Environmental Disturbance and Life Histories: Principles and Examples[1]

D. M. LEHMKUHL

Department of Biology, University of Saskatchewan, Saskatoon, Sask. S7N 0W0

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While many environmental disturbances have no readily detectable effect on aquatic invertebrates in the short term, they may prevent normal reproduction and cause eventual local extinction of a species. Small temperature changes may interfere with diapause signals and prevent completion of the life cycle. Heavy metals and toxic substances may drastically reduce reproduction rates in species exposed to sublethal levels. Dissolved salts and pH affect organisms at abnormally high or low levels but most mechanisms are unknown. It is concluded that relatively little information is available on the effects of environmental disturbances on life cycles. Available information, however, is sufficient to provide evidence of many problems that require attention.

Key words: life histories, benthos, environmental disturbances, toxic substances, diapause, temperature, heavy metals

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Bien que, à court terme, plusieurs perturbations de l'environnement n'affectent pas sensiblement les invertébrés aquatiques, elles peuvent empêcher une reproduction normale et entraîner l'extinction locale d'une espèce. De faibles changements de la température peuvent interférer avec les signaux des diapauses et interrompre le déroulement complet du cycle biologique. Les métaux lourds et les substances toxiques peuvent abaisser de façon dramatique le taux de reproduction d'espèces exposées à des niveaux sublétaux. Les sels dissous et le pH affectent les organismes lorsque leurs niveaux sont anormalement élevés ou bas, mais la plupart des mécanismes nous sont inconnus. Nous arrivons à la conclusion qu'on connaît très peu les effets des perturbations de l'environnement sur les cycles biologiques. Les connaissances que nous possédons suffisent toutefois à nous indiquer que plusieurs problèmes demandent à être étudiés.

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THE purpose of this paper is to discuss the effects of various environmental disturbances on life histories of aquatic macroinvertebrates. The task has been difficult because of the breadth of the area to be covered and also the lack of research data that are clearly relevant. Some of the examples are of organisms that are not truly benthic, and the examples are far from being a review of the known data.

The relationships between life histories and environmental disturbances are usually subtle and difficult to detect. For example, a dam constructed on the Clinch River, a warmwater Alabama river, changed it into a Annual Meeting of the North American Benthological cold-water river through release of 10°C water from the hypolimnion throughout the year (Tarzwell 1938). Almost all of the warmwater benthic fauna was eliminated. Tarzwell (1938) hoped that the river would soon be colonized by cold-water, trout stream insects and that it would change into a trout stream. He also felt that typical trout stream food organisms could be stocked in the river if natural colonization did not occur. Despite repeated attempts at stocking of trout, the Clinch River never developed into a trout stream, and according to Isom (1971), no one up to that time had *proved* why the efforts failed, although low oxygen levels in the water from the hypolimnion were held to be responsible.

My interest in the problem of the effects of environmental disturbances on life histories developed when I found a virtual absence of aquatic life in an area of the Saskatchewan River where all observations indicated that water quality was excellent (Lehmkuhl 1970, 1972, unpublished data). This river is inhabited by a unique community of mayflies, including *Anepeorus*, *Ametropus*, and *Pseudiron*, and I began searching for them in the vicinity of Saskatoon. As I moved upriver, away from the city, I expected to find a greater abundance and diversity of benthic fauna. However, collections became progressively depauperate, even though the river appeared to be physically "healthy." I suspected that Gardiner Dam, located approximately

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100 km upstream was responsible. The question was why and how.

Low dissolved oxygen concentrations could be ruled out, since the effect would hardly be expressed 50–100 km downstream from the dam. By comparing water quality in the depauperate south branch of the river with the normal north branch of the river, it was possible to eliminate many possible factors, e.g. toxins, water chemistry, pH, substrate, food, etc. It was finally apparent that a changed annual temperature profile was responsible for eliminating the organisms. For example, at least the mayfly, *Ephoron album* could not reproduce in the area influenced by the dam because it was not receiving known diapause "signals." The temperature on any given date during the year was not harmful to the organisms, but the sequence of temperatures and the overall temperature decline was responsible for the ecological death of many species (Lehmkuhl 1972; and see review by Ward 1976b).

Failure of colonization by cold-water insects in the Clinch River may be similarly explained. Cool water itself was not the only requirement for the survival of trout stream species. Life history requirements had to be met. Low dissolved oxygen concentrations may have been a problem but certainly was not the only problem involved.

This paper will document examples of other perturbations that may have disturbed the life histories of other species of aquatic invertebrates.

Nutrients and Ions

Very little precise information is available on the ecological significance and effects of nutrients and ions on aquatic life. Theoretically, the absence of essential ions would be limiting factors to the occurrence of benthic invertebrate species. For example, Nduku and Harrison (1976) found 2 mg/L Ca^{++} to be the lower limit of survival for the snail *Biomphalaria pfeifferi* when cultured in a calcium bicarbonate medium and 4 mg/L was needed for the population to thrive. Snails in calcium sulfate cultures had lower survival, indicating the importance of the bicarbonate buffer. Snails in natural waters were limited to areas with calcium concentrations of at least 5 mg/L and no snails of any species were found below 2 mg/L Ca^{++}. Adult snails would not lay eggs in natural waters with calcium concentrations under 5 mg/L, and low calcium concentrations inhibited egg production, reduced the hatching rate in eggs, and caused distorted shells in juveniles. These relationships would not be easy to detect in either field studies or short-term laboratory studies. Detailed and sophisticated life history studies were necessary.

Most life history disturbances result from excesses of nutrients and ions rather than insufficiencies. In the middle ranges of natural concentrations, I was unable to find any data to show that "normal" fluctuations have an adverse effect on aquatic invertebrates. Organisms appear to thrive over a rather wide range of concentrations (e.g. Hannon and Young 1974).

Pulses of road salt (primarily Cl^-) of up to 800 mg/L had no effect on drift patterns of aquatic insects (Crowther and Hynes 1977). However, permanent chloride concentrations of between 1000 and 2340 mg/L have caused the disappearance of many common species and an overall impoverishment of stream fauna (Crowther and Hynes 1977).

At even higher levels, such as in brackish water or inland saline lakes, most organisms are able to osmoregulate to a point, but species begin to drop out as ion concentrations increase (Wichard et al. 1973, 1975; Tones 1979; Rawson and Moore 1944).

Tones (1979) found that the beetle *Hygrotus salinarius* was able to osmoregulate in the adult stage but that haemolymph concentration in larvae was controlled by the salinity of the medium. Adults and larvae, therefore, tolerated salinity by different means. One would expect that larvae that lack the power to osmoregulate would be more sensitive than adults to abnormal changes in ion concentration.

pH

pH is widely regarded as being important in determining the distribution of organisms, but I did not encounter any data that specifically described mechanisms or vulnerable life cycle stages.

Individual species can tolerate extreme ranges of values in nature. Sprules (1975) found that in a series of acid-stressed lakes, some species of phytoplankton occurred over a range of 3.8–7, but that a large group of species dropped out at about pH 5.

Levels of pH ~4 cause a significant decrease in diversity of aquatic insects (Canton and Ward 1977). Fluctuations of pH 7 ± 1 are considered to be insignificant (Hannon and Young 1974).

Apparently more work is necessary on pH at sublethal levels, especially as it affects life cycle processes and behavior.

Heavy Metals

Heavy metals such as copper, lead, zinc, silver, and mercury are becoming increasingly recognized as severe environmental contaminants. They are highly toxic to fish, less so to invertebrates (Nehring 1976; Renzoni and Bacci 1976), and in many cases are a threat to the health of man. Winner and Farrell (1976) described the following lethal and chronic effects of copper on four species of *Daphnia*: (1) Acute toxicity ranged from 54 to 86.5 μg/L (72-h LC 50). (2) Sublethal chronic exposure to copper did not alter maturation time or frequency of reproduction in parthenogenetic females of *D. magna*, but it shortened the life span of females and reduced brood size, greatly affecting reproductive output. Copper stimulated larger broods in some cases, but this was offset by shorter life spans of the females and thus fewer broods. In other species of *Daphnia*, sublethal concentrations reduced brood size. (3) Instantaneous rate of population growth (*r*) was significantly reduced by copper stress in three of the four species of *Daphnia*, and reproduction stopped in the three most sensitive species below the lethal level.

Other studies show that sublethal concentrations of heavy metals ultimately affect life histories of invertebrates. Test solutions of $\frac{1}{10}$–$\frac{1}{200}$ of the known lethal dose of copper sulfate caused significant metabolic disorders in the snail *B. alexandrina* (Ishak and Mohamed 1975). While this paper does not directly discuss life histories, it seems obvious that low levels of copper sulfate would drastically affect reproduction because of apparently irreversible physiological damage to the organism.

Sublethal concentrations of cadmium, zinc, and chromium in lake sediments caused an avoidance reaction by larval *Chironomus tentans* (Wentsel et al. 1977). While application of these results to the field is difficult, implications of the avoidance response should be considered in future studies.

Bioaccumulation of heavy metals by many invertebrates may mean that even low concentrations of heavy metals may alter community structure by shortening life span and inhibiting reproduction. Benthic communities are probably undergoing massive perturbations under the influence of what we consider to be nonproblematic, low heavy metal concentrations.

Biocides and Other Toxins

Schober and Lampert (1976) tested sublethal effects of the herbicide Atrazin on the reproductive rates of *D. pulex* and brine shrimp (*Artemia*). In *D. pulex*, concentrations of 1 mg/L reduced cumulative reproduction by about 25%. Ten milligrams per litre was nearing the level of acute toxicity. At this concentration all animals died within 12 d and reproduction was $<40\%$ the control rate. While the mechanisms and vulnerable stages are not known, low concentrations (compared to acute toxic levels) have a striking effect on total population growth.

Sublethal concentrations or residues of pesticides may have a stimulatory effect on reproduction (e.g. Dittrich et al. 1974). Recall that at certain levels, sublethal chronic concentrations of copper stimulated reproductive rates in *D. magna*. This phenomenon, hormoligosis, is thought to result from stimulation by small quantities of a stressor. Therefore even very low sublethal chronic concentrations of toxins and biocides could drastically alter community composition by stimulating reproduction in some species or reducing reproduction rates in others. Research in this area has only begun. It would be ironic if we have created our own agricultural and forest pest problems by maintaining a stimulatory level of pesticide residues.

Insect development inhibitors are a type of pesticide consisting of juvenile hormone analogs that cause death at molting (Miura and Takahashi 1974). These materials affect the molting process of a wide range of nontarget arthropods (especially crustaceans and insects), but I found no information on the possible stimulatory effects of sublethal dosages.

Changes in Physical Parameters of Watersheds

Drastic changes in physical features such as current velocity, water level fluctuations, substrate, etc. can eliminate sensitive species while allowing tolerant ones to thrive. Some information is available from studies of newly established habitats (e.g. Williams and Hynes 1976) that indicate that insects, worms, crustaceans, and molluscs constantly invade new habitats from surrounding areas. Competition and ability to reproduce in the new habitats soon molds a new community. "Fine tuning" may occur through such processes as conditioning of water by another life stage. Growth promoting substances are produced by the snail *B. glabrata* (Thomas et al. 1975). Both growth rates and natality are higher in water that has been conditioned by the presence of adults than in water that has not. Thus, various subtle aspects of life histories (e.g. fecundity, vagility, and competitive ability) control community structure and composition in freshwater invertebrates.

Fisher and LaVoy (1972) found that water level fluctuations below a hydroelectric dam produced a freshwater "intertidal zone." The basic problem was periodic desiccation which would obviously affect immobile and vulnerable life stages. This problem has been recognized for many years (Grimås 1965). Fish food organisms and aquatic plants are drastically affected. Similar problems have been documented by Radford and Hartland-Rowe (1972) and reviewed and discussed by Ward (1976a).

Changes in current velocity and substrate act selectively on individual species and on individual life history stages. A sandy stream substrate, caused by a mining operation, formed an effective barrier to upstream movement in insect nymphs and larvae except for heavy-cased *Dicosmoecus* sp. (Leudtke and Brusven 1976). Larvae and pupae of *Pycnopsyche* spp. exhibited species specific substrate preference and behavioral sequences (Mackay 1977). Lehmkuhl and Anderson (1971) reported changes in habitat preference as nymphs of *Paraleptophlebia temporalis* matured. Kovalak (1976) found an interaction between temperature and currents that influenced positioning on brick substrates by the caddisfly *Glossosoma nigrior*. Faunal changes in areas of siltation or altered current velocity are therefore predictable. More precise studies on such relationships are needed.

Temperature

The literature suggests that no natural factor is as important as temperature, because, while pH and nutrients appear to be tolerated by organisms over a wide range, a change in temperature of a single degree Celsius can be significant.

Britt (1962) showed that the mayfly *E. album* required a strict sequence of temperatures to allow hatching and growth to maturity. Eggs would not hatch until being warmed after exposure to 0°C. Development differed at 0 and 1.3°C, indicating the degree of sensitivity. Actual hatching is stimulated by a rise in temperature to 10–13°C.

Horsfall (1974) described a similar sequence of events for hatching and growth of the mosquito *Aedes stimulans*. Eggs experience temperatures of 20–25°C after oviposition in summer followed by 4°C or below for 6 mo. In the spring, the eggs hatch after temperatures rise to >4°C. Eggs will not hatch unless exposed to 4°C or less.

A laboratory growth study of larvae of the blackfly *Simulium venustum* is summarized in Table 1 (Mokry 1976). Combining laboratory data and field temperature observations, Mokry (1976) was able to provide a growth model for *S. venustum* (Table 2).

The leech *Helobdella stagnalis* produced two generations per year in a comparatively warm pond in British Columbia but only a single generation per year in a cooler pond in Alberta (Davies and Reynoldson 1976). Thus, increases in temperature associated with thermal pollution could easily increase the number of leeches in an aquatic ecosystem. In contrast, Aston and Brown (1975) found that reproduction in the leech *Erpobdella octoculata* was apparently regulated by day length, and the life cycle pattern was similar in five different sampling stations in a thermally polluted river.

TABLE 1. Response of blackfly larvae (*Simulium venustum* to various temperatures (Mokry 1976).

Temp (°C)	Survival (%)	Observations
5	0	— eggs hatched, no growth, 1st instar died after 10 d
10	0	— larvae developed to second instar, died after 21 d
12	0	— larvae developed to 4th instar, died after 33 d
15	10	— development completed to pupal stage, 36 d
18	15	— development completed to pupal stage, 29 d
20	16	— development completed to pupal stage, 25 d
22	20	— development completed to pupal stage, 22 d
24	5	— development completed to pupal stage, 20 d

TABLE 2. Growth model for the blackfly *Simulium venustum* based on field and laboratory data (Mokry 1976).

Generation	Month(s)	Temp	Larval duration
1st	May–June	cool spring	54 d
2nd	July	$\bar{x} \sim 18$°C	1 mo
3rd	Aug.	$\bar{x} \sim 18$°C	1 mo
4th (rare)	Sept.	cooler	variable, overwinters as eggs

Further examples of the effects of temperature on the life cycles of a variety of aquatic organisms are available. The turbellarian *Phaenocora typlops* requires temperatures below 5°C to stimulate egg development (Young 1974). Temperatures above 9°C are required to stimulate hatching. The egg resting stage was an obligate diapause rather than being initiated by environmental stimuli. Thermal pollution that did not allow temperatures to drop below 5°C in winter could exterminate the species.

The planarian *Polycelis tenuis* has a higher reproductive rate at lower temperatures than *P. nigra* which explains the wider distribution of *P. tenuis* (Lascombe et al. 1975).

There is also evidence that organisms are able to acclimate or compensate for temperature changes. Planktonic crustaceans were able to develop at the normal rate at cooler than normal temperatures (Munro and White 1975; Munro 1974). Similarly, Langford (1975) did not find a significant change in insect emergence patterns in a river warmed as much as 8 deg above normal.

Thus, a wide variety of invertebrates (arthropods, leeches, flatworms) have distinct temperature requirements, and minor alterations of temperature by thermal pollution can cause drastic effects on the animal community. This applies to extreme climates (e.g. Canada) and also to relatively mild climates (e.g. England). I concluded several years ago (Lehmkuhl 1972) that thermal regime alteration caused faunal depletion up to 100 km downstream from a hypolimnion drain reservoir, and that other factors were of secondary importance. After this review, I find no reason to change my mind about the overriding importance of temperature.

Discussion

I am left with two impressions after reviewing the literature for this paper: (1) In contrast to even 5 yr ago, when very few papers relevant to this discussion were available, we now find that much valuable information has been published. (2) Much is yet to be done. Just enough information is available to let us begin to see the outlines of this new problem. Many authors are commenting on this fact. For example, Schober and Lampert (1976) have warned that the determination of acute toxicity in pesticides has little relevance to the determination of ultimate ecological consequences and that long-term studies involving sublethal concentrations are necessary.

Likewise, Stockner and Antia (1976) (discussing algae) warn of the dangers of confusing short-term "shock" responses with long-term "habituation" responses. They note that sometimes, after the "shock" is over, the organism may adapt and live quite well with the new disturbance. Short-term studies of acute effects may mislead in two ways: (1) they may fail to detect ecologically meaningful problems, and (2) they may direct undue attention to a brief "shock" reaction.

Cairns (1976) feels that many subtle environmental perturbations caused by heated waste water are so difficult to detect that the research community is unprepared to meet the challenge, and that frequently inappropriate data are gathered. The truth of Cairns' statement is borne out by the contents of the volume in which it appears (Cairns 1976), which consists largely of descriptive studies or the results of experiments involving acute effects. I stress, again, that acute effects have little to do with ultimate ecological consequences.

Ellis (1976) (discussing marine benthos) raises the matters of judgement and cost–benefit analysis in relation to studies of benthos. As we all know, it is usually impossible to identify all the organisms collected in samples to species. To now suggest that detailed life history or other long-term studies be made on every species is not only impossible from a practical point of view, but perhaps unnecessary from a scientific point of view. It seems that we need a new conceptual framework for benthological data that will point the way to future work.

For example, toxic materials not only cause immediate death in high concentrations, but they may have equally devastating effects in the long-term at sublethal levels. They may affect fecundity, longevity, behavior, or may cause stress-induced stimulatory effects on reproduction. The effects of altered temperature may be equally complex. Generations may be lost or gained, or there may be reproductive failure. It would be useful to compile a checklist of environmental disturbances and the types of impact that they may have on life histories to reduce the danger of overlooking important yet difficult-to-detect relationships. While the references cited in this paper could be used as a beginning checklist, its brevity and incompleteness would illustrate the amount of work yet to be done, both in the laboratory and in the library. Note, for example, that while ions and pH are routinely measured, the significance of fluctuations around normal readings are obscure. After such a checklist is expanded and refined, it would be possible to quickly identify potential problems, determine whether or not appropriate data had already been gathered, and decide upon the research required.

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