University of Groningen

Moving (in) water

van Duren, Luca Ancel

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2000

[Link to publication in University of Groningen/UMCG research database](#)

The copepod *Temora longicornis* Müller

The calanoid copepod *Temora longicornis* (Müller) is one of the most abundant copepod species in temperate waters of the northern hemisphere. Like most calanoids, it creates a feeding current with which it perceives food and draws food towards the mouth appendages. Swimming and feeding are therefore closely linked. *T. longicornis* is often described as a herbivorous filter feeder, foraging mainly on unicellular algae, but field studies have also indicated that *T. longicornis* can switch to a carnivorous mode. In laboratory cultures *T. longicornis* thrives best on a mixture of different algae and larger heterotrophic flagellates.

Its life cycle comprises 12 instars, 6 nauplius larvae and 6 copepodid stages, C6 being the adult. The nauplii differ from the copepodids not only in size and morphology but also in swimming behaviour.

Feeding

Behaviour in response to different food concentrations

The routine swimming mode, which is linked to feeding in all but the first nauplius stages of the copepod *T. longicornis*, differs between the nauplii and the copepodids. The nauplii swim intermittently, alternating between short swimming bouts (0.6 - 5 s) and short pauses (0.4 - 4.3 s). The swimming behaviour of the smallest feeding stage (N2) is not affected by the concentration of food in the environment. The largest nauplius stages react to an increased food concentration by increasing the percentage of time spent swimming.

All copepodid stages move their feeding appendages nearly 100% of the time. These instars can therefore only increase their feeding effort by increasing their limb beat frequency, and hence their swimming speed. At very low and at extremely high food concentrations, adult females show low swimming speeds, while showing increased swimming speeds at intermediate concentrations. This response agrees with expectations based on the optimal foraging theory. Males behave differently from the females. Not only is their average swimming speed higher at similar food conditions, but they also maintain a very high swimming speed at very high food concentrations. Neither the males nor females showed any obvious differences in turning behaviour at different food concentrations.

Kinematics

High speed film recordings at 500 frames s⁻¹ of the motion pattern of the feeding appendages and the escape movement of the swimming legs revealed that the two swimming modes are essentially very different. While foraging, the first three mouth appendages (antennae, mandibular palps and maxillules) create a backwards motion of water with a metasynchronous beating pattern, while the maxillae and the

---

maxillipeds face th
maxillule. On avera

Hydrodynamic ana

Particle In
image of the flow g
longicornis. By sca
velocity and veloci
laminar, and was
laterally, with high
feeding appendage
morphology of the
the antennules, whi
which could interfe

In both th
resembles that of
copepodid (C1) are
the steepness of the
relationship was fou
on the contrary, sh
increasing body siz
also relative to body
the smaller copepo

Energetic cost of t

The energ
the energy dissipati
varied from 3.43 10
copepods. Both nau
with increasing bo
nauplii. The copep
energetic cost of th
the regression line
energetic cost of th
total energy budget

maxillipeds face the opposite direction, the maxilla being in counter phase with the maxillule. On average, limb beat frequencies of around 40 Hz were measured.

Hydrodynamic analysis of the feeding currents

Particle Image Velocimetry was used to construct a quasi 3-dimensional image of the flow generated by the feeding appendages of the different instars of *T. longicornis*. By scanning layers of flow, detailed information was obtained on flow velocity and velocity gradients. The flow around adult feeding *T. longicornis* was laminar, and was symmetrical viewed dorsally, but highly asymmetrical viewed laterally, with high levels of vorticity on the ventral side. The flow rate through the feeding appendages varied between 77 and 220 ml day^{-1} per individual. The morphology of the flow field ensured that water was entrained over the full length of the antennules, while the antennae were kept out of areas with high velocity gradients which could interfere with distant mechano- or chemoreception.

In both the nauplii and the copepodids, the general shape of the flow field resembles that of the adult stages. The last nauplius stage (N6) and the smallest copepodid (C1) are similar in size. For these instars the size of the feeding current and the steepness of the velocity gradients were very similar. In the nauplii no significant relationship was found between the volume of influence and body weight. Copepodids, on the contrary, show a very steep increase in volume of the feeding current with increasing body size. The slope of this regression line is greater than 1, indicating that also relative to body weight, larger copepodids have a larger volume of influence than the smaller copepodid stages.

Energetic cost of the feeding current

The energetic cost of the feeding current could be estimated on the basis of the energy dissipation due to viscous friction in the feeding currents. Dissipation rates varied from 3.43 10^{-13} W for the smallest nauplii to 2.55 10^{-10} W for the largest adult copepods. Both nauplii and copepodids tended to an increase in energy dissipation rate with increasing body weight, although this correlation was not significant for the nauplii. The copepodids showed a much steeper and very significant increase in energetic cost of the feeding current with increasing body weight. This relation fitted the regression line log(P) = -11.99 + 1.61*log(AFDW). For all instars the total energetic cost of the feeding current amounted to only a very small percentage of the total energy budget.

Predator avoidance and escape

Avoiding detection

Swimming behaviour of adult female and adult male instars was tested in clean water in the presence of food algae and in water from an aquarium with planktivorous fish (grey mullet, *Chelon labrosus*). The water from the aquarium with the fish had a considerable effect on the swimming behaviour of the copepods. Both males and females show much lower swimming speeds in fish water compared with clean water. In clean water the males swim significantly faster than the females, while in fish water, both males and females show an average swimming speed of about 2.5 mm s^{-1}. Female copepods that have been starved for 18 - 24 hrs still show a significant decrease in swimming speed in fish water. However, the starved females do not reduce their swimming speed as far as the non-starved animals.

Avoiding capture

All instars of *T. longicornis* show very rapid escaping behaviour. The smallest stages (N1 and N2) can reach escape speeds of 15 - 32 mm s^{-1}, corresponding to 90 - 189 body lengths per second. The largest nauplii and the smallest copepodids on average reach escape speeds of 33 mm s^{-1} (90 body lengths s^{-1}). C1 instars show on average slightly slower escape responses than the similar sized N6, with speeds ranging between 15 and 39 mm s^{-1} (45 -119 body lengths s^{-1}).
Adult *T. longicornis* can reach escape velocities of over 100 mm s^{-1}, ranging between 34 and 143 body lengths s^{-1}.

Nauplii have only three pairs of appendages with which they have to perform both the feeding motion as well as escape responses. The copepodids perform their high speed evasive movements with the swimming legs. The kinematics and the co-ordination of the escape motion is quite different from the beat pattern of the feeding appendages during routine swimming. During escape movements the mouth appendages stop moving and the large antennules are folded backwards, resulting in a streamlined body shape. The appendages move metachronally (beating in an adlocomotor sequence) only during the power stroke. The recovery stroke is synchronised. Of the four normal sized swimming legs, p4 is the first to start the power stroke, when it has completed its power stroke and has reached its extreme posterior position, p3 starts and completes its power stroke, then p2 and finally p1. When p1 has reached its extreme position, all four swimming legs start the combined recovery stroke, which is much slower than the individual power strokes. During escape responses, beat frequencies of the swimming legs between 44 and 117 Hz were measured. The maximum tip speed of the feeding appendages during routine swimming is similar during the power stroke and the recovery stroke, while during the escape response the power stroke of an individual leg is faster than the recovery stroke.

174

While the feeding current around a copepodid remains stable for a long time, the escape response produced with the swimming legs is highly unstable. During escape responses in adults a vortex ring appears behind the animal, which dissipates over time. Several seconds after cessation of swimming leg movement an enlarged volume of influence and an increased rate of energy dissipation can still be measured. The formation of a vortex ring behind the moving limbs indicates that this type of locomotion is based on inertia. During escape responses the rate of energy dissipation due to viscous friction increases by up to two orders of magnitude compared to foraging, and the average amount of power delivered by the swimming legs is 60 - 400 times higher than during foraging.

As mentioned earlier, the escape velocities of the similar sized N6 and C1 are of the same order of magnitude. Reynolds numbers associated with escape swimming in these stages range around 10. However, very marked differences are found in the flow morphology of the escape responses of these two stages. The flow around the escaping nauplius is essentially similar to the feeding current. The velocities are higher and the velocity gradients are larger, but the shape is the same. The flow around an escaping copepodid resembles that of the adults in the formation of a vortex ring. It appears that the first copepodid stage of *T. longicornis* is not quite large and fast enough to efficiently employ an inertia based swimming mode. This leads to the hypothesis that other aspects of copepodid morphology must offer sufficient advantages to outweigh the disadvantages of the relatively poor escaping performance, and increased detection risk, of this stage.

Mate seeking

Behavioural responses to pheromones

Studies by other researchers (e.g. Doall *et al.*, 1998) have shown that male *T. longicornis* are able to pick up and trace the chemical trails from females up to several seconds after the female has passed through. This is now thought to be the most important system of mate location. However, the experiments described in this thesis have revealed that *T. longicornis* adults also show other types of behaviour that eventually may lead to an increased encounter probability between males and females.

The fact that males swim faster than females may be linked to a mate seeking strategy, with the female behaviour geared towards optimising food intake and the males investing more energy in searching and risking higher probability of encountering a predator. The males showed a reduction in the frequency of escape behaviour in water with female pheromones present and even more so in the presence of females. Females were shown to react to the smell of males with little "hops", quite distinct from both their normal smooth swimming motion and escape responses. These hops are likely to be signals intended to increase the encounter probability with males.

175

Hydrodynamic properties of the signal produced by hops

Laser sheet Particle Image Velocimetry was used to investigate the flow fields associated with hops as produced by adult females in response to male pheromones, and compared these to the flow of the feeding current of an adult female. During and immediately after a hop the flow field around the copepod shows a marked difference from that of a foraging animal. During foraging, the highest velocity gradients are located around the feeding appendages of the copepod. During a hop, high velocity gradients are located behind the animal. About 0.5 s after the start of swimming leg movement, effects of the hop have virtually dissipated and the flow field resembles that around a foraging animal.

The estimated volume of influence of the individual investigated increased about twelve fold during the hop compared with the situation around a foraging animal. Since the volume of influence around a hopping copepod is not spherical, but extends much further backward than forward, the distance from the animal to the edge of the volume of influence can be increased about four fold. Assuming this can be translated into an increase in detection distance of a similar order of magnitude this would lead to a 16 fold increase in encounter probability. The signal would of course also create additional risk of being noticed by a predator. Furthermore the rate of viscous energy dissipation within the copepod's volume of influence increased nearly 80 fold. Hops may therefore serve to increase encounter probability, but due to the short duration of the effect and high costs and risks they would only be adaptive when other cues have indicated that suitable sexual partners are in the vicinity. The fact that females increase their frequency of hops in response to male pheromones indicates an active form of communication among copepods.

176