

THERMAL REGIME ALTERATION AND VITAL ENVIRONMENTAL PHYSIOLOGICAL SIGNALS IN AQUATIC ORGANISMS

Reprinted from:

Thermal Ecology, J.W. Gibbons and R.R. Scharits (eds.)
AEC Symposium Series (CONF 730505) p. 216-222.
1974.

D. M. LEHMKUHL

Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada

ABSTRACT

In temperate climates, characterized by distinct warm and cold seasons, many aquatic insects are dependent upon key temperatures to initiate embryological development, signal eclosion from the egg, control the rate of growth, and stimulate emergence of adults. Deep reservoirs with hypolimnion drains cause a type of thermal pollution by releasing a summer cool but winter warm outflow. No lethal temperatures are involved, but the lack of or the abnormal timing of signals as a result of the reservoir exterminated most of the intermediate members of a food chain up to 70 miles downstream of a reservoir. The principle of the altered thermal regime would apply to any source of unseasonably warm or cool water.

Meaningful life-cycle and reproductive data are scarce in the published literature, but the validity of the principle can be illustrated with the examples from the Ephemeroptera.

The discharge of thermal effluents into a natural habitat may affect organisms living in the habitat in several different ways. In severe cases organisms may be killed outright; in less severe cases metabolic rates may be altered (Krenkel and Parker, 1969; Becker, 1973). These are the immediate effects. The situation becomes more complicated when we add the time factor. Organisms may be tolerant of a thermal alteration at one stage of their life cycle but sensitive to the same change at a different stage. Finally, we must acknowledge that in addition to heating abnormal cooling is also a type of thermal pollution. I base these latter statements on my studies of the benthic insect community at the outflow of a large reservoir on the Saskatchewan River. No lethal temperatures are involved, but the reservoir discharges a summer cool and winter warm outflow compared to the natural thermal regime. This thermal alteration has almost completely eradicated the benthic insect community for a number of miles downstream from the outlet (Lehmkuhl, 1972).

The explanation of this extinction can be found in the physiological and biochemical literature. It is well known that in terrestrial animals, for example,

such phenomena as migration and mating behavior are often initiated through hormonal and other physiological systems, which are stimulated by ambient temperature and photoperiod, or day length. In aquatic organisms the essential environmental stimuli are often thermal. Diapause, an obligatory state of arrested development, is found in hundreds of species of insects, and it can occur at any stage of the life cycle, depending on the species. Diapause is often broken by thermal stimuli (Mansingh, 1971). Elimination of an essential temperature sequence by a reservoir, for example, can mean the death of a species as certainly as would the exposure of the organisms to a lethal temperature. I feel that these subtle, long-term effects of alteration of the thermal regime which lead to reproductive death rather than immediate physiological death of members of the aquatic community need more emphasis. I should like to support my statements with some examples.

THERMAL REQUIREMENTS

Figure 1 shows the life cycle of the mayfly *Ephoron album* (Say) along with the seasonal thermal regime of the unaltered Saskatchewan River. Also given are the thermal requirements of this species found by Britt (1962) in laboratory studies. Eggs will not develop until they have been exposed to freezing temperatures, nymphs will not hatch from the egg until the temperature rises to about 10°C, and nymphs will not mature unless the temperature reaches 18 to 20°C and remains there for several months. These requirements are met in the unaltered river, where the species is present. Downstream of the reservoir in the area of summer cool and winter warm water temperatures, however, the species is absent. My conclusion is that the species was eliminated below the reservoir because it did not receive the sequence of stimuli and temperature conditions to which it had adapted through a long evolutionary process. In relation to this symposium, it would not matter if the thermal alteration was a result of effluent from a reservoir or from a power plant. Essential temperature requirements could be eliminated in either case.

FLEXIBILITY

My next point is that, although some insect species have strict thermal requirements, they also possess a certain amount of flexibility. Figure 2 shows the life cycle of the widespread mayfly species *Paraleptophlebia debilis* (Walker) along with the thermal regimes in two widely separated areas, the lowland Oak forests of coastal Oregon (Lehmkuhl and Anderson, 1971) and the boreal forest east of the Rocky Mountains in the Province of Alberta (Clifford, 1969). On the basis of the long resting period in the egg stage, it seems safe to infer that diapause is present and that freezing temperatures are essential to stimulate egg development and hatching. While the two areas differ significantly in appearance

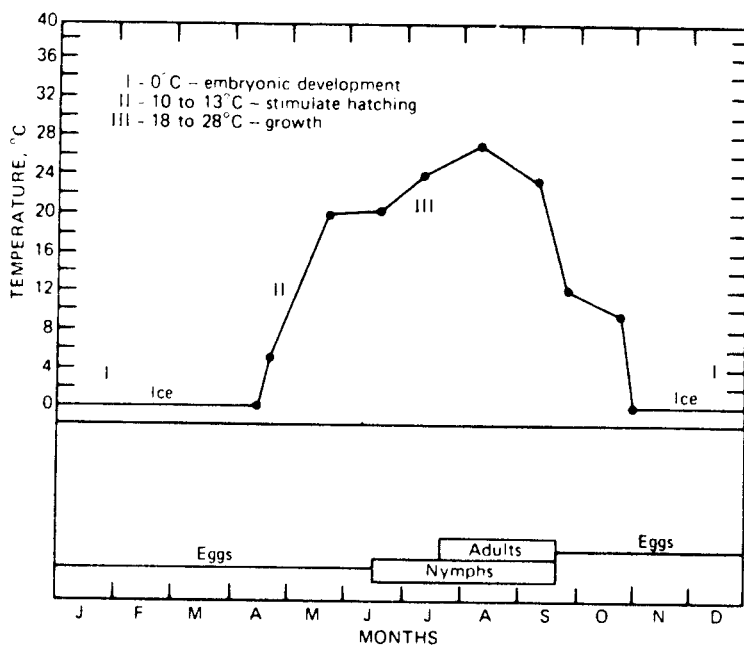


Fig. 1 Seasonal distribution of *Ephoron album* (lower), seasonal temperature regime in Saskatchewan River (upper), and temperature requirements of the species (Britt, 1962). The compatibility of species requirements, life cycle events, and field conditions are illustrated.

and the thermal regimes are different at first glance, both temperature regimes have in common a period of freezing temperatures in winter and a period of warm temperature in summer. Both habitats provide the essential stimuli and other thermal requirements of the species. The life cycles differ only in the duration of stages, for example, the limited flight time of adults in Alberta. My point is that the species is flexible enough to occur in different temperature regimes so long as the essential stimuli are present. In another study involving a spring-fed river that is within the range of the species but has a flat temperature curve, the species is rare (Lehmkuhl, 1969). Perhaps the species is rare in the spring-fed river because the freezing requirement is absent, making normal reproduction impossible. The occurrence of the odd specimens could be genetic heterogeneity (Mansingh, 1971).

MAN-MADE TEMPERATURE REGIMES

Technological projects involving thermal discharges often create flat temperature curves such as those found in a spring-fed river. Figure 3 shows annual

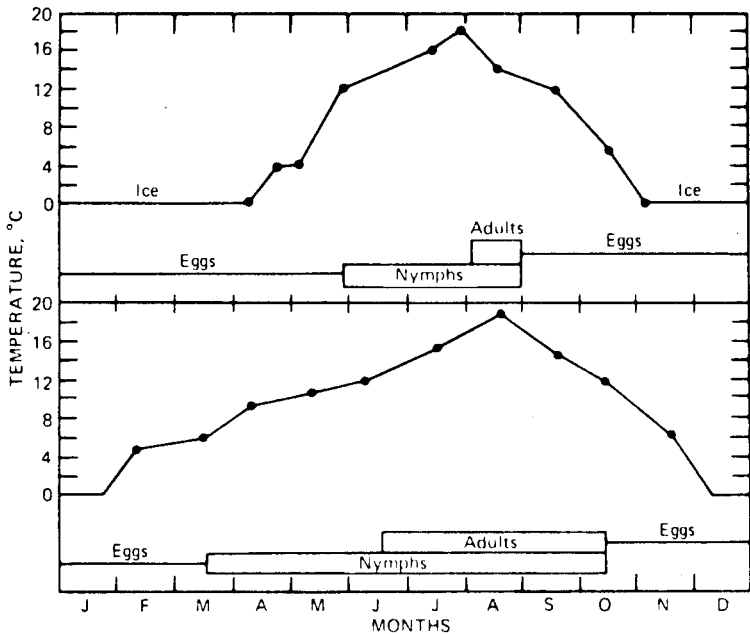


Fig. 2 Flexibility of the life cycle of *Paraleptopplebia debilis* (Walker) under different thermal regimes. Upper curve, northern boreal forest (53°N), Edmonton, Alberta (data from Clifford, 1969). Lower curve, coastal lowland stream (44°N), Corvallis, Oregon (data from Lehmkühl, 1969). Freezing temperatures terminate diapause and the warm summer period allows growth; thus the species can occur in both areas.

temperature curves in the South Saskatchewan River at an unaltered site above the reservoir and at the outflow of the reservoir. A summary of the organisms found at each site is also shown. The normal river is characterized by a sharp increase in temperature in spring and a sharp drop in autumn. A diverse fauna is present. At the outflow the hypolimnion drain prevents ice from forming in winter, even in 30°F-below-zero air temperatures. In spring and summer the large body of cool water in the reservoir keeps temperatures low in the channel below the outlet. The area at the outflow is best described as a biological desert. No lethal temperatures are involved, and I can find no other factors, such as depleted oxygen or altered water chemistry, which would explain the depletion of the fauna. All the evidence, whether physiological or ecological, points to the same conclusion. Stimuli essential for the completion of life cycles were eliminated by the reservoir. The effect on the aquatic community would be the same if the temperature curve were flattened by a reservoir or a power plant.

Work remains to be done to prove how widely these conclusions apply, but much is already known. Time and space prevent me from entering into the details of the great mass of scattered life-history data and unassimilated

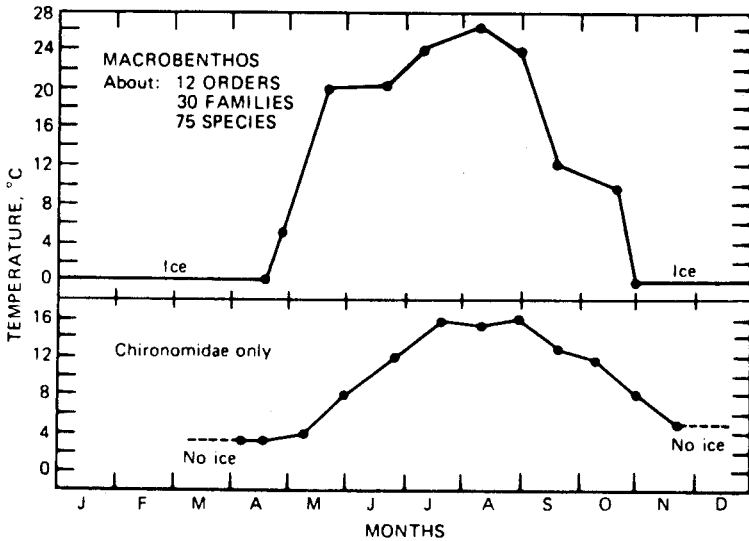


Fig. 3 Temperature regimes at the reservoir outflow (lower curve) and in the unaltered river (upper curve). The paucity of fauna at the outflow indicates that the limits of flexibility of species have been exceeded. Freezing temperatures and warm summer temperatures, both requirements, are absent at the outflow.

physiological facts that support the thermal-regime—physiological-stimulus approach to thermal ecology. Several examples must suffice. Annala (1969) provides data on voltinism (number, control, and timing of generations), thermal sums, and lethal temperatures in the terrestrial beetle genus *Ips* indicating that the phenomena under discussion are not limited to aquatic insects. Trpis, Haufe, and Shemanchuk (1973) point out that a sequence of environmental temperatures and other conditions are necessary for the hatching of eggs and subsequent development of the floodwater mosquito *Aedes sticticus*. Elsewhere I have inferred that what is true for certain mayflies is also true for many other insects (Lehmkuhl, 1972). Brewer (1964) described the summer—fall—winter temperature sequence that is essential for the development of the copepod *Diaptomus stagnalis*, and he states that in principle the “resting stage” in copepods is the same as diapause in insects. Finally, I should like to mention the well-known phenomenon of “dormancy” in plants and the fact that some vascular plants have requirements for strict temperature sequences (Ware, 1972).

It would be interesting to know how many species of plankton, aquatic plants, benthic crustaceans, game fishes, and marine organisms are susceptible to temperature-regime alteration. To find out, we would need data so that a model of thermal requirements spanning several generations could be plotted, as in Fig. 4 for the mayfly *Ephoron album*. We could then simply superimpose the

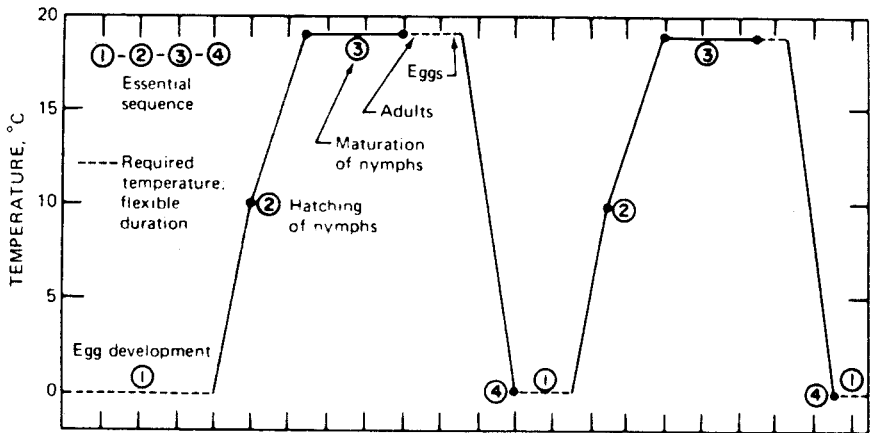


Fig. 4 Graphic model of the thermal requirements of *Ephoron album* spanning two generations. Models could be developed for all important species for comparison with actual or potential thermal regimes.

experimentally derived model on the actual thermal regime of a given area. Problem areas concerning a given species could be quickly identified, and future effects of projects in the planning stage could be predicted. While it is possible for biologists to stress the "diversity-of-life" and "all-species-are-different" points of view, I feel that many common features in life cycles will be found if we look for them because organisms of many different groups have evolved and adapted to the same conditions. If we accumulate more knowledge of the life cycles of aquatic organisms, we should be able to design technological projects in such a way that man could receive the benefits but minimize the negative impact on the environment and natural communities. Perhaps power plants and reservoirs should be constructed together and outflows manipulated so that the natural temperature regimes are duplicated.

ACKNOWLEDGMENT

The research reported here was supported by grants from the National Research Council of Canada.

REFERENCES

- Annala, Erikki, 1969, Influence of Temperature upon the Development and Voltinism of *Ips typographus* L. (Coleoptera, Scolytidae), *Ann. Zool. Fennici*, 6: 161-208.
- Becker, C. D., 1973, Development of *Simulium* (Psilozia) *vittatum* Zett. (Diptera: Simuliidae) from Larvae to Adults at Thermal Increments from 17.0 to 27.0°C, *Amer. Midl. Nat.*, 89: 246-251.

- Brewer, R. H., 1964, The Phenology of *Diaptomus stagnalis* (Copepoda: Calanoida). The Development and the Hatching of the Egg Stage, *Physiol. Zool.*, **37**: 1-20.
- Britt, N. W., 1962, Biology of Two Species of Lake Erie Mayflies, *Ephoron album* (Say) and *Ephemera simulans* Walker, *Bull. Ohio Biol. Surv.*, **5**: 70.
- Clifford, H. F., 1969, Limnological Features of a Northern Brown-Water Stream, with Special Reference to the Life Histories of the Aquatic Insects, *Amer. Midl. Nat.*, **82**: 578-597.
- Krenkel, P. A., and F. L. Parker (Eds.), 1969, Biological Aspects of Thermal Pollution. Vanderbilt University Press, Nashville, Tenn.
- Lehmkuhl, D. M., 1972, Change in Thermal Regime as a Cause of Reduction of Benthic Fauna Downstream of a Reservoir, *J. Fish. Res. Board Can.*, **29**: 1329-1332
- , 1969, Biology and Downstream Drift of Some Oregon Ephemeroptera, Ph. D. Thesis, Oregon State Univ., Corvallis.
- , and N. H. Anderson, 1971, Contributions to the Biology and Taxonomy of the *Paraleptophlebia* of Oregon (Ephemeroptera: Leptophlebiidae). *Pan-Pac. Ent.*, **47**: 85-93.
- Mansingh, Ajai, 1971, Physiological Classification of Dormancies in Insects, *Can. Ent.*, **103**: 983-1009.
- Trpis, M., W. O. Haufe, and J. A. Shemanchuk, 1973, Embryonic Development of *Aedes* (O.) *sticticus* (Diptera: Culicidae) in Relation to Different Constant Temperatures, *Can. Ent.*, **105**: 43-50.
- Ware, Stewart, 1972, Growth and Dormancy in *Talinum* Rhizomes, *Ecology*, **53**: 1195-1199.