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PII: S1385-1101(09)00003-3
DOI: doi: 10.1016/j.seares.2009.01.002
Reference: SEARES 674

To appear in: *Journal of Sea Research*

Received date: 25 September 2008
Revised date: 18 December 2008
Accepted date: 6 January 2009

Please cite this article as: Saage, Andrea, Vadstein, Olav, Sommer, Ulrich, Feeding behaviour of adult Centropages hamatus (Copepoda, Calanoida): Functional response and selective feeding experiments, *Journal of Sea Research* (2009), doi: 10.1016/j.seares.2009.01.002

# Feeding behaviour of adult *Centropages hamatus* (Copepoda, Calanoida): Functional response and selective feeding experiments.

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**A B S T R A C T**

The feeding behaviour of adults of the marine calanoid copepod *Centropages hamatus* was studied in laboratory experiments with ciliates and phytoplankton as food sources. The ingestion rate of algal (flagellates, diatoms) and ciliate prey (oligotrichs) as a function of prey concentration could be described by a Holling type III functional response, with close to zero ingestion rates at concentrations below 5 µg C $l^{-1}$. In general, ingestion of ciliates was higher than ingestion of algae, and maximum feeding rates by adult males reached were half the feeding rates of adult females at prey concentrations exceeding 50 µg C $l^{-1}$. When diatoms and ciliates were offered together *C. hamatus* (both sexes) fed exclusively on ciliates as long as they contributed with more than 5% to the mixture. This indicates the capability of active prey selection and switching between suspension feeding and ambush predation. Therefore, the feeding behaviour of adult *C. hamatus* can be characterised as omnivorous with a preference for larger motile prey. This implies a trophic level above two, if there is a sufficient abundance of protozoan food available.

## 1. Introduction

The perception of the trophic role of calanoid copepods has changed during the last decades. Traditionally they were viewed as pure herbivores that act as a link between primary production and planktivorous fish [1,2,3]. Further research showed that copepods are not herbivorous but mostly omnivorous, with microzooplankton being a component of their diet [e.g. 4,5,6,7]. To which extent phytoplankton and microzooplankton contribute to the diet of copepods, i.e. the relative proportion of herbivory and carnivory, is still a matter of debate. The degree of, respectively, herbivory and carnivory has consequences for food chain length, and thus the efficiency of energy transfer to higher trophic levels, and the top-down control on phytoplankton and microzooplankton [8,9,10,11,12].

Copepods have two main feeding modes, suspension and ambush feeding [13]. Both are selective in different ways. Suspension feeding implies a selection based on limb morphology and prey behaviour, because motile food items will partially escape from the

feeding current, whereas ambush feeding relies on detecting prey by hydromechanical signals created by prey movements which induce a deformation of the laminar flow around them and thus leads to detection of motile prey [14,15,16,17,18].

Except for eggs at appropriate size and detrital particles, immotile prey is usually algal. Therefore, copepods that live in surface waters and only capture immotile prey can be considered mostly herbivorous. Motile prey consists of moving algae (e.g. flagellates) and microzooplankton, such as ciliates. Suspension feeding and ambush feeding do thus not exactly coincide with herbivory and carnivory, but a more herbivorous tendency may be related to suspension feeders and a more carnivorous to ambush feeding copepods.

We chose *Centropages hamatus* as our study organism, because it is widespread in coastal waters of the North Atlantic ocean and adjacent seas and an abundant representative of medium-sized (around 1 mm) epipelagic copepods [19] which form an important part of the diet of pelagic planktivorous fish, such as herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) [20]. *C. hamatus* can occur in abundances up to 722 Ind $m^{-3}$ and is capable of ingestion of daily means reaching 0.85% of phytoplankton carbon and 8.23% of copepod nauplii present [21]. The contribution of ciliates to the diet of *C. hamatus* has been reported to be negligible [22], which does seem unlikely from our own experience with copepod feeding behaviour. Both suspension feeding, i.e. creating a feeding current, and ambush feeding, i.e. long periods of sinking combined with apparent catching movements, have been observed for *C. hamatus* [23,24].

The aim of the present study was to investigate the functional response of *C. hamatus* on immotile as well as on small and large motile prey, whether it prefers ciliates over algal prey, and whether there is a difference in feeding between males and females.

## 2. Materials and methods

### *2.1. Culture and maintenance of experimental organisms*

*Centropages hamatus* was caught in the Kiel fjord (salinity 15 -18; 54°19' - 54°23' N; 10°08' - 10°10' E) with a 200 µm-plankton-net (WP2 Closing Net, Hydro-Bios, Kiel). The net had a collecting cylinder (diameter 16 cm, length 30 cm) that was closed at the bottom to avoid the copepods from being damaged. The maximum catching depth was 18 metres. Adult males and females were picked out and kept in three litre jars (~ 30 - 50 Ind $l^{-1}$) with filtered, autoclaved seawater (same salinity as in the fjord) at 10°C (experiments with ciliate prey) or 15°C (experiments with only algal prey), and regularly fed an algal mixture consisting of the flagellate *Rhodomonas* sp. and the diatom *Thalassiosira weissflogii* in surplus concentrations until used in the experiments. One day prior to the experiments which included ciliate prey *C. hamatus* was fed the oligotrich ciliate *Rimostrombidium caudatum* in addition to the algal mixture. Summed up, four experiments were performed in July and October 2005 and in May and June 2006. The maintenance time of the copepods in the laboratory ranged from three to eight days (see table 1 for details).

*Rhodomonas* sp. and *T. weissflogii* were grown at 15°C in Drebes-medium [25], but the nutrient concentrations were increased to values typical for F/2-medium [26]. The light cycle was 12 h light : 12 h darkness. The algae species originated from stock cultures at the Leibniz Institute of Marine Sciences, Kiel.

*R. caudatum* was isolated in March 2006 from the Kiel fjord (water temperature 3°C). The ciliate culture was kept in cell tissue flasks filled with 0.2 µm filtered, autoclaved sea water in a climate chamber at a final temperature of 10°C at a light intensity between 100 and 150 µmol $m^{-2}$ $s^{-1}$. In regular intervals the ciliates were fed the marine flagellate *Rhodomonas* sp. grown under the same conditions as mentioned above.

### *2.2. Experiments*

The copepods were incubated in darkness for six hours at different prey concentrations. A plastic pipette was used to transfer the copepods to 100 ml brown glass

bottles with filtered, autoclaved seawater. The experiments were started by adding the prey organisms, and stopped by adding acid LUGOL´s solution to a final concentration of 1%. Two replicates were set up for each food concentration and for each sex.

In functional response experiments *C. hamatus* females and males were offered *Rhodomonas* sp., *T. weissflogii*, and *R. caudatum* as food (for detailed information on the experimental setup see table 1). At the end of the experiments, the prey cells were counted and measured using an inverted microscope [27]. Carbon content was computed based on cell volume and a value of 0.14 pg C $\mu m^{-3}$ and 0.19 pg C $\mu m^{-3}$ for algal and ciliate prey, respectively [28, 29].

In the selective feeding experiment, *C. hamatus* was offered a mixture of ciliate (*R. caudatum*) and algal (*T. weissflogii*) prey at varying concentrations (detailed information is given in table 1). The overall concentration of ciliate and algal prey together ranged between 251 and 403 µg C $l^{-1}$. Experimental bottles were incubated in darkness at 10°C. The determination of the cell biomass at the end of the experiment followed the procedure given above for the functional response experiments.

*2.3. Calculations of clearance and ingestion rates*

For all experiments the ingestion rate ($I$) (µg C $Ind^{-1}$ $l^{-1}$) was calculated after Nejstgaard and colleagues [30; adapted from 31] with $I = CR \cdot \overline{C}$, where $CR$ is the clearance rate (ml $Ind^{-1}$ $h^{-1}$) and $\overline{C}$ is the average food concentration (µg C $l^{-1}$), calculated as the logarithmic mean.

For the functional response experiments $CR$ was calculated after Lucas [32] with $CR = \left[1/t \cdot LN\left(C_1 / C_2\right)\right]$, where $C_1$ is the final food concentration in the controls without copepods, $C_2$ the final food concentration in the replicates, and $t$ the incubation time (d).

For the selective feeding experiment a correction for the ciliate grazing on the diatom was necessary. The clearance rate for the copepod community on diatoms $CR_{cop,dia}$ and on

ciliates $CR_{cop,cil}$ was calculated after Tokle [33] with $CR_{cop,dia} = \mu_{dia} - r_{dia} - \left(CR_{cil,dia} \cdot \overline{C}_{cil}\right)$ and $CR_{com,cil} = \mu_{cil} - 1/t \cdot \left[LN\left(C_{cil2} / C_{cil1}\right)\right]$, where $C_{cil1}$ and $C_{cil2}$ are the final concentrations (µg C $l^{-1}$) of ciliates from the controls without copepods and from the replicates with copepods, respectively, and $t$ the incubation time (d). $\overline{C}_{cil}$ is the average ciliate concentration (µg C $l^{-1}$), calculated as the logarithmic mean. For $CR_{cil,dia}$, the clearance rate of the ciliates on the diatoms, a constant value, calculated from the start concentrations before incubation and the controls without copepods (data not shown), of 0.33 ml µgciliateC$^{-1}$ $h^{-1}$ was applied. An average $\mu_{cil}$ of 0.017 $h^{-1}$ (± 0.008 SE) was applied. $\mu_{dia}$ is a constant factor of -0.0216 $h^{-1}$ (± 0.0101 SE) and was estimated by linear regression of the specific rate of change for diatom vs. ciliate biomass in the bottles without copepods. $r_{dia}$ is an additional factor to correct for diatom growth during incubation [33].

To get the individual clearance rates all $CR$ values were divided by copepod density (Ind $ml^{-1}$).

## 3. Results

Ingestion rate values which were negative or outliers were excluded from regressions (in the functional response experiments with ciliate and diatom prey: one and two ingestion rate values, respectively, due to irregularities in corresponding start values; in the selective feeding experiment: ingestion of diatoms; Box Plot; mean ± standard deviation (SD), distance from mean (times SD) for males and females, respectively: 4.14 ± 13.09 ml Ind$^{-1}$d$^{-1}$, 8.6 times SD, and 0.71 ± 7.7 ml Ind$^{-1}$d$^{-1}$, 28.4 times SD). They are shown as square symbols in all graphs, as are all calculated negative values which were set zero for illustration. A type III functional response model was fitted to the data by non-linear regression using least square and the Gauss-Newton method. If the parameter $N$ in the model is not significantly different from one, the model reduces down to a type II functional response. This was evaluated based on estimated Wald Confidence Intervals [34]. Clearance rates are mathematically

directly linked to ingestion rates (see section 2.3., equation $I = CR \cdot \overline{C}$ ) and are therefore not shown in distinct graphs.

*3.1. Functional response experiments*

Ingestion increased with prey concentration in all three functional response experiments and can be described by Holling type III functional response curves [35], irrespective of prey and sex of the copepods. Both male and female *C. hamatus* showed highest ingestion rates on ciliate prey with maximum values of 7.10 µg C $Ind^{-1}$ $d^{-1}$ and 11.01 µg C $Ind^{-1}$ $d^{-1}$, respectively. Ingestion of diatoms and flagellates were similar (maximum values feeding on diatoms: males: 1.12 µg C $Ind^{-1}$ $d^{-1}$, females: 1.66 µg C $Ind^{-1}$ $d^{-1}$; feeding on flagellates: males: 1.30 µg C $Ind^{-1}$ $d^{-1}$, females: 2.22 µg C $Ind^{-1}$ $d^{-1}$), but a factor of four and seven lower, than maximum ingestion of ciliates, for females and males, respectively. Saturation in ingestion was reached around 50 µg C $l^{-1}$ with algal prey, whereas with ciliate prey maximum ingestion for both sexes was reached at prey concentrations > 100 µg C $l^{-1}$. Detailed information on the fitted regression curves is given in table 2. For males feeding on flagellate prey no maximum ingestion rate could be identified, due to the missing saturation in ingestion at concentrations below 80 µg C $l^{-1}$. Therefore the model could not be fitted to the data (Fig. 1c).

The lowest prey concentration in all three functional response experiments varied between 2.62 and 4.69 µg C $l^{-1}$. At these low concentrations, clearance rates were similar between adult males and females with diatom prey. Feeding on motile prey (ciliates and flagellates) females showed higher maximum clearance rates than males with 16.46 and 7.15 µg C $Ind^{-1}$ $d^{-1}$, respectively. Here female *C. hamatus* also reached saturation in ingestion at lower prey concentration than males (Fig. 1).

*3.2. Selective feeding experiment*

When offered a mixture of the ciliate *R. caudatum* and the diatom *T. weissflogii*, ingestion of ciliates of both sexes followed a Holling type III response [35] (Fig. 2a). The estimated maximum ingestion rates for males and females were 7.30 and 12.50 µg C $Ind^{-1}$ $d^{-1}$, respectively. Clearance and ingestion of diatoms was very irregular and did not follow a trend. In a number of cases, theoretically impossible negative values were calculated for the ingestion rate, because of the scatter in the cell counts. Ingestion rates of diatoms were close to zero for most of the diatom concentrations, except the highest ones which corresponded to the lowest ciliate concentrations (Fig. 2).

The ingestion rates were used to calculate the composition of the diet of *C. hamatus*, after setting calculated negative ingestion values to zero. A plot of percent ciliate carbon in the diet versus percent ciliate carbon in the food offered reveals that *C. hamatus* switches to almost pure ciliate feeding as soon as ciliates exceed 5% of the offered food carbon (Fig. 3). This threshold might even be as low as 1% for the females (Fig. 3), and is in line with Tokle and colleagues [36] who found similar values for female *C. hamatus* when ciliates were offered in varying concentrations together with algal prey at a constant surplus food concentration. Calculation of a selectivity index was performed after Jacobs [37], and showed a clear preference of *C. hamatus* for ciliates in the selective feeding experiment (Table 4).

## 4. Discussion

The feeding behaviour of *Centropages hamatus* can be characterised as omnivorous with the ability of selective feeding. Increasing clearance rate with increasing prey concentration suggests a feeding threshold for *C. hamatus* ~ 5 µg C $l^{-1}$, which seems to be similar for both algal and ciliate prey. This is different from other small copepods which do not seem to have a feeding threshold [38 (*A. clausi*),39 (*A. tonsa*),40 (*Pseudocalanus* sp.)]. A comparison of the 95% confidence intervals (data not shown) of the fitted non-linear regressions of all performed experiments showed that there is no difference in ingestion rates between the sexes at lower prey concentrations (< 100 µg C $l^{-1}$). At higher prey

concentrations (> 100 µg C $l^{-1}$) ingestion of ciliates by females was higher by a factor of approximately two compared to ingestion by male *C. hamatus*, both in the functional response and selective experiment. Thus, female copepods seem to be more effective predators at higher prey concentrations where the maximum ingestion capacity is limiting the food uptake. Contrarily there seems to be no difference in feeding between males and females at lower prey concentrations when food uptake is limited by the maximum search rate. Female *C. hamatus* in our experiment showed similar, low ingestion on the diatom (except the two values considered as outliers) and the flagellate (Fig. 1b and c). This suggests that also the motile but small flagellate is ingested via suspension feeding, as is the immotile diatom. The ingestion by females on ciliates at the same concentration range, on the other hand, was twice as high (Fig. 1a). This we interpret as indication for ambush feeding as reported for *C. hamatus* by Tiselius and Jonsson [23]. At lower prey concentration ambush feeding results in higher clearance rates [41], which then in turn gives higher ingestion rates (see section 2.3., equation $I = CR \cdot \overline{C}$ ). Male *C. hamatus* showed a relatively constant and low clearance on ciliate prey in the functional response experiment. This relatively constant clearance rate of males in contrast to females might be explained by suspension feeding. But in the selective feeding experiment there was no such difference between the sexes in clearance of ciliates at lower concentrations. Here males even showed higher maximum clearance than females. Thus the lower clearance by male *C. hamatus* in the functional response experiment might be explained by the individual nutritional status of the copepods causing individual variability associated with feeding behaviour [42]. Furthermore, the speed of the feeding current of *C. hamatus* is 0.79 mm $s^{-1}$ at a distance of 1 mm from the antennules [43]. The prey ciliate in our experiments was *R. caudatum* which swims in spirals, but can perform rapid escape jumps when disturbed (personal observation). Spiral swimming ciliates of the genus *Strombidium* (some *Strombidium* species lately have been transferred to the genus *Rimostrombidium*) reach swimming velocities between 0.36 and 1.00 mm $s^{-1}$, and for escape jumps a velocities between 0.81 and 1.02 mm $s^{-1}$ have been observed [13,44]. Hence, *C. hamatus* likely could not capture an escaping *R. caudatum* within its feeding current, and in conclusion must have actively selected the ciliate prey, i.e.

used ambush feeding. In the selective feeding experiment the two high ingestion rate values on diatoms for the replicates with lowest ciliate / highest diatom concentration are considered to be outliers (see section 3) as they with an ingestion of 40 and 20 µg C $Ind^{-1}$ $d^{-1}$ by male and female, respectively (Fig. 2b) give unrealistic high values for *C. hamatus* [21,22,45]. Copepods can ingest up to 148% of their own body carbon per day [46], which for *C. hamatus* equals ~10.5 µg C $Ind^{-1}$ $d^{-1}$, assuming an average body carbon content of ~7.1 µg C $Ind^{-1}$ [47]. Naturally occurring ciliate abundances usually do not exceed 35 µg C $l^{-1}$ [48,49], but *R. caudatum* can in bloom situations reach maximum abundances of 3060 µg C $l^{-1}$ [50] which is one magnitude higher than the highest ciliate concentration in our ciliate experiments. At concentrations around 35 µg C $l^{-1}$ *C. hamatus* had an ingestion rate of ~2 and ~4 µg C $Ind^{-1}$ $d^{-1}$ in the functional response experiment and selective feeding experiment, respectively, which equal 28 to 56% of body carbon. *C. hamatus* is very efficient in capturing ciliates [51]. The copepods might have started to feed on diatoms when no more ciliates were left in the treatment with lowest ciliate concentration, but even this would not explain these very high ingestion rates for diatoms of 40 and 20 µg C $Ind^{-1}$ $d^{-1}$ by male and female, respectively (Fig. 2b).

The ingestion of ciliates by *C. hamatus* in the selective feeding experiment might show a more realistic pattern than in the functional response experiment, because saturation of the functional response seemed to start at ciliate concentrations of ~ 50 µg C $l^{-1}$ (Fig. 2a), which are common values for ciliate abundances in natural ecosystems [48,49]. For our experiments we assumed that the copepods fed continuously during incubation, at a rate they would use during night under natural conditions. Because the experiments were stopped after a few hours, daily rates were calculated by multiplying “rates per hour” with 24. This implies a continuous feeding over the whole day, which might not necessarily be true for natural copepod communities.

Earlier studies seldom used male copepods in feeding experiments. For the larger *Calanus* spp. none or little feeding by adult males has been reported [52,53]. In our study adult males of the small copepod species *C. hamatus* reached ~50% of female maximum clearance and ingestion rates, similar to rates found for male individuals of the similar sized

*Acartia tonsa* [54]. Reduced energy demand compared to females, which require much energy for egg production (our experiments fell in the reproductive season of *C. hamatus* (April to November) [55] or the smaller body size itself, compared to females, might be reasons for lower maximum feeding rates of male copepods [54,56].

During the 1990s the traditionally accepted role of diatoms as important and nutritionally adequate food source became questioned [57,58,59]. Several authors provided evidence for their nutritional inadequacy [e.g. 60,61,62,63,64]. Some authors even stated that diatoms are not only poor food, but toxic for developing embryos because of certain aldehydes [65], but the issue remains controversial [66]. Murray and Marcus [67] showed for *C. hamatus* that simple unialgal or mixed diets are not the best food supply at all developmental stages, but that "an optimal diet fosters growth and survival at all stages and maximizes viable egg production, to ensure high recruitment to the next generation". Younger stages of *C. hamatus* might have different feeding strategies and therefore prey preferences than older stages, analogue to other small copepods, e.g. early copepodites of *Acartia clausi*, which under certain prey concentrations spend more time on suspension feeding than later stages [68], and CI to CIII stages of *A. tonsa*, which ingest more diatoms than stages CIV to adult [69]. On the other hand, Ismar and colleagues [70] have shown that *A. tonsa* can complete its entire life-cycle both on a monodiet of *Rhodomonas* sp. and *T. weissflogii*, but *Rhodomonas* sp. was the better food.

The present study shows, that adult stages of the copepod *C. hamatus* can ingest both ciliates and algae, but prefer ciliates when these occur in sufficient abundances. *C. hamatus* seems to be able to switch between suspension and ambush feeding [23,24] in adaption to the current composition of the prey assemblage and / or the energy demand of the individual copepod.

**Acknowledgments**

This research has been supported by the Deutsche Forschungsgemeinschaft under contract number SO 145 / 25-1.

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**Figure legends**

Figure 1 - *Centropages hamatus*. Ingestion rates of males (m; filled) and females (f; open) on *Rimostrombidium caudatum* (a), *Thalassiosira weissflogii* (b), and *Rhodomonas* sp. (c). Error bars indicate Mean ± standard error. Square symbols are outliers for males (filled) and females (open). Note the different scaling of the x- and y-axes. Lines are fitted regressions, see table 2 for details.

Figure 2 - *Centropages hamatus*. Ingestion rates of males (m; filled) and females (f; open) on a mixture of *Rimostrombidium caudatum* (a) and *Thalassiosira weissflogii* (b) (see section 2 for details). Square symbols are outliers for males (filled) and females (open). Error bars indicate Mean ± standard error. Note the different scaling of the x- and y-axes. Lines are fitted regressions, see table 2 for details.

Figure 3 - *Centropages hamatus*. Feeding of males (m; filled) and females (f; open) on ciliates when offered a mixture of *Rimostrombidium caudatum* and *Thalassiosira weissflogii* (see section 2 for details). Error bars indicate Mean ± standard error.

Table 1 - *Centropages hamatus*. Detailed overview over the experiments (functional response and selective feeding).

| Experiment | Functional response | | | Selective feeding |
|---|---|---|---|---|
| Prey species | *Rhodomonas* sp. | *T. weissflogii* | *R. caudatum* | *T. weissflogii*<br>*R. caudatum* |
| Prey size [ESD in µm] | 11 | 12 - 27 | 35 - 50 | 12 - 27<br>35 - 50 |
| Temperature [°C] | 15 | 15 | 10 | 10 |
| Start concentration [µg C $l^{-1}$] | 4.7, 10.8, 17.3, 35.7, 57.1, 75.0, 102.2 | 2.7, 2.8, 4.4, 5.6, 8.4, 18.8, 25.9, 28.8, 35.7, 47.6 | 3.9, 5.6, 10.2, 26.4, 45.9, 58.8, 95.4, 99.9, 117.4, 176.6, 208.6, 266.3 | 463.6, 384.6, 379.9, 371.4, 313.7, 289.6, 266.6, 187.0, 116.6, 3.7<br>0.7, 1.7, 3.4, 4.6, 9.2, 14.4, 28.1, 64.0, 130.2, 240.2 |
| Start replicates [µg C $l^{-1}$] | 1 for each concentration | 1 for each concentration | 1 for 10, 13, 60, 100, and 300 | 1 for each concentration |
| Treatment replicates per concentration | 2 for each sex | 2 for each sex | 2 for each sex | 2 for each sex |
| Copepods per bottle | 5 | 5 | 5 | 5 |
| Control replicates [µg C $l^{-1}$] | 2 for 4.7, 35.7, and 102.2 | 2 for 2.7, 18.8, and 47.6 | 1 for each concentration | 1 for each concentration |
| Copepod sampling day | 12 July 2005 | 27 October 2005 | 8 May 2006 | 13 June 2006 |
| Experiment day | 19 July 2005 | 31 October 2005 | 16 May 2006 | 16 June 2006 |

ESD: Equivalent spherical diameter

Table 2 - Statistics for the ingestion rates of *Centropages hamatus*. Variables, predicted coefficients, and significances. The model of the fitted regression is $I = I_{\max} \cdot \overline{C}^N / \left(K^N + \overline{C}^N\right)$ with $\overline{C} = K$ at $I = \frac{I_{\max}}{2}$ and criteria for type III functional response of $N > 1$. For units see section table 3. Predicted maximum ingestion rates are shown in bold, $R^2$ is observed vs. predicted values.

| **Ingestion** | | | | | | |
|---|---|---|---|---|---|---|
| **Functional response experiments** | | | | | | |
| **Prey** | **Sex** | **$I_{max}$** | **N** | **K** | **$R^2$** | **p** |
| *R. caudatum* | male | **7.1471** | 7.4913 | 117.2750 | 0.9965 | <0.0001 |
| | female | **16.4626** | 1.0227 | 164.8548 | 0.8692 | 0.0003 |
| *T. weissflogii* | male | **0.9185** | 2.1966 | 5.9242 | 0.6783 | 0.0189 |
| | female | **2.6154** | 1.3152 | 28.7718 | 0.9545 | 0.0004 |
| *Rhodomonas* sp | male | **no $I_{max}$ data**, so model fit is not possible | | | | |
| | female | **2.2012** | 10.2031 | 45.9913 | 0.9630 | 0.0014 |
| **Selective feeding experiment** | | | | | | |
| *R. caudatum* | male | **7.3391** | 1.3020 | 16.7040 | 0.9514 | <0.0001 |
| | female | **12.4965** | 1.9930 | 33.6458 | 0.9117 | 0.0002 |

Table 3 - Abbreviations.

| Abbreviation | Unit | Meaning |
|---|---|---|
| C | - | Carbon |
| d | - | Day |
| h | - | Hour |
| Ind | - | Individual |
| l | - | Litre |
| µg | - | Microgram |
| $\mu m^3$ | - | Cubic micrometer |
| | | *In general* |
| $I$ | µg C $Ind^{-1}$ $d^{-1}$ | Ingestion rate |
| $I_{max}$ | µg C $Ind^{-1}$ $d^{-1}$ | Maximum ingestion rate |
| $CR$ | l $Ind^{-1}$ $d^{-1}$ | Clearance rate |
| $\overline{C}$ | µg C $l^{-1}$ | Average food concentration |
| $C_0$ | µg C $l^{-1}$ | Food concentration at start of incubation time |
| $C_1$ | µg C $l^{-1}$ | Food concentration in control bottles at end of incubation time |
| $C_2$ | µg C $l^{-1}$ | Food concentration in treatment bottles at end of incubation time |
| $K$ | µg C $l^{-1}$ | Half saturation value |
| $t$ | h | Incubation time |
| | | *Selective feeding experiment* |
| $CR_{cop,cil}$ | l $Ind^{-1}$ $d^{-1}$ | Clearance rate of copepods on ciliates |
| $CR_{cop,dia}$ | l $Ind^{-1}$ $d^{-1}$ | Clearance rate of copepods on diatoms |
| $CR_{cil,dia}$ | l $Ind^{-1}$ $d^{-1}$ | Clearance rate of ciliates on diatoms |
| $\overline{C}_{cil}$ | µg C $l^{-1}$ | Weighted average ciliate concentration during incubation |
| $C_{cil1}$ | µg C $l^{-1}$ | Ciliate concentration in control bottles at end of incubation time |
| $C_{cil2}$ | µg C $l^{-1}$ | Ciliate concentration in treatment bottles at end of incubation time |
| $\mu_{cil}$ | - | Factor correcting for ciliate growth during incubation |
| $\mu_{dia}$ | - | Factor correcting for diatom growth during incubation |
| $r_{dia}$ | - | Additional factor correcting for diatom growth during incubation |

Table 4 - Selectivity index ($D$) of *Centropages hamatus*. $D$ was calculated after Jacobs [37], with $D = 1$: preference, $D = 0$: no preference / no rejection, $D = -1$: rejection. $C_0$ are the start concentrations in the replicates of ciliates and diatoms. Numbers in *italic* are defined as outliers (see section 3).

| **Selectivity index** | | | | | |
|---|---|---|---|---|---|
| Selective feeding experiments | | | | | |
| Ciliate prey | | | Diatom prey | | |
| | male | female | | male | female |
| $C_0$ | $D$ | $D$ | $C_0$ | $D$ | $D$ |
| *0.7* | *0.24* | *0.79* | *463.6* | *-0.24* | *-0.79* |
| 1.7 | 0.95 | 0.92 | 384.6 | -0.95 | -0.92 |
| 3.4 | 0.95 | 1.00 | 379.9 | -0.95 | -1.00 |
| 4.6 | 0.78 | 1.00 | 371.4 | -0.78 | -1.00 |
| 9.2 | 0.91 | 1.00 | 313.7 | -0.91 | -1.00 |
| 14.4 | 1.00 | 1.00 | 289.6 | -1.00 | -1.00 |
| 28.1 | 1.00 | 1.00 | 266.6 | -1.00 | -1.00 |
| 64.0 | 1.00 | 0.79 | 187.0 | -1.00 | -0.79 |
| 130.2 | 1.00 | 1.00 | 116.6 | -1.00 | -1.00 |
| 240.2 | 1.00 | 1.00 | 3.7 | -1.00 | -1.00 |