JOURNAL OF PLANKTON RESEARCH | VOLUME 28 | NUMBER 4 | PAGES 429–436 | 2006

Effects of nitrogen stressed algae on different *Acartia* species

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Received September 7, 2005; accepted in principle January 10, 2006; accepted for publication February 1, 2006; published online February 3, 2006

Communicating editor: K.J. Flynn

We studied the reproductive response of two copepod species, Acartia tonsa and Acartia clausii, fed algae with different C:N ratios (4.5 and 9.1 molar ratios respectively) in order to investigate the influence of nutritional imbalances on calanoid copepods egg production. Adult females were incubated with the cryptophyte Rhodomonas sp. at saturating concentrations. The algae were cultured under nitrogen depleted and sufficient conditions. Ingestion rates of the animals fed with different algae and their response in terms of egg production and hatching success of the eggs were quantified. Both species produced more egg when fed with nitrogen-limited algae. Ingestion rates and egg hatching differed between species, but were not significantly affected by the quality of the food. The only difference between the two species in their reaction to food quality was that A. tonsa increased the number of resting eggs, whereas no resting egg production was observed in A. clausii when fed with nitrogen limited algae. These results support the recent suggestion that a moderately high prey C:N ratio (10–15) supports a higher egg production than a C:N ratio substantially <10.

INTRODUCTION

Copepod ingestion and production rates are influenced by physical and biological environmental factors (Runge, 1984; Ambler, 1986; Rothschild and Osborn, 1988). A considerable body of literature already exists on the influence of the feeding environment on the growth and reproduction of a wide number of zooplankton species (Mayzaud *et al.*, 1998; Gomez-Gutierrez and Peterson, 1999; Nejstgaard *et al.*, 2001; Turner, 2004). Based on these findings, it has become increasingly clear, that not only food quantity determines the success of zooplankton in their environment, but that differences in food quality may be just as important (Kiørboe *et al.*, 1985; Houde and Roman, 1987; Støttrup and Jensen, 1990; Kleppel and Burkart, 1995; Koski *et al.*, 1998; Khanaychenko, 1999; Klein Breteler and Koski, 2003; Jones and Flynn, 2005).

One of the main aspect of food quality under study in marine systems is the biochemical composition of the food, or more specifically the fatty acid spectrum of the different algal groups (Klein Breteler and Gonzalez, 1988; Jónasdóttir *et al.*, 1995; Kleppel and Burkart, 1995; Müller-Navarra, 1995). Other food quality factors that have been investigated, especially in freshwater systems, include the nutrient content of the food, or more specifically the C:N:P stoichiometry, the morphology and biochemical components such as amino acids and sterols (Urabe and Watanabe, 1992; Ederington *et al.*, 1995; Frost *et al.*, 2005). In fact, several authors have shown that even within a single algal species the quality as food for zooplankton can vary dramatically as a result of differences in growth conditions (Jónasdóttir, 1994; Jónasdóttir and Kiørboe, 1996; Urabe and Sterner, 2001; Boersma and Kreutzer, 2002; Jones *et al.*, 2002; Villar-Argaiz and Sterner, 2002; Jones and Flynn, 2005).

In the field, several studies have followed growth and reproduction of copepods throughout blooms of phytoplankton, during which growth conditions of the algae change dramatically as a result of nutrient and/or light depletion (Fransz, 1976; Tang and Dam, 1999; Kleppel and Hazzard, 2000). Typically, the C:nutrient ratios in the algae continually increase throughout the bloom (Ambler, 1986; Båmstedt, 1988; Jónasdóttir *et al.*, 1998; Touratier *et al.*, 1999; Van Nieuwerburgh *et al.*, 2004). However, during a phytoplankton bloom factors may change both independently or in correlation with others, it is thus difficult to link changes in egg production of

doi:10.1093/plankt/fbi131, available online at www.plankt.oxfordjournals.org

consumers to any single specific factor in complex natural systems.

It is often argued that macronutrient stoichiometry of the food is an important factor for the trophic transfer in marine food webs (Burdloff *et al.*, 2002; Jones *et al.*, 2002; Klein Breteler and Koski, 2003; Anderson *et al.*, 2004; Jones and Flynn, 2005; Mitra and Flynn, 2005). However, the effect of algae growth conditions on the growth and reproduction of zooplankton is rarely studied directly in laboratory settings. This study seeks to fill this gap in our knowledge, which is especially important for the development of more realistic ecosystem models, as they often do not include different quality values of food (Checkley, 1980; Mitra and Flynn, 2005).

Copepods of the genus *Acartia* have a worldwide distribution. They do not have large lipid reserves and hence normally react to experimental treatments rapidly (Kiørboe *et al.*, 1985). Moreover, many species can be found with overlapping distributions and slightly different phenology or habitat preferences. For example, adult *A. clausii* is found in the mouth of rivers, whereas *A. tonsa* is mainly restricted to the upper reaches of estuaries (Chinnery and Williams, 2004). The species co-occur in the Maine Estuary (Lee and McAlice, 1979), in the Gullmarfjord (Tiselius, 1998) and in the Wadden Sea (Klein Breteler and Gonzalez, 1982). In our experiments, we used *A. clausii* and *A. tonsa*, as they both are found in the North Sea, and their abundances differ with the time of year. *Acartia tonsa* mainly occurs in summer–autumn, whereas *A. clausii* dominates in winter–spring (see also Lee and McAlice, 1979), which could cause the species to have different strategies to deal with nitrogen depletion of the food. *Acartia* species are known to distinguish between different nutritional microcapsules (Poulet and Marsot, 1978) and single algal species with different nutrient content (Houde and Roman, 1987; Cowles *et al.*, 1988). This suggests that differences in nutritional content of the algae can be of importance in nature (Timmermans *et al.*, 2004). Based on their phenology, we hypothesize that *A. tonsa* and *A. clausii* have different strategies in dealing with phytoplankton blooms. Hence, to determine the effects of different growth conditions of the algae on life history parameters of these copepods, we compared the reproductive responses to a model prey algae, *Rhodomonas* sp., in nitrogen sufficient (beginning of bloom) and nitrogen limited (end of bloom) culture conditions. Ingestion rates, egg production, egg size, egg hatching and resting egg production were measured.

METHODS

Acartia tonsa and *A. clausii* were reared in 5 L beaker batch cultures under 16:8h light:dark cycle and a temperature of 15–16°C. They were supplied in excess (> 300 µg C L^{-1} day^{-1}) with batch cultures of the cryptophyte algae *Rhodomonas* sp. The different *Rhodomonas* cultures were kept in 5 L bottles under similar conditions as the copepods. One set of cultures was kept in full *F*/2 medium (Guillard, 1975) and the other one in *F*/2 medium without nitrogen. Both cultures were started with the same cell concentration originating from the same stock culture. After 3 days the algae culture in low nitrogen medium showed signs of nitrogen limitation, visible as changes in the colour (from red to green) and decreased growth (Fig. 1a). Furthermore, C:N ratios of the nitrogen depleted cells increased steadily, whereas the *Rhodomonas* sp. cultures that received nitrogen showed relatively

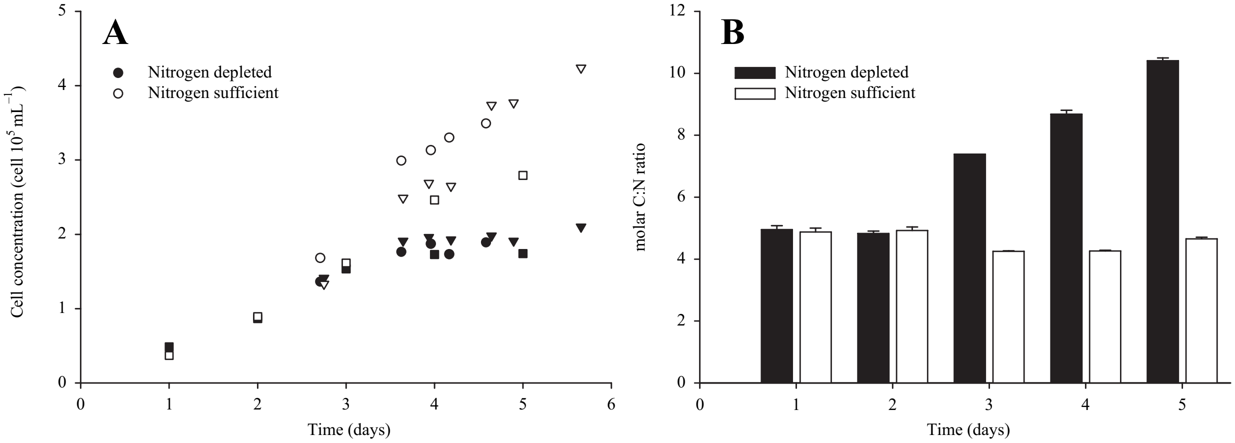

Fig. 1. *Rhodomonas* sp. Development of cell densities (panel A) and molar C:N ratios (panel B) in cultures grown in different media; nitrogen depleted (filled symbols) and nitrogen sufficient (open symbols); Different symbol shapes represent different experiments. Error bars denote standard error of the mean.

constant C:N ratios (Fig. 1b). The particulate carbon and nitrogen content of the algae was measured with a Fison EA 1108 CHN analyser after filtering 30–50 mL of the algal culture onto a combusted Whatman GF/C filter and storing at −20°C. Based on this, nitrogen depleted and nitrogen sufficient *Rhodomonas* sp. cultures were timed so that the nitrogen limited culture was on the verge of crashing at the beginning of the experiment while the nitrogen sufficient culture was still growing fast (after 4 days). The C:N ratio (molar) of nitrogen depleted cells was 9.05 (±0.8 SD; $n = 6$) after 4 days, whereas the C:N ratio of algae in the medium with nitrogen was 4.49 (±0.2 SD; $n = 6$). The C:N ratios were similar in all the three experiments.

Groups of 10 adult female copepods and 4 adult males were selected gently and placed into 1140 mL bottles, which were filled with 0.45 μm filtered artificial sea water. The artificial seawater was made up with commercial sea salt (Aqua Marin) and distilled water with a final salinity of 32–33. This solution contained no additional nitrogen to prevent nitrogen deficient algal cultures receiving nitrogen during the incubations. The cell concentration in the cultures was determined with a CASY particle counter (Schärfe Systems, Reutlingen, Germany) and was adjusted to a concentration of 13 000 cells m L^{-1} (corresponding to about 500 μg C L^{-1}) in the incubation bottles. This is a non-limiting food concentration for the copepods (Roman, 1977; Kiørboe *et al.*, 1985). To prevent sedimentation of the food, the bottles were mounted on a plankton wheel and rotated with 1 rpm at 15°C in a temperature controlled room. Every day, the copepods were transferred gently with a pipette into new bottles with fresh *Rhodomonas*. After 2 days of incubation, the egg production per female during the previous 24 h was determined by carefully filtering the water through a submerged 50 μm sieve and rinsing the eggs into small Petri dishes. The copepods were counted and transferred to incubation bottles with fresh medium. The eggs were counted and transferred into fresh artificial seawater. To determine hatching success the eggs were kept at 15°C, in a light:dark cycle of 16:8 h and recounted after 4 days of incubation. Total duration of the experiment was 3 days. The whole experiment was carried out three times during 6 months to test for the robustness and repeatability of the observed responses.

The core program of the three experiments to measure egg production and hatching success was identical, but small modifications were made to investigate additional aspects. In two experiments, we measured the ingestion rates of the copepods using the equations by Frost (1972) to investigate whether the reactions to the different algae were caused by differences in ingestion. This was done with three replicates of the bottles with copepods and three replicate controls without animals. Furthermore, we investigated whether the response is dependent on the quantity of the food by adding an extra algae treatment with only half of the algal biomass in one experiment. In another experiment, we determined the average egg sizes by measuring 30 eggs from each treatment using a SIS video imaging system. We kept the unhatched eggs of this experiment for a period of 3 weeks at the same temperature to establish the percentage of the eggs that can be considered resting eggs. Those that were still intact after 3 weeks were considered to have entered a dormancy period, other eggs disintegrate after this period. Normally at 17°C, eggs of *A. tonsa* hatch within 2 days, or disintegrate (Ambler, 1986).

RESULTS

The copepods showed significant feeding in all experiments (Fig. 2): the 95% confidence interval of the mean

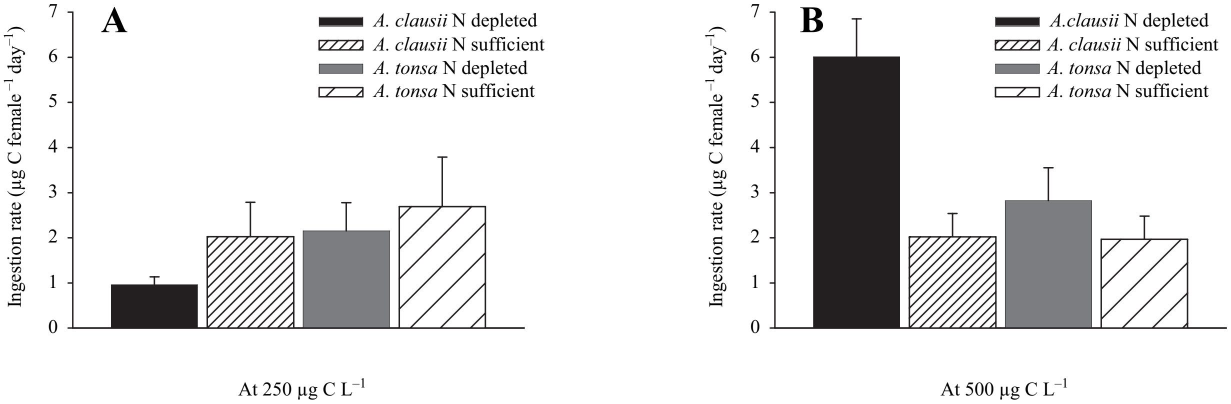

Fig. 2. *Acartia tonsa* and *Acartia clausii*. Ingestion rates of nitrogen depleted and nitrogen sufficient *Rhodomonas* sp.; error bars denote the standard error of the mean at algae concentration of 250 μg C L^{-1} (panel A) and at 500 μg C L^{-1} (panel B).

did not include zero. At the low food concentration (250 µg C L^{-1}) there were no significant differences in ingestion rates between the nutrient depleted and sufficient diets (ANOVA $F_{1,8}$ = 0.78, P = 0.402) or between the species ($F_{1,8}$ =1.05; P = 0.335; Fig. 2a). At the higher concentration (500 µg C L^{-1}) the ingestion rates were significantly different between the diets (ANOVA $F_{1,16}$ =11.20; P = 0.004) and between the species $F_{1,16}$ =5.02; P = 0.040, Fig. 2b). A Tukey post hoc test (Table I) revealed that the difference was due to the higher ingestion rate of *A. clausii* feeding on nitrogen depleted food. The amount of carbon ingested was in the range of 1–6 µg C female^{-1} day^{-1} in all experiments.

When incubated with high food concentrations (500 µg C L^{-1}), *A. clausii* generally produced eggs at a lower rate than *A. tonsa*, but both species increased their egg production rates significantly in nitrogen depleted food, relative to when feeding nitrogen sufficient *Rhodomonas* (Fig. 3). Although there was a difference in magnitude of the response between the experiments causing a significant experiment effect in the ANOVA (Table II), the patterns observed in the different experiments were robust. This pattern was also visible when the females were fed the lower concentration (250 µg C L^{-1}); a highly significant effect between food types ($F_{1,8}$ = 11.26; P = 0.009), and a significant species effect ($F_{1,8}$ =12.16; P = 0.008), with a marginally significant interaction between species and food type indicating that the species reacted in a similar way ($F_{1,8}$ = 5.31; P = 0.050) (Fig. 4).

Table I: Acartia clausii (A.c.) and Acartia tonsa (A.t.)

	A.c. N sufficient	*A.c.* N depleted	*A.t.* N sufficient
A.c. N depleted	**0.006**		
A.t. N sufficient	1.000	**0.006**	
A.t. N depleted	0.862	**0.031**	0.838

Tukey post hoc test: effect of nutritional conditions on the ingestion rates per female and day at 500 µg C L^{-1} (significant values are in bold).

Table II: Acartia clausii and Acartia tonsa

Effect	Degree of freedom $_{\text{effect}}$	Mean squares	Variance ratio	*P*
Species	1	1086.81	51.42	**<0.001**
Nutritional condition	1	468.08	22.14	**<0.001**
Experiment	2	79.39	3.76	**0.034**
Species versus nutrition	1	0.16	0.01	0.932
Species versus experiment	2	388.97	18.40	**<0.001**
Nutrition versus experiment	2	118.52	5.61	**0.008**
Three-way	2	16.23	0.77	0.472
Error	32	21.14		

ANOVA: testing the effect of nutritional conditions on the egg production rates per female and day in three experiments (significant values are in bold).

Hatching success was not significantly affected by food type, and both species showed similar levels of hatching, ranging from 40 to 100% in the different experiments but with no significant differences between the

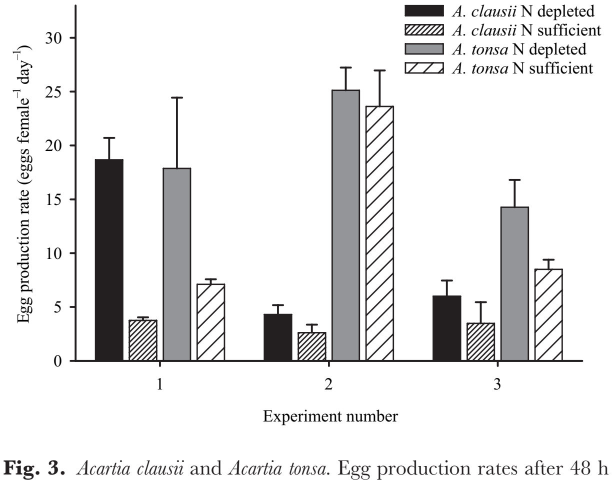

Fig. 3. *Acartia clausii* and *Acartia tonsa*. Egg production rates after 48 h incubation in either nitrogen depleted or nitrogen sufficient *Rhodomonas* sp. cultures at a food concentration of 500 µg C L^{-1}; error bars denote standard error of the mean.

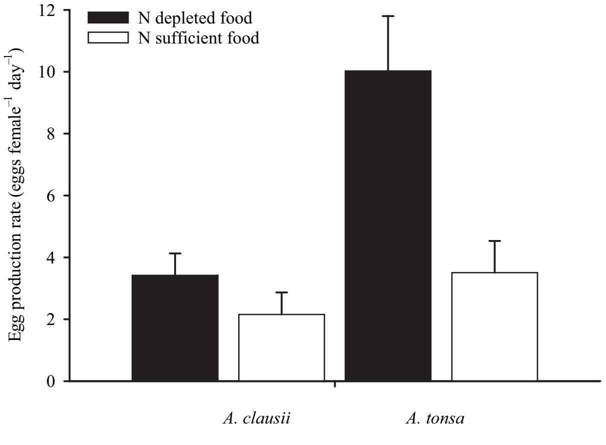

Fig. 4. *Acartia clausii* and *Acartia tonsa*. Egg production rates after 48 h incubation in 250 µg C L^{-1} of nitrogen depleted *Rhodomonas* sp. (filled bars) or nitrogen sufficient *Rhodomonas* sp. cultures (open bars); error bars denote standard error.

treatments (Fig. 5). *Acartia tonsa* always produced a certain percentage of resting eggs, whereas we did not observe resting egg production by *A. clausii*. Between the two food types the difference in the percentage of resting eggs produced was, however, not significant ($\chi^2 = 0.045$; $n = 134$; $P = 0.83$, Fig. 6). We did observe differences in the size of the eggs produced by both species in the different food treatments. While *A. clausii* decreased the size of the eggs slightly under nitrogen limitation, the opposite was found for *A. tonsa,* although both changes were small (ANOVA: Interaction Species*Nitrogen treatment, $F_{1,116} = 4.27$; $P = 0.041$).

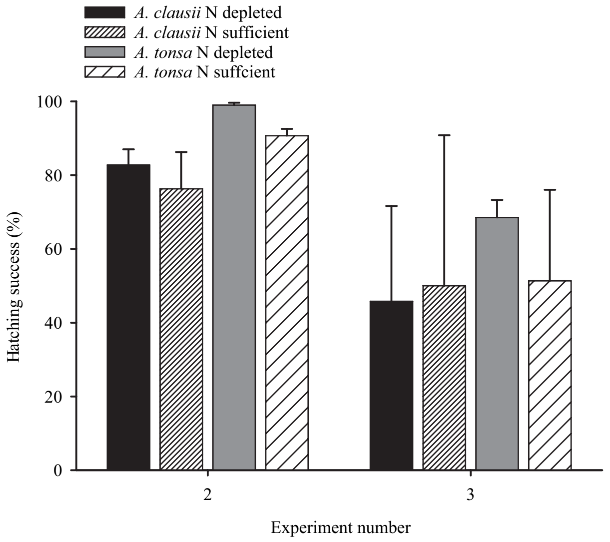

Fig. 5. *Acartia clausii* and *Acartia tonsa.* Hatching success after feeding nitrogen depleted or nitrogen sufficient *Rhodomonas* sp.; error bars denote standard error.

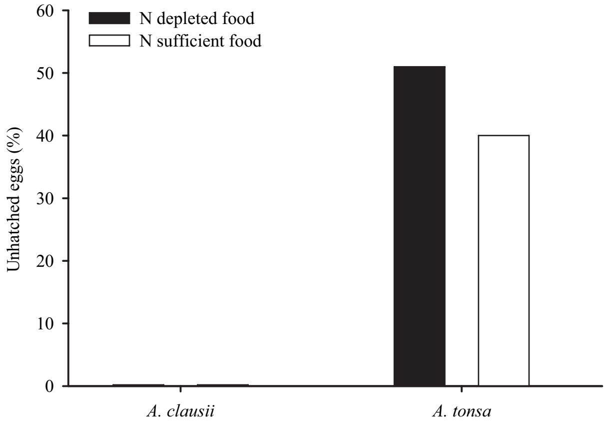

Fig. 6. *Acartia clausii* and *Acartia tonsa,* experiment 1. Production of resting eggs after feeding nitrogen depleted or nitrogen sufficient *Rhodomonas* sp.

DISCUSSION

It is well established that egg production rates and abundances of copepods generally increase during blooms of phytoplankton (Bautista *et al.*, 1994; Schmidt *et al.*, 1998; Titelman and Tiselius, 1998). However, since many factors change simultaneously it is not well understood what directly causes these changes during such blooms. Food availability and quality are key factors determining secondary production (Klein Breteler and Gonzalez, 1988; Kleppel, 1992), but copepods also react to the increase in temperature during spring blooms in temperate regions (Halsband and Hirche, 2001). Here we focus on the effects of nitrogen limitation of the food on egg production of two copepods.

Both species of *Acartia* showed higher egg production when feeding *Rhodomonas* sp. grown under nitrogen limitation, not only when food concentrations were high (500 μg C L^{-1}), but also when the animals were supplied with lower (250 μg C L^{-1}) algae concentrations. This was surprising, as previous work in marine and freshwater systems has indicated that nitrogen limited food has a lower quality than food with higher nitrogen content (Checkley, 1985; Anderson and Hessen, 1995; Müller-Navarra, 1995; van Donk and Hessen, 1995; Jones *et al.*, 2002; Jones and Flynn, 2005). As there was only one case of significantly different feeding rate (higher ingestion for *A. clausii* feeding on nitrogen limited algae at high concentrations, Fig. 2b, Table I; see also Plath and Boersma, 2001), the significant differences in egg production between the algae treatments and copepod species (Table II) cannot be explained by differences in C-ingestion rates, especially since ingestion by *A. clausii* of nitrogen limited algae in the lower concentration (250 μg C L^{-1}) showed the opposite trend compared to the higher concentration (Fig. 2). Several reports (van Donk *et al.*, 1997) have shown that both phosphorus limited and nitrogen limited algae may be more difficult to digest than algae grown under balanced nutrient conditions, because the former may increase the thickness of their cell wall. This, however, is less likely to happen with a cryptophyte because they do not have such a cell wall, but a periplast only (Lichtle, 1979).

A decrease in reproductive output is often explained by a direct limitation of the nutrient under study, or by a concordant change in the biochemical composition of the algae (Lacoste *et al.*, 2001; Jones and Flynn, 2005). The fatty acid spectrum of algae changes under nitrogen limitation, with a lower percentage of highly unsaturated fatty acids (HUFA) in nitrogen limited algae (Reitan *et al.*, 1994). These fatty acids are essential to many consumers, and hence a decrease in their content in the algae would cause a decrease in their quality as food for zooplankton

(Elser *et al.*, 2001). Most likely, however, the HUFA content of cryptophytes is high enough to meet the nutritional requirements of the copepods, even when the algae are nitrogen limited (Koski *et al.*, 1998), as the saturation thresholds for fatty acids are very low for most zooplankton species (Becker *et al.*, 2004).

Copepod eggs may also have a higher C:N ratio than body tissue as a result of the higher lipid content of the eggs (Pond *et al.*, 1996). Hence, it could be that under nitrogen limitation (carbon surplus) the best strategy for a copepod is to produce more eggs to decrease the excess carbon (but see Jones and Flynn, 2005; Klein Breteler *et al.*, 2005). Such excess carbon eggs could have a different size or be of lower quality (Guisande and Harris, 1995; Kleppel and Hazzard, 2000), but then one would expect differences in hatching success, which we did not observe, neither was there a consistent pattern in egg sizes between the treatments.

The C:N content of the algae increased from 5 to 10 under nitrogen limitation. Although this increase is substantial, even under nitrogen limitation the C:N content of the algae is still fairly close to the Redfield ratio, and hence it is likely that the animals were at least not very nitrogen limited even when feeding on the nitrogen limited algae. In fact, a recent study by Boersma and Elser (in press) argues that the response of animals to changes in C:nutrient ratios in their food should be unimodal, with a maximum at the threshold elemental ratio. One explanation for our results could hence be that the decrease in nitrogen content of the algae brought it closer to this ratio, as with a copepod C:N ratio around 5, assuming 30% gross growth efficiency for carbon, the theoretical threshold for nitrogen limitation for copepods could be as high as 15 (Urabe and Watanabe, 1992). Accordingly, a dynamic energy budget model (Kuijper *et al.*, 2004) showed a dome-shaped reaction to prey C:N ratio with a gross growth efficiency (egg production) for N increasing from prey with a C:N ratio at 5, peaking between 10 and 15 and decreasing again at higher ratios. Thus, the results presented here strongly support the results of Urabe and Kuijper (Urabe and Watanabe, 1992; Kuijper *et al.*, 2004), and Boersma and Elser (in press) suggesting a higher egg production at a prey C:N ratio of 9.05 compared to at 4.49, due to a combination of different C and N requirements for maintenance and reproduction.

General life history theory predicts that reduced life expectancy should change resource allocation decisions in favour of increased reproductive effort (Clutton-Brock, 1984; Bollens and Stearns, 1992). However, the dependence of reproductive investment on cues of low life expectancy has rarely been recorded. It could be that our observation of changing reproductive effort as a result of nitrogen depletion is such a response to a change in life expectancy, as this might mean that the bloom is reaching its end. Although not visible as a significant interaction between species and food type, *A. tonsa* seems to be the more responsive species of the two. Interestingly, *A. tonsa* also increased the proportion of eggs which might be resting eggs as well as the size of the eggs produced, which could be a precaution against potential deteriorating food conditions. These were the only differences we observed between the two species under study with respect to the reaction to the differences in feeding conditions.

In conclusion, we show that both *Acartia* species reacted to *Rhodomonas* prey grown in nitrogen depleted cultures with an increase in egg production. This was explained by a better fit with the total nutritional C and N requirements of the copepods for maintenance and egg production on the N depleted algae prey with a C:N ratio of approximately 9.1, compared to the N-replete cultures with a C:N ratio of appr. 4.5. Further research, especially with longer incubations, is necessary to differentiate potential physiological reactions from using nitrogen depletion as information on bloom development. In the meantime, we can only stress the points made by Mitra and Flynn (2005) that it is essential to incorporate nutrient stoichiometry of the food when studying copepod production.

ACKNOWLEDGEMENTS

We are most grateful to Colleen Jamieson for her generous support in the experimental work and her teamwork. Further we thank Karin Bickmeyer for technical assistance with CHN measurements, Annette Ficker for cell counts and the other members of the Helgoland Foodweb Project for the interesting discussions and constructive comments on previous versions of the manuscript. This study was funded as a part of the GLOBEC-Germany programme by the German Federal Ministry of Education and Research (BMBF). Thanks are also due to Lars Gutow and Anne Sell for critically reading the manuscript. We also would like to thank Reinhold Müller and Jens Nejstgaard for comments that greatly improved earlier versions of this manuscript.

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