LATERAL MOVEMENTS VERSUS STATIONARITY - ADAPTIVE ALTERNATIVES IN BENTHIC INVERTEBRATES TO THE SEASONAL ENVIRONMENT IN A BOREAL RIVER

by

Tommy I. Olsson

Department of Ecological Zoology

and

Department of Public Health

and Environmental Studies

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Tommy I. Olsson

University of Umeå, Department of Ecological Zoology / Department of Public Health and Environmental Studies, S-901 87 Umeå, Sweden.

ABSTRACT

Benthic invertebrates inhabiting boreal rivers are exposed to very large seasonal variations in their physical environment. The extremes are in winter when the littoral area freezes solid and in spring when water flow increases rapidly. In the North Swedish river Vindelälven, the invertebrates fell into three main categories according to their seasonal lateral distribution. One category of animals was stationary in the littoral zone and let itselt freeze into the ice, adopting a "take it" alternative. The category consisted of many species belonging to several higher taxa. By overwintering in ice, the animals avoided predation for nearly half the year and they were in the productive littoral at the same time as they thawed out from the ice in spring. On the other hand the animals had to withstand sub-zero temperatures. A typical representative for this category of animals was the semivoltine snail Gyraulus acronicus. It is a less mobile species connected to dense stands of macrophytes, which are found only in the littoral zone of the river. Nearly the whole population was found overwintering successfully enclosed in ice. Its shell and epiphragm could serve as mechanical protection when frozen into the ice. G. acronicus was cold-hardy only during late autumn and early winter, but it could stand prolonged sub-zero exposure during the proper time. A second category of animlas avoided being frozen by performing lateral movements to deeper parts of the river, adopting the "leave it" alternative. No species tested in this category were found cold-hardy. It consisted of mobile species known to utilize sedimentated detritus which was only found in greater amounts in the littoral zone of the river. In springtime, prior to spring flood peak, these species colonized promptly the former frozen zone. This behaviour was most pronounced in several lentic mayfly species. An extreme case of migratory behaviour was found in the mayfly Parameletus chelifer which not only moved towards the river bank but continued up into small tributaries. The shoreward movements of mayflies both allowed the nymphs to avoid the high current velocities in the central part of the river during spring flood time and to utilize the food resources in the flooded areas. A third category of animals avoided the ice by living stationary in the sublittoral zone, adopting the "never face it" alternative. This category was dominated by filter feeders.

Key words: Benthic invertebrates, cold-hardiness, ice, migrations, overwintering, river, seasonal variations, spatial distribution, spring flood, water level.

LIST OF PAPERS

This thesis is a summary and discussion of the following papers, which will be refered to by their Roman numerals.

I. Olsson, T. and Söderström, O. 1978. Springtime migration and growth of <u>Parameletus chelifer</u> (Ephemeroptera) in a temporary stream in northern Sweden. - Oikos 31:284-289.

II. Olsson, T. I. 1981. Overwintering of benthic invertebrates in ice and frozen sediment in a North Swedish river. - Holarct. Ecol. 4:161-166.

III. Olsson, T. I. 1982. Overwintering sites and freezing tolerance of benthic invertebrates in a North Swedish river. - Cryo-Letters (in press).

IV. Olsson, T. I. 1983. Seasonal variations in the lateral distribution of mayfly nymphs in a boreal river. - Holarct. Ecol. (in press).

V. Olsson, T. I. Overwintering strategies and cold-hardiness of gastropods in a boreal river (manuscript).

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INTRODUCTION

Benthic invertebrates inhabiting boreal rivers are exposed to very large seasonal variations in their physical environment. These variations are most prominent during two different seasons; in winter when the littoral areas freezes solid and in spring when the water-flow increases rapidly.

The river fauna has mainly three distributional alternatives to survive in this changing environment; (1) to be stationary in the exposed microhabitat, the "take it" alternative, (2) to possess seasonal lateral movements to less exposed microhabitats, the "leave it" alternative or (3) to be stationary in a less exposed microhabitat, the "never face it" alternative. In the first alternative the animals have to be behaviourally and physiologically adapted to exposed conditions. The other two alternatives base on behavioural avoidance of adverse conditions.

The following discussion emphasizes the physical environment the animals have to cope with depending on alternative distributional patterns and the adaptive advantages of these alternatives. Special reference is made to the problems with freezing of the littoral area during winter and the subsequent flooding in springtime.

The investigated part of the North Swedish river Vindelälven was ice-covered from mid-November until early May (IV). During this period the zone which was frozen solid developed gradually to a maximum extent (32-35 m) at mid-April (IV). Ice thickness within this zone was 30-50 cm and maximum frost penetration into the sediment 30-40 cm (II,IV). The temperature beneath the ice fell very slowly and the lowest temperature (-4°C) was recorded soon before ice-brake (II).

"TAKE IT" ALTERNATIVE

A stationary animal in the littoral zone has to tolerate being frozen into the ice or sediment (II,IV,V). These animals have to be cold-hardy as the temperature at the overwintering site falls below zero. They also have to be tolerant to the mechanical forces exerted when water crystalizes (Danks 1971). An enclosure in ice also means an inescapable arrest in the development of the animals concerned.

The observed temperature (-4°C) is below the haemolymph melting point of freshwater animals (II). Further, aquatic animals are exposed to an external nucleator, the surrounding ice, which usually has been considered to prevent supercooling (Salt 1963). However, internal growth of ice crystals could be prevented by thermal hysteresis factors. Thermal hysteresis factors have been demonstrated not only in arctic fish (De Vries 1971, DeVries et al. 1970), but recently also in molluscs (Thede et al. 1976) and insects (Duman 1979, Husby & Zachariassen 1980, Zachariassen & Husby 1982). Thus, if not case of thermal hysteresis, supercooling is prevented and the animals have to be freezing tolerant i.e. to stand an extracellular ice formation in their tissues.

Thus, animals possessing the "take it" alternative have to be cold-hardy, they have to stand the mechanical stresses of ice and they should not be dependent on winter growth to complete their development at the proper time.

Adaptive advantages of this alternative are complete avoidance of winter predation in the bosom of the ice and to be in a productive littoral area at the same moment as they thaw out from the ice. The last point must be important for less mobile species.

Many species belonging to several higher taxa (Nematoda, Gastropoda, Oligochaeta, Hirudinea, Trichoptera and Chironomidae) were shown to be capable of overwintering in the frozen hydrolittoral zone (II). Taxa which were abundant in this zone, except Asellus aquaticus L., were found to have survival rates as high as 80-100 % when thawed out from ice samples (II). In addition, it was shown that many species, but not all, developed cysts, cocoons or other special resting stage constructions that can serve as mechanical protections during the enclosure in ice. Such species were Gyraulus acronicus Ferrusac, Lumbriculus variegatus (Müll.), Agrypnia obsoleta Hagen, Oecetis ochracea Curtis, Molanna albicans Zett., M. angustata Curtis and some chironomid species (II).

A typical representative for the "take it" alternative is the pulmonate snail G. acronicus. Nearly the whole population of this snail overwintered in the frozen littoral zone (V). G.

acronicus was not cold-hardy during the summer but cold-tolerance developed in October (V). In specimens not frozen into the ice the cold-hardiness was lost again as early as in January (V). Both age classes of this semivoltine species developed cold-tolerance (V). Thus it seems more important at what time of year *G. acronicus* is frozen into the ice than the duration of the cold exposure (II,V). The seasonal pattern of cold-hardiness suggests that the inner part of the hydro-littoral zone, which freezes at the time of maximum cold-tolerance in this species is the optimal overwintering site (V). These experiment-results are in agreement with observed distributions in the field (V). The shell and the epiphragm construction of *G. acronicus* can serve as mechanical protections during the enclosure in ice (II). It is a less mobile species connected to dense stands of macrophytes (Økland 1969) which is only found in the littoral zone of the river.

"LEAVE IT" ALTERNATIVE

A second way of coping with the seasonal environment is to perform seasonal lateral movements to less exposed microhabitats (III). To the migratory group of animals belong many ephemerid species (III,IV), many plecopteran species (III) and the crustaceans *Pallasea quadrispinosa* (Sars) (III) and *A. aquaticus*.

There must be a high selection pressure on not cold-hardy animals to avoid the frozen littoral zone in winter. No species tested in cold experiments, belonging to the migratory group of animals has been found cold-hardy (P. quadrispinosa, A. aquaticus, Heptagenia fuscogrisea Retz., Leptophlebia marginata L., and L. vespertina L.) (II).

A typical representative for the group of animals possessing this alternative is the mayfly species L. vespertina. This species is not cold-hardy (II). It is a species found in high numbers where the bottom substrate consists of greater amounts of sedimentated detritus (Brittain 1978). Such conditions are only found in the littoral zone of the river (IV). It is a mobile species that moves out into deeper parts of the river as the hydrolittoral freezes solid and it colonizes promptly the former frozen zone in springtime (IV). A substantial part of its growth (about 30 %) takes place during the ice-covered period (Brittain 1978).

The avoidance behaviour in not cold-hardy animals seems very well adapted, except in A. aquaticus (II). During three years of sampling in the frozen zone only 5 specimens of L. vespertina while over 500 specimens of A. aquaticus were found (II,IV). A. aquaticus had about the same distributional pattern as L. vespertina during the winter i.e. it kept very near the ice (IV). Contrary to L. vespertina very many A. aquaticus were apparently trapped by the ice. The survival rate of A. aquaticus found in the ice was only 2 % (II).

"NEVER FACE IT" ALTERNATIVE

The third alternative was adopted by a group of species that avoids coming in contact with ice by living stationary in the sublittoral zone (III). To the stationary sublittoral group belong amongst others the mussles (Anodonta cygnaea L. (III) and Sphaerium spp., the prosobranch snail Valvata piscinalis Müll. (III,V) and the ephemeropteran species Ephemera danica Müll. and Baetis digitatus Bgtss. (IV). The only species in this category tested in cold experiments, V. piscinalis, was not cold-hardy at any time of the year (V). A species adopting this alternative ought not to be dependent on the amount of macrophytes or organic detritus deposits in the littoral.

Accordingly most of the species in this category were filter feeders i.e. the burrowing mayfly nymph E. danica (Otto & Svensson 1981) and the mussles Sphaerium spp. and A. cygnaea.

THE SPRINGTIME COLONIZATION

In the investigated part of the river Vindelälven minimum flow occurs in mid-April, ice brake during the first part of May and spring flood maximum often the last week in May (IV). During this period the water flow increases from about 30 $m^3 s^{-1}$ to 1000 $m^3 s^{-1}$ and the water level rises about 4 m (IV). The rise in water level results in a flooding of the geolittoral areas including alluvial meadows (I). During spring flood, the central parts of the river are exposed to high current velocities while the current speed in the flooded areas is very low (IV).

As the littoral area thawed out and became flooded the animals belonging to the "leave it" category promptly colonized the former frozen zone (IV). Shoreward migrations were most pronounced in several lentic mayfly species which colonized the uppermost geolittoral and stayed there till emergence (IV). The plecopteran species also occupied the uppermost geolittoral but this behaviour seems more restricted to time of emergence (Lillehammer 1965). More lotic ephemeropteran species did not exhibit the same aggregation in the uppermost geolittoral (IV). They stayed in the hydrolittoral zone, like most of the non-ephemeropteran species.

The fact that species common in lentic habitats were found in uppermost geolittoral, while lotic species did not show the same aggregation near the shore, indicates that this is an adopted behaviour to avoid high current speeds of central parts of the river during spring flood (IV). In addition it enables the animals to utilize the amount of detritus found in the uppermost geolittoral during spring flood (IV).

An extreme case of migratory behaviour was found in the mayfly Parameletus chelifer Bgtss. The nymphs of this species did not only move towards the river-banks but continued migrating up into small tributaries. By this behaviour the nymphs left the main river before spring flood peak (I). A similar behaviour has been reported in the North American mayfly species Leptophlebia cupida (Say) (Neave 1930, Hayden & Clifford 1974). It is suggested that this behaviour allows the nymphs to escape from the springtime turbulence of the main stream (Clifford et al. 1979). This is probably also of importance in P. chelifer. On the other hand this study also indicates that the nymphs take advantage of the rich food supply and the moore favourable temperature conditions in the alluvial meadows (I).

CONCLUDING REMARKS

This study has demonstrated that the frozen zone is an important overwintering site for several benthic invertebrate species in boreal rivers. The results are not in agreement with earlier suggestions regarding overwintering of benthic invertebrates in running waters: "The habitat of benthic insects therefore never freezes, ..." (Hynes 1970) and "Surface ice does not usually come into direct contact with invertebrates, although when it does freeze them in it apparently kills them (Brown et al. 1953)" (Hynes 1972).

Further studies on cold-hardiness and overwintering strategies are of vital importance for the understanding of the ecology of boreal running waters, as well as for predictions of consequences of human activities like water regulations and heat extractions from lake and river sediments.

In my opinion future research in this field should concentrate on (1) physiological preparations for overwintering of benthic invertebrates at sub-zero temperatures and the environmental factors involved in the control of these adjustments, (2) flexibility of the cold-hardiness patterns within a species depending on latitudes and habitats, and (3) evaluation of different strategies i.e. to obtain comparative data of survival rate and reproductive success of animals adopting different overwintering alternatives.

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