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Growth impacts of Saharan dust, mineral nutrients, and CO_2 on a planktonic herbivore in southern Mediterranean lakes

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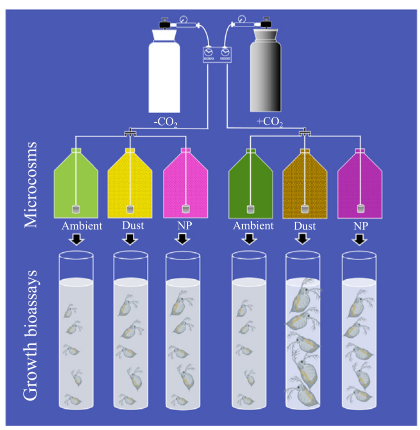
HIGHLIGHTS

- Impact of multiple global stressors on *Daphnia* growth rates was investigated in Mediterranean lakes.
- No single effect of rising CO_2 was detected unless supplemented with Saharan dust or inorganic nutrients.
- These factors affected the growth of Daphnia via alteration in the quantity of its food.
- CO_2 effects on herbivores are expected to intensify as the Mediterranean region becomes dustier.

GRAPHICAL ABSTRACT



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ABSTRACT

Rising levels of CO_2 can boost plant biomass but reduce its quality as a food source for herbivores. However, significant uncertainties remain as to the degree to which the effect is modulated by other environmental factors and the underlying processes causing these responses in nature. To address these questions, we carried out CO_2-manipulation experiments using natural seston from three lakes under nutrient-enriched conditions (mimicking eutrophication and atmospheric dust-input processes) as a food source for the planktonic *Daphnia pulicaria*. Contrary to expectations, there were no single effects of rising CO_2 on herbivorous growth. Instead, synergistic $CO_2 \times$ nutrient interactions indicated that CO_2 did not support higher zooplankton growth rates unless supplemented with dust or inorganic nutrients (nitrogen, N; phosphorus, P) in two of three studied lakes. The overall positive correlation between zooplankton growth and seston carbon (C), but not seston C:P, suggested that this was a food quantity-mediated response. In addition, we found that this correlation improved when the data were grouped according to the nutrient treatments, and that the response was largest for dust. The synergistic $CO_2 \times$ nutrient effects reported here imply that the effects of rising CO_2 levels on herbivorous growth may be strongly influenced by eutrophication processes and the increase in dust deposition predicted for the Mediterranean region.

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1. Introduction

Carbon dioxide (CO_2) increase in the atmosphere is perhaps the most notorious global-change anomaly, from around 230 ppm in preindustrial times to over 400 ppm today and, based on the model used for future projections, its concentration is expected to reach 750 to 1000 ppm in the next hundred years (IPCC, 2013). Studies on the influence of atmospheric CO_2 on aquatic ecosystems have shown that CO_2 addition promotes the growth (Kim et al., 2013) and production of phytoplankton (Jansson et al., 2012), as less light energy is required to operate the carbon-concentrating mechanisms (Hopkinson et al., 2011). However, various adverse effects has also been reported. These include the pH decline of surface ocean waters by >0.1 units since the beginning of Industrial Revolution (Orr et al., 2005). Increased pCO_2 levels in aquatic environments can shift the carbonate buffer system towards more acidic conditions, which can affect carbonate and bicarbonate chemistry and ultimately alter the structure of phytoplankton communities due to differences in the competitive ability of species (Shi et al., 2017) and their susceptibility to lower pH values (Hurd et al., 2011; Kroeker et al., 2013). Also higher pCO_2 levels can alter food quality for herbivores by rising the C:N:P ratios of autotrophs (Riebesell et al., 2007; Verschoor et al., 2013). Thus, some studies have reported a decrease in the growth rate of herbivores with monospecific diets in response to rising CO_2 levels (Urabe et al., 2003; Schoo et al., 2013), although these adverse effects were mitigated when herbivores were offered multialgal diets (Urabe and Waki, 2009). While these studies provide valuable perspectives on the food-quality effects of CO_2, it remains unassessed whether these findings can be translated to the outside world. This is because in experiments using natural seston mixtures (living and nonliving suspended matter in a water body), as opposed to controlled assays with single or multialgal diets, not all carbon (C) is equally edible for zooplankton. For example, *Daphnia* are filter feeders that ingest algae and detritus, but also bacteria which can be an important source of nutrients due to the flexibility in their P content with up to 3% of bacterial dry mass (Godwin and Cotner, 2015). In addition, most studies that investigate the effects of CO_2 have been conducted under *ad libitum* food concentrations and, therefore, do not separate effects of food quality from those of food quantity that are likely to prevail in low- to medium-trophic conditions. Lastly, the influence of CO_2 on herbivores is most often studied independently, whereas the interactive effect of CO_2 with other factors is noticeably lacking.

From this ecological background, it is becoming increasingly clear that realistic studies on the effects of increased CO_2 not only need to consider natural seston mixtures but also the effect of multiple interactive factors. For example, there is evidence showing that nutritional conditions of phytoplankton determine their response to rising CO_2 (Verspagen et al., 2014). Higher levels of nutrients might be a consequence of anthropogenic eutrophication processes induced by the discharge of limiting nutrients contained in detergents, sewage or fertilizers into the aquatic ecosystems. At the same time, human activities are also affecting the Earth's nutrient budgets by altering atmospheric concentrations of key gases and bulk dust aerosols (Sala et al., 2000; Hartmann et al., 2013). Mineral dust particles are produced mainly by the disintegration of aggregates following creeping and saltation of larger soil particles over deserts and other arid surfaces (Koch, 2001; Zhao et al., 2006). Dust aerosols not only exert a major radiative effect on the Earth's energy balance, but also constitute major vectors for nutrient transfer (e.g., iron [Fe], P or N) between distant worldwide regions, affecting the productivity of ecosystems (Herut et al., 2002). Thus, P deposition due to increased dust and biomass burning emissions has increased by 1.4 times the preindustrial rate (Brahney et al., 2015). The Sahara and the Sahel are by far the largest sources of dust particles (Prospero and Lamb, 2003), contributing ~56% of the Earth total dust emissions (Jickells and Moore, 2015), and particularly in the nearby Mediterranean basin where the occurrence and intensity of desert dust episodes are increasing (Bullejos et al., 2010; Gkikas et al., 2013). However, the role of dust on ecosystem productivity is still controversial (Gallisai et al., 2014). Some experimental studies have shown that mineral-dust inputs can strongly stimulate the primary production of P-limited communities (González-Olalla et al., 2017), boosting the biological pump and reinforcing the role of oligotrophic areas as key CO_2 sinks (Cabrerizo et al., 2016). In contrast, other studies have reported negative effects of dust inputs on phytoplankton growth due to the presence of toxic microelements such as copper (Paytan et al., 2009; Jordi et al., 2012). In addition, the impact of dust deposition on microbial plankton can be quite heterogeneous as a result of the uniqueness in the intensity (Gallisai et al., 2016) and composition of aerosols (anthropogenic versus mineral; e.g. Marín et al., 2017).

There is increasing awareness among scientist that the effect of multiple factors are key to understand how species and biological interactions respond to all the stressors that are acting on an ecosystem at a given time (Villar-Argaiz et al., 2018a). So far, there is empirical evidence showing that CO_2 and nutrients interactively impact the growth and elemental content of primary producers (Verspagen et al., 2014), but the extent of their joint effect to the next trophic level of herbivores in nature is quite unexplored. Finally, the overall net effects of dust, specifically its interactive effect with CO_2 on zooplankton are largely unknown (Christou et al., 2017). To examine the single and interactive effects of CO_2, Saharan dust and mineral nutrients on herbivorous growth, we designed a series of microcosm experiments composed of two steps. In the first, we exposed natural seston from three southern Mediterranean lakes to the effects of CO_2 (ambient and elevated levels), dust, and inorganic nutrients. In the second, we tested the nutritional suitability of the raised seston on the growth of the cladoceran *Daphnia pulicaria* as a target species. The following specific hypothesis were tested: (1) the single effect of CO_2 enhances the growth rate of *D. pulicaria* and, (2) inorganic nutrients and dust synergistically increase the role of CO_2 on *D. pulicaria* growth rate. The experimental manipulation proposed here should provide with relevant information on how future scenarios of augmented eutrophication and dust might offset or enhance CO_2 effect on planktonic food webs.

2. Material and methods

2.1. Study sites

This study was conducted in three Mediterranean lakes in southern Spain. Two of these lakes (Dulce [37°3′10.96″ N, 4°50′6.78″ W] and Archidona [37°6′31.87″ N, 4°18′9.20″ W], province of Malaga) are hard-water lakes with high carbonate/bicarbonate content. However, while Lake Dulce is a temporary shallow lake that dries out during the summer period, Archidona is a permanent, deeper lake. The third lake (Cogollos [37°12′29.47″ N, 3°10′1.06″ W], province of Granada) is a low-alkalinity lake located on a siliceous bedrock. The three lakes covered a moderate trophic gradient according to their Total Phosphorus (TP) content from the oligotrophic Lake Cogollos to the mesotrophic Lake Dulce (TP: 15.2–39.8 μg P L^{-1}).

2.2. Field sampling

These lakes were sampled in 2014 (Lake Dulce in May 27; Lake Archidona in June 2) and 2015 (Lake Cogollos in March 1) at a station located at the maximum depth of each lake. Vertical profiles of radiation (UVR at 305, 320, and 380 nm and photosynthetically active radiation, PAR) were measured at noon using a submersible BIC compact 4-channel radiometer (Biospherical Instruments Inc., San Diego, CA, USA). Diffuse attenuation coefficients for downward irradiance (k_d) were determined from the slope of the linear regression of the natural logarithm of downwelling irradiance vs. depth for each wavelength range considered (n > 200 per profile). Vertical profiles of pH and temperature were measured using a multi-probe system (YSI MPS-556, YSI Incorporated, OH, USA). A representative water-column sample for each