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Influence of phytoplankton diets on the ingestion rate and egg production of *Acartia clausi* and *A. lilljeborgii* (Copepoda: Calanoida) from Bahía de La Paz, Gulf of California

Influencia de dietas de fitoplancton en la tasa de ingesta y producción de huevos de *Acartia clausi* y *A. lilljeborgii* (Copepoda: Calanoida) de la Bahía de La Paz, Golfo de California

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ABSTRACT

Different phytoplankton diets were tested on *Acartia clausi* and *A. lilljeborgii* from Bahía de La Paz to determine their effect on survival, egg production, and ingestion rate. Female copepods were fed diatom strains (*Chaetoceros* sp., *Cylindrotheca closterium, Odontella longicruris*, and *Dytilum brightwelli*), dinoflagellate strains (*Scrippsiella* sp., *Gyrodinium* sp., *Prorocentrum micans,* and *P. rhathymum*), and one Raphidophyceae (*Chattonella* sp.). After 24 h of incubation in darkness at 24 °C, survival with various phytoplankton diets was above 91%. *Gyrodinium* sp. produced the lowest survival in both copepod species (44.5% in *A. clausi* and 89.6% in *A. lilljeborgii*). Dinoflagellate diets provided the highest egg production. *A. clausi* had higher egg production when fed with *P. rhathymum*, *P. micans*, *Gyrodinium* sp., *Scrippsiella* sp., and *Chattonella* sp. *A. lilljeborgii* had a higher egg production with *Scrippsiella* sp., *P. micans*, *Gyrodinium* sp., and *Chaetoceros* sp. Ingestion rates were higher in both *Acartia* species with two diatom diets (*O. longicruris* and *Chaetoceros* sp.), *P. rhathymum* and *Chattonella* sp. These results suggest that both *Acartia* species respond to nutritional quality of phytoplankton in a short time. Higher ingestion rates did not necessarily result in higher egg production, suggesting that the link between ingestion and egg production may be in what is eaten, rather than in how much. The response in egg production seems to be species specific, but in general was higher with dinoflagellate diets, suggesting a higher food quality compared with diatoms (excepting *Chaetoceros* sp.).

Key words: *Acartia clausi*, *Acartia lilljeborgii*, Bahía de La Paz, egg production, grazing rate.

RESUMEN

Se probaron diversas dietas de fitoplancton en *Acartia clausi* y *A. lilljeborgii* de la Bahía de La Paz, para determinar su efecto en la supervivencia, producción de huevos y tasa de ingesta. Se alimentaron hembras de copépodos con cepas de diatomeas (*Chaetoceros* sp., *Cylindrotheca closterium, Odontella longicruris* y *Dytilum brightwelli*), de dinoflagelados (*Scrippsiella* sp., *Gyrodinium* sp., *Prorocentrum micans* y *P. rhathymum*) y una rafidofita (*Chattonella* sp.). Después de 24 h de incubación en oscuridad a 24 °C, la supervivencia con las diversas dietas fue mayor a 91%. Sólo al alimentar a *A. clausi* con *Gyrodinium* sp. la supervivencia fue baja (44.5%). Con las dietas de dinoflagelados se obtuvo la mayor producción de huevos. *A. clausi* presentó una mayor producción de huevos al alimentarse con *P. rhathymum*, *P. micans*, *Gyrodinium* sp., *Scrippsiella* sp. y *Chattonella* sp. *A. lilljeborgii* presentó una mayor producción de huevos con *Scrippsiella* sp., *P. micans*, *Gyrodinium* sp. y *Chaetoceros* sp. La tasa de ingesta en ambas especies de *Acartia* fue mayor con dos dietas de diatomeas (*O. longicruris* y *Chaetoceros* sp.), *P. rhathymum* y *Chattonella* sp. Estos resultados sugieren que ambas especies de *Acartia* responden en un lapso corto de tiempo a la calidad nutricional del fitoplancton. Las mayores tasas de ingesta no necesariamente resultaron en una mayor producción de huevos, sugiriendo que la relación entre la tasa de ingesta y la producción de huevos pudiera estar relacionada con la calidad alimenticia, más que con la cantidad ingerida. La respuesta en la producción de huevos en ambos copépodos parece ser específica para cada especie, sin embargo en general, las dietas de dinoflagelados parecen tener una mayor calidad nutricional comparadas con las diatomeas con la excepción de *Chaetoceros* sp.

Palabras clave: *Acartia clausi*, *Acartia lilljeborgii*, Bahía de La Paz, producción de huevos, tasa de ingesta.

INTRODUCTION

Copepods are the dominant mesozooplankton in marine environments, representing up to 80% of its total biomass (Kiørboe, 1998). In Bahía de La Paz, few dominant species have been reported. *Acartia clausi* (Giesbrecht, 1892) and *A. lilljeborgii* (Giesbrecht, 1889) are the most abundant species throughout the year and are important contributors to secondary production of the bay (Palomares-García *et al*., 2003).

Several studies have demonstrated that egg production rate in copepods can be used to estimate feeding conditions (Dagg, 1977; Saiz *et al*., 1993), but few studies have been done in subtropical zones to support this hypothesis. Egg production is regulated by several environmental factors, such as temperature (Koski & Kuosa, 1999), salinity (Pagano *et al*., 2004), female size (Koski & Kuosa, 1999), diurnal rhythms (Pagano *et al*., 2004), food abundance (Kleppel, 1993; Pagano *et al*., 2004), food type (Murray & Marcus, 2002; Ceballos & Ianora, 2003), and food quality (Kleppel & Burkart, 1995).

In situ daily egg production rates of *A. clausi* and *A. lilljeborgii* have been estimated on a seasonal basis in Bahía de La Paz, however the factors influencing variations in production rates have not been defined (Palomares-García *et al*., 2003; Pacheco-Chávez *et al*., 2005). During winter, average daily egg production rates for *A. clausi* and *A. lilljeborgii* were 12 ± 4 eggs female^{-1} day^{-1} and 23 ± 6 eggs female^{-1} day^{-1}, respectively, and increased with high nutrient and chlorophyll *a* (Chl *a*) concentrations in a well-mixed water column (Palomares-García *et al*., 2003). Pacheco-Chávez *et al*. (2005) found in autumn an egg production for *A. lilljeborgii* and *A. clausi* of 16.8 ± 7.8 eggs female^{-1} day^{-1} and 8.7 ± 4.9 eggs female^{-1} day^{-1}, respectively. Daily egg production increased with Chl *a* concentration during autumn, but no correlation was found in spring and winter. These results suggest that seasonal changes in phytoplankton species composition could be influencing egg production.

The determination of grazing rates and egg production of copepods with different phytoplankton species can lead to a better understanding of the environmental factors that define the ecological niches of the copepods, leading the way to a description of environmental controls on community composition and on food web structure. The goal of this study was to determine the effect of different phytoplankton diets (dinoflagellates, diatoms, and one raphidophyte) on survival, ingestion rate, and egg production, in *Acartia clausi* and *A. lilljeborgii* from Bahía de La Paz under laboratory conditions.

MATERIALS AND METHODS

Clonal cultures of several algae (*Odontella longicruris* (Greville) Hoban, *Chaetoceros* sp., *Cylindrotheca closterium* (Ehrenberg) W. Smith, *Ditylum brightwellii* (West) Grunow in Van Heurck, *Prorocentrum rhathymum* Loeblich, Shirley *et* Schmidt, *P. micans* Ehrenberg, and *Chattonella* sp. were obtained from Bahía de La Paz on the western side of the Gulf of California. *Scrippsiella* sp. and *Gyrodinium* sp. were collected in Bahía de Topolobampo on the eastern side of the Gulf of California. Vegetative cells were collected by vertical tows with a 20-µm phytoplankton net. The cell concentrate was sieved through a 60-µm mesh screen to eliminate larger organisms. The concentrate was placed in a 250-ml culture container filled with filtered seawater. In the laboratory, phytoplankton vegetative cells were isolated with micro-pipettes under an inverted microscope. Single cells and chains were transferred to 96-well plates with modified f/2 medium according to Anderson *et al*. (1984) and maintained at 24 ± 1 °C with 150 µmol photons m^{-2} s^{-1} overhead illumination supplied with cool-white fluorescent lights.

Culture media were prepared with seawater obtained from Ensenada de La Paz, a lagoon at the southern end of Bahía de La Paz (~35 psu). Seawater used for the preparation of culture media was filtered through GF/F filters with 0.7 µm pore size and sterilized in an autoclave at 121°C at 1.1 kg cm^{-2} for 20 minutes. Cultures from wells were transferred to 50-mL culture tubes for maintaining the strains.

Dinoflagellate and Raphidophyte strains were grown in modified f/2 medium (Anderson *et al*., 1984) and silica was added for diatom strains. Batch cultures were grown in 1-L polycarbonate vials and maintained under conditions described above. All strains were offered as diets during exponential growth phase.

Carbon content was estimated from cell volume, based on length and width measurements of 30 cells from each strain according to Strathmann (1967). Cell volume and carbon content of phytoplankton diets are presented in Table 1. Cell volume varied from 31 to 60,421 µm^3. Initial carbon concentration varied between 800 and 1,000 µg C L^{-1}. Only *Gyrodinium* sp. was used with an initial concentration of 400 µg C L^{-1}.

Copepods were collected superficially with a 333-µm plankton mesh net from Bahía de La Paz. Plankton samples were transferred to the laboratory in iceboxes filled with seawater. In the laboratory, adult females of *Acartia clausi* and *A. lilljeborgii* were separated under a stereoscopic microscope and acclimated for two hours in filtered seawater, at 24 °C and 35 psu.

For the different phytoplankton diets that were tested, 30 adult females were transferred to 1-L plastic flasks with 500-ml filtered seawater through GF/F filters and incubated in darkness at 24 °C at 35 psu for 24 h. There were three replicates of each treatment within each trial. To determine the phytoplankton growth rate, two flasks without copepods were incubated under the conditions previously described. At the beginning and end of each trial, 2-ml sub-samples of phytoplankton were fixed in Lugol´s iodine solution (Throndsen, 1978). Large cells were counted on 1-ml Sedgwick-Rafter counting slides; a Neubauer counting slide was used for smaller cells. At least 400 cells were counted for each sample. Cell density was used to calculate exponential growth rates according to Guillard (1973), and female ingestion rates according to the equation of Frost (1972):

$$I = ((V \times g)/N) \times C$$

$$g = (\ln Ci - \ln Cf)/(t + k)$$

where, V = volume of cell suspension in each flask (ml), g = grazing coefficient, N = number of copepods in each flask, C = cell concentration (cells ml^{-1}), Ci = initial cell concentration (cells ml^{-1}), Cf = final cell concentration (cells ml^{-1}), t = time (hours), and k = phytoplankton growth rate/hour. Additionally, copepods in filtered seawater without phytoplankton were incubated by triplicate; these represented the initial reproductive conditions of females and were used as control values for each experiment.

After incubation for 24 h, adult females in each bottle were gently separated through a 200-µm mesh screen; eggs and nauplii were collected in a 50-µm mesh screen. Surviving females, eggs, and nauplii were counted.

The percentage data were arcsine-transformed, whereas values for ingestion rates and egg production were log-transformed prior to statistical analyses. An ANOVA test was applied ($p \leq 0.05$), followed by Tukey's post hoc analyses. All statistical analyses used the STATISTICA™ v.6 (StatSoft, Inc.).

RESULTS

After incubation for 24 h, survival of adult females of *Acartia lilljeborgii* and *A. clausi*, fed with different phytoplankton diets was above 91.3% (Table 1). When *A. clausi* and

Table 1. Cell volume, carbon content, initial carbon concentration of phytoplankton strains and survival (mean ± SD) of *Acartia clausi* and *A. lilljeborgii* fed with the phytoplankton strains. * ANOVA test, p <0.05.

Phytoplankton diets	Cell volume (µm^3)	Carbon content (pg cell^{-1})	Initial concentration (µg C L^{-1})	A. lilljeborgii survival (%)	A. clausi survival (%)
Odontella longicruris	18,536	650	1,000	96.7 ± 4.7	97.9 ± 3.6
Chaetoceros sp.	31	650	1,000	92.5 ± 10.4	91.3 ± 12.2
Cilyndrotheca closterium	68	9	800	96.8 ± 3.3	93.1 ± 7.2
Dytilum brightwellii	60,421	1,593	800	96.7 ± 3.2	94.1 ± 2.4
Scrippsiella sp.	2,478	352	800	96.5 ± 3.3	98.9 ± 2.0
Gyrodinium sp.	486	83	400	89.6 ± 1.9*	44.5 ± 14.7*
Prorocentrum micans	6,898	873	800	98.8 ± 2.0	98.9 ± 1.9
P. rhathymum	8,575	1,059	800	97.7 ± 2.0	95.7 ± 4.9
Chattonella sp.	35,626	3,740	1,000	95.9 ± 3.6	95.4 ± 5.3
Without food				98.4 ± 1.9	97.2 ± 2.8
Average				95.7	90.0

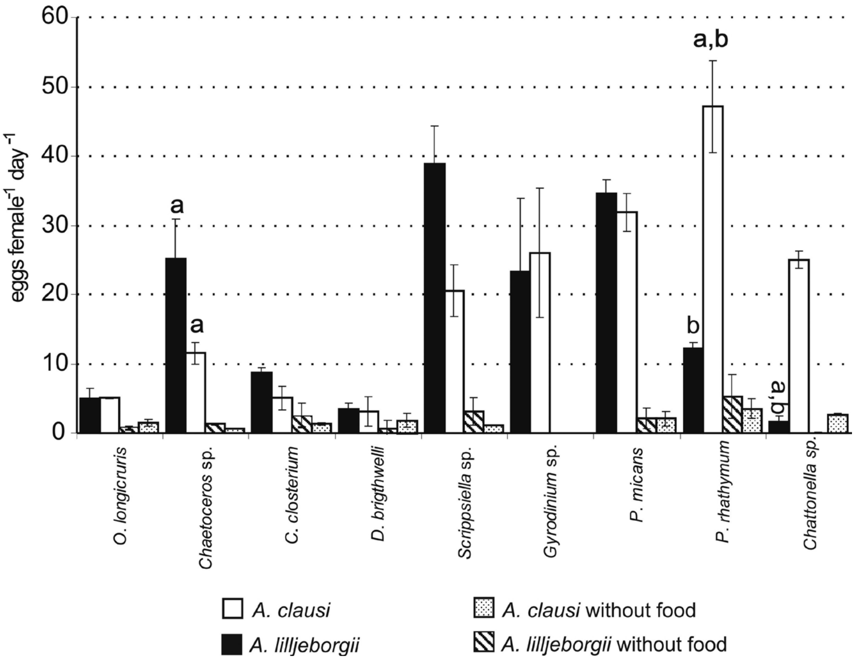

Fig. 1. Average (± SD) egg production in *Acartia lilljeborgii* and *A. clausi* with different phytoplankton diets and without food. a = significant difference with diatom diets; b = significant difference with dinoflagellate diets (ANOVA test, $p < 0.05$).

A. lilljeborgii were fed *Gyrodinium* sp. survival was significantly lower (44.5% and 89.6% respectively). Due to the elevated mortality obtained with this diet, higher cell concentrations of *Gyrodinium* sp. could not be used. Average survival of adult females of *A. lilljeborgii* with the other diets was higher (95.7%) than for *A. clausi* (90%).

Different responses in egg production in *A. clausi* and *A. lilljeborgii* were observed with the same diet (Fig. 1). In general, the highest production was obtained with dinoflagellates. *A. lilljeborgii* had significantly superior production rates when fed with *Scrippsiella* sp. (38.8 ± 5.5 eggs female^{-1} day^{-1}), *Prorocentrum micans* (34.6 ± 2.0), and *Gyrodinium* sp. (23.3 ± 10.5) compared to *P. rhathymum* and *Chattonella* sp. Of the diatoms diets, *Chaetoceros* sp. (25.1 ± 5.8 eggs female^{-1} day^{-1}) produced a significantly higher production rate than the other diatom diets. With the Raphidophyceae, *Chattonella* sp., a mild production occurred (<5.7 eggs). *A. clausi* also had significantly higher egg production with dinoflagellates (20.5 to 47.1 eggs female^{-1} day^{-1}), particularly with *P. rhathymum* (47.1 eggs female^{-1} day^{-1}). With *A. clausi*, *Chattonella* sp. favored a greater egg production (25.0 ± 1.2 eggs female^{-1} day^{-1}) than with *A. lilljeborgii*. When fed diatoms, *A. clausi* had a moderate egg production (≤11.5 eggs female^{-1} day^{-1}), only when fed *Chaetoceros* sp. a significantly higher egg production than other diatoms diets was observed.

Ingestion rates were significantly higher in both copepods when fed *Chaetoceros* sp., *Odontella longicruris*, *Prorocentrum rhathymum,* and *Chattonella* sp. (Fig. 2). In both copepods, the lowest ingestion rates (below 300 ng C copepod^{-1} hr^{-1}) occurred with *Cylindrotheca closterium*, *Dytilum brightwelli*, *Scrippsiella* sp., and *Gyrodinium* sp. Ingestion rates were different with a *Prorocentrum micans* diet; *A. lilljeborgii* had a superior average ingestion rate than *A. clausi*.

Both *Acartia* species had greater ingestion rates (above 700 ng C copepod hr^{-1}) with particle sizes from 9 to 40 × 10^3 µm^3 (Fig. 3). When particle sizes were larger or smaller, ingestion rates were below 300 ng C copepod^{-1} hr^{-1}, with the exception of the *Chaetoceros* sp. diet.

DISCUSSION

This is the first study in the Subtropical Pacific where several regional phytoplankton strains were used to determine the survival, ingestion rate, and egg production in two of the most abundant *Acartia* species in the region: *A. clausi* and *A. lilljeborgii*. Worldwide, several studies on egg production have been performed in *A. clausi*, however scarce information exists on *A. lilljeborgii*, a species with a more tropical-subtropical distribution. Our results clearly show the heterogeneous effects of phytoplankton diets on both copepods specifically on survival, egg production, ingestion rate, and cell size *vs.* ingestion rates in darkness at 24 °C.

No significant differences were observed in the survival of *A. lilljeborgii* and *A. clausi* with the different phytoplankton diets,

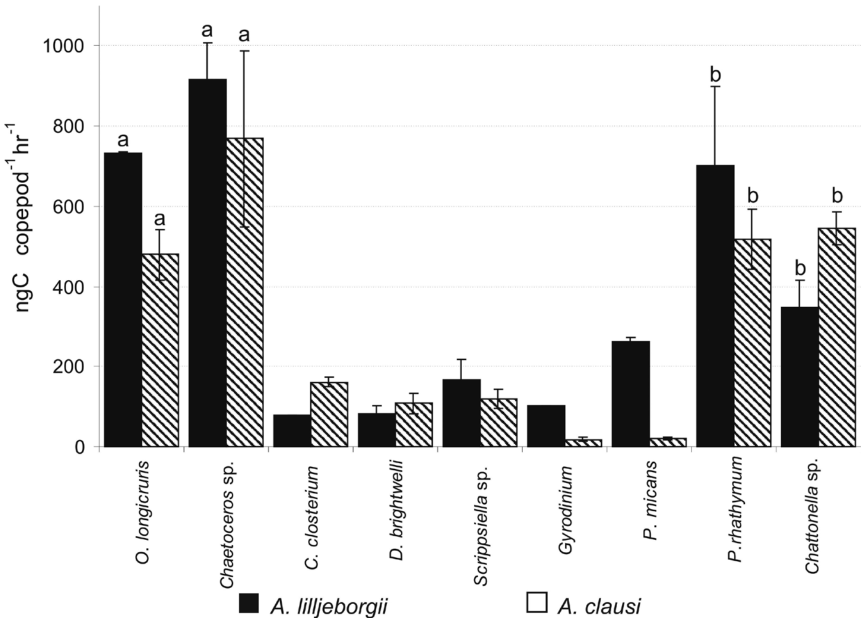

Fig. 2. Average (± SD) ingestion rates (ng C copepod^{-1}hr^{-1}) of *Acartia lilljeborgii* and *A. clausi* fed different phytoplankton diets. a = significant difference with diatom diets; b = significant difference with dinoflagellate diets (ANOVA test, $p < 0.05$).

with the exception of *Gyrodinium* sp. which produced a high mortality. In general, there was a high survival (>91.3%) in the different experiments and in filtered seawater (data not shown). High survival of copepods in filtered seawater also occurred in *Temora longicornis* O. F. Müller and *Pseudocalanus elongatus* (Boeck, 1865) (Koski & Klein-Breteler, 2003). In general, the lower average survival of *A. clausi* (90%) compared with *A. lilljeborgii* (95.7%) with different diets suggests that *A. clausi* is more sensitive to secondary metabolites of phytoplankton or to incubation conditions. Koski & Klein-Breteler (2003) believe that low or high survival in copepods is species specific. High mortality when fed *Gyrodinium* sp. suggests rejection, possibly due to the presence of toxic substances. The possible toxicity of our *Gyrodinium* strain requires further research.

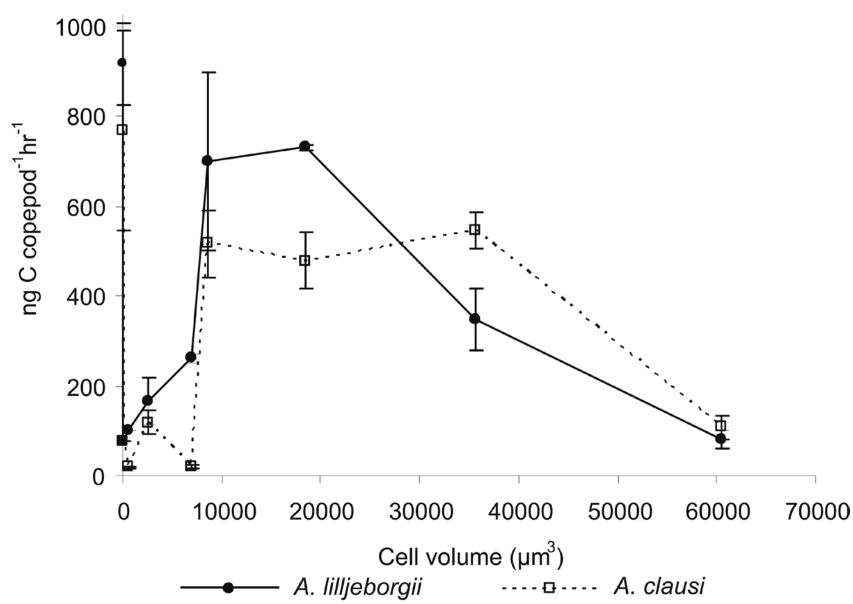

Fig. 3. Ingestion rate (ng C copepod^{-1} hr^{-1}) versus cell volume (µm^3). *Acartia lilljeborgii* and *A. clausi*. Average (± SD).

In general, the highest egg production occurred with dinoflagellate diets (*Scrippsiella* sp., *Gyrodinium* sp., *Prorocentrum micans, P. rhathymum*), and with one diatom (*Chaetoceros* sp.). Egg production was dependent on food type and with some diets species-specific responses were observed, *Chattonella* sp. and *P. rhathymum* induced high egg production only in *A. clausi*; *Chaetoceros* sp. and *Scrippsiella* sp. induced a higher egg production in *A. lilljeborgii.* The response of egg production to diet in *A. clausi* and *A. lilljeborgii* occurred in a short time, confirming observations of Tester & Turner (1990). Greater egg production with dinoflagellate diets suggests that these species could have a higher food quality if they were non toxin producers or if copepods were insensitive to toxic metabolites. *A. clausi* is capable of ingesting the toxic dinoflagellate *Gymnodinium catenatum* Graham with no apparent adverse effects in the ingestion and egg production rates (Palomares-García *et al*., 2006). *A. clausi* also ingested more toxic cells of *Alexandrium minutum* Halim as its concentration increased; with this diet hatching success and nauplii production decreased (Frangópulos *et al*., 2000).

Egg production rates were significantly reduced with diatom diets, with the exception of *Chaetoceros* sp. Based on egg production rates, *Ditylum brightwelli, Cylindrotheca closterium*, and *Odontella longicruris* were clearly inadequate for both copepod species. Several laboratory studies showed that diatoms, at high concentrations ($\geq 10^3$ cells ml^{-1}), are deleterious to copepod reproduction (Ban *et al*., 1997). Ingestion of diatoms by adult female copepods can be followed by low egg production and low hatching success, including abnormal egg and nauplii development (Hyung-Ku & Poulet, 2000; Lee *et al*., 1999). Other studies demonstrated that some diatoms species produce toxic unsaturated aldehydes that block embryogenesis (Ceballos & Ianora, 2003) or deform nauplii (Ianora *et al*., 2004).

Studies of the effect of Raphidophyte species on copepod production are scarce. Many marine *Chattonella* species are ichthyotoxin producers, related to reactive oxygen species (Oda *et al*., 1994), brevetoxins (Onoue & Nozawa, 1989), and polyunsaturated fatty acids (Skeen *et al*., 2002). The response of *Acartia omorii, A. tonsa*, and *A. hudsonica* to different toxic Raphidophyte species varies from not eating, rejection of food, and reduced fecundity (Uye & Takamatsu, 1990). *A. lilljeborgii* and *A. clausi* did not reject the diet of *Chattonella* sp. and a reduction in egg production was only observed in *A. lilljeborgii*. Production of toxic metabolites needs to be confirmed in this species.

In general, *A. clausi* and *A. lilljeborgi* seem to be very efficient in transforming ingested material into egg production, this has also been observed in *A. tonsa,* which rapidly adapts energetically to changing food conditions and seems well adapted to the fluctuating but occasionally high food concentrations characteristic of coastal waters (Kiørboe *et al*., 1998). This could also be the case for *A. clausi* and *A. lilljeborgii* which have a coastal distribution (Mauchline, 1998).

In general, average egg production was higher than production obtained under field conditions in Bahía de La Paz for both *Acartia* species, probably caused by the amount of cells ingested. Highest average egg production was 11.9 eggs female^{-1} day^{-1} in Bahía de La Paz for *A. clausi* (Palomares-García *et al*., 2003). For *A. lilljeborgii*, the rates were from 6.1 to 15.3 eggs female^{-1} day^{-1} (Gómez-Gutiérrez & Peterson, 1999; Palomares-García *et al*., 2003).

Ingestion rates varied significantly with diet, varying from 19 to 917 ng C copepod^{-1} hr^{-1}, and seem to be related to cell size. Both *Acartia* species had higher ingestion rates with *Odontella longicruris, Chaetoceros* sp., *Prorocentrum rhathymum,* and *Chattonella* sp. Cell volume could have influenced higher ingestion rates (ranging from 9,000 to 40,000 µm^3), with the exception of *Chaetoceros* sp., however this species forms long chains and, in culture forms dense aggregations that probably facilitated ingestion. It is possible that small cells (<500 µm^3) and large cells (>60,000 µm^3) are difficult to capture and/or manipulate (Frost, 1977; Hansen *et al*., 1994). The similar size-limits for ingestion of particles could indicate that both *Acartia* species share the same trophic level.

Clearly, ingestion and egg production rates in *Acartia clausi* and *A. lilljeborgii* are dependent on food type. Higher ingestion rates not necessarily resulted in higher reproductive rates. These results suggest that, under natural conditions, egg production of *A. clausi* and *A. lilljeborgii* probably could increase when higher abundances of dinoflagellates are found in the bay.

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