LIFE HISTORY CHARACTERISTICS AS A DETERMINANT OF THE RESPONSE OF MAYFLIES AND STONEFLIES TO MAN-MADE ENVIRONMENTAL DISTURBANCE (EPHEMEROPTERA AND PLECOPTERA)

John E. Brittain

Freshwater Ecology and Inland Fisheries Laboratory
University of Oslo
Sars gate 1, 0562 Oslo 5, Norway

ABSTRACT

The degree to which a particular species of mayfly or stonefly is susceptible to man-made environmental disturbances, such as river regulation or pollution, is determined in many cases by the life history strategies displayed by that species. Certain strategies are hypothesised as advantageous. These include asynchronous development, flexible voltinism, long egg development and insensitivity to changes in temperature. The ability to rapidly colonise denuded habitats is also of importance, as is the ability to escape difficult conditions by moving into less affected microhabitats.

INTRODUCTION

Lotic insects, including mayflies and stoneflies, are subject to both natural and man-induced disturbance and change (Resh *et al.* 1988). Man-made perturbations include organic and metal pollution, acidification, river regulation and increased frequency of drought or floods. Life history attributes provide the framework for the ability of aquatic insects to withstand such environmental disturbance and to recolonise denuded habitats. In this paper life history attributes of mayflies and stoneflies considered advantageous or disadvantageous are put forward, together with specific examples.

EGG DEVELOPMENT

The egg stage in mayflies and stoneflies has fewer environmental requirements than the nymphal stage and is therefore often better able to survive the temporal instability frequently associated with disturbance (Hawkins 1990). It can therefore be advantageous to have a long egg stage coupled with a short period of active nymphal growth. Among the mayflies, the European species, *Ephemerella ignita* (Poda), successful in regulated rivers, displays these characteristics. It has a long period of egg development and hatching (Bohle 1972, Elliott 1978), followed by a short period of summer nymphal growth (Bournaud *et al.* 1987). Similar strategies are seen in certain Plecoptera, such as the European *Leuctra* (Saltveit *et al.* 1987) and many Australian *Dinotoperla* (Hynes and Hynes 1975, Yule 1985). Egg diapause in certain species provides an additional opportunity to avoid unfavourable conditions.

The more robust eggs of several stonefly species are able to withstand freezing (Brittain and Mutch 1984, Lillehammer 1987, Gehrken 1989), an advantage during low flows in cold climates. In contrast, low flows or cessation of flow in warm climates often necessitate a drought resistant egg stage.

TEMPERATURE RELATIONSHIPS

River regulation and thermal discharges invariably produce temperature changes in the downstream reach. The temperature relationships, both in the egg and nymphal stage, will be crucial in determining the species' ability to survive. Strict temperature limits or specific temperature cues will be disadvantageous under changed conditions and will often lead to extinction (Lehmkuhl 1972). However, certain species have neither strict temperature limits nor development and growth that is greatly temperature dependent. For example, unlike most mayflies, egg development in the North American, *Tricorythodes minutus* Traver, is little influenced by temperature (Newell & Minshall 1978a, Brittain 1990). This, coupled with flexible voltinism, rapid growth and an ability to withstand silting (Newell and Minshall 1978b) has enabled it to be successful below dams (Brittain and Saltveit 1989).

SIZE AND SHAPE

Small size and a cylindrical shape enable mayfly and stonefly nymphs to seek refuge in gravel and stone substrates during pollution episodes or under low flows. The stonefly genera, *Alloperla* s.l. (Chloroperlidae) and *Leuctra*, show such characteristics and are frequently abundant in regulated rivers (Saltveit et al. 1987). The early instars of several species live down in the hyporheic (Stanford & Ward 1988) and are equally or better able to survive environmental vicissitudes than the immobile egg stage.

COLONIZATION

A pollution incident may eradicate most or all of the population of a particular mayfly or stonefly species. The ability to rapidly colonize and build up a new population in such a denuded habitat is of prime importance in determining the species' success. Colonization can occur by the oviposition of aerial adults, upstream movement, downstream drift or movement upwards from the hyporheic (Williams and Hynes 1976). The contribution from these various sources will vary with species and situation, although drift would seem to be the major source (Williams and Hynes 1976, Townsend and Hildrew 1976). Mayflies are generally more abundant in downstream drift than stoneflies, and members of the genus *Baetis* often exhibit high drift rates (Clifford 1972, Brittain and Eikeland 1988). At least over short distances, adult mayflies are also more successful at dispersal then adult stoneflies. They fly more readily and have extremely high fecundities (Brittain 1982, 1990).

DEVELOPMENTAL SYNCHRONY

Many species of mayfly and stonefly display synchronous development with little variation in nymphal size or state of egg development at any point in time in order to maximize the benefit from optimal conditions. This has the disadvantage that the whole population may be exterminated if the habitat is affected by pollution or other disturbance affecting a particular life history stage. However, certain species and genera "hedge their bets" and display a range both in size and life cycle stage at a given point in time. The development of several Australian mayflies and stoneflies is more asynchronous than many northern temperate species (Hynes and Hynes 1975, Campbell 1986), although not always so (Marchant *et al.* 1984, Yule 1985). On this basis it would be expected that disturbance would have less effect in Australia than elsewhere.

There are, however, several northern temperate species which by virtue of their asynchrony are successful in disturbed systems. These include several mayflies in the genus *Baetis* and the leptophlebiid mayfly, *Choroterpes mexicanus* Allen, which is a seasonal polyvoltine species with three overlapping generations per year and is abundant in the regulated Brazos River (McClure and Stewart 1976). Although advantageous in terms of disturbance, asynchronous emergence may be a disadvantage. The chances of meeting a mate are reduced and there is little chance of predator saturation (Butler 1984).

VOLTINISM

Flexible voltinism is linked to developmental synchrony and is also an important determinant of a species' ability to cope with pollution and other environmental disturbances. The life cycle plasticity of the European *Baetis rhodani* Pictet and the North American *B. tricaudatus* Dodds has undoubtedly contributed to their success in regulated rivers and running waters in general. Their life cycles vary from a fairly synchronous univoltine cycle in cold water habitats to a wide range of more or less synchronous multivoltine cycles, sometimes with overlapping cohorts (see Clifford 1982). This provides the potential to maintain a viable population, even though one cohort or generation may be exterminated by unfavourable environmental conditions (*e.g.* Brittain *et al.* 1984), as well as to exploit new and favourable conditions (*e.g.* Wallace and Gertz 1986, Rader and Ward 1989).

CONCLUDING REMARKS

In many cases the mayfly and stonefly species that are able to survive and even benefit from pollution, regulation and other man-made disturbances are generalists with wide ecological limits. On the other hand, specialists, with narrow ecological limits are often reduced in numbers or exterminated. The stonefly, *Isoperla quinquipunctata* (Banks) is one of the few stoneflies surviving below hypolimnetic release dams in North America. It has wide environmental limits (Knight and Gaufin 1966), but may be excluded by competition in habitats with more diverse faunas. This is also probably the case with several stoneflies tolerant of organic pollution, such as the European, *Nemoura cinerea* (Retzius) and *Nemurella pictetii* Klapâlek. They are widespread, but usually in low numbers except where species diversity is low through natural or man-made causes. Thus, although mayfly or stonefly densities may increase after man-induced environmental change, diversity is invariably reduced (Landa 1984). In contrast, natural perturbation may increase diversity by creating a wider variety of ecological niches (Resh *et al.* 1988).

Factors other than life history parameters are also important in determining a species' response to man-made environmental disturbance and change. These include the individual species' tolerance to specific pollutants, although this also seems to be related to the species' general ecological tolerance. Community interactions, such as changes in predation pressure and food availability can also bring about species change (Power *et al.* 1988). Nevertheless, life history parameters provide the framework within which the species response takes place. Certain mayfly and stonefly species and genera with their wide ecological requirements, life cycle plasticity and ability to rapidly colonize demanded habitats are clearly able to cope with and even profit from human intervention in freshwaters.

ACKNOWLEDGEMENT

I am grateful to Svein Jakob Saltveit for reading and commenting on the manuscript.

REFERENCES

Bohle, H. W. (1972): Die Temperaturabhangigkeit der Embryogenese und der embryonalen Diapause von *Ephemerella ignita* (Poda) (Insecta, Ephemeroptera). Oecologica (Berl.),10: 253-268.

Bournaud, M., H. Tachet, and A. L. Roux (1987): The effects of seasonal and hydrological influences on the macroinvertebrates of the Rhone River, France. II. Ecological aspects. Arch. Hydrobiol./Suppl., 76: 25-51.

Brittain, J. E. (1982): Biology of mayflies. Ann. Rev. Entomol., 27: 119-147.

Brittain, J. E. (1990): Life history strategies in Ephemeroptera and Plecoptera. pp. 1-12. *In*: Mayflies and Stoneflies: Life Histories and Biology. Campbell, I. (ed.). Kluwer Academic Publishers, Dordrecht. 366 p.

Brittain, J. E. and T. J. Eikeland (1988): Invertebrate drift - a review. Hydrobiologia, 166: 77-93.

Brittain, J. E., A. Lillehammer and R. Bildeng (1984): The impact of a water transfer scheme on the benthic macroinvertebrates of a Norwegian River, pp. 189-199, *In*: Regulated Rivers, Lillehammer, A., and S. J. Saltveit (eds.), Universitetsforlaget, Oslo, 540 p.

Brittain, J. E. and R. A. Mutch (1984): The effect of water temperature on the egg incubation period of *Mesocapnia oenone* (Plecoptera) from the Canadian Rocky Mountains. Can. Entomol., 116: 549-554.

Brittain, J. E. and S. J. Saltveit (1989): A review of the effect of river regulation on mayflies (Ephemeroptera). Regulated Rivers, 3: 191-204.

Butler, M. G. (1984): Life histories of aquatic insects. pp. 24-55. *In*: The Ecology of Aquatic Insects. Resh, V. H. and D. M. Rosenberg, (eds). Praeger Publishers, New York. 625 p.

Campbell, I. C. (1986): Life histories of some Australian siphlonurid and oligoneuriid mayflies (Insecta: Ephemeroptera). Austr. J. Mar. Freshwat. Res., 37: 261-288.

Clifford, H. F. (1972): A year's study of the drifting organisms in a brownwater stream of Alberta. Can. J. Zool., 50: 975-983.

Clifford, H. F. (1982): Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. Quaest. Entomol., 18: 15-90.

Elliott, J. M. (1978): Effect of temperature on the hatching time of eggs of *Ephemerella ignita* (Poda) (Ephemeroptera, Ephemerellidae). Freshwat. Biol., 8: 51-58.

Gehrken, U. (1989): Diapause termination in eggs of the stonefly *Arcynopteryx compacta* (McLachlan) in relation to dehydration and cold hardiness. J. Insect Physiol., 35: 377-385.

Hawkins, C. P. (1990): Relationships between habitat dynamics, food availability, and growth patterns of ephemerellid mayflies from western North America. pp. 35-42. *In*: Mayflies and Stoneflies: Life Histories and Biology. Campbell, I. (ed.). Kluwer Academic Publishers, Dordrecht. 366 p.

Hynes, H. B. N. and M. E. Hynes (1975): The life-histories of many of the stoneflies (Plecoptera) of south-eastern mainland Australia. Austr. J. Mar. Freshwat. Res., 26: 113-153.

Knight, A. W. and A. R. Gaufin (1966): Altitudinal distribution of stoneflies (Plecoptera) in a Rocky Mountain drainage system. J. Kansas Ent. Soc., 39: 668-675.

Landa, V. (1984): Studies on aquatic insects in Czechoslovakia with regard to changes in the quality of water in the last 20-30 years. pp. 317-321, *In*: Proc. 4th Int. Conf. Ephemeroptera, Landa, V., T. Soldán and M. Tonner (eds), CSAV, Ceske Budejovice. 345 p.

Lehmkuhl, D. M. (1972): Changes in the thermal regime as a cause of reduction of benthic fauna downstream of a reservoir. J. Fish. Res. Bd.

Canada, 29: 1329-1332.
Lillehammer, A. (1987): Diapause and quiescence in eggs of *Systellognatha* stonefly species (Plecoptera) occuring in alpine areas of Norway. Annls Limnol., 23: 179-184.
Marchant, R., A. Graesser, L. Metzeling, P. Mitchell, R. Norris and P. Suter (1984): Life histories of some benthic insects from the La Trobe River, Victoria. Austr. J. Mar. Freshwat. Res., 35: 793-806.
McClure, R. G. and K. W. Stewart (1976): Life cycle and production of the mayfly *Choroterpes (Neochoroterpes) mexicanus* Allen (Ephemeroptera: Leptophlebiidae). Ann. Entomol. Soc. Am., 69: 134-144.
Newell, R. L. and G. W. Minshall (1978a): Life history of a multivoltine mayfly, *Tricorythodes minutus*: an example of the effect of temperature on the life cycle. Ann. Entomol. Soc. Am., 71: 876-881.
Newell, R. L. and G. W. Minshall (1978b): Effect of temperature on the hatching time of *Tricorythodes minutus* (Ephemeroptera: Tricorythidae). J. Kansas Entomol. Soc., 51: 504-506.
Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B. Moyle, B. Statzner and I. R. Wais De Bagden (1988): Biotic and abiotic controls in river and stream communities. J. N. Am. Benthol. Soc., 7: 456-479.
Rader, R. B. and J. V. Ward (1989): Influence of impoundments on mayfly diets, life histories, and production. J. N. Am. Benthol. Soc., 8: 64-73.
Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar (1988): The role of disturbance in stream ecology. J. N. Am. Benthol. Soc., 7: 433-455.
Saltveit, S. J., J. E. Brittain and A. Lillehammer (1987): Stoneflies and river regulation - a review. pp. 117-129. *In*: Regulated Streams, Craig, J. F. and J. B. Kemper, (eds.), Plenum, New York, 431 p.
Stanford, J.A. and J. V. Ward (1988): The hyporheic habitat of river ecosystems. Nature, 335 (6185): 64-66.
Townsend, C. R. and A. G. Hildrew (1976): Field experiments on the drifting, colonization and continuous redistribution of stream benthos. J. anim. Ecol., 45: 759-772.
Wallace, J. B. and M. Gurtz (1986): Response of *Baetis* mayflies (Ephemeroptera) to catchment logging. Am. Midl. Nat., 115: 25-41.
Williams, D. D. and H. B. N. Hynes (1976): The recolonization methods of stream benthos. Oikos, 27: 265-272.
Yule, C. M. (1985): Comparative study of the life cycle of six species of *Dinotoperla* (Plecoptera: Gripopterygidae) in Victoria. Austr. J. Mar. Freshwat. Res., 36: 717-735.

Table 1. A summary of mayfly and stonefly life history attributes generally advantageous or disadvantageous in disturbed habitats.

	ADVANTAGEOUS	DISADVANTAGEOUS
EGG DEVELOPMENT	Long	Short
TEMPERATURE RELATIONSHIPS	Eurytherm Temp. independent	Stenotherm Temp. dependent
NYMPHAL SIZE	Small	Large
NYMPHAL DEVELOPMENT	Asynchronous	Synchronous
LIFE CYCLE	Flexible Multivoltine	Fixed Univoltine