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Copepod growth and diatoms: insensitivity of *Acartia tonsa* to the composition of semi-natural plankton mixtures manipulated by silicon:nitrogen ratios in mesocosms

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Abstract The feeding selectivity and the growth and reproductive success of the copepod *Acartia tonsa* have been studied in mesocosms fertilized at different Si:N ratios (0–1.75:1) and, therefore, at different compositions of the phytoplankton communities. Phytoplankton composition showed a strong response to nutrient ratios, with diatoms comprising >90% at Si:N ratios >1:1 of total biomass as opposed to <20% at the lowest ratio. *A. tonsa* strongly preferred feeding on motile prey (flagellates and ciliates) to feeding on diatoms. Nevertheless, diatoms comprised a substantial part of the diet at the highest Si:N ratios. *A. tonsa* egg production and the final (after 4 weeks) abundance of adults and copepodites showed no response to Si:N ratios while nauplii production slightly increased with Si:N ratios. It is concluded that the frequently reported deleterious effect of diatoms on copepod reproduction is rather unusual when copepods are confronted with a naturally diverse phytoplankton assemblage instead of clonal cultures in the laboratory.

Keywords Copepods · Diatoms · Food chain · Plankton

Introduction

Since the mid 1990s, the community of marine plankton ecologists has been upset by the "diatom–copepod paradox" (Ban et al. 1997). Originally, diatoms and copepods were considered to be the perfect planktonic analogues of grass and ungulates in savannah ecosystems, diatoms being the most important primary producers and copepods the most important herbivores. As early as ca. 25 years ago, it became clear that protozoan grazing on picoplankton (<2 μm) can contribute more to the C flux between the first and the second trophic level than the "grazing food chain" (diatoms–copepods), particularly in oligotrophic oceans (Calbet and Landry 2004). Nevertheless, diatom mass growth in areas of nutrient-rich upwelling and during the spring bloom of temperate and cold seas has still been considered to form the basis of the grazing food chain in the oceans (Legendre 1990) and thus the primary avenue of energy transfer from primary producers to fish production. This image has changed since the mid 1990s with an increasing number of culture studies demonstrating a detrimental impact of diatoms on embryonic development of copepods (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). Field studies have shown both adverse effects of diatoms (Miralto et al. 1999; Pierson et al. 2005) and favourable effects (Irigoien et al. 2002). Even grazing selectivity in favour of diatoms has been demonstrated in copepods under natural conditions (Meyer-Harms et al. 1999; Irigoien et al. 2000) while other studies have reported a feeding preference for Protozoa and flagellates (Nejstgaard et al. 1997). An overview of the literature published up until 3 years ago can be found in Paffenhöfer et al. (2005). The increasing number of studies has lead to

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an increasingly idiosyncratic picture, i.e. species (diatom and copepod spp.) and context dependence of the conclusions.

From an ecosystem perspective, a more holistic approach is necessary. If deleterious diatom effects are species dependent, behavioural flexibility of copepods (switching food selection) and species replacements between copepods might retain food chain transfer efficiency fully or to some extent, even if some diatoms are toxic for some copepods. While the question "are some diatoms toxic for some copepods?" has to be answered by a clear "yes", it is still an open question whether the usual species mix in natural diatom blooms would be harmful to copepods. This question has two sub-questions: does the effect depend on diatoms in the diet or on diatoms in the environment, i.e. toxic substances released into the water?

As a first step towards a more holistic experimentation, I manipulated phytoplankton composition by adding nutrients at different Si:N and Si:P ratios to indoor mesocosms. These mesocosms were stocked with non-feeding nauplius II larvae of the copepod *Acartia tonsa*, to follow copepod food selection, ontogeny and reproduction in response to different compositions of the microbial plankton community. High Si:N and Si:P ratios have frequently been reported to favour diatom dominance in the plankton community (Egge and Jacobsen 1997; Sommer 1994, 1998; Sommer et al. 2002, 2004, 2005). *A. tonsa* has been chosen, first because it is an important copepod species in many temperate and subtropical coastal marine environments and is also widely used in aquaculture (Knuckey et al. 2005). The second reason for the choice was even more important: adults and copepodites of *Acartia* have been shown to be able to switch between suspension feeding and ambush feeding sensu Tiselius and Jonsson (1990), the former being more suitable for immotile prey, e.g. diatoms, and the latter for motile prey, e.g. ciliates and flagellates (Saiz and Kiørboe 1995; Kiørboe et al. 1996; Takahashi and Tiselius 2005).

Materials and methods

The experiments were performed in 80-cm-deep, 300-l mesocosms in temperature-controlled rooms at 18°C and a 14:10-h light:dark cycle. Surface irradiance during the light phase was 200 µmol quanta m^{-2} s^{-1} photosynthetic active radiation (PAR). Assuming a carbon–chlorophyll conversion ratio of 50:1 and a chlorophyll specific attenuation coefficient of 0.015 (µg chlorophyll $l^{-1})^{-1}$ (Tilzer 1983), average mixed layer light intensity (calculated after Riley 1957) in the 80-cm-deep mesocosms would not have dropped to <60 µmol quanta m^{-2} s^{-1} PAR even at the highest biomass levels attained in the experiment. On 30 August 2006, eight mesocosms were filled with natural plankton suspension from the Kiel Fjord (Western Baltic Sea). Mesozooplankton was removed by a 150-µm mesh-size screen. In order to produce a high phytoplankton biomass and to avoid exhaustion of phytoplankton by zooplankton grazing early in the experiment, rather high nutrient additions were chosen: 5 µmol PO_4^{3-} l^{-1}, 45 NO_3^- µmol l^{-1}. The added Si:N ratios were 0, 0.25, 0.5, 0.75, 1.0, 1.25, 1.5, and 1.75:1. Dissolved background concentrations were negligible. *A. tonsa* nauplii of the pre-feeding stage NII were added at target densities of 30 individuals l^{-1} from stock cultures. The N:P ratio was kept close to the transition ratio from N to P limitation for average phytoplankton in order to promote coexistence of N- and P-limited phytoplankton (Sommer 1998).

The content of the mesocosms was gently stirred by a propeller in order to assure a homogeneous distribution of the plankton. In previous experiments (Sommer et al. 2007) this form of mixing had been found to be harmless to phyto- and zooplankton. The experiments lasted for 4 weeks. Prior to sampling, the mesocosms were mixed by a paddle to assure re-suspension of phytoplankton which could have settled to the bottom. Moreover, the bottom of the mesocosm was sampled for sedimented algae at the end of the experiment. Samples of 250 ml for phytoplankton, Protozoa, *A. tonsa* eggs and nauplii were taken weekly and fixed with Lugol's iodine. Phytoplankton and Protozoa were counted according to Utermöhl's (1958) inverted microscope method. If abundant enough, at least 100 individuals of each dominant species were counted, thus giving 95% confidence limits of ca. ±20%. Twenty cells of each species were measured microscopically to calculate cell volumes after approximation to standard geometric figures (Hillebrand et al. 1999) and converted to C according the Menden-Deuer and Lessard (2000). *A. tonsa* adults and copepodites were sampled weekly by a plankton net (100-µm mesh size, 10-l sample volume) and counted under a dissecting microscope. On day 21, ten individuals of each copepodite stage and adult females from each mesocosm were examined semi-quantitatively for remains of diatom frustules in their guts. Abundance of diatom remains was classified by the scores 0 (none), 1 (few), 2 (medium), 3 (many), and 4 (full). A more exact quantification was impossible because most diatom frustules in the gut were crushed.

Classification of protists as "edible" and "inedible" for *A. tonsa* was based on the size limit in Sommer et al. 2005 and Sommer and Sommer (2006), i.e. protists >500-μm^3 particle size were considered edible. This simple size limit was applicable because the scarcely edible armoured dinoflagellates were negligible.

Grazing rates of *Acartia* on phytoplankton and Protozoa were measured from day 14 to 21 and from day 21 to 28. Dialysis tubes were filled with plankton suspension from

each mesocosms without *Acartia*. The tubes were then incubated at mid-depth in the mesocosms. The tubes extended from 15 to 65 cm depth. Three replicate dialysis tubes were incubated in each mesocosm. Within the tubes, the algae and Protozoa received the same growth conditions (light, temperature, nutrients) as in the mesocosms without being subject to grazing by *Acartia*. The population grazing rates (G; in day^{-1}) could thus be calculated by the difference between the net growth rate in the mesocosms (r_m) and the net growth rate in the tubes (r_t in day^{-1}, mean of three replicate tubes per mesocosms).

$$G = r_t - r_m$$

Growth rates (r) were calculated from cell numbers (N) at the beginning (t_1) and the end (t_2) of the incubation:

$$r = (\log^e N_2 - \log^e N_1)/(t_2 - t_1)$$

The analysis of growth and grazing rates was restricted to three species, each representing one group: *Thalassionema nitzschioides* (diatoms), *Rhodomonas salina* (phytoflagellates), and oligotrichous ciliates of the medium size class (20–30 μm). The choice of *R. salina* (on average 96% of edible flagellate biomass) and of the medium-sized oligotrichs (on average 76% of ciliates) was based on biomass dominance in their functional groups. *T. nitzschioides* was not dominant among diatoms (on average 8% of diatom biomass), but was the diatom species with the highest cell number and the only diatom species present in reliably countable numbers in all mesocosms during the grazing incubations. The method assumes that r_t is not influenced by second-order effects of copepod removal, e.g. enhanced grazing rates of ciliates in the absence of copepod grazing. This assumption is justified by previous studies (Sommer et al. 2005; Sommer and Sommer 2006), which had demonstrated a complete absence of overlap in the feeding size spectra of summer ciliate assemblages and copepods, i.e. near zero ciliate grazing on the phytoplankton large enough for copepods. After termination of the experiments, samples were taken from the bottom of the mesocosms to see whether sinking of pelagic algae could have biased the estimates of loss rates. The biofilm at the bottom of the mesocosms was extremely patchy and contained almost exclusively benthic diatoms (mainly *Melosira nummuloides*, *Tabularia fasciculata*, *Achnanthes brevipes*) but areal densities of planktonic algae on the bottom were negligible. Therefore, no correction of phytoplankton loss rates for sinking losses was needed.

Community ingestion rates (I) on edible diatoms, ciliates, and edible flagellates were calculated by assuming grazing rates on *Thalassionema* to be representative of those for edible diatoms, grazing rates on the 25-μm oligotrichs to be representative of those for ciliates, and grazing rates on *Rhodomonas* to be representative of those for edible flagellates:

$$I_i = G_i \times B_i$$

where i is the index for the different food categories and B biomass expressed in C (geometric mean of start and end value).

Net production rates of copepod eggs were estimated by calculating the area under the egg or nauplii abundance versus time curve and dividing this area by the development times of eggs and nauplii. These are primarily temperature dependent (Mauchlin 1998) and could be calculated from equations in the literature for 18°C: 1.6 day for egg development (McLaren 1966; McLaren et al. 1969 for *A. tonsa*) and 7.15 day for naupliar development (McLaren 1978 for the congeneric species *Acartia clausii*). However, the calculated rates are just net production rates, not gross production rates because of unmeasured mortality. In the case of eggs, also cannibalism by adults has to be considered.

Results

Protist (phytoplankton plus Protozoa) biomass in the mesocosms increased rapidly and reached a peak after 2–3 weeks (shown for Si:N = 0.1 and 1.75:1 in Fig. 1). Thereafter, biomass declined. Maximal biomass levels were quite similar between treatments (5.9–9 mg C l^{-1}) without any trend across the Si:N gradient. While initially edible protists dominated, the share of inedible ones increased towards the end of the experiment. As expected, the relative contribution of diatoms to protist biomass increased with Si:N. This applied both to edible protists (shown for the averages over the entire experiment in Fig. 2) and to the entire protist community (not shown). Pigmented flagellates contributed far more to total biomass than ciliates, unpigmented flagellates were marginal.

All *Acartia* stages had remains of diatoms in their guts except for some of the individuals from the mesocosms with the lowest Si:N ratios. A plot of gut fullness (median vales for each stage and mesocosm) shows two patterns (Fig. 3): gut fullness increases with diatom biomass in a saturating way; at the same level of diatom biomass, the younger stages (CI–CIII) have fuller guts than the older ones (CIV–adults).

Calculated grazing rates are population grazing rates, i.e. the composite result of different life cycle stages with different rates and food preferences. Therefore, it was impossible to calculate grazing rates per copepod individual. The calculated grazing rates of the *Acartia* population on the diatom *Thalassionema nitzschioides* were low and ranged from ca. 0.04 to 0.065 day^{-1} without any tendency

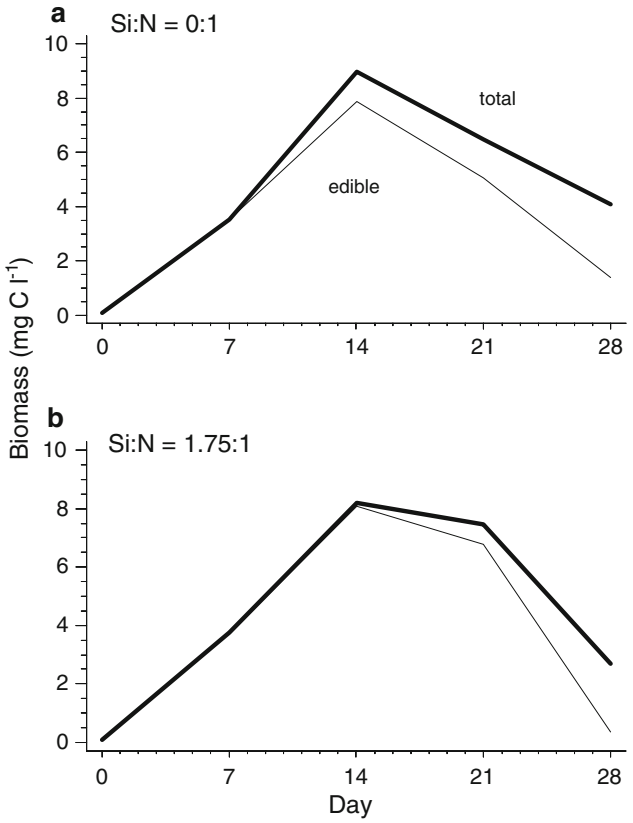

Fig. 1 Time course from 0 to 28 days of total (*continuous thick line*) and edible (*continuous thin line*) protist biomass (μg C l^{-1}) in the mesocosms fertilized at an Si:N ratio of **a** 0:1 and **b** 1.75:1. Protists were classified as "edible" for *Acartia tonsa* if they exceeded 500 μm^3

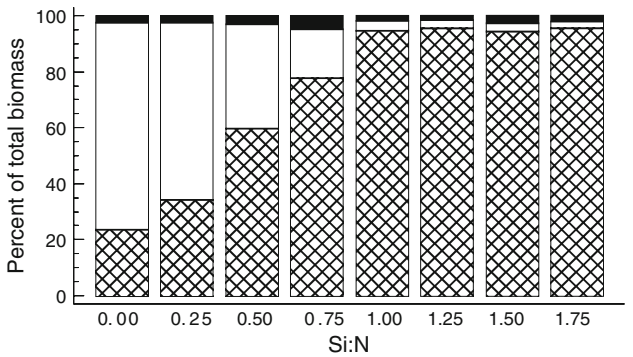

Fig. 2 Percent of edible protist biomass for ciliates (*black*), pigmented flagellates (*white*), and diatoms (*hatched*) at Si:N ratios from 0:1 to 1.75:1; mean values of entire experiment

to change with diatom biomass (Fig. 4a). Conversely, the grazing rates on the phytoflagellate *Rhodomonas salina* (Fig. 4b) and on medium-sized oligotrichous ciliates (Fig. 4c) were low (around 0.1 day^{-1}) at high biomass levels of motile prey and high (up to 0.55 day^{-1}) at low biomass levels, indicating increased clearance rates at low

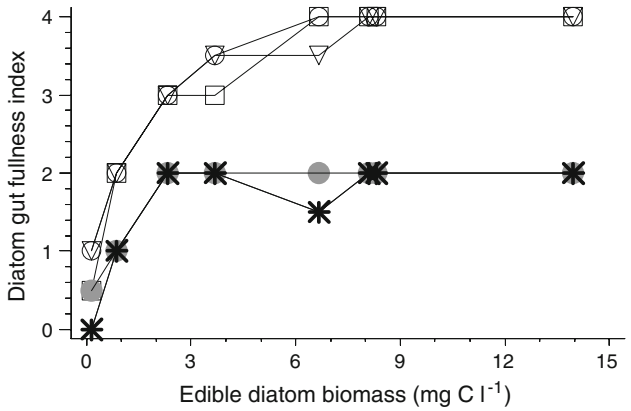

Fig. 3 Median of diatom feeding by *Acartia tonsa* (diatom gut fullness index) at six developmental stages in response to edible diatom biomass. *A. tonsa* stages are C1 (*open circle*), C2 (*inverted triangle*), C3 (*square*), C4 (*plus*), C5 (*multiplication symbol*), and adults (*grey circle*)

biomass of motile prey. Grazing rates on the ciliates and on *Rhodomonas* did not differ significantly (paired *t*-test, $t = -1.565$; $P = 0.1385$). Therefore, ingestion rates on ciliates and edible flagellates were lumped and related to the biomass of motile, edible prey. A non-linear regression analysis provided a satisfactory fit of a Michaelis–Menten-type saturation model both for the two grazing experiments individually and for the pooled data from both experiments (Table 1).

While the three prey types analysed in the grazing experiments were not the only representatives of their functional group in the plankton of the mesocosms, it is still possible to calculate at least a tentative estimate of diet composition. For that purpose, I assumed that the grazing rates on edible diatoms equalled the ones on *T. nitzschioides*, the grazing rates on edible flagellates the ones on *Rhodomonas salina*, and the grazing rates on ciliates the ones on the oligotrichous ciliates. This assumption seems a plausible approximation, because a previous copepod grazing experiment (Sommer et al. 2005) had shown negligible differences between the grazing rates on food items within the edible food categories. Ingestion rates (I) for the different food categories were calculated by multiplying the biomass (geometric mean of incubation interval) of the different functional groups with the grazing rates on their "representatives" by the entire *Acartia* population. Because of the similarity of *Acartia*'s response to *Rhodomonas salina* and oligotrichous ciliates the ingestion rates were pooled. Ingestion ratios (IRs) of motile prey (I_{motile}:I_{total}) were compared to the relative contribution of motile, edible protists to total edible biomass in the environment ("biomass ratio"). A regression analysis according to the model $y = ax^b$ yielded almost identical results for both grazing experiments and the pooled data:

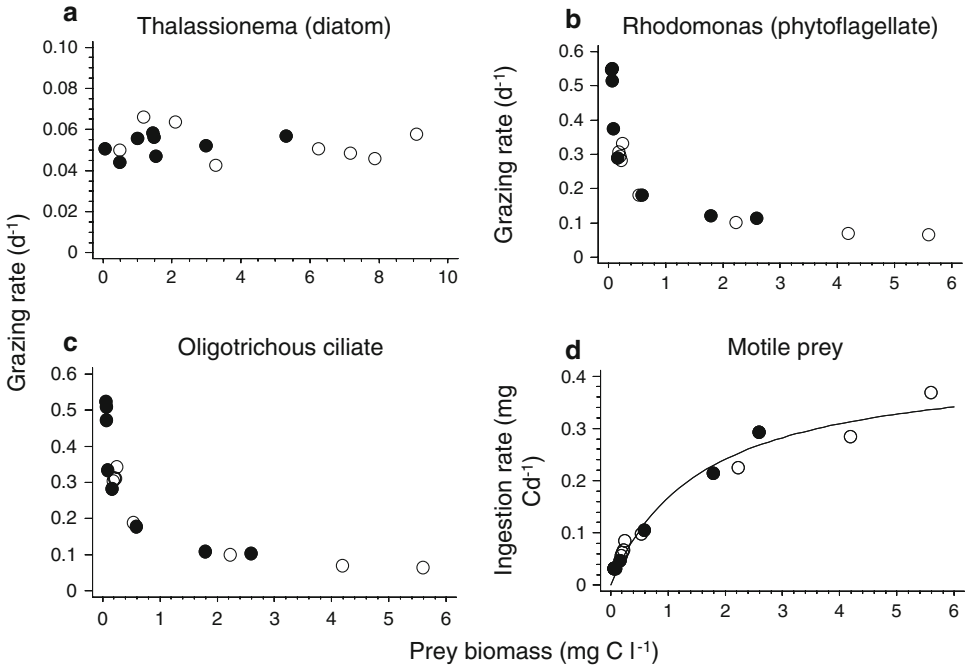

Fig. 4 Population grazing rates of *A. tonsa* during grazing experiment 1 from day 14 to 21 (*open circle*) and experiment 2 from day 21 to 28 (*filled circle*) as a function of prey biomass (geometric means of incubation interval). Grazing rates on **a** the diatom *Thalassionema nitzschioides* as a function of diatom biomass, **b** the phytoflagellate *Rhodomoas salina* as a function of motile prey biomass, **c** the medium-sized oligotrichous ciliates as a function of motile prey biomass. **d** Ingestion rate of motile prey as a saturating function of motile prey biomass (parameters of fitted Michaelis–Menten curve in Table 1)

Table 1 Nonlinear regression analysis according to the model $I = (I_{max} \cdot F)/(F + k)$ of population ingestion rates (I) on motile prey on biomass of motile prey

Experiment	I_{max} (µg C l^{-1} day^{-1}) ± SE	k (µg C l^{-1}) ± SE	r^2	n
1	427 ± 45.8	1,584 ± 470	0.956	8
2	492 ± 100	1,992 ± 784	0.973	8
Pooled data	431 ± 32.7	1,577 ± 299	0.968	16

Experiment 1: $IR = 0.95BR^{051(\pm 0.03)}$, $r^2 = 0.977$, $P < 0.0001$

Experiment 2: $IR = 1.08BR^{0.49(\pm 0.04)}$, $r^2 = 0.957$, $P < 0.0001$

Pooled data: $IR = 1.01BR^{0.50(\pm 0.03)}$, $r^2 = 0.954$, $P < 0.0001$

The plot in Fig. 5 shows that only at a very high dominance of motile prey are ingestion ratios similar to biomass ratios in the environment. At 10% motile prey in the environment, motile prey would make up ca. 30% of the diet, and at 1% in the environment still ca. 10% of the diet. There is no indication for switching in favour of a more abundant prey, which would show up as a sigmoid pattern in a linear plot of IR on biomass ratio.

Initially, nauplii numbers began to decrease because of development into copepodites. New eggs began to appear in the mesocosm with Si:N = 0–0.5:1 on day 7, while at the higher Si:N ratios the first eggs appeared on day 14 (Fig. 6). Subsequently, there was an increase of nauplii reaching abundance maxima between 592 and 988 l^{-1} in

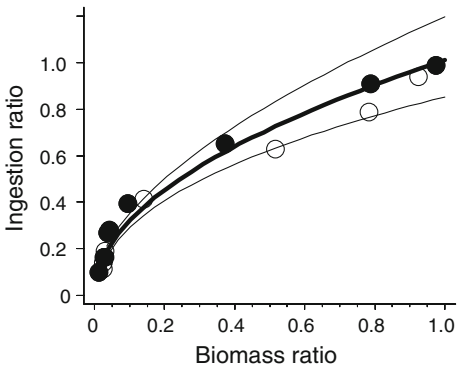

Fig. 5 Ingestion ratio versus biomass ratio of motile prey during days 14–21 (*open circle*) and days 21–28 (*filled circle*); regression line (*continuous thick line*), 95% confidence limits for pooled data set (*continuous thin line*)

the different mesocosms. Adult plus copepodite numbers increased rather steadily and reached maximal levels between 59 and 114 l^{-1} at the end of the experiment in all mesocosms. There was no relationship between the final abundance and Si:N ratios or edible diatom biomass. Similarly, egg production rates were unrelated to Si:N ratios, while nauplii production rates showed a weak, but significant, increasing trend with Si:N ratios and with the share of diatoms in the diet, calculated as mean for both grazing experiments (Fig. 7):

$$P_n = 130.7 + 104.0\,\mathrm{Si:N}; \quad r^2 = 0.668; \quad P = 0.0132$$

$$P_n = 103.5^{*} + 213\,\mathrm{IR}_{diat}; \quad r^2 = 0.816; \quad P = 0.002$$

where P_n is the nauplii production rate (in N l^{-1} day^{-1}) and $IR_{diatoms}$ the ratio $I_{diatoms}/I_{total}$.

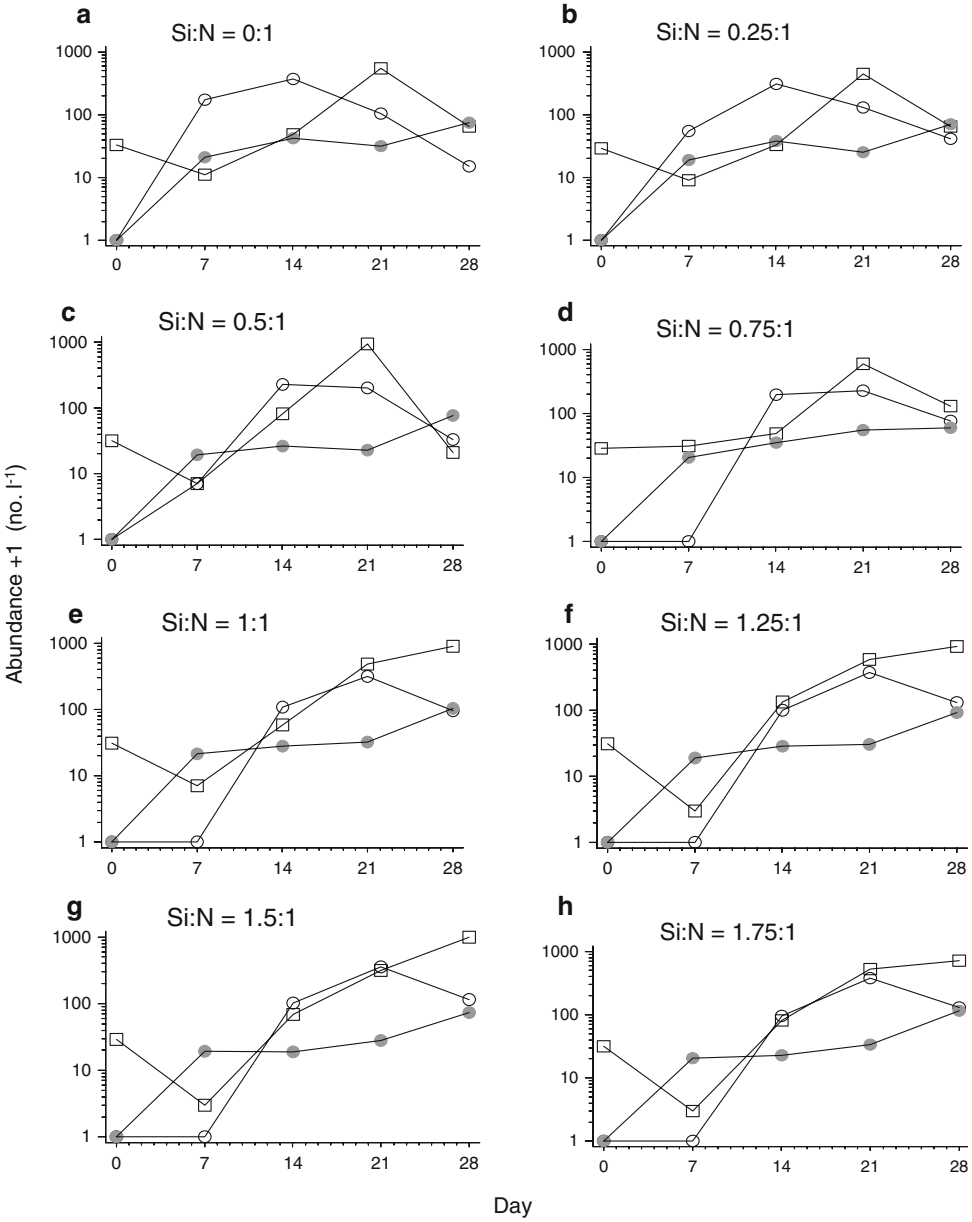

Fig. 6 **a**–**h** Temporal abundance change of *A. tonsa* eggs (*open circle*), nauplii (*square*), and copepodites plus adults (*grey circle*) at eight different Si:N ratios

Discussion

A. tonsa has been reported repeatedly to be able to shift between suspension and ambush feeding and thus between feeding on diatoms and motile protists (Saiz and Kiørboe 1995; Kiørboe et al. 1996; Takahashi and Tiselius 2005). The plot in Fig. 5 shows a clear behavioural preference for feeding on motile prey and no switching in favour of a relatively more common prey type at a certain diatom:motile prey ratio. Instead, it is obvious that the over-representation of motile prey in the diet becomes bigger the smaller its share is in the environment.

The composite nature of feeding by a mixture of different developmental stages is also the main reason why

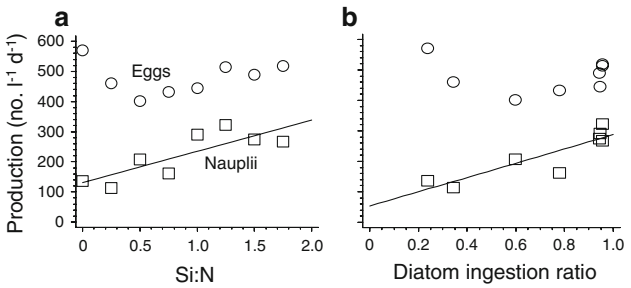

Fig. 7 Egg (*open circle*) and nauplii production (*square* and *regression line*) in response to **a** Si:N fertilization ratios and **b** ingestion ratios of diatoms, defined as the ratio of diatoms biomass ingested to total biomass ingested, mean between both experiments

the half-saturation parameters in Table 1 cannot be compared to functional response curves in the literature based on one food type—one developmental stage (usually adult) experiments. The dependence of ingestion rates on food concentrations is not always analysed using a Michaelis–Menten model, but from the graphical representations it is easy to estimate the food concentration at which 50% of I_{max} are reached. The literature values of the half-saturation constant range form ca. 200 to 600 μg C l^{-1} (Frangoulos et al. 2000; Besiktepe and Dam 2002; Thor et al. 2002; Dam and Colin 2005; Maneiro et al. 2005; Tirelli and Mayzaud 2005; Colin and Dam 2007; Henriksen et al. 2007) and are thus 2.5–7.5 times smaller than the half-saturation constants in Table 1.

The flat response of diatom grazing rates to diatom concentrations implies a linear response of ingestions rates which clearly contradicts any usual functional response model at food concentrations above the incipient limiting level. It may be suspected that a density-independent loss factor applying to the mesocosms but not to the dialysis tubes could have caused the erroneous calculation of a positive grazing rate on diatoms. However, sedimentation as the only plausible density-independent loss factor can be excluded, Moreover, the gut content analysis indicated feeding on diatoms and fuller guts at higher ambient diatom concentrations. Therefore, diatom feeding is taken as a fact.

In spite of the clear behavioural preference for motile prey, dominance of diatoms in the diet at the higher Si:N ratios did not harm growth and reproduction of *A. tonsa*. Egg production rates and the final number of copepodites/adults were not affected by Si:N ratios or diatom dominance and the production rate of nauplii showed even a slight positive response. Thus, there was neither a toxic effect of diatoms in the environment nor of diatoms in the diet on the growth and reproduction of *A. tonsa*. On the other hand, nutritional deficiency, e.g. lack of essential polyunsaturated fatty acids (Jónasdottir and Kiørboe 1996; Jonasdottir et al. 2002; Koski and Klein Breteler 2003) cannot be ruled out. However, even 90% diatoms in the diet did not lead to a reduced reproduction of *A. tonsa.* This means that 10% flagellates and ciliates in the diet must have sufficed to compensate for any nutritional deficiency of diatoms. This seems to deviate from much of the recent literature on the diatom–copepod paradox, but some specific differences to the typical one phytoplankton clone—one copepod experiments have to be kept in mind.

The diatom assemblage in my experiments was rather diverse, with seven species sufficiently abundant to warrant counting, plus numerous rare species which could be neglected during counting. In addition, it seems probable that there was substantial clonal diversity within species because of the large inoculum size (300-l natural plankton suspension).

Even at the highest diatom dominance, *A. tonsa* had the chance to ingest 10% non-diatom food. This value seems low at first sight because it implies a diet consisting of 90% diatoms. Nevertheless, it might be important during the critical phase of egg production. Ianora et al. (2003) have shown that the adverse effects of toxic diatoms on egg production and hatching rates can be reversed within a few days if diatoms are replaced by flagellates as food. Thus, even toxic diatoms can be a reasonable energy source for most of the somatic growth of copepods if they are replaced by other food during a short period at the right time. While critically important for females during reproduction, non-diatom food can be a minor component of a copepod's lifetime diet.

The literature on diatom–copepod interactions has become increasingly detailed. Meanwhile aldehydes and fatty acid hydroperoxides have been identified as the toxic compounds (Ianora et al. 2004; Wichard et al. 2005; Fontana et al. 2007) and it has been shown that these compounds are produced by mechanical cell rupture (Pohnert 2000; Fontana et al. 2007). The toxic effect has been identified as being particularly harmful to embryogenesis and thus to reduce the hatching success of eggs (Chaudron et al. 1996; Poulet et al. 2006). In other laboratory studies, no toxic effect was found, but under some environmental conditions, poor food quality, e.g. a low content of highly polyunsaturated fatty acid, could explain reduced hatching success (Jónasdottir and Kiørboe 1996; Jonasdottir et al. 2002; Koski and Klein Breteler 2003). Also the extent of diatom nutrient limitation has been found to be decisive for their nutritional value (Jones et al. 2002), sometimes mediated by unfavourable fatty acid profiles under nutrient limitation (Klein Breteler et al. 2005). Field studies have sometimes supported the idea of negative diatom effects on copepods (Miralto et al. 1999, 2003; Pierson et al. 2005) while other studies have reported successful copepod growth and reproduction during dense diatom blooms (Irigoien et al. 2000, 2005), including occasional feeding selectivity in favour of diatoms (Irigoien et al. 2003; Meyer-Harms et al. 1999). Obviously, effects are highly species (diatoms and copepods) and context dependent.

The seven diatoms species abundant enough for reliable counts (*Cerataulina pelagica*, *Chaetoceros curvisetus*, *Dactylosolen fragilissimus*, *Nitzschia acicularis*, *Pseudonitzschia* cf. *pungens*, *Rhizosolenia setigera*, *and T. nitzschioides*) have so far not been reported harmful for *A. tonsa* or other *Acartia* spp. However, three of the species have been reported to be toxic for other copepods: *Chaetoceros curvisetus* for *Temora stylifera* (Koski et al. 2008), *N. acicularis* for *Calanus chilensis* (Poulet et al. 2007b), and *R. setigera* for *Calanus helgolandicus* (Poulet

et al. 2007a). Other species of *Chaetoceros* have been found toxic for *A. tonsa* and other *Acartia* spp. (Ban et al. 1997; Jónasdottir and Kiørboe 1996; Vargas et al. 2006). A survey of the occurrence of polyunsaturated aldehydes (PUAs), the class of substances most commonly held responsible for diatom toxicity, in 71 diatom species (Wichard et al. 2005) did not list any of the species in the mesocosms as containing PUAs, but several other *Chaetoceros* spp.

The increasing level of detail and biochemical resolution in the laboratory has provided interesting insights into chemical ecology, but from an ecosystem perspective the big questions remain open: do diatoms interrupt the efficiency of energy and matter transfer from primary production to copepod production, and thereby indirectly to fish production? If this is the case, why is the ratio fish production:primary production higher in diatom-dominated upwelling systems (ca. 1%) than in oligotrohic systems dominated by nano- and picophytoplankton (ca. 0.4%) (Iverson 1990; Sommer et al. 2002)? While it is premature to give a final answer, some speculation might be possible: the deleterious diatom effects on copepods might be comparable to the effects of toxic plants on herbivores in grassland ecosystems, i.e. might be a problem locally and under specific circumstance, but unimportant for large-scale budgets. The in situ effect should be smaller than anticipated from single-species laboratory experiments because:

1. Even under high diatom natural dominance there are always alternative food sources.
2. Natural diatom assemblages are usually mixed, which increases the probability of non-toxic species or strains.
3. Natural copepod assemblages are usually mixed, which increases the probability of resistant species.
4. Even if diatoms are toxic, they have to be avoided by copepods only during a relatively short part of their life cycle (Ianora et al. 2003).

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References

Ban S, Burns C, Castel J, et al. (1997) The paradox of diatom copepod interactions. Mar Ecol Prog Ser 157:287–293

Besiktepe S, Dam HG (2002) Coupling of ingestion and defecation as a function of diet in the calanoid copepod *Acartia tonsa*. Mar Ecol Prog Ser 229:151–164

Calbet A, Landry MR (2004) Phytoplankton growth, microzooplankton, and carbon cycling in marine systems. Limnol Oceanogr 49:51–57

Chaudron Y, Poulet SA, Laabir M, et al. (1996) Is hatching success of copepod eggs diatom density-dependent? Mar Ecol Prog Ser 144:185–193

Colin SP, Dam HG (2007) Comparison of the functional and numerical responses of resistant versus non-resistant populations of the copepod *Acartia hudsonica* fed the toxic dinoflagellate *Alexandrium tamarense*. Harmful Algae 6:875–882

Dam HG, Colin SP (2005) *Prorocentrum minimum* (clone Exuv) is nutritionally insufficient, but not toxic to the copepod *Acartia tonsa*. Harmful Algae 4:575–584

Egge JK, Jacobsen A (1997) Influence of silicate on particulate carbon production in phytoplankton. Mar Ecol Prog Ser 147:219–230

Fontana A, d'Ippolito G, Cutignano A, et al. (2007) LOX-induced lipid peroxidation mechanism responsible for the detrimental effect of marine diatoms on zooplankton grazers. Chem Biochem 8:1810–1818

Frangoulos M, Guisande C, Maneiro I, et al. (2000) Short-term and long-term effects of the toxic dinoflagellate *Alexandrium minutum* on the copepod *Acartia clausi*. Mar Ecol Prog Ser 203:161–169

Henriksen CI, Saiz E, Calbet A, et al. (2007) Feeding activity and swimming patterns of *Acartia grani* and *Oithona davisae* nauplii in the presence of motile and non-motile prey. Mar Ecol Prog Ser 331:119–129

Hillebrand H, Duerselen C-D, Kirschtel D, Pollingher U, Zohary T (1999) Biovolume calculation for pelagic and benthic microalgae. J Phycol 35:403–424

Ianora A, Poulet SA, Miralto A (1995) A comparative study of the inhibitory effect of diatoms on the reproductive biology of the copepod *Temora stylifera*. Mar Biol 125:279–286

Ianora A, Poulet SA, Miralto A (2003) The effects of diatoms on copepod reproduction. A review. Phycologia 42:351–363

Ianora A, Miralto A, Poulet SA, et al. (2004) Aldehyde suppression of copepod recruitment in blooms of a ubiquitous planktonic diatom. Nature 429:403–407

Irigoien X, Harris RP, Verheye HM, et al. (2002) Copepod hatching success in marine ecosystems with high diatom concentrations. Nature 419:387–389

Irigoien X, Head RN, Harris RP, et al. (2000) Feeding selectivity and egg production of *Calanus helgolandicus* in the English Channel. Limnol Oceanogr 45:44–54

Irigoien X, Titelman J, Harris RP, et al. (2003) Feeding of *Calanus finmarchicus* nauplii in the Irminger Sea. Mar Ecol Prog Ser 262:193–200

Irigoien X, Verheye HM, Harris RP, et al. (2005) Effect of food composition on egg production and hatching success rate of two copepod species (Calanoides carinatus and Rhincalanus nasutus) in the Benguela upwelling system. J Plankton Res 27:735–742

Iverson RL (1990) Control of marine fish production. Limnol Oceanogr 35:1593–1604

Jónasdottir SH, Kiørboe T (1996) Copepod recruitment and food composition: do diatoms affect hatching success? Mar Biol 125:743–750

Jonasdottir SH, Gudfinnsson HG, Gislason, Astthorsson OS (2002) Diet composition and quality for *Calanus finmarchicus* egg production and hatching success off south-west Iceland. Mar Biol 140:1195–1206

Jones RH, Flynn KJ, Anderson TR (2002) Effect of food quality on carbon and nitrogen growth efficiency in the copepod *Acartia tonsa*. Mar Ecol Prog Ser 235:147–156

Kiørboe T, Saiz E, Viitasalo M (1996) Prey switching behaviour in the planktonic copepod *Acartia tonsa*. Mar Ecol Prog Ser 143:65–75

Klein Breteler WCM, Schogt N, Rampen S (2005) Effect of diatom nutrient limitation on copepod development: role of essential lipids. Mar Ecol Prog Ser 219:125–130

Knuckey RM, Semmens GL, Mayer RJ, et al. (2005) Development of an optimal microalgal diet for the culture of the calanoid copepod *Acartia sinjiensis*: effect of algal species and feed concentration on copepod development. Aquaculture 249:339–351

Koski M, Klein Breteler WCM (2003) Influence of diet on copepod survival in the laboratory. Mar Ecol Prog Ser 264:73–82

Koski M, Wichard T, Jónasdottir SH (2008) "Good" and "bad" diatoms: development, growth, and juvenile mortality of the copepod *Temora longicornis* on diatom diets. Mar Biol 154:719–734

Legendre L (1990) The significance of microalgal blooms for fisheries and export of particulate organic carbon in the oceans. J Plankton Res 12:681–699

Maneiro I, Iglesias P, Guisande C, et al. (2005) Fate of domoic acid ingested by the copepod *Acartia clausi*. Mar Biol 148:123–130

Mauchlin J (1998) The biology of calanoid copepods. Academic Press, San Diego

McLaren IA (1966) Predicting development rates of copepod eggs. Biol Bull 131:457–469

McLaren IA (1978) Generation lengths of some temperate marine copepods–estimation, prediction and implications. J Fish Res Board Can 35:1330–1342

McLaren IA, Corkett CJ, Zillioux EJ (1969) Temperature adaptations of copepod eggs from the arctic to the tropics. Biol Bull 137:486–493

Menden-Deuer S, Lessard EJ (2000) Carbon to volume relationships for dinoflagellates, diatoms, and of the protist plankton. Limnol Oceanogr 45:569–579

Meyer-Harms B, Irigoien X, Head R, Harris R (1999) Selective feeding on natural phytoplankton by *Calanus finmarchicus* before, during, and after the 1997 spring bloom in the Norwegian Sea. Limnol Oceanogr 44:154–165

Miralto A, Barone G, Romano G, et al. (1999) The insidious effect of diatoms on copepod reproduction. Nature 402:173–176

Miralto A, Guglielmo L, Zagami G, et al. (2003) Inhibition of population growth in the copepods *Acartia clausi* and *Calanus helgolandicus* during diatom blooms. Mar Ecol Prog Ser 254:253–268

Nejstgaard JC, Gismervik I, Solberg PT (1997) Feeding and reproduction by *Calanus finnmarchicus,* and microzooplankton grazing during mesocosm blooms of diatoms and the coccolithophore *Emilinana huxleyi*. Mar Ecol Prog Ser 147:197–217

Paffenhöfer GA, Ianora A, Miralto A, et al. (2005) Colloquium on diatom–copepod interactions. Mar Ecol Prog Ser 286:293–305

Pierson JJ, Halsband-Lenk C, Leising AW (2005) Reproductive success of *Calanus pacificus* during diatom blooms in Dabob Bay, Washington. Prog Ocean 67:314–331

Pohnert G (2000) Wound-activated chemical defence in unicellular planktonic algae. Angew Chem Int Ed 39:4352–4354

Poulet SA, Ianora A, Miralto A, Meijer L (1994) Do diatoms arrest embryonic development in copepods? Mar Ecol Prog Ser 111:79–96

Poulet SA, Cueff A, Wichard T, et al. (2007a) Influence of diatoms on copepod reproduction. III. Consequences of abnormal oocyte maturation on reproductive factors in *Calanus helgolandicus*. Mar Biol 152:415–428

Poulet SA, Escribano R, Hidalgo P, et al. (2007b) Collapse of *Calanus chilensis* reproduction in a marine environment with high diatom concentration. J Exp Mar Biol Ecol 352:187–199

Poulet SA, Wichard T, Ledoux JB, et al. (2006) Influence of diatoms on copepod reproduction. I. Field and laboratory observations related to *Calanus helgolandicus* egg production. Mar Ecol Prog Ser 308:129–142

Riley GA (1957) Phytoplankton of the North Central Sargasso Sea. Limnol Oceanogr 2:252–270

Saiz E, Kiørboe T (1995) Predatory and suspension feeding of the copepod *Acartia tonsa* in turbulent environments. Mar Ecol Prog Ser 122:147–158

Sommer U (1994) The impact of light intensity and daylength on silicate and nitrate competition among marine phytoplankton. Limnol Oceanogr 39:1680–1688

Sommer U (1998) From algal competition to animal production: enhance ecological efficiency of *Brachionus* with a mixed diet. Limnol Oceanogr 43:1393–1396

Sommer U, Sommer F (2006) Cladocerans versus copepods: the cause of contrasting top-down controls in freshwater and marine phytoplankton. Oecologia 147:183–194

Sommer U, Stibor H, Katechakis A, Sommer F, Hansen T (2002) Pelagic food web configuration at different levels of nutrient richness and their implications for the ratio fish production:primary production. Hydrobiologia 484:11–120

Sommer U, Hansen T, Stibor H, Vadstein O (2004) Presistence of phytoplankton responses to different Si:N ratios under mesozooplankton grazing pressure: a mesocosm study with NE Atlantic plankton. Mar Ecol Prog Ser 278:67–75

Sommer U, Hansen T, Blum O, Holzner N, Vadstein O, Stibor H (2005) Copepod and microzooplankton grazing in mesocosms fertilised with different Si:N ratios: no overlap between food spectra and Si:N influence on zooplankton trophic level. Oecologia 142:274–283

Sommer U, Aberle N, Engel A, Hansen T, Lengfellner K, Sandow M, Wohlers J, Zöllner E, Riebesell U (2007) An indoor mesocosm system to study the effect of climate change on the late winter and spring succession of Baltic Sea phyto- and zooplankton. Oecologia 150:655–667

Takahashi K, Tiselius P (2005) Ontogenetic change of foraging behaviour during copepodite development of *Acartia clausii*. Mar Ecol Prog Ser 303:213–223

Thor P, Cervetto G, Besiktepe S, et al. (2002) Influence of two different green algal diets on specific dynamic action and incorporation of carbon into biochemical fractions in the copepod *Acartia tonsa*. J Plankton Res 24:293–300

Tilzer M (1983) The importance of fractional light absorption by photosynthetic pigments for phytoplankton productivity in Lake Constance. Limnol Oceanogr 28:833–846

Tirelli V, Mayzaud P (2005) Relationship between functional response and gut transit time in the calanoid copepod *Acartia clausi*: role of food quantity and quality. J Plankton Res 27:557–568

Tiselius P, Jonsson PR (1990) Foraging behaviour of six calanoid copepods: observations and hydrodynamic analysis. Mar Ecol Prog Ser 66:22–33

Utermöhl H (1958) Zur Vervollkommnung der quantitativen Phytoplankton Methodik. Mitt Int Ver Theor Angew Limnol 9:263–272

Vargas C, Escribano R, Poulet SA (2006) Phytoplankton food quality determines time-windows for successful zooplankton reproductive pulses. Ecology 87:2992–2999

Wichard T, Poulet SA, Halsband-Lenk C, et al. (2005) Survey of the chemical defence potential of diatoms: screening of fifty-one species for α, β, γ, δ-unsaturated aldehydes. J Chem Ecol 31(4):949–958