the same growth rate at the four sites. The presence of newly hatched larvae was different since they occurred 1–2 months earlier in the river Vassbygdelvi than in the river Aurland.

DISCUSSION

The life cycle of mayflies is in most cases dependent on temperature and food resources (Brittain and Saltveit, 1989). These parameters are directly or indirectly impacted by regulation for hydropower. The natural temperature regime of a river may be modified in several ways by impoundment, depending on type of water release. Hypolimnion release will normally reduce the temperature in downstream stretches during summer, but to some extent increase the temperature in winter (Ward and Standford, 1982). Surface release can increase the temperature during summer. Reduction in flow from unregulated catchments at lower levels will give increased temperature as colder water is transferred away from the river as observed in the Aurland watershed. Many studies have shown that emergence occurs earlier during warmer conditions (Vannote and Sweeney, 1980; Ward and Standford, 1982).

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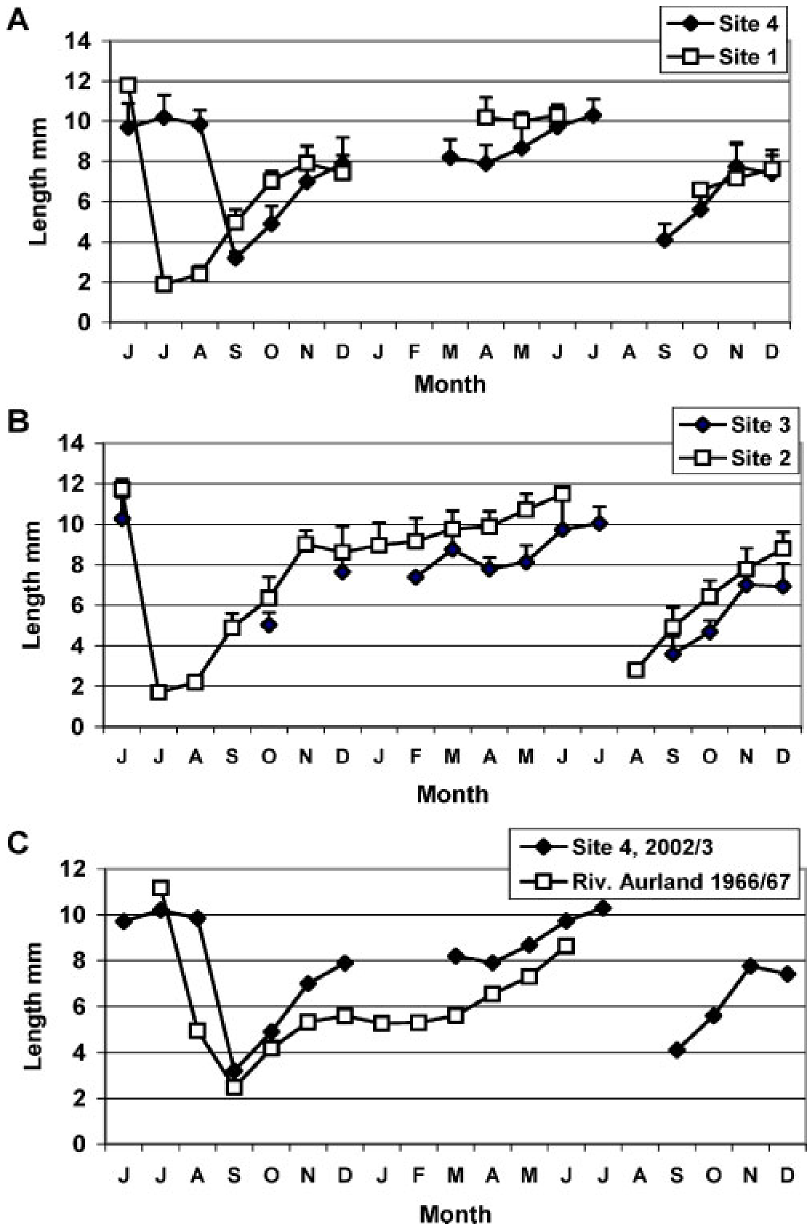

Figure 5. Mean length of larvae of *E. aurivillii* from June 2002 to December 2003. A: Sites 1 and 4, (B) sites 2 and 3. C: Site 4 compared with larval length from 1966/1967, after Larsen (1968). This figure is available in colour online at www.interscience.wiley.com/journal/rra

However, this may vary depending on the species concerned. Gregory *et al*. (2000) found that April temperature was the best predictor for emergence of a Californian mayfly. Degree-day accumulation for egg incubation has been studied for several Australian mayfly species (Suter and Bishop, 1990; Brittain and Campbell, 1991; Brittain, 1995). Generally the studied species hatched successfully between 9 and 25°C. For European mayfly species, the minimum temperature for successful hatching could be as low as 3°C (Elliott, 1972; Humpesch, 1980). Incubation time can vary from a few days to about 20 for Australian species (Suter and Bishop, 1990; Brittain and Campbell, 1991; Brittain, 1995), while this period can be longer for northern hemisphere species (see Bohle, 1972; Elliott, 1978; Newell and Minshall, 1978). The number of degree-days accumulation required for development has been

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Table I. Results of size comparisons of *E. aurivillii* for the four sites, using Wilcoxon Sum Rank Test

	Site 1	Site 2	Site 3	Site 4
Site 1		4/13	7/10	8/13
Site 2	0.31		8/11	10/15
Site 3	0.7	0.73		2/12
Site 4	0.62	0.67	0.17	

The fraction indicates the number of significant tests/number of total tests. The tests were done for each month during the sampling period.

shown to increase at lower temperature (Elliott, 1978; Suter and Bishop, 1990; Brittain and Campbell, 1991). The number of degree-days for egg incubation may increase in the low temperature regime of the Aurland watershed and raise the demand for degree-days in *E. aurivillii*.

Food resources, consisting of fine or coarse particular organic material as well as algae will impact life cycles. These resources are more or less dependent on the flow regime, as reduced flow increases sedimentation of organic material. This can increase or decrease the density of insects and cause changes in the species structure and diversity (Hynes, 1970; Armitage, 1976; Ward and Standford, 1982; Brusven, 1984; Lillehammer and Saltveit, 1984; Brittain and Saltveit, 1989). The largest alterations will take place if the system changes from a typical lotic to a lentic one (Brittain and Saltveit, 1989; Fjellheim *et al*., 1993). In addition to sedimentation of fine organic particles, lentic conditions will also favour algal growth and enhance the conditions for grazers or scrapers (Spence and Hynes, 1971; Williams and Winget, 1979).

In the rivers Aurland and Vassbygdelvi, no shift in voltinism has been recorded since regulation (Raddum *et al*., 2005; Fjellheim and Raddum, 2006). All recorded species had univoltine life cycles. Most of them had synchronous egg hatching, growth of larvae and emergence, while a few showed several cohorts at the same time. *E. aurivillii* belonged to the group of species with synchronous egg hatching, larval growth and emergence.

In the river Vassbygdelvi, degree-days accumulation was estimated to be 1500 before regulation. In this temperature regime *E. aurivillii* was not recorded. The species was, however, at the same time recorded in river Aurland (Larsen, 1968) holding about 1800–1900 degree-days. Flow patterns were principally similar up and downstream of lake Vassbygdvatn before regulation, except for the flow buffering effect of the lake.

The relationship between larval length and degree-days accumulation was very similar for the different sites both in rivers Vassbygdelvi and Aurland. The growth was linear with the temperature and the necessary degree-days from early hatched to emerging larva were in the range of 1500–1600 for all sites. To fulfil the life cycle we must add the necessary degree-days for oviposition and egg incubation. There are few studies dealing with the temperature demands for completion of life cycles among mayflies. Taylor and Kennedy (2003) found that an average of 1709 degree-days was necessary for larvae of *Caenis latipennis* to develop. In addition, eggs took 132 degree-days to develop. The aquatic stage therefore needed >1800 degree-days. Similar findings have been found for caddisflies (Georgian and Wallace, 1983; Krueger and Waters, 1983; Robinson and Minshall 1998). Our findings for larval development of *E. aurivillii* are in the same range. We conclude that the species need >1600 degree-days for egg and larval development. This can explain the absence and the presence of the species in the river Vassbygdelvi before and after regulation, respectively.

The difference in larval size between rivers Vassbygdelvi and Aurland was significant at most dates. Newly hatched larvae were recorded 1–2 months earlier in the river Vassbygdelvi than in the river Aurland. The delay in the development of the larvae in the river Aurland followed the population until emergence and was in accordance with number of degree-days recorded during the larval period.

Low temperature after egg deposition can increase the egg incubation time (Suter and Bishop, 1990; Brittain and Campbell, 1991; Brittain, 1995). Late egg hatching can in turn shorten the period with the best temperature for growth of larvae in the river Aurland. The increased flow and decreased temperature in the river from the middle of July will therefore depress the life cycle development of *E. aurivillii* during the most important period of larvae development. We conclude that these conditions are the major explanation for the delay in emergence.

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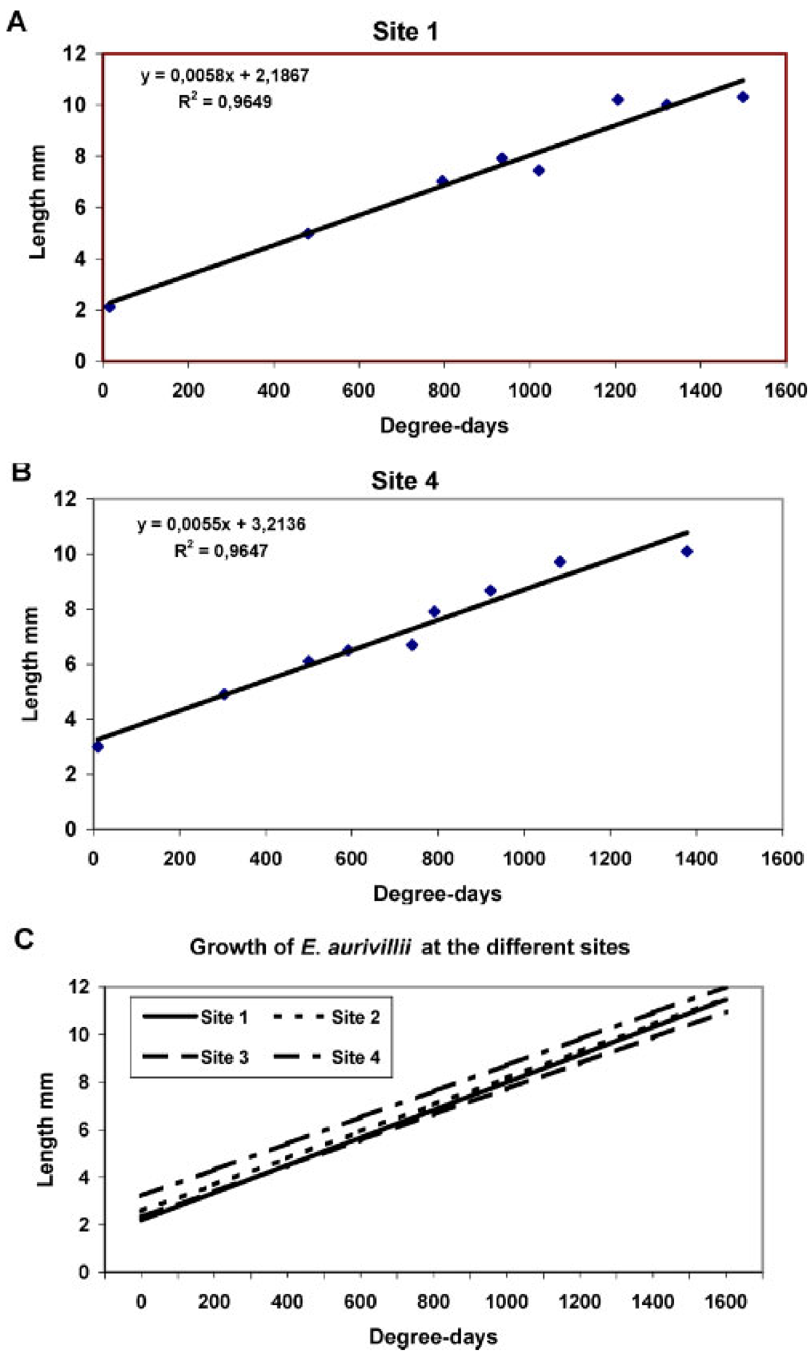

Figure 6. A: Growth of *E. aurivillii* at site 1. B: Growth of *E. aurivillii* at site 4. C: Comparison of growth regression curves at sites 1, 2, 3 and 4. This figure is available in colour online at www.interscience.wiley.com/journal/rra

CONCLUDING REMARKS

E. aurivillii has a synchronous 1-year life cycle that needs >1600 degree-days to be fulfilled. The species was absent from river stretches with lower temperatures, but became abundant when the temperature increased above this limit. The local distribution of *E. aurivillii* can therefore vary considerably in rivers with degree-days

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fluctuating around 1600. Emergence and egg hatching was strictly related to water temperature and differed up to 2 months when comparing cold (1700–1800 degree-days) and warm (2200–2300 degree-days) conditions. Man-made changes in the temperature regime may therefore cause changes in life cycle timing as well as in the distribution of the species within watersheds.

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REFERENCES

Armitage PD. 1976. A quantitative study of the invertebrate fauna of the river Tees below Cow Green Reservoir. *Freshwater Biology* **6**: 229–240.

Baekken T, Fjellheim A, Larsen R. 1984. Benthic animal production in a weir basin in Western Norway. In *Regulated Rivers*, Lillehammer A, Saltveit SJ (eds). Universitetsforlaget: Oslo; 223–232.

Bohle HW. 1972. Die Temperaturabhängigkeit der Embryogenese und der embryonalen Diapause von *Ephemerella ignita* (Poda) (Insecta, Ephemeroptera). *Oecologia (Berl.)* **10**: 253–268.

Brittain JE. 1995. Egg development in Australian mayflies (Ephemeroptera). In *Current Directions in Research on Ephemeroptera*, Corkum LD, Ciborowski JJH (eds). Canadian Scholars Press Inc.: Toronto; 307–316.

Brittain JE, Campbell IC. 1991. The effect of temperature on egg development in Australian mayfly genus *Coloburiscoides* (Ephemeroptera: Coloburiscidae) and its relationship to distribution and life history. *Journal of Biogeography* **18**: 231–235.

Brittain JE, Saltveit SJ. 1989. A review of the effect of river regulation on mayflies (Ephemeroptera). *Regulated Rivers: Research and Management* **3**: 191–204.

Brusven MA. 1984. The distribution and abundance of benthic insects subjected to reservoir-release flows in the Clearwater River, Idaho, USA. In *Regulated Rivers*, Lillehammer A, Saltveit SJ (eds). Universitetsforlaget: Oslo; 167–180.

Crawley MJ. 2002. *Statistical Computing: An Introduction to Data Analysis Using S-Plus*. Wiley: Chichester; 761.

Elliott JM. 1972. Effect of temperature on the time of hatching in *Baetis rhodani* (Ephemeroptera: Baetidae). *Oecologia (Berl.)* **9**: 47–451.

Elliott JM. 1978. Effect of temperature on the hatching time of eggs of *Ephemerella ignita* (Poda) (Ephemeroptera: Ephemerellidae). *Freshwater Biology* **8**: 51–58.

Faugli. 1994. The Aurland catchment area—the watercourse and hydropower development. *Norsk Geografisk Tidsskrift* **48**: 3–7.

Fjellheim A, Håvardstun J, Raddum GG, Schnell ØA. 1993. Effects of increased discharge on benthic invertebrates in a regulated river. *Regulated Rivers: Research and Management* **8**: 179–187.

Fjellheim A, Raddum GG. 2006. Growth and voltinism in the aquatic insects of a regulated river subject to groundwater inflows. (This vol.).

Frost S, Huni A, Kershaw WE. 1971. Evaluation of a kicking technique for sampling stream bottom fauna. *Canadian Journal of Zoology* **49**: 167–173.

Georgian T, Wallace JB. 1983. Seasonal production dynamics in a guild of periphytongrazing insect in a south Appalachian stream. *Ecology* **64**: 1236–1248.

Gregory JS, Beesley SS, Van Kirk RW. 2000. Effect of springtime water temperature on the time of emergence and size of *Pteronarcys californica* in the Henrys Fork catchment, Idaho, USA. *Freshwater Biology* **45**: 75–83.

Hellen BS, Saegrov H, Kaalaas S, Urdal K. 2005. Fish investigations in the Aurland and Flaam watersheds, year report for 2005\, (in Norwegian). *Raadgivende Biologer AS, Report No. 897*, Bergen 79.

Humpesch UH. 1980. Effect of temperature on the hatching time of eggs of five *Ecdyonurus* spp. (Ephemeroptera) from Austrian streams and English streams, rivers and lakes. *The Journal of Animal Ecology* **49**: 317–333.

Hynes HBN. 1970. *The Ecology of Running Waters*. University Press: Liverpool; 555.

Krueger CC, Waters TF. 1983. Annual production of macroinvertebrates in three streams of different water quality. *Ecology* **64**: 840–850.

Larsen R. 1968. Investigation of the fauna and ecology of the benthos in river Aurland. (in Norwegian). *Unpublished Thesis*, University of Bergen, 268.

Lillehammer A, Saltveit SJ. 1984. The effect of the regulation on the aquatic macroinvertebrate fauna in the river Suldalslågen, Western Norway. In *Regulated Rivers*, Lillehammer A, Saltveit SJ (eds). Universitetsforlaget: Oslo; 201–210.

Newell RL, Minshall GW. 1978. Life history of a multivoltine mayfly *Tricorythodes minutus*: an example of the effect of temperature on the life cycle. *Annals of the Entomological Society of America* **71**: 876–881.

Raddum GG. 1978. Effects of regulation on the benthic fauna in Aurland watershed. *LFI, University of Bergen, Report*, 25, 49 pp. (in Norwegian).

Raddum GG, Fjellheim A. 1993. The effect of changed waterflow on the mayfly *Baetis rhodani* in the regulated river Aurland, western Norway. *Regulated Rivers: Research and Management* **8**: 49–61.

DOI: 10.1002/rra

Raddum GG, Fjellheim A, Barlaup B, og Åtland Å. 1991. Investigations of bentos in the Aurland watershed: a comparision between the situation before and after regulation. *LFI, University of Bergen, Report*, 70, 69 pp. (in Norwegian).

Raddum GG, Fjellheim A, Velle G. 2005. The population structure of benthos in river Aurland in relation to changes in discharge and temperature. *Report: Miljøbasert vannføring nr. 3, NVE*, Oslo. 49 pp. (in Norwegian).

Robinson CT, Minshall GW. 1998. Macroinvertebrate communities, secondary production, and life history patterns in two adjacent streams in Idaho, USA. *Archive für Hydrobiologie*, **142**: 257–281.

Spence JA, Hynes HBN. 1971. Differences in benthos upstream and downstream of an impoundment. *Journal of the Fish Research Board of Canada* **28**: 35–43.

Suter PJ, Bishop JE. 1990. Post-development of eggs of south Australian mayflies. In *Mayflies and Stoneflies, Life History and Biology*, Campbell IC (ed.). Kluwer Academic Press: Dordecht, Netherlands; 85–94.

Taylor JM, Kennedy JH. 2003. Cohort dynamics of an overwintering *Caenis latipennis* population in Honey Creek, Oklahoma, U.S.A. In *Research Update on Ephemeroptera & Plecoptera*, E Gaino (ed.). University of Perugia: Perugia, Italy; 201–204.

Tvede AM. 1994. Discharge, water temperature and glaciers in the Aurland river basin. *Norsk Geografisk Tidsskrift* **48**: 23–28.

Vannote RL, Sweeney BS. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *The American Naturalist* **115**: 667–695.

Ward JV, Standford JA. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annual Review of Entomology* **27**: 97–117.

Williams RD, Winget RN. 1979. Macroinvertebrate response to flow manipulation in the Strawberry River, Utha, U.S.A. In *The ecology of Regulated Streams*, Ward JV, Standford JA (eds). Plenum: New York; 365–376.

DOI: 10.1002/rra