

REPRESSION OF COPEPOD FEEDING AND FECUNDITY BY THE TOXIC HAPTOPHYTE *PRYMNESIUM PATELLIFERUM*

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Late copepodids and adults of *Acartia clausi* GIESBRECHT showed no mortality when kept in a very dense culture (10^9 cells l^{-1}) of a toxic strain of the haptophyte *Prymnesium patelliferum* GREEN, HIBBERD & PIENAAR, for 48 h at 26-28 PSU. However, the haptophyte had strong negative effects on copepod egestion and reproduction rates, both when the haptophyte was offered as the only food, and when offered in mixtures with *Rhodomonas baltica* KARSTEN *sensu* ZIMMERMANN, an alga known to be ingested and support reproduction in *Acartia*. The rates were depressed already at concentrations of $0.1-0.3 \cdot 10^6$ cells l^{-1} of *P. patelliferum*, and decreased further with increasing concentration of the haptophyte. At typical bloom concentrations ($\geq 4 \cdot 10^6$ cells l^{-1}) of *P. patelliferum*, the rates were no greater than those of starved copepods. These results demonstrates that zooplankton feeding and reproduction in coastal waters may be constrained by presence of toxic haptophytes, also when these algae occur in moderate concentrations and mortality is not registered.

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INTRODUCTION

Potentially toxic haptophytes occur world-wide, and toxic blooms of *Prymnesium* species have been known for almost hundred years (MOESTRUP 1994). Seasonal blooms of haptophytes from the genera *Prymnesium* and *Chrysochromulina* have caused considerable loss in cultivated fish and other marine organisms in both brackish and marine coastal waters, especially around Scandinavia during the last decade (GRANÉLI & al. 1993; EDVARDSEN & PAASCHE in press). Today blooms of toxic haptophytes are considered a permanent threat to Scandinavian mariculture (GRANÉLI & al. 1993).

The toxic potential of most haptophyte species is still poorly studied, and most such studies report on acute toxicity to the 'laboratory organism' *Artemia* spp., cytological material, microalgae or fish (see reviews by MOESTRUP 1994; EDVARDSEN & PAASCHE in press). Toxic effects on copepods have received little attention, despite that copepods have a central role in the marine food web, both as mediators of energy to higher trophic levels, such as commercial fish (e.g. CUSHING 1995), and as selective predators with a potentially important role in plankton community development (e.g. RIEGMAN & al. 1993; VERITY & SMETACEK 1996, and references therein). NIELSEN & al. (1990) reported low *in situ* concentrations

and activities, and high mortality, of bacteria, microzooplankton and copepods within the subsurface bloom of *Chrysochromulina polylepis* MANTON & PARK in the Kattegat 1988. However, their following laboratory experiments with cultures of *C. polylepis* isolated from the bloom, did not reproduce the copepod mortality observed *in situ*, and egg production was reduced only in monocultures of the haptophyte, but not in polycultures with *R. baltica*. VALKANOV (1964) demonstrated acute toxicity of field collected *Prymnesium* (cf. *patelliferum*, see GREEN & al. 1982) on a large number of organisms. However, in contrast to most other organisms tested, the copepods (*Cyclops* sp. and *Calanipeda* sp.) did not display acute mortality or signs of 'exhaustion' even after 3 d exposure to $1.1 \cdot 10^8$ cells l^{-1} . In accordance with these observations, NEJSTGAARD & al. (1995) found no mortality, or visible effect on swimming activity for *Calanus finmarchicus* GUNNERUS exposed to ichthyotoxic *P. patelliferum* at a concentration of 10^9 cells l^{-1} for 2 d, although feeding on the haptophyte was strongly constrained at much lower concentrations.

Here we report on sublethal effects of *P. patelliferum* GREEN, HIBBERD & PIENAAR on feeding and reproduction of *Acartia clausi* GIESBRECHT, an important calanoid copepod in the food web of brackish and coastal waters (cf. HANSSON & al. 1990, TESTER & TURNER 1991).

MATERIALS & METHODS

Algae

Two similar sized algae were used in the experiments; the haptophyte *Prymnesium patelliferum* (7-9 µm equivalent spherical diameter, ESD), and the cryptophyte *Rhodomonas baltica* KARSTEN *sensu* ZIMMERMANN (6-8 µm ESD). *P. patelliferum* was isolated by Torbjørn M. Johnsen in Hylsfjorden, Western Norway (59°33' N, 6°24' E) in August 1989, during a *P. parvum/patelliferum* bloom associated with high fish mortality (KAARTVEDT & al. 1991; EIKREM & THRONDSSEN 1993). Stock cultures were kept at 26-28 practical salinity units (PSU), 10° C, in f/2 medium (GUILLARD & RYTHER 1962), and a 14/10 L/D light cycle at ca 15 µmol m⁻² s⁻¹. It was distinguished from *P. parvum* by TEM at the start of the experimental period (A. LARSEN, pers. commn). A hepatocytic cell test demonstrated a high toxicity of the *P. patelliferum* strain used (NEJSTGAARD & al. 1995). *R. baltica* was bought from IFREMER, Brest, France. It is a well studied food algae for cultures of copepods, such as *Acartia* spp., and was offered in surplus concentrations (11 · 10⁶ cells l⁻¹, equivalent to ca 900 µg carbon l⁻¹, cf. STØTTRUP & JENSEN 1990; NEJSTGAARD & al. 1995). *P. patelliferum* used in the acute toxicity test was grown in a 5 l batch culture until early stationary phase (25 d), using f/2 medium diluted to f/20, and a 14/10 L/D light cycle at ca. 25 µmol m⁻² s⁻¹. *P. patelliferum* used in other experiments was grown under similar conditions, but in 5 l semicontinuous

cultures diluted every 3 to 5 d, to keep cells in late exponential growth phase (≥ 0.1 d⁻¹). *R. baltica* was kept under similar conditions, but using f/2 medium and continuous culture with daily renewal of 15-25 %. Algae ESD, growth, and cell concentrations were monitored daily on a model ZM Coulter Counter. Food suspensions were prepared by diluting cultures with GF/F filtered sea water immediately before the experiments. Cultures and experiments were kept at 13° C and 26-28 PSU.

Copepods and incubation experiments

Adults of *Acartia clausi* were isolated from surface waters of Byfjorden (60°27' N, 5°17' E), north of Bergen, Norway in December 1993, and were cultured in 90-l tanks, using a mixture of *Isochrysis galbana* PARKE, *R. baltica* and *Oxyrrhis marina* DUJARDIN, as described in KLEIN BRETELER & GONZALEZ (1986).

Two series of experiments were performed with *A. clausi* between 20-24 February, and 7-11 March 1994, respectively. Females were pipetted individually into 33 ml polystyrene vials, which were carefully locked with polyethylene snap caps, excluding all air, mounted on an incubation wheel (ca 1 RPM), and incubated for four 24-hour periods (day 0-3) in dim light. After each 24-h period living females were transferred to new vials, whereafter egg and faecal pellets were enumerated directly in the vial under a dissection microscope at 50x. At day 0, all females were incubated in 11 · 10⁶ *R. baltica* l⁻¹ to stimulate egg

Table 1. Experiment I, *Acartia clausi*. Faecal pellet egestion, egg production and hatching success when incubated in different concentrations of *Rhodomonas baltica* (R) and *Prymnesium patelliferum* (P). Number in brackets denotes ± 95 % confidence intervals for the mean (n = 8).

Algae suspension (10 ⁶ cells l ⁻¹)		Faecal pellet egestion (female ⁻¹ d ⁻¹)		Egg production (female ⁻¹ d ⁻¹)		Hatching success (%)
R	P	Day 1	Day 2 and 3	Day 1	Day 2 and 3	Day 1-3
11	0	17 (3)	14 (6)	19 (3)	15 (3)	68 (6)
11	0.25	15 (4)	13 (4)	16 (5)	13 (2)	62 (5)
11	4.0	8 (2)	2 (2)	9 (4)	4 (3)	58 (9)
0	0.25	2 (2)	0 (0)	11 (5)	2 (2)	39(27)
0	4.0	2 (1)	1 (0)	7 (3)	1 (1)	41(22)
0	0	1 (1)	1 (1)	8 (2)	3 (2)	62(13)

Table 2. Experiment II, *Acartia clausi*. Symbols are as in Table 1.

Algae suspension (10 ⁶ cells l ⁻¹)		Faecal pellet egestion (female ⁻¹ d ⁻¹)		Egg production (female ⁻¹ d ⁻¹)	
R	P	Day 1	Day 2 and 3	Day 1	Day 2 and 3
11	0	13 (5)	25 (3)	20 (6)	23 (3)
11	0.10	17 (5)	20 (6)	14 (7)	13 (3)
11	0.25	7 (5)	13(10)	9 (3)	10 (8)
11	0.63	5 (3)	15 (8)	9 (3)	6 (4)
11	1.6	14 (6)	9 (6)	12 (2)	8 (5)
11	4.0	4 (2)	7 (4)	12 (4)	6 (3)
11	10	1 (1)	2 (2)	8 (3)	3 (2)
0	0	0 (0)	0 (0)	9 (2)	2 (1)

production. At the start of day 1, egg-producing females were pipetted in a random order into vials containing the experimental food suspensions (eight parallels treatment⁻¹, see Tables 1 and 2 for treatments). The experimental food suspensions were renewed at the start of days 2 and 3. In experimental series I, nauplii were counted in the vials 48 h after females were removed. Hatching success was defined as the percentage nauplii hatched from the eggs produced.

RESULTS

Late copepodids and adults of *Acartia clausi* showed no mortality, or visible effect on swimming activity when held in very dense early stationary phase cultures (10^9 cells l⁻¹) of *Prymnesium patelliferum* for 48 h. However, females of *A. clausi* showed strong sublethal effects correlated with the ambient concentration of *P. patelliferum*. Faecal pellet production (egestion) and egg production rates for females incubated in different mono-cultures of *P. patelliferum* were not significantly different from those for individuals incubated in filtered water (Table 1). This shows that *P. patelliferum* was not appreciably ingested and it did not support egg production in *A. clausi*.

Addition of *P. patelliferum* to cultures of *Rhodomonas baltica* significantly depressed egestion and egg production rates in *A. clausi* with increasing concentration of *P. patelliferum* (Tables 1, 2). After 3 days exposure to $\geq 6.3 \cdot 10^5$ *P. patelliferum* l⁻¹, females had produced significantly ($p < 0.01$, Scheffé's test, ZAR 1996) less faecal pellets and eggs, compared to females offered *R. baltica* alone (Figs 1, 2). At the highest concentrations of *P. patelliferum* ($4 \cdot 10^6$ l⁻¹) numbers of accumulated faecal pellets and eggs at day 3 were still not significantly different from that for starved animals ($p > 0.14$, Scheffé's test).

At $2.5 \cdot 10^5$ *P. patelliferum* l⁻¹, however, accumulation of faecal pellets and eggs was only slightly affected in experiment I, while it was significantly depressed ($p < 0.04$, Scheffé's test) at both 1.0 and $2.5 \cdot 10^5$ *P. patelliferum* l⁻¹ in experiment II. This suggests that the cell specific toxic effect increased slightly in the *P. patelliferum* culture between the experiments.

The accumulation of nauplii emphasised the pattern of egg accumulation in experiment I (Fig. 1), and the hatching success tended to decrease in presence of *P. patelliferum* (Table 1). However, the samples were relatively small and consequently there were no significant differences in hatching success between the treatments.

DISCUSSION

Copepodid tolerance for *Prymnesium* toxins

The copepodids of *A. clausi* appeared to have a very high tolerance for the toxic *P. patelliferum*. The *P. patelliferum*

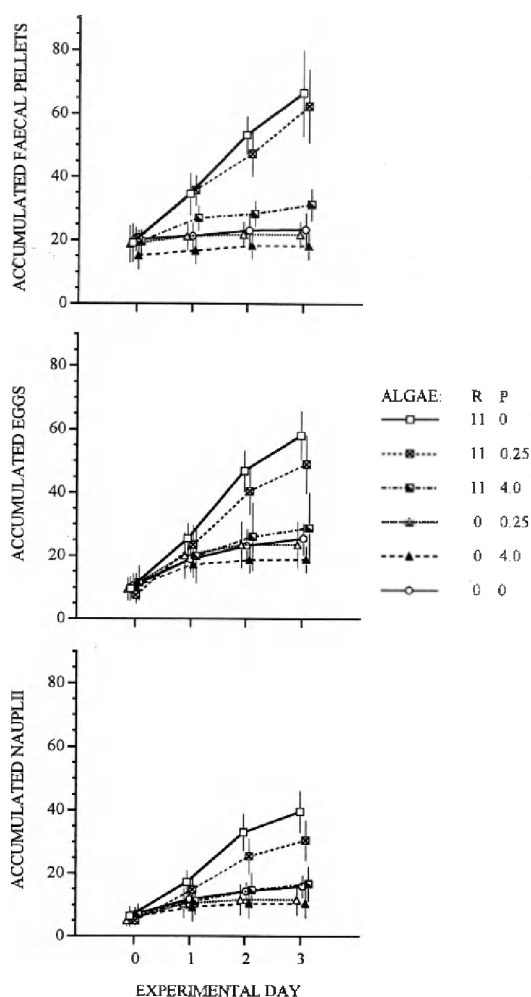


Fig. 1. Experiment I, *Acartia clausi*. Accumulated faecal pellets, eggs and nauplii per female exposed to different concentrations of the algae: *Rhodomonas baltica* (R) and *Prymnesium patelliferum* (P), (10^6 cells l⁻¹). Day 0-values were obtained after 24 h incubation with *R. baltica* ($1.1 \cdot 10^7$ cells l⁻¹). Y-bars denotes 95 % confidence intervals for the mean. Data points are separated on the X-axis for clarity.

strain used here was isolated during a bloom that caused severe fish mortality in 1989 (KAARTVEDT & al. 1991; EIKREM & THRONDSEN 1993). Later this strain demonstrated a high toxicity to hepatocytes (NEJSTGAARD & al. 1995), and allelopathic effects on *Pavlova lutheri* (DROOP) GREEN, and *Emiliania huxleyi* (LOHMANN) HAY & MOHLER (NEJSTGAARD & EVENSEN, own obs.). A simultaneously isolated *P. patelliferum* strain showed toxicity to *Artemia* nauplii (LARSEN & al. 1993). However, the survival of

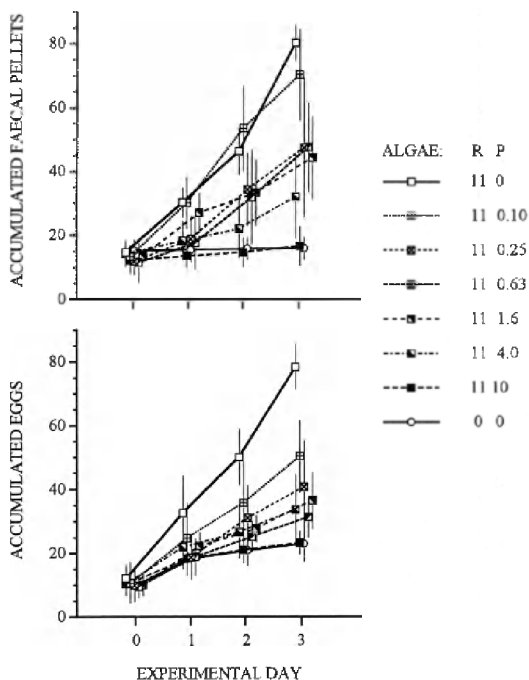


Fig. 2. Experiment II, *Acartia clausi*. Algae suspensions are as in Table 2, symbols are otherwise as in Fig. 1.

A. clausi was not influenced by two days exposure to 10^9 *P. patelliferum* l^{-1} , a concentration that is at the upper limit of previously reported maximal concentrations found in the field ($1.6 \cdot 10^9$ cells l^{-1} , EDVARDSEN & PAASCHE in press), and by far exceeds concentrations that may cause extensive fish kills ($\leq 2.2 \cdot 10^6$ cells l^{-1} , KAARTVEDT & al. 1991). Similar results have been reported for other copepods, while most other tested organisms, including other crustaceans such as *Artemia* spp., die at much lower concentrations of *Prymnesium* spp. (VALKANOV 1964; NEJSTGAARD & al. 1995; LARSEN & al. 1993).

Sublethal effects

A. clausi did not feed or reproduce in monocultures of *P. patelliferum*. The observed egg production during day 1 in copepods not showing significant egestion is explained by the time lag for conversion of ingested food into egg production, which is on the order of day(s), whereas egested gut material reflects the feeding activity within the last hour(s) (e.g. KJØRBOE & TISELIUS 1987; TESTER & TURNER 1990). Thus the very low egestion rates imply that the haptophyte is not ingested by *A. clausi*.

The egestion and reproduction by *A. clausi* in suspensions with the food algae *R. baltica*, decreased when *P. patelliferum* was added. However, in the mixtures of *R. baltica* and low concentrations of the haptophyte, the copepods appeared to keep up a steady egestion and egg production rate even after three days. This would not be expected if copepods were accumulating toxins by ingestion, until incapacitated, as has been shown for toxic dinoflagellates (IVES 1987). Alternatively, if the copepod rejects toxic cells behaviourally (cf. HUNTLEY 1986) one might expect a negative effect due to handling time of the non ingested *P. patelliferum*. But this effect should be limited as *R. baltica* was present in surplus concentrations, and the copepods were adapted to feed on *R. baltica* as it was used in the copepod cultures. However, when *P. patelliferum* was present at bloom concentrations ($\geq 4 \cdot 10^6$ cells l^{-1}) in the food mixtures, egestion and egg production rates were not significantly different from those of starved animals. *P. patelliferum*, as well as *P. parvum* and *Chrysochromulina polylepis* are known to produce exotoxins that have generalised membrane effects (EDVARDSEN & PAASCHE in press). This suggests that the copepods may instead have been affected by toxins from *P. patelliferum* in the ambient water. Similar grazing inhibition of normally palatable cells suspended in medium with inhibitory extracellular substances has previously been found for dinoflagellates (e.g. HUNTLEY & al. 1986).

Toxic effects in the field

Haptophytes may lose their inhibitory effects *in vitro*, and toxicity may be a species-specific, or even strain-specific feature, with a complex and still largely unknown coupling to *in situ* growth conditions (as discussed in e.g. EDVARDSEN & PAASCHE in press). Field studies during blooms of the haptophytes *Phaeocystis* spp. indicate that they are not extensively preyed upon by copepods during their exponential growth phase (HANSEN 1995, and references therein), but may be utilised when the algae becomes senescent (ESTEP & al. 1990). NIELSEN & al. (1990) reported increased mortality, low activity and low abundance of copepods, microzooplankton and bacteria in the *C. polylepis* bloom in 1988, while the opposite was true during the decline of the bloom. Accordingly, monocultures of *C. polylepis* isolated from the bloom did not support copepod egg production in the following laboratory experiments. However, the cultures in NIELSEN & al. (1990) did not reproduce the copepod mortality observed *in situ*, and there was no reduction in egg production rates when *C. polylepis* was offered together with *R. baltica*. This suggests that lab studies, such as the one presented here, may significantly underestimate the negative effects of potentially toxic haptophytes *in situ*. Further, toxin pro-

duction from *Prymnesium* spp. is the most pronounced when ambient inorganic phosphorus concentrations are low (SHILO 1967; LARSEN & al. 1993), as has been recorded during blooms of *P. patelliferum* and *P. parvum* (AURE & REY 1992; THINGSTAD & al. 1993). The *P. patelliferum* cultures used in the study of sublethal effects were kept in late exponential growth phase by dilution with f/20 medium every 3 to 5 days, and are not likely to have been phosphate-limited. Thus it is likely that the results presented here represent a minimum estimate of the toxic potential of *P. patelliferum*.

Although there are several records of bloom and sub-bloom concentrations of *Prymnesium* from coastal waters (EDVARDSEN & PAASCHE in press), the abundance of haptophytes in natural water samples has probably been underestimated, or often even completely overlooked, because they have a small cell size and usually do not fix well (EIKREM & THRONDSSEN 1993).

We conclude that toxic haptophytes, such as *P. patelliferum* may not only cause occasional conspicuous bloom effects, such as fish kills, but they may also have a substantial impact on the plankton food chain in coastal waters, by constraining the zooplankton feeding and reproduction even at commonly occurring sub-bloom concentrations.

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