



Future climate change scenarios differentially affect three abundant algal species in southwestern Australia



Charlie M. Phelps^{a, *}, Mary C. Boyce^b, Megan J. Huggett^{a, b}

^a Centre for Marine Ecosystems Research, School of Science, Edith Cowan University, 270 Joondalup Dr, Joondalup, 6027, Australia

^b Centre for Ecosystem Management, School of Science, Edith Cowan University, 270 Joondalup Dr, Joondalup, 6027, Australia

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ABSTRACT

Three species of macroalgae (*Ecklonia radiata*, *Sargassum linearifolium*, and *Laurencia brongniartii*) were subjected to future climate change conditions, tested directly for changes in their physiology and chemical ecology, and used in feeding assays with local herbivores to identify the indirect effects of climatic stressors on subsequent levels of herbivory. Each alga had distinct physical and chemical responses to the changes in environmental conditions. In high temperature conditions, *S. linearifolium* exhibited high levels of bleaching and low maximum quantum yield. For *E. radiata*, the alga became more palatable to herbivores and the C:N ratios were either higher or lower, dependent on the treatment. *Laurencia brongniartii* was effected in all manipulations when compared to controls, with increases in bleaching, blade density, and C:N ratios and decreases in growth, maximum quantum yield, blade toughness, total phenolics and consumption by mesograzers. The differential responses we observed in each species have important implications for benthic communities in projected climate change conditions and we suggest that future studies target multi-species assemblage responses.

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1. Introduction

Temperate reef systems form a significant global resource, and through activities such as tourism and fisheries have been estimated to contribute up to \$US5 billion per year to some national economies. The basis of such reefs are the canopy-forming macroalgal assemblages of kelp and furoids, which have significant ecological importance (Steneck et al., 2002) including roles in the foundation of the marine food web (Koch et al., 2013), nutrient retention and cycling and CO₂ storage (Koch et al., 2013) as well as providing a three-dimensional habitat for many marine taxa (Egan et al., 2013). Understory macroalgae also play a significant role in temperate marine ecosystems (Clark et al., 2004) and algal communities containing both canopy and understory species are more productive than singular, homogenous populations (Middelboe and Binzer, 2004). In addition, for some herbivore species, reproductive success is dependent on the canopy/understory dynamics and different algal species are used as a habitat for varying life history stages (Williamson et al., 2004). In Australia, temperate reefs

mostly consist of kelp-dominated assemblages on rocky reefs, which occur along over 8000 km of the southern coastline and are considered to be global diversity hotspots (Irving and Connell, 2006; Bennett et al., 2016).

Algal assemblages are shaped in part by levels of herbivory that effects the growth, survival and reproductive success of individuals (Vergés et al., 2014; Franco et al., 2015). Levels of herbivory are often related to the nutritional value of the plant material and the number of herbivores present (Cebrian et al., 2009) and herbivory can have a substantial impact on the ecosystem. For example, in marine systems grazing causes an average of 68% reduction in the biomass of benthic primary producers (Poore et al., 2012). Mesograzers are small, mobile herbivores such as amphipods, isopods, gastropods, polychaetes, small crabs and shrimps, found in high abundances in marine benthic communities (Duffy and Hay, 2000; Cruz-Rivera and Hay, 2000). Mesograzers inhabit, consume and construct nests on macroalgae (Poore et al., 2013) using the macroalgae as a shelter for protection from the physical stresses of the ocean (Gestoso et al., 2011) and as a refuge from predators (Huang et al., 2006). Marine mesograzers can consume between 2 and 23% of their body mass daily, with the exception of amphipods which have been recorded to ingest >100% of their body weight daily (Ruesink, 2000). Individually, mesograzers have a small impact on

* Corresponding author.

E-mail address: c.phelps@ecu.edu.au (C.M. Phelps).

their host algae (Ruesink, 2000). At high densities, often in the tens of thousands per square meter, their combined consumption can impact algal biomass significantly (Poore et al., 2009).

Climate change is the biggest threat to the global environment (Hughes, 2003; Koch et al., 2013). In marine environments, increases in ocean temperature and $p\text{CO}_2$ associated with anthropogenic CO_2 emissions are affecting the physiology and chemistry of all marine life (Harley et al., 2006; Scherner et al., 2016). When foundation or keystone species, such as canopy forming algae, are physically or chemically affected by climate-mediated changes the effects can affect other organisms in all trophic levels (Vergés et al., 2014). Changes in climatic conditions can alter macroalgal physiology affecting the photosynthetic rate, growth (Li et al., 2013), blade mass (Niinemets, 2001), level of bleaching (Xiao et al., 2015), nutrient content (Reich et al., 2006) and can impact production of chemical defenses through changes in phenolic content (Cronin and Hay, 1996b). Climate change can also have a drastic impact on the distribution range of species, and result in poleward shifts in many marine communities (Cheung et al., 2009). In addition, temperature-related shifts in temperate macroalgal communities can be exacerbated by high rates of herbivory and increased consumption rates can also prevent the re-establishment of macroalgal species when they are lost from the edges of their distribution range (Bennett et al., 2015).

Here, we carried out climate change experiments on three algal species commonly found in Australian temperate reefs. After exposing algae to various combinations of temperature and ocean acidification we completed a series of algal physiological and chemical response tests, and mesograzers feeding assays. We aimed to answer two questions: (1) How do projected climate change conditions affect the physiological and chemical aspects of macroalgae in terms of growth, bleaching, maximum quantum yield, blade toughness, density, phenolic content and nutrient content?; and (2) Are the feeding rates of mesograzers impacted by macroalgae that have been subjected to climate change conditions?

2. Methods

2.1. Study site, organisms and sampling design

Sargassum linearifolium (Turner) C. Agardh is a canopy-forming, brown macroalga that occurs in rocky tropical (Schaffelke, 1999) and temperate regions worldwide (Stiger et al., 2004). *Ecklonia radiata* (C. Agardh) J. Agardh is a temperate, canopy-forming brown kelp found on reefs in Australia, New Zealand and South Africa (Phillips et al., 1997; Wernberg et al., 2003) and *Laurencia brongniartii* (J. Agardh) is a subtropical red algal species, found in subtidal zones in Australia, Japan and the Caribbean Sea (Nishihara et al., 2004). These three algal species were collected and used in three experiments in February (*S. linearifolium*), March (*E. radiata*) and August (*L. brongniartii*) 2015. *Sargassum linearifolium* and *E. radiata* were collected haphazardly from 0.5 to 2 m depth at Hillarys Beach, Perth, Western Australia (31° 49' 14" S, 115° 44' 12" E). *Laurencia brongniartii* were collected similarly from Point Peron, Rockingham, Western Australia (32° 16' 18" S, 115° 41' 17" E).

Medium sized (approximately 250–530 mm in total length for *E. radiata* and *S. linearifolium* and 125–195 mm in total length for *L. brongniartii*) algae (20), were collected with their holdfasts intact, placed within individual aquaria, measured for maximum quantum yield and acclimated to the mean summer temperatures in Perth (20.5 °C) (Navy Metoc, 2015: <http://www.metoc.gov.au/products/data/ausstst.php>) for a period of 48 h, before increasing the $p\text{CO}_2$ and temperature gradually over a 12 h period. *Allorchestes compressa* (Dana) amphipods were collected from the surf zone at Quinns Rocks, Western Australia. The amphipods were carefully

dislodged from beach wrack using a mesh collection bag and placed in aquaria at Edith Cowan University where successive generations were reared on a mixed algal diet to supply new individuals for each experiment. *Allorchestes compressa* is a common surf zone amphipod in Western Australia (Crawley and Hyndes, 2007) and was used here due to the ease of large scale culture and its ready consumption of a range of macroalgae (Crawley et al., 2007). Two species of gastropod, *Strigosella lepida* (Philippi, 1846) and *Thalotia conica* (Gray, 1827) from the family Trochidae were collected 24 h prior to each feeding experiment from the subtidal zone in Rockingham, Western Australia (32° 16' 18" S, 115° 41' 17" E). To ensure adequate numbers of gastropods of similar size (5–6 mm shell base diameter), an equal number of individuals from each species were collected and used in each feeding assay.

2.2. Experimental conditions

The experimental design consisted of four reservoir tanks with a 2 × 2 design following Russell et al. (2009). The treatments included (1) the ambient control: 20.5 °C, pH 8.1, (2) decreased pH: 20.5 °C and pH 7.6, (3) increased temperature: 25.5 °C, pH 8.1 and (4) both increased temperature and decreased pH: 25.5 °C (Table 1). The combination of 25.5 °C and pH 7.6 represent the upper threshold for local near-future climate predictions (2070–2100) (IPCC, 2007). Temperature was controlled using aquarium heaters (200 W; Aqua One) placed in reservoir tanks and pH (NIST) was adjusted with a self-regulating CO_2 controller (Aquatronica). Fluorescent lights (Sylvania 36 W) providing ca 40 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (water surface) were placed above treatment tanks on a 14:10 h light:dark cycle to mimic natural conditions (Perth Observatory, 2014). Treated seawater entered the 50 L treatment tanks at $\sim 40 \text{ L h}^{-1}$, returning via filtration to the reservoir tank. Tank pH, temperature and salinity were monitored daily and total alkalinity was measured using a Metrohm 716 Titrimo weekly (method adapted from (Williams et al., 2009)). $p\text{CO}_2$ was calculated with CO2SYS (Pierrot et al., 2006). After 14 days final measures, described below, were taken and replicate pieces of algae were stored at -80 °C for plant chemistry analysis, nutrient analysis and for use in the reconstituted feeding experiments.

2.3. Algal physical and chemical measurements

To assess the impact of experimental treatments, growth, tissue toughness, C:N ratio, maximum quantum yield, density and total phenolic content were measured. Tissue toughness, C:N, density and total phenolic content was measured post (Day 14) exposure to the treatment conditions. Growth and maximum quantum yield measurements were done prior (Day 1) and at Day 14 after exposure to the treatment conditions, and additional maximum quantum yield measurements were taken prior to acclimation. New growth occurs in the apex of each frond within *S. linearifolium* and *L. brongniartii*, and therefore total length from the holdfast to apical tip along the main frond axis was measured (Baer and Stengel, 2010). For *E. radiata*, growth occurs at the base of the algae and instead the hole punch method was applied (method adapted from Mann and Kirkman (1981)). To estimate tissue toughness, a custom-made penetrometer (following method developed by Duffy and Hay (1991)) was used to measure the force needed to penetrate a central region of new growth fronds. Density was measured as blade mass per square centimeter (BM/cm^2). Fresh, new growth blades were cut to fit accurately into a 100 mm^2 area and weighed to gain a measurement of g/mm^2 fresh weight, a proxy for BM/cm^2 (methods adapted from McClendon (1962)).

Bleaching was characterized as visible whitening of the blade tissue due to the loss of surface integrity within algae, following

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