

# On the feeding of copepods on *Thalassiosira partheneia* from the Northwest African upwelling area

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**ABSTRACT:** Copepod feeding on the colony-building diatom *Thalassiosira partheneia* was studied in spring 1975 in the Northwest African upwelling area. Healthy, whole colonies of *T. partheneia* (diameter ~ 1 cm) were offered as food as well as single cells (diameter ~ 9 µm) after disintegration of the colonies. In addition, comparative experiments were carried out with the dinoflagellate *Scrippsiella trochoidea*. None of the 13 copepod species studied was able to feed on the entire colony. However, feeding on single cells after disintegration of the colonies was found for 4 copepod species studied. The actual quantity of food intake ranged from 14.7 to 124.0 % body carbon per day. The lowest values were obtained for *Calanus helgolandicus*, the highest for *Temora stylifera*.

## INTRODUCTION

*Thalassiosira partheneia* Schrader, a small centric diatom (~ 9 µm diameter), is the most striking phytoplankton species in the Northwest African upwelling area. This alga forms colonies of sizes up to 5 cm in length and up to 1 cm in diameter, each with several hundred up to 25,000 cells (Elbrächter and Boje, 1978). So far, little is known about the possible role of *T. partheneia* as a food source for zooplankton. Small protozoans such as heterotrophic dinoflagellates, ciliates and amoebae live within healthy colonies and seem to feed on single cells (Elbrächter and Boje, 1978). *T. partheneia* also seems to be a food source for filter-feeders but only after disintegration into short chains and single cells. This disintegration, shown in culture experiments, can be due to senescence and damage due to excess light (Elbrächter and Boje, 1978). According to Elbrächter (pers. comm.) it is unlikely that colonies are destroyed by large grazers or by turbulence under culture conditions. At 60 to 75 m water depth, Elbrächter and Boje (1978) observed mainly single cells up to  $130,000\ l^{-1}$ .

During a cruise of R. V. 'Meteor' in spring 1975 to the Northwest African upwelling area, the role of *Thal-*

*siosira partheneia* as a possible food source for copepods was investigated. The question addressed was: are copepods able to take advantage of the mass distribution of this alga and, if so, in what form does this occur, i.e. can copepods utilize the big colonies and/or do they only feed on *T. partheneia* after disintegration into single cells? Comparative studies were carried out using the dinoflagellate *Scrippsiella trochoidea* (Stein) Loeblich III as food supply.

## MATERIAL AND METHODS

Copepods used in experiments were collected in the upper 60 m with a Helgoländer Larvae net of 300 µm mesh size during a '*Thalassiosira partheneia*'-project on Station C6 (Position: 21° 21.4' W, 17° 40.8' N; February 8, 1975). Hauls were taken at night. Only healthy animals were used for experiments.

*Thalassiosira partheneia* was sampled at daytime by bucket from the surface of the same sampling site. Colonies visible by naked eye were picked out by pipette and transferred into 1-l glass jars filled with 0.2 µm filtered seawater. To obtain single cells of *T. partheneia*, colonies collected 10 d before the experiments at the same station were exposed to intense light ( $40\ \mu E\ m^{-2}\ s^{-1}$ ) without changing the medium. The condition of the algae was checked every day under a stereomicroscope.

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*Scrippsiella trochoidea* was prepared from cultures cultivated by Elbrächter (Clone BAH ME 64).

Ten to 20 adults were placed in 2 l of filtered seawater. After 1 d, the respective algal suspension was added to the beakers and the copepods were prefed for 20 to 24 h. During preconditioning, food levels were the same as in the experiments. Each experimental set included at least 1 control beaker (i.e. without copepods). No rotation of the beakers was possible, but the motion of the ship helped to keep the algae in suspension as regular checks demonstrated. Particle concentration in experiments with single cells of *Thalassiosira partheneia* and with *Scrippsiella trochoidea* was checked on board with a Coulter Counter Channelyzer Model Z<sub>B</sub>. At the beginning and end of each experiment, 6 subsamples of 100 ml each from different parts of the beakers (2 from the surface, 2 from the middle, 2 from the bottom) were preserved with formalin (end concentration: 2 %) and counted with an inverted microscope at a magnification of 400 × (*T. partheneia*) and of 250 × (*S. trochoidea*). At least 200 cells were counted from each subsample. The relative coefficient of variation between the subsamples was low for all experiments ( $V_r < 4.9\%$ ). Average cell volume and carbon content of the algae were estimated after Smetacek (1975). Experiments were run in dim light for 8 to 10 h at 15 °C. *In situ* temperatures in the upper 60 m at Station C6 ranged from 15° to 17 °C (Brockmann et al., 1977). Filtration and ingestion rates were calculated after Frost (1972).

For studies on the possible feeding on colonies of *Thalassiosira partheneia*, 13 different copepod species were used (Table 1). In the 81 experiments conducted, the algae were labelled with radioactive carbon (<sup>14</sup>C) or phosphorus (<sup>32</sup>P) for 1 to 3 d and then supplied as food. Only colonies of similar length (1.5 to 2.0 cm)

Table 1. Copepod species used in experiments with colonies of *Thalassiosira partheneia*, separated according to their feeding behaviour

Copepod species	Cephalothorax length (mm)	Feeding behaviour
<i>Calanoides carinatus</i> , ♀	2.3	Filtration
<i>Calanus helgolandicus</i> , ♀	2.2	Filtration
<i>Rhincalanus nasutus</i> , ♀	4.4	Filtration
<i>Eucalanus crassus</i> , ♀	2.9	Filtration
<i>Acartia clausi</i> , ♀	0.9	Mixed
<i>Centropages chierchiae</i> , ♀	1.4	Mixed
<i>Centropages chierchiae</i> , ♂	1.2	Mixed
<i>Temora stylifera</i> , ♀	1.2	Mixed
<i>Temora stylifera</i> , ♂	1.0	Mixed
<i>Anomalocera patersoni</i> , ♀	3.0	Grasping
<i>Candacia armata</i> , ♀	1.9	Grasping
<i>Oncaea conifera</i> , ♀	0.5	Grasping
<i>Corycaeus</i> sp.	1.0	Grasping

were used; the length was measured at the beginning and end of each experiment. Experiments were run for 7 to 48 h. During that time, the colonies were buoyant; this was checked several times. Radioactivity in water and colonies was measured at the beginning and end of the experiments. Copepods were removed after experiments, sorted into scintillation vials and counted in a liquid scintillation counter.

## RESULTS

Table 1 lists the 13 different copepod species used as potential consumers of healthy colonies of *Thalassiosira partheneia*. None of the copepod species, in spite of the various feeding modes represented, fed on the colonies, i.e. became radioactive, and no faecal pellets were produced.

To find out whether copepods can utilize the single cells of *Thalassiosira partheneia* (single cell: 9 × 4 μm, 18 pgC), experiments were conducted with 6 different copepod species (*Calanoides carinatus*, *Calanus helgolandicus*, *Centropages chierchiae*, *Temora stylifera*, *Candacia armata*, *Oncaea conifera*). No feeding could be ascertained in the case of the 2 raptorial species, *C. armata* and *O. conifera*, but the other 4 species did indeed feed on *T. partheneia* as shown in Figs. 1 to 4. The figures include the results obtained from feeding experiments using *Scrippsiella trochoidea* (20 μm, 390 pgC) as food source. Initial phytoplankton carbon concentration ranged between 4 and 99 μgC l<sup>-1</sup> for *S.*

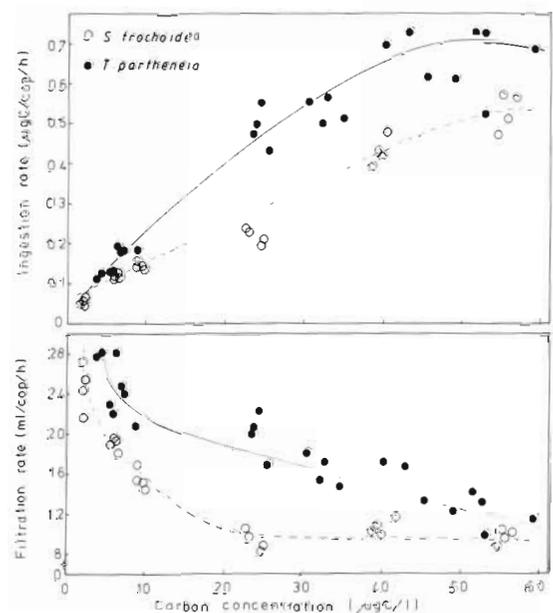


Fig. 1. *Calanoides carinatus*. Filtration rate and ingestion rate on single cells of *Thalassiosira partheneia* (solid line) and *Scrippsiella trochoidea* (broken line) plotted against mean food concentration

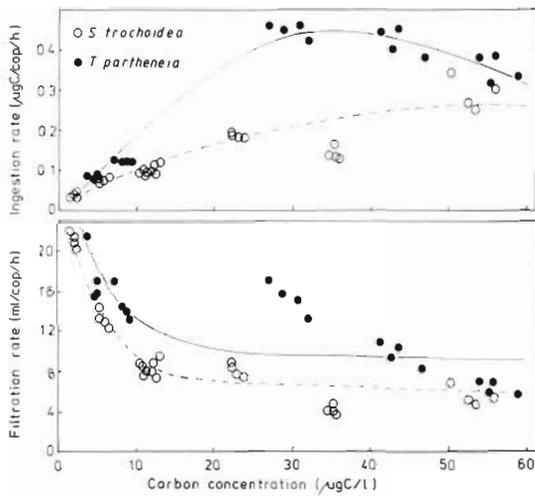


Fig. 2. *Calanus helgolandicus*. Filtration rate and ingestion rate on single cells of *Thalassiosira partheneia* (solid line) and *Scrippsiella trochoidea* (broken line) plotted against mean food concentration

*trochoidea* and between 9 and 84  $\mu\text{gC l}^{-1}$  for single-cell *T. partheneia*.

The 2 filter-feeding species, *Calanoides carinatus* and *Calanus helgolandicus*, showed higher filtration rates on the smaller *Thalassiosira partheneia* (Figs. 1 and 2); the 2 mixed-mode species, on *Scrippsiella trochoidea* (Figs. 3 and 4). Filtration rates were in any case higher at low food concentrations, decreasing with increasing food densities.

The quantity of food ingested and the maximum rations are summarized in Table 2. Dry-weight of deep-frozen copepods was determined and converted to carbon after Lenz (1974). The amount eaten per individual per day is expressed as percentage of carbon content of the copepods. The difference obtained for both phytoplankton species offered as food is relatively low in *Calanoides carinatus* and *Calanus helgolandicus*, compared with *Temora stylifera* and *Centropages chierchiae*, which ingested *Scrippsiella*

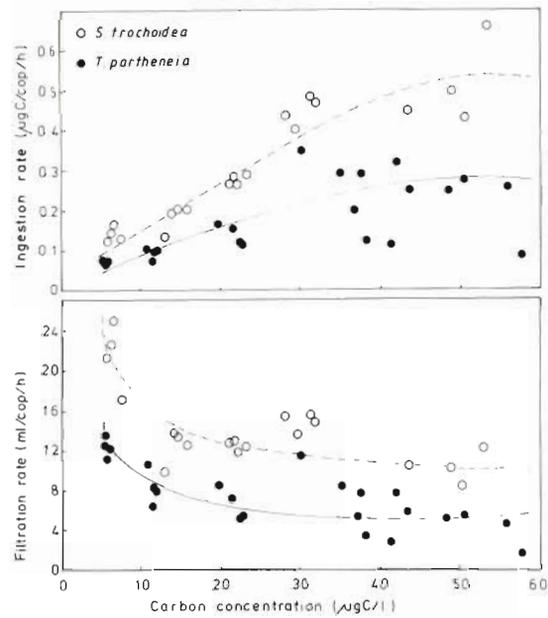


Fig. 3. *Centropages chierchiae*. Filtration rate and ingestion rate on single cells of *Thalassiosira partheneia* (solid line) and *Scrippsiella trochoidea* (broken line) plotted against mean food concentration

*trochoidea* more efficiently than *Thalassiosira partheneia* (1.5 and 1.9 times, respectively).

## DISCUSSION

The average value for food intake is about 40 to 60 % of body weight per day for late copepodids and adult copepods (Parsons et al., 1977). The food intake expressed as percentage of body carbon was below this average value in experiments with *Calanoides carinatus* and *Calanus helgolandicus* feeding on both algal species and with *Centropages chierchiae* feeding on *Thalassiosira partheneia*. Under experimental conditions, *Temora stylifera* consumed a quantity of food

Table 2. Quantity of food ingested

Copepod species	Algae species	Food density		Max. ration obtained ( $\mu\text{g C cop}^{-1} \text{d}^{-1}$ )	Max. ration (% body C $\text{d}^{-1}$ )
		Min. ( $\mu\text{g C l}^{-1}$ )	Max.		
<i>Calanoides carinatus</i>	<i>T. partheneia</i>	4.1	59.6	17.63	29.38
	<i>S. trochoidea</i>	2.0	56.5	13.66	22.77
<i>Calanus helgolandicus</i>	<i>T. partheneia</i>	3.9	58.8	10.99	19.63
	<i>S. trochoidea</i>	1.8	55.9	8.21	14.66
<i>Centropages chierchiae</i>	<i>T. partheneia</i>	5.2	57.4	8.22	29.36
	<i>S. trochoidea</i>	5.7	53.2	15.68	56.00
<i>Temora stylifera</i>	<i>T. partheneia</i>	4.4	53.1	11.04	78.86
	<i>S. trochoidea</i>	4.4	58.5	17.36	124.00

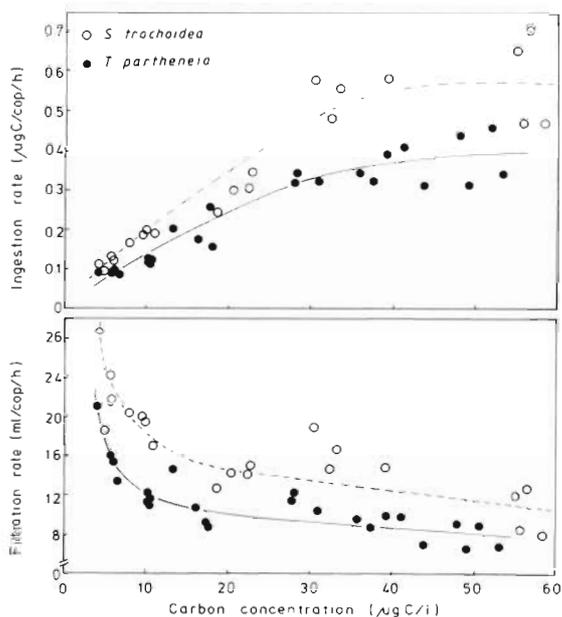


Fig. 4. *Temora stylifera*. Filtration rate and ingestion rate on single cells of *Thalassiosira partheneia* (solid line) and *Scrippsiella trochoidea* (broken line) plotted against mean food concentration

equivalent to a greater proportion of its body weight than the 3 other species. Similar observations for another *Temora* species (*T. longicornis*) were reported by Marshall and Orr (1966) and Poulet (1978).

It appears that the copepods are not able to feed on healthy, whole colonies of *Thalassiosira partheneia*. Nevertheless, single cells, after disintegration, are ingested by copepods. The high filtration rates on individual cells of *T. partheneia* are contrary to those reported by Conover (1956) and Mullin (1963), in which decreasing filtration rates with senescent phytoplankton cultures as food supply were observed. It is even more remarkable that *Calanoides carinatus* and *Calanus helgolandicus* grazed less efficiently on cultures of the larger dinoflagellate *Scrippsiella trochoidea* in good physiological state than on single celled *T. partheneia* at comparable food concentrations.

Considerable discussion has focused on the feeding response of zooplankton at very low food concentrations (e.g. Parsons et al., 1967; Frost, 1975; Muck and Lampert, 1980). Frost's (1975) results indicate that there was an interrelationship between food size and the concentration at which feeding rates decreased; large phytoplankton cells were grazed more efficiently at low food levels than smaller ones. Frost (1975) calculated from earlier data, threshold concentrations for *Calanus pacificus* varying between 95 and 13  $\mu\text{gC l}^{-1}$ , depending on the different sizes (diameters between 11 and 87  $\mu\text{m}$ ) of single centric diatoms offered.

Schnack (in prep.) described for the copepods *Calanoides carinatus* and *Centropages chierchiae* zero feeding below 0.9  $\mu\text{gC l}^{-1}$  when offered the centric diatom *Thalassiosira eccentrica*, whereas feeding was observed at the same food concentration when the motile dinoflagellate *Gymnodinium splendens* was offered.

Average phytoplankton and protozooplankton carbon (PPC/PZPC) concentration in the upper 75 m at Station C6 was about 7.5  $\mu\text{gC l}^{-1}$ ; the highest value of 57  $\mu\text{gC l}^{-1}$  was found at 5 m depth (Petersen, 1978). *Thalassiosira partheneia* constituted the major part (84%),  $\mu$ -flagellates and the diatoms *Chaetoceros* and *Leptocylindrus* and ciliates were the other organisms reported (Petersen, 1978). About 53% of *T. partheneia* were found in colonies at the surface, whereas in deeper layers the proportion of cells within colonies increased (Elbrächter and Boje, 1978). Total particulate carbon concentration (POC), however, was 154  $\mu\text{gC l}^{-1}$  in the upper 75 m, with a maximum value also at 5 m of 222  $\mu\text{gC l}^{-1}$  and a minimum value of 114  $\mu\text{gC l}^{-1}$  at 40 m depth (Lenz, unpubl.). The experimental concentrations were within the range of PPC and PZPC, but below the natural POC concentration.

The present study was not designed to study the feeding behaviour of copepods at low food concentrations. However, it is interesting to note that all 4 copepod species showed higher filtration rates at the lower mean food concentrations (below 10  $\mu\text{gC l}^{-1}$ ) which is in contrast to the data reported by Frost (1975).

Frost (1972) found for *Calanus pacificus* that maximum filtration rate increased with increasing particle size during feeding on monospecific cultures of centric diatoms, i.e. filtration rates were size dependent. On this basis, *Scrippsiella trochoidea* should be taken more efficiently than *Thalassiosira partheneia*, which is true for the pair *Temora stylifera* and *Centropages chierchiae*. *Calanoides carinatus* and *C. helgolandicus*, however, showed higher filtration rates on *T. partheneia* at similar food concentration, despite the smaller size and senescence of the algae. *S. trochoidea* differs from *T. partheneia* both in size and motility. Hence, the encounter rate should be higher for the dinoflagellate. The observed difference between the 4 copepod species can be associated with the difference in their feeding behaviour: *C. carinatus* and *C. helgolandicus* are primarily filter-feeding species, whereas *T. stylifera* and *C. chierchiae* are strongly omnivorous.

As described by Elbrächter and Boje (1978), disintegration into single cells is a common phenomenon for *Thalassiosira partheneia*. The results shown here suggest that *T. partheneia* is a suitable food organism in older upwelled waters and in deeper layers where the colonies disintegrate due to senescence. It should

be mentioned that the colonies of *T. partheneia* are not gelatinous. The short individual chains are held together by a thicker central thread and many twisted marginal ones (Elbrächter and Boje, 1978). Such colonies disintegrate much faster than gelatinous ones and one might expect the physiological state of the algal cells at disintegration to be still sufficiently good to serve as food for grazers. As pointed out already, the larger colonies of *T. partheneia* were not eaten by copepods of different feeding modes.

Similar experiments run with colonies of the gelatinous *Phaeocystis pouchetii* in the Antarctic in 1980 showed the same negative results for filter feeding copepods (*Calanus propinquus*, *Rhincalanus gigas*, *Eucalanus* sp.); however, copepods with a mixed and a raptorial feeding mode (*Metridia gerlachei* and *Pareuchaeta antarctica*, respectively) did feed on the colonies (Schnack, unpubl.). Feeding on *P. pouchetii* by different, mainly omnivorous, copepod species in the North Sea has been reported by Lebour (1922), Jones and Haq (1963) and Weise (1982). However, the *P. pouchetii* colonies used by Weise as well as by Schnack in their feeding experiments were generally much shorter than those of *Thalassiosira partheneia* used in the present study (0.05 to 1.5 mm compared with 1.5 to 2.0 cm).

From these results one might speculate that colony building in the phytoplankton represents an adaptation to discourage grazing, particularly of those filter-feeding copepods that are characteristic of diatom blooms. Raptorial species might well be discouraged by the size of larger colonies. Possibly, the greater amount of jelly in larger colonies of gelatinous species might be the reason for their apparent unpalatability. However, the fact that a non-gelatinous species such as *Thalassiosira partheneia* is also not relished in colony-form would indicate that size indeed is the decisive factor. This assumption is supported by the observations of Ferguson et al. (1982) and Thompson et al. (1982) who showed that (in a lacustrine environment), smaller colonies of the gelatinous cyanophyte *Microcystis* were eaten by zooplankton but not the larger, older colonies. None of the copepod species were adapted to feeding on *T. partheneia*. It remains to be seen whether other animals (such as salps and euphausiids) are able to feed on the large colonies of this diatom.

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