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Latitudinal and seasonal effects on short-term acclimation of floating kelp species from the South-East Pacific

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ABSTRACT

Floating seaweeds are important dispersal vehicles for many organisms in cold-temperate waters between latitudes 30° and 60°. Molecular studies suggested that long-distance rafting of seaweeds is more prevalent at the polar edges of their distribution but knowledge about their physiological status at high latitudes is limited. Seasonal short-term field experiments were conducted along a latitudinal gradient (30°, 37° and 54°S) with floating kelps *Macrocystis pyrifera* and *Durvillaea antarctica*. Kelps were tethered at the sea surface for 14 d during austral winter and summer to examine their acclimation potential in floating conditions. Biomass changes, reproductive status and physiological traits (chlorophyll *a* fluorescence, pigments, phlorotannins and antioxidant capacity) were evaluated after 7 d and 14 d of floating. Biomass changes (positive or negative) depended on species and latitude: at low latitudes (Coquimbo) both species lost biomass during both seasons while at mid latitudes (Concepción) they grew during summer but not in winter. Species-specific responses were observed at high latitudes (Pta. Arenas) with floating *M. pyrifera* growing in summer and *D. antarctica* in winter. Both species were able to maintain reproductive status mainly in winter, but at mid latitudes *M. pyrifera* also showed high reproductive activity during summer. Physiological adjustment was detected for both species at day 7 and upheld until the end of the experiment (14 d). Latitudinal changes in photosynthetic variables (maximum quantum yield and pigments) were more evident in summer conditions, *M. pyrifera* showing decreases in F_v/F_m and pigment levels at low and high latitudes while in *D. antarctica* these variables increased with latitude. Phlorotannin contents varied with latitude but showed an opposing pattern in the two kelp species, with high concentrations at low latitudes for *M. pyrifera* and at high latitudes for *D. antarctica*. The floating kelps maintained high antioxidant capacity during the experiments. The short-term acclimation responses support the hypothesis of long-distance dispersal at high latitudes for both floating kelp species. The acclimation potential differed between the two species depending on the season, especially at mid and high latitudes. Summer conditions were favorable for floating *M. pyrifera* at high latitudes and for both species at mid latitudes in which a combination of increasing radiation and moderate temperature can stimulate growth. The results confirm that kelp rafting is favored at mid/high latitudes but suggest that in polar waters (>60°) low temperatures and light limitations might suppress growth of floating seaweeds.

1. Introduction

Floating patches of various seaweed species occur throughout the world´s oceans, although they are most abundant in temperate and cold waters of both hemispheres (30°–60°) (Kingsford, 1992; Hinojosa et al., 2010, 2011; Thiel et al., 2011; Rothäusler et al., 2012). Long-distance rafting of buoyant, brown seaweeds contributes to the dispersal of marine biota (Edgar, 1987; Thiel and Gutow, 2005; Fraser et al., 2011). Molecular studies confirm the importance of dispersal and recolonization by floating seaweeds especially at high latitudes, where seaweed rafts must cross long distances of open ocean without intermediate stepping stones (e.g. *Ascophyllum* - Olsen et al., 2010; *Durvillaea* -

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Fraser et al., 2009, 2011; *Fucus* - Coyer et al., 2011; *Macrocystis* - Macaya and Zuccarello, 2010a, 2010b). However, the morphological and physiological mechanisms that allow long-distance dispersal of floating seaweeds are not well understood.

Some seaweed species are able to continue floating, growing, and even reproducing for extended time periods after detachment (Macaya et al., 2005; Martinez et al., 2006; Hernández-Carmona et al., 2006; McKenzie and Bellgrove, 2008; Rothäusler et al., 2009, 2011a, 2011b; Tala et al., 2013). However, during their voyage biotic factors, including grazing (by snails, urchins, crustaceans), fouling (by bryozoans, stalked barnacles, epiphytic algae) (Thiel and Gutow, 2005; Rothäusler et al., 2009; Gutow et al., 2012), and abiotic factors such as high water temperatures, intense solar radiation and nutrient depletion negatively affect the floating seaweeds, limiting their persistence at the sea surface (Hobday, 2000; Karsten et al., 2001; Vandendriessche et al., 2007; Rothäusler et al., 2011b; Graiff et al., 2013). Even though initial physiological acclimation can occur, the decline in growth and reproductive capacity are the main changes suppressing the colonization potential of floating kelps (Hobday, 2000; Macaya et al., 2005; Hernández-Carmona et al., 2006; Vandendriessche et al., 2007; Rothäusler et al., 2009, 2011b).

Depending on their geographic origin (latitude) or the time (season) when they are detached, floating seaweeds are confronted with variable environmental conditions during rafting (Wooster and Sievers, 1970; Macaya et al., 2005; Komatsu et al., 2007; Rothäusler et al., 2009; Tapia et al., 2014). In summer, high temperature and solar radiation may affect the photosynthetic efficiency and pigment concentration and cause an increase in tissue degradation, thereby contributing to the sinking of floating kelps (Rothäusler et al., 2009, 2011c; Graiff et al., 2013). In contrast, during winter the conditions at the sea surface are more moderate and floating kelps can persist for longer time periods (Graiff et al., 2013; Tala et al., 2013). Solar radiation shows a general gradient decreasing from the equator towards the poles with greater seasonal changes at higher latitudes than at low latitudes (Kain, 1989). Latitudinal gradients in temperature follow a similar general pattern as radiation (Silva et al., 2009). Consequently, it is expected that floating kelps show efficient acclimation mechanisms that allow them to persist longer at the sea surface during winter and at higher latitudes than during summer and at mid-low latitudes. Current knowledge on the growth and physiology of floating seaweeds and the environmental factors influencing their persistence at the sea surface is mainly limited to mid and low latitudes (<40°S) and experimental conditions (e.g. Vandendriessche et al., 2007; Rothäusler et al., 2009, 2011a, 2011b, 2011c; Graiff et al., 2013). Considering that floating seaweeds are abundant at higher latitudes (>40°S) (Smith, 2002; Hinojosa et al., 2010, 2011; Rothäusler et al., 2012; Wichmann et al., 2012), long-distance rafting appears most relevant at these latitudes (Fraser et al., 2009; Macaya and Zuccarello, 2010a; Fraser et al., 2011; Cumming et al., 2014).

Two important floating kelps *Macrocystis pyrifera* (L.) C. Agardh (Laminariales) and *Durvillaea antarctica* (Chamisso) Hariot (Fucales) are very common along the Chilean coast between 30°S and 55°S (Collantes et al., 2002; Macaya et al., 2005), and their abundances show a clear latitudinal trend in concordance with benthic sources (more abundant in the south) (Macaya et al., 2005; Hinojosa et al., 2010, 2011; Wichmann et al., 2012). In both species, molecular studies support the idea of high dispersal potential with similar genetic structure between distant populations (Fraser et al., 2009, 2010; Macaya and Zuccarello, 2010a, 2010b). In addition to the temperature gradient, there are latitudinal gradients in solar radiation and nutrient supply (upwelling) along the Chilean coast (Cabrera et al., 1995; Thiel et al., 2007; Silva et al., 2009). Consequently, the lifetime of kelp rafts is expected to increase towards higher latitudes. In this sense, the Chilean coast offers an excellent *in situ* laboratory to test the combined latitudinal and seasonal effects on floating kelps using experimental field studies.

Based on the above considerations it was hypothesized that floating kelps *M. pyrifera* and *D. antarctica* are performing better at high latitudes where environmental conditions favor long-term rafting, reproduction and physiological acclimation. In order to test this hypothesis, herein short-term field experiments were conducted to determine the morphological (biomass change), physiological (chlorophyll *a* fluorescents in *PS*II, pigments, phlorotannin contents, and antioxidant capacity) and reproductive status of floating kelps *M. pyrifera* and *D. antarctica* tethered at three sites along the Chilean coast (30°S–54°S, spanning a distance of more than 2500 km) during contrasting seasons (winter vs. summer).

2. Materials and methods

2.1. Experimental zones and sites.

The latitudinal and seasonal effects of floating conditions on adult individuals of *M. pyrifera* and *D. antarctica* were examined in field experiments. The *in situ* experiments were conducted during austral winter 2013 (July–September) and summer 2013/2014 (December–February) for each species separately. Experiments were conducted at low (Coquimbo, Herradura Bay: 29°57′S, 71°20′W), mid (Concepción, Dichato: 36°29′S, 72°54′W) and high latitudes (Punta Arenas, Puerto del Hambre: 53°36′S, 70°55′W) (Fig. 1). These study sites allowed to examine the latitudinal gradient in environmental conditions to which floating rafts are exposed along the coast of the SE Pacific, including extremes of low and high latitudes. Benthic populations of both species occur along this range, with abundances that vary according to factors such as hard substratum availability and wave-exposure (Santelices et al., 1980; Collantes et al., 2002; Buschmann et al., 2004; Mansilla and Avila, 2007). Molecular studies in *D. antarctica* had shown that the populations from central Chile (32°–44°S) are genetically different from the populations of southern Chile (49°–56°S) (Fraser et al., 2009, 2010) whereas *M. pyrifera* showed a homogenous genetic structure along the Chilean coast (Macaya and Zuccarello, 2010b).

2.2. Environmental conditions during the study.

Throughout the experimental period, at each experimental site temperature (°C) and light (Klux) in the upper water layers were monitored every 5 min using a HOBO® Pendant Temperature-Light Datalogger

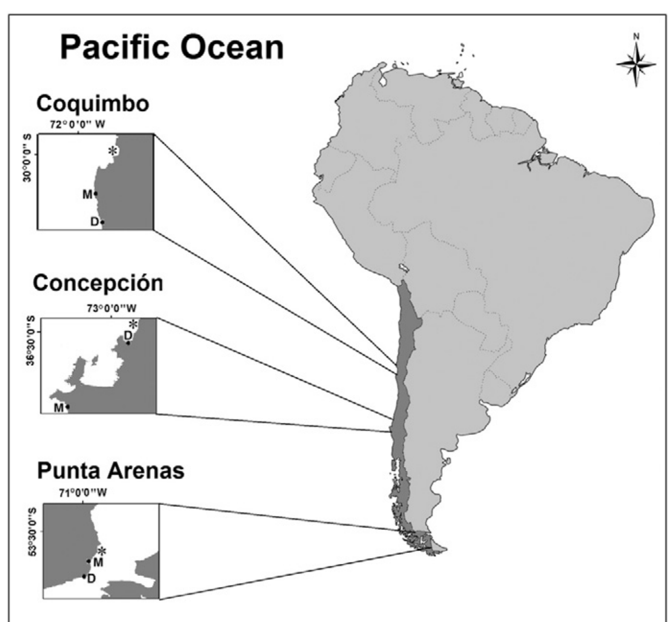

Fig. 1. Map of Chile with the three study sites. Experimental sites (asterisk), and *Macrocystis* (M) and *Durvillaea* (D) source population for Coquimbo, Concepción and Punta Arenas.