



## The deleterious effect of diatoms on the biomass and growth of early stages of their copepod grazers



Cinzia Brugnano<sup>a,\*</sup>, Antonia Granata<sup>a</sup>, Letterio Guglielmo<sup>a</sup>, Roberta Minutoli<sup>a</sup>, Giacomo Zagami<sup>a</sup>, Adrianna Ianora<sup>b</sup>

<sup>a</sup> Department of Biological and Environmental Sciences, University of Messina, Viale F. d'Alcontres 31, 98166, S. Agata, Messina, Italy

<sup>b</sup> Co-ordinator Functional and Evolutionary Ecology Laboratory and Public Aquarium, Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Naples, Italy

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### ABSTRACT

Diatoms are key phytoplankton species in the world oceans and essential in the transfer of energy through marine food chains. Their beneficial role has been questioned after the discovery that some diatom species produce teratogenic compounds such as polyunsaturated aldehydes and other oxylipins that induce abortions, poor larval development and high offspring mortality in many invertebrates. To test whether maternal and post-embryonic diatom diets affected development in the copepod *Paracartia latisetosa*, we carried out experiments in which the PUA-producing diatom *Skeletonema marinoi* (SKE) was fed to this copepod species. Controls were run with the dinoflagellate, *Prorocentrum minimum* (PRO), which does not produce any of these compounds. Four treatments were tested: both mothers and progeny always fed on either SKE or PRO, and those in which mothers received either PRO or SKE, and neonates were switched to the other diet. Our results show that a SKE/SKE diet induced lower egg production and egg viability, as well as slower embryonic development than the control diet. Naupliar development was negatively affected with the diatom diet which blocked the metamorphosis of larvae at N3, 4 days after hatching, compared to the control diet that allowed for normal naupliar development in 10 days. Nauplii reared on PRO and spawned by females fed on SKE were able to complete development, but only after 11 days, whereas larvae reared on SKE spawned by females fed on PRO were arrested at the N5 developmental stage, 12 days after hatching. Apoptotic TUNEL-positive nauplii were detected with the SKE diet, indicating imminent death. Significant differences were also recorded by comparing biomass of equivalent naupliar stages obtained for each treatment, and the overall mean biomass female<sup>-1</sup> day<sup>-1</sup> for each diet. Growth inhibition due to oxylipin-producing diatoms may have important consequences on prey-predator relationships and on the biomass flux through marine food chains.

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### 1. Introduction

In the last two decades numerous studies have reported on the harmful effects of some diatom diets (e.g. *Chaetoceros curvisetum*, *difficilis Chaetocero*, *Ditylum brightwellii*, *Phaeodactylum tricorutum*, *Skeletonema costatum*, *Thalassiosira rotula*, *Thalassiosira weissflogii*) on the reproduction and development of several copepod species (e.g. *Acartia clausi*, *Calanus helgolandicus*, *Calanus pacificus*, *Temora stylifera*) (reviewed by Caldwell, 2009; Leflaive and Ten-Hage, 2009; Ianora and Miralto, 2010). Harmful effects include a reduction in egg production and hatching success, and the production of abnormal teratogenic nauplii showing poor post-embryonic development and high mortality (Ianora and Poulet, 1993; Ianora et al., 1995, 1996, 2004; Poulet et al., 1994, 1995; Uye, 1996; Miralto et al., 1995, 1999; Starr

et al., 1999; Turner et al., 2001; Pohnert et al., 2002; Dutz et al., 2008; Koski, 2008; Wichard et al., 2008). It is now generally accepted that these antigrowth effects are due to the production of a plethora of compounds such as polyunsaturated aldehydes (PUAs) and other metabolites collectively termed as oxylipins, caused by damage of diatom cells as it occurs during copepod feeding (Pohnert, 2000; Pohnert and Boland, 2002; D'Ippolito et al., 2003; Fontana et al., 2007). These compounds were identified for the first time by Miralto et al. (1999) as 2-trans-4-cis-7-cis-decatrienal, 2-trans-4-trans-7-cis-decatrienal and 2-trans-4-trans-decadienal, produced by diatoms as a chemical defense against grazing pressure by herbivores (Pohnert, 2000; Pohnert and Boland, 2002). In fact, quantification experiments on intact algae did not reveal the presence of any of these oxygenated fatty acid degradation products, whereas after mechanical cell rupture, the concentration of defensive secondary metabolites, such as PUAs, increased within seconds after cell rupture (Fontana et al., 2007). Inhibition of copepod egg hatching success has been shown to depend on diatom density (Chaudron et al., 1996; Starr et al., 1999), because diatom

\* Corresponding author.

E-mail address: [cinzia.brugnano@unime.it](mailto:cinzia.brugnano@unime.it) (C. Brugnano).

inhibitors may be partially metabolized by digestive enzymes when concentrations are low enough for hydrolysis. All these laboratory studies were prompted by in situ evidence of the negative effect of these algae on biological communities (Miralto et al., 1999; Nejstgaard et al., 2001; Ianora et al., 2004). However, the effect can be diatom-species-specific (Ban et al., 1997) but also strain-dependent differences can induce different responses in feeding, egg production and hatching rates (Ask et al., 2006; Dutz et al., 2008). Different copepod species also react differently in their reproductive response to specific algal diets (Ianora et al., 2003; Md Amin et al., 2011). Lauritano et al. (2012) showed that enzymes involved in free radical detoxification were up-regulated after both 24 and 48 h of exposure to a diatom diet in a Swedish population of the copepod *C. helgolandicus*, after 24 h in the Atlantic population of the same species, but not in the Mediterranean population of *C. helgolandicus*. These data suggest an immediate specific capability of the Swedish and Atlantic populations to protect themselves against radical toxicants indicating strong population-level variations in copepod detoxification mechanisms to reduce diatoms possibly explaining why diatoms at times do not always reduce hatching success (e.g. Irigoien et al., 2002; Dutz et al., 2008).

Other possible causes for reduced hatching success include differential nutritional quality of diatoms (Jónasdóttir and Kjørboe, 1996), and insufficient nutrient uptake in the copepod gut caused by a rapid passage time during algal feeding by copepods (Dutz et al., 2008). Any of these causes (specific capability of some copepods to protect themselves against radical toxicants, differential nutritional quality of diatoms or insufficient nutrient uptake) could have been the possible cause of the absence of deleterious effects of a diatom diet on the Benthopelagic calanoid species *Pseudocyclops xiphophorus*, even if this copepod was fed on *Skeletonema marinoi*, a well-known PUA-producing species (Brugnano et al., 2008).

Until recently, most studies have focused on the negative effects of maternal diatom diets on copepod egg production and hatching success, and to a lesser extent on the effects on embryonic and postembryonic development. Negative effects of diatom diets on copepod development rates with increasing mortality until adulthood were first observed on *T. stylifera* and later in *C. helgolandicus* (Carotenuto et al., 2002; Ianora et al., 2004). Ianora et al. (2004) were the first to report that an improvement in the survivorship of larvae is strongly related to maternal diet thereby demonstrating that a good maternal diet is determinant to assure high offspring survival. Carotenuto et al. (2011) further demonstrated the importance of maternal and neonate diets not only for the development and survivorship of the offspring but also in determining sex differentiation in *T. stylifera*.

The object of our current study is the copepod species *Paracartia latisetosa* (Calanoida, Acartiidae, Kriczaguin, 1873). This planktonic calanoid shows a wide distribution range, extending from the Atlantic and Indian Oceans to Mediterranean coastal neritic environments and coastal lagoon systems (Rose, 1933; Dussart, 1982), where it often accounts for the major part of the copepod assemblage. The effects of the diatom species, *S. marinoi*, were tested because it is known to produce heptadienal, octadienal and octatrienal PUAs and other bioactive secondary metabolites, such as oxylipins, upon cell wounding (Fontana et al., 2007). The goal of the present study was to test the effects of a diatom with respect to a control non-diatom diet on the egg production, hatching success, embryonic and naupliar development in relation to both a maternal and larval diet in this euryhaline and opportunistic copepod species. Since it has been shown that the longer females are exposed to a diatom diet, the stronger the deleterious effects on the offspring (e.g. Chaudron et al., 1996), cohorts spawned after Day 1, 2 and 3 of maternal feeding on *S. marinoi* and the control dinoflagellate *Prorocentrum minimum*, which does not produce any of these metabolites, were observed. In addition, the hypothesis that maternal and naupliar diatom diets control not only the number of offspring, which has already been shown (Ianora et al., 2004; Carotenuto

et al., 2011), but also the quality of naupliar stages, in terms of larval biomass was tested.

## 2. Materials and methods

### 2.1. Study area

Lake Faro (38° 16' N, 15° 38' 20" E) is a coastal ecosystem located in the northeastern tip of Sicily that has a surface area of 263,600 m<sup>2</sup> and a maximum depth of 29 m. It has typical features of a meromictic ecosystem, i.e. an oxic epilimnion (surface to 10–12 m) and an anoxic hypolimnion (15 m to the bottom), characterized by large fluctuations in physico-chemical parameters, especially temperature (10–28 °C), salinity (34–37) and dissolved oxygen (ranging from absent, near the bottom in the central area, to 8.3 mg/l at the surface along the shore). These layers are separated by a metalimnion, within which strong blooms of anoxygenic phototrophic bacteria cause the periodic development of a red water layer (Genovese, 1963; Truper and Genovese, 1968). Physical and chemical stratification is particularly sharp in summer, when anoxia typically extends up to the lower mixolimnion and conspicuous blooms of photosynthetic sulfur bacteria develop. Diatoms represent the most conspicuous phytoplankton group during the summer bloom, whereas dinoflagellates are more abundant in spring (Giuffrè and Pezzani, 2005). The occurrence of *S. marinoi* (cf. *costatum*) was reported in the Lake Faro (Giuffrè, 2011) and some species of the genus *Prorocentrum* were occasionally present (Giuffrè and Pezzani, 2005). *P. latisetosa* is the dominant copepod species in Lake Faro. It is present the year-round but attains peak abundances in the summer-autumn period in surface layers (Zagami and Guglielmo, 1995; Brugnano and Zagami, 2013; Pansera et al., 2014).

### 2.2. Sampling methods

Samples were collected during the period of maximum *P. latisetosa* abundance, in summer. Zooplankton hauls were performed along a central north–south transect, ranging between 30 and 75 m in length, using a WP2 plankton net (200 µm mesh size and 57 cm mouth diameter). The net was towed horizontally at 2 to 3 m below the surface. Zooplankton samples were placed in plastic containers and immediately taken to the laboratory. There, *P. latisetosa* specimens were sorted from the zooplankton under a stereomicroscope, and gently transferred to an aquarium containing 100 mL of sea water, sterilized in an autoclave for 15 min at 121 °C. The aquarium was placed in a thermostatic-cell at 18 °C. Individuals were maintained under starvation in this aquarium for 24 h to reduce the effect of past feeding history of females and allow complete gut emptying.

### 2.3. Phytoplankton cultures

Both clones of the diatom *S. marinoi* (cell volume = 196 µm<sup>3</sup>, carbon content 20.7 pg cell<sup>-1</sup>) and the dinoflagellate *P. minimum* (cell volume = 1340 µm<sup>3</sup>, carbon content 177.1 pg cell<sup>-1</sup>) used in these experiments were from the culture collection of the Zoological Station “A. Dohrn” of Naples. Both clones were used in several previous studies testing the impact of the oxylipin-producing diatom *S. marinoi* on copepod hatching success and the non-oxylipin producing dinoflagellate *P. minimum* as a control (e.g. Ianora et al., 2004; Fontana et al., 2007). *S. marinoi* was grown in Guillard's F/2 medium Sigma-Aldrich Sigma-G0154, and *P. minimum* in Walne medium. Cultures of both species were kept in a thermostatic cell at 18 °C under a 12L:12D light cycle. Cultures were replicated every 7 days in order to have ~7-day-old cultures to offer to copepods and their nauplii during their exponential growth phases to exclude different toxicity related to growth phase (Barofsky et al., 2010).

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