



# Physical and biogeochemical correlates of spatio-temporal variation in the $\delta^{13}\text{C}$ of marine macroalgae



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## ABSTRACT

Carbon isotope ratios ( $^{13}\text{C}/^{12}\text{C}$ ) can be used to trace sources of production supporting food chains, as  $\delta^{13}\text{C}$  undergoes relatively small and predictable increases ( $\sim 0.5\%$ ) through each trophic level. However, for this technique to be precise, variation in  $\delta^{13}\text{C}$  signatures of different sources of production (baseline sources) must be clearly defined and distinct from each other. Despite this,  $\delta^{13}\text{C}$  in the primary producers of marine systems are highly variable over space and time, due to the complexity of physical and biogeochemical processes that drive  $\delta^{13}\text{C}$  variation at the base of these foodwebs. We measured spatial and temporal variation in the  $\delta^{13}\text{C}$  of two species of macroalgae that are important dietary components of grazers over temperate reefs: the small kelp *Ecklonia radiata*, and the red alga *Plocamium preissianum*, and related any variation to a suite of physical and biogeochemical variables. Patterns in  $\delta^{13}\text{C}$  variation, over different spatial (10 s m to 100 km) and temporal scales (weeks to seasons), differed greatly between taxa, but these were partly explained by the  $\delta^{13}\text{C}$  of dissolved inorganic carbon (DIC) and light. However, while the  $\delta^{13}\text{C}$  in *E. radiata* was not related to water temperature, a highly significant proportion of the spatio-temporal variation in  $\delta^{13}\text{C}$  of *P. preissianum* was explained by temperature alone. Accordingly, we applied this relationship to project (across temperate Australasia) and forecast (in time, south-western Australia) patterns in *P. preissianum*  $\delta^{13}\text{C}$ . The mean projected  $\delta^{13}\text{C}$  for *P. preissianum* in the study region varied by only  $\sim 1\%$  over a 12-month period, compared to  $\sim 3\%$  over 2000 km. This illustrates the potential scale in the shift of  $\delta^{13}\text{C}$  in baseline food sources over broad scales, and its implications to food web studies. While we show that those relationships differ across taxonomic groups, we recommend developing models to explain variability in  $\delta^{13}\text{C}$  of other baseline sources to facilitate the interpretation of variation in  $\delta^{13}\text{C}$  of consumers in food webs, particularly where data for baselines are absent over broad scales.

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## 1. Introduction

Carbon isotope ratios of  $^{13}\text{C}/^{12}\text{C}$  (expressed as  $\delta^{13}\text{C}$ ) can be used to trace sources of production supporting food chains, as  $\delta^{13}\text{C}$  is generally considered to undergo relatively small and predictable increases ( $\sim 0.5\%$ ) through each trophic level (Olive et al., 2003). Combined with  $\delta^{15}\text{N}$  (e.g.  $^{15}\text{N}/^{14}\text{N}$ ), which often reflect shifts in trophic position (Jennings et al., 2008),  $\delta^{13}\text{C}$  has been used to determine the structure of food webs, e.g. rainforests (McGlynn et al., 2009), and infer diet and trophic niche of consumers (Bearhop et al., 2004). However, this often relies on the premise

that the  $\delta^{13}\text{C}$  between sources of production form groups that display marked differences in their  $\delta^{13}\text{C}$  (O'Leary, 1988). Unfortunately, taxa within these groups often have highly varied and/or overlapping  $\delta^{13}\text{C}$  signatures (Hanson et al., 2010). These variations are often not fully considered, despite having been recognised as a problem for foodweb ecologists for many years (Stephenson et al., 1984; Fenton and Ritz, 1989), which has been highlighted in recent literature (e.g. Cloern et al., 2002; Guest et al., 2010; Hyndes et al., 2013; Dethier et al., 2013). Such spatial and temporal variation may mask or distort subsequent interpretations and our ability to gain an accurate understanding of food webs, trace the movement of animals between habitats, or develop predictions of  $\delta^{13}\text{C}$ .

Broad predictions of  $\delta^{13}\text{C}$  variation in autotrophs are developing rapidly for terrestrial systems over temporal and particularly spatial scales. This has led to the development of predictive

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modelling of plant- $\delta^{13}\text{C}$  patterns across time (e.g. Kodama et al., 2008; Marron et al., 2008) and landscapes or 'isoscapes' (Hobson et al., 2012; Powell et al., 2012). These have helped identify the geographic patterns of migratory or wide-ranging species, e.g. insects (Miller et al., 2011), birds (Hobson et al., 2012) and primates (Crowley, 2012). However, these broad predictions are only just emerging for marine environments, due to the complexity of physical and biogeochemical processes that drive  $\delta^{13}\text{C}$  variation at the base of these food webs.

In marine systems, macroalgae form an extremely diverse group of primary producers with contrasting taxonomy, morphology and physiology (Carvalho and Eyre, 2011; Keith et al., 2013) and provide an important baseline food source in food webs in a range of ecosystems (Steneck et al., 2003). Furthermore, considerable  $\delta^{13}\text{C}$  variation has been reported over temperate reefs between individuals of the same species depending on site and season (Dethier et al., 2013). As the dynamics in the  $\delta^{13}\text{C}$  of macroalgae are strongly influenced by the physiological mechanisms by which dissolved nutrients are assimilated (Raven et al., 2002), the surrounding physical and biogeochemical environment may therefore account for spatial and temporal variations in  $\delta^{13}\text{C}$ . Moreover, these physiological responses will likely vary between taxa with different physical adaptations and life history traits (Raven et al., 2002), whereby different sources of production may be distinguished from each other.

Studies from estuaries or under controlled laboratory conditions have shown that an increase in irradiance produces a higher demand for carbon, and in some taxa the energy required to assimilate relatively  $\delta^{13}\text{C}$  enriched  $\text{HCO}_3^-$  over relatively depleted  $\text{CO}_2$  (Cornelisen et al., 2007). Water motion and salinity regulate the diffusive boundary layer, which determines the mode of carbon assimilation and level of fractionation, whereas temperature controls metabolism and photosynthesis (Booth and Beardall, 1991; Cornelisen et al., 2007). As the variables of temperature, salinity, light and depth are widely available and commonly recorded (through extensive oceanographic and remote sensing data), linking these variables with autotroph- $\delta^{13}\text{C}$  could represent a valuable method for making broad predictions of spatial and temporal variations in marine environments. Furthermore, such relationships could be used to predict the response of  $\delta^{13}\text{C}$  in marine autotrophs to continued increases in seawater temperatures (e.g. Wernberg et al., 2011) and  $\text{CO}_2$  (e.g. Doney et al., 2009), and so adjust for such differences when comparing past, present and future  $\delta^{13}\text{C}$  data from temperate systems.

Research describing  $\delta^{13}\text{C}$  in marine macroalgae has primarily been focused on spatial variation (e.g. Guest et al., 2010; Vanderklift and Wernberg, 2010) and those that have combined both spatial and temporal scales are often limited to only a few sampling periods (e.g. Hyndes et al., 2013; Dethier et al., 2013). Furthermore, few studies have attempted to link  $\delta^{13}\text{C}$  in marine macrophytes with their physical and biogeochemical environment. In situ environmental variables have, however, been correlated with the  $\delta^{13}\text{C}$  of phytoplankton (Rau et al., 1982; Lara et al., 2010), and even their consumers. Barnes et al. (2009) showed spatial variation in  $\delta^{13}\text{C}$  of filter-feeding scallops was strongly correlated with temperature, which was thought to be propagated through their phytoplankton diet. As a result, they were able to predict up to 79% of the spatial  $\delta^{13}\text{C}$  variation in species of fish, using a single variable model of bottom temperature. In another study by MacKenzie et al. (2011), the effect of sea surface temperature (SST) was indirectly linked to the  $\delta^{13}\text{C}$  in Atlantic salmon (again through phytoplankton) and used to determine the geographic locations of feeding grounds. The case for macroalgae is, however, very different to phytoplankton. Phytoplankton are sampled in bulk, giving a production weighted mean of  $\delta^{13}\text{C}$ , whereas macroalgae are sampled individually, and

$\delta^{13}\text{C}$  among taxa that occupy the same habitats, can have very different spatial (Vanderklift and Wernberg, 2010) and temporal patterns (Dethier et al., 2013). This suggests that differences exist among taxa in the way the environmental factors interact with their physiological mechanisms for capturing and storing carbon. Understanding these  $\delta^{13}\text{C}$ /environmental relationships could provide a better understanding of shifts in  $\delta^{13}\text{C}$  of baseline sources to more accurately interpret  $\delta^{13}\text{C}$  values in food web studies (Barnes et al., 2009).

In this study, we describe  $\delta^{13}\text{C}$  in two taxonomically contrasting macroalgae on temperate subtidal reefs over various spatial (10 s m to 100 km), and temporal (weekly to seasonal) scales over a 13-month period. The kelp *Ecklonia radiata* is abundant along the southern coasts of Australia and New Zealand, and supports food webs in that region (Guest et al., 2010; Vanderklift and Wernberg, 2010). Similarly, the red alga *Plocamium preissianum* represents foliose red algae, which are abundant and support food webs in temperate reef and seagrass systems (McClanahan, 2008; Shepherd and Edgar, 2013). Secondly, we analysed spatial and temporal  $\delta^{13}\text{C}$  variations against a suite of physical and biogeochemical variables, including those where relationships could be conveniently applied to extensive oceanographic and remote sensed data. We then used our subsequent models to project (in space) and forecast (in time) patterns in  $\delta^{13}\text{C}$  to determine if environmental variables could be used for predictions in  $\delta^{13}\text{C}$  and whether these could facilitate interpretation of food web data and generation of hypotheses.

## 2. Materials and methods

### 2.1. Study area

Our study was conducted over subtidal reefs along the lower west coast of Australia. A characteristic feature of this coastline is the presence of limestone reefs running parallel to the shore that are exposed to prevailing south-westerly oceanic swells (Sanderson, 2000). These reefs dissipate wave energy, forming gradients of water velocity from high-energy offshore reefs to protected inshore reefs. The region is also considered oligotrophic due to the Leeuwin Current that prevents the development of any major upwellings (Pearce and Griffiths, 1991). The climate is Mediterranean with seawater temperatures ranging from 17 °C in winter rising to 24.5 °C in late summer (Smale and Wernberg, 2009).

### 2.2. Sampling design

Our spatial sampling was conducted on reefs in early autumn 2013 (18th - 20th March), and encompassed three spatial scales. These included three regions: Quinn's Rocks (31°41'09'S, 115°40'26'E), Marmion Marine Park (31°49'13'S, 115°43'01'E) and Shoalwater Islands Marine Park (32°19'43'S, 115°41'23'E), with four sites within each region, and five replicates within each site (Fig. 1). Each region was separated by 10 s of km (regional scale), while sites were spaced > 1 km apart (site scale), and replicates taken 10 s of m apart (replicate scale). At each site, and from a depth of between 5 and 7 m, we collected by hand using SCUBA, replicate samples of two taxonomically contrasting macroalgae: the small kelp *Ecklonia radiata* (of the order Laminariales) and the red alga *Plocamium preissianum* (of the order Plocamiales). Macroalgae were collected as whole, and only mature individuals were taken (~55 cm *E. radiata*, ~20 cm *P. preissianum*), as young and old plants can vary significantly in their  $\delta^{13}\text{C}$  (Fredriksen, 2003).

Our temporal sampling followed the same protocol but from just two sites within Marmion Marine Park (Little Island (LI) and Marmion Reef (MR), Fig. 1). At these sites, we sampled every month

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