

New oxylipins produced at the end of a diatom bloom and their effects on copepod reproductive success and gene expression levels



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ABSTRACT

Diatoms are dominant photosynthetic organisms in the world's oceans and are considered essential in the transfer of energy to higher trophic levels. However, these unicellular organisms produce secondary metabolites deriving from the oxidation of fatty acids, collectively termed oxylipins, with negative effects on predators, such as copepods, that feed on them (e.g. reduction in survival, egg production and hatching success) and, indirectly, on higher trophic levels. Here, a multidisciplinary study (oxylipin measurements, copepod fitness, gene expression analyses, chlorophyll distribution, phytoplankton composition, physico-chemical characteristics) was carried out at the end of the spring diatom bloom in April 2011 in the Northern Adriatic Sea (Mediterranean Sea) in order to deeply investigate copepod–diatom interactions, chemical communication and response pathways. The results show that the transect with the lowest phytoplankton abundance had the lowest copepod egg production and hatching success, but the highest oxylipin concentrations. In addition, copepods in both the analyzed transects showed increased expression levels of key stress-related genes (e.g. heat-shock proteins, catalase, glutathione S-transferase, aldehyde dehydrogenase) compared to control laboratory conditions where copepods were fed with the dinoflagellate *Prorocentrum minimum* which does not produce any oxylipins. New oxylipins that have never been reported before for microalgae are described for the first time, giving new insights into the complex nature of plant–animal signaling and communication pathways at sea. This is also the first study providing insights on the copepod response during a diatom bloom at the molecular level.

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1. Introduction

Diatoms are a key component of aquatic food webs and have traditionally been considered an optimal food source for the reproduction and development of planktonic grazers, mainly crustacean copepods, and essential in the transfer of energy to higher trophic levels (as reviewed by Ianora and Miralto, 2010). Intense blooms that negatively impact the hatching success of calanoid copepods have been described worldwide, including the North Adriatic Sea (Miralto et al., 1999, 2003), Gulf of Bothnia (Baltic Sea; Ask et al., 2006) and Dabob Bay (Washington, USA;

Halsband-Lenk et al., 2005). The North Adriatic bloom can last for several months (February to April) and is mostly dominated by the diatom *Skeletonema marinoi* with the phytoplankton assemblage becoming more heterogeneous toward the end of the bloom (Ribalet et al., 2014). During the bloom, *S. marinoi* co-occurs with the copepod *Calanus helgolandicus*, a calanoid copepod dominant in the North East Atlantic and Adriatic Sea (Mauchline, 1998; Papadopoulos et al., 2005).

Numerous studies have shown that several species of diatoms produce polyunsaturated aldehydes (PUAs) and a plethora of other metabolites, collectively termed oxylipins (Cutignano et al., 2006; d'Ippolito et al., 2004, 2009; Fontana et al., 2007a; Wichard et al., 2005), that are oxygenated fatty acid degradation products with toxic effects on reproductive processes in crustacean copepods (Fontana et al., 2007b; Ianora et al., 2004) and cladocerans

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(Carotenuto et al., 2005), echinoderm sea urchins (Romano et al., 2010) and sea stars (Caldwell, 2009; Guenther et al., 2009), polychaete worms (Caldwell et al., 2002; Simon et al., 2010), and ascidians (Lettieri et al., 2015; Tosti et al., 2003). Oxylipins have multiple biological and biochemical effects inducing the disruption of gametogenesis, gamete functionality, fertilization, embryonic mitosis, and larval fitness and competence (Caldwell, 2009). The specific type and quantity of oxylipins produced differs between diatom species and strains (Gerecht et al., 2011; Ianora and Miralto, 2010) and also depends on the different nutrient regimes (Ribalet et al., 2007, 2009) or various growth stages (d'Ippolito et al., 2009; Ribalet et al., 2007; Vidoudez and Pohnert, 2008), and could explain why some blooms may be more toxic than others. Other microalgal groups, such as Chrysophytes, Chlorophytes and Prymnesiophytes (Barbosa et al., 2016; de Los Reyes et al., 2014; Hansen and Eilertsen, 2007), as well as many macroalgae (Barbosa et al., 2016) are also known to produce both PUAs and other oxylipins. As suggested by Gerecht et al. (2011) and Casotti et al. (2005), oxylipins may function as signaling molecules and may be released in higher quantities under unfavorable conditions such as those encountered at the end of phytoplankton blooms (Ribalet et al., 2014). These stressful conditions may alter phytoplankton population dynamics such as succession and bloom termination (Vardi et al., 2006).

Several papers reported on the insidious effects of diatom metabolites during almost mono-specific blooms (e.g. *Skeletonema marinoi*, *Pseudonitzschia galaxiae* and *Chaetoceros* spp; Ianora et al., 2004, 2015; Miralto et al., 1999) or when copepods were fed monoalgal diets during feeding experiments in the laboratory (Brugnano et al., 2016; Ianora and Miralto, 2010; Li et al., 2006). In this study, phytoplankton–copepod interactions, secondary metabolite production and copepod gene expression changes are investigated during an oceanographic cruise conducted at the end of the spring diatom bloom in April 2011 in the North Adriatic Sea

(Mediterranean Sea). In particular, expression level analyses of a series of target genes involved in generic stress response, general detoxification and drug metabolism, aldehyde detoxification, antioxidant activities and apoptosis regulation are studied in *Calanus helgolandicus* in order to also investigate possible defense mechanisms activated in natural conditions.

2. Methods

2.1. Experimental design

An oceanographic cruise was conducted during the spring diatom bloom in the North Adriatic Sea (Mediterranean Sea) in April 2011 (ENVADRI2011, 7–20 April 2011) on board the R/V Urania within the framework of the EU Life+ project EnvEurope. Two transects were analyzed (i.e. Goro and Rimini; Fig. 1 and Table 1) each with three stations: Goro (ST2, ST3, ST4) and Rimini (ST2, ST3, ST4). For all locations, ST2 was the closest to shore, while ST4 was the outermost station.

At each station, the following samples/parameters were collected: 10 female copepods for fitness measurements (egg production, hatching success and fecal pellet production), 15 female copepods for gene expression analysis (5 females were pooled for each replicate), and two phytoplankton samples (one for chemical analysis and one for phytoplankton identification). An additional copepod sample (5 copepod females) was collected at each station, for gene expression analysis under controlled laboratory conditions. Data of physical parameters were obtained with a Sea Bird SBE 911 probe; temperature, salinity and oxygen saturation were measured with a CTD (conductivity, temperature and depth) profiler. The data (i.e. the mean of the values measured along the water column for each station) are reported in Table 1. The pH values were between 8.16 and 8.2 as also observed by Catalano et al. (2014). Sampling site names, sampling depths,

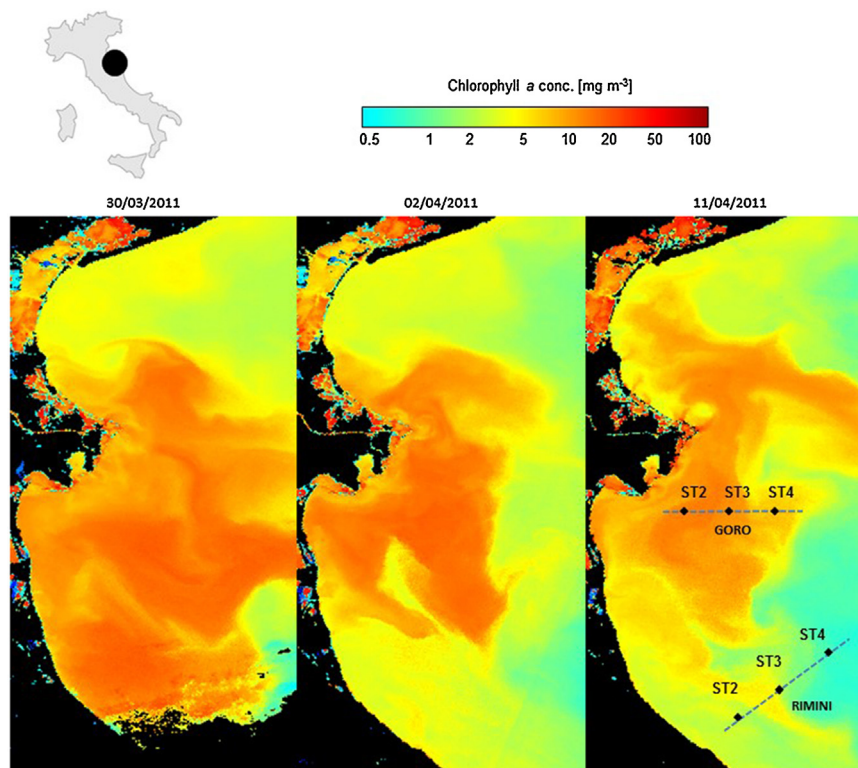


Fig. 1. Map of the sampling site. Color intensities represent Chlorophyll concentrations (mg m^{-3}) for the sampling period (11 April 2011) and some days before (30 March 2011 and 2 April 2011).

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