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Isoprene fluxes from warm temperate and tropical seagrass communities

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ABSTRACT: Isoprene is an important biogenic volatile organic compound (BVOC), with a contribution to annual greenhouse gas emissions similar to that of methane in terms of carbon equivalent. Isoprene is mostly produced by terrestrial vegetation, although marine ecosystems also play an important role in isoprene production. Here, we report isoprene fluxes from warm temperate seagrass communities dominated by specific seagrass species (*Posidonia australis, Zostera muelleri* and *Halophila ovalis*) in Wallis Lake, NSW, Australia, and from tropical seagrass communities (*H. ovalis*/*Halodule uninervis* mixed patches) on Lizard Island, QLD, Australia. *P. australis* and *Z. muelleri* were net isoprene sinks (−0.6 ± 0.1 and −3.4 ± 2.0 nmol m^{-2} h^{-1}, respectively), whereas *H. ovalis* (2.4 ± 0.2 nmol m^{-2} h^{-1}) and mixed patches of *H. ovalis*/*H. uninervis* (13.2 ± 3.2 nmol m^{-2} h^{-1}) were a net source of isoprene, indicating that seagrass communities can be both a source of and a sink for isoprene on a local scale depending on species. Overall, isoprene effluxes were more than 5 times higher on Lizard Island than in Wallis Lake, likely due to higher temperatures and prolonged sunlight on Lizard Island during the time of measurement. Wallis Lake and Lizard Island seagrass communities emit isoprene to the water column at an average rate of −0.3 and 8 mg m^{-2} yr^{-1}, respectively. Seagrass communities are a benthic source of isoprene in coastal waters, but only make a small contribution (2.3 Gg C yr^{-1}) to the global marine isoprene flux (11.6 Tg C yr^{-1}).

KEY WORDS: BVOC · Biogenic volatile organic compound · Benthic incubations · *Zostera* · *Halophila* · *Posidonia* · *Halodule*

1. INTRODUCTION

Isoprene is one of the most important biogenic volatile organic compounds (BVOCs) on the planet, with emissions similar to those of methane in terms of carbon equivalents (Arneth et al. 2007, Menon et al. 2007). Isoprene is climatically important, with about 50% of secondary organic aerosol (SOA) formation in the atmosphere being due to isoprene photooxidation (Claeys et al. 2004, Liao et al. 2007). The hydroxy-driven oxidation of isoprene enhances particle growth and increases the capacity of aerosols to act as cloud condensation nuclei (CCN), causing a negative feedback loop in sea surface warming via the production of low-level shading clouds (Claeys et al. 2004, Meskhidze & Nenes 2006). On the other hand, in terrestrial environments isoprene derived SOAs have the potential to influence cirrus cloud formation, potentially causing a net warming effect on global climate (Wolf et al. 2020). Isoprene has also been found to play a key role in the formation of tropospheric O_3 in the presence of nitrous oxide (NO_x) in polluted air (Fehsenfeld et al. 1992, Pierce et al. 1998, Li et al. 2007). As a result, isoprene not only contributes to O_3 formation in the troposphere, leading to enhanced greenhouse effect, but also serves as a sink for oxidants in the marine boundary layer, which increases the residence time of greenhouse gases such as carbon

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monoxide and methane, ultimately leading to global warming (Poisson et al. 2000). It remains unclear to what degree isoprene oxidation in the atmosphere contributes to warming and cooling on a global scale.

While isoprene has traditionally been considered a terrestrial gas, with 90% of the isoprene on Earth being released into the atmosphere by vegetation (Guenther et al. 1995), it is now well established that marine ecosystems also play an important role in isoprene production (Alcuna Alvarez et al. 2009, Arnold et al. 2009, Exton et al. 2013). In the open ocean, algal biomass drives isoprene production (Bonsang et al. 1992, Yokouchi et al. 1999), whereas in shallow, benthic marine habitats close to the coast, microbial communities are the major drivers of isoprene concentrations (Alcuna Alvarez et al. 2009, Shaw et al. 2010, Exton et al. 2012).

Isoprene production is strongly positively correlated with increases in temperature and light (Monson & Fall 1989, Shaw et al. 2003, Broadgate et al. 2004), with isoprene emissions metabolically linked to photosynthesis (Monson et al. 1992, Guenther et al. 1995, Dani et al. 2017). Terrestrial studies have identified that the rate of isoprene emissions increases exponentially with temperature before reaching a clearly defined plateau at temperatures higher than 30°C, demonstrating high sensitivity to temperatures between 25 and 30°C in terrestrial systems (Guenther et al. 1993, Pugh et al. 2013). Other drivers of isoprene production include abiotic stressors such as droughts and oxidative stress (Velikova et al. 2006, Sharkey et al. 2008, Loreto & Schnitzler 2010). However, although nitrogen and phosphorus have been linked to an increase in productivity and growth in seagrass (Udy et al. 1999, Eyre & Ferguson 2002, Eyre et al. 2011b), nutrient availability has yet to be definitively linked to isoprene production (Shaw et al. 2010), with varying results from previous studies (Evans 2009, Zindler et al. 2014).

To date, isoprene has been found in a variety of marine systems, with phytoplankton being one of the main marine isoprene producers in the ocean (Broadgate et al. 1997, Baker et al. 2000, Shaw et al. 2003). Isoprene production has also been measured from macroalgae (McKay et al. 1996, Broadgate et al. 2004), cyanobacteria (Lindberg et al. 2010), intertidal benthic microalgae (Exton et al. 2012), microbial communities (Alcuna Alvarez et al. 2009), coral-associated *Symbiodinium* (Exton et al. 2013), coral mucus (Swan et al. 2016), and coral reef carbonate sediments with microphytobenthos (MPB) (Hrebien et al. 2020b). Isoprene production has been found to be species dependent in seaweed (Broadgate et al. 2004) and provides a source of carbon and energy to marine heterotrophic bacteria (Alcuna Alvarez et al. 2009).

Seagrasses are highly productive per unit area, constituting a key habitat for many marine organisms (Hughes et al. 2003). Seagrass beds are extremely complex ecosystems, with a great diversity and abundance of epiphytes composed mainly of microscopic algae (Moncreiff et al. 1992), and a benthic microflora composed mostly of pennate diatoms (Daehnick et al. 1992) and a rich microbial community, which combined are referred to as the seagrass MPB. All seagrass bed components contribute significantly to the primary production and autotrophic biomass of these communities (Borum et al. 1984, Moncreiff et al. 1992). Epiphytic algal biomass can equal or exceed that of the seagrass leaves (Moncreiff et al. 1992), ranging from 1 to 68% of the total leaf surface area (Borum et al. 1984), and can contribute up to a 56% increase in primary productivity within a seagrass bed (Morgan & Kitting 1984). Since microalgae, diatoms, and bacteria can all produce isoprene, seagrass communities are expected to be a source of isoprene in the marine environment. However, there has been no measurement of benthic isoprene flux in seagrass communities to date.

In this study, we thus aimed to measure isoprene flux from seagrass communities dominated by 4 species (*Zostera muelleri*, *Posidonia australis, Halophila ovalis*, and *Halodule uninervis*) from both tropical (Lizard Island) and warm temperate (Wallis Lake) locations along the east Australian coast using benthic chamber deployments. Since temperature and, to a lesser extent, sunlight are known environmental drivers of isoprene production, we hypothesised that isoprene fluxes would be greater during the day than at night, with higher concentrations and fluxes at the tropical site than at the warm temperate site. Furthermore, shallow coastal marine habitats have the potential to endure dramatic temperature changes over the course of a day (Hancke & Glud 2004), which will potentially lead to greater isoprene fluctuations. Because isoprene production has been detected in carbonate sands on Lizard Island (Hrebien et al. 2020b), it was expected that seagrass habitats within carbonate sediments would produce more isoprene as they become vegetated by seagrass and other isoprene producing organisms within the community. It was also expected that increased nutrients would lead to greater seagrass primary productivity and therefore increase isoprene production as a result. Given that seagrass beds constitute an interface between the terrestrial and marine world and 90% of isoprene emissions are

sourced terrestrially, we hypothesised that seagrass communities make a significant contribution to global marine isoprene fluxes.

2. MATERIALS AND METHODS

2.1. Study sites

The first study was conducted from 13 to 20 March 2018 (early autumn) in Wallis Lake, Forster, NSW, Australia. This shallow, warm temperate, coastal lagoon is located approximately 360 km north of Sydney, NSW (Fig. 1) and has seawater temperatures ranging from 23 to 26°C in the summer and 18 to 20°C in the winter (BOM 2019). Wallis Lake has an open water area of 90 km^2 with 33 km^2 (37%) seagrass coverage, a mean depth of 1.8 m (Eyre & Maher 2010, Maher & Eyre 2012, Eyre et al. 2016) with a semi-diurnal tidal range of 2 m, and a net production of 55 g C m^{-2} yr^{-1} (Maher & Eyre 2011). A detailed description and map of the estuary is provided in Eyre & Maher (2010). Sampling occurred within 50 m of the mainland shore along a concrete jetty behind Miles Island (32° 11′ 09.2″ S, 152° 30′ 39.3″ E; Fig. 1A, D,E). The sampling location was chosen due to the presence of adjacent seagrass communities, which were visually assessed as ecologically healthy (thick canopy cover, aboveground biomass visually rich in chlorophyll, evidence of new growth present, and presence of epiphytes). Measuring within the same location ensured that environmental conditions such as depth, light, and water movement varied minimally between species. This sheltered location also ensured optimal conditions for benthic chamber deployments. Consecutive chamber incubations were conducted over 4 communities containing densely vegetated areas of *Zostera muelleri* and *Posidonia australis,* lightly vegetated *Halophila ovalis* (Fig. 2A–C, respectively), and non-vegetated bare sediments (not pictured) (Dekker et al. 2003, Maher & Eyre 2010). Three chamber replicates over each substrate type and one blank chamber were used for each incubation period. *Z. muelleri* have an aboveground biomass (mean + SE) of 69.1 ± 40.7 g dry wt m^{-2}, belowground biomass of 38.2 ± 24.0 g dry wt m^{-2} and a sediment porosity of 0.66 ± 0.01 (vol:vol); *P. australis* have an aboveground biomass of 25.6 ± 3.8 g

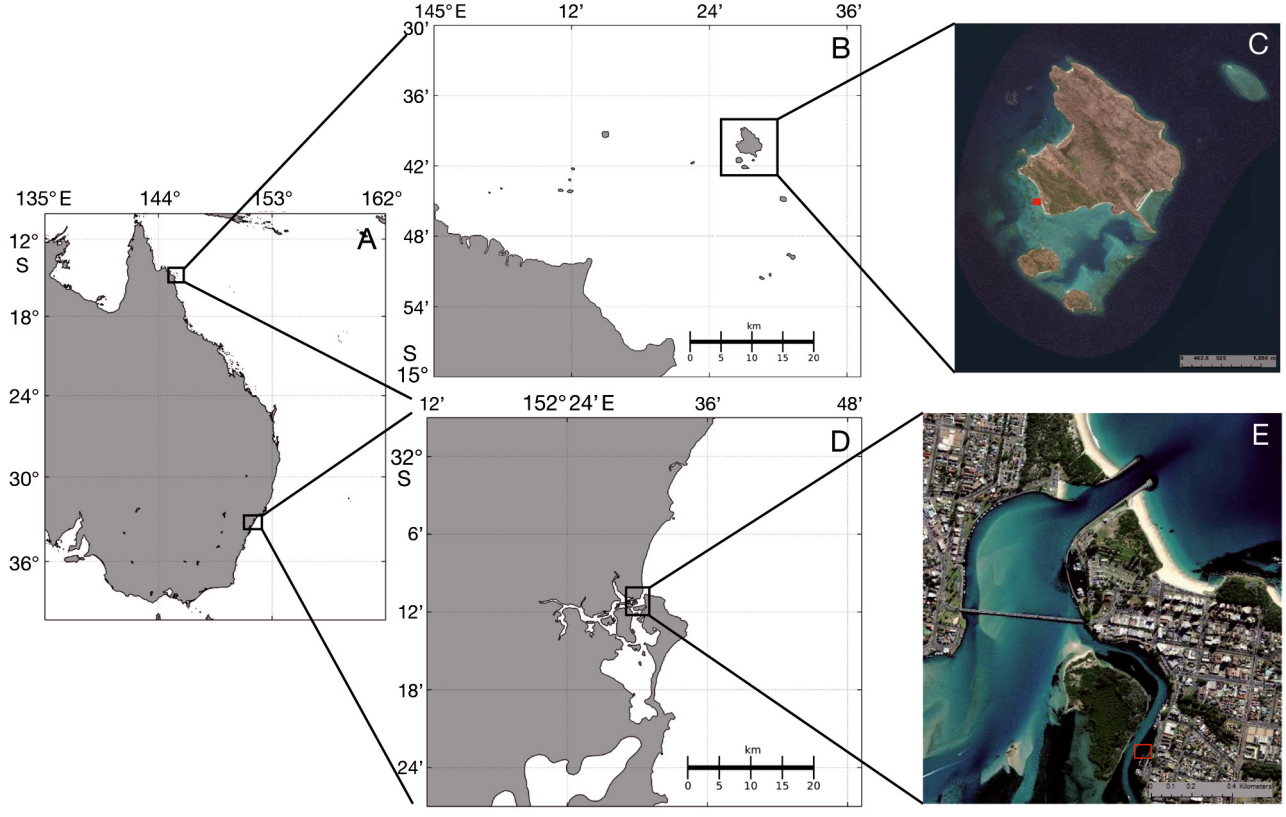

Fig. 1. Location of (A–C) Lizard Island, QLD (14° 40′ 36.6″ S 145° 26′ 48.4″ E) and (A, D–E) Wallis Lake, NSW (32° 11′ 09.2″ S, 152° 30′ 39.3″ E) in Australia. Study sites are indicated by red boxes in panels C and E

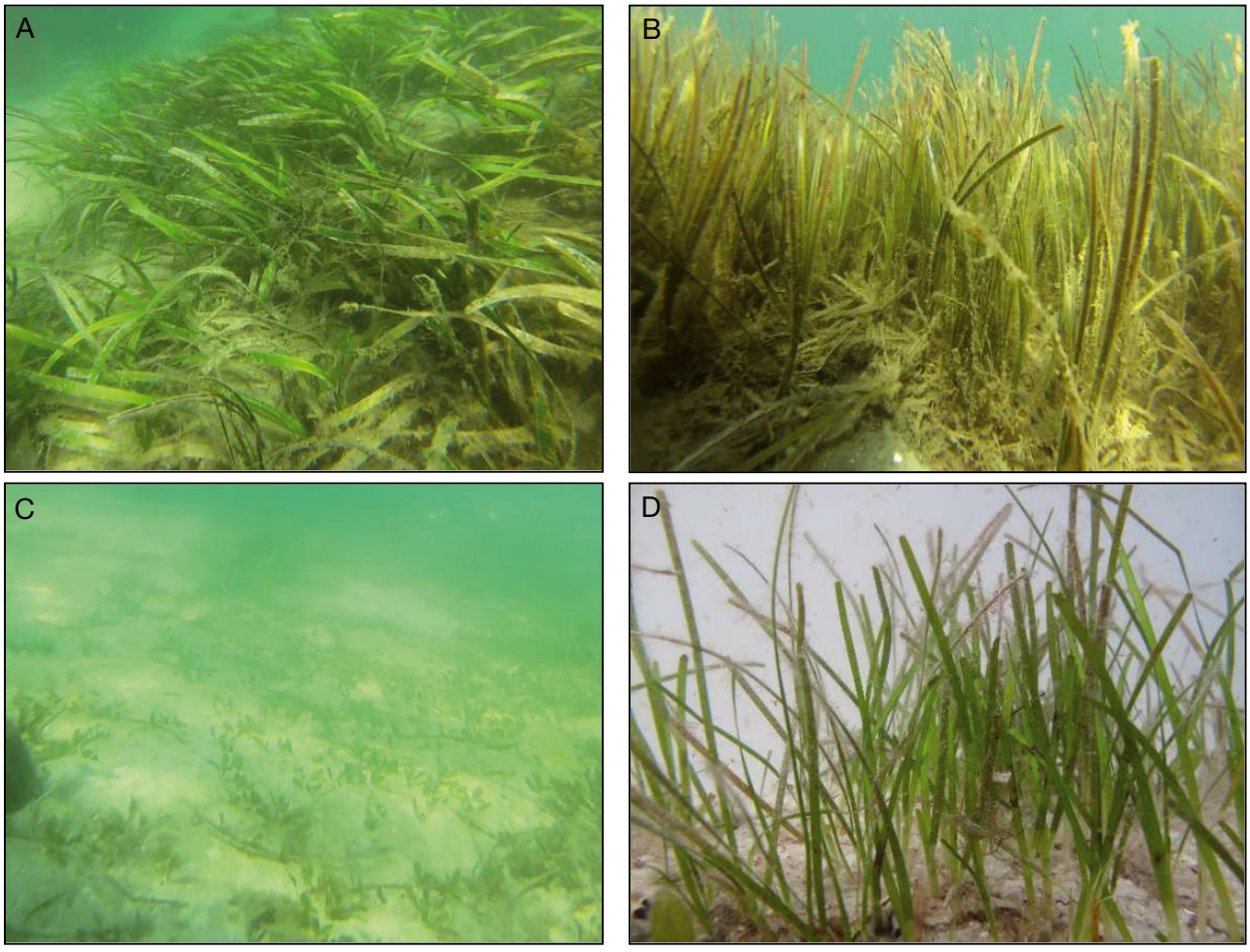

Fig. 2. Photos of seagrass beds used for benthic chamber deployments at (A–C) Wallis Lake, NSW and (D) Lizard Island, QLD. (A) *Posidonia australis*, (B) *Zostera muelleri*, (C) *Halophila ovalis*, and (D) mixed seagrass patch containing *H. ovalis* and *Halodule uninervis*

dry wt m^{-2}, belowground biomass of 44.8 ± 9.7 g dry wt m^{-2} and a sediment porosity of 0.63 ± 0.06 (vol:vol); and *H. ovalis* have an aboveground biomass of 2.4 ± 0.1 g dry wt m^{-2}, belowground biomass of 2.4 ± 0.3 g dry wt m^{-2} and a sediment porosity of 0.44 ± 0.05 (vol:vol) (Camillini 2020). Biomass was measured in Wallis Lake at the time of this study.

All seagrass communities contained MPB and epiphytes and the bare sediments were covered in plant detritus and MPB (visual observation, Fig. 2).

The second study was conducted from 27 to 28 October 2018 (mid spring) within the Lizard Island Group, located 270 km north of Cairns, QLD, northern Great Barrier Reef, Australia (Fig. 1). Located in a tropical climate, with average seawater temperature of 24°C in the winter and 29°C in the summer (AIMS 2020), the Lizard Island National Park area covers 150 km^2 with 0.18 km^2 (1.2%) seagrass coverage (Saunders et al. 2015). Net production of C m^{-2} yr^{-1} has not yet been determined. The Lizard Island Group (from here on referred to as Lizard Island) is situated between the coast and outer barrier reef on the mid continental shelf and is made up of 4 granite islands surrounded by fringing reefs. Together, these islands enclose a lagoon reaching up to 10 m in depth with a semi-diurnal tidal range of 3 m. The lagoon is comprised of patch reefs and seagrass meadows mainly dominated by *Halophila* species *H. ovalis*, *H. spinulosa*, and *H. decipiens*, with partial coverage of *Thalassia hemprichii* and *Halodule uninervis* in shallow water (York et al. 2018). A single species habitat comparable to Wallis Lake was not available on Lizard Island at the time of sampling; therefore, sampling occurred within 50 m of shore off the southwestern side of the main Lizard Island (14° 40′ 36.6″ S 145° 26′ 48.4″ E;

Fig. 1A–C) over a mixed seagrass patch containing *H. ovalis* (visually estimated as 40% of the patch measured) and *H. uninervis* (visually estimated as 60% of the patch measured). This location ensured a similar depth to that of Wallis Lake (~1.8 m), which would provide similar conditions for light availability and water movement. Bare sediments adjacent to the seagrass were not measured due to permit and time constraints. Although plant detritus and MPB were present, this seagrass bed had relatively clean leaves (few epiphytes; Fig. 2D) in comparison with Wallis Lake (Fig. 2A–C). The sediments at the study site were fine carbonate sand and mud (McKenzie et al. 1997). Mixed patches of *H. ovalis* and *H. uninervis* on Lizard Island measured mid-spring had an aboveground biomass of 2.7 ± 2.8 g dry wt m^{-2} and belowground biomass of 6.5 ± 3.8 g dry wt m^{-2} (Saunders et al. 2015). Biomass and sediment porosity were not measured at the time of the study due to permit constraints.

Due to logistical constraints, sampling at similar times of the year was not possible; however, based on gross and net photosynthesis, intermediate seasons (spring and autumn) are more representative of averaged conditions than summer or winter, due to the higher respiration rates associated with summer temperatures (Dennison 1987). Since isoprene production is linked to photosynthesis, it is thus likely that intermediate seasons also represent average conditions in terms of isoprene emission.

2.2. Chamber incubations

Benthic isoprene fluxes were measured using 55 l benthic flume-chambers (Eyre et al. 2011b, Camillini et al. 2021). Briefly, Perspex chambers with rounded ends, 680 × 300 × 300 mm, and sediment surface area of 0.08 m^2 were used in triplicate over seagrass beds or bare sediments (Fig. 3). Lateral flow across the seagrass was produced using an inflow bar positioned 1 cm from the lid on one end and a parallel outflow bar located 1 cm from the bottom of the chamber on the other side. A pump with regulated flow was attached to each inlet and outlet via 5 m hoses to produce a closed-circuit lateral flow at 5 l min^{-1} across the seagrass community, mimicking *in situ* flows. The flow rate was chosen based on average current velocities within seagrass beds (Koch & Gust 1999, Heiss et al. 2000). Chambers were placed over each of the seagrass communities or bare sediment sites in direct sunlight and left open for about 3 h with circulating flow to allow for the sediments and seawater profile to settle before sealing the chambers. Great care was taken not to step on the seagrass bed as the chambers were placed. Collapsible 20 l bags were filled with *in situ* seawater at the time of chamber deployment and attached to the chambers to ensure that the same ambient seawater replaced water removed during sampling. Water was also collected from a blank bag to account for changes in water chemistry over time. One hour prior to sampling, chambers were sealed

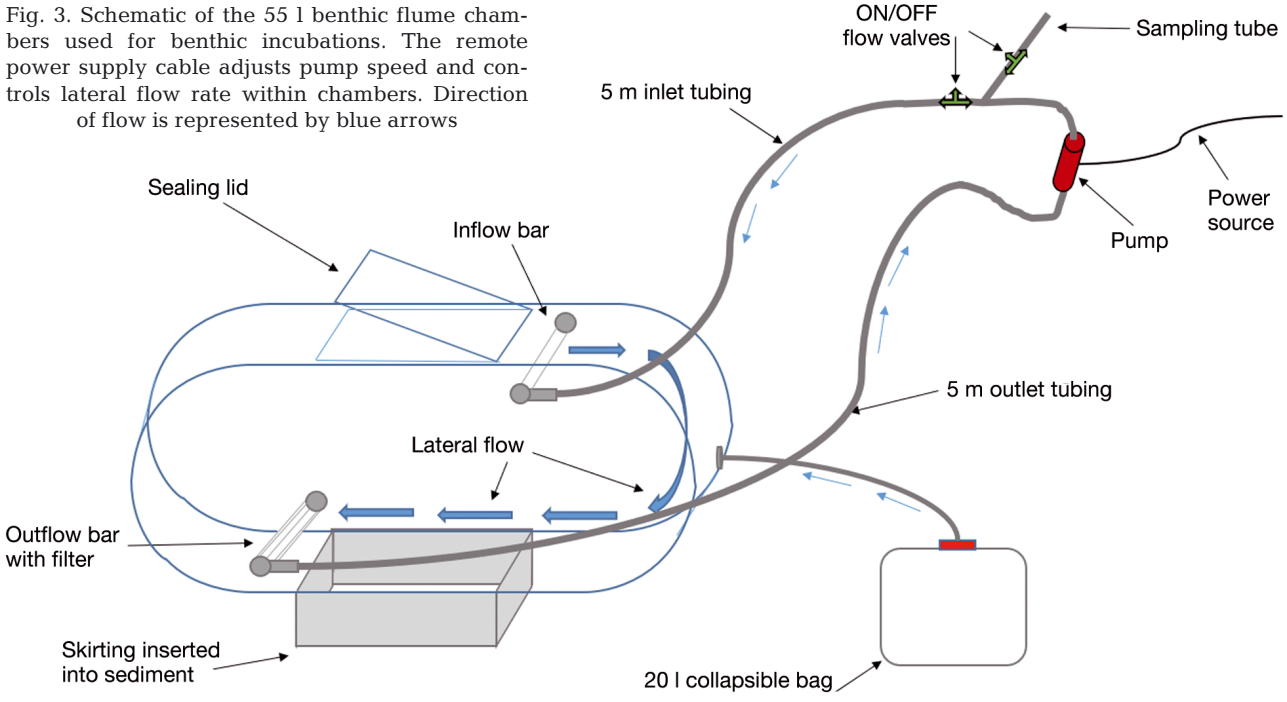

Fig. 3. Schematic of the 55 l benthic flume chambers used for benthic incubations. The remote power supply cable adjusts pump speed and controls lateral flow rate within chambers. Direction of flow is represented by blue arrows

ensuring no bubbles were trapped inside the chambers. A blank chamber with a false bottom containing only seawater was used as an incubation control to remove production from phytoplankton and other isoprene producing organisms in the water column (Fig. A1 in the Appendix). Chambers were sampled every 4 h for 24 h over a diel cycle.

2.3. Sampling

Three chambers were deployed and sampled over each seagrass community and one blank chamber with a false bottom containing only water was deployed for each sampling period. Water samples were collected from each chamber by slowly filling 450 ml amber glass Schott bottles to the top from a T-piece outlet placed upstream of the water pumps. Sub samples for all parameters and physico-chemical measurements were taken from the 450 ml bottles. At Wallis Lake, all samples were preserved immediately following sampling; however, on Lizard Island, all sample bottles were transported to the Lizard Island Research Station in a water bath to ensure temperature was maintained at *in situ* conditions, and preserved within 45 min of collection.

Isoprene samples were collected by extracting 70 ml of seawater from the 450 ml sample bottles, which was syringed into 100 ml amber glass sample bottles using a glass syringe mounted with Teflon tubing to ensure that sample bottles were filled from bottom up without bubbles. Sample bottles were immediately sealed with aluminium crimp top caps with Teflon septa (PTFE/S, Agilent Technologies). All isoprene samples were treated with 150 µl $HgCl_2$ using a needle syringe and stored in the dark at 4°C. Nutrient samples were collected from the 450 ml bottles as follows: two 10 ml nutrient samples were collected into 15 ml centrifuge tubes after filtering using 0.45 µM cellulose acetate syringe filters and frozen at −20°C until analysis. Temperature (± 0.1°C) and dissolved oxygen (DO; ± 0.01 mg l^{-1}) of each 450 ml sample bottle were measured using a Hatch HQ 30d meter and Luminescent DO probe. Additionally, temperature (°C) in Wallis Lake was also recorded using a Hydrolab HL4 Multiparameter Sonde (OTT HydroMet) every 15 min for the duration of each incubation. Photosynthetic active radiation (PAR) was recorded every 10 min within all chambers using HOBO loggers (UA-002-64) on Lizard Island (13 h light:11h dark cycle) and Wallis Lake (12 h light:12 h dark cycle). HOBO Lux units were calibrated using a Li-Cor-192 light meter to convert to µmol photons m^{-2} s^{-1} (Camillini 2020). Light data for *P. australis* is not available due to logger being shaded by the leaves within the chamber.

2.4. Analytical methods

2.4.1. Isoprene and nutrient analysis

Isoprene analysis was conducted within 30 d of collection by gas chromatography using cumulative headspace injections (Hrebien et al. 2020a). Briefly, isoprene samples were analysed on a gas chromatograph (GC; Agilent Technologies 6890N) coupled with a mass selective detector (MSD; Agilent Technologies 5973N) and a multipurpose sampler (MPS; Gerstel 2XL) set up with a 2.5 ml syringe. The was operated in selective ion mode (SIM) mode with selected ion mass of 67, 68, and 53. Prior to measuring samples, a 6 point calibration ranging from 29 to 1429 pM was performed onto the GC using isoprene standard (Sigma Aldrich; Ref 59240). The precision (coefficient of variation; CV) for this method is 2.6% for natural samples, accuracy based on recovery is 74–84%, and detection limit is 15 pM.

Nutrient samples of ammonium (NH_4^+) and phosphate (PO_4^{3-}) were analysed using a Lachat flow injection analysis system; details of the methods, errors and detection limits are described in McKee et al. (2000).

2.4.2. Benthic flux calculations

Net flux for isoprene and nutrients (nmol m^{-2} h^{-1}) was calculated using the following equation:

$$F = \frac{\Delta S \times v}{A \times \Delta t} \quad (1)$$

where ΔS is the change in solute concentration corrected for the addition of replacement water (nmol l^{-1}):

$$S = [[\text{initial concentration} \times \text{chamber volume (l)}] - [\text{volume withdrawn (l)} \times \text{blank concentration}]] / [\text{chamber volume (l)} - \text{volume withdrawn (l)}] \quad (2)$$

and v is the volume of the chamber (l), A is the chamber surface area (m^2), and Δt is the time elapsed between samples (h). Dark benthic fluxes were calculated using concentrations from dusk to dawn (19:00–06:00 h in Wallis Lake and 18:00–06:00 h on Lizard Island), while light benthic fluxes were calculated using concentrations from dawn to dusk (06:00–19:00 h in Wallis Lake and 06:00–18:00 h on Lizard Island) the following day.

2.4.3. Benthic metabolic rates

Benthic metabolic rates for respiration (R), net primary productivity (NPP), gross primary productivity (GPP), and production to respiration ratio (P:R) were calculated based on DO fluxes (mmol O_2 m^{-2} h^{-1}), using the following equations (Eyre et al. 2011b):

$$R = \text{Dark DO flux} \times -1 \quad (3)$$

$$NPP = \text{Light DO flux} \quad (4)$$

$$GPP = NPP + R \quad (5)$$

$$P{:}R = GPP \times \text{daylight h} / (R \times 24) \quad (6)$$

2.4.4. Statistical analysis

Data was analysed using a univariate general linear model (GLM) with Bonferroni adjustment for multiple comparisons ($\alpha = 0.05$) to look at differences between species and locations (SPSS statistics 26). When referring to locations, Wallis Lake includes all species present (*P. australis, Z. muelleri*, and *Halophila ovalis*), while Lizard Island includes the single mixed patch measured (*H. ovalis* and *Halodule uninervis*). Prior to analysis, dependent variables (light, dark, and net isoprene fluxes; R, NPP, GPP, and P:R; and light, dark, and net nutrient fluxes) were tested for normality using a Shapiro-Wilks test and data that were not normally distributed ($p < 0.05$) were transformed. Isoprene and R were reciprocal ($1/x$) transformed and PO_4^{3-} was square (x^2) transformed. All other data (NH_4^+, NPP, GPP, P:R) were normally distributed. Light and dark measurements were analysed using an unpaired *t*-test. Correlations between data were determined using a linear regression model.

3. RESULTS

3.1. Temperature and light

Temperature was significantly higher on Lizard Island (mid-spring) than in Wallis Lake (mid-fall) for all incubations (Table 1; unpaired *t*-test, $t_{df} = 160$, $p < 0.01$). Likewise, light was significantly greater on Lizard Island than in Wallis Lake during the *Zostera muelleri* incubation (Fig. 4; $t_{df} = 286$, $p = 0.005$). Over 24 h there was no significant difference between light intensities during the *Halophila ovalis* incubation in Wallis Lake and the incubation on Lizard Island. However, PAR was significantly greater for the first 5 h of sunlight on Lizard Island ($t_{df} = 58$, $p = 0.03$) than during the *H. ovalis* incubation in Wallis Lake and remained significantly higher between the hours of 14:00 and 16:00 ($t_{df} = 22$, $p = 0.01$).

3.2. Nutrients, PO_4^{3-} and NH_4^+

H. ovalis communities produced significantly more PO_4^{3-} in the dark (mean ± SE: 2.3 ± 0.7 µmol m^{-2} h^{-1}) than in the light (−1.7 ± 0.1 µmol m^{-2} h^{-1}; Fig. 5E; $t_{df} = 16$, $p = 0.01$) and *Z. muelleri* communities produced

Table 1. Sea surface temperature ranges (°C) for each study location measured *in situ* and historically (Lizard Island: 2014–2020; Wallis Lake: 2014–2019)

Location	Range (± 0.1°C)	Mean (°C)	Historical range (°C)	Source
Wallis Lake, NSW	22.4–26.4	24.5	18–20 (winter) 23–26 (summer)	(BOM 2019)
Lizard Island, QLD	26.1–30.5	27.9	23–25 (winter) 29–31 (summer)	(AIMS 2020)

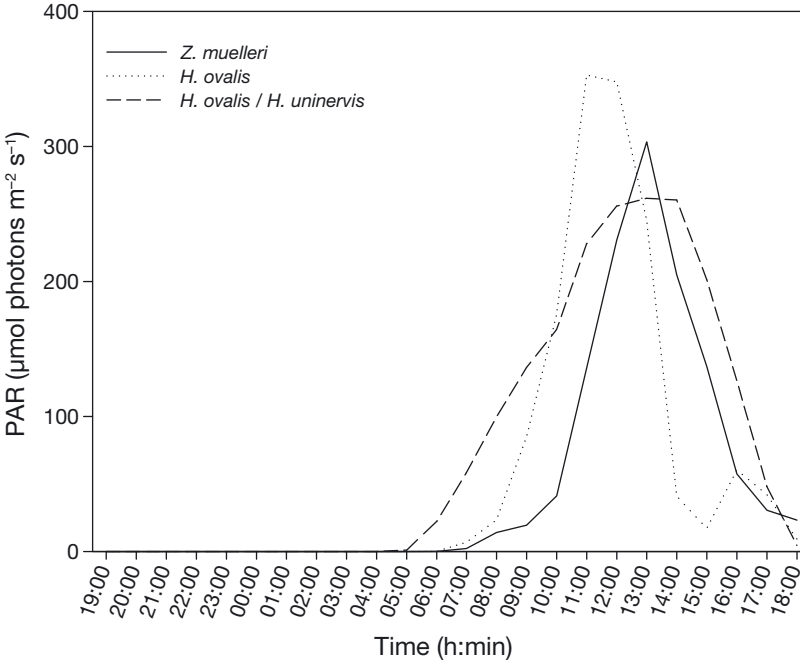

Fig. 4. PAR (photosynthetic active radiation; µmol photons m^{-2} s^{-1}) for *Zostera muelleri* and *Halophila ovalis* in Wallis Lake and the mixed patch of *H. ovalis* and *Halodule uninervis* on Lizard Island

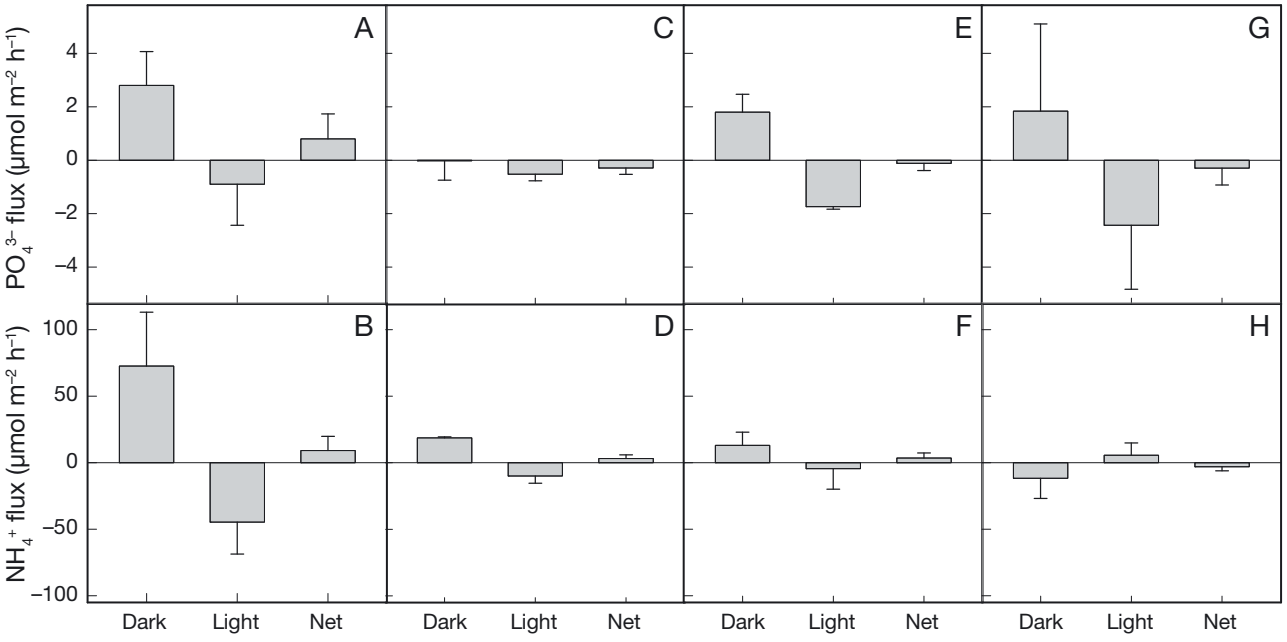

Fig. 5. Mean light, dark, and net PO_4^{3-} and NH_4^+ fluxes from (A,B) *Posidonia australis*, (C,D) *Zostera muelleri*, and (E,F) *Halophila ovalis* in Wallis Lake, and (G,H) a mixed seagrass patch of *H. ovalis* and *Halodule uninervis* on Lizard Island. Three chambers were deployed and sampled for each seagrass community. Error bars indicate SE

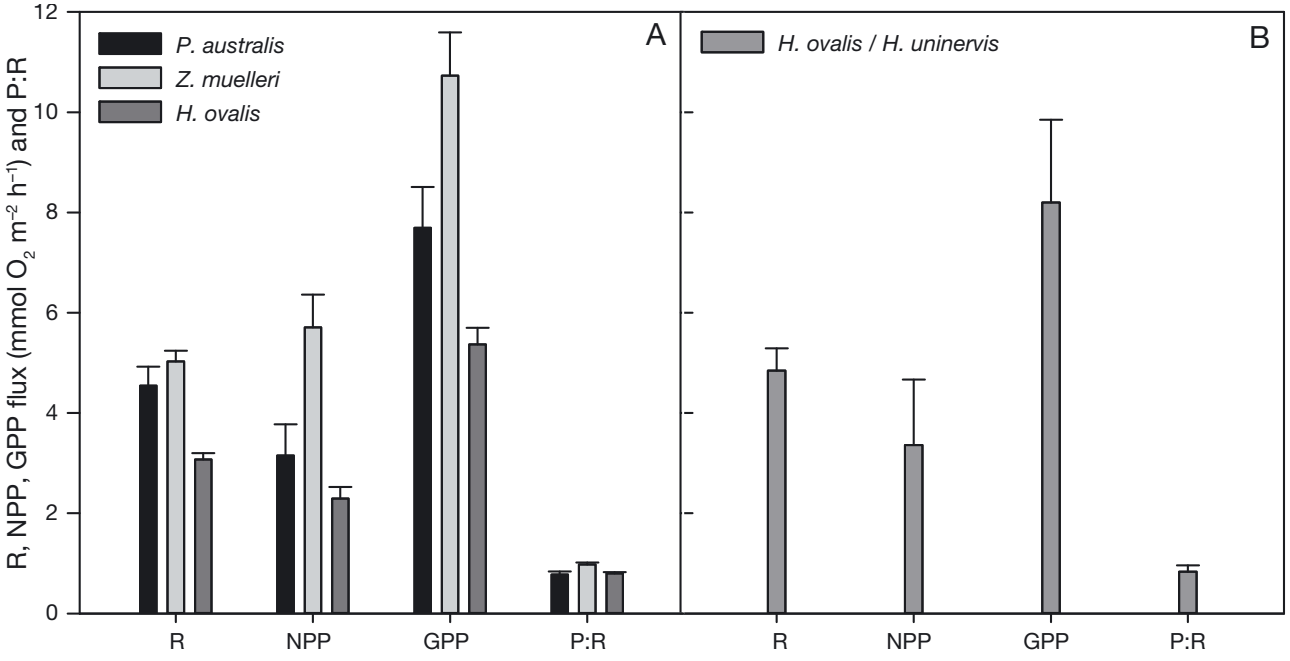

Fig. 6. Mean respiration (R), gross primary production (GPP), net primary production (NPP), and photosynthesis to respiration ratio (P:R) over (A) *P. australis*, *Z. muelleri*, and *Halophila ovalis* at Wallis Lake and (B) a mixed seagrass community containing *H. ovalis* and *Halodule uninervis* on Lizard Island. Three chambers were deployed and sampled for each seagrass community. Error bars indicate SE

significantly more NH_4^+ in the dark (18.7 ± 0.7 µmol m^{-2} h^{-1}) than in the light (–9.9 ± 5.4 µmol m^{-2} h^{-1}; Fig. 6D; t_{df} = 16, $p < 0.01$) in Wallis Lake. There were no significant differences in nutrient production between any other species in Wallis Lake or Lizard Island. Water column nutrient concentrations were on average 0.23 µmol l^{-1} for PO_4^{3-} and 0.16 µmol l^{-1} for NH_4^+ in Wallis Lake, and 0.05 µmol

l^{-1} for PO_4^{3-} and 0.87 µmol l^{-1} for NH_4^+ on Lizard Island (average of all open water samples taken during measurements).

3.3. Respiration and photosynthesis

Halophila ovalis beds had significantly lower R than *P. australis* and *Z. muelleri* in Wallis Lake and mixed seagrass *H. ovalis* and *Halodule uninervis* on Lizard Island (Fig. 6A,B; GLM, $F = 7.75$, $p = 0.02$, $p = 0.02$, $p = 0.03$, respectively). In Wallis Lake, GPP was also significantly greater in *Z. muelleri* than in *H. ovalis* communities (GLM, $F = 4.57$, $p = 0.04$, respectively) and NPP was significantly greater in *Z. muelleri* beds than *H. ovalis* and *P. australis* beds (GLM, $F = 7.71$, $p < 0.01$, $p = 0.04$). There was no significant difference between NPP on Lizard Island and any species in Wallis Lake and P:R was not significantly different between species or sites (Fig. 6A–C; GLM, $p > 0.05$).

3.4. Isoprene flux

In Wallis Lake, there were light, dark, and net isoprene effluxes from the benthic community to the water column for *Halophila ovalis* and bare sediments, and light isoprene effluxes for *P. australis* and *Z. muelleri*. There were dark and net isoprene uptakes for *P. australis* and *Z. muelleri* (Fig. 7A). In Wallis Lake, *Z. muelleri* produced significantly more isoprene in the light (mean (±SE) 0.9 ± 1.4 nmol m^{-2} h^{-1}) than in the dark (–8.6 ± 3.0 nmol m^{-2} h^{-1}; $t_{df} = 4$, $p = 0.05$) while *H. ovalis* produced significantly more isoprene in the dark (5.6 ± 0.6 nmol m^{-2} h^{-1}) than in the light (0.5 ± 0.5 nmol m^{-2} h^{-1}; $t_{df} = 4$, $p < 0.01$). No other species showed significant differences between light and dark isoprene fluxes, nor were there any significant differences in isoprene flux between species in Wallis Lake. Bare sediments showed no change between light, dark or net isoprene flux (for all comparisons, $t_{df} = 4$, $p = 1.00$); furthermore, errors for all bare sediment measurements were greater than the flux, indicating they were not significantly different from zero.

On Lizard Island, there were light, dark, and net isoprene effluxes in the mixed seagrass beds of *H. ovalis* and *Halodule uninervis* (Fig. 7B). Lizard Island net isoprene fluxes (mean ±SE) 13.2 ± 3.2 nmol m^{-2} h^{-1}) were significantly higher than all net isoprene fluxes across all species measured in Wallis Lake (GLM, $f = 14.287$, $p < 0.01$). While not significant, the highest dark and light isoprene fluxes were observed on Lizard Island, ranging from –6.5 to 17.0 nmol m^{-2} h^{-1} (mean ±SE) 7.4 ± 7.1 nmol m^{-2} h^{-1}) and 0.72 to 29.3 nmol m^{-2} h^{-1} (19.0 ± 9.2 nmol m^{-2} h^{-1}) respectively (Fig. 7B).

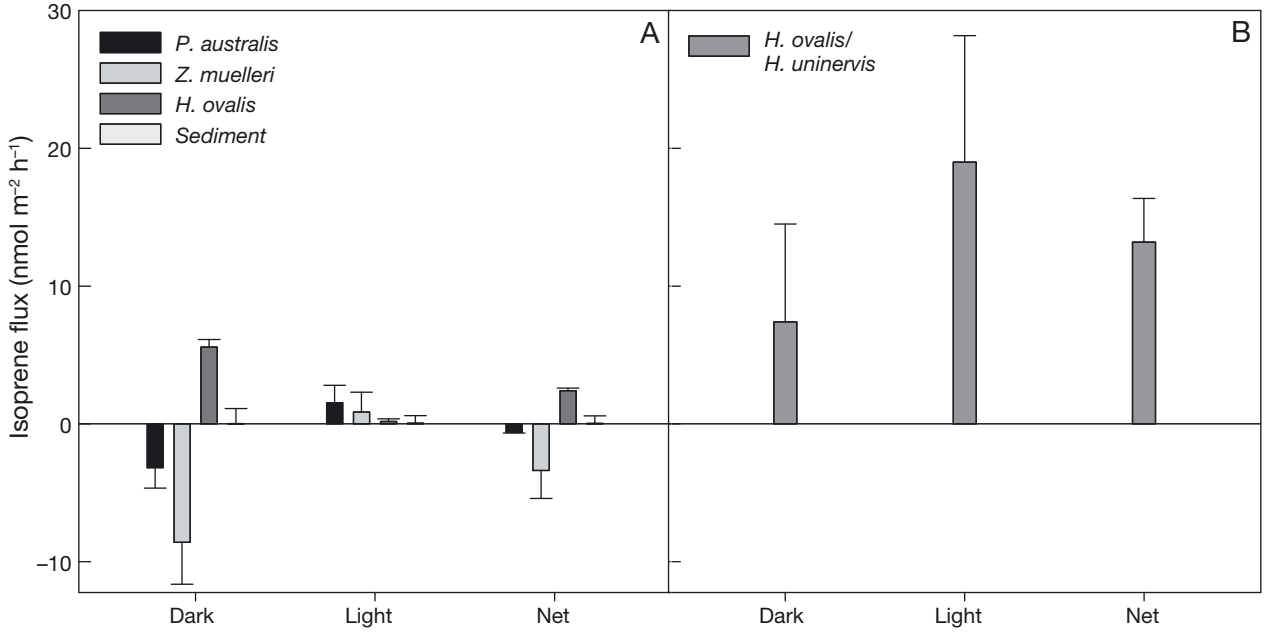

Fig. 7. Mean light, dark, and net isoprene fluxes over (A) 3 species of seagrass (*P. australis*, *Z. muelleri* and *Halophila ovalis*) and bare sediments in Wallis Lake, and (B) mixed seagrass bed containing *H. ovalis* and *Halodule uninervis* on Lizard Island. Three chambers were deployed and sampled for each seagrass and bare sediment community. Error bars indicate SE

3.5. Significant correlations

In Wallis Lake, isoprene fluxes negatively correlated with PO_4^{3-} and NH_4^+ in P. australis beds (Fig. 8A,B; PO_4^{3-}: $R^2 = 0.455$, p = 0.046, n = 9 and NH_4^+: $R^2 = 0.771$, p = 0.009, n = 7). Isoprene fluxes positively correlated with PO_4^{3-} in *Halophila ovalis* patches in Wallis Lake (Fig. 8C; $R^2 = 0.852$, $p < 0.001$, n = 9); however, isoprene fluxes negatively correlated with PO_4^{3-} in mixed seagrass containing *H. ovalis* and *Halodule uninervis* on Lizard Island (Fig. 8D; $R^2 = 0.543$, p = 0.024, n = 9). There were no significant correlations for *Z. muelleri*.

4. DISCUSSION

4.1. Seagrass habitats are both a source of and sink for isoprene in the water column

This study is the first to report benthic isoprene fluxes from seagrass communities. Seagrass communities from both tropical (Lizard Island) and warm temperate (Wallis Lake) regions were a source of and sink for isoprene in the marine environment, with this pattern being highly species-specific. For instance, *Halophila ovalis* and *Halodule uninervis* were net sources of isoprene in the water column, whereas an

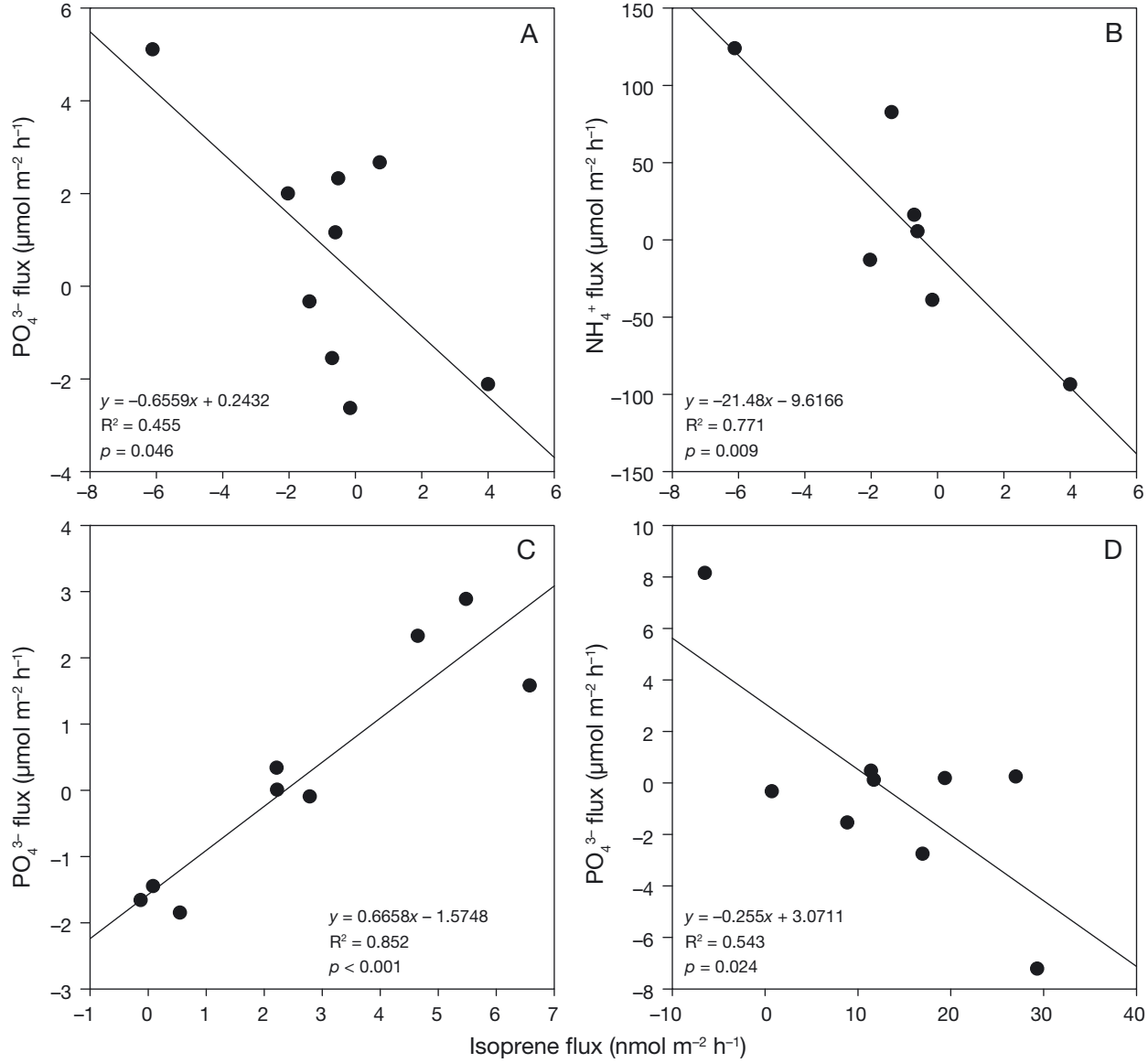

Fig. 8. Significant correlations between parameters measured over (A,B) *P. australis* and (C) *Halophila ovalis* (n = 7–9, varies due to missing data) at Wallis Lake and (D) mixed seagrass beds containing *H. ovalis* and *Halodule uninervis* on Lizard Island (n = 9)

Table 2. Benthic isoprene fluxes

Source	Locations	Net flux (nmol m^{-2} h^{-1})	Reference
Sediments	Wales, UK	0.0004	(Bravo-Linares & Mudge 2007)
Sediments (MPB)	Essex, UK	8.2 ± 1.2	(Exton et al. 2012)
Sediments (MPB)	Heron Island, QLD	10.0 ± 1.1	(Hrebien et al. 2020b)
Sediments (MPB)	Lizard Island, QLD	3.9 ± 0.9	(Hrebien et al. 2020b)
Sediments	Wallis Lake, NSW	0.0 ± 0.6	Current study
Seagrass			
P. australis	Wallis Lake, NSW	−0.6 ± 0.1	
Z. muelleri	Wallis Lake, NSW	−3.4 ± 2.0	
H. ovalis	Wallis Lake, NSW	2.4 ± 0.2	
H. ovalis/*H. uninervis*	Lizard Island, QLD	13.2 ± 3.2	

uptake of isoprene was measured in *Z. muelleri* and *P. australis* beds. Isoprene fluxes from mixed patches containing *H. ovalis* and *H. uninervis* on Lizard Island were higher than previous benthic fluxes from sediments containing MPB on Heron Island and Lizard Island (Australia) as well as in Essex (UK) (Table 2). This was expected, as seagrass has a much higher biomass than non-vegetated carbonate sands or sediments dominated by MPB. Similar to sandy sediments measured in Wales (UK), non-vegetated sediment incubations in Wallis Lake had very low to no flux (Table 2), indicating that benthic isoprene fluxes likely exclusively come from segrasscommunities, which include above- and belowground seagrass biomass as well as epiphytes and MPB, although *H. ovalis* effluxes in Wallis Lake were still quite low. While benthic incubations provide the advantage of *in situ* measurements, they do not allow separate components within seagrass beds to be isolated. This highlights the need for additional studies to determine individual isoprene production and consumption from each component within seagrass communities.

4.2. The drivers of isoprene production in seagrass communities are species-specific

Isoprene fluxes were typically greater during the day than at night in both temperate (Wallis Lake) and tropical (Lizard Island) habitats, suggesting that most of the isoprene production in seagrass communities is driven by photosynthesis. This is consistent with the negative correlation between isoprene and both NH_4^+ and PO_4^{3-} in *P. australis* and in mixed seagrass patches containing *Halophila ovalis* and *Halodule uninervis* (Fig. 5), which indicate NH_4^+ and PO_4^{3-} uptakes through seagrass community productivity (Eyre & Ferguson 2002, Eyre et al. 2011a). A number of studies have shown an increase in isoprene production due to the influence of photosynthesis (Guenther et al. 1995) as well as temperature and light (Monson & Fall 1989, Broadgate et al. 2004). In Wallis Lake, *Z. muelleri* and *P. australis* had a significantly greater GPP and R than *H. ovalis* (Fig. 6), which, combined with an uptake of isoprene at night in both *Z. muelleri* and *P. australis*, suggests an absence of isoprene production in the dark combined with isoprene uptake by either the seagrass or associated microbial community (Alcuna Alvarez et al. 2009).

On Lizard Island, although isoprene efflux from mixed seagrass patches containing *H. ovalis* and *H. uninervis* was higher during the day (mean ± SE 19.0 ± 9.2 nmol m^{-2} h^{-1}) than at night (7.4 ± 7.1 nmol m^{-2} h^{-1}), an efflux of isoprene was still observed at night, suggesting isoprene production via a different pathway than photosynthesis. Benthic bacteria can both produce and consume isoprene, although this is species dependent (Shaw et al. 2003, Alcuna Alvarez et al. 2009). Isoprene production by terrestrial bacteria has been demonstrated at night (Kuzma et al. 1995) due to the breakdown of stored carbohydrates in plant cells in the absence of light (Lerdau et al. 1997). Furthermore, unicellular green algae produce isoprene in the dark via heterotrophic use of exogenous glucose at the same rate as they produce isoprene in the light via photosynthesis (Dani et al. 2020). These mechanisms could be occurring in seagrass habitats. A similar pattern was also observed in MPB (Exton et al. 2012, Hrebien et al. 2020b), cyanobacterial cultures (Shaw et al. 2003), and macro-algae (Broadgate et al. 2004), suggesting that seagrass habitats behave in a similar way to other benthic systems.

In Wallis Lake, *H. ovalis* exhibited higher isoprene efflux at night (mean ± SE 5.6 ± 0.6 nmol m^{-2} h^{-1}) than during the day (0.2 ± 0.2 nmol m^{-2} h^{-1}). This might reflect the uptake of isoprene by bacteria during the day, although this is more likely to occur at night (Alvarez et al. 2009). Due to its morphology, it is also

possible that *H. ovalis* can become O_2 stressed, and an O_2 surplus from productivity during the day would diffuse from seagrass leaves through the roots and rhizomes, oxygenating and enriching the sediments (Pedersen et al. 1998, Greve et al. 2003, Rasmusson 2015). This phenomenon, known as radial O_2 loss (ROL), could lead to an increase in isoprene production from MPB at night. While ROL occurs in other species, it is directly related to the available light to leaf ratio, with the zone of ROL in *H. ovalis* extending more than twice as far as that in *Z. muelleri* (Martin et al. 2019). Furthermore, the higher isoprene efflux at night compared to other species could be due to the microbial community associated with *H. ovalis,* which could be more productive and contain more heterotrophic organisms that produce isoprene at night than that associated with *P. australis* or *Z. muelleri* (Dani et al. 2020). However, the abundance and composition of bacteria communities in these seagrass beds has not been measured in this study and thus should be the focus of future investigations.

H. ovalis had significantly lower isoprene flux during the day than other seagrass species, which could be linked to a difference in productivity as GPP, NPP, and R were significantly lower in *H. ovalis* than in *Z. muelleri* (Fig. 6). *Halophila* spp. are extremely sensitive to UV-B irradiation, which can inhibit photosynthesis (Halldal 1964, Drew 1979, Foyer et al. 1994). For example, *H. ovalis* is highly physiologically responsive when exposed to moderate irradiances (500 µmol photons m^{-2} s^{-1}) and oxidative stress, triggering photoprotective responses such as non-photochemical quenching and clumping of chloroplasts, which would limit the amount of light being absorbed (Phandee & Buapet 2018). *Halodule* spp., on the other hand, have a higher physiological tolerance for UV-B irradiance stress, with photo-repair mechanisms to reduce photosynthetic inhibition (Trocine et al. 1981). The low-relief growth form of *Halophila* spp. usually enables shading from other, larger species as well as epiphytes and detritus (Trocine et al. 1981). However, the study site at Wallis Lake did not have shade from other species and individual leaves were more exposed to light. While maximum irradiance only reached 353 µmol photons m^{-2} s^{-1}, it is still possible that isoprene produced during the day was immediately photooxidised due to higher light penetration throughout the water column, with UV-B associated stress leading to a decrease in productivity (Foyer et al. 1994, Phandee & Buapet 2018) and potentially a decline in isoprene production. Therefore, it is possible that the difference in day primary production rates between Wallis Lake and Lizard Island (Fig. 6) is linked to the presence of both *H. uninervis* and *H. ovalis*, with one being responsible for production during the day and the other at night, respectively. In terrestrial plants, oxidative stress can increase isoprene production under increased levels of UV-B radiation (Loreto & Velikova 2001); however, the physiological function of isoprene in seagrass and other marine systems is not yet understood. For example, while isoprene is released as a thermoregulator in terrestrial plants, this is not the case in phytoplankton in the open ocean (Shaw et al. 2003).

Isoprene production in seagrass communities was species-specific, which has also been demonstrated in seaweed (Broadgate et al. 2004) as well as in phytoplankton (Milne et al. 1995) and bacteria (Alvarez et al. 2009). Temperate seagrass communities dominated by *P. australis* and *Z. muelleri* were found to be net sinks for isoprene. While both species emit isoprene during the day, increased uptake at night resulted in a net uptake over the diel cycle. In Wallis Lake, *P. australis* was twice as productive as *Z. muelleri* during the day (mean ±SE 1.5 ± 1.3 nmol m^{-2} h^{-1} and 0.9 ± 1.4 nmol m^{-2} h^{-1} respectively), which is expected since it is proportionally nearly 3 times the size of *Z. muelleri* (aboveground biomass: mean ±SE 69.1 ± 40.7 g dry wt m^{-2} and 25.6 ± 3.8 g dry wt m^{-2}, respectively) (Camillini 2020). Furthermore, isoprene uptake in *Z. muelleri* was more than twice the uptake of *P. australis* at night (mean ±SE −8.6 ± 3.0 nmol m^{-2} h^{-1} and −3.2 ± 1.5 nmol m^{-2} h^{-1} respectively). Compared to *H. ovalis* or *H. uninervis, P. australis* and *Z. muelleri* have larger leaves, which constitute a greater surface area for macrophytes, microalgae and bacteria to grow. Visual observations suggest that both *P. australis* (Fig. 2A) and *Z. muelleri* (Fig. 2B) had a substantially greater macrophyte community than *H. ovalis* (Fig. 2C) and the mixed patch of *H. ovalis and H. uninervis* (Fig. 2D), which had cleaner leaves. Therefore, it is likely that the higher isoprene uptake in *P. australis* and *Z. muelleri* is due to the presence of macrophytes and associated microbial community (Broadgate et al. 2004, Alvarez et al. 2009). In contrast, *H. ovalis* emitted isoprene during light and dark periods in both locations, indicating that seagrass communities dominated by *H. ovalis* can be considered a net source of isoprene in the water column.

4.3. Isoprene fluxes from tropical and warm temperate regions across different species

Isoprene fluxes were significantly greater on Lizard Island (tropical habitat) than in any species or

sediment in Wallis Lake (temperate zone) (Table 2). Since isoprene production is driven by light and temperature, with isoprene production generally increasing exponentially with temperature (Guenther et al. 1995, Pugh et al. 2013), tropical habitats likely have higher isoprene emissions (Exton et al. 2015). Although the study in Wallis Lake was conducted in mid-March (early autumn), temperatures ranged from 22.4 to 26.4°C, with the average temperature (24.5°C) falling within the summer temperature range (23–26°C). On the other hand, the study on Lizard Island was conducted in late October (mid-spring), with measured temperatures ranging from 26.1 to 30.5°C, with the average temperature (27.9°C) falling just under the summer temperature range (29–31°C). The optimal temperature for growth and productivity in temperate seagrass species ranges from 11.5 to 26°C, whereas for subtropical and tropical species optimal temperatures range from 23 to 32°C (Lee et al. 2007). Temperatures in Wallis Lake were within the thermal optima for temperate seagrasses *P. australis* and *Z. muelleri*, although both species represented a sink for isoprene. On the other hand, tropical/subtropical species *Halophila ovalis* was within optimal temperature range for tropical seagrass growth and productivity at both locations, with Wallis Lake and Lizard Island representing the lower and upper ends of the range, respectively. Since isoprene emissions are metabolically linked to photosynthesis (Monson et al. 1992, Guenther et al. 1995, Dani et al. 2017), overall higher temperature and increased hours of light (Fig. 6) in the tropics were likely the main factors influencing isoprene production in this study. Based on average temperature ranges at each location and the optimum range for seagrass growth and productivity, it was predicted that isoprene production would be higher on Lizard Island for the tropical and subtropical species *H. ovalis* and *H. uninervis,* with the annual temperature range (23–31°C; Table 1) being close to the temperature optima for these species (23–32°C). Wallis Lake is likely to have *Halodule uninervis* with the annual temperature range (23–31°C; Table 1) being close to the temperature optima for these species (23–32°C). Wallis Lake is likely to have lower isoprene production, with maximum temperatures only reaching the lower end of the optimal scale and most of the year falling below optimal temperatures for H. ovalis (18–26°C; Table 1). It is thus possible that during the winter no isoprene is produced at all in *H. ovalis*.

Seasonal variability in seagrass usually increases productivity during spring and summer and decreases productivity in fall and winter as temperature significantly affects photosynthesis and respiration, which are considered as major growth factors in seagrass (Lee & Dunton 1996, Lee et al. 2005). In this study, it is likely that Wallis Lake seagrass productivity was low due to lower temperatures, while on Lizard Island, seagrass productivity was high due to increasing temperatures, with our measurements reflecting this seasonal pattern. As mentioned earlier, this study is likely representative of yearly average seagrass production; however, additional studies measuring seasonal maximums and minimums in isoprene production need to be conducted to understand the true contribution of these seagrass communities to local and global isoprene budgets.

H. ovalis in Wallis Lake and the mixed *H. ovalis*/*H. uninervis* on Lizard Island showed similar trends, with isoprene production in both light and dark. However, the isoprene fluxes from these species were significantly higher on Lizard Island than in Wallis Lake, with isoprene effluxes measuring nearly 20 times greater in the light and 2 times greater in the dark, resulting in a 10 times greater net efflux. While temperature and light are drivers of isoprene production in the tropics, it was not feasible to measure *H. uninervis* on its own, which makes it difficult to determine whether there could also be a species-specific element causing higher isoprene fluxes on Lizard Island.

The aboveground biomass for *H. ovalis* (mean ± SE 2.4 ± 0.1 g dry wt m^{-2}) in Wallis Lake and for the mixed seagrass *H. ovalis* and *H. uninervis* (2.7 ± 2.8 g dry wt m^{-2}) on Lizard Island were similar; however, the belowground biomass on Lizard Island (6.5 ± 3.8 g dry wt m^{-2}) was almost 3 times greater than that in Wallis Lake (2.4 ± 0.3 g dry wt m^{-2}). To build the root system necessary for the sediment composition, assimilated carbon needs to be allocated from aboveground biomass to belowground biomass via photosynthesis (Hemminga 1998). Since roots and rhizomes need nutrient uptake for growth and colonisation, nutrient availability is also a factor to consider when comparing belowground biomass. In Wallis Lake, resources for growth are likely to be more readily available within the water column, whereas on Lizard Island, nutrients likely come from porewater where uptake by belowground biomass is key, although further research is necessary to confirm this.

4.4. Seagrass as a source of isoprene to the water column

In Wallis Lake, *P. australis covers* 4.4% of the total lake area, *Z. muelleri* 21.2% and *Halophila ovalis*

5.27 % (Eyre & Maher 2010). Using a total lake area of 90 km^2 and a total net isoprene flux rate of –0.3 mg m^{-2} yr^{-1} for all species, seagrass communities in Wallis Lake were found to be a sink for isoprene, with a total uptake of –0.008 T C yr^{-1}. While *H. ovalis* was found to emit small amounts of isoprene at 1 mg m^{-2} yr^{-1} (0.006 T C yr^{-1}), its 5 % coverage within the lake was not enough to counteract the lack of isoprene production from *P. australis* (0 mg m^{-2} yr^{-1}, –0.001 T C yr^{-1}) or the uptake from *Z. muelleri* (–2 mg m^{-2} yr^{-1}, –0.034 T C yr^{-1}).

On Lizard Island, *H. ovalis* and *Halodule uninervis* constitute 0.33 % of the total reef area (Saunders et al. 2015). Using a total reef area of 150 km^2 for Lizard Island, and a net isoprene flux rate of 8 mg m^{-2} yr^{-1}, we estimated that mixed seagrass communities of *H. ovalis* and *H. uninervis* emit 0.003 T C yr^{-1} from Lizard Island. While net isoprene flux rates were more than 10 times greater on Lizard Island (net: 13.21 ± 3.2 nmol m^{-2} h^{-1}) than for all species in Wallis Lake (combined net: –0.53 ± 0.8 nmol m^{-2} h^{-1}), the small seagrass coverage on Lizard Island for these 2 species makes their contribution insignificant, even in comparison to carbonate sediments on Lizard Island, which emit 0.09 T C yr^{-1} of isoprene (Hrebien et al. 2020b).

Using a global area of 350 000 km^2 for seagrass (Duarte 2017), and an average annual isoprene flux rate for Wallis Lake and Lizard Island of 8 mg m^{-2} yr^{-1} (min: 2, max: 13), the global isoprene flux from these seagrass species is estimated to range from 0.74 to 4.52 Gg C yr^{-1} with a global net isoprene flux estimated to be 2.3 Gg C yr^{-1}. This is slightly higher than the estimated global isoprene flux from coral reef carbonate sediments (0.52 Gg C yr^{-1}) (Hrebien et al. 2020b); however, it is still much lower than estimated global isoprene flux from phytoplankton (0.66 Tg C yr^{-1}) (Conte et al. 2020), and only a small contribution to the global marine isoprene flux of 11.6 Tg C yr^{-1} (Luo & Yu 2010).

While we acknowledge the uncertainties of extrapolating from only 2 locations and a few seagrass species, it is still worthwhile to put our findings into a global context. As it stands, this 'back of the envelope' estimate is not meant to be an absolute value, as it contains a percentage of error due to lack of seasonal sampling, does not take into account fluctuations of light and temperature throughout the year, and is constrained by a small sample size. However, it helps to see how the snapshot measured in this study compares to global estimates and other studies, and indicates that isoprene sources and sinks from seagrass are perhaps more important on a local scale than on a global scale. Additional studies across a wider range of seagrass communities dominated by different seagrass species in both tropical and temperate climates and across different seasons capturing the minimum and maximum temperature range over the year are required to obtain a more accurate estimate of how seagrass contributes to the global isoprene budget. Furthermore, additional studies on epiphytes and microbial communities are needed to determine the contribution of each component of seagrass communities. Nevertheless, this study has provided seagrass community isoprene emissions in coastal waters and identified new knowledge gaps to be explored.

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Appendix.

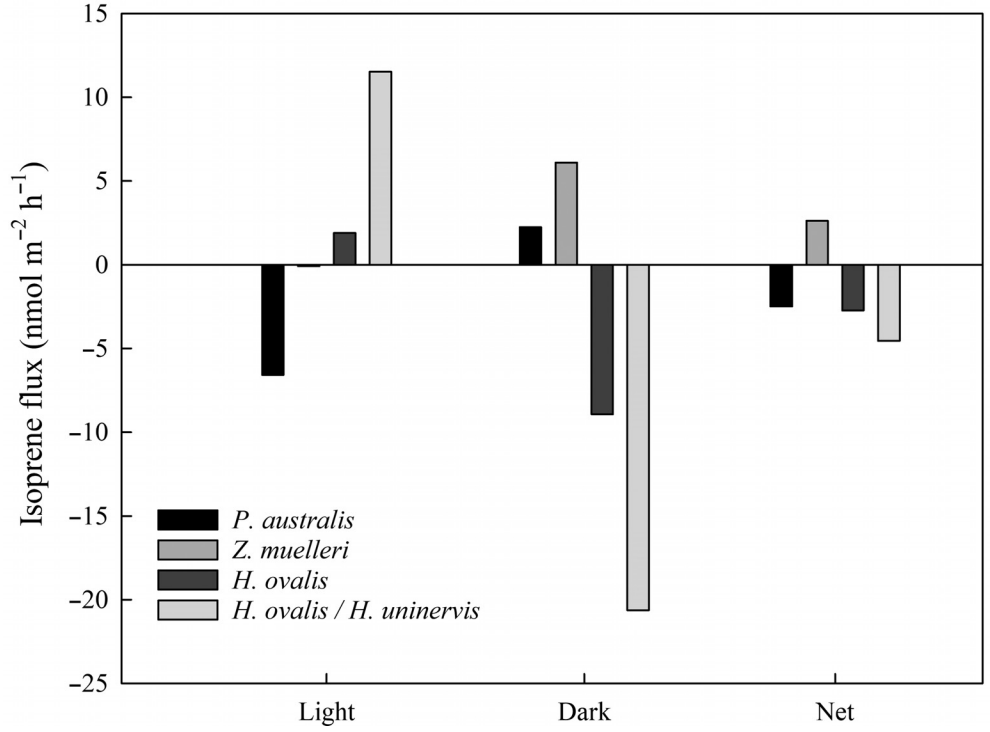

Fig. A1. Light, dark, and net isoprene fluxes within false bottom blank chambers in conjunction with incubations over 3 species of seagrass (*P. australis*, *Z. muelleri*, and *Halophila ovalis*) in Wallis Lake and one mixed seagrass bed containing *H. ovalis* and *Halodule uninervis* on Lizard Island (n = 1)

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