

Best wishes,
Hynden

Movements of marsh-dwelling invertebrates

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SUMMARY. 1. Invertebrate movement was monitored in a parkland marsh in central Alberta, Canada, for 24 h periods every 2 weeks during the ice-free season. Stationary plankton nets captured organisms moving towards or away from shore.

2. Movement occurred throughout the sampling programme, particularly during the warm summer months. Most organisms were night active and exhibited directional movements. *Hyaella azteca* (Saussure) and *Caenis simulans* McDunnough constituted most of the catch.

3. Although there was a significant positive seasonal relationship between maximum water temperature and total numbers of animals captured, no physical factor appeared to control movement on a daily basis.

Introduction

Invertebrate movement in lentic waters is often related to prematuration activity or seasonal environmental changes. Prior to emergence, insect larvae may move from deep, open areas to shallow, shaded, shoreline regions of lakes or ponds (Moon, 1935; Verrier, 1956; Hall, Cooper & Werner, 1970). Seasonal activity is associated with physical changes in the environment, particularly water temperature (Gibbs, 1979). In spring (after ice melt), there is movement shoreward from open areas as invertebrates occupy peripheral areas of the basin throughout the open water season; later, invertebrates retreat to the basin centre before ice formation in autumn (Wesenberg-Lund, 1908; Wodsedalek, 1912; Lundbeck, 1926; Eggleton, 1931; Moon, 1935, 1940; Gibbs, 1979). Marine invertebrates also have been

shown to retreat to deeper waters to avoid freezing conditions (Vermeij, 1978).

Invertebrate movement typically has been inferred from changes in benthic density (Wodsedalek, 1912; Eggleton, 1931; Gibbs, 1979). On the basis of a benthic colonization study of littoral regions of Windermere, Moon (1935) suggested that invertebrates moved continually (particularly during flood conditions), following the rise and fall of water levels. Corkum (1979) also observed that benthic densities of invertebrates varied with fluctuations in marsh water levels.

This study was designed to monitor the magnitude of actual onshore/offshore movements of marsh invertebrates throughout the open water season and to examine factors that might induce such movement.

Study area

The study was conducted in a marsh (surface area: 61.4 ha, volume: 2×10^5 m³, maximum

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depth: 1.2 m) on the Clifford E. Lee Nature Sanctuary located within the aspen parkland region of central Alberta, Canada (53° 24' N, 113° 47' W). The marsh, having a characteristic U-shaped basin, is one of several shallow, permanent waterbodies situated on sand dunes formed during post-glacial times. Ice cover usually occurs from late October until mid-April and reaches a thickness of up to 80 cm in March.

Extensive stands of bulrush, *Scirpus validus* Vahl., surround the marsh. The entire marsh is littoral in character; bladderwort, *Utricularia vulgaris* L., occupies nearshore areas and stonewort, *Chara* sp., occurs in the central basin.

Methods

Invertebrate movement was monitored using stationary plankton nets. Nets were 1 m long with a mesh size of 180 μm and a circular opening of 0.05 m². A stone was placed in the tapered end of each net, providing shelter for invertebrates. Two rods attached to the rim of

the net opening, 180° apart, were used to anchor nets and facilitate removal. Nets were set on the substrate at the border between shoreline and open water areas as defined by the distribution of emergent aquatic plants. Water depths at which nets were set ranged from 0.5 to 1 m. Sampling was conducted from a rowing boat to minimize bottom disturbance.

Five pairs of nets were positioned at equal intervals around one bay of the marsh for 24 h every 2 weeks throughout the ice-free season (24 April to 23 October). One net of each pair faced shoreward; the other was open to the marsh centre. Nets were positioned at dusk, emptied the following dawn and again at dusk. There was a total of fourteen sampling periods (5 June to 23 October 1979; 24 April to 22 May 1980), and for each period twenty samples of invertebrates were obtained (5 sites \times 2 net directions \times 2 light phases).

Although organisms were able to enter or leave the samplers at all times, movement was inferred from the net contents at the end of each light phase. Planktonic invertebrates (Cladocera and Ostracoda) were ignored in these analyses.

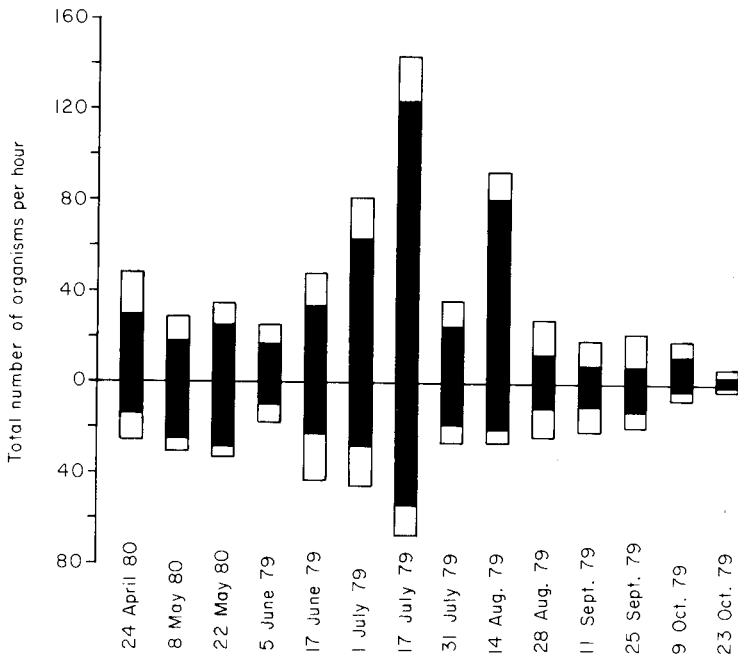


FIG. 1. Total number of organisms captured in nets per hour moving away from shore (above horizontal line) and towards shore (below horizontal line). Black and white portions of histograms represent organisms caught in the night and day, respectively.

Shoreline water level was measured by means of a graduated rod positioned in the marsh. Water depth and temperatures (throughout the water column) were recorded at each of the five net locations and at the marsh centre. Placement of nets around the marsh was designed to detect possible differences in movement due to wind. To eliminate potential lunar effects, samples were taken during the first or last quarter phases of the moon.

Results

Patterns of invertebrate movement

Summary data of catches of abundant taxa obtained during the fourteen sampling periods are presented in Figs. 1 and 2. Catches were expressed as number of organisms per hour. A total of 11,695 organisms was removed from the nets and the majority (66.1%) of these were captured at night (Fig. 1). Nocturnal activity was pronounced from late April until mid-August ($P < 0.05$); however, no significant dif-

ference in diel activity occurred during the last five sampling periods (G-statistic goodness-of-fit test; Sokal & Rohlf, 1969). Movement (61.6%) was primarily directed away from shore towards the centre of the marsh. This was most evident in mid-summer (1, 17 July and 14 August 1979).

Many taxa were night active. These included, in decreasing order of abundance, *Hyalella azteca* (Saussure), *Caenis simulans* McDunnough, *Oligochaeta*, *Tanytarsini*, *Cloeon* sp., and *Tanypodinae*. Larvae of two caddisfly species, *Mystacides interjecta* (Banks) and *Agrypnia pagetana* Curtis, were day active. Overall, two species (*Hyalella azteca* and *Caenis simulans*) constituted about a third (31.9%) of the total net catch.

The amphipod, *H. azteca*, occurred most frequently in the nets, constituting 17.6% of all animals. The majority of amphipods were retrieved during one sampling period (mid-July) and, of these, most were immatures moving toward the marsh centre (Fig. 2).

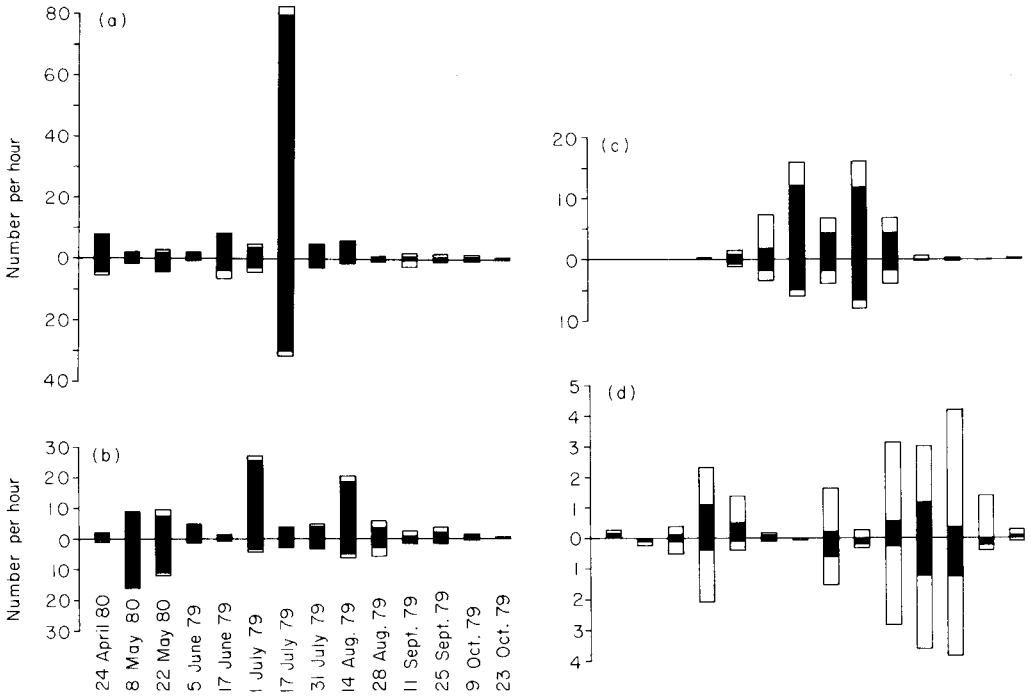


FIG. 2. Total numbers of four species captured in nets per hour moving away from shore (above horizontal line) and towards shore (below horizontal line) for (a) *Hyalella azteca*, $n=2057$; (b) *Caenis simulans*, $n=1678$; (c) *Cloeon* sp., $n=891$; (d) *Mystacides interjecta*, $n=413$. Black and white portions of histograms represent organisms caught in the night and day, respectively.

Mayfly nymphs, *C. simulans*, were more evenly distributed than *H. azteca* in the net catch throughout the sampling programme (Fig. 2). In May (the second and third sampling periods), large, mature nymphs of *C. simulans* moved shoreward. A mass emergence occurred on 30 June 1979 and sporadically thereafter until late September. On 1 July and 14 August 1979 (sixth and ninth sampling periods), large numbers of small nymphs were caught moving towards the marsh centre.

Nymphs of the mayfly *Cloeon* sp. were captured from mid-June to early September, moving primarily toward the marsh centre (Fig. 2). Emergence occurred during the summer months and a swarm of imagoes was noted in late August.

Mystacides interjecta, the most abundant day active organism, constituted a minor component (3.5%) of the total catch. Two seasonal activity peaks were noted (early June and late August to late September, Fig. 2). Emergence occurred in late June.

Factors influencing movement

There were no significant differences ($P>0.05$) in the catches of *H. azteca* or *C. simulans* among the five sample sites during the fourteen sample periods [Friedman's two-way analysis by ranks (date×site); Elliott, 1971]. Day and night catches were analysed separately

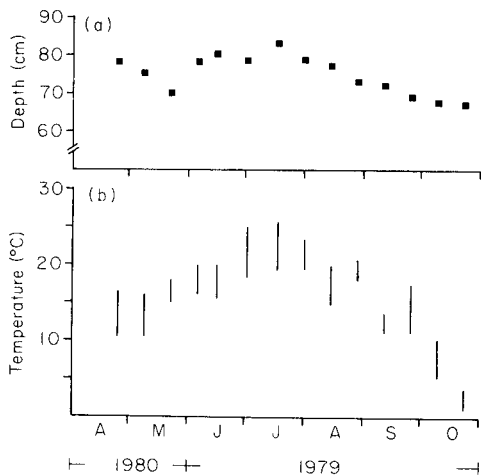


FIG. 3. Shoreline water levels (a) and maximum and minimum water temperatures (b) recorded at fourteen sample periods (24 April to 22 May 1980; 5 June to 23 October 1979).

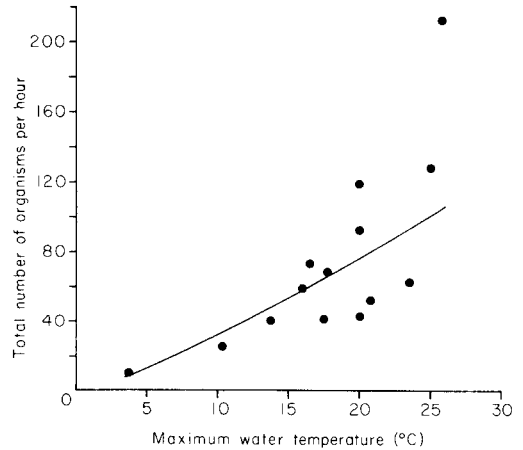


FIG. 4. Relationship between maximum water temperature and the total number of organisms captured per hour for the fourteen sample periods, $Y=1.60 X^{1.285}$.

as were onshore and offshore facing net catches. It was concluded that neither wind nor wave action had any detectable effect on the movement of these major taxa.

Shoreline water level and range of water temperatures recorded during the sampling periods are presented in Fig. 3. Maximum water temperature (25.8°C) was recorded on 17 July 1979. Water level fluctuations were minimal.

A stepwise multiple regression analysis (Draper & Smith, 1966) was used to determine the influence of maximum water temperature, depths at which nets were set and water level on each of four taxa (*H. azteca*, *C. simulans*, *Cloeon* sp., *M. interjecta*) as well as on the total number of organisms captured. All variables were transformed $[\ln(x+1)]$ to equalize variances. None of the factors examined had an effect on movement of individual taxa ($P>0.05$). However, there was a significant positive relationship between maximum water temperature and the total number of animals caught in nets ($R^2=0.58$, $P<0.05$; Fig. 4). Most organisms moved during mid-summer at water temperatures greater than 20°C.

Discussion

Marsh invertebrates appeared to move continually on- and offshore throughout the open water season, particularly during the warm

summer months. Most organisms were active nocturnally, exhibiting directional movements. Patterns of total invertebrate movement were due mainly to two species (*H. azteca* and *C. simulans*) and although movement was associated with the relative stage of invertebrate development, it was not necessarily related to pre-maturation activity.

Most amphipods collected were immatures moving toward the marsh centre. This pattern may reflect dispersal resulting from crowded conditions created by the new cohort. Kajak & Kajak (1975) suggested that dispersal of *H. azteca* from a locale occurs once food resources become limiting. On the basis of benthic samples, Anderson & Hooper (1956) showed that the turnover rate of *H. azteca* was 90% between 22 May and 10 July. They suggested that amphipods may have been moving shoreward during this period.

Invertebrate movement, inferred from changes in benthic density, has been correlated with numerous physical factors including wave action (Moon, 1934), fluctuating water levels (Wesenberg-Lund, 1908; Moon, 1935), water depth (Rawson, 1930; Eggleton, 1931; Thut, 1969; Kajak & Dusage, 1975a, b; Thorp & Diggins, 1982), temperature (Wesenberg-Lund, 1912; Gibbs, 1979), lunar and tidal rhythms (Mileikovsky, 1970) or a combination of these factors. Shifts in zones of invertebrate concentration also have been reported in reservoirs (Nursall, 1952; Fillion, 1967) and presumably are related to fluctuating water levels.

In this study, light phase appears to be the major factor inducing invertebrate movement. Within each light phase, however, none of the physical factors examined affected movement of individual taxa. Because water depth was homogeneous throughout the marsh, rates of temperature change were similar at the marsh centre and nearshore. Maximum water temperature, however, was significantly associated with total invertebrate movement. Although water temperature may affect overall activity, and hence degree of invertebrate movement, it does not appear to control the direction of movement in this marsh.

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