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Copepod feeding behaviour and egg production during a dinoflagellate bloom in the North Sea

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Abstract

Feeding strategies of copepods were studied during a dinoflagellate-dominated bloom in the North Sea in August 2001. The aim of this study was to evaluate the importance of mesozooplankton grazing as a biological loss factor of harmful algal blooms under natural conditions. Therefore, ingestion, egestion and egg production experiments were performed with the most abundant copepod species *Calanus helgolandicus*, *Temora longicornis* and *Acartia* sp. feeding on the natural phytoplankton community. *Dinophysis norvegica* and *Ceratium furca* were the most abundant dinoflagellate species at the time of the experiments. Grazing experiments as well as examination of fecal pellet content revealed *C. helgolandicus* fed efficiently on *D. norvegica*. Ingestion rates up to 47 cells female^{-1} h^{-1} were measured and a large proportion of the *C. helgolandicus* fecal pellets contained intact *D. norvegica* cells. *Dinophysis* cells were rarely seen in fecal pellets produced by *T. longicornis*, and never observed in pellets produced by *Acartia* sp. The ingestion rate of *C. furca*, which was the dominating *Ceratium* species, mimicked that of *D. norvegica*. *C. helgolandicus* grazed significantly on *C. furca* (16 cells female^{-1} h^{-1}), while the ingestion rate of *T. longicornis* was low and *Acartia* sp. was not able to graze on *C. furca*. Egg production experiments revealed that 92% of the *C. helgolandicus* females produced eggs. The specific egg production rate and the proportion of females producing eggs among *T. longicornis* were low. This field experiment clearly shows that some copepod species feed efficiently on *D. norvegica* and *C. furca* under natural conditions, which may affect the bloom development of these dinoflagellates.

Keywords: Copepods; Dinoflagellates; Grazing; HAB; North Sea

1. Introduction

Most bloom-forming species of phytoplankton are not harmful and serve as energy resource at the base of the food web. Only about 40 phytoplankton species, mainly dinoflagellates, are known to produce potent toxins and belong to a group of algae, which are able to form harmful algal blooms (HABs) (Hallegraeff, 1993). HABs occur worldwide but cause concerns mainly in near-coastal waters through commercial losses for tourism or aquaculture. Filter-feeding shellfish, zooplankton and herbivorous fish can act

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as toxin vehicles to higher trophic levels, including humans. The transfer of toxins through the marine food web is an important aspect of the dynamics of HABs, and the increasing interest in utilizing coastal waters for aquaculture gives rise to an increased awareness of toxic algal species. There is still little knowledge about the biological factors regulating the formation and decline of HABs. Since the maximum growth rates reported for large dinoflagellates are rather low compared to fast growing diatoms and other flagellates (Smayda, 1997), it becomes obvious that other processes benefit the bloom development of such species. The success of a phytoplankton species is not only dependent on their specific growth rate, but the difference between growth and loss must be favourable. Mesozooplankton, as one of the main grazers on phytoplankton, could play a key role in the control, structure and development of dinoflagellate blooms. However, knowledge about interactions between toxic phytoplankton and their potential grazers are rudimentary (reviewed by Turner and Tester, 1997; Turner et al., 1998). The effect of HABs on grazers is variable and appears to be situation specific. Some grazers are adversely affected by phycotoxins, whereas there are no apparent effects on others. Most experiments carried out within this field deal with grazing on cultures or concentrated samples only, which makes a direct comparison to natural conditions difficult. Grazing studies should extend beyond unialgal cultures to include ingestion on naturally co-occurring non-toxic as well as toxic phytoplankton in natural assemblages (Turner and Tester, 1997; Turner et al., 1998).

Large dinoflagellates of the genus *Ceratium* and *Dinophysis* are commonly observed in the North Sea. Blooms of these species may be harmful by either producing toxins (*Dinophysis*) or by the formation of high biomass (*Ceratium*), which subsequently may lead to oxygen deficiency in the bottom layer in areas of reduced water exchange (e.g. Falkowski et al., 1980). *Dinophysis* produces diarrhetic shellfish poisoning (DSP) toxins, which cause unpleasant, but not dangerous digestive problems for humans. *Dinophysis* spp. usually occur in concentrations of 10^2–10^3 cells l^{-1}, with only few reports of blooms with more than 10^3 cells l^{-1} (Maneiro et al., 2000). Little is known about the interactions between copepods and *Dinophysis* spp., mainly because it has not been possible to culture this dinoflagellate (Sampayo, 1993), and only few in situ grazing measurements exist. Most experiments were carried out with concentrated water samples (e.g. Carlsson et al., 1995; Maneiro et al., 2000, 2002), and there is a lack of in situ observations with the natural phytoplankton assemblages. Studies of zooplankton grazing on *Ceratium*-dominated blooms are also few; *Ceratium* spp. are generally believed to be a poor food source for copepods due to their size and/or shape (Hargrave and Geen, 1970; Granéli et al., 1989). The development of dense *Ceratium* blooms usually takes place in autumn and has been associated with a decline in mesozooplankton (Smetacek, 1981). Laboratory experiments suggest that only larger copepod species (e.g. *Centropages hamatus* and *C. typicus*) and cladocerans are able to graze on ceratians (Nielsen, 1991).

The present work is part of the BIOHAB program, which attempts to study the biological control of HABs in European coastal waters. The aim of this study was to evaluate the importance of mesozooplankton grazing as a biological loss factor of HABs under natural conditions. During a Lagrangian experiment in the North Sea, we investigated whether or not the prominent copepod species significantly impacted the *Dinophysis* spp. and *Ceratium* spp. population through their grazing. Besides grazing and fecal pellet production experiments, egg production was measured to analyse if dinoflagellates affect copepod production processes.

2. Material and methods

Data were collected and experiments performed during two drift experiments with RV HEINCKE in August 2001 (HE-152) in the North Sea (~56°N, ~7°E). The area was scanned by transects and hydrographical stations to determine the three-dimensional distribution of dinoflagellates. The transect work, with on-board cell counts of the most prominent dinoflagellate species, identified patches of enhanced dinoflagellate concentrations. The centre of the patch was marked with a drifting array, composed of a drogue located in the centre of the bloom (15–25 m) and marked at the ocean surface with a GPS equipped buoy. All samples were taken close to the buoy.

Copepods for experiments were collected by vertical net tows (30–0 m) using a WP2 zooplankton

net (180 μm mesh size). After retrieval, zooplankton was gently transferred from the cod-end into 10 l of surface water and transferred to a temperature-controlled room (in situ temperature, 15 ± 1 °C). Females of the dominant zooplankton species (*Calanus helgolandicus*, *Temora longicornis*, *Centropages* sp. and *Acartia* sp.) were incubated to measure ingestion, egestion and egg production. Incubation water was taken from the chlorophyll maximum and pre-screened through a 200 μm mesh to remove larger grazers.

2.1. Grazing

The grazing experiments were conducted with four or five experimental bottles and one or two controls without copepods. From 6 to 25 females (depending on species) were transferred into 1180 ml bottles. The bottles were carefully closed to prevent any air bubbles and placed onto a plankton wheel (1 rpm) in an on-deck flow-through incubator to maintain uniform cell distribution at in situ temperature. Experiments were conducted for 24 h in dim light. Cell concentrations were measured from sub-samples preserved with Lugol's iodine solution prior to, and after the experiments. All phytoplankton species were counted under an inverted microscope (Utermöhl, 1958) and grazing rates were calculated (according to Frost, 1972). Since algal growth rate was sometimes higher in experimental bottles than in control bottles, negative grazing values were obtained in some experiments. These values were treated as zero filtration and ingestion when average grazing values were calculated.

2.2. Fecal pellet production

Fecal pellet production rate is closely related to feeding behaviour, and can be used as an alternative approach for studying grazing. During the present study, fecal pellet production experiments were conducted to provide an independent data set to evaluate the results of the grazing experiments. Four experimental jars and one control jar (0.9 l) were filled with water for determination of fecal pellet production and carried out parallel to the grazing experiments. In each experimental jar, three to five copepods were placed into a suspended insert with mesh on both ends, which allowed the pellets to fall through and prevented coprophagy and/or similar destruction of the pellets by the copepods (for details, see Urban-Rich et al., 1999; Wexels Riser et al., 2002). The experiments were carried out in dim light in a temperature-controlled room (in situ temperature, 15 ± 1 °C) for 6 h. The short incubation time was necessary to avoid food limitation. However, to exclude the impact of diel feeding, the experiments were performed with staggered start times, covering an entire day. The average fecal pellet production was calculated since there were no significant differences in production rates during day and night. At the end of each incubation experiment, the copepods were removed and the contents of the experimental and control bottles sieved through a 20 μm mesh and preserved with buffered formaldehyde (2% final concentration). The fecal pellets were counted under an inverted microscope with phase contrast and ocular micrometer (Zeiss IM 35), and photographs taken with a Nikon 500 digital camera. Samples were also prepared for scanning electron microscopy (as described in Wexels Riser et al., 2003).

2.3. Egg production

Egg production experiments were performed with *C. helgolandicus*, *T. longicornis* and *Acartia* sp. Females were incubated individually in 100 ml spawning chambers filled with water from the chlorophyll maximum. Prior to the experiments, the incubation water was examined carefully under a binocular to check for unwanted introduction of nauplii and eggs. Light and temperature conditions were as described for the fecal pellet production experiments. Eggs were counted after 6, 12 and 24 h to look for signs of cannibalism on the freshly produced eggs since cannibalism is known for *Calanus* and *Temora* (e.g. Kiørboe et al., 1985; Daan et al., 1988; Laabir et al., 1995). Females were removed after 24 h and hatching success determined after another 24 h incubation of the eggs.

3. Results

Even though the present field study was carried out as a Lagrangian experiment, there were significant

Table 1
Initial concentrations, clearance rates (F) as ml female^{-1} h^{-1}, and ingestion rates (I) as cells female^{-1} h^{-1} in 24 h grazing experiments performed with the abundant copepod species present during a dinoflagellate bloom in the North Sea

Species	Initial concentration (cells l^{-1})	*Calanus helgolandicus*		*Temora longicornis*	
		F	I	F	I
Dinoflagellates <20 μm	48240	3.1 ± 0.1	151.3 ± 3.7	0.8 ± 0.1	38.2 ± 3.9
Dinoflagellates 20–50 μm	4720	5.2 ± 0.8	24.4 ± 3.8	1.6 ± 0.1	7.7 ± 0.4
Dinoflagellates >50 μm	480	6.3 ± 1.2	3.0 ± 0.6	1.4 ± 0.8	0.7 ± 0.4
Ciliates	80	4.7 ± 2.8	0.4 ± 0.2	1.5 ± 0.9	0.1 ± 0.1
Diatoms	960	7.4 ± 2.7	7.1 ± 2.7	2.2 ± 0.4	2.1 ± 0.4
Dinophysis norvegica	9940	3.1 ± 0.4	33.8 ± 4.4	0.1 ± 0.1	1.5 ± 0.9
Other *Dinophysis* spp.	200	3.8 ± 1.1	0.8 ± 0.2	0.7 ± 0.3	0.1 ± 0.1
Ceratium furca	2420	6.7 ± 0.7	16.5 ± 1.7	1.2 ± 0.1	2.9 ± 0.2
Other *Ceratium* spp.	480	4.5 ± 0.6	1.9 ± 0.3	1.2 ± 0.3	0.5 ± 0.1
Species	Initial concentration (cells l^{-1})	*Centropages* sp.		*Acartia* sp.	
		F	I	F	I
Dinoflagellates <20 μm	10240	0.4 ± 0.2	3.8 ± 2.1	0.4 ± 0.3	4.2 ± 2.9
Dinoflagellates 20–50 μm	3840	0.7 ± 0.5	2.7 ± 2.1	1.0 ± 0.2	3.7 ± 0.6
Dinoflagellates >50 μm	230	0.5 ± 0.4	0.1 ± 0.1	0	0
Ciliates	160	1.9 ± 1.2	0.3 ± 0.2	0.4 ± 0.4	0.1 ± 0.1
Diatoms	240	2.4 ± 1.4	0.6 ± 0.3	0.9 ± 0.1	0.2 ± 0.01
Dinophysis norvegica	5920	0.2 ± 0.1	1.1 ± 0.6	0	0
Other *Dinophysis* spp.	100	0.2 ± 0.2	0	0.1 ± 0.1	0
Ceratium furca	980	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Other *Ceratium* spp.	500	0.3 ± 0.3	0.1 ± 0.1	0.4 ± 0.2	0.1 ± 0.1

Standard error is given.

differences in phytoplankton abundance and composition between stations. In general, the phytoplankton was dominated by dinoflagellates. Abundances for two stations are given in Table 1. Dinoflagellates smaller then 20 μm mainly comprised *Gymnodinium* species, and *C. furca* and *D. norvegica* were abundant during the entire cruise. The highest concentrations were generally found at 15–25 m depth (Gisselson et al., 2002). During the first leg of the cruise, *D. norvegica* dominated the dinoflagellate biomass, with cell concentrations ranging between 500 and 18,000 cells l^{-1} and making up 40–85% of the total dinoflagellate community larger than 50 μm. *Ceratium furca* was less abundant, with concentrations ranging from <100 up to 2000 cells l^{-1}. During the second leg, *C. furca* was the dominant species, with up to 11,000 cells l^{-1}, while *D. norvegica* concentrations reached ~1200 cells l^{-1} (Gisselson et al., 2002). Maximum chlorophyll a concentrations during the first and second leg varied between 2.3–2.5 and 0.9–2.9 μg l^{-1}, respectively (C. Brussaard and M. Veldhuis, personal communication).

3.1. Grazing

The 24 h grazing experiments revealed that *C. helgolandicus* fed on *D. norvegica*, with an average ingestion rate of 34 cells female^{-1} h^{-1} (Fig. 1). The ingestion rates for *T. longicornis* and *Centropages* sp.

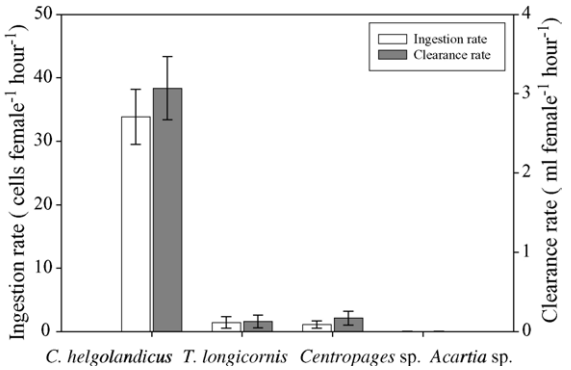

Fig. 1. Mean (±S.E.) 24 h ingestion (white bars) and clearance rates (grey bars) on *Dinophysis norvegica* by four copepod species prominent during the drift study.

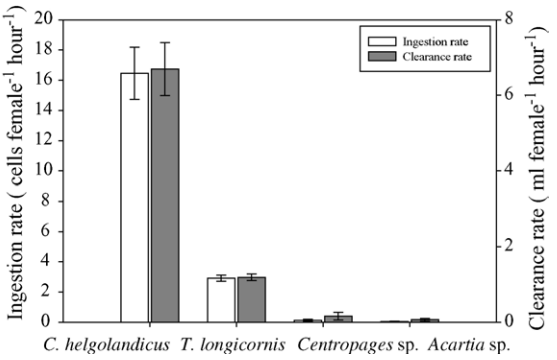

Fig. 2. Mean (±S.E.) 24 h ingestion (white bars) and clearance rates (grey bars) on *Ceratium furca* by four copepod species prominent during the drift study.

were 1.5 and 1.1 cells female^{-1} h^{-1}, respectively, while *Acartia* sp. was not found to graze on *D. norvegica* (Fig. 1). The grazing rates on *C. furca* showed a pattern similar to that with *D. norvegica*. *C. helgolandicus* ingested, on average, 16 cells female^{-1} h^{-1}. *T. longicornis* ingested 2.9 cells female^{-1} h^{-1} and neither *Centropages* sp. nor *Acartia* sp. grazed on *C. furca* (Fig. 2). In these experiments, *D. norvegica* made up ~75% of the dinoflagellate community larger than 50 μm, while *C. furca* comprised between 13 and 18%. Grazing rates on the total pytoplankton community are summarized in Table 1. Clearance rates for *C. helgolandicus* ranged between 3.1 and 7.4 ml female^{-1} h^{-1} for the different prey species. Maximum rates, both for *T. longicornis* and *Centropages* sp., were ~2 ml female^{-1} h^{-1} when grazing on diatoms.

For *C. helgolandicus* and *T. longicornis*, additional 6 h experiments were performed with staggered start times covering an entire day (Table 2). In these experiments, a maximum ingestion rate of 47 *D. norvegica* female^{-1} h^{-1} was found for *C. helgolandicus* at an initial cell concentration of ~13,000 cells l^{-1}.

3.2. Fecal pellet production

Fig. 3 shows the average fecal pellet production rates measured during the 6 h experiments. The concentration of dinoflagellates >50 μm in the incubations ranged from 6500 to 7800 cells l^{-1}, of which *D. norvegica* comprised about 85% and *C. furca* made up 10–15%. *C. helgolandicus* and *T. longicornis* produced about 0.6 fecal pellets copepod^{-1} h^{-1}. Production rates were 0.2 and 0.3 fecal pell-ets copepod^{-1} h^{-1} for *Centropages* sp. and *Acartia* sp., respectively. Close examination of the fecal pellet content revealed that most of the fecal pellets from *C. helgolandicus* were filled with unbroken *D. norvegica* cells (Fig. 4). *Dinophysis* spp. cells were rarely seen in fecal pellets produced by *T. longicornis*, and never observed in pellets produced by *Acartia* sp. and *Centropages* sp.

3.3. Egg production

Egg production rates of *C. helgolandicus* and *T. longicornis* were measured twice during the cruise. Fig. 5 summarizes both experiments, since there were no significant differences. All incubated females were included in the calculations, whether they spawned or not. This inclusion is crucial in establishing the egg production of the copepod populations in the field. 92% of the *C. helgolandicus* present produced eggs during the 24 h incubation ($n = 25$); the average egg

Table 2
Clearance rates (F) as ml female^{-1} h^{-1} and ingestion rates (I) as cells females^{-1} h^{-1} of *Calanus helgolandicus* and *Temora longicornis* at different time intervals

Copepod species	Time	*Dinophysis norvegica*			*Ceratium furca*		
		Start (cells l^{-1})	F	I	Start (cells l^{-1})	F	I
Calanus helgolandicus	02:30–08:30 p.m.	4200	2.2 ± 1.1	9.1 ± 4.6	440	9.2 ± 2.6	4.1 ± 1.1
	08:30 p.m.–02:30 a.m.	18040	2.4 ± 1.1	43.8 ± 15.2	1960	7.2 ± 2.2	14.0 ± 4.4
	03:00–09:00 a.m.	13280	3.5 ± 1.0	46.8 ± 13.7	580	6.1 ± 2.2	3.5 ± 1.3
Temora longicornis	03:30–09:30 p.m.	400	1.2 ± 1.2	0.5 ± 0.5	420	3.5 ± 0.3	1.5 ± 0.1
	09:00 p.m.–03.00 a.m.	220	5.8 ± 1.0	1.1 ± 0.2	640	1.7 ± 1.1	1.1 ± 0.7
	04:00–10:00 a.m.	280	6.0 ± 1.7	1.7 ± 0.5	200	3.9 ± 1.7	1.7 ± 0.3
	11:00 a.m.–05:00 p.m.	200	1.8 ± 0.7	0.4 ± 0.1	1060	5.5 ± 1.4	5.8 ± 1.4

Note variations in the start population of *Dinophysis norvegica* and *Ceratium furca*.

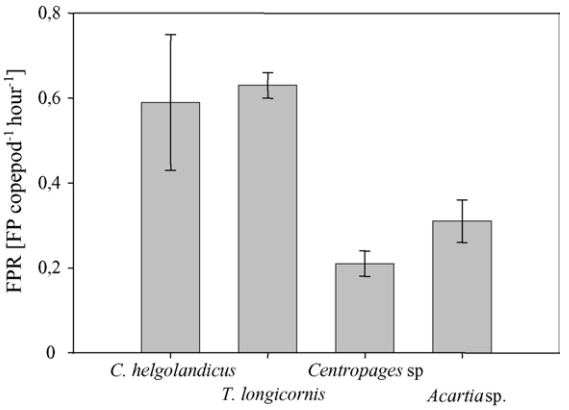

Fig. 3. Mean fecal pellet (FP) production rate (FPR), with standard errors, of abundant copepod species when grazing on the natural phytoplankton community during a dinoflagellate bloom.

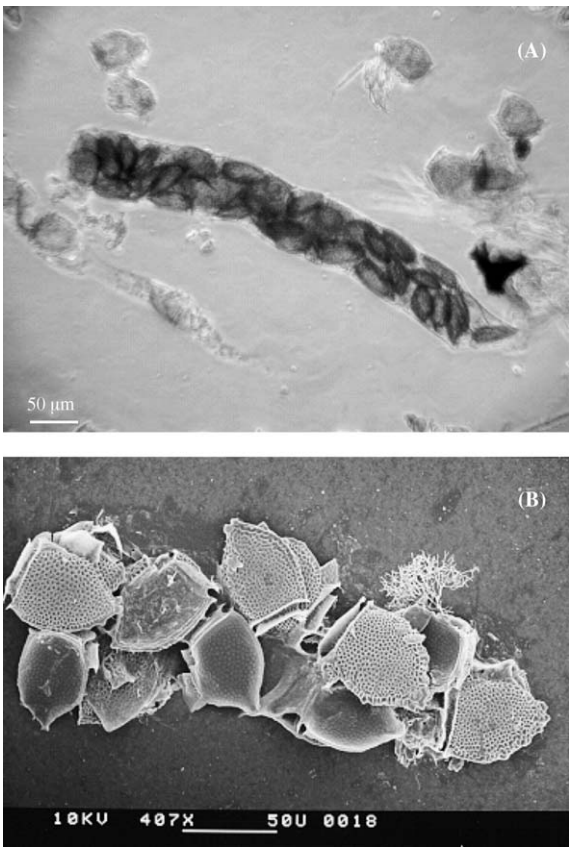

Fig. 4. (A) light microscope, (B) scanning electron photographs of fecal pellets from *Calanus helgolandicus* containing *Dinophysis norvegica* in grazing experiments on the natural plankton community during a drift study in the North Sea.

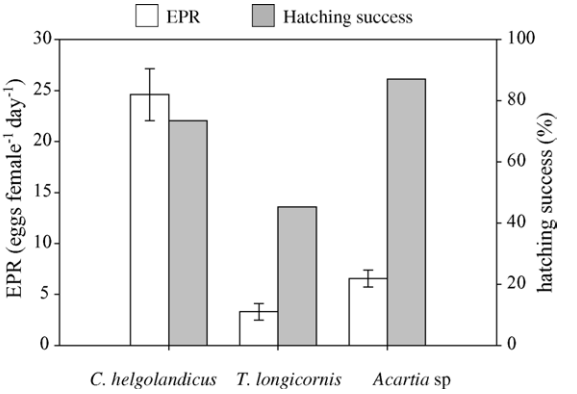

Fig. 5. Egg production rate (EPR) (mean ± S.E.) and hatching success for *Calanus helgolandicus*, *Temora longicornis* and *Acartia* sp. after 24 h incubation in natural seawater.

production rate was 24.6 ± 2.6 eggs female^{-1} day^{-1}. After 24 h incubation, 74% of the eggs hatched. 17% of *T. longicornis* females produced eggs (n = 63), with an average egg production rate of 3.3 ± 0.8 eggs female^{-1} day^{-1}, and only 45% of the eggs hatched after 24 h. Experiments were performed with natural water collected at the chlorophyll maximum. Offering an alternative food to *T. longicornis* reduced its cannibalism on its own eggs or nauplii (Daan et al., 1988). However, *T. longicornis* and *C. helgolandicus* frequently fed on their own eggs. By counting the produced eggs every 6 h, it was possible to correct for this behaviour, but the production rates given for these two species must be considered as minimal estimates.

The egg production rate of *Acartia* sp. was 6.5 ± 0.8 eggs female^{-1} day^{-1}; 83% of the incubated females produced eggs (n = 24). Hatching success was highest for this species, with 87% of the eggs hatched after 24 h of incubation. There was no indication of egg cannibalism by the *Acartia* sp.

4. Discussion

Field studies investigating the interactions between HABs and copepods produced variable results, ranging from no apparent effects from phytoplankton toxins (reviewed by Turner and Tester, 1997; Turner et al., 1998; Lincoln et al., 2001) to avoidance and mortality (Fiedler, 1982; Huntley, 1982). Potential, adverse effects of phytoplankton toxins on copepods might include selective or limited grazing, and

reduced egg production and egg hatching. These aspects were the focus of our investigations e.g. to determine the potential impact of copepods on the development and fate of *D. norvegica* and *C. furca* blooms in the North Sea.

4.1. Grazing impact of copepods on HABs

Grazing experiments as well as microscope examination of fecal pellets clearly showed that *C. helgolandicus* fed on *D. norvegica* (see also Wexels Riser et al., 2003). The fecal pellets of *T. longicornis* contained only single, undigested cells of *D. norvegica*, consistent with the results of the grazing experiments. This presence of *Dinophysis* spp. cells in fecal pellets of *T. longicornis*, grazing on an autumn bloom of the smaller species *D. acuminata*, has been reported by Maneiro et al. (2002). For *Acartia* sp., no ingestion could be detected and no cells were seen within the fecal pellets. Turner and Anderson (1983) observed that *D. acuminata* was not grazed by *A. clausi*, and Maneiro et al. (2000) also showed that *A. clausi* was unable to feed on *Dinophysis* spp., while the copepods *T. longicornis* and *Oithona nana* were able to do so. In contrast, Carlsson et al. (1995) found *A. clausi* grazed significantly on *D. acuminata*. We observed that *C. helgolandicus* fed efficiently on *C. furca*, but these results could not be confirmed by fecal pellet examination. The assumption that *C. furca* is unsuitable food for copepods due to size and structure (Hargrave and Geen, 1970; Granéli et al., 1989) is obviously not generally true.

Elbrächter (1973) observed that copepods sucked out the cellular contents of *C. tripos* cells, a mechanism noticed earlier by Wickstead (1962). This capacity enables copepods to graze on larger *Ceratium* species. Hence, an increase in empty *Ceratium* shells should have been observed in the experimental bottles compared to the controls, but this was not the case. Further investigations and direct observations are needed to answer the question how copepods graze on cells such as *Ceratium*. The phase of cell division, which usually occurs diurnally synchronized within a *Ceratium* population (Weiler and Chisholm, 1976), may be a favourable time for copepods to graze on them. During cell division, half of the cellulose cell plates of *Ceratium* have to be substituted, thus the dividing cells are exposed until the cell walls are rebuild (Elbrächter, 1973). It may be possible, that dinoflagellates of the genus *Ceratium* are susceptible for copepod grazing only during their phase of cell division. Synchronized cell division within a population may protect them against such selected grazing, since copepods are not able to correspond such an event. For corroboration or rejection of this hypothesis additionally grazing experiments with staggered starts and a duration of 6 h were carried out. The diurnal feeding behaviour of *C. helgolandicus* and *T. longicornis* were investigated. *C. furca* exhibited a clearly diurnal synchronized cell cycle with a maximum in cells with incomplete horn generation (newly divided cells) between 8 and 11 a.m. during the present field study (Gisselson et al., 2002). However, problems arise because the initial population of dinoflagellates varied greatly between the different experiments (Table 2). Therefore, it is difficult to interpret diurnal differences in the ingestion or clearance rates. But, it became again obvious that *C. helgolandicus* can graze very efficiently on *D. norvegica* and *C. furca* and maximum ingestion rates as high as 47 *D. norvegica* cells female^{-1} h^{-1} and 14 *C. furca* cells female^{-1} h^{-1} were observed (Table 2). In Fig. 6, ingestion rates for *C. helgolandicus* and *T. longicornis* are plotted against the initial concentration of *D. norvegica* for all grazing experiments. One *C. helgolandicus* fecal pellet, on average, contained 19 ± 2.5 cells fecal pellet^{-1}, as found in an additional experiment carried out during the present cruise (see Wexels Riser et al., 2003), the ingestion rate can also be calculated for the fecal pellet experiment, and is included in this figure. As expected, ingestion rates of *C. helgolandicus* increased with increasing initial cell concentration. It is well documented that *Calanus* exhibits higher ingestion rates with increasing food availability, and this rate asymptotically approaches a maximum (e.g. Frost, 1972; Gamble, 1978). Maximum ingestion rate on *D. norvegica* seems to be achieved at about 75 cells female^{-1} h^{-1}. Ingestion rates for *T. longicornis* remained low, even during high *D. norvegica* concentrations.

4.2. Influence of the dinoflagellate bloom on the reproduction processes

Egg production rates are influenced by several factors, with the availability and quality of food the

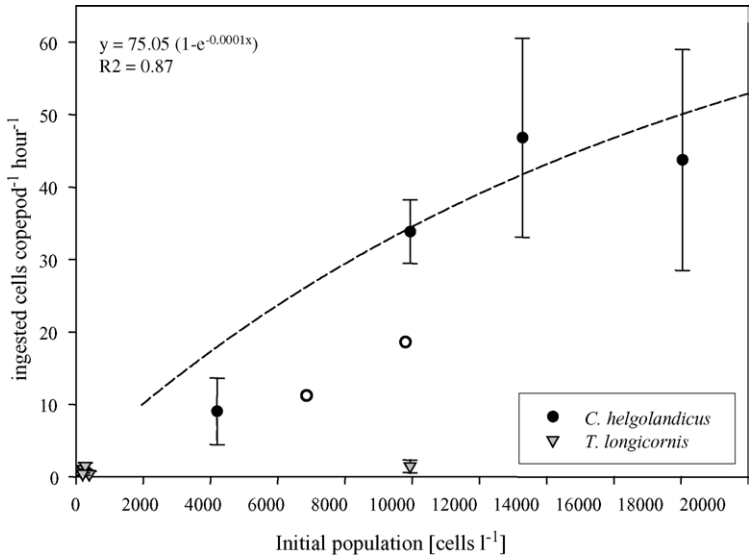

Fig. 6. Ingestion rates for *Calanus helgolandicus* (filled circles) and *Temora longicornis* (triangles) grazing on *Dinophysis norvegica* plotted against the *D. norvegica* initial population in experiments (mean ± S.E.). The open circles indicate the calculated ingestion rate from the fecal pellet experiment in this study and Wexels Riser et al. (2003). Regression line is the Ivlev model fit to the data of *C. helgolandicus* ingestion rates.

most important ones. Since there were no reference stations during the cruise outside the dinoflagellate bloom, egg production rates must be compared to other studies, carried out in this region at the same time of the year. The low egg production rates for *T. longicornis* and *Acartia* sp. found during this study fell into the same range found during other studies (Nielsen, 1991; Fransz et al., 1989), and can therefore hardly be related to the dinoflagellate bloom. However, hatching success and the proportion of females producing eggs among *T. longicornis* were low, indicating these copepods experienced less favourable conditions. High hatching success and high percentages of the incubated *C. helgolandicus* and *Acartia* sp. females producing eggs lead to the assumption that they were in good condition during the study. *Centropages* sp. was in bad shape throughout the experiments: ectoparasites were observed on the carapax of the copepods. Low fecal pellet production and low grazing rates may result from this infection.

4.3. Selective feeding behaviour and prey size

Low growth rates of dinoflagellates compared to other phytoplankton species of the same size (Smayda, 1997) lead to the question if selective grazing by copepods may contribute to dinoflagellate blooms by preferring other species. Despite the high abundance of *D. norvegica*, ingestion and clearance rates by *T. longicornis* remained low. Few complete cells were observed within some of the fecal pellets, which show that they are able to graze on larger *Dinophysis*. Since only complete cells were found within the fecal pellets of the copepods, it is likely that the mechanical stability of the *D. norvegica* cell is very high. Therefore, it may be that the copepod species under investigation were unable to fracture them with their mandibles. Mechanical stability of diatoms was tested by Hamm et al. (2003), but is not known to be tested for dinoflagellates yet. The fact that *D. norvegica* cells were neither observed within the fecal pellets of *Acartia* sp. nor ingestion was detected, suggests that the cells are simply too large to be grazed by the smaller species. Hansen et al. (1994) concluded that the average ratio of the size of the predatory copepod to that of its prey ranges from 10:1 to 30:1 (average 18:1), size being determined as the equivalent spherical diameter (ESD). The ESD of *A. clausi* is ~350 μm and a cell volume of 18,000 μm^3 for *D. norvegica* (Smetacek, 1975) gives an ESD of 33 μm. The predator prey ratio is therefore in the upper range. However, *Acartia* sp. was found not to graze on *D. norvegica*. In general, the ability of copepods to ingest

their prey is not only dependent on the size ratio. Structural characteristics like the stability of a cell must also be taken into account.

4.4. Contribution of fecal pellets to pathways for DSP toxins

Fecal pellets containing *Dinophysis* cells, as observed for *C. helgolandicus*, may contribute to pathways of DSP through the food web, which are usually not considered during studies of the fate of HABs. Vertical flux and recycling of fecal pellets then become an important aspect how toxins are distributed in and transferred through the water column. The contribution of fecal pellets to the vertical flux of particulate organic carbon varies a lot, and can range from <1 to 99% (Smetacek, 1980; Bathmann et al., 1987; Viitasalo et al., 1999; Wexels Riser et al., 2001). The recycling of fecal pellets in the water column seems to be highly dependent on the zooplankton community structure and may be linked to different feeding behaviour (Viitasalo et al., 1999; Wassmann et al., 1999, 2003).

Copepods can be highly efficient in breaking down fecal pellets, while ingesting only a small portion of the pellet (Lampitt et al., 1990), while cyclopoid copepods, particularly of the genus *Oithona* are believed to graze on fecal pellets (González and Smetacek, 1994). Such behaviour reduces the vertical export of fecal material. Whether or not fecal pellets are exported or recycled within the water column may significantly affect the distribution and concentrations of toxins throughout the water column. Sinking fecal pellets may channel the otherwise slowly sinking phytoplankton cells rapidly to greater depth. Therefore, ''toxic'' fecal pellets containing *Dinophysis* potentially are an important vehicle vectoring toxins to the benthic food web.

4.5. Potential grazing impact on the investigated dinoflagellate bloom

With the abundance of copepods within the water column, counted for selected stations, it was possible to calculate the potential grazing impact on the in situ dinoflagellate community. On average 2600 *C. helgolandicus* m^{-2} were present in the upper 30 m during this study, including CV stages, male and female copepods. Due to this relatively low abundance and the very high concentrations of dinoflagellates, their grazing impact on the standing stocks of *D. norvegica* and *C. furca* were both calculated to be less then 5%, assuming the same grazing impact for CV stages and males as measured in the experiments with females. *T. longicornis* abundance was about 14,000 animals m^{-2} (0–30 m), including CV stages, males and females. Therefore, the mean grazing impact of *T. longicornis* on *C. furca* was about 5%, while the average impact on the standing stock of *D. norvegica* was calculated to be 3% day^{-1}. Data on the distribution of copepods within the water column are not available. Zooplankton abundance was integrated over the upper 30 m of the water column, while the water for the experiments was always taken from the chlorophyll maximum. It is therefore possible that the actual copepod grazing pressure on dinoflagellates is lower, or even higher, because of a horizontal mismatch or match between the copepods and the dinoflagellates.

Problems arise for general interpretations and comparison between the different results due to strong fluctuations in the dinoflagellate abundances. Fluctuations and horizontal patchiness within the vertical distribution may result from active or passive movements of the cells within the water column. Water sampling with Niskin bottles may therefore lead to incomplete vertical sampling of the whole phytoplankton community. Furthermore, it is possible that strong winds pushed the buoy with the drifter out of the bloom centre and led to sampling of different water masses. However, the general ability to ingest harmful algal species like *D. norvegica* and *C. furca* could be shown for *C. helgolandicus* and *T. longicornis*. Hence, the influence of copepods on the development and the fate of a HAB is dependent on the species composition and abundance.

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