Mar Biol (2008) 154:335–343
DOI 10.1007/s00227-008-0928-9

RESEARCH ARTICLE

Effect of food concentration and type of diet on *Acartia* survival and naupliar development

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Received: 9 January 2008 / Accepted: 5 February 2008 / Published online: 21 February 2008

Abstract We have performed life table experiments to investigate the effects of different food types and concentrations on the larval development and survival up to adulthood of *Acartia tonsa*. The food species offered comprised a wide taxonomic spectrum: the pigmented flagellates *Isochrysis galbana*, *Emiliania huxleyi*, *Rhodomonas* sp., *Prorocentrum minimum*, the diatom *Thalassiosira weissflogii*, grown on medium offering enriched macronutrient concentrations and the ciliate *Euplotes* sp. initially cultured on *Rhodomonas*. For the ciliate species, also the functional response was studied. In order to avoid limitation by mineral nutrients, food algae have been taken from the exponential growth phase of the nutrient replete cultures. The suitability of *Rhodomonas* as a food source throughout the entire life cycle was not a surprise. However, in contrast to much of the recent literature about the inadequacy or even toxicity of diatoms, we found that also *Thalassiosira* could support *Acartia*-development through the entire life cycle. On the other hand, *Acartia* could not complete its life cycle when fed with the other food items, *Prorocentrum* having adverse effects even when mixed with *Rhodomonas* and *Thalassiosira*. *Isochrysis* well supported naupliar survival and development, but was insufficient to support further development until reproduction. With *Emiliania* and *Euplotes*, nauplii died off before most of them could reach the first copepodite stages. *Acartia*-nauplii showed a behavioral preference for *Euplotes*-feeding over diatom feeding, but nevertheless *Euplotes* was an insufficient diet to complete development beyond the naupliar stages.

Communicated by X. Irigoien.

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Introduction

The traditional view of copepods as herbivores became challenged during recent years (Kleppel et al. 1991; Kleppel 1993; Lonsdale et al. 1996; Sommer and Sommer 2006; and references therein). The relative importance of herbivory and carnivory (mainly on protozoans) is related to the feeding behaviour: Suspension feeders creating a feeding current to transport immotile or slowly swimming prey to the mouthparts tend to be more herbivorous. Ambush feeders waiting for the turbulence signal created by a swimming organism tend to be more carnivorous (Jonsson and Tiselius 1990).

Diatoms forming the basis of the grazing food chain in the oceans (Legendre 1990) have become controversial as a food source for copepods. Since the mid 1990s, there have been an increasing number of culture studies demonstrating a detrimental impact of diatoms on copepod larval development (Ianora et al. 2004; Poulet et al. 1994), including species of the genus *Acartia* (Miralto et al. 2003). While some laboratory studies have shown that diatoms can also suppress egg production and hatching rates of copepods (Ianora et al. 1995, 2003), others show that copepod egg production can be increased or unaffected depending on the diatom species in the diet (Poulet et al. 2006). Contrasting effects of diatom diet on copepods are reported from the

field. Studies from the Mediterranean Sea illustrate deleterious effects of diatoms on copepod reproduction (Miralto et al. 1999) and depression of reproductive success at high *Thalassiosira* abundance has been reported for *Calanus pacificus* from Dabob Bay, Washington (Pierson et al. 2005). Yet, other work provides evidence for the importance of diatoms as copepod food (Irigoien et al. 2002), and grazing selectivity in favour of diatoms has been demonstrated in copepods under natural conditions (Meyer-Harms et al. 1999; Irigoien et al. 2000). The diatom *Thalassiosira weissflogii* has been proved to constitute a high-quality food source for copepod development (Klein Breteler et al. 2005), including *Acartia tonsa* (Støttrup and Jensen 1990; Jónasdottir and Kiørboe 1996). Investigation into the chemical defence potential of a wide range of diatom species detected polyunsaturated aldehyde release also in several species of the genus *Thalassiosira* including *T. rotula* and *T. pacificus*, but no PUA were found in *T. weissflogii* (Wichard et al. 2005). Under N-saturated conditions, *A. tonsa* has been proved to ingest the diatom *T. weissflogii* preferentially over *Emiliania huxleyi* and *Aureodinium pigmentosum*, an alternative dinoflagellate food source, indicating selectivity for this diatom species in copepods especially under nutrient-sufficiency as may be found during early spring bloom conditions in the field (Jones et al. 2002).

Our study organism, *Acartia tonsa* is an important copepod species in many temperate and subtropical coastal marine environments and also widely used in aquaculture (Knuckey et al. 2005). While adult copepod feeding is a widespread research topic, including studies on *Acartia* (e.g., Houde and Roman 1987; Durbin et al. 1990; Støttrup and Jensen 1990; Kleppel and Burkart 1995; Chinnery and Williams 2004), little attention has so far been given to feeding and food requirements of nauplii (see Knuckey et al. 2005; Rey et al. 2001; Swadling and Marcus 1994).

In this study, we used a number of easily culturable protist species, the diatom *Thalassiosira weissflogii* (10–24 μm diameter), the flagellates *Rhodomonas* sp. (Cryptophyta, 18–24 μm length), *Emiliania huxleyi* (Coccolithophorales, 5–8 μm), *Isochrysis galbana* (Prymnesiophyta, 6–10 μm), and *Prorocentrum minimum* (Dinophyta, 16–20 μm), and the ciliate *Euplotes* sp. (45–65 μm). Those diets represent a wide diversity of food sizes and taxonomic groups. Effects of diet on marine copepod recruitment have so far been described by three distinct functional responses: egg production rate, egg hatching success and larval somatic growth (Poulet et al. 2007). We here investigate survival and development until adulthood in dependence of food concentration and type of diet offered—focussing on life-cycle completion from the first feeding stage onward. *Acartia tonsa* was fed with those food organisms throughout its juvenile life cycle in order to compare their suitability as a food source serving nauplii as well as adults, with the further aim of identifying potential inhibitory impacts of the respective taxa on *Acartia* development and survival.

Methods

Media for the phytoplankton cultures were prepared by enriching sterile filtered seawater with macro- and micronutrients. Medium I (Table 1; modified Von Stosch and Drebes 1964) was used for stock monocultures of *Prorocentrum minimum*, *Isochrysis galbana*, and *Emiliania huxleyi*. About 1 mL of a micro-nutrient mix composed of EDTA (Titriplex III), Fe and Mn, resulting in end-concentrations of 1 μmol L^{-1}, respectively, and 100 μL vitamin mix containing Vitamins H, B_1 and B_{12} (0.0002, 0.0005, and 0.00004 mol L^{-1} initially) were added per litre. Medium II (Table 1), a Provasoli enriched seawater medium especially suited for diatoms, was used for *Thalassiosira weissflogii*. Trace elements and vitamins were added in proportion to the nitrogen offered as 800 μL Provasoli-Enrichment per litre (PES; Mix I-III). Medium III (Table 1; Provasoli 1963, modified by U. Sommer) was used to culture *Rhodomonas*. A 50 mL of these stock monocultures, respectively, were transferred into 250 mL Erlenmeyer cylinders and 50 mL culture medium (Medium IV, Table 1) was added to each monoculture. The medium applied was enriched in concentrations of macronutrients. Microminerals were added in the same concentration as specified for Medium I above, vitamin concentrations were doubled by adding 200 μL L^{-1} of the described vitamin mix. The monocultures were consequently kept slightly stirred at 16–18°C at constant light. Medium was added in amounts of 50 mL steps as required, so that final volumes of the batch cultures matched 3 × 250 mL per diet species. Cultures were grown until concentrations >600 μg C L^{-1} were reached, and were consequently diluted 1:4 with culture medium when 2,000 μg C L^{-1} were exceeded. In order to avoid limitation by mineral nutrients, food algae for the copepods have been taken from the exponential growth phase of cultures. For a wide array of species, nutrient replete growth results in a cellular stoichiometry similar to the Redfield-ratio, i.e., C:N:P = 106:16:1 (Goldman et al. 1979; Sommer 1991a, b). This means all required nutrients were offered in surplus concentrations for build-up of the targeted biomass concentrations, sufficient to sustain growth over a 48 h period in the subsequent grazing experiments. Exponentially growing algae were also used to feed the ciliate *Euplotes*. According to all literature published so far on zooplankton (summarized in Sterner and Elser 2002) nutrient replete algae do not lead to mineral nutrient limitation of zooplankton feeding on them.

Table 1 Macronutrient end-concentrations in media used for stock cultures (μmol L^{-1})

	Medium I	Medium II	Medium III	Medium IV
N	80	30	550	700
P	5	2	36	25
Si	10	80	–	140

Medium I Von Stosch and Drebes; *Medium II* Provasoli-enriched seawater medium used for culturing *Thalassiosira weissflogii*; *Medium III* Provasoli-enriched seawater medium used for culturing *Rhodomonas*; *Medium IV* medium used in algal cultures for feeding experiments, Von Stosch and Drebes stem solutions added in higher concentrations to match *f*/2

Ciliates of the genus *Euplotes* were kept in culture on a *Rhodomonas* diet. Cell abundance was determined by inverted microscopy (Utermöhl 1958). Algal biomass was measured as cell volume and converted to biomass (μg C L^{-1}) according to Menden-Deuer and Lessard (2000). For *Rhodomonas*, the more specific factor by Møller and Nielsen (2001) was used and ciliate biomass was calculated according to Putt and Stoecker (1989).

Acartia eggs were left to hatch in filtered seawater at 20°C. Nauplii at the pre-feeding stage, naupliar stage II, were transferred into filtered, sterilized seawater in 200 mL tissue culture flasks. The cultures were kept at 20°C at 12 h light/darkness intervals. Each culture flask contained 20 nauplii. The four algal species were offered at four concentrations for each species, ranging from 37 to 300 μg C L^{-1} for *T. weissflogii*, *Rhodomonas* sp., *P. minimum* and *E. huxleyi*. For *I. galbana* the food concentrations were reduced to 19–150 μg C L^{-1}, because we were unable to reach sufficiently dense stock cultures of *I. galbana* to prepare food densities of 300 μg C L^{-1}. The food gradient was chosen to provide a range from low to optimal concentrations according to Koski and Klein Breteler (2003). *Euplotes* was offered at higher concentrations, 75–600 μg C L^{-1}, as we also wanted to test a previously reported adverse effect of high *Euplotes* densities on *Acartia* nauplii. In one additional series of treatments, a mixture of *Rhodomonas* sp., *T. weissflogii* and *P. minimum* was offered. Concentrations in these mixed treatments were regulated to add up to comparative values as in the monodiet treatments, with equal individual contributions of the different algal species to carbon biomass, matching 12–100 μg C L^{-1}, respectively. Two parallel unfed controls were set up with each series of experiments. In all treatments, culture flasks were renewed every 48 h, the nauplii were individually transferred into filtered and autoclaved seawater, and the food was added in the initial concentrations again. Experiments were run over 8 days, respectively, or until the culture died out. The *I. galbana* treatment was run over 10 days.

In order to compare the response of survival to the different food types and concentrations death rates (*d*; in day^{-1}) were calculated by linear regression of $\log^e$-transformed abundance (*N*) data on time (in day), defining the negative slope of the regression as *d*. In the case of zero abundances towards the end of the survival experiments *N* was replaced by $(N + 1)$ for the entire regression.

To analyse the process of development, naupliar stages III–VI and the first copepodite stages were attributed individual scores, with an increment of one per instar and nauplius stage I and II receiving score 1 (modified Knuckey et al. 2005). A development index, DI, for each treatment at any given time was calculated according to Villegas and Kanazawa (1979).

$$\mathrm{DI} = \Sigma(NS)$$

where *N* was the number of copepods at certain stage and *S* the assigned stage value. This developmental index constitutes a combined measure of developmental time and survival and was therefore chosen to reflect the species' performance on the alternatively offered diets. It provides a means of detecting long survival at arrested development as well as fast development at high mortality rate and thus unravels mal-adaptation to a diet offered more reliably than either of these parameters on its own. The development was observed every 8 h for the first 2 days and afterwards in 16 h intervals. The mean velocity of naupliar development was assessed in the surviving animals. It was established as the slope of the linear trends from the start of the experiments until day 2, because later some cultures died out. Single treatments are unreplicated, but as the same diets were offered in different concentrations, requirements for regression analysis are fulfilled (Tables 2, 3).

Grazing on the ciliate *Euplotes* in monodiet was checked over 24 h in smaller NIII–NIV and larger NV–NVI nauplii at all ciliate concentrations, respectively. For this purpose, 50 mL samples were fixed by Lugol's iodine before and after the chosen time interval, and ciliate abundance as carbon biomass L^{-1} was calculated by the method described above. Grazing rate was calculated as

$$g = [(\ln N_c - \ln N_0) - (\ln N_g - \ln N_0)]/t$$

where N_c is final concentration of ciliates in ungrazed controls, N_g is final concentration of ciliates in grazing treatments, and *t* measured in days. Multiplying grazing rates by food concentration and dividing by number of nauplii per litre in the respective treatments calculated ingestion rates. In a separate series of experiments, *Euplotes* was offered to *Acartia* nauplii at a surplus concentration of the diatom *T. weissflogii*. Grazing on the ciliate was investigated as described above.

Table 2 Relationship between death rate (d, in day^{-1}) and food concentration (F; in µg C L^{-1}) for the different food types analyzed according to the regression model $d = aF^b$

Food concentration values have been replaced by $(F + F_{min}/2)$ because the regression model does not accept zeros

Species	ln a	b	r^2	P
Isochrysis galbana	1.541 ± 1.014	−1.061 ± 0.257	0.788	0.0182
Rhodomonas sp.	0.687 ± 0.278	−0.739 ± 0.067	0.968	0.0004
Thalassiosira weissflogii	0.378 ± 0.453	−0.595 ± 0.109	0.881	0.0055
Mix	−0.274 ± 0.209	−0.304 ± 0.050	0.901	0.0038
Prorocentrum minimum	−0.348 ± 0.312	−0.261 ± 0.075	0.751	0.0254
Euplotes sp.	−0.240 ± 0.326	−0.079 ± 0.070	0.242	0.3211
Emiliania huxleyi	−0.574 ± 0.226	−0.035 ± 0.055	0.093	0.5571

Table 3 Michaelis–Menten equation fitted to the dependence of developmental velocities (V; in stages day^{-1}) on food concentration

Species	$V_{max} - V_c$	k	r^2
Isochrysis galbana	0.979 ± 0.050	11.06 ± 2.89	0.970
Rhodomonas sp.	0.984 ± 0.054	43.00 ± 9.23	0.989
Thalassiosira weissflogii	0.866 ± 0.176	42.52 ± 30.97	0.886
Mix	0.538 ± 0.043	7.93 ± 6.52	0.999
Prorocentrum minimum	0.596 ± 0.015	8.95 ± 2.17	0.997
Euplotes sp.	0.903 ± 0.051	58.39 ± 14.43	0.988
Emiliania huxleyi	1.021 ± 0.026	125.18 ± 72.30	0.920

Since nauplius I–III development does not depend on feeding, mean developmental velocities of controls (V_c) have been substracted: $V - V_c = [(V_{max} - V_c)F]/(F + k)$

Results

Acartia had high survival rates when fed with *Rhodomonas* sp., *T. weissflogii* and *Isochrysis galbana* (Fig. 1). Survival of nauplii was considerably poorer with *P. minimum* and the mixed diet. *E. huxleyi* and *Euplotes* sp. supported the poorest survival, almost as poor as in the unfed controls. The dependence of death rates on food concentration (F; in µg C L^{-1}) could be described by a multiplicative regression according to the model $d = aF^b$. Since this regression model does not tolerate zero values of the independent variable, food concentrations were replaced by $(F + F_{min}/2)$. A more negative value of b would indicate better food quality. A b value not significantly different from zero would indicate worthless food, e.g., no better survival with food than without food. A positive b value would indicate a toxic effect stronger than starvation. *I. galbana*, *Rhodomonas* sp., and *T. weissflogii*, were good food types for survival, *P. minimum* and the mixed diet poor ones, and *E. huxleyi* and *Euplotes* sp. were worthless (Table 2, Fig. 2).

The development index increased initially in all food treatments, but it stabilized at a high level only in the treatments fed with *Rhodomonas* sp., *T. weissflogii* and *Isochrysis galbana* (Fig. 3) while in the other food treatments the high mortality led to a pronounced decrease of DI after an initial increase. The velocity of naupliar development could be described by a modified Michaelis–Menten function relating the velocity to food concentration:

$$V - V_c = [(V_{max} - V_c)F]/(F + k)$$

where V is developmental velocity (stages day^{-1}), F food concentration (µg C L^{-1}), V_c mean developmental velocity of the controls, V_{max} maximal developmental velocity, and k half-saturation constant. The modification by substracting V_c was made in order to account for the food-independent development of the non-feeding stages NI and NII. Food quality in dependence of concentration can be inferred from the resulting values of parameters: high food quality at low concentrations is reflected by a steeper initial slope $[(V_{max} - V_c)/k]$ of the Michaelis–Menten curve; high food quality at high concentrations by a high saturation rate. The equation produced good to excellent fits (Table 3, Fig. 4) with high determination coefficients, well-constrained estimates of V_{max} but in some cases unsatisfactorily big standard errors for k. With *Rhodomonas* sp., *I. galbana*, *T. weissflogii*, *E. huxleyi*, and *Euplotes* sp. high values of V_{max} were reached, while V_{max} values for *P. minimum* and the *Prorocentrum*-containing mixed diet were only slightly more than half of the other values.

While *I. galbana* was equal if not better than *Rhodomonas* sp. and *T. weissflogii* in promoting naupliar survival and development, only the latter two species were adequate for *Acartia* to complete its entire life cycle. Egg production and subsequent hatching of nauplii was observed with the highest *T. weissflogii* concentration and at all food concentrations of *Rhodomonas*. There were only minor difference in the velocities of naupliar development supported by both food algae. On *Rhodomonas* at the highest concentration, first reproduction occurred already after 96 h, while at the end of the experiment (190 h) the second generation started to reproduce. In the *Rhodomonas*-treatment with 150 µg C L^{-1} reproduction was observed after 163 h, and in the lowest two concentrations after 190 h, respectively. When fed with the highest *T. weissflogii*-concentration, the reproduction of the first *Acartia*-

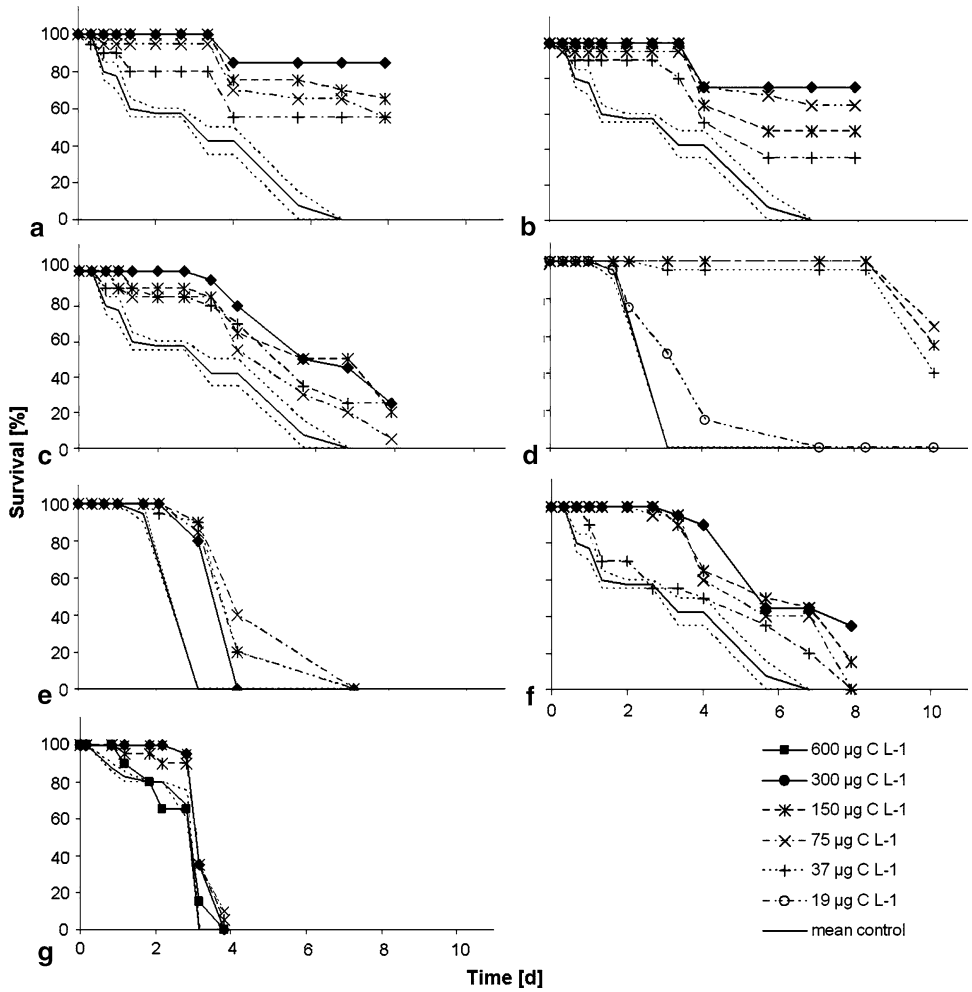

Fig. 1 Survival of *Acartia* nauplii (%) against time; diets offered: **a** *Rhodomonas* sp., **b** *Thalassiosira weissflogii*, **c** *Prorocentrum minimum*, **d** *Isochrysis galbana*, **e** *Emiliania huxleyi*, **f** mixed food (*Rhodomonas* + *Thalassiosira* + *Prorocentrum*), **g** *Euplotes* sp.

generation started at 190 h. On the other hand, *Acartia* raised on *T. weissflogii* produced markedly more eggs than animals that had fed on *Rhodomonas* (judgement by eyes, no counts performed).

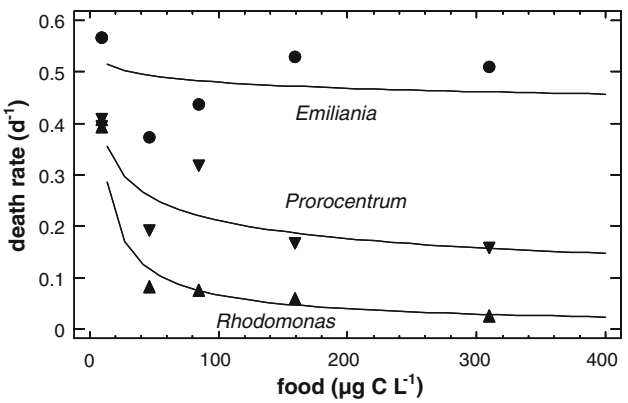

Fig. 2 Dependence of *Acartia* death rates on food concentrations when fed with *Rhodomonas* sp. (*filled triangles*), *Prorocentrum minimum* (*filled inverted triangles*), and *Emiliania huxleyi* (*filled circles*)

When fed with *I. galbana*, *Acartia* only reached the first two copepodite stages within the 12-day period in spite of the high survival rates and the fast early development. On a diet of the dinoflagellate *Prorocentrum minimum*, with few exceptions, copepodites did not develop at all. The same phenomenon could be observed in the treatments when animals were fed a mixture of *P. minimum*, *Rhodomonas* sp. and *T. weissflogii*, while the latter two species in monodiet could sustain *Acartia* during its entire life cycle. However, when these genera were offered in combination with the dinoflagellate, development indices remained below 80 (Fig. 3f). This reflects the fact that nauplii did not on average moult into copepodites on the mixed diet in spite of the fact, that 2/3 of the mixture consisted of the nutritionally adequate species *Rhodomonas* sp. and *T. weissflogii*. This indicates an adverse effect of *P. minimum* beyond nutritional inadequacy. Rearing nauplii on *E. huxleyi* or on the ciliate *Euplotes* did not lead to the development of any copepodite stages. On *Euplotes* in monodiet, progression between the early naupliar stages occurred relatively quickly, as indicated by the high V_{max} value (Table 3). However, mortality after about 80 h

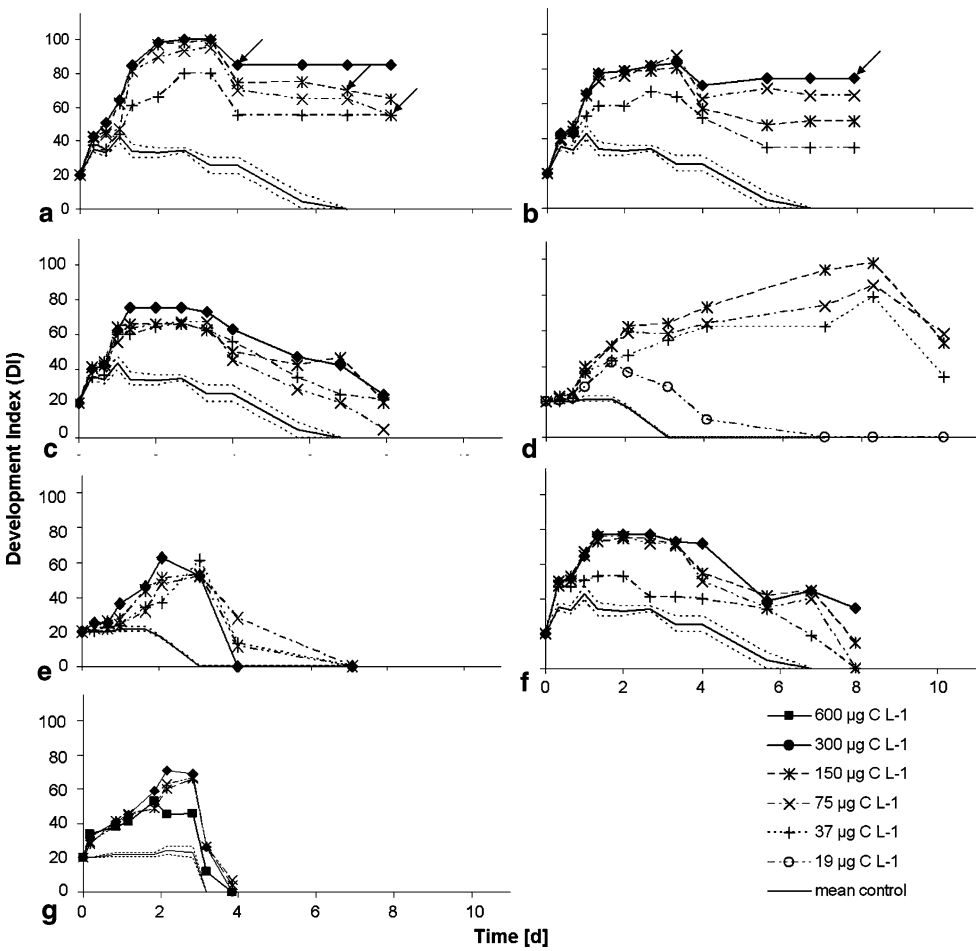

Fig. 3 Development index, DI, of the following treatments against time: **a** *Rhodomonas* sp., **b** *Thalassiosira weissflogii*, **c** *Prorocentrum minimum*, **d** *Isochrysis galbana*, **e** *Emiliania huxleyi*, **f** mixed food (*Rhodomonas* + *Thalassiosira* + *Prorocentrum*), **g** *Euplotes* sp; *arrows* indicate occurrence of egg production

increased abruptly (Fig. 1f), resulting in the death of all animals before the next sampling 96 h after the start of the experiment.

Grazing of *Acartia* nauplii on *Euplotes* could be recorded at all naupliar stages in all treatments (Fig. 5). The grazing effect on ciliate abundances was significant for 300, 150 and 75 µg C L^{-1} treatments in NIII–NIV nauplii as well as in NV–NVI nauplii.

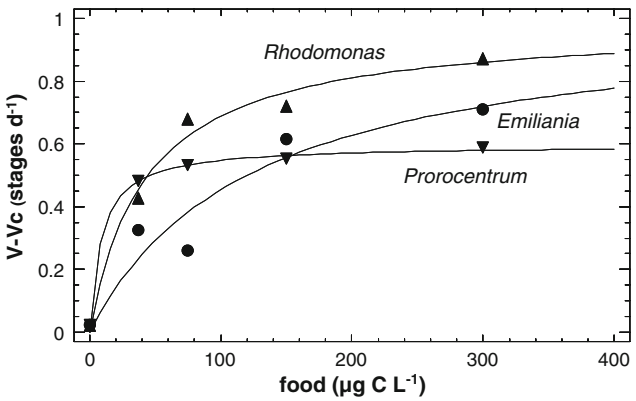

Fig. 4 Velocity of *Acartia* development (stages day^{-1}) in dependence on food concentration (µg C L^{-1}) when fed with *Rhodomonas* sp. (*filled triangles*), *Prorocentrum minimum* (*filled inverted triangles*), and *Emiliania huxleyi* (*filled circles*)

Ingestion rates *I* of *Acartia* nauplii on *Euplotes* assumed values between 0.29 and 1.12 µg C Ind^{-1} day^{-1} (Fig. 6). Except for one outlier of $I = 2.3$ µg C Ind^{-1} day^{-1} data conformed relatively closely to Holling's type II curvilinear functional response. The functional response curve was fitted by Michaelis–Menten-type saturation function:

$$I = (I_{\max}F)/(F + k)$$

where $I_{\max}$ is maximum ingestion rate, F food concentration, and k half-saturation constant. Data for the nauplius III–IV and nauplius V–VI stages were pooled, because they apparently fell on the same response curve. Curve fitting was performed by non-linear regression analysis. The resultant curve parameters were:

$$I_{\max} = 1.24 \pm 0.12 \ \mu \text{ g C Ind}^{-1}\,\text{day}^{-1};$$
$$k = 122.5 \pm 37.6 \ \mu \text{ g C L}^{-1}; \quad r^2 = 0.87.$$

The $I_{\max}$ estimate corresponds to about 30% of the ingestion rates reported for adult *Acartia* grazing on smaller ciliates (3 µg C Ind^{-1} day^{-1} at 60 µg C L^{-1}; Tokle 2006).

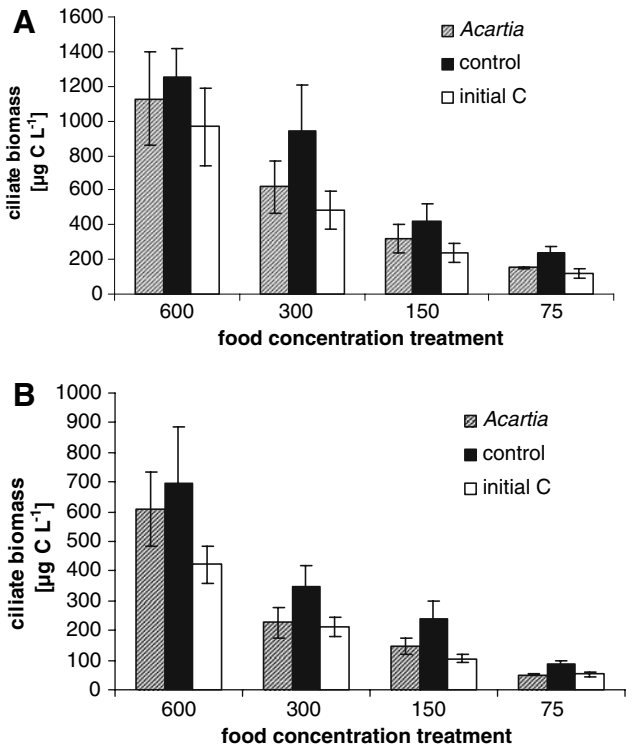

Fig. 5 Grazing of *Acartia* nauplii (**a** stages NIII–NIV, **b** stages NV–NVI) on the ciliate *Euplotes* over 24 h at different food concentrations; comparison of grazing treatments against ungrazed controls: *black patterned bars* against *black bars*; *white bars* ciliate *C* concentrations at the start of the experiment for reference

Grazing on *Euplotes* was not altered at surplus levels of the diatom *T. weissflogii* (Fig. 6), bold-faced x symbols, not included in regression analysis. Small and large nauplii equally ingested as much ciliate biomass, when the diatom food source was available as when *Euplotes* was the sole food source provided. Hence, a strong preference for the ciliate food was demonstrated by the *Acartia* nauplii, irrespective of their developmental state.

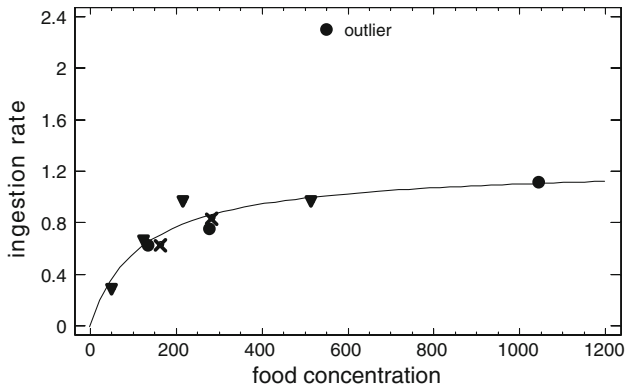

Fig. 6 *Acartia* naupliar ingestion rates (Ind^{-1} L^{-1}) of *Euplotes* sp. against ciliate concentration (µg C L^{-1}); *filled circles* NIII–IV, *filled triangles* NV–VI, *cross* plus *Thalassiosira*

Discussion

Among the food species studied, *Rhodomonas* sp. was obviously the optimum food providing high survival rates, a fast naupliar development and a fast copepodite development. *T. weissflogii* was second best, leading also to high naupliar survival rates and fast development, but to slower copepodite development. The successful use of *T. weissflogii* as a food organism is in contrast with the experimentally based view that diatoms in general are bad diet for raising copepods (Ianora et al. 1995, 2003; Miralto 1999; Paffenhöfer et al. 2005), while it agrees to field studies supporting a positive nutritional role of diatoms (Irigoien et al. 2002). It is now well illustrated that not all diatom species per se are toxic, but even taxa lacking toxic metabolites can be insufficient to support copepod recruitment and development in mono-diet (Jones and Flynn 2005). While defence chemicals of diatoms can be diverse (Fontana et al. 2007) and widely present (Wichard et al. 2005) there are obviously species that lack the detrimental effects originally presumed for the entire taxon, and among these can be adequate and high quality food sources for copepods.

All other species were inadequate in terms of supporting the entire life cycle of *Acartia*, but this inadequacy manifested itself in different impacts on the ontogeny. The smallest (*E. huxleyi*) and the largest (*Euplotes* sp.) species supported fast early naupliar development but induced death rates similar to starvation conditions. The offered biomass levels of *E. huxleyi* matched those of larger food organisms offered in other treatments. Equal biomass at smaller cell size implies higher abundance of individuals and thus higher encounter rates. Probably, *Emiliania* is too small to be captured efficiently. Top-down studies illustrate that algae smaller than 10 µm, or of a volume less than 500–1,000 μm^3, are not effectively grazed by copepods (Katechakis et al. 2004; Irigoien et al. 2003; Sommer et al. 2000). Thus *E. huxleyi* might be a biochemically good food which is sub-optimal in terms of capture mechanics. *I. galbana*, a species used frequently (often in its tropical form) as a food alga in aquaculture, was an optimal food during the early life cycle stages but failed to support subadult development. *P. minimum* had an adverse effect on naupliar survival and on developmental speeds. The negative effect was weaker than starvation, but strong enough to make mixtures with adequate food supply of *Rhodomonas* and *T. weissflogii* inadequate. This contrasts with previous studies which used *P. minimum* as a control treatment against the negative impacts of diatoms as *T. rotula* on copepod hatching success (Chaudron et al. 1996) and embryonic (Poulet et al. 1994) as well as postembryonic development (Carotenuto et al. 2002), and to reverse effects of diatom monodiets on copepod egg production (Poulet et al. 2006). *P. minimum*

has thus been documented to be a good diet for copepod reproduction and early development, but here is shown as inadequate to support *A. tonsa* during its entire life-cycle due to a weak toxicity effect beyond nutritional inadequacy. A recent study assessing the impacts of *P. minimum* on *A. tonsa* stated the insufficiency of this species as a food source, but did not report toxic effects (Dam and Colin 2005). An adverse effect of dinoflagellates on copepod egg production has been reported for *Calanus helgolandicus* in the field (Irigoien et al. 2000).

The maternal effects largely influencing the functional response parameters of marine copepod reproduction (Poulet et al. 2007) are beyond the scope of this study. Yet, they may be presumed as equal between experiments as *Acartia* eggs of the same sample were non-systematically distributed into the respective treatments.

The data presented here demonstrate that *Acartia* nauplii of all feeding stages are capable of ingesting ciliates as large as *Euplotes*. *Euplotes* is even ingested if it is mixed with surplus levels of a well edible diatom. In fact, the presence of the diatom did not even reduce the functional response to *Euplotes* density, thus indicating a feeding preference for the ciliate, as has been frequently reported from the field (Kleppel et al. 1991; Kleppel 1993; Lonsdale et al. 1996; Stoecker and Egloff 1987). Adults and copepodites of *Acartia* have been shown to be able to switch between suspension feeding and ambush feeding, the former being more suitable for immotile prey and the latter for motile prey (Saiz and Kiørboe 1995; Kiørboe et al. 1996; Takahashi and Tiselius 2005). Obviously, nauplii are capable of the same types of behaviour and are not deterred or inhibited in their feeding by the large size of *Euplotes*, which is bigger than the majority of ciliates usually found in the marine pelagic. It remains surprising, however, why *Acartia*-nauplii should show a preference for a ciliate obviously unsuitable to support their development when offered a nutritionally adequate diatom as an alternative. The behavioural trigger (mechano-sensory detection of a swimming prey; Jonsson and Tiselius 1990) must be unrelated to the food quality. From a fitness perspective, such selection behaviour is only adaptive if the actively swimming prey organism encountered in the natural environment is usually a better food than *Euplotes*.

Acknowledgments We thank Nicole Aberle-Malzahn for *Acartia* eggs, Andrea Saage for medium and for a stock culture of *Euplotes*, and Cordula Stielau for algal stock cultures. These experiments were carried out in the frame of the GLOBEC project.

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