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Quantifying air–sea CO_2 fluxes above desert-fringing coral reefs in the northern Red Sea revealed by eddy covariance.

Hamish McGowan[1], Shai Abir[2,3], Nadav Lensky[2,3], Yonathan Shaked[4]

[1]Weather and Climate Science Research Alliance, The University of Queensland, Brisbane, Australia.
[2] The Hebrew University of Jerusalem, Jerusalem, Israel.
[3] Geological Survey of Israel, Jerusalem, Israel.
[4] Interuniversity Institute for Marine Sciences, Eilat, Israel.

Corresponding author: Hamish McGowan, email: h.mcgowan@uq.edu.au

Abstract. Eddy covariance (EC) measurements of air-sea CO_2 exchange over desert fringing coral reefs in the Gulf of Eilat (Aqaba) (GoE), northern Red Sea, show these ecosystems are net sinks of atmospheric CO_2. This result contrasts with marine productivity models and bulk formula calculations based on water chemistry that are often used methods to determine the magnitude and direction of the CO_2 flux with the atmosphere over coral reefs. These studies have often concluded that coral reefs are net sources of CO_2 to the atmosphere with only rare cases finding otherwise. Our EC measurements find coral reefs in the GoE may absorb around 4.5 times more carbon from the atmosphere than other marine and terrestrial ecosystems and only slightly less than some tropical rainforests. This highlights the need for further direct measurements of air-sea CO_2 exchanges over coral reefs in different environmental settings so their role in the global carbon cycle can be accurately quantified.

1. Introduction

Understanding net ecosystem – atmosphere CO_2 exchange (Net Ecosystem Exchange (NEE)) is crucial to inform policy responses to anthropogenic global warming. Quantification of NEE has therefore become a major focus of initiatives to directly measure ecosystem CO_2 exchanges. The eddy covariance (EC) method provides the only direct representative measure that captures the multi-scaled and complex processes controlling ecosystem – atmosphere trace gas fluxes including CO_2. These span a spectrum of time and space scales of 15 orders of magnitude (Baldocchi, 2003; Baldocchi, 2014; Mauder et al., 2021). EC is therefore the cornerstone of AmeriFlux (Novick et al., 2018), EUROFLUX (Aubinet et al., 1999), OzFlux (Beringer et al., 2016) and Asiaflux (Yu and Hirano, 2021) which seek to quantify NEE by direct measurement and contribute to the global FLUXNET program (Baldocchi et al., 2001). Substantial advances have therefore been made in understanding terrestrial ecosystems CO_2 fluxes. In contrast, direct measurement of CO_2 flux over lacustrine and marine ecosystems remains dominated by time and space limited observations at disparate locations, none more so than over coral reefs – the rainforests of the oceans (Knowlton, 2001; Swart, 2013).

Coral reefs represent 0.1 to 0.25% of the global marine environment with at least 1 billion people benefiting from their ecosystem services (Cinner, 2014; Anthony et al., 2017; Souter et al., 2021). They are at risk from warming sea surface temperatures (SSTs), ocean acidification, overfishing, pollution, mining, and tourism. While the ecological importance of coral reefs is unquestionable, their role in carbon budgets is uncertain. Previous research suggested coral reefs may absorb ≈ 2 % of annual anthropogenic CO_2 emissions (≈720 Mt), while others have stated coral reefs are sources of atmospheric CO_2 (144 Mt to 504 Mt) (Kinsey & Hopley, 1991; Ware et al., 1992; Borges et al., 2005). These estimates of CO_2 exchange were based on marine productivity models or bulk formulas that use calculations of the CO_2 partial pressure (pCO_2) difference across the air-sea interfacial boundary multiplied by an estimated gas transfer velocity (Wanninkhof, 2014; Terlouw et al., 2019). Other studies have used point measurements of water pH, temperature, and chemistry to estimate reef water pCO_2 which is then compared against atmospheric CO_2 concentration to determine the CO_2 flux gradient (Hannan et al., 2020; Moav-Barzel et al., 2023). A limitation of these studies is that their focus has often been on scleractinian corals which define coral reefs, and the associated carbonate chemistry. However, coral reefs are highly complex ecosystems with for example, low-lying algae including algal turfs, crustose coralline algae or cyanobacteria that are often considered as dead coral, pavements or "bare space" covering up to 70% of coral reefs (Bahartan et al., 2010; Tebbett et al., 2023). Photosynthesis by these algae can significantly draw down CO_2, thereby lowering the pCO_2 in the water column overlying coral reefs (Anthony et al., 2013) resulting in net influx of CO_2 (Kayanne, 2025).

Direct measurements of air-sea NEE using EC with measurement footprints of >20,000 m^2 have found coral reefs to be net sinks of CO_2, at times an order of magnitude larger than reported by bulk formula and productivity models (McGowan et al., 2016, 2022a, 2022b; Rey-Sánchez et al., 2017). The large measurement footprint of EC ensures truly representative and instantaneous measurements of NEE. Importantly, it captures the influence of environmental factors on NEE such as water temperature, wind speed, humidity, currents and tides. However, these studies were conducted for only a few days to several weeks and may not have captured the full range of conditions expected on coral reefs. For example, McGowan et al. (2022a) presented only seven weeks of air-sea CO_2 EC flux data from over coral reefs in the GoE (13 September – 1 November 2020). The focus of this short-term study was on a comparison between air-sea CO_2 flux over the fringing coral reefs and the adjacent ocean in the GoE, and the possible influence of dust deposition events on air-sea CO_2 exchange. Similarly, McGowan et al., (2022b) highlighted the spatial heterogeneity of air-sea CO_2 exchange at Heron Reef on the humid subtropical southern Great Barrier Reef, Australia. Here the reef flat was identified as a net source of CO_2 to the atmosphere, while concurrently adjacent lagoons were found to be net CO_2 sinks, although the measurement period was short being around two weeks only in duration (McGowan et al., 2016).

Using data on water chemistry, tropical fringing coral reefs at Mo'orea, Tahiti were found to be CO_2 sinks, whereas a neighbouring barrier reef flat was a CO_2 source. This was attributed to the possible effect of the relative coverage of algae with coral dominated reefs hypothesized to be sources of CO_2, while those with substantial algae coverage were CO_2 sinks (Gattuso et al., 1997). More recently, analysis of water chemistry over fringing coral reefs on the South China coast during summer found coral reefs in this region to be CO_2 sinks with mean influx values of 12.3 to 19.2 mmol CO_2 $m^{-2}d^{-1}$. These air-sea CO_2 exchanges were believed to be dependent on hydrodynamics and algae cover (Yan et al., 2024). This highlights the importance of community structure of coral reef ecosystems in air – sea CO_2 exchange. Factors that may influence this observation either directly or indirectly include hydrodynamics, coastal development, river discharges, deposition of aerosols, nutrient runoff from aquiculture, local changes in atmospheric CO_2 concentrations, and synoptic meteorology.

Corals affect air-sea CO_2 exchanges through changing the $p\mathrm{CO_2}$ in the water overlying the reef via photosynthesis/respiration and calcification/dissolution across the day–night cycle (Falter et al., 2013). During the day, photosynthetic activity consumes CO_2, while at night, respiration consumes O_2 and produces CO_2. Calcification and dissolution raise the $p\mathrm{CO_2}$ in the water with the precipitation of 1 mol of $CaCO_3$ releasing approximately 0.6 mol of CO_2 to the seawater. Variability in the $p\mathrm{CO_2}$ in the water overlying a coral reef will therefore reflect biogeochemical, hydrodynamic, and meteorology processes. For example, dust deposited on the fringing coral reefs at Eilat, Israel was found to supply nanomolar amounts of essential bioelements to the coral symbionts leading to enhanced chlorophyll concentrations and photosynthesis (Blanckaert et al., 2022). This fertilization of the coral reef by dust is believed to lower the $p\mathrm{CO_2}$ in the water overlying the reef leading to a net influx of atmospheric CO_2 (McGowan et al., 2022a). Water temperature also significantly influences air-sea CO_2 exchanges with lower sea surface temperatures increasing CO_2 solubility causing a net downward flux to the water (Van Scoy et al., 1995; Gray et al., 2012).

Here we present results from the direct measurements of air-sea CO_2 exchange over a coral reef made using the EC method. Research was conducted in the hyper-arid environment of the GoE, Israel where evaporative cooling of water provides a thermal refugia for corals, which have evolutionary traits believed to further protect them from extreme water temperatures (Fine et al., 2013; Abir et al., 2022; Kochman-Gino & Fine 2023). The measurement period extends the previously published study of McGowan et al (2022a) by 22 weeks encompassing spring and winter seasons thereby representing the longest continuous direct measurement record of air-sea CO_2 exchange over a coral reef. Results are compared to previously published

EC NEE measurements for coral reefs in humid environments, and carbon exchanges over other marine and terrestrial ecosystems.

2. Materials and Methods

2.1 Study Site

This study was conducted from 3 September 2020 to 2 March 2021 (181 days) along the northwest shore of the GoE (Figure 1a, b), an almost rectangular region of the Gulf in the northern Red Sea roughly 6 × 10 km with steep lateral boundaries with a maximum depth of ~800 m (Carlson et al., 2012). Along this section of coast more than 40 coral genera are regularly identified, with the most common genera comprising of Stylophora, Acropora, Montipora, Echinopora, Cyphastrea, Goniastrea, Porites, Dipsastrea and Stylophora pistillata. Coral coverage averages approximately 25%, with rock making up around 20%, dead coral 5%, and the remaining being loose substrate of sand and shell fragments (Shaked & Genin, 2020) as seen beneath the EC measurement footprint (Figure 1d, e, f). Epilithic algae has been found to cover from less than 20% to around 70% of the reef substrate at our site (Bahartan et al., 2010) and is the dominant reef cover globally (Tebbett et al., 2023, 2025). The alongshore current is predominantly from north to south in response to prevailing northerly winds blowing from the Arava Valley, with a semidiurnal and diurnal barotropic tide range of ~1 m (Shaked & Genin, 2018). Tidal currents between approximately 4 to 7 cm s^{-1} have been measured near our field site (Figure 1) in water depths from 0 – 28 m during autumn and winter (Carlson et al., 2021) and were approximately aligned with the shoreline and the dominant northerly winds. Lateral (cross-shore direction) wind stresses are small although local hydraulics and the thermal gradient between the shallow shoreline water and adjacent deeper ocean may drive some lateral water exchange over the reef (Monismith et al., 2006). As a result, water moving over the coral reef beneath the EC measurement footprint is most likely to have travelled parallel to the shoreline over many hundreds of meters of reef flat beforehand. It is therefore unlikely that advective processes such as the onshore transport of ocean water significantly influence our EC measurements. Measurement footprint filtering further minimises the influence of for example, the adjacent ocean on our EC CO_2 flux measurements. Fish farms that operated for almost 20 years approximately 7 km northeast of our study site were removed in June 2008, and within six months sediment organic matter decreased (Oron et al., 2014). Subsequent storm induced sediment overturning events enabled the removal of all residual nutrients from the northern GoE.

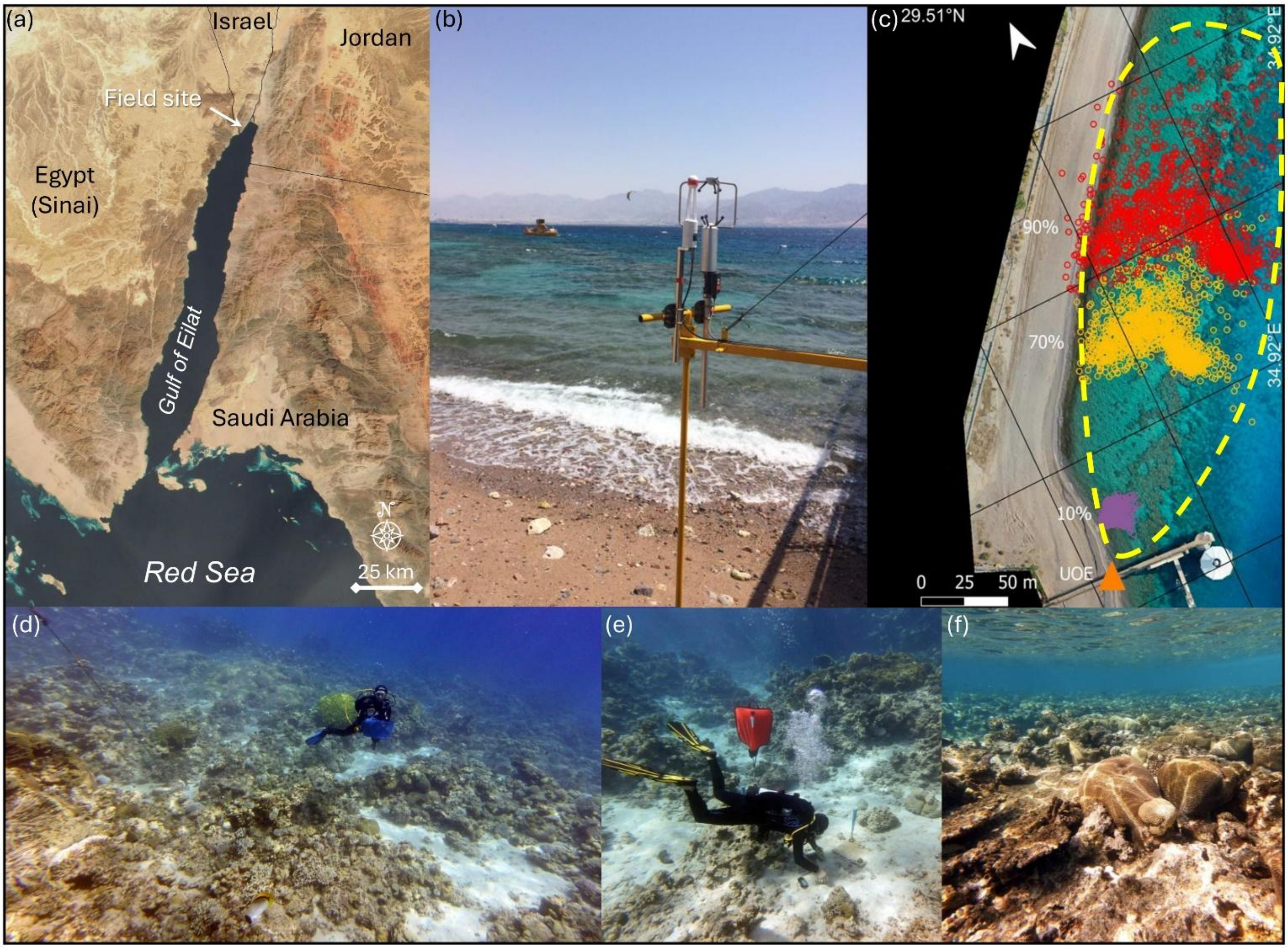

Figure 1. Location map of the EC field site in the northern GoE (a) with the EC instrumentation (b). The spatial characteristics of the EC measurement footprint highlighting the percentile of the distances from which the data was collected by the EC (i.e.10%, 70% and 90%) over the coral reef (c). The approximate boundary of the EC footprint is indicated following wind direction filtering by the yellow dashed line (c), with the EC system represented by the orange triangle (c). Photographs of the coral reef beneath the EC measurement footprint (8 November 2022) at water depths 6 to 8 m showing the seaward margin of the forereef near the reef slope (d), benthic composition of the forereef (e), and shallow reef flat with a water depth of around 1 m (f).

2.2 Direct Measurement of Air-Sea Coral Reef Ecosystem CO_2 exchange

CO_2 flux (F) is defined as:

$$F = \bar{\rho}\,\overline{w'c'} \qquad (1)$$

where ρ is the mole density of dry air (mol m^{-3}), c is the CO_2 concentration (dry mixing ratio, µmol mol^{-1}) measured by a fast-response infra-red gas analyser (IRGA) (open or closed path), and the vertical wind velocity w (m s^{-1}) is measured by a sonic anemometer. The prime denotes the fluctuations from the mean, while the overbar indicates time average (Burba 2013).

Measurements of air-sea CO_2 exchanges over coral reefs in the northern GoE were made using an EC system attached to the pier of Eilat's Coral World Underwater Observatory (UOE) (29°30′15.43″N and 34°55′6.68″E) at 2.5 m above mean sea level (Figure 1b). The EC system consisted of a 3D sonic anemometer (RM Young 81000), an open-path IRGA (Li-Cor 7500), a net radiometer (Kipp and Zonen CNR1), and ancillary sensors including a SI-4H1 infrared radiometer (Apogee Instruments, Inc.) for measured water skin temperature (McGowan et al., 2022; Abir et al., 2022). The Li-Cor 7500 open-path gas analyzer has been used successfully in many geographic locations to provide direct measurement of CO_2 in coastal and marine environments (McGowan et al., 2016, 2022; Andersson et al., 2016; Chien et al., 2018; Rutgersson et al., 2020). To minimize the potential influence of salt, dust, and biogenic films on CO_2 measurements, the Li-Cor 7500 gas analyzer was regularly washed to ensure the optical sensors were clean to minimize hygroscopic contamination leading to erroneously high CO_2 measurements. The hyper-arid climate of the GoE field site also minimizes potential cross-sensitivity of CO_2 measurements to water vapor.

Half-hourly CO_2 fluxes were calculated using EddyPro® Software v7.0 and included correction for anemometer tilt, air density variability (Webb et al., 1980), frequency response, and sensor separation (Burba, 2013; Massman, 2004). Wind speed measurements were standardized to a height of 10 m above the surface. A wind direction filter was applied to exclude measurements made when wind was directed onto the EC measurement footprint from the deep sea (> 40 m) and land (Kljun, 2004) (excluded wind directions 90 to 360°). Examples of the EC measurement percentiles and approximate footprint boundary are overlaid on the fringing coral reefs in water depths from 0 to 40 m in Figure (1c). Low quality data (flags ≥ 2) were removed from analysis as determined by steady state and developed turbulence tests (Mauder & Foken 2004). Finally, spike removal was conducted so that CO_2 flux was restricted to ±15 µmol m^{-2} s^{-1} (McGowan et al., 2022a). Individual gaps (30 minutes) in the CO_2 flux record were filled with the average of the preceding and following data points. For gaps larger than one 30-minute observation period missing data were filled using the mean diurnal variation (MDV) technique (Moffat et al., 2007) where the missing CO_2 value is replaced with the mean value of the adjacent days at the same time of day with the window set at 5 days in this study. No data gap exceeded 3.54 days (n = 1) with all remaining data gaps < 15 hrs. This approach to gap filling of the CO_2 flux record was selected in preference to other methods such as Artificial Neural Network algorithms which ideally require lengthy (> 1yr) and complete training data records where the influence of the drivers of CO_2 flux is well known (Boudhina et al. 2018; Mahabbati et al. 2021). These methods are most suited to filling large gaps exceeding one to two weeks and not a few hours where an approach such as MDV is more appropriate (Falge et al., 2001; Nemitz et al., 2018). Furthermore, the synoptic meteorology of our field site does not undergo frequent dramatic changes such as experienced at midlatitude locations meaning that the corresponding 30-minute observation period(s) in our 5-day window reflect CO_2 fluxes under similar meteorological conditions. Prior to gap filling there were 5157 mean 30-minute CO_2 flux data points with a mean CO_2 flux of -2.599 µmol m^{-2} s^{-1} (SD 3.632 µmol m^{-2} s^{-1}). Following the MDV gap filling there was 8500 mean 30-minute CO_2 flux data points (increase of 25.5%) with a mean CO_2 flux of -2.165 µmol m^{-2} s^{-1} (SD 3.441 µmol m^{-2} s^{-1}). Therefore, the effect of the MDV gap filling was a slight decrease (0.434 µmol m^{-2} s^{-1}) in the mean CO_2 influx over the coral reef.

2.3 Particle concentration in the atmosphere

Aerosol <10 µm in diameter (PM10) concentrations were obtained from the Israel Ministry of Environmental Protection monitoring program at Eilat, which uses Thermo Scientific FH62-C14 continuous particulate monitors. These measure the mass concentration of suspended particulate matter using beta attenuation, with average half hourly PM10 values reported here.

3. Results

3.1 Air-sea meteorology and CO_2 exchange

Air-sea CO_2 flux measured over the fringing coral reef at the UOE site in the GoE is presented with concurrent measurements of associated meteorology in Figure 2. The seasonal transition from late summer conditions with afternoon air temperatures of around 40 °C (Figure 2d) and water temperatures greater than 30 °C (Figure 2c) to cooler winter conditions was marked by an abrupt transition in early November 2020. This is most evident in ΔT as a step change from conditions where the air was warmer than the water to where the water was predominantly warmer than the air (Figure 2h). There was no concurrent effect on CO_2 flux (Figure 2f) with this rapid "flip" in ΔT (Figure 2h).

Daytime wind speed maxima were at their minimum during winter reflecting a weaker local sea breeze (Figure 2a). The northerly wind that regularly blows from the Arava Valley onto the northern GoE because of the valley channelling synoptic winds and the inland penetration of the Mediterranean Sea breeze was also weaker. CO_2 flux was dominated by negative values (blue shading) indicating influx from the atmosphere to the water (Figure 2f). This influx doesn't show obvious correlation with other variables including aerosols (PM10) (Figure 2e) which are primarily minerogenic entrained from the surrounding deserts. They have previously been linked to fertilization of the coral reefs in the GoE and possible CO_2 influx (McGowan et al., 2022; Blanckaert et al., 2022).

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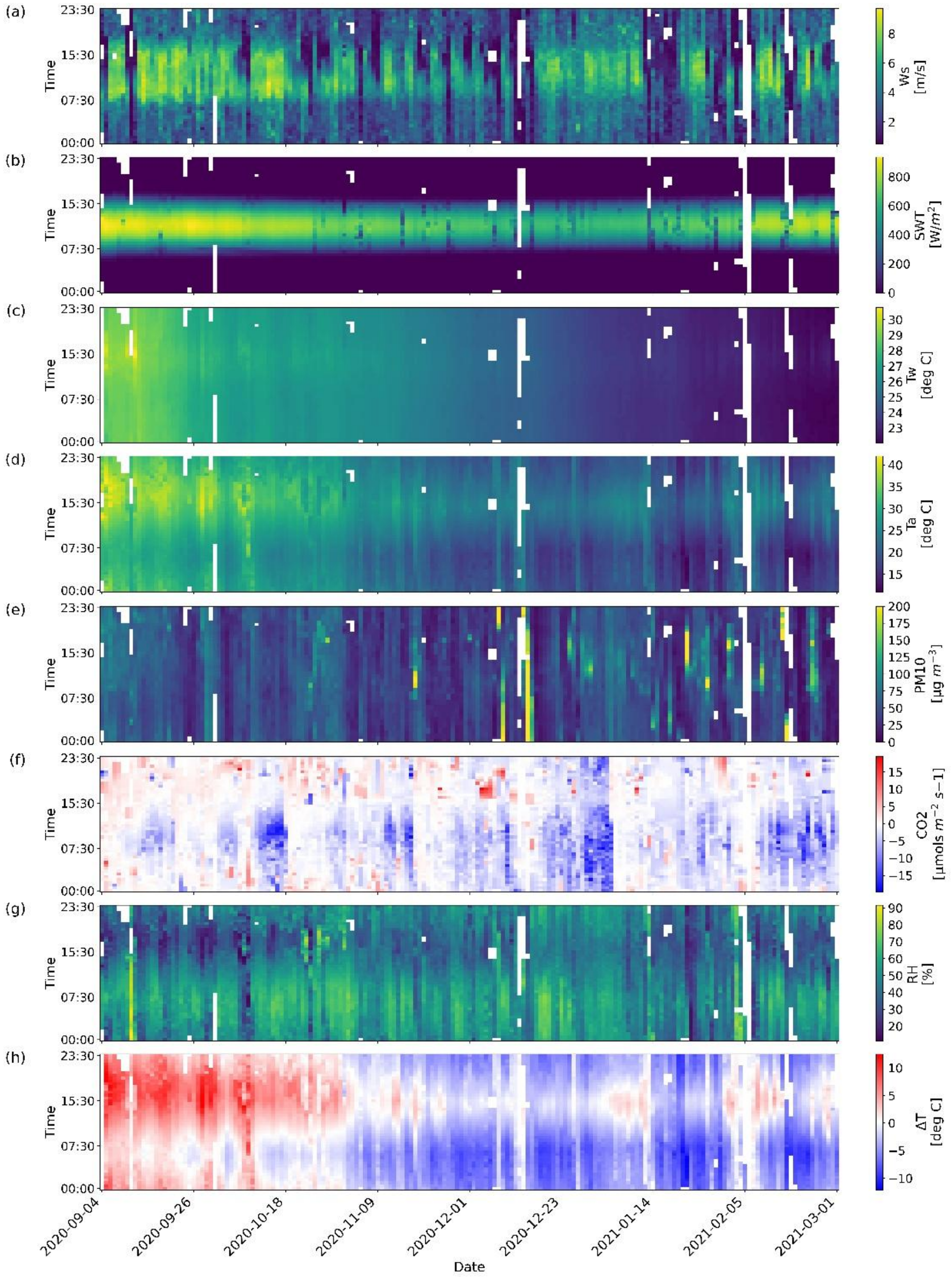

Figure 2. Heat map of measured wind speed (Ws) (a), incoming shortwave solar irradiance (SW) (b), water temperature (Tw) (c), air temperature (Ta) (d), particulate matter 10 microns in diameter or less (PM10) (e), carbon dioxide (CO_2) (f), relative humidity (RH) (g), and difference between air and water temperature (ΔT) (h), for the period 3 September 2020 to 2 March 2021 measured at the UOE field site. All times are local time (UTC +3 hrs).

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PM10 concentrations averaged 49.8 µg m^{-3} over the observation period with a maximum 30-minute concentration of 1200 µg m^{-3}. The absence of evidence of correlation between CO_2 flux and PM10 (r = 0.06) may reflect that such relationships are event specific and linked to dust chemistry, time of day, and prevailing coastal hydrodynamics. For example, at 0930 hrs 17 November 2020 CO_2 flux reached -18.90 µmols m^{-2} s^{-1} (influx) and then rapidly increased to +4.9 µmols m^{-2} s^{-1} (efflux) at 2100hrs 18 November 2020. This followed a dust event during the morning of the 18 November 2020, when PM10 concentrations peaked at 314 µg m^{-3} at 1100 hrs. Net CO_2 fluxes then remained positive (efflux) over the following days. In comparison, one month later PM10 concentrations peaked at 295 µg m^{-3} at 0600 hrs on 15 December 2020 after which net CO_2 fluxes became negative at 1900 hrs on 15 December 2020 and then increasingly negative (influx) until early January 2021.

Incoming solar radiation was not correlated with CO_2 flux (r -0.07). The introduction of a 3-hour lag between CO_2 flux and positive solar irradiance to allow for coral symbionts to respond to solar irradiance resulted in a change of sign with r = 0.08. CO_2 flux was negatively correlated with windspeed (r = -0.49) and relative humidity (r = -0.32). Accordingly, as windspeed and relative humidity increased, CO_2 influx increased. CO_2 flux displayed a positive correlation with air temperature (r = 0.40) and water skin temperature (r = 0.38) indicating that as air and water skin temperature decreased CO_2 influx increased. Over the entire 181-day monitoring period the mean 30-minute CO_2 flux measured by EC over the fringing coral reefs at Eilat was -2.07 (SD 3.74) µmols m^{-2} s^{-1} and displayed a weak trend of increasing influx from late summer into early winter (Figure 3a). This trend was not significantly correlated with the increase in measured daily Chlorophyll-a concentrations from late October to mid-December 2020 (Figure 3b) as confirmed by an R2 value of 0.1 nor PM10 concentrations (Figure 3b). This suggests that algae in the water column over the coral reef did not significantly influence air-sea CO_2 exchange.

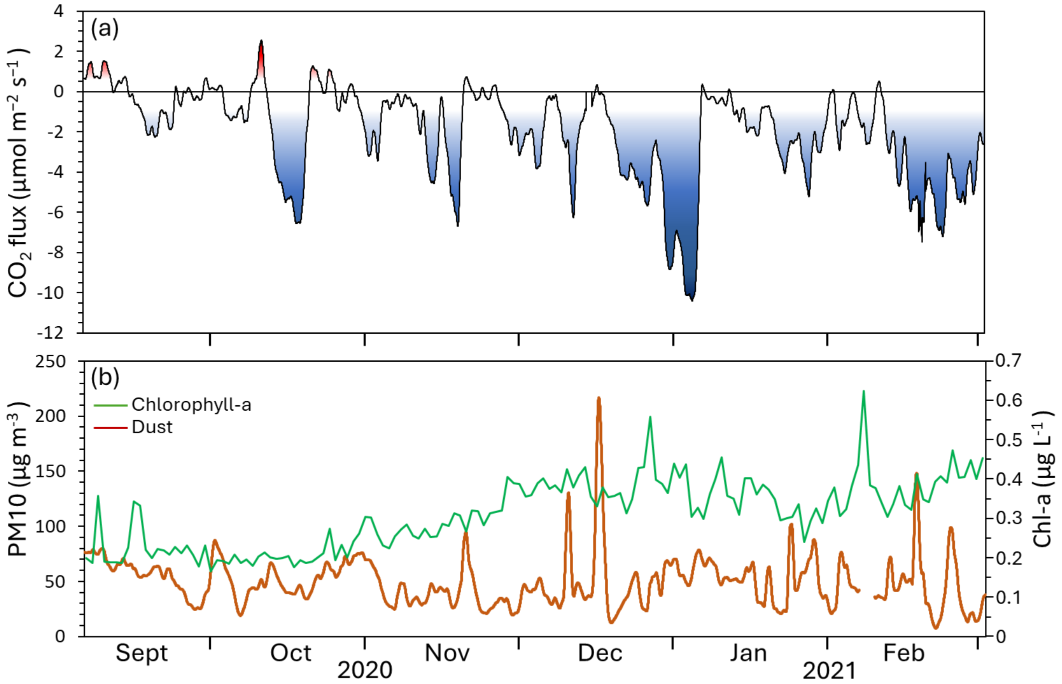

Figure 3. Time series (24 hr moving average) of EC CO_2 flux measurements made over the coral reef at the UOE field site (a), and PM10 concentrations measured at Eilat approximately 6.25 km to the northeast of the EC site (b), and Chl-a concentrations measured in water samples collected between 7 to 9 am daily approximately 200 m south of the UOE EC site 230 (b).

3.2 Diurnal CO_2 fluxes over coral reefs

The mean diurnal CO_2 flux cycle measured over the coral reef at Eilat for 181 days displayed a clear cycle with mean maximum influx -4.67 µmol m^{-2} s^{-1} in the early to mid-morning following sunrise, and a mean minimum efflux early evening after sunset 235 of 0.09 µmol m^{-2} s^{-1} (Figure 4). The most significant variability in CO_2 flux cycle occurred from late evening through to midday with notably less variability late afternoon and in the two to three hours following sunset as indicated by the standard deviation plots (Figure 4). The diurnal CO_2 flux cycle lagged the mean water skin temperature which displays relatively constant variability over the 181 days by around 4.5 hrs (Figure 4) indicating that both meteorological and biophysical processes are likely controlling air-sea CO_2 flux. Namely, photosynthesis following sunrise lowers reef water pCO_2 relative to 240 the atmosphere, while respiration and calcification from early afternoon onward including possible dark (nocturnal) calcification following sunset likely increased the reef water pCO_2 relative to the atmosphere. Following sunset the net downward CO_2 flux then became slowly increasingly negative which continued throughout the night as the water skin temperature decreased. Following sunrise, the surface water began to warm but the concurrent onset of photosynthesis likely continued to lower the water *p*CO_2 relative to the overlying atmosphere resulting in increasing CO_2 influx until late morning (Figure 4).

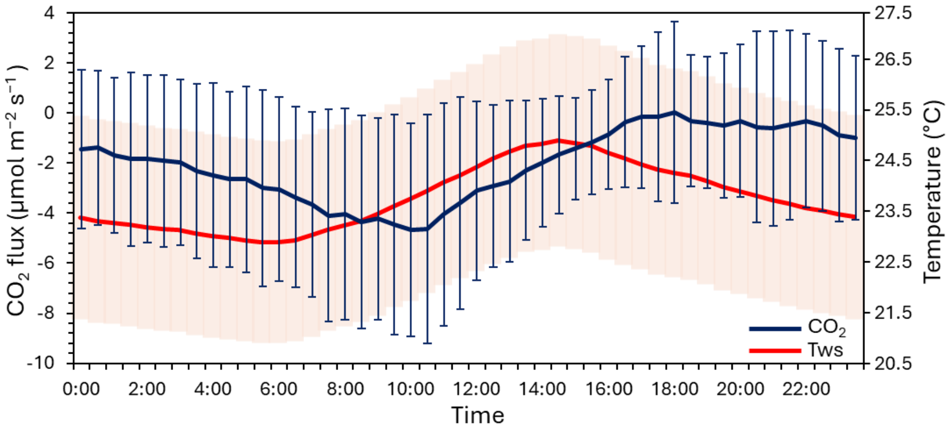

Figure 4. Mean 30-minute diurnal CO_2 flux and water skin temperature (Tws) for the full 181-day measurement period 3 September 2020 to 2 March 2021 with corresponding standard deviations (CO_2 flux blue bars; Tws pink shading).

Seasonally, following sunrise in late summer (September) there was rapid increase in the mean CO_2 influx of -2 µmol m^{-2} s^{-1} between 0600 hrs and 0730 hrs highlighting the substantial effect of the onset of photosynthesis (Figure 5a). The rate of CO2 influx then remained similar until 1000 hrs when it began to decrease as the mean water skin temperature reached 28 °C before peaking at 30.6 °C at 1300 hrs. The coral reef then remained a source of CO_2 to the atmosphere through until midnight after which net CO_2 flux remained close to zero until 0600 hrs (Figure 5a). During winter (January) the mean diurnal CO_2 flux cycle displayed the same general characteristics as observed during late summer (September) however, it remained negative indicating that the reef was a net CO_2 sink. The effect of the onset of photosynthesis on CO_2 influx was again clear by the rapid increase in CO_2 influx around 6:30AM following sunrise (Figure 5b). CO_2 influx then gradually decreased over the following hours reaching its mean minimum in the early evening of -0.25 µmol m^{-2} s^{-1} at 2000 hrs (Figure 5b) corresponding to a water skin temperature of 20.6 °C. In both months the standard deviation of the mean CO_2 flux was reasonably large reflecting daily variability throughout the month of the biophysical and hydrometeorological factors that control air – sea CO_2 exchange. However, during January and September the period with less variability in CO_2 flux was late afternoon into early evening (Figure 5a, b).

3.3 Carbon fluxes over coral reefs and other ecosystems

The measured CO_2 flux over the fringing coral reefs at Eilat was used to calculate the associated carbon (C) flux and then extrapolated to a mean annualised value for ease of comparison with reported measurements from other ecosystems. These

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include other marine environments, commercial pine plantations and tropical rainforests measured also by EC. These ecosystems are regularly highlighted as important global carbon sinks (Chambers et al., 2001; Brienen et al., 2015; Chan et al., 2018) (Table 1). Our results show that the mean net influx of C over coral reefs at Eilat ranges from around 4.5 times greater than reported in the literature for mangrove forests and cool temperate forests, to slightly more than subtropical commercial pine plantations only slightly less than the examples presented for Brazilian rainforests (Table 1). The net influx of C over coral reefs at Eilat is significantly greater than measured over the ocean in both tropical and high latitude locations (Table 1) although caution is warranted given the short observation periods of these measurements and their extrapolation to annual values.

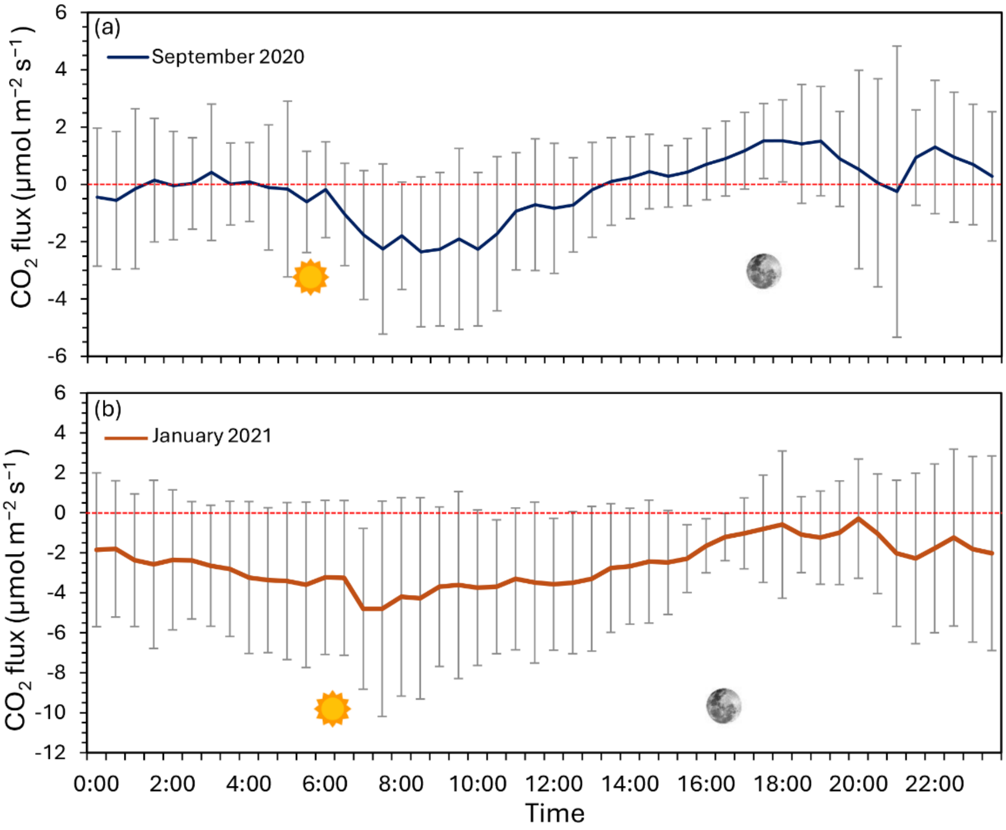

Figure 5. Late summer (September 2020) (a) and winter (January 2021) (b) diurnal mean 30-minute CO_2 fluxes and corresponding standard deviations (bars) with sunrise and sunset indicated. The horizonal red dashed line indicates 0 net air-sea CO_2 flux.

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Table 1. Examples of mean C exchange over different ecosystems calculated from CO_2 flux measurements compared to measurements made over coral reefs in the GoE including this study. All measurements were made using EC systems and therefore represent direct ecosystem – atmosphere C exchange. Published C fluxes have been converted to annual values for ease of comparison with ± 1 standard deviation shown if provided in the original publication.

Location (duration of observation)	**Ecosystem**	**t C ha yr^{-1} (SD) (negative influx)**
Eilat, Israel (3 Sept 2020 – 2 March 2021: 181 days) [This study]	Healthy fringing coral reefs only.	-7.8 ± 14.17
Eilat, Israel (1 April to 27 August of 2009: 142 days) (Rey-Sánchez et al., 2017)	Healthy fringing coral reefs and adjacent ocean.	-3.97 ± 5.3
Heron Reef, Great Barrier Reef, Australia (9-18 June 2009 & 3-7 February 2010) (McGowan et al., 2016)	Shallow lagoon with coral patches and bommies, and sand	-10.75
Maine, USA. (7 yrs) (Hollinger et al., 2004)	~90-year-old spruce dominated forest	-1.74 ± 0.46
Changbai Mountain Natural Reserve, northeastern China (1 yr) (Wang et al., 2010)	Montane forest (Dominant species Pinus koraiensis Sieb. et Zucc. (34%), Tilia amurensis Rupr. (42%)).	-1.88
Brazilian Amazon Basin - mean of 3 sites. (3 – 5 yrs) (Fu et al., 2018)	Brazilian rainforest	-10 ± 1.37
Central Japan (1 yr) (Saigusa et al., 2002)	Cool-temperate deciduous forest	-2.14
Bribie Island, Subtropical eastern Australia (2.5 yrs) (Lowry et al., 2021)	Coastal wetland (Dominant species - *Melaleuca quinquenervia*)	-5.61 ± 5.30
Bribie Island, Subtropical eastern Australia (2.5 yrs) (Lowry et al., 2021)	Pine plantation (*Pinus elliottii var. elliottii x Pinus caribaea var. hondurensis*)	-6.31 ± 4.53
Arctic Ocean (30 Jun–1 Aug 2019) (Dong et al., 2021)	Arctic Ocean	-1.62
Arctic Ocean (5 Aug–29 Sep 2019) (Dong et al., 2021)	Arctic Ocean	-2.62
Tropical Atlantic (9–16 Oct 2018) (Dong et al., 2021)	Tropical Atlantic Ocean	-0.40
Pichavaram, southeast India (1 yr) (Gnanamoorthy et al., 2020)	Mangrove forest	-1.83

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4. Discussion

Ecosystem productivity models, microscale chamber gas flux exchange measurements, and water – atmosphere chemistry studies have typically concluded that coral reefs are net sources of CO_2 to the atmosphere (Ware et al., 1992; Gattuso et al., 1999; Borges et al., 2005; Terlouw et al., 2019; Kayanne, 2025). Direct EC measurements of coral reef – atmosphere CO_2 flux (NEE) at ecosystem scale presented here show that the fringing coral reefs of the GoE are net sinks of atmospheric CO_2, and that they may sequester almost the same amount of atmospheric C as some Brazilian rainforest sites (Fu et al., 2018) (Table 1). Our results are aligned with a previous independent EC study of CO_2 flux in the GoE conducted over 142 days from April to August 2009. This study measured a mean CO_2 influx of -1.05 (SD 1.4) μmol m^{-2} s^{-1} at a site approximately 280 m south from our UOE site (Rey-Sánchez et al., 2017). However, the measurement footprint of this EC study extended beyond the coral reef and over the adjacent ocean with water depths from 40 to 550 m which have been found to absorb around 50% less CO2 on average than the fringing coral reefs (McGowan et al., 2022a). These measurements were made through late spring and summer, namely outside the months of the measurements present here, but they showed also that the coral reefs of Eilat were a net CO_2 sink (Rey-Sánchez et al., 2017). Rey-Sánchez et al., (2017) found CO_2 fluxes to be positively correlated with air temperature but negatively correlated with wind speed with high flux rates (influx) at night believed to be the result of higher diffusivity of CO_2 into the colder water.

Water skin temperature has been shown to significantly influence air-sea CO_2 exchange over oceans with the sensitivity of the pCO_2 in sea water estimated at > 4% °K of temperature change (Longhini et al., 2015; Woolf et al., 2016). Our results show that the diurnal air-sea CO_2 flux over the coral reefs at Eilat is highly correlated to the water skin temperature and that a 4.5 hr lag exists between water skin temperature maxima and minima and air-sea CO_2 flux maxima and minima throughout the diurnal CO_2 flux cycle (Figure 4a). During winter (January 2021) when the mean water skin temperature was < 22.7 °C the coral reef remained a CO_2 sink throughout the diurnal cycle. CO_2 influx over coral reefs in cooler winter months has also been reported at Coroa Vermelha on northeastern Brazil (Longhini et al., 2015). Cooling of the water skin temperature over lying the coral reefs at Eilat by the emission of thermal radiation is enhanced by evaporative cooling as the dry desert air blows over the coral reefs leading to 3.2 m of evaporation annually (Abir et al., 2022).

Collectively the CO_2 flux results from EC over the coral reefs at Eilat are aligned with research conducted near our field site three decades earlier when community productivity and calcification were calculated using the pH-O_2 method (Barnes & Lazar, 1993). This study found that the production:respiration ratio over the reef was 1.6:1 indicating the reef was a CO_2 sink at rates like those we report using EC. Similar production:respiration ratios have been reported for reef flats in Hawaii and elsewhere (Atkinson & Grigg, 1984).

Disparity between published CO_2 flux studies showing coral reefs as sources of CO_2 and results presented here showing that coral reefs in the GoE may be very significant net sinks of atmospheric CO_2 likely arise from: i) the often very small measurement/water sample footprints (i.e. cm^3 to a few m^2) of non-EC research which are often conducted in proximity to scleractinian coral dominated areas and do not fully represent the complexity of coral reef ecosystems and the effects of for example, epilithic algae, ii) short duration measurements (minutes to a few days), iii) incorrect assumptions about gas transfer velocities, iv) air – sea pCO_2 gradients calculated from point sampling of water chemistry and assumed atmospheric CO_2 concentrations from measurements made 10s to 100s of kilometres from the water sampling sites, and v) the role of meteorology and in particular water skin temperature on CO_2 solubility and air-sea exchange (Yan et al., 2011, 2016; Massaro et al., 2012; Lønborg et al 2019; Hannan et al., 2020). These studies that have often presented microscale site and time specific observations do not capture the heterogenous properties of complex coral reef ecosystems and their environment. Site factors that influence air – sea CO_2 flux such as ecosystem composition, meteorology, water temperature, hydrodynamics, wave environment, terrestrial runoff and aquifer seepage are all captured by EC measurements because of their large footprint which extends over thousands of square meters.

At Heron Reef on the southern Great Barrier Reef, Australia concurrent EC measurements found the shallow lagoon to be a net CO_2 sink (-2.27 µg m^{-2} s^{-1}), while the adjacent reef flat was a net source of CO2 ($+3.40$ µg $m{-}2$ $s{-}1$) to the atmosphere (McGowan et al., 2016). Here, seepage of CO_2 enriched water at low tide from the coral cay (Heron Island) was believed to contribute to the supersaturation of reef flat waters with CO_2 resulting in net evasion of CO_2 to the atmosphere. Concurrently over the shallow lagoon, photosynthesis by the benthic microalgae and corals was thought responsible for a net CO_2 influx (McGowan et al., 2016). Such variability highlights the need for ecosystem scale and multi-seasonal to annual continuous direct measurements of CO_2 flux over coral reefs.

While the majority of non-EC coral reef CO_2 flux studies have reported coral reefs as net sources of CO_2, scleractinian coral communities at two sites on Dapeng Peninsula in the South China Sea have also been found to be very weak net CO_2 sinks (0.48 ± 0.04 to 0.85 ± 0.20 µg m^{-2} s^{-1}) (Yang et al., 2023). Coral reefs at Lombok, Indonesia have also been found to be net CO2 sinks (0.07 to 0.56 µg m^{-2} s^{-1}) during October, but they switched to net sources in April (Afdal et al., 2023).

Recently interest has emerged in potentially establishing new or restoring coral reefs to potentially sequester CO_2. It has been estimated that floating coral nurseys with 106 coral colonies per 1 km2 could potentially sequester the equivalent of 110 t of CO_2 per year (Zhang et al., 2022). Thus, such coral reef restoration initiatives would not only have direct ecological benefits but would potentially sequester atmospheric CO_2 (Kayanne, 2025). A clearer understanding of the role of coral reefs in the carbon cycle as sources or sinks in different geographic and climate regimes, and their net impact on global atmospheric carbon is therefore required.

There remain differences in the determination of whether coral reefs are net sources or sinks of atmospheric CO_2, and the factors that may cause coral reefs to switch from source to sink and vice versa. For example, during our measurement period we found no clear and persistent association between dust fertilization of corals in the GoE and CO_2 flux as previously postulated and supported by in aquaria studies with GoE corals and dust (McGowan et al 2022a; Blanckaert et al., 2022). This may reflect variability in dust source chemistry, prevailing meteorology and hydrodynamics over the GoE coral reefs and the associated impact of coral photosynthesis. EC provides the only direct measurement method that can accurately quantify air-sea CO2 exchange at ecosystem scale that accounts for changes in water chemistry including that caused by the deposition of aerosols, coral reef hydrodynamics, meteorology, and coral reef ecology. Accordingly, EC should be used whenever possible to quantify air-sea CO2 exchanges over coral reefs and in preference to other methods including those that rely on estimated gas transfer velocities.

5. Conclusion

The uncertainty as to whether coral reefs act as a net source or sink of atmospheric CO_2 has prevailed for more three decades (Kayanne, 2025). However, there is growing evidence through research as we present here that when continuous direct measurement is undertaken at ecosystem scale, coral reefs such as those in the GoE are net sinks of atmospheric CO_2, potentially far exceeding CO_2 sequestration by commercial forestry plantations and only slightly less than some tropical rainforests although the areal extent (measurement footprint) of such EC studies that we cite for comparisons are unknown. Mean air – sea CO_2 flux (NEE) measured by EC from late summer to the end of winter (181 days) over the fringing coral reefs in the GoE was -2.165 (SD 3.441) μmol m^{-2} s^{-1} which equates to around -7.8 (SD 14.17) t C ha yr^{-1} assuming CO2 flux remains of similar magnitude during spring and summer – an assumption supported by an independent study (Rey-Sánchez et al., 2017). These results further highlight the value of ecosystem services provided by coral reefs and should strengthen the justification for their protection from a range of threats including global warming.

Our research also highlights the need to extend direct measurement of air – sea CO_2 exchanges over coral reefs to other locations and climate regimes such as the Indian, Pacific and Atlantic Oceans. Such research should, if possible, attempt to trace CO_2 pathways in the water overlying coral reefs including possible lateral transport and dissolution. For example, neither this study nor that of Rey-Sánchez et al., (2017) measured the concurrent pCO_2 in water overlying the coral reef and adjacent ocean to determine the influence of the tidal exchange of water under the EC measurement footprint on measured CO_2 flux. Measurements should be made over at least one full year, preferably longer, to capture all meteorological, hydrodynamic and biophysical processes that can reasonably be expected to affect CO_2 flux over coral reefs. This should include the possible influence of aerosol deposition on the productivity of coral reefs such as Ningaloo Reef – the world's largest fringing coral reef located under the northwest dust transport pathway from Australia. At locations where fertilization of coral reefs occurs by the deposition of aerosols in low-nutrient, low-chlorophyll marine environments, and where evaporative cooling of the water skin temperature is enhanced by local meteorological conditions, then the ability of coral reefs to behave as sinks of atmospheric CO_2 may be most evident.

Data Availability Statement.

Data and its descriptions used to create all figures in this paper are available (McGowan et al., 2025).

Author contributions

HM initiated the research and wrote the manuscript with contributions from NL, YS and SA. SA analysed EC data and prepared Figure 2. NL and SA managed instrumentation, while HM and NL obtained funding to support the research.

Competing interests

The authors declare no competing interests nor conflicts of interest.

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