Swimming behaviour in *Monoporeia affinis* (Crustacea: Amphipoda) — dependence on temperature and population density

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Abstract

Swimming speed and swimming activity of the nocturnally active benthic amphipod *Monoporeia affinis* were measured in water temperatures from 3 to 18°C and different population densities in the laboratory. Swimming speed increased with increasing temperature. Increasing water temperature reduced the percentage of active animals in the population, as measured by a “freeze frame” technique. At 7 and 10°C a higher percentage of the population was active in higher animal densities. In all tested conditions swimming activity was highest at about 1 h after light-off and lowest shortly before the predicted time of light-on. The consequences of the documented behavioural responses to environmental stimuli are discussed in relation to population dynamics. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

The ecologically important amphipod *Monoporeia [Pontoporeia] affinis* is a nocturnal swimmer capable of substantial migration. During the day it normally stays burrowed into the bottom mud. Because of its occasionally very high abundance it constitutes an important food source for many fish species (Aneer, 1975). The numbers of *Monoporeia* may oscillate strongly, as described by Segerstråle (1933) and locally the abundance may change rapidly even on a few days scale (Donner et al., 1987). Factors affecting its vertical and horizontal migration have been extensively studied by Donner and
In a laboratory experiment, based on automatic activity counts, Lindström and Fortelius (1992) found both positive thermotaxis and a decrease in activity induced by increasing temperature. Thus increasing temperatures may lead to accumulation of animals.

In this study we document the relation between swimming speed and water temperature. In part, the aim of the study was to exclude the possibility that fewer activity counts in higher temperatures are due to an unexpected decrease in swimming speed. We also re-analysed the original video-recordings from former experiments (Lindström and Fortelius, 1992), for direct counts of the percentage of animals active in different temperatures. In addition we tested the effect of population density on activity in three temperatures.

2. Material and methods

2.1. The animals

Animals were collected with a van Veen bottom sediment grab or with an Ockelmann bottom sledge at about 30 m depth in the Tvärminne Storfjärd basin (part of the Baltic Sea, salinity \( \approx 0.65\% \)) nearby the Tvärminne Zoological Station, where this investigation was performed. They were kept in storage tanks with sediment from the sampling site at \( 3^\circ C \) in darkness until collected for experiments. The experiments took place in a temperature controlled room in a 300 cm long, 35 cm deep and 4.8 cm wide aquarium in demarcated sections separated by latticed walls, thus allowing water from the total volume to pass freely (Lindström and Fortelius, 1992). Flow-through was not used, as that could have introduced not wanted horizontal migration of the animals in the concurrent direction (Lindström, 1991). Only adult animals (length \( \approx 7–9 \) mm) were used. The light regime in the room was a 12:12 h light–dark cycle (L 07:00–19:00). Light intensity and spectral composition at the water surface mimicked the light conditions at about 30 m depth at the sampling locality in the summer at noon: intensity, \( \approx 10^{16} \) qu m\(^{-2}\) s\(^{-1}\), spectral maximum at \( \approx 565 \) nm (Lindström and Nilsson, 1988; Lindström, 2000a,b). The experiments were performed in the autumn, when the animals are most active (Lindström and Lindström, 1980a).

Water temperature was adjusted slowly (\( \approx 0.4^\circ C \) h\(^{-1}\)) by changing room temperature in steps of 3°C. The active cooling from 18 to 3°C at the end of the experiment was completed in 12 h. The temperature was measured with permanently installed thermocouples at three depths in the aquarium. In the temperature experiments the demarcated aquarium section was 36 cm long. The 120 animals in the aquarium corresponded to an animal density of about 6300 m\(^{-2}\). In the density/activity experiment, 190 and 19 animals, respectively, were tested simultaneously in two 25 cm long adjacent aquarium sections. Here the animal densities corresponded to 16 000 and 1600 animals m\(^{-2}\) respectively, which are ecologically relevant densities. Keynäs and Keynäs (1978) found 7000–12 000 ind. m\(^{-2}\) in this area, and Segerstråle (1933)
reported a maximum of 26 000 animals m\(^{-2}\). Andersin et al. (1978) found a long-term abundance cycle lasting 6–7 years and oscillating between about 1000 and 3000 ind. m\(^{-2}\) in the Gulf of Bothnia, and Segerstråle (1937) described a collapse from about 7800 to 100 ind. m\(^{-2}\) in just 4 years time.

2.2. Video recording system

As the animals are nocturnal swimmers, staying in the bottom mud during the day, investigations on its behaviour has to be done using infrared light which is invisible to the animal (Donner and Lindström, 1980). A black-and-white video camera (Javelin J7242X) capable of recording in infrared (IR) was mounted on a wagon moving on rails in front of the aquarium at a focusing distance of 80 cm. The IR light source consisted of four IR emitting diodes (Opto Diode Corp. OD-663, peak emission 880 nm). Additional filters (Schott RG 850, 1% transmittance in 820 nm) cut out the light visible for the animals (Donner and Lindström, 1980; Lindström and Meyer-Rochow, 1987). The IR illumination system could be moved in synchronised motion with the camera above the aquarium. With a “video-limit” device (Lindström and Fortelius, 1992) two contrast sensitive areas could be generated on the video screen. These are subsequently called video sensors. Animals passing a video sensor induced on-off signals which were fed into a computer, (Fig. 1 in Lindström and Fortelius, 1992).

2.3. Swimming speed

The swimming speed of \(M. \text{ affinis}\) was measured from pre-recorded films of the animals swimming behaviour. The speed of single animals was measured in front of a grid of 2 cm squares. Horizontal swims of 10–34 cm with maximum deviation from the horizontal plane by 2 cm were marked on the screen at the squares of beginning and end of the swim. Then the video sensors were moved into the middle of these squares, the video sequence was re-run and the time between the on-signals from the two sensors was recorded. Thus the length of the animal did not influence the measurement. The animals were, however, able to move in a horizontal direction perpendicular to the main path, as the width of the aquarium was 4.8 cm. In case of clear blurring of the image, or clear turns or speed changes, the swim was excluded. For each temperature 34–35 swim paths were recorded. Mean swim path for all recordings was 24.4±5.6 (mean±S.D.) cm. The paths recorded were chosen at about equal numbers from three 15 min recording sessions of each activity period, i.e., 1 h after light-off, at midnight, and 1 h before light-on (below).

2.4. Number of animals active

Lindström and Fortelius (1992) analysed \textit{Monoporeia's} nocturnal swimming activity in different temperatures from video recordings using two vertical 12 mm long video sensors responding to passing animals (see above). The swimming activity of the 120 animals was recorded in IR light for 15 min three times a night; 1 h after light off, at midnight, and 1 h before light-on (Lindström and Fortelius, 1992, Fig. 4). The same
video recordings were now re-analysed manually by counting swimming animals. During each 15 min video recording the video frame was frozen ten times at exactly 60 s intervals, and the animals seen on the still picture were counted.

2.5. Activity level and time of the day

The results from the activity/temperature experiments (Lindström and Fortelius, 1992) were analysed in terms of animals active during each nightly period. The number of animals swimming were counted using the freeze method. The average number of animals (ten “freeze-counts”) for the three periods of each night were pooled and the mean number of animals of each period was then expressed as a percentage of the total activity. In Fig. 3 the results from the 20 days of recording were averaged.

2.6. Percentage of animals active in different densities

Two adjacent sections of the aquarium, containing 19 and 190 animals respectively, were recorded simultaneously on video twice a day at 00:30 and 12:30 for 27 days. Length of recordings was 15 min, light period was between 08:30 and 20:30. The numbers of actively swimming animals were counted using the video freeze method described above, at 3, 7 and 10°C. For 3°C, 70 still frames were analysed, for 7 and 10°C, 100 frames each. For technical reasons, the video view did not cover more than 61 and 72% of the areas of the sparse and dense sections respectively in this experiment. The numbers of animals active were thus calculated from the numbers seen, correcting for the reduced field sizes.

3. Results

3.1. Swimming speed

The swimming speed of the animals was strongly affected by changing temperature. At the lowest temperature, 3°C, the average speed in horizontal direction was 3.81±0.47 cm s⁻¹ (N = 34). By increasing temperature the speed increased to 5.59±0.66 cm s⁻¹ at 18°C (N = 35) (Fig. 1). The speed increase followed a logarithmic function, y = 2.83 + 2.10 Log x (F = 314.22, P < 0.0001). The shape of the curve indicates that maximum speed still has not been reached at 18°C. Mature males occasionally made extremely fast short rushes (up to 12 cm s⁻¹). The fast swims were recorded over short distances, mostly deviating from the horizontal direction. They were not included in the averages above. At none of the tested temperatures did the swimming speeds differ between the three nights.

3.2. Number of animals active in different temperatures

At the beginning of the experiment about 30 of the 120 animals were swimming actively in 3°C. By increasing temperature from 3 to 6°C and further to 9°C, the number
of swimming animals decreased. A subsequent temperature increase to 12, 15 and 18°C did not depress the number of active animals further (Fig. 2). On the day between night 17 and 18, temperature was lowered to 3°C degrees again. This resulted in an almost instant increase in number of swimming animals back to (and slightly over) the initial number at the beginning of the experiment.

3.3. Activity and time of day

The results in Fig. 2 were pooled in terms of recording period of the day. Of the three recording periods, the activity was in most cases highest during the period 1 h after light-off, decreasing towards midnight. The activity, calculated as a percentage of the total activity recorded, was lowest during the period 1 h before light-on (Fig. 3).

3.4. Effect of population density

The percentage of animals swimming at 3, 7 and 10°C was measured at two population densities, 1600 and 16 000 animals m⁻². No animals were seen during the light period. In darkness more animals were active in the higher density at a given
Fig. 2. Number of animals active at different temperatures. Each point represents the mean of ten observations±S.D. Filled circles, 1 h after light-off, open, at midnight, and half-filled, 1 h before light-on.

At 7 and 10°C the difference was statistically significant (Mann–Whitney, \( P = 0.0199 \) and 0.0001, respectively).

4. Discussion

4.1. Swimming speed

Current velocities of 10–20 cm s⁻¹ are not uncommon along the coast of the Baltic Sea (Laakkonen et al., 1981). Donner et al. (1987) got high numbers of *M. affinis* in a trap standing on the bottom at times of falling sea water level in a bay. This indicated a passive transport of the animals with the outgoing current. They mentioned that a water current of 20 cm s⁻¹ would transfer a passively floating *Monoporeia* a distance of 720 m h⁻¹. Lindström (1991) found that *Monoporeia* migrates in a concurrent direction at least in current speeds, lower than 0.37 cm s⁻¹ (0.22 m min⁻¹) at 10°C. In the present study, the animal’s swimming speed at 10°C was about 4.9 cm s⁻¹. Active migration towards the current would in that case decrease the unintentional “backward” distance to about 544 m. At 18°C the hypothetical distance would shrink to 518 m. However, at 9–18°C very few animals were swimming (Fig. 2). At the low speed currents (0.37 cm s⁻¹)
tested by Lindström (1991), the animal’s concurrent migration was seen clearly only at moments of descending into the bottom mud at, or slightly before, light-on. Because the concurrent migration seemed to be locked to the time of descent only, there is still a considerable risk for a population to be carried away by water currents. So far it is not known how *Monoporeia* reacts to currents stronger than 1.3 cm s\(^{-1}\) (Lindström, unpublished), at which speed the animals had no difficulties to remain in an upstream direction. Theoretically, at 3\(^{\circ}\)C the animals should be able to withstand a current of 3.8 cm s\(^{-1}\) and at 18\(^{\circ}\)C about 5.6 cm s\(^{-1}\) if swimming continuously.

In late autumn, pregnant females almost cease to swim while the males swim almost continuously (Lindström and Fortelius, 1992). Their mostly irregular swimming paths and the position of the antennae extended in four directions indicate that the males try to cover as large a water volume as possible in search for females (unpublished observations). It is, however, not possible to compare the swimming speeds of males and females during other than the breeding seasons, because the males cannot be distinguished from the females until after the last or the last but one moult before maturation (Segerstråle, 1950).

Part of the explanation for the reduced swimming speed in low temperatures may be found on cell membrane level. Kivivuori and Lagerspetz (1982) showed that both the rising and the falling phases of the action potentials in medial giant axons from crayfish
became slower with decreasing temperature. This might well slow down the onset of the next action potential, which might affect the swimming speed. There is also an alternate explanation. The viscosity of water changes with temperature. At 3°C it is about 150% of that at 18°C in Antarctic waters (Macdonald and Wells, 1991; Macdonald, personal communication). The smaller an organism, the more water viscosity will affect its locomotion. *M. affinis*’ average swimming speed at 18°C was indeed 147% of that at 3°C.

4.2. Number of animals active, and activity per animal in different temperatures

At higher temperatures, fewer amphipods were swimming (Fig. 2). Unfortunately it was not possible to tell if the same animals were active from night to night. The recovery of swimming activity to the initial level at 3° after a 14-day period of temperature raised in steps showed that the animals had not been harmed by the high temperature, at least on a short time scale. At the beginning of the experiment, about 25% of the 120 animals were active. Lindström and Lindström (1980a) reported that in most cases about 50% of the animals were actively swimming at 4°C during the first half of the night. Their experimental set-up was however different and the observations were not quantified. Marzolf (1965) reported that at most, 7.4% of Lake Michigan *Ponto poreia hoyi* became pelagic at any one time (Segerstråle, 1977).

The present results confirm the claim by Lindström and Fortelius (1992) of a reduced part of the population swimming at higher temperatures.
4.3. Activity and time of the day

The nocturnal activity was highest during the first of the three recording periods, 1 h after light-off (Fig. 3). Lindström and Lindström (1980a) recorded the swimming activity of *M. affinis* hour by hour during different seasons. They found an inherent change in the nocturnal activity pattern during the seasons depending on the natural light cycle, that continued also in the laboratory although the light:dark (L:D) cycle was retained at 12:12 h. The natural light cycle changes from L:D 18:6 by mid-summer to L:D 6:18 by mid-December at the Tvarminne Zoological Station (59° 50’ N 23° 15’ E). The activity pattern found in the present investigation is similar to the pattern of October swimming in *M. affinis* (Lindström and Lindström, 1980a,b; Fig. 4). They found that the activity was highest 1–2 h after light-off, depending on a readiness to swim immediately after light-off. This was explained as an endogenous expectation of short days in late autumn. On the other hand the onset of swimming was very much slower in summertime, with a short activity maximum and an activity decrease starting several hours before light-on. This was considered an adaptation of the endogenous rhythm to expected short nights in the summer (Lindström and Lindström, 1980a,b). Activity changes depending on the natural light cycle and the changes in the daily activity cycles stress the necessity to standardise experimental observation to season and time of the day in *M. affinis*, and probably also in other animals.

4.4. Population density and effect of temperature changes

The percentage of the population active depended on population density. As temperature was increased, leading to fewer active animals, the activity decrease was smaller in the higher population density (Fig. 4). The number of animals per sediment surface area increased the probability of nocturnal activity in *M. affinis*. The mechanism for this might be increased levels of social facilitation or other expressions of physical disturbance and crowding. *M. affinis* migrates in the direction of higher temperature when descending to the bottom at, or just before light-on (Lindström and Fortelius, 1992). This behaviour may lead to increased population density in the direction of higher temperature, which, in turn, enhances swimming activity. Together with the increased swimming speed these factors may all support migration in the direction of “warmer”. *M. affinis* is known to migrate upwards in the sediment when disturbed, while the co-occurring amphipod *Pontoporeia femorata*, tends to burrow deeper upon disturbance (Hill and Elmgren, 1987). Both species feed almost exclusively on organic matter in the uppermost centimetre of the sediment (Lopez and Elmgren, 1989). High population densities will decrease the amount of food available in the surface layer, which also might induce increased swimming activity in search for spots of higher nutritional value. Marzolf (1965) showed a positive correlation between the abundance of *Pontoporeia hoyi* and the amount of bacterial organic matter in the sediments of Lake Michigan. Lindström (unpublished) noted that *M. affinis* may even become day-active if the population density becomes very high. Unsuitable bottom substratum and increased salinity have also been shown to induce day-time swimming in *M. affinis* (Lindström and Lindström, 1980a,b; Lindström and Fortelius, 1992).
Individuals of *M. affinis* clearly have the capacity for behavioural responses to changes in local conditions. Both phenological and stochastic phenomena lead to measurable responses at the population level. The characteristic endogenous diurnal activity rhythm of this species seems to be tuned to a variety of environmental stimuli in a highly sophisticated manner. One interesting example is the almost 50% increase in swimming speed corresponding to a rise in water temperature from 3 to 18°C, which indicates a dramatic variation in the migratory potential of *M. affinis*.

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References


