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Increased temperature but not pCO_2 levels affect early developmental and reproductive traits of the economically important habitat-forming kelp *Lessonia trabeculata*

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ABSTRACT

The effects of ocean warming and ocean acidification on developmental and reproductive traits of *Lessonia trabeculata* were evaluated. Meiospores were cultured for 35 days in an experimental mesocosm where temperature (~15 and 19 °C) and partial CO_2 pressure (pCO_2, ~400 and 1300 μatm) were controlled. The results indicate that germination was reduced at 19 °C, whereas the increase of pCO_2 only had effects at 15 °C. Likewise, the increase in temperature significantly affected the vegetative growth of female gametophytes. Sex ratio was not affected significantly by any of the variables studied. Fertility and reproductive success decreased by about 50% at 19 °C. The pCO_2 levels had no significant effects on most early developmental traits. The results suggest that ocean warming or periodic warming events (e.g. an El Niño event) might affect the recruiting capacity of this or other similar species by affecting their early developmental stages.

1. Introduction

On the Chilean coast, the kelp *Lessonia trabeculata* (known locally as "huiro palo") is one of the species with the highest primary production rate (Tala and Edding, 2007). This species is considered a bioengineer for providing food and forms a three-dimensional habitat for the development of a large number of marine invertebrates and fishes (Villouta and Santelices, 1984; Vásquez and Buschmann, 1997; Villegas et al., 2008). Furthermore, the kelps hold economic importance in Chile as raw material in the extraction of alginates, a polymer used in various industries, e.g., textiles, pharmaceutical and has even been reported to have possible agricultural applications (Vásquez and Fonck, 1993; Edding and Tala, 2003; Chandia et al., 2004). *L. trabeculata* is one of the most economically exploited seaweed in Chile; total landing records indicate an average extraction of 47,000 tons per year in the last ten years (SERNAPESCA, 2016). This species has a heteromorphic diplohaplont life cycle (Fig. 1) with a generational alternation between a macroscopic diploid phase (2n) and a microscopic haploid phase (n) that are morphologically different (Edding et al., 1994). The meiospores, or kelp microscopic phases, do not have mechanisms of parental or structural protection to face the abiotic conditions and therefore they are more sensitive to environmental factors than their macroscopic phases (Edding et al., 1994; Schiel and Foster, 2006).

The increase in atmospheric CO_2 concentration since the industrial revolution has caused two important shifts in the world's oceans: an increase in the seawater temperature, known as ocean warming (OW) and a decrease in the seawater pH, known as ocean acidification (OA) (Levitus et al., 2001; Caldeira and Wickett, 2003; IPCC, 2014). Research on climate change has generated a range of possible future scenarios based on the evolution of accumulated emissions of anthropogenic carbon dioxide or Representative Concentration Pathways (RCPs), where the more drastic scenario (RCP8.5) suggests that by the end of the year 2100, the sea surface temperature will increase by 3.2 °C and the pH will decrease by 0.4 units in most regions of the world (Caldeira and Wickett, 2005; Meinshausen et al., 2011; Gattuso et al., 2015). However, in the north-central coast of Chile, local evidence indicates that from 1979 to 2006, there was a cooling at a rate of −0.2 °C per decade, linked by the intensification of the South Pacific anticyclone as a consequence of global warming (Falvey and Garreaud, 2009). On the other hand, evidence also suggests episodic events of warming in

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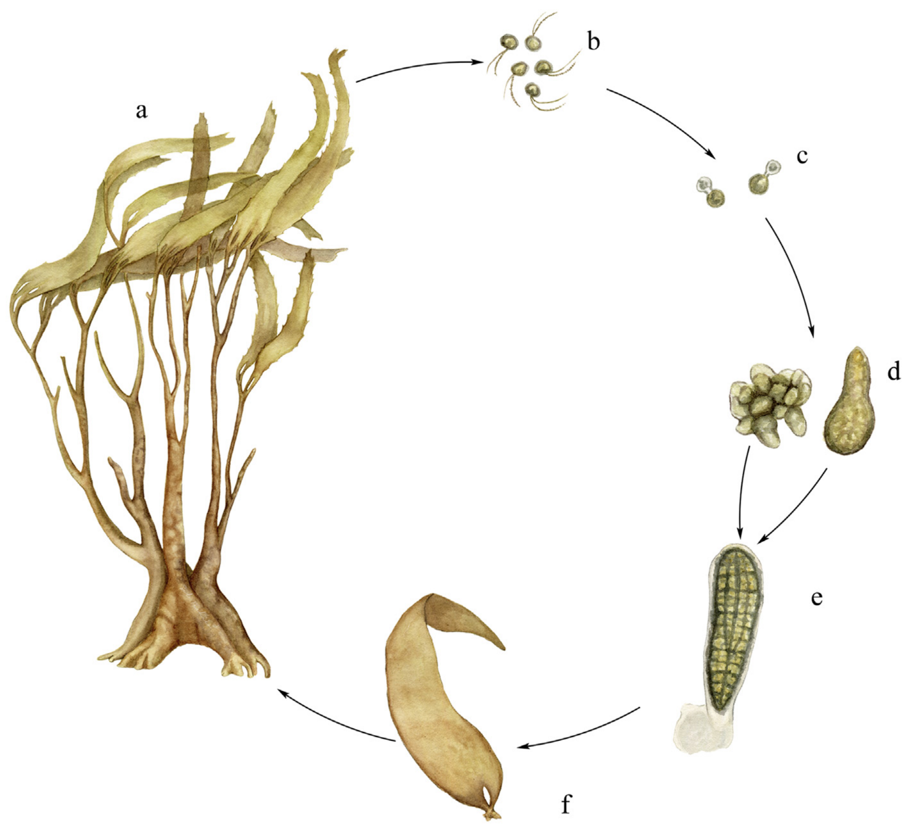

Fig. 1. Schematic representation of the life cycle *Lessonia trabeculata*. It begins with the meiosis of the cells forming the sporangial soro on the adult sporophyte fronds (a). Then the release of the meiospores to the environment occurs (b). This meiospores are set (c) and germinate to form the female and male gametophytes (d), responsible for the formation of the microscopic sporophyte (e) and then the macroscopic sporophyte (f). Drawing by Solange Pacheco.

response to an increase in the frequency of El Niño-like conditions as a consequence of increasing concentrations of greenhouse gases (Timmermann et al., 1999).

There is considerable evidence in the literature to suggest that light, ultraviolet radiation and temperature are key abiotic factors for early developmental and reproductive traits in different kelp species such as germination, gametophyte development, reproductive success and photosynthetic efficiency (Lüning, 1980; Avila et al., 1985; Fonck et al., 1998; Buschmann et al., 2004; Nelson, 2005; Roleda, 2009; Redmond, 2013; Murúa et al., 2013; Roleda, 2016). Temperature is considered the most important factor in the regulation of seaweed reproduction as well the factor which directly control the onset of seaweed reproduction (Liu et al., 2017). In this sense, the kelps have optimal conditions for the development of their early stages which, depending on the species, are modulated by the locality and the season (Buschmann et al., 2004; Tala et al., 2004; Murúa et al., 2013). For example, populations of *L. trabeculata* from Coquimbo in north-central Chile (30°15′ S; 71°30′ W) reach the highest fertility between the austral autumn and winter months, while the same species from Maicolpué in southern Chile (40°36′ S; 73°46′ W) has the highest fertility during the austral spring months (Tala et al., 2004; Murúa et al., 2013). Thus, among seaweed, temperature can strongly control geographic distribution by modulating the survival, growth and the reproduction of sporophytes and gametophytes (van den Hoek, 1982; Bartsch et al., 2013). For example, it has been observed that *Lessonia spicata* (southern to 30° S) show clear reproductive limits associated with temperature (Oppliger et al. 2012). This study suggests that the northern distribution limit for *L. spicata* is reached when the seawater temperature is 20 °C, at which the production of gametes by their gametophytes is inhibited. However, it have been demonstrated that reproduction of the sporophytes has a narrower thermic tolerance range than the reproduction and growing range tolerance limit recorded for gametophytes (Bartsch et al., 2013).

The independent effect of OA and its interactive effect with temperature or light has not shown clear effects on early developmental or reproductive traits of kelps (Roleda et al., 2012; Gaitán-Espitia et al., 2014; Xu et al., 2015; Leal et al., 2017a; Leal et al., 2017b). For example, in *Macrocystis pyrifera* from Santa Barbara, California (34°25′ N; 119°57′ W), the synergic effect of an increased temperature (18 °C) and reduced seawater pH (~7.5) significantly decreased germination rate (Gaitán-Espitia et al., 2014). Whereas, in *M. pyrifera* from Hamilton Bay, Otago Harbour (45°47′ S; 170°38′ E), no significant effects of pH in isolation or in combination with temperature on germination rate were observed (Leal et al., 2017a; Leal et al., 2017b). Furthermore, in *Saccharina japonica*, pH reductions at low and high light intensities delay gametogenesis and significantly restrict fertilization, respectively (Xu et al., 2015). In this regard, the OA not only involves a decrease in pH, but also implies a modification in the proportions of inorganic carbon (C_i) species, increasing aqueous CO_2 (aq) and HCO_3^-, and decreasing CO_3^{2-} (Feely et al., 2004). The main source of C_i for photosynthesis in seaweed is CO_2 (aq) from bulk seawater. However, seaweed can also uptake CO_2 by simple diffusion or by HCO_3^- uptake and catalyze the accumulation of CO_2 around RuBisCO through the inorganic carbon concentrating mechanism or CCM (Raven, 1997; Giordano et al., 2005). Therefore, changes in the proportions CO_2/HCO_3^- could exert some type of key control for photosynthesis (Hurd et al., 2009; Cornwall et al., 2012). To our best knowledge, no information is available about the primary C_i source or mechanisms of carbon uptake of *Lessonia trabeculata*. However, the primary C_i source that support photosynthesis for another kelp species, such as *M. pyrifera*, is mainly HCO_3^- (Fernández et al., 2014). Thus AO is expected to benefit primary production by facilitating the acquisition of C_i for photosynthesis (Hurd et al., 2009; Cornwall et al., 2012), and the different observed responses in reproduction and development of kelps could be associated with different mechanisms of carbon uptake (Cornwall et al., 2012).

In the present study, we used a multi-stressor experimental approach to examine changes in developmental and reproductive traits of microscopic phases of the kelp *L. trabeculata* in response to different levels of temperature (~15 vs. 19 °C) and pCO_2 (~400 vs. 1300 μatm).