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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.

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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