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Significant carbonate production on a temperate reef system in southwestern Australia

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A R T I C L E I N F O

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A B S T R A C T

Calcifying organisms support key geo-ecological functions in shallow tropical and temperate reefs worldwide, including creating habitat structure, producing sediments, and supporting reef accretion. These functions depend on the carbonate budget: the balance between calcium carbonate production and erosion. While carbonate budgets are well characterized in tropical coral reefs, the carbonate budgets of temperate rocky reefs, and their variability across spatiotemporal scales, remain much less well understood. Here, we quantify the carbonate budget of a seaweed-dominated rocky reef ecosystem within the world's largest cool-water carbonate depositional system. We first measured the seasonal and annual calcification rates of key calcifying groups (mobile invertebrates, corals, and coralline algae) across depths of 5, 10 and 18 m at two sites. Using a census-based approach, we then estimated how reef-scale gross carbonate production and erosion varied over depth. Crustose coralline algae exhibited calcification rates similar to those recorded in tropical studies, but their calcification was 2–7 times lower than that of corals. At the reef scale, gross carbonate production ranged from 9 to 2369 g $CaCO_3$ m^{-2} yr^{-1}, and was dominated by crustose and articulated coralline algae at shallow depths (68–96 % of the total production, 5–10 m depth), with corals becoming the principal contributors (58–62 %) at greater depths. Mobile invertebrates (gastropods and sea urchins) were minor contributors to carbonate production overall (1–3 %). Sea urchins entirely drove bioerosion however, which was relatively low (8–114 g $CaCO_3$ m^{-2} yr^{-1}) and increased with depth. Although the average net carbonate production in the studied temperate reefs (216–671 g $CaCO_3$ m^{-2} yr^{-1}) is relatively low compared to that of healthy coral reefs in the region (1400–3880 g $CaCO_3$ m^{-2} yr^{-1}), the vast expanses of seaweed-dominated rocky reefs in the study area and globally suggest that these ecosystems may play an underappreciated role in cool-water and global carbonate production. Indeed, preliminary estimates suggest that carbonate production across Australia's temperate Great Southern Reef could be comparable to tropical systems renowned for their high carbonate production such as the Great Barrier Reef.

1. Introduction

The coastal ocean is a hotspot of biogeochemical activity, cycling and storing globally-significant quantities of carbon and nutrients (Liu et al., 2010). Central to this processes is the production and accumulation of calcium carbonate ($CaCO_3$), with over half of the $CaCO_3$ accumulation—and a quarter of the production— occurring in shallow ecosystems alone (e.g. coral reefs, seagrass meadows) (Milliman, 1993; O'Mara and Dunne, 2019). In addition to its role in the carbon cycle, the biogenic production of $CaCO_3$ in shallow habitats also underpins several key ecological and geological functions. For example, the complex carbonate structures formed by calcifying organisms support biodiversity and help dissipate wave energy, reducing coastal erosion (Adey et al., 2013; Pratchett et al., 2015; Steneck, 1986). Additionally, the breakdown of that carbonate contributes to reef accretion and to the production of sand and sediments, which helps maintain beaches and sandy islands. Tropical reefs have long been considered hotpots of $CaCO_3$ production, receiving intense research effort since the 1950s (Chave et al., 1972; Goreau, 1963; Lange et al., 2020; Rodgers, 1957; Stearn et al., 1977). In contrast, the carbonate production of temperate and subtropical waters has received comparatively less research attention (Henrich et al., 1995; James et al., 2013; Smith, 1972), even though

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carbonate sediments can be widespread in these areas (Freiwald, 1995; James et al., 1994; O'Connell et al., 2012), and evidence shows some temperate and subtropical organisms produce $CaCO_3$ at rates comparable to tropical species (Bosence, 1980; Canals and Ballesteros, 1997; Chave, 1967; Freiwald and Henrich, 1994; Oliveira et al., 2025; Smith, 1972). As a consequence, little is known about carbonate cycling in temperate reefs. This knowledge gap is particularly relevant in the context of ongoing climate-driven changes in abundance of calcifying and bioeroding organisms, and our understanding of whether temperate reef ecosystems are net carbon sources or sinks (Filbee-Dexter et al., 2023; Pessarrodona et al., 2023).

Past and present climate-driven declines in the abundance of corals have reduced the net carbonate production of tropical coral reefs worldwide, impacting their ability to sustain geo-ecological functions (Davis et al., 2021; Perry et al., 2018a). Temperate reefs are also undergoing rapid transformations under climate change, including changes in the abundance of calcifying organisms. The populations of tropical and subtropical corals are expanding in temperate regions worldwide (Korea: Denis et al., 2015; Lee et al., 2022; Japan: Kato et al., 2018; Yamano et al., 2011; Western Australia: Marsh, 1992; Ribeiro et al., 2022; Sahin, 2023), and overfishing of sea urchin predators and ocean warming have caused the formation of barrens dominated by sea urchins and coralline algae (Filbee-Dexter and Scheibling, 2014; Ling et al., 2015). Understanding how the geo-ecological functions associated with carbonate production in temperate reefs are responding to such changes requires establishing a carbonate budget baseline. Yet, knowledge about the key organisms controlling the biological production and erosion of carbonate, and how these processes vary across spatiotemporal scales, is currently lacking for most temperate coastlines.

In tropical reefs, $CaCO_3$ production is predominantly produced by scleractinian corals (hereafter corals), with additional contributions by calcified algae (e.g. articulated and encrusting corallines, *Halimeda* spp.), molluscs, and foraminifera (Perry et al., 2018b; Wilson et al., 2009). All of these taxa can occur on temperate reefs (Smith, 1972) (Fig. 1), albeit their abundance and growth rates may differ. High-latitude temperate reef environments are considered to be unfavourable for coral growth and coral reef formation, with the distribution, abundance and recruitment of corals declining with latitude (Chave, 1967; Chong et al., 2023; Grigg, 1981; Price et al., 2019). Despite this, corals can be locally abundant in temperate reef communities (Thomson and Frisch, 2010 and references therein), where they can calcify at rates similar than tropical species (Ross et al., 2018). Coralline algae are another one of the key carbonate producers in tropical and temperate reefs worldwide (Smith, 1972). To date however, most calcification studies on temperate corallines have focused on free-living rhodoliths and/or been conducted in the lab (see reviews by Cornwall et al., 2023, 2019). In contrast, comparatively little is known about *in situ* calcification of encrusting forms, which are amongst the most abundant temperate marine organisms (Steneck, 1986). Mobile invertebrates such as gastropods and echinoderms are often major contributors to carbonate sediment deposits (Bonesso et al., 2022; Montaggioni et al., 2009), but their carbonate production rates are seldom directly measured (Hart and Kench, 2007; Hily et al., 2013; Massé, 1999), and are often omitted from carbonate budgets studies due to a lack of data (Perry et al., 2015). Yet, invertebrate carbonate production rates can be high at local scales (e.g. >4 kg $CaCO_3$ m^{-2} yr^{-1}, California, Smith, 1972; 2.4 kg $CaCO_3$ m^{-2} yr^{-1}, Brittany, Hily et al., 2013), prompting calls to explicitly consider them in global biogeochemical models (Lebrato et al., 2010a). Invertebrates like sea urchins can also function as important bioeroders on tropical reefs, removing carbonates at rates that equal or exceed carbonate production as they feed by scraping algae and other organisms off hard substrate (Bak, 1994). The extent of sea urchin bio-erosion on temperate reefs, and its influence on the total carbonate budget, remains however poorly understood (Thilakarathna et al., 2022).

The temperate coast of southern Australia is the largest deposition zone of cool-water carbonate sediments on the globe (James et al., 1994), and as such is a globally-significant hotspot of production and burial of carbonates. This coastline is lined by seagrass habitats and a system of interconnected rocky reefs dominated by seaweed forests – the Great Southern Reef (Bennett et al., 2016), which features a diverse range of calcifying organisms (James et al., 2013; James and Bone, 2011a). Although the contributions of these organisms to Australian carbonate sediments are well established (James and Bone, 2011b), their actual production rates, and their spatiotemporal variation, remain largely unknown. This limits our understanding of the relative

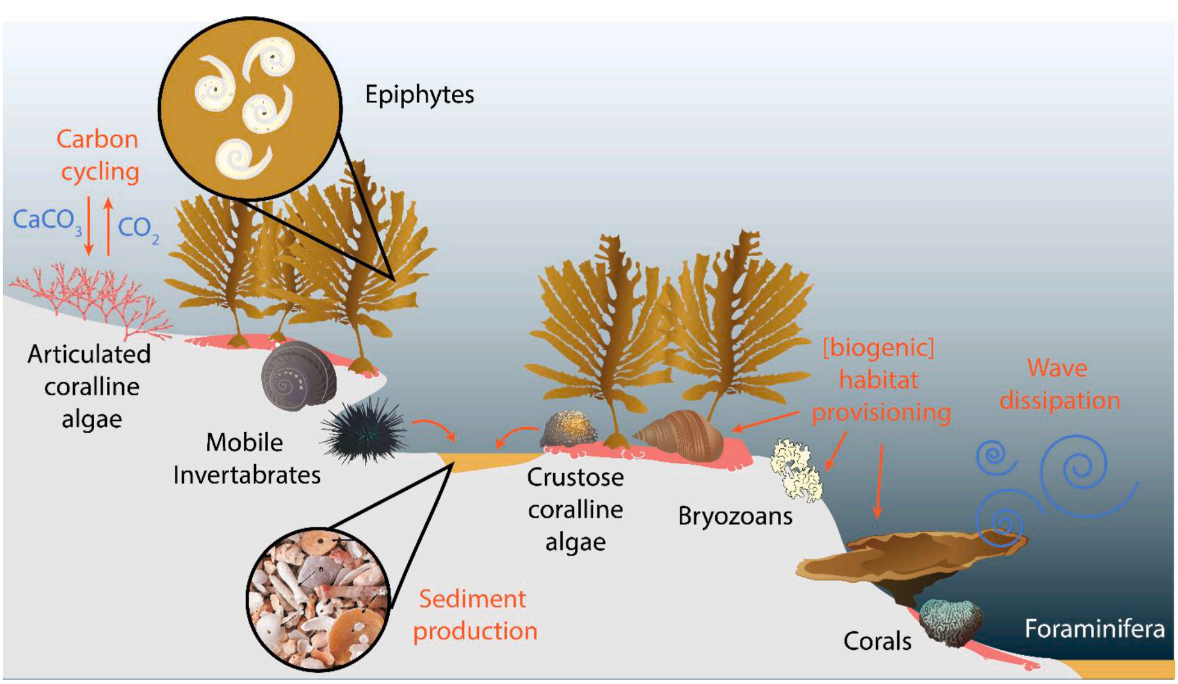

Fig. 1. Schematic diagram of the main carbonate producers and bioeroders of a temperate rocky reef, and some of the geo-ecological functions they provide (in orange). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

importance of this carbonate-producing habitat at continental and global scales, and our ability to predict whether these reefs will be able to sustain key geo-ecological services such as habitat provision, sand production, or coastal protection into the future. Here, we provide the first estimates of $CaCO_3$ production and erosion for Australian temperate rocky reefs, and explore how reef carbonate budgets vary with depth. Our results provide a new understanding of the carbonate sedimentology of Australia, and yield key insights on how carbonate budgets may respond to ongoing and future changes in the abundance of calcifying taxa.

2. Methods

2.1. Study area and design

We quantified the net carbonate production of two temperate rocky reefs in Marmion Lagoon (31°46', 115°40), a limestone reef system located near Perth in southwestern Australia. Reefs within the lagoon are separated by areas of coarse quartz and calcium carbonate sand which is resuspended and deposited on the reef surfaces intermittently. The surveyed reefs spanned a depth gradient from shallow (5 m), intermediate (10–11 m) to deep (18 m) depths before transitioning to sand. All reefs sampled in this study were located on the outer reef line, and therefore are fully exposed to the wind and swell-generated waves, which dominate the hydrodynamic regime in the study region. The reefs host a diverse algal assemblage (Wernberg and Goldberg, 2008), with the canopy being dominated by the small kelp *Ecklonia radiata*, and the fucoid *Scytothalia dorycarpa* becoming codominant as depth increases.

We used a census-based approach (see Fig. S1 for schematic representation of the study design) to quantify reef net carbonate production— i.e. the balance between gross carbonate production and bioerosion, also known as carbonate budget. Census-based carbonate budgets quantify the contributions of individual taxa to each of these processes, providing a 'snap-shot' of the reef's budget condition from days to years (Lange et al., 2020). Gross carbonate production results from the net calcification of calcifying organisms (e.g. as corals, algae, mobile and sessile invertebrates, foraminifera), while bioerosion results from the removal of carbonate by parrotfishes, sea urchins, sponges and other organisms that live within the calcium carbonate structure of the reef (Chave et al., 1972; Lange et al., 2020; Perry et al., 2018b). Carbonates can also get removed via chemical dissolution and physical processes (Eyre et al., 2018), but these were not considered here. As the calcification rates of temperate calcifying organisms likely differ from those in the tropical literature, we also determined the calcification of key temperate crustose coralline and coral taxa.

2.2. Seasonal calcification rates

We quantified the seasonal net calcification rates of crustose coralline algae (CCA) and two of the most abundant species of coral (*Plesiastrea versipora*, *Coelastrea aspera*; Tuckett et al., 2017, Results) using the buoyant weight technique. Net calcification includes secondary calcification processes such as infilling of the older skeleton and skeletal dissolution as well as the mortality and loss of skeleton (Lewis et al., 2017). Individual coral colonies (4–46 cm^2) and fragments of CCA (3–60 cm^2, *Lithophylloideae* and *Lithophylloideae* and *Hydrolithoideae*) were originally collected from 5 (CCA) and 10 (corals) meters depth at our study sites and brought into climate-controlled aquaria for acclimation for two weeks. Colonies/fragments were fixed to numbered plexiglass tiles using marine epoxy and left for two (CCA) and five (corals) more weeks in aquaria with flow-through water to check for epoxy-related mortality. Tiles were then deployed at each reef (n = 8–12 tiles per depth within each site, 2 sites per depth), with coral tiles only being deployed at 10 m depth at the two sites. CCA tiles were secured under the seaweed canopy by cable-tying them to kelp holdfasts or holes within the reef, thus emulating their natural position (Fig. S2). Tiles were haphazardly positioned on the substrate approximately 25–100 cm apart in an area that was around 5 m^2. Coral tiles were deployed on PVC frames in large canopy gaps, away from negative effects from the seaweed canopy (Ribeiro et al., 2022). The tiles were retrieved/redeployed approximately every 3 months (see Table S1 for deployment and collection schedule) to measure seasonal growth rates. Upon retrieval, tiles were brought to the laboratory where all biofouling was carefully removed, and each tile was buoyantly weighed to the nearest 0.001 g by freely suspending the tiles from a fishing line below an electronic scale in a basket full of seawater. Tiles were redeployed to their respective sites/depths within less than a week. When necessary, replicates that were lost were replaced with new ones. Net organismal calcification (mg $CaCO_3 \cdot cm^{-2}$ organism day^{-1}) was then estimated as:

$$x = \frac{W1 - WO}{(A0 + A1)/2} \Big/ d$$

where W0 and W1 are the initial and final dry weights normalized to the surface area (initial and final surface area: A0 and A1) of each colony/fragment and divided by the number of days (d) in that particular season. The surface area of coralline algae was determined using the aluminum foil technique (Marsh, 1970), whilst area of corals was determined using the geometric method following (González-Barrios and Álvarez-Filip, 2018) assuming hemispheric growth. The dry weights (W) were calculated as:

$$W = W_{sw}\frac{\rho CaCO_3}{\rho CaCO_3 - \rho sw}$$

where W_{sw} is the buoyant weight, ρ_{sw} is the density of seawater calculated from temperature and salinity during each measurement, and $\rho\, CaCO_3$ is the density of the dominant skeletal mineral (2.71 g cm^{-3} for high-magnesium calcite for CCA, and 2.93 g cm^{-3} for aragonite for corals).

2.3. Reef carbonate production

2.3.1. Mobile invertebrates

The reef-scale carbonate production (g $CaCO_3 \cdot m^{-2}$ reef yr^{-1}) of mobile calcifying invertebrates was determined based on their abundance (individuals m^{-2}) and shell growth rates (g $CaCO_3$ yr^{-1} ind^{-1}). The abundance and test diameter or shell size of echinoids and gastropods (>2.5 cm shell length) was determined along three (5 and 10 m) to four (18 m) 50 × 1 m belt transects at each reef and depth. We only considered these two invertabrate groups as they are highly abundant in the study area (Richards et al., 2016; Vanderklift and Kendrick, 2004), are responsible for the majority of carbonate production within their phyla (Lebrato et al., 2010b), and other mobile calcifying taxa (e.g. ophiuroids, boring bivalves) are challenging to survey *in situ*. To calculate the expected yearly test/shell growth of each individual and species, we used a von Bertalanffy growth model (VBGM) with parameters obtained from the literature (Table 1). We converted the expected shell growth (in cm) to dry shell weights (in g) using species-specific length-weight relationships obtained from recently dead (empty) shells (gastropods) and the literature (echinoid tests, Lebrato et al., 2010b), thus yielding annual test/shell carbonate production (g $CaCO_3$ yr^{-1} ind^{-1}). We assumed sea urchin tests were 75.1 % carbonate (Lebrato et al., 2010b) and gastropod shells were 100 % carbonate. We then derived a species-specific mortality risk using data from the literature (Table 1) and applied it to our dataset to estimate which individuals from our data would stochastically perish after a year. To obtain the reef-scale carbonate production, we then divided the sum of the expected yearly carbonate produced by all surviving mobile invertebrates (g $CaCO_3$ yr^{-1}) of the same species within a transect by the transect area (50 m^2).

2.3.2. Benthos

The reef-scale carbonate production of benthic calcifiers (corals, crustose and articulated coralline algae, bryozoans; g $CaCO_3$· m^{-2} reef yr^{-1}) was determined by multiplying their abundance (% cover of reef, i.e. the area of a calcifying organism in a m^2 of reef) by their net annual calcification rates (g CaCO3 cm^{-2} organism yr^{-1}). Annual calcification rates for CCA and corals were obtained by summing the average seasonal rates (g $CaCO_3$· cm^{-2} day^{-1}) multiplied by the length of each season (91–92 days). For the areal calcification rates, we used the depth and site-specific rates derived from this study. Rates for bryozoans were derived from Smith and Nelson (1994), and rates for articulated coralline algae were obtained from a growth study on the tropical species *Amphiroa tribulus* (157.7 mg CaCO3 cm^{-2} yr^{-1}, control treatment at 24°C—the summer temperature of our study sites; Vásquez-Elizondo and Enríquez, 2016), *Amphiroa* being the dominant genus of articulated coralline algae in the study area. At each site, the percent cover of benthic calcifiers was quantified by placing five 0.25 m^2 quadrats at 5 m intervals along a 25 m transect. Six transects (n = 30 quadrats) were laid at 5 and 10 m depth and eight transects (n = 40 quadrats) were laid at 18 m depth. The percent cover of benthic calcifying taxa within each quadrat was estimated *in situ* using the point intersect method (50 points per quadrat). We assumed that coral species not included in the experiments above would calcify at a rate average of the two species studied here, as most coral species in our survey were of the same growth form (massive/submassive; Pratchett et al., 2015).

2.3.3. Epiphytes

We estimated the production of epiphytes by weighing the calcifying epiphytes on the dominant canopy former *Ecklonia radiata* (n = 15 plants per site/depth), and estimating the age of the plants using their annual growth marks, thus yielding the biomass $CaCO_3$ accumulated per year of plant growth.

2.4. Reef carbonate bioerosion

To calculate reef bioerosion we multiplied sea urchin abundances from the surveys above by published bioerosion rates of sea urchins species present in the study area (Table 2). Bioeroding fishes (e.g. parrotfishes) are largely absent from the study area (Tuya et al., 2009), and were therefore not considered. Bioerosion by macro (sponges, bivalves,

Table 1

Life-history parameters used to model the carbonate production of the principal mobile calcifying invertebrates. L∞ (asymptotic maximum length) and *k* (growth rate coefficient) were used to predict yearly test/shell growth (cm) using a von Bertalanffy Growth Model, which was then converted to $CaCO_3$ weights using a test/shell length-weight power relationship (for gastropods: Weight = a × $Length^b$, for echinoids: Weight = [(a × Length) – b]*0.7512). We then applied a stochastic natural mortality rate (M, instantaneous annual mortality) to the surveyed populations to predict the individuals that would survive after a year of growth. R^2 gives the Pearson correlation of the shell length-weight relationships.

Species	L∞ (cm)	*k* (yr^{-1})	M (yr^{-1})	Parmeters' region	a	b	R^2	n	References
GASTROPODS									
Dicathais orbita	5.22	0.405	0.6162	Thomson and Fish-hook Bay, Rottnest Island, WA	0.1134	3.2548	0.953	9	(Phillips and Campbell, 1968, 1974)
Turbo kenwilliamsi	6.61	0.8157	0.38[c]	Rottnest Island & Cheyenne Beach WA	1.3425	0.5365	0.96	18	Joll (1975)
Turbo jourdani	22.1[a]	0.4307[b]	0.38[c]	Cottesloe, WA	0.5353	2.2023	0.98	9	Joll (1975)
Lunella torquata	9.89[a]	0.4307	0.38[c]	Cottesloe, WA	0.8234	2.6071	0.968	31	Joll (1975)
Astralium tentorum	5.3[a]	0.299[b]	1.83[b]	Kaikoura, New Zealand	0.252	3.1132	0.987	15	Robinson (1992)
ECHINOIDS									
Echinometra mathaei	4.96	0.277	0.1450	Rottnest Island, WA	0.492	0.8202	0.84	36	(A Ebert, 2013; Ebert, 1982)
Heliocidaris erythrogramma	7.619	0.191	0.0976	Point Peron, WA	3.49[f]	15.414[f]	0.93	40	(Ebert, 1982; Pederson and Johnson, 2008)
Centrostephanus tenuispinus	9.218[d]	0.247[d]	0.0640[d]	Port Jackson, NSW	0.492	0.8202	0.84	36	Ebert (1982)
Phyllacanthus irregularis	11.6[a]	0.247[e]	0.0640[e]		0.492	0.8202	0.84	36	

[b]Based on congeneric *Lunella torquata* (Joll, 1975).
[a] Adjusted following L∞ = Lmax/0.95, where Lmax is the maximum length observed in the population (Pauly, 1984).
[b] Based on the similarly-sized temperate turbinid *Turbo smaragdus* (Robinson, 1992).
[c] Based on the large temperate turbinid *Turbo sarmanticus* (Pulfrich and Branch, 2002).
[d] Based on the congeneric species C. rodgersii from Eastern Australia (Ebert, 1982).
[e] Assumed to be similar than *C. tenuispinus* based on similar diets and demography (Vanderklift et al., 2006; Vanderklift and Kendrick, 2004).
[f] Length-weight equation was obtained for wet weight, which was then converted to dry weight based on a wet-dry weight conversion factor (Lebrato et al., 2010a).

Table 2

Bioerosion rates of different species of sea urchins encountered in the study. TD = Test diameter.

Species	Data's Region	Erosion rate (g $CaCO_3$ ind^{-1})	Notes	Reference
Centrostephanus tenuispinus	Perth, WA	242.9 (<6.5 cm TD) 313.6 (6.5–7 cm TD) 334.3 (>7 cm TD)	Sum of seasonal averages at one site for 2015. Bioerosion = ingestion rate × ($CaCO_3$ content – experimentally-derived reworked $CaCO_3$)	Thilakarathna et al. (2022)
Echinometra mathaei	Ningaloo Reef, WA	194.2 ± 70	Average of five sites. Individuals collected at first light to estimate daily ingestion rate winter 2011. Bioerosion = ingestion rate × $CaCO_3$ content	Langdon (2012)
Heliocidaris erythrogramma	Perth, WA	0	Drift feeder, minimal $CaCO_3$ content in guts.	(Vanderklift et al., 2006; Vanderklift and Kendrick, 2005)
Phyllacanthus irregularis	Perth, WA	121.4 (<6.5 cm TD) 157.1 (6.5–7 cm TD) 167.1 (>7 cm TD)	Assumed to be half of *C. tenuispinus* as it contains 40 % less sand/rock in gut contents	Vanderklift et al. (2006)
Holopneustes porossissimus	Sydney, NSW	0	Lives off the substratum	(Steinberg, 1995, pers. obs.)

worms) and microborers (cyanobacteria, fungi) was not determined because rates are poorly characterized in temperate areas. Sponge bioerosion is likely to be low in our study system however as boring sponges (e.g. order Clionaida) are rare in temperate Australia (McDonald and Fromont, 2005; Roberts and Davis, 1996).

2.5. *Statistical analysis*

We examined differences in the seasonal calcification rate (mg $CaCO_3$ cm^2 day^{-1}) of CCA between sites (2 levels, fixed factor) and depths (3 levels, fixed factor) using linear models in the R statistical environment (R Development Core Team, 2016). For corals, calcification rates were compared between species (2 levels, fixed factor) and sites (2 levels, fixed factor) only, as tiles were deployed solely at 10 m depth. "Season" was included as a fixed factor in all models with 3 levels for corals and 4 levels for CCA. Data was log(x+1) transformed to meet model assumptions, with model fit assessed using quantile-quantile and residual vs. fitted value plots, Kolmogorov-Smirnov, and outlier tests via the DHARMa package (Hartig, 2020).

To test whether the composition of benthic and mobile calcifiers varied across depths (3 levels, fixed factor) and sites (2 levels, fixed factor), we used a permutation multivariate analysis of variance (PERMANOVA) with 9999 unrestricted permutations in PRIMER 6.0 with the PERMANOVA add-on. For each abundance response variable (density for invertebrates and percent cover for benthic calcifiers), we generated a similarity matrix based on Bray-Curtis distances of square-root transformed data. In the analysis of benthic calcifiers, a dummy variable was added to account for quadrats with zero calcifiers (e.g., sand), and transect was included as a nested random factor within each site-depth combination (n = 5 quadrats per transect). Transects were the replicate units in the mobile calcifier analysis (n = 3–4 transect per site-depth combination). To determine whether within-group variation differed between levels of each factor, we conducted a permutational analysis of multivariate dispersion (PERMDISP). Finally, similarity percentage analysis (SIMPER) identified which species or taxa contributed to the similarity between depths and sites.

Differences in total gross carbonate production and total bioerosion (g $CaCO_3$ m^2 yr^{-1}) between sites (2 levels, fixed factor) and depths (3 levels, fixed factor) were examined using generalized linear models fitted with a Gamma distribution and a log-link function. To account for the large number of zeroes (reflecting the absence of benthic or mobile producers/eroders), we used zero-inflated models within the `glmmTMB` package (Brooks et al., 2017). Model fit was assessed as described above.

3. Results

3.1. *Seasonal calcification rates*

Seasonal calcification rates of CCA ranged between −0.48 (i.e. net dissolution/skeletal loss) and 0.78 mg $CaCO_3$ cm^{-2} organism day^{-1}, generally peaking during early austral autumn and early winter. Seasonal patterns varied however across depths (significant Depth × Season interaction; Table S2, $p < 0.05$), being less pronounced at 18 m compared to shallower depths. Calcification rates were significantly lower at Site 2 (Table S1, $p < 0.001$, Fig. 2), which also showed more reduced seasonality in growth rates (Depth × Season interaction; Table S2, $p < 0.05$). Seasonal calcification rates of colonies of *Plesiastrea versipora* ranged from 0.04 to 3.36 mg $CaCO_3$ cm^{-2} day^{-1}, while calcification of *Coelastrea aspera* colonies was significantly higher (linear model, Table S2, $p < 0.01$), and ranged from 0.12 to 1.77 mg $CaCO_3$ cm^{-2} day^{-1} (Fig. 2). Coral calcification rates were significantly higher in summer, remaining similar throughout the other seasons (linear model, Table S2, $p < 0.001$). Unlike coralline algae, coral calcification rates did not significantly vary between sites. Overall, after accounting for

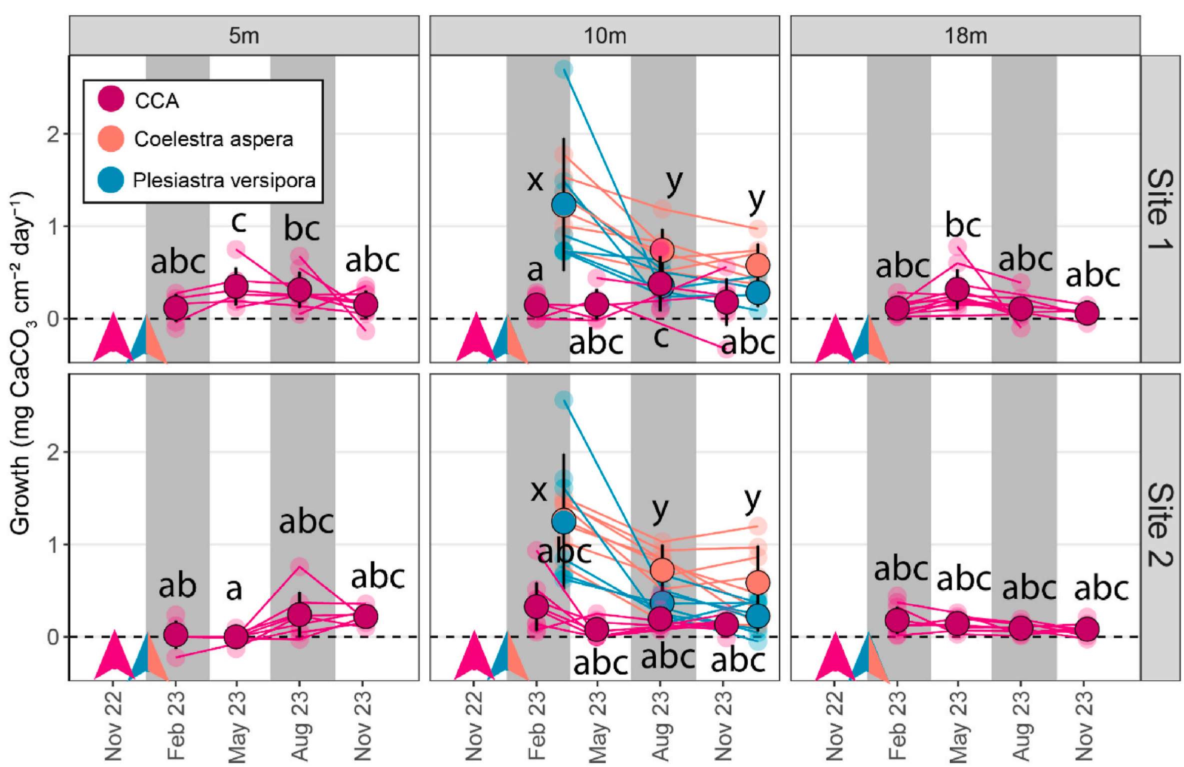

Fig. 2. Area-normalized calcification rates of crustose coralline algae (CCA) and coral colonies of *Plesiastrea versipora* and *Coelastrea aspera* on experimental tiles at their collection date. CCA tiles were deployed from November 2022 to November 2023, whilst coral tiles were deployed from December 2022 to December 2023. Initial deployment dates are indicated by arrows. Large dots indicate means ± standard deviation, while small dots indicate individual-level values, and lines follow individuals through time. Letters denote significant differences between depths, sites and time points (coral and CCA tiles were examined separately). Note CCA tiles deployed in May at the 10 m depth were mistakenly secured to the wrong site, hence why the lines skip the third time point.

seasonal variation, annual calcification rates of corals (*P. versipora*, 200.7 ± 71.5 mg $CaCO_3$ cm^{-2} yr^1; *C. aspera* 299.1 ± 59.9 mg $CaCO_3$ cm^{-2} yr^1, mean ± sd) were 2.5–7.5 higher than those of CCA, which ranged from a minimum 44.2 ± 27.9 mg $CaCO_3$ cm^{-2} yr^1 (mean ± sd) at 18 m in Site 2, and a maximum of 84.7 ± 32.2 mg $CaCO_3$ cm^{-2} yr^{-1} at 5 m in Site 1.

3.2. Reef carbonate production

3.2.1. Mobile invertebrates

The assemblage of mobile calcifiers was relatively diverse, with a total of 16 species (5 echinoids and 11 gastropods) being recorded across all surveys. Invertebrate assemblages did not vary significantly between

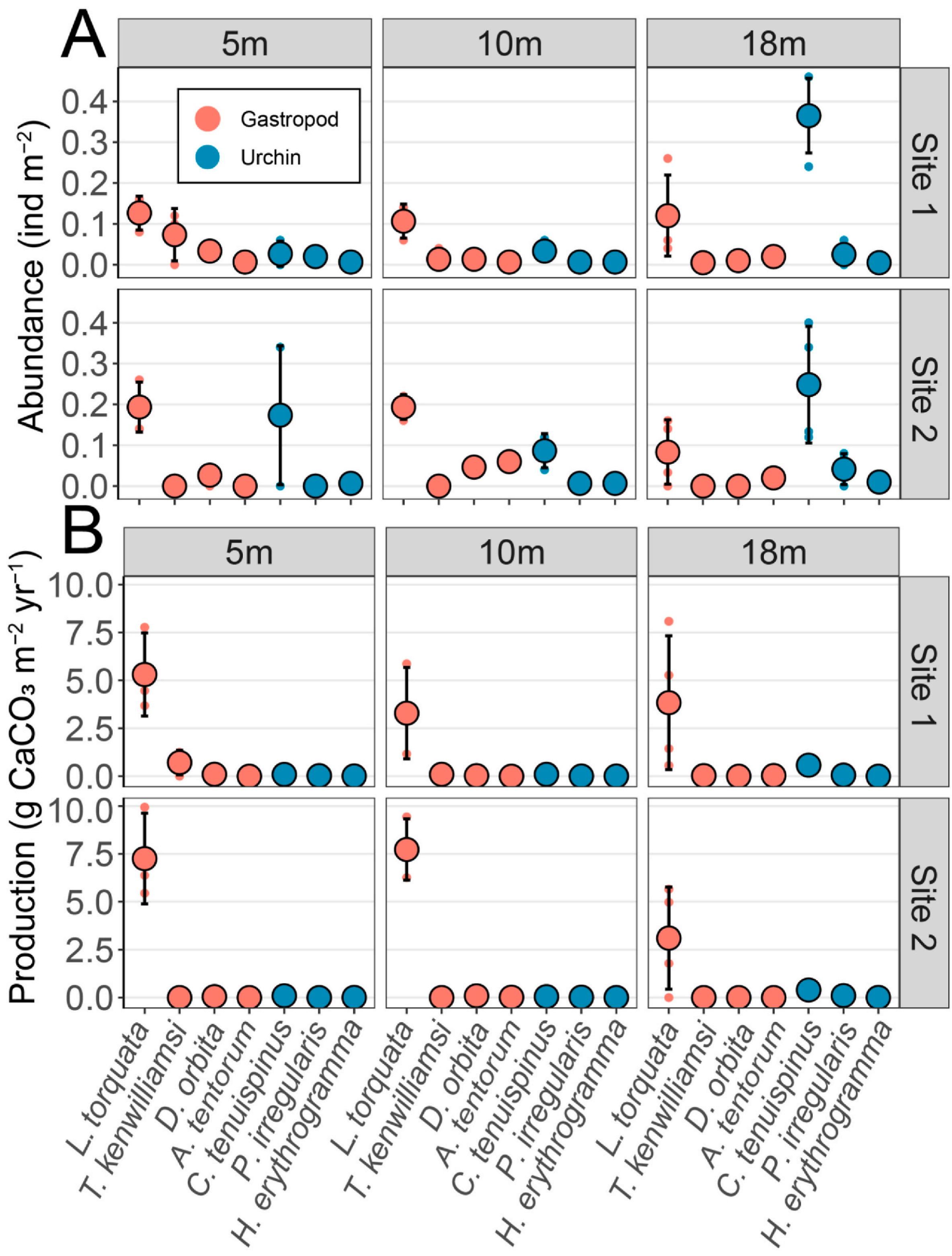

Fig. 3. Abundance (A) and carbonate production (B) of different species of mobile invertebrates across depths and sites. For illustration purposes, only species with an abundance greater than 0.005 ind m^{-2} across all our sites are shown. Small dots show the transect-level abundance (n = 3–4 per site) within each site, whilst larger dots and error bars denote the mean and standard deviation (SD). Genus names are *Lunella, Turbo, Dicathais, Centrostephanus, Phylacanthus and Heliocidaris*.

sites but varied significantly with depth (PERMANOVA, Table S3). Dissimilarities were greatest between the shallow (5 m) and deep sites (18m), and were mostly driven by higher abundances of the sea urchins *C. tenuispinus* and *Phyllacanthus irregularis* at greater depths, with *Lunella (Turbo) torquata* being more abundant at shallower depths (Fig. 3A, SIMPER, Table S4). Despite the diverse mobile invertebrate calcifier assemblage, gross carbonate production at the reef scale was largely dominated by a single species: *L. torquata* (Fig. 3B). Production of *L. torquata* individuals increased with shell length until peaking at 5–6 cm (50 g $CaCO_3$ ind^{-1} yr^{-1}), and then steeply declined after individuals grew beyond 7 cm (Fig. S3). Overall, invertebrate carbonate production did not vary significantly across sites or depths and was relatively low, ranging from 0.2 to 10.6 g $CaCO_3$ m^{-2} yr^{-1}.

3.2.2. Benthos

The assemblage of benthic calcifiers was comprised of 20 taxa (8 corals, 8 articulated corallines, 3 bryozoans and crustose corallines). Crustose corallines were the dominant calcifying taxa across all sites and depths (Fig. 4A, Fig. S4). There were no significant differences in the benthic calcifying assemblage between sites, but there were significant differences with depth (PERMANOVA, Table S3). These were largely driven by differences in the total abundance of crustose corallines, as well as articulated corallines (*Amphiroa anceps*, *A. gracilis*, *Jania* sp.) being more abundant at shallow sites and coral species (e.g. *Paragoniastrea australiensis*, *Coelastrea aspera*) being more abundant at depth (SIMPER, Table S4). The gross reef-scale production of different benthic calcifiers varied strongly with depth, being a product of their abundance as well as calcification rate (Fig. 4B). With the exception of the 5 m depth at Site 1, where production was only 90 g $CaCO_3$ m^{-2} yr^{-1}, production by CCA was relatively high at 5 and 10 m, with site averages ranging 285–400 g $CaCO_3$ m^{-2} yr^{-1}. Production of articulated algae peaked in the shallows (5 m Site 1267 ± 50 g $CaCO_3$ m^{-2} yr^{-1}; mean ± SE), while production of corals peaked at depth (18 m Site 2295 ± 82 g $CaCO_3$ m^{-2} yr^{-1}), where it was also the principal contributor to total gross carbonate production Fig. 5). Production by bryozoans was negligible across all sites (<1 g $CaCO_3$ m^{-2} yr^{-1}), while production of canopy epiphytes was nil (not shown in Fig. 4) as none of the plants examined had calcifying epiphytes.

3.3. Reef carbonate bioerosion

Transect-level bioerosion ranged from 0 to 128 g $CaCO_3$ m^{-2} yr^{-1},

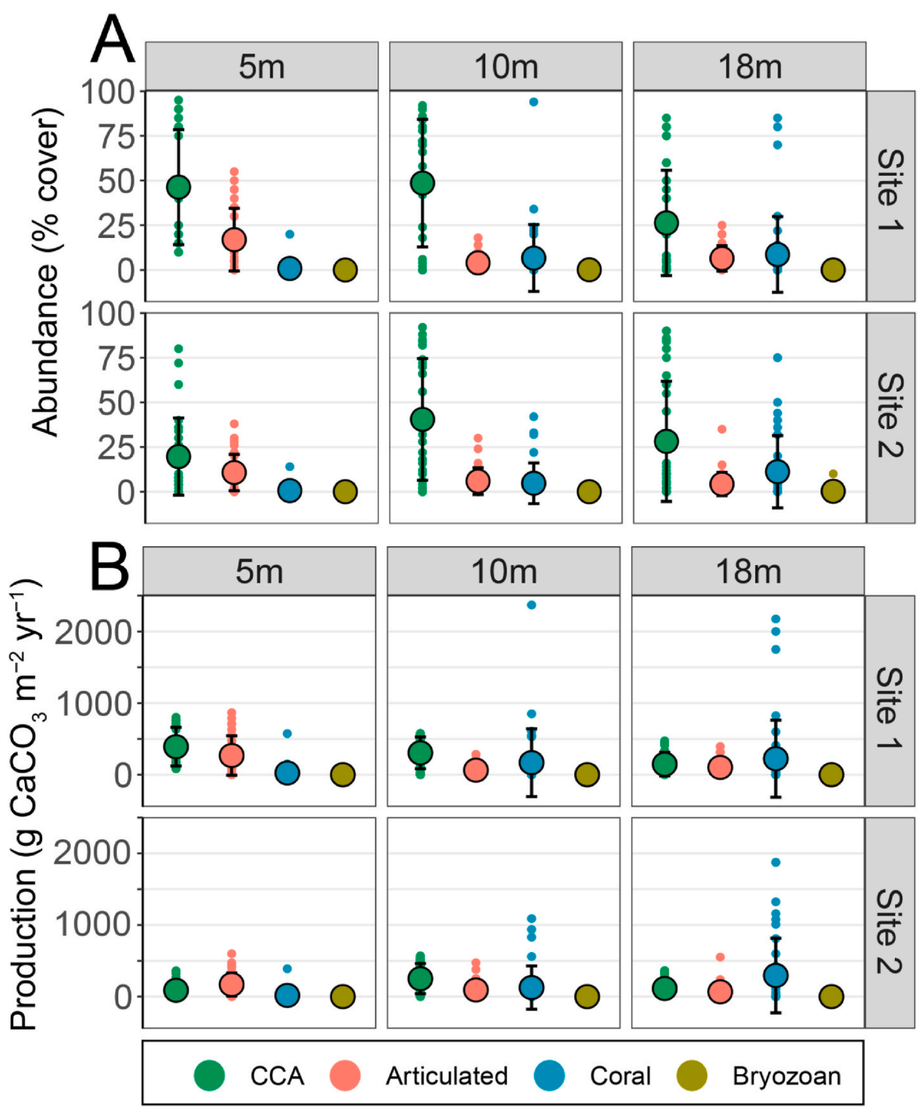

Fig. 4. Abundance (A) and carbonate production (B) of different benthic calcifying groups across depths and sites. Small dots show the quadrat-level abundance (n = 30–40 per site) within each site, while larger dots and error bars denote the mean and standard deviation (SD). CCA refers to crustose coralline algae, whilst articulated refers to articulated coralline algae.

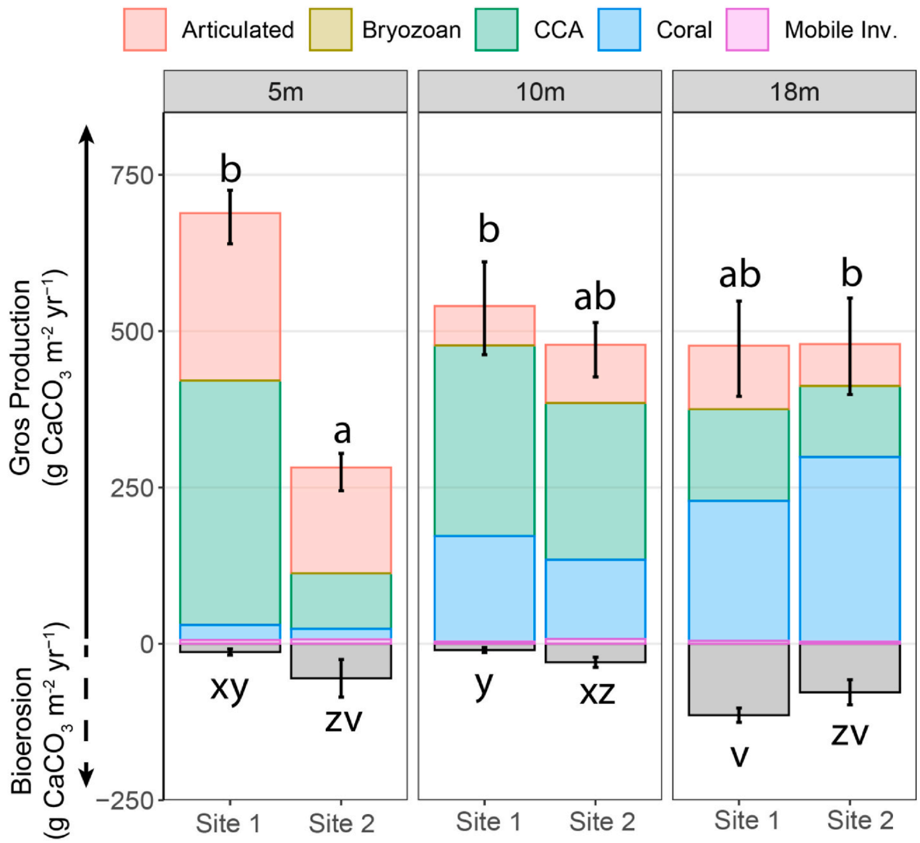

Fig. 5. Total gross carbonate production (positive values) and total erosion (negative values) between sites and depths. Colors indicate the average relative contribution of each calcifying group to total production. Letters denote significant differences between depths and sites (production and bioerosion were examined separately). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

and was largely driven by the abundance of the diadematid sea urchin *C. tenuispinus* (Fig. S5). Bioerosion varied significantly between sites and was significantly different between depths (Table S5), being greatest at the deepest depths (78–114 g $CaCO_3$ m^{-2} yr^{-1} on average) where the abundance of sea urchins was also highest (Fig. 3A).

3.4. Total gross and net production

The total gross production of the studied sites ranged between 9 and 2369 g $CaCO_3$ m^{-2} yr^{-1}, with shallow 5 m depths recording both the lowest (272 ± 30 g $CaCO_3$ m^{-2} yr^{-1}; Site 2) and highest (684 ± 43 g $CaCO_3$ m^{-2} yr^{-1}; Site 1) average production. Overall, total gross production did not vary with depth (Fig. 5, Table S5, GLMM, $p = 0.07$), albeit Site 2 did show significantly lower production in the shallowest depth (significant Depth × Site interaction, GLMM, $p < 0.001$). Average net production ranged from 216 to 671 g $CaCO_3$ m^{-2} yr^{-1}, both recorded at the shallowest depths. Bioerosion removed a minor fraction (4–7 %) of the production at 10m, being more important at depth (23–30 %).

4. Discussion

A longstanding but prevailing view among geologists and ecologists is that biogenic $CaCO_3$ production, and therefore the ecosystem services this function supports, is most prominent in tropical latitudes (Grigg, 1981; O'Mara and Dunne, 2019; Rodgers, 1957), where coral reefs are hotspots of carbonate production and erosion (Chave et al., 1972; Ogden, 1977; Stearn et al., 1977). Although this view was contested early on (Chave, 1967; Smith, 1972), studies quantifying reef carbonate production outside the tropics have remained extremely scarce, preventing a comprehensive evaluation of this assumption. Here, we found that the average seasonal and annual calcification rates of crustose coralline algae (40–82 mg $CaCO_3$ cm^{-2} yr^{1}) and corals (200–299 mg $CaCO_3$ cm^{-2} yr^{1}) in the studied temperate reefs were comparable to those reported from tropical and subtropical locations (Cornwall et al., 2023; Foster et al., 2014). Although calcification rates are often reported to decline at high latitudes (Grigg, 1981; Harriott, 1999; Marsh, 1992; Norzagaray-López et al., 2015), these findings are often location, study, and/or species-specific (e.g., see Ross et al., 2015; Short et al., 2015), with multi-species meta-analyses of calcification often failing to find general patterns between calcification and latitude (Cornwall et al., 2023; Ross et al., 2019). That is likely because calcifying organisms at high latitudes exert strong physiological control of their calcifying fluid to adapt and/or acclimate to their localized thermal regime (Ross et al., 2019).

At the reef scale, average gross carbonate production in south-western Australia ranged between 281 and 688 g $CaCO_3$ m^{-2} yr^{-1}, adding to a growing body of literature that shows carbonate production in temperate reefs is not necessarily negligible (Canals and Ballesteros, 1997; Cebrián et al., 2000; Smith, 1972). These estimates are similar than production in shallow subtropical waters, which is also often dominated by coralline algae (e.g. Abrolhos Bank, Brazil 437–745 g m^{-2} y^{-1}, Reis et al., 2016; Queimada Grande, Brazil, 126 g m^{-2} y^{-1}, Randi et al., 2021) and are within the range of $CaCO_3$ production by rhodolith beds (7–2700 g m^{-2} yr^{-1}; Teed et al., 2020). Our estimates are also comparable to those of marginal coral reefs worldwide (e.g. eastern Pacific 250–430 g $CaCO_3$ m^{-2} yr^{-1}, Norzagaray-López et al., 2015; NW Australia, 620-1100 g $CaCO_3$ m^{-2} yr^{-1}, Dee et al., 2024; Singapore, 620 g $CaCO_3$ m^{-2} yr^{-1}, Januchowski-Hartley et al., 2020) but are about 2–6 times lower than the average of coral reefs in the Indian Ocean (1410 ± 3020; Perry et al., 2018a). Still, the high production rates we found in some areas (up to 2369 g $CaCO_3$ m^{-2} yr^{-1} in quadrats dominated by corals), highlight the importance of further research into temperate carbonate budgets. This is particularly relevant in light of worldwide declines in carbonate production of coral reefs (Cornwall et al., 2021; Davis et al., 2021; Perry et al., 2018a), and potential future gains as corals and other species increase in abundance at temperate latitudes (Price et al., 2019; Sahin, 2023; Yamano et al., 2011; but see Mizerek et al., 2021).

Total gross carbonate production did not show any consistent patterns with depth, although the relative contribution of different calcifying groups did vary markedly. Production in shallow reefs (−10 m) was dominated by coralline algae (68–96 % of the total production), their production declining consistently with depth. This was due to lower abundances of crustose coralline algae at 18 m rather than differences in CCA calcification rates, which showed no consistent trends with depth (Table S2). One possible explanation may be the light regimes under the kelp canopy being similar across depths, or CCA acclimating to low light and being able to compensate growth and calcification (Ju-Hyoung et al., 2013). The algal dominance of shallow temperate carbonate budgets contrasts with tropical budgets, where corals are the primary contributors to gross production (Cornwall et al., 2021; Lange et al., 2020; Perry et al., 2018a). Corals contributed minimally (4–7 %) to total gross production in the budgets of the shallows, but their contribution increased with depth, being highest (58–62 %) at 18 m where coral abundance also peaked. Although corals are widespread across depths along the southwest of Australia (Marsh and Veron, 1988), their establishment and development in the shallows is strongly limited by abrasion by the seaweed canopy (Ribeiro et al., 2022), leading to low abundances in areas where seaweeds dominate (Kato et al., 2018; Mulders et al., 2022; Ribeiro et al., 2022; Ross et al., 2021).

Overall, mobile invertebrates contributed minimally to reef-scale carbonate production, with production being largely dominated by a single species: *Lunella torquata*. Average *L. torquata* densities at our study sites (0.08–0.19 ind. m^{-2}) are in the same range as those previously reported for southwestern Australia (0.1–0.5 ind. m^{-2},Vanderklift and Kendrick, 2004; 0.32 ind. m^{-2}, Wernberg et al., 2008) but relatively lower than elsewhere in Australia (1.1 ind. m^{-2} South Australia, Clarkson and Shepherd, 1985; Eastern Australia, 0.2–7 ind. m^{-2}, Ettinger-Epstein and Kingsford, 2008). The carbonate contribution of this gastropods may thus be more important in other locations, albeit our results suggest this contribution is likely to remain limited to the shallows, where *Lunella* is mostly abundant (see also Ettinger-Epstein and Kingsford, 2008). Other calcifying groups such as bryozoans or sea urchins also contributed minimally to gross carbonate production. Unlike in other temperate reefs, where bryozoans can completely cover the blades of algae and reach biomasses of up to 7 kg m^{-2} (Chave, 1967), epiphytes were not common in the canopy-forming algae of our study area. The total abundance of sea urchins at our study sites (0.05–0.4 ind. m^{-2}) is somewhat lower than other reefs in the study area (0.2 ind. m^{-2}, Thilakrarathna, 2017; 0.2–7 ind. m^{-2}, Vanderklift and Kendrick, 2004), but their small contribution to carbonate production was driven by their slow growth rates, not abundance (Fig. S5).

In contrast, however, sea urchins played a key role in bioerosion, which was largely driven by the diadematid *Centrostephanus tenuispinus*. About a quarter of the carbonate produced at our sites was putatively eroded, with bioerosion rates being greatest at 18 m, where *C. tenuispinus* was more abundant. Sea urchins are likely restricted from shallower reefs due to the whiplash-action of large kelps under the action of heavy ocean swell and a lack of high-complexity substrate, as documented for the eastern Australian species of *Centrostephanus* (*C. rodgersii*; Ling and Keane, 2018; Perkins et al., 2015). In our study location, *C. tenuispinus* is often found in high-relief areas or associated with foliaceous corals in kelp-free areas (authors' pers. obs), which likely offer shelter from predators (Andrew, 1993). Average urchin bioerosion in the studied reefs (10–114 g $CaCO_3$ m^{-2} yr^{-1}) was within the range of western Indian Ocean coral reefs (0–750 g $CaCO_3$ m^{-2} yr^{-1}; (Perry et al., 2018a), despite size-specific bioerosion rates of *C. tenuispinus* (1.4–4.5 g CaCO3 $urchin^{-1}$ day^{-1}; Thilakrarathna, 2017) being somewhat lower than those reported for tropical sea urchins (Perry et al., 2018b; Thilakarathna et al., 2022). The degree to which sea urchins bioeroded the carbonate produced at our study sites will however likely depend on local food availability as well as the type of substratum. Bioerosion rates are higher in areas where *C. tenuispinus* has to actively graze the substrate due to lower availability of standing macroalgae (Thilakrarathna, 2017). This further reinforces the idea that bioerosion is greater at depth, where macroalgae are less abundant (unpubl. data).

The carbonate production rates established in our study are likely to be an underestimate, as important calcifying groups were not included (e.g. foraminifera) or their contribution underestimated due to their cryptic nature (bryozoans, other echinoderms). These groups are often major components of the carbonate sediments encountered around temperate Australia (James et al., 2013; James and Bone, 2011a, 2011b) but their calcification rates are difficult to quantify *in situ* (Smith and Key, 2019). Other census-based carbonate budgets also do not include these groups, however, making our estimates largely comparable to previous studies. Our carbonate production estimates, based on belt transects, do not fully account for the reef's three-dimensional complexity, and the presence of calcifying organisms in cryptic spaces (e.g. CCA in pockets or crevices, Goatley and Bellwood, 2011), therefore yielding underestimates of the total calcifying area of reef. Preliminary surveys using a method that incorporates rugosity (Perry et al., 2018b) suggest that the values presented here are underestimated by 1.2–1.5 times (Pessarrodona & Attlan, unpub. data). On the other hand, the production rates of deeper coral assemblages may be overestimated, as we assumed their calcification was equal to those in shallower water (10 m). Declines in coral growth rates and calcification with depths however are non-uniform and species-specific (Hubbard and Scaturo, 1985; Huston, 1985; Lange et al., 2020), and therefore require further investigation. Another limitation of our study is the use of literature values for articulated coralline algae. Whilst we used data from a congener of the dominant taxa in the study area (*Amphiroa* spp.), establishing *in situ* calcification rates of the different species should be a priority for future research.

Our results have important implications for our understanding of the carbon cycle of kelp forests, and the ongoing debate about the net source or sink nature of kelp and other coastal vegetated ecosystems (Bach et al., 2021; Filbee-Dexter et al., 2023). Calcification releases CO_2 by reducing seawater alkalinity, a process that can partially or fully offset photosynthetic carbon drawdown if that CO_2 reaches the atmosphere (Bach et al., 2021; Kalokora et al., 2020). Most studies to date have found macroalgae forests to be strong net atmospheric CO_2 sinks (see review in Pessarrodona et al., 2023), which suggests that the CO_2 released by calcification is re-fixed in the system (Kalokora et al., 2020) and/or of lower magnitude than the carbon drawn during photosynthesis. Shifts from kelp-dominated states to states dominated by calcifiers—such as sea urchin barrens or coral-dominated seascapes—may however substantially alter this balance, warranting further study of the source/sink dynamics of calcifier-dominanted habitats (Schubert et al., 2024).

Our study establishes a valuable baseline for understanding what a typical carbonate budget looks like in temperate Australian rocky reefs. Australian temperate reefs are experiencing rapid changes however, both in the abundance of the main calcifiers, as well as bioeroders. There has been an increase in the abundance of temperate and tropical coral species along the warmer sections of the southwestern Australian coastline (Marsh, 1992; Ribeiro et al., 2022; Sahin, 2023), likely a result of competitive release following seaweed declines (Ribeiro et al., 2022; Tuckett et al., 2017). Our results suggest that ongoing (Edgar et al., 2023; Wernberg et al., 2016) and future declines in forest-forming seaweeds (Martínez et al., 2018), and concurrent expansions of corals will dramatically increase reef carbonate production. Given that the dominant calcifying mobile invertebrate *L. torquata* is strongly associated with forest-forming seaweeds (Ettinger-Epstein and Kingsford, 2008;

Smoothey, 2013) we can also expect future declines in the contribution of this group. In fact, declines in the abundance of this gastropod have already been recorded after a marine heatwave drove the loss of kelp habitat (Mulders and Wernberg, 2020). Little information is available regarding long-term trends in the abundance of coralline algae, but predictions can be made based on laboratory experiments and well-established canopy-understory interactions (Irving and Connell, 2006). Although most warm-temperate species appear to be resistant and resilient to future warming conditions (Cornwall et al., 2019), crustose corallines are likely to be negatively affected by declines in forest cover (Irving and Connell, 2006). In contrast, articulated corallines will likely be benefited by the decrease in cover and increase in canopy gaps (Irving and Connell, 2006), especially considering abundant species such as *Amphiroa anceps* also appear to be resilient to warming (Mccormack, 2014).

The lack or low abundance of key bioeroding groups (e.g. parrotfishes, boring sponges) in temperate areas suggests bioerosion rates are likely to be low, maintaining positive carbon budgets. Transitions from seaweed forests to sea urchin barrens may change this balance however, with bioerosion rates of up to 1 kg $CaCO_3$ m^{-2} yr^{-1} being recorded in reefs with a superabundance of urchins (Thilakarathna et al., 2022). The densities of some sea urchins in southeastern Australia have increased 75 % over the last 15 years (Ling and Keane, 2018), with the formation of barrens expected to increase in southern temperate Australia and decrease in warmer regions (Davis et al., 2023). In the study area, the key bioeroder *C. tenuispinus* also has increased in recent decades, probably in response to warming (Mulders and Wernberg, 2020; Smale et al., 2017). The expansion of tropical and subtropical parrotfishes in temperate areas is also likely to drive major changes in temperate carbonate budgets (Bennett et al., 2015), although bioerosion by parrotfishes will likely depend on substrate type and availability.

Overall, our results highlight that temperate rocky reefs dominated by seaweed forests can act as important producers of carbonate. The fact that reefs across other areas of temperate Australia have similar abundances of calcifying algae and invertebrates (Edgar et al., 2023; Ettinger-Epstein and Kingsford, 2008; Irving and Connell, 2006) suggests that our findings are likely representative of the Great Southern Reef (Bennett et al., 2016), a system of interconnected rocky reefs stretching through the bottom half of the continent. The carbonate production encountered here is similar to that of other seaweed-dominated temperate reefs worldwide (Southern California, 80–915 g $CaCO_3$ m^{-2} yr^{-1}, Smith, 1972; NW Mediterranean, 290–464 g $CaCO_3$ m^{-2} yr^{-1}, Canals and Ballesteros, 1997; SW Mediterranean, 549-1310 g $CaCO_3$ m^{-2} yr^{-1}, Cebrián et al., 2000), suggesting that temperate seaweed forests may be an overlooked carbonate producing habitat. Importantly the global area of seaweed forests is several times higher than that of more well-studied carbonate producing benthic habitats (e.g. coral reefs, seagrass meadows) (Duarte et al., 2022; Lyons et al., 2024), suggesting temperate $CaCO_3$ factories may be of global relevance, and need to be considered. For instance, assuming that our values are representative of the rest of temperate reefs of southern Australia, gross carbonate production of the Great Southern Reef is about 33.8 Mt yr^{-1} (given a rocky reef area of 71,389 km^2 between 0 and 30 m; Bennett et al., 2016). This compares well with similarly coarse estimates of the reef-scale carbonate production of the Great Barrier Reef, which is estimated to produce ca. 50 Mt yr^{-1} (Vecsei, 2004). The rapidly changing ecology of seaweed forests worldwide thus urges a more detailed understanding of these potentially important carbonate producing habitats, the geo-ecological services that they provide, and how these may change in the future.

CRediT authorship contribution statement

Albert Pessarrodona: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Océane Attlan:** Writing – review & editing, Methodology, Investigation. **Thomas Wernberg:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Albert Pessarrodona reports financial support was provided by Australian Research Council. Oceane Attlan reports financial support was provided by Holsworth Wildlife Research Endowment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107416.

Data availability

Data are available on request to the corresponding author.

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