Swimming behaviour of developmental stages of the calanoid copepod *Temora longicornis* at different food concentrations

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ABSTRACT: The swimming behaviour of developmental stages of the marine calanoid copepod *Temora longicornis* was studied using 2-dimensional observations under a microscope and a 3-dimensional filming technique to analyze swimming mode, swimming speed and swimming trajectories under different food concentrations. The nauplii swam intermittently in a stop-and-go fashion. The swimming behaviour of the smallest feeding stage (N2) did not change with different food concentrations. The largest nauplius stages reacted to an increased food concentration by increasing the percentage of time spent swimming. All copepodid stages swam continuously, their mouthparts moving nearly 100% of the time. Copepodids can therefore only increase their feeding effort by increasing their limb beat frequency. Adult females showed low swimming speeds at very low food concentrations, higher swimming speeds at intermediate concentrations and low swimming speeds at very high food concentrations. This agreed with expectations based on the optimal foraging theory. Males behaved differently from the females. Not only was the average swimming speed of males higher at similar food conditions, but they also maintained a very high swimming speed at very high food concentrations. This increased swimming activity in the males may be linked to a mate seeking strategy. Neither males nor females showed any obvious differences in turning behaviour at different food concentrations.

KEY WORDS: Copepods · Swimming behaviour · Instars · Food concentration · Searching strategy · *Temora longicornis*

INTRODUCTION

Copepod feeding behaviour has been shown to be a complex process with large differences among species and even differences among individuals of the same species (Price 1988, Paffenhöfer 1994). Copepods are able to perceive food quality and quantity through chemo- and mechanoreception and are able to modify their mode of feeding and the intensity of their movements according to this information (DeMott 1990, Vanderploeg et al. 1990).

The calanoid copepod *Temora longicornis* (Müller) is not only very abundant in temperate waters of the northern hemisphere, it is also of great ecological sig-

nificance in many areas. It represents 35 to 70% of the total copepod population in the southern bight of the North Sea (Daan 1989), and in Long Island Sound, USA, *T. longicornis* is able to remove up to 49% of the daily primary production (Dam & Peterson 1993). 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 small algae and its feeding apparatus is thought to be consistent with this description (Tiselius & Jonsson 1990.) But field studies have also indicated that *T. longicornis* can switch to a carnivorous mode when necessary, e.g. during a *Phaeocystis* bloom (Hansen & van Boekel 1991, Fransz et al. 1992). Kleppel (1993) found that

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although the largest part of the diet of this species consisted of algae, the proportion of microzooplankton in the diet is larger than the proportion found in the environment, suggesting that *T. longicornis* has a positive preference for this type of food. This finding seems to be consistent with the ideas of Gerritsen & Strickler (1977), who concluded that cruising predators hunting for slowly moving prey would probably be versatile in their hunting techniques and should be able to adopt other modes of prey capture depending on the amount and type of available prey.

In laboratory cultures *Temora longicornis* thrives best on a mixture of different algae and larger heterotrophic flagellates (Klein Breteler & Gonzales 1986).

An efficient feeding strategy should involve maximizing the probability of encountering food. Gerritsen & Strickler (1977) found that 3 factors influenced encounter probability: (1) The encounter radius: copepods can probably influence their perception range by varying the flow field created with their mouth appendages. (2) Swimming speed: a higher swimming speed increases encounter probability. Copepods can either move their appendages faster or slower or vary the time they spend swimming or not swimming. (3) The concentration of food items in the environment: although copepods cannot alter the food concentration in their environment directly, they can decide to stay in a particular profitable area by following a complex swimming path, or to leave a patch by swimming straight out of it (Buskey 1984).

With a model based on optimal foraging theory, Lehman (1976) predicted a low filtering rate at very low and at very high food concentrations, with higher filtering rates at intermediate concentrations. The idea is that foraging animals in an environment with a low food concentration should adopt an energetically inexpensive foraging strategy. At higher food concentrations they can afford to adopt a more expensive but also more rewarding searching strategy. When the encounter rate with food becomes higher than the maximum ingestion rate the filtering rate should also go down. Yule & Crisp (1983) found that *Temora longicornis* had a higher limb beat frequency in the presence of algae than in filtered sea water Dam (1986) showed that for *T. longicornis* clearance rates are indeed reduced at higher food concentrations. For *Acartia tonsa* clearance rates peak at a particular food concentration and are lower at both low and very high food concentrations (Kiørboe et al. 1985).

Most studies concerned with feeding behaviour of copepods have been carried out with adult females. Those studies of different developmental stages indicate that there are considerable differences in food intake (Klein Breteler & Gonzales 1986) and selectivity (Berggreen et al. 1988, Swadling & Marcus 1994). This indication has large implications because the concentrations of subadults are higher than adult *Temora longicornis* (Daan 1989, Fransz et al. 1992).

In this study, swimming behaviour of different stages of *T. longicornis* was analyzed under 2 different food concentrations. In addition, the swimming behaviour (speed and path) of adult males and females was analyzed under 5 different food concentrations; the results are compared to theoretical predictions on optimal foraging as well as to the results of other experimental work.

MATERIAL AND METHODS

Temora longicornis was cultured in the laboratory as described by Klein Breteler (1980). All stages were fed on algae from continuous cultures, either *Dunaliella tertiolecta* (7 μm diameter) or a mixture of *Rhodomonas* sp. (7 μm) and *Isochrysis galbana* (5 μm). The larger hetrotrophic flagellate *Oxyrrhis marina* (13 μm) was present in the culture as an additional food source. Culture temperature was 15°C. Concentration of cells in the cultures was regularly checked by microscopic counts.

To study swimming behaviour of the different stages at high enough magnification to enable appendage movements to be observed, a black and white video camera fitted with a 35 mm macro lens and either a 15 or a 20 mm extension ring was mounted over a Petri dish (Ø 9 cm, depth 1.2 cm). The volume of water in the petri dish was not restrictive for the movement of the nauplii and younger copepodids; 1.2 cm is about 30 body lengths for a C1, the largest instar tested in this set-up. Illumination was provided by a cold light source (150 W). The camera could be moved by hand to follow individuals over a limited range. The behaviour of swimming copepodids and nauplii was video recorded (Sony U-matic SP).

The video tapes were subsequently analyzed using an event recorder developed in the laboratory of the Dept of Marine Biology at the University of Groningen, Haren, The Netherlands. This event recorder is fitted with 16 keys; each key can be set to code for a particular behaviour Every time a key is pressed the time is registered with an accuracy of up to 0.1 s. The event recorder is capable of storing up to 2500 events. Behaviours were considered to be mutually exclusive.

To analyze the swimming speed and trajectory of free swimming copepods in 3 dimensions, a filming set-up was constructed based on the apparatus used by Ramcharan & Sprules (1989) Through a set of mirrors 2 orthogonal views of an aquarium (10 × 10 × 12 cm), representing the *x-z* and *y-z* plane, were pro-
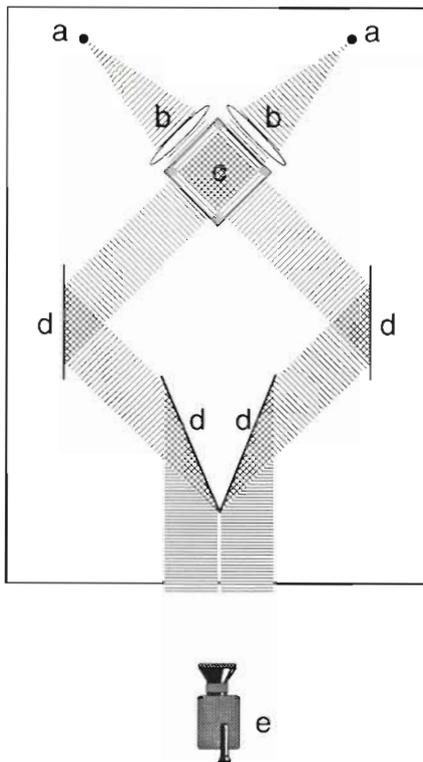
Fig. 1. Schematic overview of the 3-dimensional experimental set-up. (a) Infrared LEDs, (b) lenses, (c) aquarium, (d) surface mirrors, (e) video camera

jected into the lens of a high resolution black and white video camera (Fig 1). Illumination was provided by 2 high output infrared LEDs ($\lambda = 880$ nm) to which the copepods did not show any behavioural response. The LEDs were placed in the focus of 2 large diameter lenses ($\varnothing$ 10 cm), each creating a parallel light beam through the aquarium into the camera. This resulted in an image with the animals showing up as black dots against a light background.

Swimming behaviour of copepods was recorded on video tape (Sony U-matic SP) at a rate of 50 half frames s^{-1} and these tapes were subsequently analyzed frame by frame using an image processing package for IBM-PC (TIM). This software package digitizes video images, divides each image into 768×512 pixels and assigns horizontal and vertical coordinates to each pixel. Software programs were developed to automatically trace the black dots, representing the silhouettes of animals, frame-by-frame, and to store the x-z and y-z coordinates. After every filming session a reference grid was recorded to measure the scale of distances in every direction.

To calculate the average swimming speed of a copepod, instantaneous velocities in every direction were calculated every 0.02 s using Lagrange's 5 points differentiation formula:

$$\frac{\mathrm{d}x}{\mathrm{d}t_{(t=n)}} = 50\left(\frac{1}{12} x_{(n-2)} - \frac{2}{3} x_{(n-1)} + \frac{2}{3} x_{(n+1)} - \frac{1}{12} x_{(n+2)} \right) \ (1)$$

The velocity in the x direction was estimated to be the mean value of 5 $\mathrm{d}x/\mathrm{d}t$ values around $t = n$ (Videler 1981). This calculation was repeated for the y and z directions.

From the swimming speed records the average swimming speed per individual was calculated.

As a measure of turning behaviour, the net to gross displacement rate (NGDR), the ratio of the linear distance between the beginning and end of a swimming path to the total distance travelled (Buskey 1984), was calculated.

Experimental procedures. *Comparison of different stages:* The swimming modes of N2, N6, and C1 were studied at 2 food situations: 0 and 10^7 *Rhodomonas* sp. cells l^{-1}. The copepods were sorted under a dissecting microscope and left to acclimatize for at least 15 min prior to filming, which was assumed to be sufficient for them to adapt their behaviour to the circumstances (Gill & Harris 1987). Both sorting and filming were carried out at 15°C.

The event recorder was set to encode for the following behaviours: 'swimming' (i.e. relatively slow continuous movement created with the mouth appendages), 'pause' (no movement of appendages, specimen sinking passively), 'jump' (i.e. very rapid movement lasting only a few tenths of a second; copepodids use their swimming legs for this) and 'not visible' (i.e. specimen temporarily out of range or out of focus of the camera). Every individual was followed for at least 30 s and for up to 2 min.

From the event recorder registrations the following parameters were calculated: the proportion of time the individual spent swimming (corrected for the time 'not visible'), the average bout length of the behaviours 'swimming' and 'pause', and the frequency of 'jumps'.

Average swimming speeds of different developmental stages were determined in the 3-dimensional set-up at 1 food concentration. All specimens came from the same copepod culture and all experiments were carried out within a few days to avoid differences in feeding history. Individuals were selected under a dissecting microscope; about 15 of the juvenile stages and 8 to 10 adults per experiment. Algae (*Dunaliella tertiolecta*) were added to 1 l of (0.45 µm) filtered seawater to obtain a concentration of 10^7 cells l^{-1} (ca 300 µg C l^{-1}). The animals were left in the filming set-up to acclimatize for about 15 min prior to filming. Average swimming speeds were calculated over sequences of 250 half frames. The number of sequences analyzed was 10, 19, 21, 11 and 14 for N2, N6, C1, adult females and adult males respectively.

Behaviour of adults at different food concentrations:
Swimming behaviour of adult females and males was studied at 5 different food concentrations, ranging from 0 to 10^8 cells l^{-1}. To avoid effects of feeding history, all the experiments for one sex were carried out within 3 d. The experiments were carried out with the same algae as were present in the copepod cultures. For the females this was *Dunaliella tertiolecta* and for the males this was *Rhodomonas* sp.

For each experiment groups of 8 to 10 females or males were selected and left in filtered seawater for 15 min to acclimatize. Subsequently algae were added to the desired concentration and the animals were left for another 15 min prior to filming. Per experiment at least 7 sequences of 400 half frames minimum were analyzed to calculate NGDR and 15 sequences of a minimum of 100 half frames were analyzed to calculate average swimming speed. The experiments with the males were carried out in duplicate.

RESULTS

Comparison of the swimming mode during feeding of different stages

The nauplius stages swam in a stop-and-go fashion. They alternated between short swimming bouts (0.6 to 5 s) and short pauses (0.4 to 4.3 s). The largest nauplius stages reacted to a situation with a higher food concentration with an increase in the proportion of time they spent swimming (Table 1). These stages achieved this by increasing the average length of the swimming bout (Table 2), while the 'pause' bouts stayed the same (Table 3). The smallest nauplii did not significantly alter their swim-to-pause ratio. Contrary to the N6 they showed longer swimming bouts in the no-food situation, but this was compensated for with longer pause bouts so the ratio stayed the same. However, the difference in swimming bout length was not significant ($\alpha = 0.05$, Mann-Whitney U-test). The most obvious change in feeding behaviour during ontogeny coincided with the most dramatic morphological change. C1 showed the same continuous swimming mode which has already been described for the adults (Tiselius & Jonsson 1990) at both food conditions (Table 1). In the no-food situation the animals occasionally showed pauses (Table 3), which accounted for the significant difference in the proportion of time spent swimming These pauses, however, were so infrequent that we could not speak of a stop-and-go swimming mode. In most protocols no pauses were observed. For an estimate of the average pause bout length, only the protocols where animals showed pauses could be used. At the higher food concentra-

tion only 2 individuals showed 1 very short pause. This makes a statistical comparison of the bout length of pauses impossible.

In all stages of *Temora longicornis* investigated, 'jumps' occurred very infrequently and appeared to be mainly escape reactions to encounters with other animals or objects such as the side of the Petri dish. Since this behaviour did not appear to be directly linked to feeding, it is omitted from further discussion.

No difference could be detected in overall swimming speed in any of the investigated juvenile stages in the 3-dimensional set-up. Their swimming speeds all ranged around 1.5 mm s^{-1}. There was however a significant difference in swimming speed between adults and younger stages, and among adults between males and females (Fig. 2) (Mann-Whitney U-test, $\alpha = 0.05$). The males swam significantly faster than the females.

Table 1 *Temora longicornis*. Proportion of time spent swimming (SE)

	0 cells l^{-1}	n	10^7 cells l^{-1}	n	p[*]
N2	0.573 (0.038)	21	0.555 (0.028)	28	ns
N6	0.575 (0.024)	22	0.687 (0.028)	20	p < 0.01
C1	0.965 (0.017)	17	0.996 (0.003)	20	p < 0.05

[*]Two-tailed probability, Mann-Whitney U-test, $\alpha = 0.05$

Table 2. *Temora longicornis*. Swimming bout length (SE) of nauplii. C1 not included since in most cases swimming bout length exceeded protocol length

	0 cells l^{-1}	n	10^7 cells l^{-1}	n	p[*]
N2	2.551 (0.302)	21	1.747 (0.138)	28	ns
N6	1.520 (0.098)	22	2.297 (0.248)	20	p < 0.01

[*]Two-tailed probability, Mann-Whitney U-test, $\alpha = 0.05$

Table 3. *Temora longicornis*. Pause bout length

	0 cells l^{-1}	n	10^7 cells l^{-1}	n	p[*]
N2	1.566 (0.212)	21	1.248 (0.120)	28	ns
N6	1.112 (0.103)	22	0.889 (0.074)	20	ns
C1	1.400 (0.441)	6[a]	0.225 (0.125)	2[a]	–

[*]Two-tailed probability, Mann-Whitney U-test, $\alpha = 0.05$
[a]Only protocols with pauses could be included. In the majority of the protocols no pauses occurred. Sample size too low for statistics

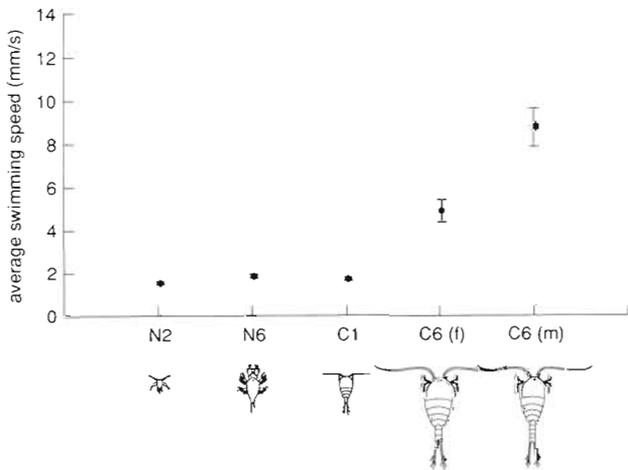Fig. 2. *Temora longicornis*. Average swimming speed of different instars at a food concentration of 10^7 cells l^{-1}. Error bars indicate SE

Behaviour of adults at different food concentrations

Female *Temora longicornis* behaved much in the way that was expected on the basis of optimal foraging theory (Fig. 3a). At very low and at extremely high food concentrations the average swimming speed was significantly lower than at intermediate concentrations. The differences between the intermediate concentrations (10^5, 10^6, and 10^7) were not significant (Mann-Whitney U-test, $p < 0.05$), while the difference between concentration 0 and the intermediate concentrations, as well as the difference between concentration 10^8 and the intermediate concentrations, were significant. The males, however, showed a slightly different picture (Fig. 3b). Their average swimming speed was significantly lower at concentration 0, but there were no significant differences at the higher food concentrations. The distribution of the swimming speeds of the males showed a very marked change. At lower food concentrations (0 and 10^5) the distributions of the swimming speeds did not differ significantly from a normal distribution (χ^2-test, $\alpha = 0.05$), but at higher food concentrations (10^6 and 10^7) the frequency distribution histogram showed 2 very distinct peaks (Fig. 4), although the picture at 10^8 was less clear. Animals were either fast or slow, but very few swam at an intermediate swimming speed. Although the average swimming speed for males at food concentrations 10^5 and 10^7 cells l^{-1} were very similar, there seemed to be a difference in behaviour between the 2 food concentrations. This phenomenon was absent in the females.

Neither in the males nor in the females could any effect of food concentration on the NGDR be detected (Fig. 5a, b). There were no significant differences for different food concentrations, nor could a trend of NGDR with food concentration be observed.
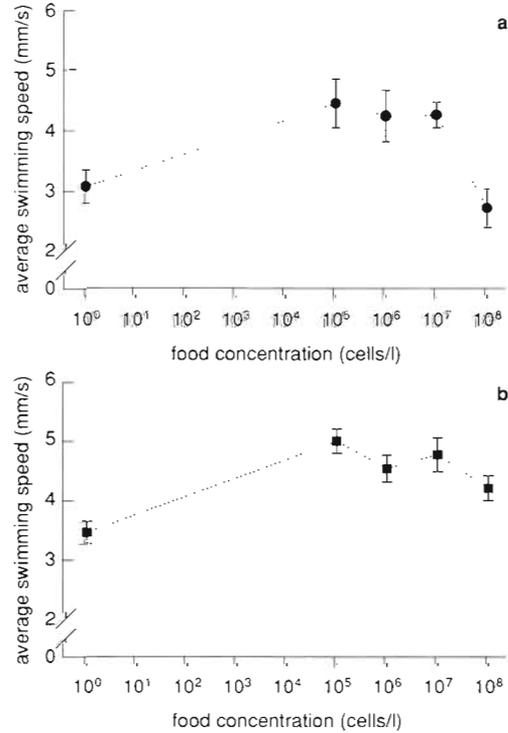

Fig. 3. *Temora longicornis*. Average swimming speed of adult (a) females and (b) males at different food concentrations. Error bars indicate SE
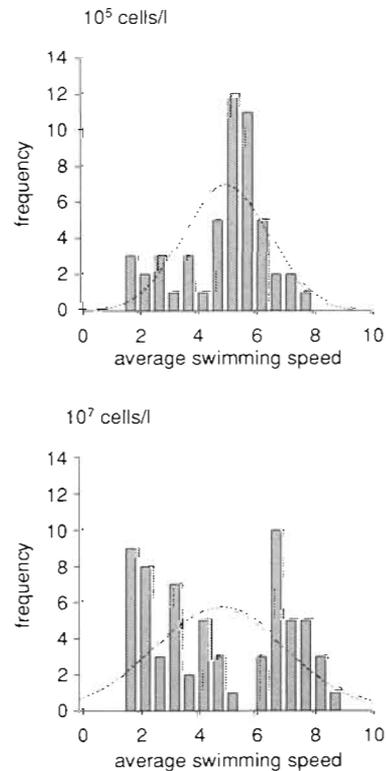

Fig. 4. *Temora longicornis*. Frequency distribution of swimming speeds of males at 10^5 and 10^7 cells l^{-1}
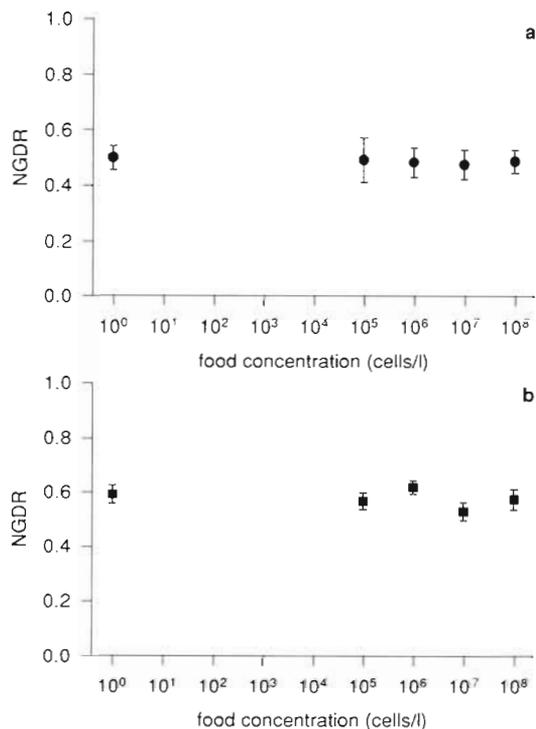
Fig. 5. *Temora longicornis.* NGDR of adult (a) females and (b) males at different food concentrations. Error bars indicate SE

DISCUSSION AND CONCLUSIONS

Swimming mode of different developmental stages

Temora longicornis is a very popular subject for studies on feeding behaviour. Most of these studies mention continuous swimming with the feeding appendages as the characteristic type of behaviour for *T. longicornis* (Yule & Crisp 1983, Gill & Harris 1987, Poulet & Gill 1988, Tiselius & Jonsson 1990). This study shows that this behaviour is indeed the case for the copepodids, but the nauplius stages show a cruise and pause swimming mode. Intermittently swimming animals can adjust their foraging effort, and as a consequence their average swimming speed, in different ways: by changing their limb beat frequency, by changing the ratio between stationary periods and swimming bouts, or by a combination of both. *Eucalanus elongatus*, an intermittently swimming copepod, decreases its time spent swimming at very low food conditions (Price & Paffenhöfer 1985). Jonsson & Tiselius (1990) also found that *Acartia tonsa* substantially increased the percentage of time its feeding appendages were active when the concentration of *Cryptomonas baltica* reached a certain threshold level. The nauplii of *T. longicornis* seemed to opt for this

mechanism, whereas the older stages fed continuously and varied their feeding effort by swimming faster or slower instead of swimming more or less, according to changing circumstances. Paffenhöfer & Lewis (1990) reported the opposite for *Eucalanus pileatus*. N5/6 of this species moved its appendages 100% of the time while the copepodids showed intermittent feeding movements, with the adult females moving their appendages a larger proportion of the time than the smaller copepodid stages.

N2, the youngest feeding nauplius stage, did not show an obvious reaction to a change in food condition. Two explanations are possible. The first possibility is that in this stage the sensory system may not yet be fully developed, and therefore changes in food availability are not detected very efficiently. The second explanation is that this stage has insufficient feeding experience and still has to learn through trial and error what is the most profitable feeding strategy. The latter hypothesis can only hold if efficient feeding develops through a learning process. Buskey (1984) could condition adult female *Pseudocalanus minutus* to react to a novel stimulus (morpholine) with increased feeding activity after these females were exposed to a mix of food algae and morpholine. Females that were not exposed to the morpholine-food mix did not show any behavioural reaction to morpholine. This result suggests that copepods have at least some power of association.

If swimming speed is considered to be directly related to filtering rate, female *Temora longicornis* behave almost exactly in accordance with the results of experiments of Frost (1975), who found that adult females of *Calanus pacificus* filtered at a reduced rate at very low food concentrations. When food supply was increased the females increased their filtering rate until some maximum rate was reached. They maintained this maximum filtering rate until a critical food density was reached, at which point they reduced their filtering rate, while maintaining a constant ingestion rate. The shape of the swimming speed curve of the adult females was also similar to the optimal filtering rate curve predicted by both Lehman (1976) and Lam & Frost (1976). Although these models predict an optimal filtering rate of zero at food densities of zero, adult *T. longicornis* never stopped swimming completely. This result agrees with the observations of Price & Paffenhöfer (1985), who found that *Eucalanus elongatus* also reduced the rate of flapping of the mouth appendages at low food concentrations, but never ceased feeding completely. Lam & Frost (1976) hypothesized that at very low food concentrations copepods could cease filtering movements and enter a searching mode. In our set-up however, it was impossible to observe if there was a difference between filtering-swimming and

searching-swimming. This topic deserves further attention but needs to be investigated with different equipment.

In our experiments the swimming speed of the females decreased only at very high concentrations of algae, which according to the models was probably a consequence of the fact that the algae used were of adequate but not optimal size for adult *Temora longicornis*. Klein Breteler et al. (1990) observed no differences in either the development time of the different stages or the average prosome length the adults reached between specimens reared on a diet of only *Rhodomonas* sp. and specimens reared on a mixed diet with *Rhodomonas*, *Isochrysis galbana* and the flagellate *Oxyrrhis marina*. However, given the choice, the adult copepods generally have a preference for larger prey (Klein Breteler 1980, Kleppel 1993). Berggreen et al. (1988) found different optimum particle sizes for different developmental stages of the copepod *Acartia tonsa*. The *Rhodomonas* sp. and the similar sized *Dunaliella tertiolecta* were probably optimal for the juvenile stages but suboptimal for the adults.

When males and females from the same culture were swimming at a relatively high food concentration, the males swam faster than the females. This is remarkable since several sources in the literature report higher food intake in females than in males (Harris & Paffenhöfer 1976, Klein Breteler & Gonzales 1986, Klein Breteler et al. 1990). The swimming behaviour of the males also deviated from the predictions of the optimal foraging theory, because at very high food concentrations they did not reduce their swimming speed. It is possibly dangerous to compare the experiments with the male and female copepods at different food concentrations directly, because the animals came from different cultures and a different food alga was used. Although both algae are small motile flagellates of similar size, we cannot exclude that there may be some difference in the quality of the food. However, the fact that males and females showed such different reactions to differences in food concentration is unlikely to be a consequence of the difference in algal species used. Gill & Crisp (1985) found that males had a significantly larger range in limb beat frequency than females. These phenomena may be linked to mate seeking behaviour. According to Gerritsen (1980) this is indeed the optimal mate seeking strategy for males looking for relatively slow-moving females. While the females concentrate on maximizing their energy intake because a large part of their energy budget is taken up by producing eggs, the males may invest some of their energy in increasing the encounter probability with females. This hypothesis is supported by the marked change in frequency distribution of the swimming speeds of the males with increasing food concentration. All the males tested came from the same culture and had therefore the same feeding history. All the experiments with the males were carried out within a few days and there were no other obvious differences (e.g. in size) that could account for this bimodal distribution at higher food concentrations. The normal frequency distribution at low food concentrations indicates that the behaviour of the males is regulated by one motivation, probably food intake. At higher food concentrations a second regulating factor seems to come into play. At these higher food concentrations those males that are looking for females can probably afford to increase their swimming speed to increase their encounter probability. A number of researchers have found changes in swimming behaviour of (usually male) copepods when they were exposed to the smell of the opposite sex or in the presence of the opposite sex (Katona 1973, Griffiths & Frost 1976, Van Leeuwen & Maly 1991). In these experiments the copepods were swimming in water from a recirculating seawater system which was free of fish and was continuously filtered, UV-sterilized and activated-carbon-filtered. Regular checks indicated that no *Temora longicornis* were living in this system. This suspected mate seeking mechanism seems to be operating without the stimulus of the presence of females. Yen (1988) found different swimming behaviour in males and females of *Euchaeta rimana*. Females moved predominantly in a horizontal plane while males had a stronger vertical component in their swimming trajectory. The copepods also showed this behaviour in the absence of the opposite sex. Unlike *T. longicornis* however, *E. rimana* males have reduced mouth parts and do not have to compromise between feeding and mate seeking.

Although the adult copepods clearly reacted to different food conditions by changing their swimming speed, they did not significantly change their turning behaviour. Changes in swimming path have been reported for copepods by a number of investigators. Williamson (1981) described an increase in looping behaviour in *Mesocyclops edax* in patches with a high food density. This predatory copepod showed tight swimming loops in water with a high concentration of prey and a straight swimming path without loops in filtered lake water. Buskey (1984) reported a lower NGDR in high food conditions for *Pseudocalanus minutus* as well as in water with chemosensory or mechanosensory feeding cues. Coughlin et al. (1992) used both NGDR and fractal dimension analysis to describe the swimming paths of larval clownfish *Amphiprion perideraion*. While the NGDR showed no clear trend due to the high levels of variance, the fractal dimension analysis indicated an increased complexity of the swimming path in higher food densities. Unfortu-

nately, the filmed sequences of swimming copepods in the 3-dimensional set-up were too short for fractal dimension analysis, so it is possible that there was a change in swimming path that could not be detected with this method. It is also possible that the absence of a reaction in swimming path was a consequence of the type of food used. As mentioned earlier, the small flagellate algae are an adequate food source for *Temora longicornis* but in the culture the adults prefer the larger heterotrophic flagellate. So the adults may have been feeding as efficiently as possible on the food present, but continued to search for better sources of food.

From these experiments we cannot conclude whether the copepods used remote detection of food availability as a cue to adjust their feeding behaviour or whether they merely reacted to a change in food intake. The algae used were well below the minimum sizes that Poulet & Gill (1988) tested in their study of mechanosensory responses of *Temora longicornis*. DeMott & Watson (1991) concluded that mechanoreception and not chemoreception is probably the primary mechanism for remote detection of algae, and on theoretical grounds the algae used seemed to be on the lower end of the scale for possible remote detection (Légier-Visser et al 1986). On the other hand the algae were motile flagellates, and although their rate of movement is limited, especially when compared to that of copepods, this motility could possibly enhance detection by mechanoreception.

This study shows that different developmental stages behave differently and that food concentration has a clear effect on behaviour. Apart from these 2 factors, there will exist a number of other factors influencing copepod behaviour. Poulet & Gill (1988) found that the beat pattern of the feeding appendages changed with different sizes of food. Larger food is perceived from a greater distance and the handling of the food is different. Poulet & Gill (1988) found that *Temora longicornis* could easily handle a large range of particle sizes and that the limb beat frequency was reduced with an increase in particle size. Abiotic factors such as temperature (Gill & Crisp 1985) and (micro)turbulence (Costello et al. 1991) affect swimming and feeding, as well as the condition and age of the animals. Tiselius & Jonsson (1990) described the feeding behaviour of female *T. longicornis* as stationary cruising and linked this to a particular feeding strategy. This seems a valid description for females feeding on small prey (algae) at very low or very high food concentrations, but it is not accurate as a general description of the feeding behaviour of the species.

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