Net ecosystem production of coral communities persisting under marginal environmental conditions

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Abstract. Coral communities in Hong Kong persist under a range of local stressors, including strong subtropical seasonality, chronic low light, and high turbidity, resulting in patchy, compositionally constrained communities relative to typical tropical reef systems. These challenging environmental conditions provide an opportunity to better understand how coral ecosystems may respond to changing ocean conditions in the future. Here, we used in-situ sensors to quantify high-resolution, community-scale net ecosystem production (NEP, organic carbon cycling) at three sites across a marine environmental gradient around Hong Kong. These communities were net respiring (negative NEP) across the gradient in both the wet (NEP_{mean}= -0.49 ± 4.83 mmol O_2 m^{-2} hr^{-1}) and dry seasons (NEP_{mean}= -0.21 ± 0.85 mmol O_2 m^{-2} hr^{-1}), with a significant increase in metabolic variability observed during the wet season (mean daily NEP range = 9.99 ± 13.34 mmol O_2 m^{-2} hr^{-1}) versus the dry season (2.38 ± 1.93 mmol O_2 m^{-2} hr^{-1}), associated with stronger variation in light and hydrographic conditions. This study adds to the small number of studies to date assessing in-situ metabolic variability of coral communities persisting under marginal environmental conditions. Understanding natural community-scale variability in organic carbon cycling is crucial for predicting how coral communities may cope with changing ocean conditions, thereby providing vital insights into the future of globally threatened coral reef ecosystems.

1 Introduction

Coral ecosystems offer crucial ecosystem services, such as supporting biodiversity hotspots, providing storm protection for coastal communities and tourism-related income (Moberg and Folke, 1999). However, the future viability of these ecosystems is threatened by a combination of global (Doney et al., 2009; Hughes et al., 2017) and local stressors (Tuttle and Donahue, 2022). We can better understand how coral communities might persist in the future by studying communities that are already surviving in challenging environments. While corals generally thrive in shallow, clear waters, coral ecosystems can persist under marginal environmental conditions and anthropogenic stressors (Schoepf et al., 2023), albeit typically with lower coral species diversity, slower growth rates, and without appreciable carbonate accretion (Heery et al., 2018). A key component of furthering understanding of how these corals are persisting in their environment is to understand how coral metabolic rates vary under local environmental stressors.

Corals in turbid, low-light environments, while having a compressed depth range (Morgan et al., 2020) and likely being more susceptible to sea-level rise due to higher light attenuation (Zweifler et al., 2021; Law and Huang, 2023), may be more resilient to future climate change due to shielding from heat and light stress (Morgan et al., 2017; Sully and Van Woesik, 2020; Rosedy et al., 2023) and may provide equal or even greater habitat capacity for associated organisms compared to clearer, higher coral cover reefs (Goatley and Bellwood 2011; Valino et al., 2026). These environments thus potentially serve as an important climate refugia (Cacciapaglia and van Woesik 2015). Hong Kong coral communities, which are subject to chronic low-light conditions and a compressed depth range (1-6 m Goodkin et al., 2011), may serve as a proxy for understanding how coral communities may change function under more restricted geographic ranges and turbid conditions in the future (Zweifler et al., 2021).

In addition to low light, coral communities around Hong Kong persist under challenging environmental conditions resulting from the subtropical climatology and local anthropogenic forcing (Goodkin et al., 2011; Duprey et al., 2017). Hong Kong's subtropical, monsoonal climate varies markedly throughout the year. The wet season, which lasts from April to October, is marked by higher water temperatures (up to 31 °C), higher nutrient and sediment loads into coastal waters, more rainfall, and decreased salinity due to increased freshwater flux. The dry season, which lasts from November to March, is distinguished by low water temperatures (down to 14 °C), little rain, and higher salinities (Morton, 1989). Other local stressors, such as sea urchin-derived bioerosion (Dumont et al., 2013; Xie et al., 2020; Yeung et al., 2021), recreational activities (Chung et al., 2013), and elevated eutrophication rates (Duprey et al., 2016), fluctuate spatiotemporally around Hong Kong and can have short- and long-term impacts on the health of coral communities. An east-west environmental-urbanization gradient linked to human populations and discharge from the Pearl River disproportionally affects Hong Kong's western waters. Therefore, most of Hong Kong's corals are now found farther away from the Pearl River Estuary, in the eastern, more oceanic waters of the territory (Duprey et al., 2020). High turbidity from elevated nutrients and sedimentation results in low-light conditions across Hong Kong. Despite these challenging environmental conditions, high coral cover areas can still be found in the Eastern waters of Hong Kong. Therefore, coral communities in Hong Kong may be classified as 'marginal' for a variety of reasons (see Schoepf et al., (2023) for 'marginal' classification details), depending on where they are located along the east-west environmental gradient. While the degree of structural marginality (coral cover, richness, community composition) can be more easily assessed with traditional benthic surveys, the functional marginality (see Brandl et al., (2019), Schoepf et al., (2023) of a coral community can only be obtained through the quantification of a core process in coral community functioning. In this study, we focus on net ecosystem production (NEP) as one measure of community-scale organic carbon cycling, allowing us to assess how this component of functional performance varies across the environmental gradient of Hong Kong.

A benthic community's NEP is proportional to the gradient in dissolved oxygen (DO; McGillis et al., 2011) of the overlying seawater column and reflects the cycling of organic carbon and the balance between photosynthesis and respiration (Andersson and Gledhill, 2013). The magnitude of NEP generated by a benthic community can change over space and time depending on the local biogeochemical environment (i.e., benthic community composition (Page et al., 2019)) and physical

environment (i.e., increased residence time (Falter et al., 2012) or wave action (Long et al., 2013)). NEP will increase DO through photosynthesis and lower DO through respiration (Turk et al., 2015; Lowe et al., 2019). Additionally, NEP will naturally fluctuate over diel to seasonal timescales and can be linked to the diversity of benthic communities (Takeshita et al., 2018), with more diverse and rich ecosystems tending to display greater metabolic variability (Page et al., 2017) and higher rates of net productivity (+NEP) (Odum and Odum 1955; Long et al., 2013; Cyronak et al., 2018). In contrast, lower rates of NEP have been associated with more degraded reef environments (Kayanne et al., 2005; Takeshita et al., 2016; McMahon et al., 2019; Webb et al., 2021). Therefore, NEP can provide insight into one critical component of ecosystem function, namely community-scale organic carbon cycling (Allgeier, 2024). This community-scale variability has not been assessed in-situ in a highly urbanized coral environment like Hong Kong, which is subject to chronic local stressors.

Globally, community-scale organic metabolism over coral habitats remains under-examined (Platz et al., 2022). In Hong Kong, measurements of coral productivity have only been made at the level of individual corals (Dellisanti et al., 2020) or in mesocosm settings (McIlroy et al., 2019), with no assessments of in-situ NEP at a community scale. Community-scale NEP can change rapidly across small spatial scales, and the results of individual coral-scale metabolic rates may not be adequate for extrapolation to the community as a whole (Page et al., 2017). Understanding natural community-level variability is thus crucial for assessing how coral communities may change under future ocean conditions. Therefore, rather than extrapolating estimates from a single species, investigations should include the metabolic signal of the whole community (Edmunds et al., 2016) to better forecast how community organic carbon cycling may change in the future (Kekuewa et al., 2021). Accordingly, the main objectives of the study were to (1) characterize the natural spatiotemporal variability in coral community organic metabolism through in-situ NEP measurements along the environmental-urbanization gradient in Hong Kong, and (2) identify environmental factors that are the primary drivers of changes in NEP. Such information on the natural variability and environmental drivers of coral community-scale organic carbon cycling is essential to understand how corals will persist under shifting local and global ocean conditions, including increasing prevalence of marginal environmental conditions.

2 Materials and methods

2.1 Study sites

Three study sites were selected to represent a spectrum of environmental conditions around Hong Kong that still support corals, from east to west: Tung Ping Chau (22.5451°N, 114.4326°E), Sharp Island (22.3639°N, 114.2903°E), and Sham Wan (22.1861°N, 114.1359°E) (Fig. 1).

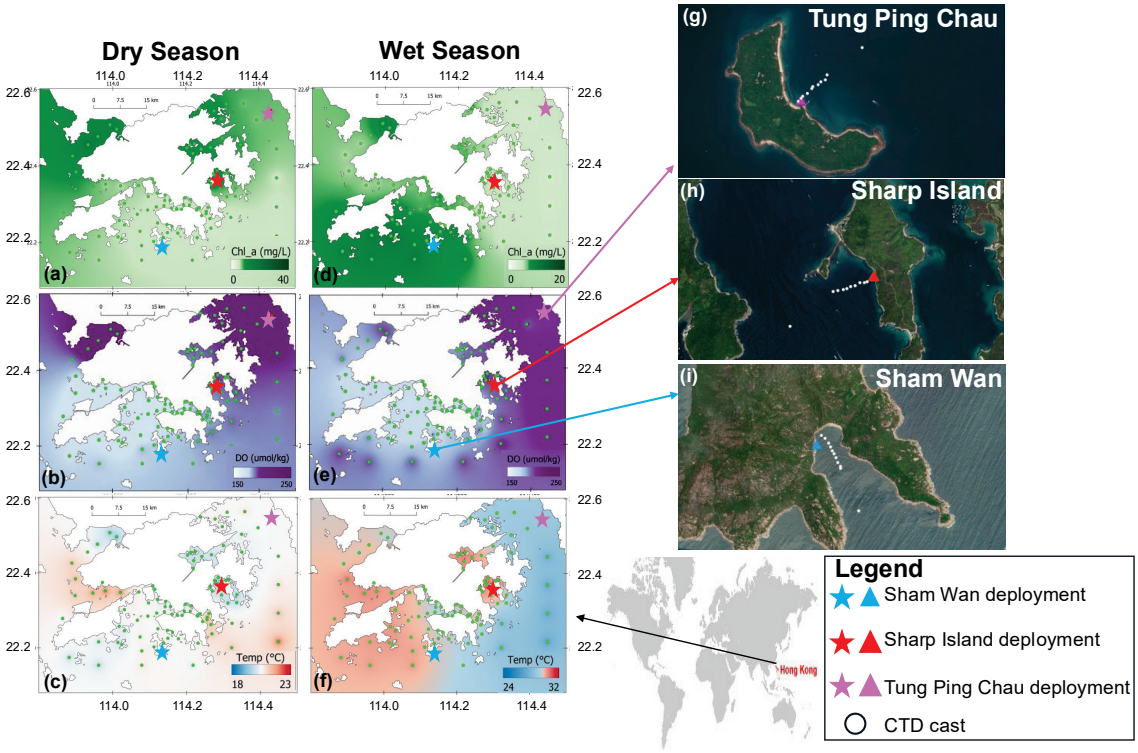

Figure 1. Marine spatial west-east environmental gradients and deployment locations around Hong Kong. Gradients during the dry (a, b, c; December 2021-January 2022) and wet (d, e, f; September-October 2022) season are shown for chlorophyll-a (a, 0-41 mg/L; d, 0-20 mg/L), temperature (b, 18-23 °C; e, 24-32 °C) and dissolved oxygen (c & f, 150-250 µmol kg^{-1}) based on Environmental Protection Department (EPD) data measured at the sampling stations shown with green dots. Gradient flux instrument deployments (see Table 1) were undertaken to characterize community-scale NEP at 3 sites: (g) Tung Ping Chau (purple star), (h) Sharp Island (green star), and (i) Sham Wan (blue star). At each site, CTD casts were undertaken along a transect denoted by the white circles. Satellite images in g-i derived from (Imagery © 2023 NASA, Map data © 2023 Google). The inset map shows the location of Hong Kong (indicated by a red square) in relation to mainland China and the northern South China Sea.

Coral ecosystems in eastern Hong Kong have high species diversity and abundance and are less affected by Pearl River discharge (Goodkin et al., 2011). Tung Ping Chau is especially isolated from the rest of Hong Kong, lying 10 km from the Hong Kong coast in Mirs Bay. While the waters surrounding Tung Ping Chau have previously been reported to have among the highest coverage and diversity of hard corals in Hong Kong (Xie et al. 2020), our surveys showed less coral cover around our deployment at Tung Ping Chau than at Sharp Island. However, Sharp Island in the past has shown evidence of higher bleaching rates than other sites in Hong Kong (Xie et al., 2020). During our deployments, outside peak summer conditions, there were no signs of significant bleaching affecting the community, likely due to rapid recovery of corals that bleached in August 2022, leading to near full recovery within months (Chung et al., 2024). The south of Hong Kong lies in the transitional zone where coral assemblages are still sporadically present, but abundances are limited by the impact of the Pearl River

discharge (Duprey et al., 2016). Sham Wan, which is located in the middle of this transition zone and dominated by rocky substrate (Yeung et al., 2021), was selected to represent the westernmost extent at which coral communities persist in Hong Kong.

The location of instrument deployments within sites were chosen based on visual inspection of the benthos by SCUBA divers such that the deployments were surrounded by relatively uniform coral communities on all sides that were roughly representative of the broader sites' composition. A summary of deployment parameters is available in Table 1. Changes in flow direction will lead to metabolism data being generated from different areas of benthic communities. Therefore, in this study, we selected deployment sites that were well surrounded, on all sides, by coral cover as uniformly high as possible to account for unpredictable flow patterns.

Table 1. Summary of deployments during the dry (2021) and wet (2022) seasons showing the location, season, deployment dates, the mean and range in depth of deployment (in m), deployment duration (in days), and mean (± S.E.) NEP value for each deployment.

Season	*Location*	*Dates*	*Depth (m)*	*Duration (days)*	NEP_{MEAN} *(mmol* O_2 m^{-2} hr^{-1}*)*
Dry	*Sham Wan*	*23–30 Dec 2021*	*5.8 (4.7-6.7)*	*7*	*-0.37 ± 1.3*
	Sharp Island	*19–26 Nov 2021*	*3.3 (2.4-4.3)*	*7*	*0.12 ± 1.3*
	Tung Ping Chau	*30 Nov – 7 Dec 2021*	*3.8 (2.7-5.2)*	*8*	*-0.22 ± 0.9*
Wet	*Sham Wan*	*28 Oct – 11 Nov 2022*	*5.7 (4.5-6.8)*	*14*	*-0.37 ± 0.6*
	Sharp Island (May)	*18–24 May 2022*	*3.7 (2.7-4.9)*	*6*	*-1.39 ± 3.0*
	Sharp Island (Oct)	*29 Sept – 6 Oct 2022*	*3.6 (2.7-4.6)*	*7*	*0.15 ± 9.4*
	Tung Ping Chau	*11–21 Oct 2022*	*2.8 (2.0-3.6)*	*11*	*-0.59 ± 2.3*

To encompass major seasonal variations, deployments were carried out at each site during the dry season (Nov-Dec 2021) and at the end of the prolonged wet season in 2022 (October 2022; Table 1). An additional deployment was completed earlier in the wet season (May 2022) at Sharp Island. Although October often marks the transition period between wet and dry season conditions, the October 2022 deployments were classified as wet season because Hong Kong temperatures remained elevated during this period. Specifically, Hong Kong experienced its hottest autumn on record in 2022, with a mean air temperature of 26.4 °C from September to November (Hong Kong Observatory, 2022). Furthermore, the mean water temperature measured during our October 2022 deployments (25.89 ±2.13 °C) was characteristic of the long-term (1991-2020) average wet season (April-October) SST values recorded by HKO (https://www.hko.gov.hk/en/cis/normal/1991_2020.htm, Table 9., Waglan Island 1400 or 1700 hours) of 26.09 ± 2.02 °C, in contrast to the long-term average dry season (Nov-March) SST value of 19.58 ± 2.65 °C. We therefore refer to these as late wet-season deployments due to the elevated water temperatures extending into our deployment periods.

2.2 Water quality data and atmospheric conditions of Hong Kong

The environmental gradient around Hong Kong was characterized using periodic monitoring data collected by the Environmental Protection Department (EPD, https://cd.epic.epd.gov.hk/EPICRIVER/marine/?lang=en, date accessed Dec 15, 2023), focusing on the monthly data from the wet (September, October 2022) and dry season (December 2021, January 2022), closest to our deployment dates (Figure 1a-f). Surface-water data collected at 1 m depth was used because it best reflects the environmental conditions experienced by local coral communities due to their typically shallow distribution (1-6 m, Goodkin et al., 2011). For monitoring sites with multiple days of observations during the period of interest, values were averaged to give one seasonal value per station. The variables examined included dissolved oxygen (DO), turbidity, chlorophyll-a (chl-a), temperature, and salinity. DO was converted from mg L^{-1} to µmol kg^{-1} for consistency in DO units used in this study. A constant density value of 1021.08 kg m^{-3}, the mean density value of the CTD casts, was used for this conversion. Using this density value was necessary for unit conversion due to pressure not being provided in the EPD dataset. Standard error of the mean (SEM) was reported instead of standard deviation (SD) with the means of the EPD data to better show variability across seasons. The examined variables were selected due to their ecological relevance to coral reef metabolic processes (Ferrier-Pages et al., 1999; Sawall et al., 2011; Long et al., 2013; Bessell-Browne et al., 2017; Nelson and Altieri, 2019) and availability across both seasonal periods during the deployment periods. Because EPD monitoring data are collected at monthly resolution, these values are used to characterize broad spatial and seasonal environmental context rather than the exact conditions experienced during each of the short-term deployments.

Atmospheric weather conditions were provided by the Hong Kong Observatory (HKO, date received Dec 22, 2022) for the period of 2013 through 2022. Atmospheric variables used in analysis were global solar radiation (MJ m^{-2} h^{-1}), wind speed (m/s) and rainfall (mm) due to their applicability in interpreting benthic light (Roth, 2014; Hochberg et al., 2024), turbidity (Riegl and Branch, 1995; Browne et al., 2014), salinity (Coles and Jokiel, 2018; Moberg et al., 1997; Manzello and

Lirman, 2003) and mixing of the water column (Dennison and Barnes, 1988; van Hoytema et al., 2016), respectively. Each of these factors could impact measured NEP and can help explain seasonal differences.

2.3 Benthic community composition

The benthic community composition of these locations, including substrate composition and the cover for each coral genus, was characterized based on underwater video surveys conducted at each site from September–October 2022. The surveys used a GoPro Hero4 Black camera to capture video transects based on a timed (5 min) swim from a roving diver, moving in a spiral motion outward and away from the deployed gradient flux system. Benthic analysis was undertaken using CoralNet (Beijbom et al., 2015). Photo quadrats were extracted from each video transect at approximately 10 second intervals. Due to poor quality (i.e., too blurry) of a few extracted images, we eventually were only able to obtain 28, 28, and 25 usable photo quadrats for Tung Ping Chau, Sharp Island, and Sham Wan, respectively. From each extracted photo quadrat, 100 random points were overlaid on each image with an annotation area set to exclude 20 % of the area from the peripheral to ensure no overlap between images. Major biotic and abiotic benthic groups (sand, rock, rubble) were annotated, and hard corals were identified to a finer genus level with notes on their health status (i.e., live and dead) when possible. Artificial items and unidentifiable or unknown objects were labelled as "Others-Abiotic" and "Unknown/Unidentifiable", respectively. Benthic community composition was presented as percent cover (%) for each benthic category. Macroalgae and turf algae were included as groups as well, but no significant coverage was identified for record at any of our sites. This finding is supported by past benthic studies completed in Hong Kong that showed algal abundance peaking during early Spring months and decreased substantially during the summer and early winter months (Yeung et al., 2021; Cheung-Wong et al., 2022).

2.4 Coral community metabolism measurement: gradient flux approach

To characterize the metabolic rates of Hong Kong coral communities, we collected autonomous measurements of benthic metabolism at high temporal frequencies (minutes) using a gradient flux (GF) approach, which tracks chemical and velocity gradients in the benthic boundary layer to estimate benthic metabolic rates (McGillis et al., 2011). The gradient flux technique has been used to assess NEP (McGillis et al., 2011; Turk et al., 2015; Takeshita et al., 2016; Coogan et al., 2022) on natural coral reefs, and at coral restoration sites (Platz et al., 2020). The GF approach relies on estimates of the mean chemical flux of DO from the benthic boundary layer to calculate NEP. In this study, the GF instrumentation consisted of two DO sensors (MiniDOT, Precision Measurement Engineering (PME), Vista, California, USA) and two velocimeters (Vector, Nortek, Norway) positioned at two heights above the benthos, Z_1 and Z_2. The lower height (Z_2) was positioned 8cm above the substrate, and the top height (Z_1) was 124cm above the substrate. It should be noted that our lower height (8cm) was positioned closer to the substrate than previous gradient flux studies (i.e. 10cm (Pisapia et al., 2019); 20cm (McGillis et al., 2011; Boles et al., 2026); 30cm (Takeshita et al., 2016)) because the coral canopy at our sites is relatively low and patchy compared to other study sites higher-relief more complex canopy settings. Therefore, this height was selected to remain within the benthic boundary layer while also avoiding direct obstruction by the benthos. The two DO sensors (accuracy = ±9.5 μmol kg^{-1}) were

cross calibrated immediately after each deployment to correct for any offset between the two sensors that could impact the DO gradient and to minimize the impact of the uncertainty associated with the sensor accuracy. Fluxes of DO (mmol m^{-2} h^{-1}) were calculated using Eq. (1) (McGillis et al., 2011; Platz et al., 2020):

$$J_{DO} = \rho u^* \kappa \left(\frac{DO_{z1} - DO_{z2}}{ln\left(\frac{z_1}{z_2}\right)} \right) \quad (1)$$

where ρ is the seawater density (kg m^{-3}), u^* is the friction velocity (m s^{-1}), κ is the Kármán constant (0.40). This value is widely used for turbulent boundary layers and is supported by observations from coastal and reef environments, where κ typically falls within 0.35–0.50 (e.g., Gross & Nowell 1983). Although κ can vary with local roughness and wave–current interactions, its inclusion in the diffusivity term is linear; therefore, using κ = 0.40 is appropriate and provides a robust estimate for our sites. As above, Z_1 and Z_2 are the higher and lower pump heights (m), respectively. DO_{zx} is the chemical concentrations (µmol kg^{-1}) at the respective heights z_x (z_1 or z_2). The friction velocity was calculated using Eq. (2) as described in McGillis et al. (2011):

$$u^* = \kappa \left(\frac{U_{z1} - U_{z2}}{ln\left(\frac{z1}{z2}\right)} \right) \quad (2)$$

where U_z is the 3-axis water velocity at the respective sensor height (m s^{-1}).

Metabolic rates are proportional to these chemical fluxes (McGillis et al., 2011) and were calculated based on Eq. (3) as:

$$NEP = -(J_{DO}) \quad (3)$$

2.5 High frequency in-situ characterization of prevailing environmental conditions

The salinity (S) of the seawater was determined using a miniature CTD sensor (Accuracy = ±0.05 mS cm-1, DEFI-CT, JFE Advantech, Tokyo, Japan) attached halfway between the two sensor heights on the GF frame. At each height, the respective velocimeter was used to measure, in addition to water velocity, the pressure (P) and temperature (T) of the seawater. Deployment settings for the Vectors were set to sample at a rate of 16hz with burst sampling interval of 60 seconds using ENU coordinate system. These settings were maintained across all deployments. During each deployment, a photosynthetically active radiation (PAR) sensor (accuracy = ± 5%, MiniPAR, PME, Vista, California, USA) was also deployed directly on the benthos next to the gradient flux system to record incident light levels, far enough away to avoid shading by the instrument. All sensors collected one data point every 60 seconds and were averaged over 10 minutes for final data analysis.

We also measured the vertical structure of the water column, in terms of T (°C), S (ppt), DO (µmol kg^{-1}), and chl *a* (mg L^{-1}), along an onshore-offshore transect across each coral community using a RINKO-profiler CTD (ASTD102, JFE Advantech, Tokyo, Japan) set to process data in 0.1 m depth bins through the water column. Due to logistical constraints, casts

were only performed during the wet season deployments. Ten casts were made per site with the exact location of each cast shown by the white dots in Fig 1g-i.

2.6 Data pre-treatment

Data was omitted when gradient flux assumptions were not met. Firstly, data were omitted when the top sensor velocity was lower than the bottom sensor velocity, showing that there was no law-of-the-wall relationship between the substrate boundary layer and the overlying water column (Platz et al. 2020). Because gradient-flux estimates require sufficient turbulent mixing, periods of very low near-bed flow were excluded. Rather than applying a single fixed velocity cutoff across all deployments, we removed observations falling below the 10th percentile of bottom-sensor velocity within each deployment. This deployment-specific threshold was selected to exclude the weakest-flow periods most likely to violate gradient-flux assumptions while accounting for differences in background flow among sites and seasons.

A non-steady state boundary layer unsuitable for gradient flux analysis was indicated when the standard deviation of the 60-second DO measurements within each 10-minute averaged time period was in the top 10% of the distribution (> 90^{th} percentile), determined for each deployment individually; data was discarded in such cases. To ensure confidence in velocity measurements, ADV vector velocities were omitted when the correlation of any individual beam was < 50 %. If > 10 % of the burst sample (more than 1 of the 10 samples in each burst) was omitted, then that burst sample was not included in the 10-minute average velocity values used for further analysis, similar to the filter methods used in Coogan et al. (2022). These data cutting steps are necessary to reduce artefactual flux measurements. The retained dataset represents only periods when all gradient flux assumptions were met, not necessarily every condition experienced during the deployment.

The 10-minute average values were used to provide time series for all environmental variables. Approximately 54.47% of the dry season data and 62.94 % of the wet season data was removed with these filters applied, averaged for all deployments, omitting for Sham Wan in the wet season, where 86.04 % of data was removed largely due to a malfunction with the bottom DO making metabolism calculations impossible. Hourly-averaged NEP rates were used for plotting these time series. Any gaps in the time series are the result of either sensor failure due to water leakage or battery malfunction or, in the case of measurements of metabolism, violations of the conditions required for gradient flux calculations described above. All calculations related to metabolism were performed in MATLAB (R2020b, The MathWorks Inc, Natick, Massachusetts, USA).

2.7 Statistical analyses

To assess spatial and diel variation in community metabolism, we conducted non-parametric statistical tests on NEP for each deployment. Analyses were performed separately for the dry season and wet season datasets. Timestamps were categorized into “Day” (7am-6pm) and “Night” (6pm-7am). Mean values were computed separately for each time category at each site. To test for significant differences in NEP between Day and Night, we applied the Mann–Whitney U test for each site individually. A Bonferroni correction was used to adjust for multiple pairwise comparisons ($\alpha = 0.05$). For deployments with valid data in both diel periods, the Mann–Whitney U statistic, raw p-value, and Bonferroni-adjusted p-value were calculated.

To identify the environmental variables most strongly associated with changes in NEP during each deployment, we quantified pairwise correlations between NEP and measured environmental parameters. Prior to this analysis, NEP values were regressed against PAR to isolate the light-driven component of NEP variability that would otherwise obscure the relationship between PAR and other measured variables (Khrizman et al., 2025). For each deployment, a simple linear model of the form:

$$NEP_{expected} = \alpha \times PAR + C \quad (4)$$

where α is the photosynthetic efficiency coefficient determined through the slope of the NEP/PAR relationship, and C is the intercept at zero irradiance. The residuals of this model,

$$NEP_{residual} = NEP_{observed} - NEP_{expected} \quad (5)$$

represent the portion of NEP variability independent of irradiance. Pearson correlation coefficients (r) and associated p-values were then computed between both the original NEP and the light-removed NEP residuals and each environmental predictor variable (water velocity, temperature, depth and salinity). Only relationships that were statistically significant ($p < 0.05$) were retained for result reporting and discussion.

Because assumptions of normality and equal variance were not met for several variables in the extracted EPD dataset, we employed the Mann-Whitney U test to determine whether median values of each parameter differed significantly between seasons. A significance threshold of $p < 0.05$ was used to identify meaningful seasonal differences. Simple linear regression was used to determine the correlation between PAR measured in-situ and global solar radiation derived from HKO weather data to examine light attenuation at the benthos. Global solar radiation was converted from Mj m^{-2} hr^{-1} to PAR units of µmol m^{-2} s^{-1} for slope comparison using a two-step process. First, global solar radiation values were converted to irradiance in watts per square meter (W m^{-2}) by multiplying by 277.78, recognizing that 1 MJ m^{-2} h^{-1} equals 277.78 W m^{-2}. Subsequently, to approximate PAR, the irradiance values were multiplied by an empirical conversion factor of 2.02 µmol J^{-1}. This factor reflects the proportion of solar energy within the PAR spectrum (400–700 nm) and is consistent with values reported in previous studies (Wang et al., 2024). The complete conversion formula is as follows:

$$PAR = Global\ solar\ radiation\ x\ 561.1 \quad (6)$$

Data from the HKO was analyzed according to a targeted dataset corresponding to the instrument deployment periods in the dry season (November–March 2021) and wet season (April–October 2022). For each environmental variable, we parsed and combined all relevant stations that measured a variable of interest (Light: Sai Kung; Wind speed; Sai Kung, Ping Chau and Lamma Island; Rainfall: Sai Kung, Ping Chau and Lamma Island). Values were grouped into wet season (April–October) and dry season (November–March) for the long-term dataset. For the deployment-time-specific dataset, seasonal grouping followed calendar year (i.e., dry = 2021; wet = 2022). We calculated seasonal means, standard deviations (±SD), and ranges for each variable. To test significant differences between wet and dry seasons within each dataset, we first assessed the normality of the data using the Shapiro-Wilk test. All variables were found to deviate significantly from a normal distribution

($p < 0.05$), so non-parametric Mann-Whitney U tests were used to compare medians between seasons. Kruskal-Wallis and associated post-hoc Dunn's test was used to test for difference in weather variables between deployments within seasons as well.

3 Results

3.1 Environmental conditions

3.1.1 Characterization of the vertical biophysical profile across sites

CTD casts measuring the range and mean (± SD) temperature, DO, and chl *a* were completed in October 2022 to assess the vertical water column structure at each site (Fig 2). DO stratification is reported as the average difference in DO (ΔDO) between the top and bottom cast from each deployment. Temperature along the Tung Ping Chau transect was spatially uniform (Fig 2b), averaging 28.0 ± 0.1 °C (range = 27.9–28.3 °C) with minimal vertical stratification ($\Delta T = T_{surface} - T_{bottom} = 0.18$ °C). Dissolved oxygen concentrations were similarly homogeneous (mean = 173.7±2.8 μmol kg^{-1}; range = 167.7-181.8 μmol kg^{-1}) with weak stratification (ΔDO=−5.45±1.92 μmol kg^{-1}) (Fig 2c). Chlorophyll concentrations were low to moderate (0.79 ± 0.28 μg L^{-1}; range = 0.35–1.42 μg L^{-1}) and exhibited weak vertical gradients (Fig 2a), indicating well-mixed, oxygenated conditions across the CTD transect. The narrow temperature and DO ranges observed in the contour plots support limited water-column stratification and low variability with distance from shore. Sharp Island displayed the greatest vertical and spatial variability among the three sites. Temperatures averaged 29.2 ± 0.4 °C (range = 28.7–29.8 °C) (Fig 2e) with a mean surface–bottom gradient of 0.8 °C, reflecting moderate thermal stratification. Dissolved oxygen varied substantially (Fig 2f), ranging from 69.45 to 183.53 μmol kg^{-1} (mean = 169.28 ± 22.60 μmol kg^{-1}) with strong stratification in DO (ΔDO =−81.53 ± 33.70 μmol kg^{-1}). The DO contour plot shows an oxygen minimum near the seabed in offshore casts. Chlorophyll concentrations (mean 0.79 ± 0.67 μg L^{-1}; range = 0.22–2.99 μg L^{-1}) (Fig 2d) increased offshore and at depth, aligning with enhanced stratification and possible subsurface productivity layers. Overall, the sharper vertical gradients at Sham Island indicate stronger water column stability and low DO conditions in deeper water compared to the other sites.

At Sham Wan, temperature averaged 25.3 ± 0.9 °C (range = 24.0–26.8 °C) (Fig 2h) with modest vertical gradients ($\Delta T \approx 0.24$ °C). Dissolved oxygen was slightly higher on average than at the other sites (153.03±14.35 μmol kg^{-1}; range = 124.00 to 178.44 μmol kg^{-1} (Fig 2i) and showed weak stratification (ΔDO = 6.16 ±1.75 μmol kg^{-1}). Chlorophyll concentrations were lower and more uniform (0.67 ± 0.37 μg L^{-1}; range = 0.06–1.48 μg L^{-1}) (Fig 2g), consistent with vertically mixed, well-flushed conditions within this semi-exposed embayment. The CTD transects highlight limited vertical structure and relatively high oxygenation throughout the water column, suggesting efficient turbulent exchange and minimal stratification.

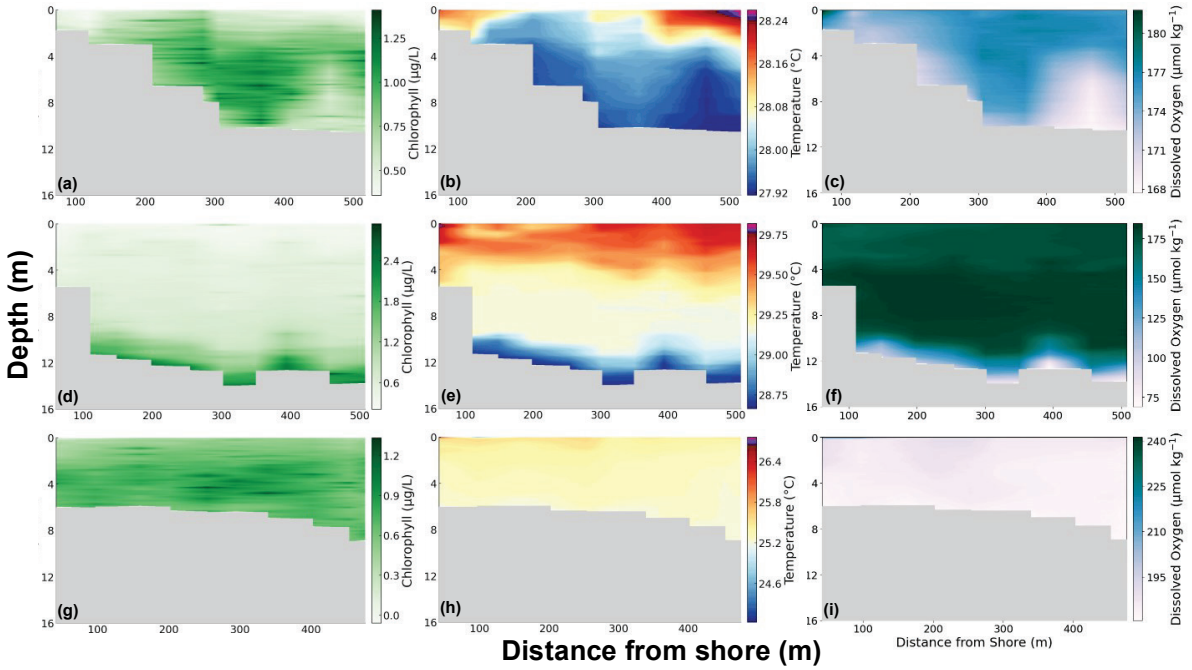

Figure 2. Vertical water column structure at each site. Contours show (A, D, G) chl a (in mg/L), (B, E, H) temperature (in °C) and (C, F, I) dissolved oxygen (in µmol kg^{-1}) based on CTD casts taken in October 2022 at each of the deployment sites. Tung Ping Chau (row 1): (A) chl a, (B) temperature and (C) DO. Sharp Island (row 2): (D) chl a, (E) temperature and (F) DO. Sham Wan (row 3) (G) chl a, (H) temperature, and (I) DO. The distance from shore of the CTD casts is shown on the x axis.

3.1.2 Seasonality in the environmental water quality gradient

Based on EPD data collected during both deployment seasons (see Table S1 for full list of means (± SEM) and ranges), the wet season was less saline, more turbid, and displayed higher temperatures and lower DO than the dry season. Mann-Whitney U-tests revealed significant differences in the means between seasons of each variable tested (p-value <0.05), except for chl-a (p-value = 0.079; Table S1). The wet season (Figure 1d, e, f) exhibited highly variable turbidity, with a mean value (± SEM) of 27.9 (±4.3) NTU. Salinity had a wide range in the wet season (17.5 to 33.9 psu) and lower DO (mean = 165.9 (±1.8) µmol kg^{-1}). Temperatures averaged 28.4 (±0.11) degrees Celsius during the wet season.

The dry season (Figure 1a, b, c) displayed less turbid, more saline water, lower temperatures, and higher DO compared to the wet season. Dry season turbidity had a mean value of 19.3 (±2.1) NTU. Salinity values ranged from 18.8 to 34.4 psu. DO had a mean value of 197.3 (±1.8) µmol kg^{-1}. Temperature dropped to a mean value of 22.6 (±0.14) degrees Celsius during the dry season.

3.1.3 Atmospheric weather conditions

During the deployment periods, weather data similarly showed significant differences between wet and dry seasons for solar radiation and wind speed. Solar radiation was higher in the wet season (1.02 ± 1.05 MJ m^{-2} h^{-1}) than in the dry season (0.86 ± 0.91 MJ m^{-2} h^{-1}; $U = 2.31 \times 10^5$, $p = 0.0052$). Wind speed was significantly greater during the wet season (4.10 ± 2.67 $m \cdot s^{-1}$) compared to the dry season (3.02 ± 2.10 m s^{-1}; $U = 6.69 \times 10^5$, $p < 0.0001$). While rainfall did not differ significantly between seasons during the specific date ranges where gradient flux deployments were being completed (wet: 0.11 ± 0.93 mm h^{-1}; dry: 0.02 ± 0.16 mm h^{-1}; $U = 5.04 \times 10^5$, $p = 0.696$), rainfall was significantly different between seasons when assessed over the entire seasonal timescale (Dry season = Nov 2021-March 2022, Wet season = April 2022-Oct 2022), with a mean (± SD) rainfall in the dry season of 0.068 ± 0.482 mm h^{-1} versus 0.329 ± 1.999 mm h^{-1} in the wet season ($U = 7.9 \times 10^7$, $p = 2.39 \times 10^{-37}$.

Weather data was also significantly different between deployment times within seasons as well. In the dry season, global solar radiation, wind speed, and rainfall were all significantly different between the Tung Ping Chau and Sham Wan deployment (Table S2). Dry-season Sharp Island deployment had significantly different wind speed and rainfall compared to Tung Ping Chau and Sham Wan, respectively. During the wet season, Tung Ping Chau and Sham Wan deployments had significantly different global solar radiation and rainfall. Additionally, Sharp Island's wind speed differed from Tung Ping Chau, and the rainfall differed compared to during the Sham Wan deployment (Table S2).

3.1.4 In-situ environmental conditions

Environmental conditions differed significantly (Man-Whitney U test, $p<0.001$) between seasons when averaged across all sites. The wet season (Figure 3g-l) had significantly higher average daytime PAR (194.21 ± 100.23 µmol m^{-2} s^{-1}) and average water temperature (25.89 ±2.13 °C) compared to the dry season (55.53 ± 34.81 µmol m^{-2} s^{-1}, 21.88 ±1.27 °C) (Figure 3a-f). Dissolved oxygen and salinity were significantly lower in the wet season (181.76 ±27.35, 32.77 ±0.59 ppt) compared to the dry season (202.25 ±14.62, 33.72 ± 0.27). The direction of the dominant water flow remained constant from dry to wet season at all three sites. (Figure S1). Sharp Island displayed the most extreme values for many of the environmental variables recorded; in the wet season it had the highest mean water temperature (28 °C), lowest mean DO (165 µmol kg^{-1}), and lowest salinity (32.1 ppt), indicating more extreme conditions at the site over and above seasonal variations. Mean values and ranges for all environmental variables measured at each site and season can be found in Supplementary Information (Table S3, Table S4).

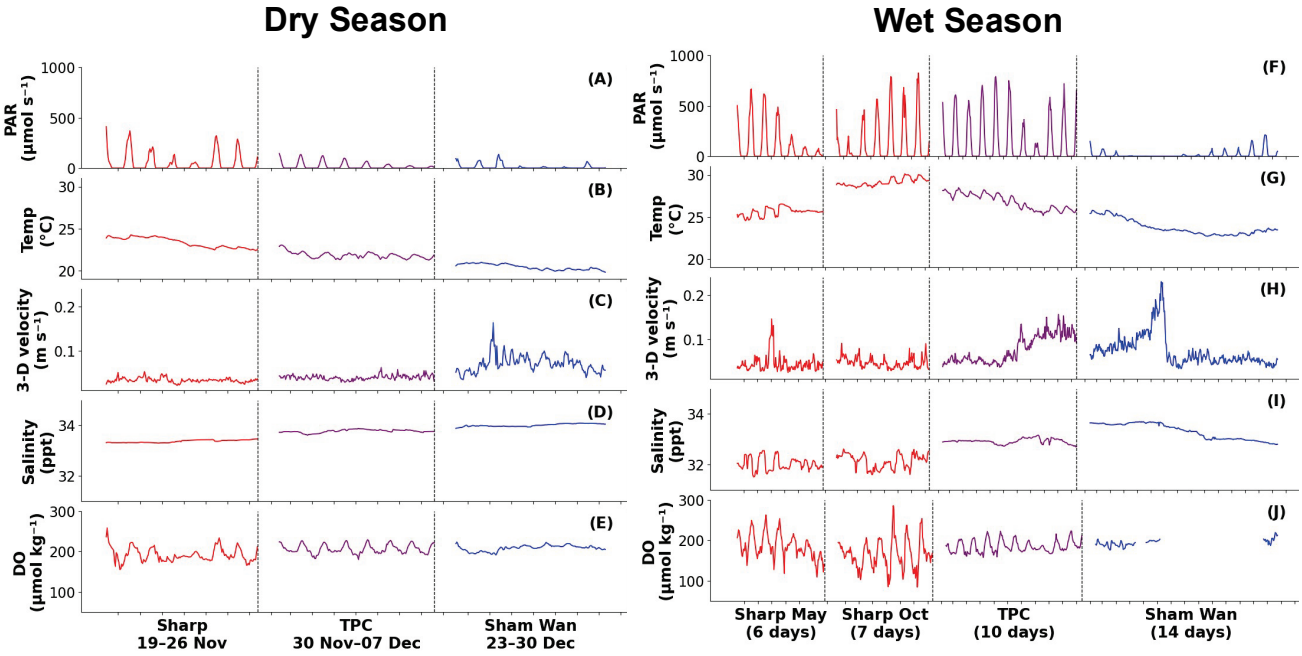

Figure 3. Comparison of prevailing environmental conditions measured during each deployment in the (a-e) dry and (f-j) wet seasons. Panels show PAR (µmol m^{-2} s^{-1}; a, f), temperature (°C; b, g), water velocity (m s^{-1}; c, h), salinity (ppt; d, i), and dissolved oxygen (µmol kg^{-1}; e, j) for Tung Ping Chau (purple lines), Sharp Island (red lines) and Sham Wan (blue lines).

3.1.5 Benthic community composition

The estimated benthic community compositions are shown in Table 2. Focusing on major components of the benthic substrate (> 1 %), Tung Ping Chau was dominated by rock/rubble (38.89 ± 24.34%), live coral (36.14 ± 29.59 %), sand (21.14 ± 16.75 %), and dead coral (4.36 ± 7.71 %). The dominant coral genera present (reported as percent of total benthic cover) were *Porites* (2.89 ± 6.75 %), *Acropora* (8.04 ± 17.52 %), and *Platygyra* (23.86 ± 21.26 %). At Sharp Island, the substrate was predominately composed of live coral (65.75 ± 22.84%), with sand (18.14 ± 14.01 %), rock/rubble (10.71 ± 8.26%), and dead coral (3.66 ± 4.05 %). Within the live coral cover, *Acropora* (46.46 ± 25.99 %), *Pavona* (17.32 ± 21.25 %) and *Porites* (1.36 ± 3.08%) dominated the site. At Sham Wan, the benthos was mainly rock/rubble (59.4 ± 24.82 %) and sand (36.6 ± 26.16%), with only a small amount of live coral (3.84 ± 7.37 %). The only coral species observed in any numbers here was *Plesiastrea* (2.72 ± 7.37 %). Its very low coral cover and dominance of rocky substrate support prior studies that show that Sham Wan is close to the westernmost extent of coral cover in Hong Kong, providing contrast with the higher coral cover communities at TPC and Sharp Island.

Table 2. Benthic community composition around the deployment locations at Tung Ping Chau, Sharp Island and Sham Wan as percentage total benthic cover. Tung Ping Chau's live coral cover was dominated by Platygyra sp. while Sharp Island was dominated by Acropora sp. Corals were largely absent from Sham Wan, which was dominated by rock/rubble and sand.

	Acropora (%)	Pavona (%)	Porites (%)	Platygyra (%)	Plesiastrea (%)	Sand (%)	Rock/Rubble (%)	Live Coral (%)	Dead coral (%)
Tung Ping Chau	8.04 ± 17.52	0.00 ± 1.50	2.89 ± 6.75	23.86 ± 21.26	0.00 ± 0.00	21.14 ± 16.75	38.89 ± 24.34	36.14 ± 29.59	4.36 ± 7.71
Sharp Island	46.46 ± 25.99	17.32 ± 21.25	1.36 ± 3.08	0.00 ± 2.60	0.00 ± 0.00	18.14 ± 14.01	10.71 ± 8.26	65.75 ± 22.84	3.66 ± 4.05
Sham Wan	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	2.72 ± 7.37	36.60 ± 26.16	59.40 ± 24.82	3.84 ± 7.37	0.00 ± 0.00

3.2 Benthic community metabolic rates

3.2.1 Dry season

Significant spatial and diel variability in NEP was detected during the dry season (Figure S2), with Tung Ping Chau and Sham Wan displaying net respiration (negative NEP) and Sharp Island NEP being slightly net productive. Diel comparisons of NEP within each site revealed significant differences between day and night (Figure 4a-c). Mann–Whitney U tests yielded statistically significant contrasts at Sharp Island ($p < 0.001$, daytime NEP = 0.31 ±1.47 mmol O_2 m^{-2} hr^{-1}, nighttime NEP = -0.31 ±0.44 mmol O_2 m^{-2} hr^{-1}) and Tung Ping Chau ($p < 0.001$, daytime NEP = 0.15 ±0.87 mmol O_2 m^{-2} hr^{-1}, nighttime NEP =-0.69 ±0.72 mmol O_2 m^{-2} hr^{-1}), indicating a shift from net production to net respiration over the diel cycle. Sham Wan did not show significant differences between day and night NEP ($p = 0.176$, daytime NEP = -0.40 ±0.36 mmol O_2 m^{-2} hr^{-1}, nighttime NEP = -0.34 ±0.30 mmol O_2 m^{-2} hr^{-1}).

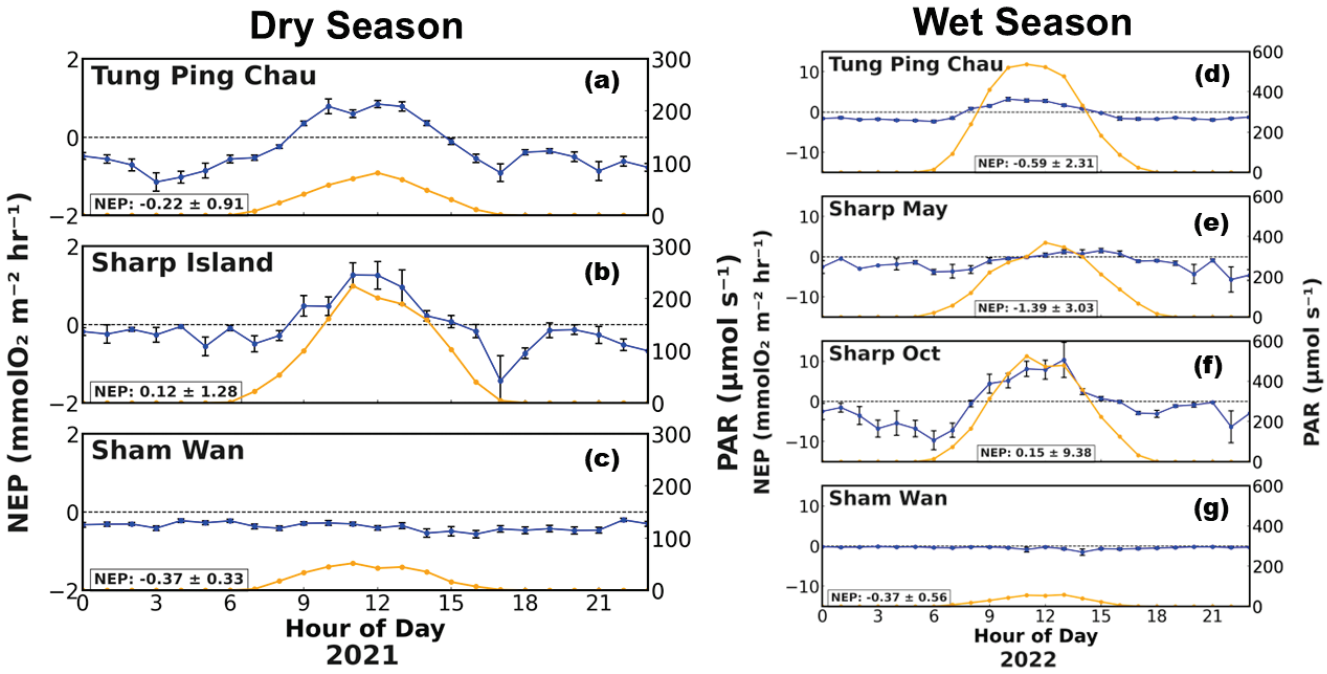

Figure 4. Diel composite plots of hourly averaged NEP (blue line) and PAR (orange line) for the dry season (a-c) and wet season (d-g) deployments. Error bars represent ± standard error of the mean NEP for each hourly bin. Text boxes show the mean ±SD NEP (mmol O_2 m^{-2} hr^{-1}). Note the expanded NEP and PAR axis ranges for the wet season figures relative to the dry season to capture the larger variability observed during the wet season.

3.2.2 Wet Season

In the wet season, all sites were net respiring (-NEP) except for Sharp Island in October which was slightly net productive. NEP also exhibited significant diel variation across all deployments (Figure S3). Mann–Whitney U tests revealed consistent and significant differences in NEP ($p < 0.001$) between day and night at all sites (Figure 4d-g). Tung Ping Chau NEP (daytime = 0.77 ±2.48 mmol O_2 m^{-2} hr^{-1}, nighttime = -1.78 ±1.28 mmol O_2 m^{-2} hr^{-1}) and Sharp Island NEP in both May (daytime = -0.63 ±2.85 mmol O_2 m^{-2} hr^{-1}, nighttime = -2.65mmol O_2 m^{-2} hr^{-1}) and October (daytime = 2.10 ±9.67 mmol O_2 m^{-2} hr^{-1}, nighttime = -1.78 ±1.28 mmol O_2 m^{-2} hr^{-1}) was significantly greater during the day than at night. Sham Wan NEP was significantly lower ($p = 0.0051$) during the day (-0.53 ±0.80 mmol O_2 m^{-2} hr^{-1}) versus the night (-0.27 ±0.28 mmol O_2 m^{-2} hr^{-1}).

3.3 Environmental drivers of NEP

3.3.1 Dry season

At Sharp Island, NEP (Figure S4**)** was strongly correlated with PAR ($r = 0.57$, $p < 0.001$), while weak negative correlations were also observed with bottom depth ($r = -0.16$, $p = 0.010$) and salinity ($r = -0.14$, $p = 0.026$). After removal of the PAR

effect, none of these variables remained significantly correlated with the NEP residuals, indicating that NEP variability at this site was almost entirely governed by light availability.

At Tung Ping Chau, NEP also showed a significant positive correlation with PAR ($r = 0.61$, $p < 0.001$), while no other environmental parameters displayed significant relationships with either NEP or NEP residual. This suggests that community metabolism at Tung Ping Chau during the dry season was tightly coupled to irradiance and largely insensitive to variation in flow, temperature, or salinity.

In contrast, Sham Wan exhibited a broader range of significant relationships. NEP was positively correlated with bottom velocity ($r = 0.14$, $p = 0.002$), negatively correlated with bottom temperature ($r = -0.22$, $p < 0.001$), and positively correlated with salinity ($r = 0.12$, $p = 0.005$). These same variables remained significant after removing the PAR effect, with NEP residuals correlated with velocity ($r = 0.14$, $p = 0.001$), temperature ($r = -0.23$, $p < 0.001$), and salinity ($r = 0.13$, $p = 0.004$). This persistence of correlations in the light-removed dataset indicates that hydrodynamic and thermal processes exerted independent control on community metabolism at Sham Wan.

3.3.2 Wet season

At Sharp Island in May (Figure S5), NEP was significantly correlated with PAR ($r = 0.53$, $p < 0.001$) and water velocity ($r = 0.24$, $p < 0.001$). After removal of the PAR effect, NEP residuals remained significantly correlated with velocity ($r = 0.17$, $p = 0.014$), temperature ($r = 0.24$, $p < 0.001$), and salinity ($r = -0.16$, $p = 0.020$), indicating additional light-independent influences on benthic organic metabolism during this deployment.

In October at Sharp Island, NEP was strongly correlated with PAR ($r = 0.63$, $p < 0.001$), as well as temperature ($r = 0.32$, $p < 0.001$), depth ($r = -0.36$, $p < 0.001$), and salinity ($r = -0.11$, $p = 0.045$). However, none of these secondary correlations persisted in the NEP residuals, demonstrating that NEP variability was primarily driven by light and diurnally covarying thermal and hydrographic changes.

At Tung Ping Chau, NEP exhibited a very strong relationship with PAR ($r = 0.72$, $p < 0.001$) and a weaker positive correlation with velocity ($r = 0.09$, $p = 0.009$). These relationships disappeared for the NEP residuals, suggesting that short-term fluctuations in flow and temperature were largely covariant with light availability.

In contrast, Sham Wan 2022 showed significant correlations of NEP with PAR ($r = 0.41$, $p < 0.001$), bottom velocity ($r = 0.12$, $p = 0.006$), and bottom temperature ($r = -0.22$, $p < 0.001$). The NEP residuals remained significantly related to both velocity ($r = 0.11$, $p = 0.012$) and temperature ($r = -0.20$, $p < 0.001$).

4 Discussion

A growing number of studies have focused on measuring community-scale NEP over coral assemblages, utilizing primarily autonomous methods (Takeshita et al., 2018; Platz et al., 2022). To our knowledge, this is the first study assessing high-resolution, in-situ NEP and associated organic carbon cycling over coral communities in a marginal, highly urbanized

environment. The three study sites occur within the broader marginal environmental setting of Hong Kong, but differ in benthic structure and coral cover. Sham Wan showed clear structural marginality, with very low coral cover and dominance of rocky substrate, whereas Sharp Island and Tung Ping Chau maintained moderate to high coral cover. Across these contrasting benthic settings, however, all sites showed low or negative short-term NEP, indicating constrained community-scale net organic carbon production during deployment periods. We therefore interpret NEP not as a complete measure of reef function or health, but as a measure of one important component of ecosystem function: the balance between photosynthesis and respiration (Brandl et al., 2019; Schoepf et al., 2023). Quantifying how this component of organic carbon cycling varies across Hong Kong's environmental gradient can help clarify how coral communities persist under local stressors and changing ocean conditions, including coastal urbanization and global change. The spatiotemporal patterns NEP here therefore provide a basis for identifying natural background variability in community carbon cycling and for assessing how communities may change under future ocean conditions.

The observed net respiration observed of Hong Kong coral communities in this study adds to a growing number of studies that challenge the notion that coral ecosystems are by default highly net productive environments (Odum and Odum, 1955; Gattuso et al., 1996). Corals are the predominant contributor to community productivity, especially in environments like our study sites where algal abundance is low. When these corals shift their metabolic balance to heterotrophic feeding rather than a dependance on photosynthetic sources, as has been shown to happen in turbid reefs (Travaglione et al., 2023), the community-scale cumulative respiration signal of the corals and other respiring organisms found in high abundance in these communities in Hong Kong, such as reef fishes (especially in high coral cover sites, Yiu et al., 2025) and sea urchins (Dumont et al., 2013; Qui et al., 2014), can outweigh autotrophic production. Interestingly, the high abundance of urchins found within Hong Kong coral communities has also been shown to be a leading cause of low algal abundance through grazing (Suarez et al., 2021), in addition to seasonality related decreases in algal populations (Yeung et al, 2021). In should also be noted that community-scale net respiration is not exclusive to turbid environments. A growing number of studies conducted in more pristine reef environments have also reported net community respiration (Kaneohe Bay, Hawaii; Falter et al., 2008, Shamberger et al., 2011; Cheeca Rocks, Florida and La Parguera, Puerto Rico; Melendez et al., 2022; Chagos Archipelago; Khrizman et al., 2025; Palmyra atoll; Takeshita et al., 2016; Florida Keys; Coogan et al., 2022). Longer timescale studies investigating organic metabolism over a wide range of coral habitats are needed to better elucidate what local factors are driving observed shifts in metabolic balance over space and time.

4.1 Spatiotemporal patterns in NEP

4.1.1 Identifying possible drivers of suppressed productivity in Hong Kong coral communities despite high coral cover

Our results support that coral cover alone may not be a reliable indicator of contemporary community-scale organic carbon production in coral communities (Page et al., 2017) , and that persistence of these communities in marginal environmental

settings may depend on mechanisms such as heterotrophic subsidies, stress-tolerant taxa, low macroalgal competition, and recovery from episodic disturbances rather than consistently high net autotrophy.

Although low light availability emerged as the dominant measured driver of NEP in this study, we interpret this as one mechanism driving the observed low NEP rather than the sole defining characteristic of the system. Low light suppresses autotrophic production of the communities, but several other possible mechanisms may be acting to increase respiration rates in these communities as well. Excessive eutrophication has been shown to be the dominant control over modern-day coral community composition in Hong Kong (Cybulski et al., 2020; Duprey et al., 2020). Elevated allochthonous nutrient inputs into coral environments have been shown to have mixed effects on coral NEP (D'angelo and Wiedenmann, 2014; Silbiger et al., 2018; Barnas et al., 2025); however, the beneficial aspects of elevated nutrients in increasing NEP largely is derived from increased production rates with adequate light levels to support it. This is not the case in Hong Kong, where the light-limiting environment stunts the positive effects of nutrients loads to NEP. In contrast, external nutrient input will increase sediment and microbial respiration (Kelly et al., 2014; Silbiger et al., 2018) and, perhaps most crucially, increase nighttime respiration rates of the coral community when no photosynthesis is occurring (Falter et al., 2011; Long et al., 2013). Therefore, when evaluating the impact that chronic eutrophication of Hong Kong coastal waters has on community organic cycling, it is likely that it enhances respiration rates at a greater rate than any positive effect it has on enhancing photosynthesis rates. The combined effects of low-light limitation on photosynthesis production and increased respiration rates driven by excess nutrient loads potentially act together to suppress NEP rates of coral communities in Hong Kong, compared to tropical oligotrophic reef counterparts.

4.1.2 Seasonality in NEP

All of our deployments, across sites and seasons, indicated that these communities are net respiring or only slightly net productive, with average net respiration rates (-NEP) ranging from -1.39 ± 3.03 to 0.15 ± 9.38 mmol O_2 m^{-2} hr^{-1}. This suggests that the coral communities across Hong Kong are limited in their photosynthetic capacity, or that respiring organisms' metabolic rates exceeds rates of photosynthesis. PAR was shown to be a consistent primary driver of NEP rates during this study, so prolonged periods of cloudy weather could have a serious effect on suppressing NEP in this region. Hong Kong generally experiences reduced light conditions (4.0 kWh m^{-2} day^{-1}(337 µmol m^{-2} s^{-1}) , Figure S6) (Hong Kong Observatory 2025) compared to other coral rich environments around the world, such as the Great Barrier Reef (5.0 - 6.0 kWh m^{-2} day^{-1}(421-505 µmol m^{-2} s^{-1}, (SolCast Pty Ltd. 2025)), the Caribbean (5.0 - 6.5 kWh m^{-2} day^{-1}(421-547 µmol m^{-2} s^{-1}, (NASA Langley Research Center 2025)), and the Red Sea (6.0 - 7.0 kWh m^{-2} day^{-1}(505-589 µmol m^{-2} s^{-1}, (SolarGIS s.r.o. 2025)). In combination with the strong net respiration signals seen during night hours in these coral communities (Mean NEP_{day} = 0.42 ± 4.21 (mmol O_2 m^{-2} hr^{-1} versus Mean NEP_{night} = -1.26 ± 2.39 mmol O_2 m^{-2} hr^{-1}), cloudy days and turbid water conditions will act in unison to suppress production rates in these communities. Despite the wet season displaying environmental conditions more conducive to positive NEP (higher PAR), these communities exhibit similar low production year-round, regardless of season. A prior mesocosm study in Hong Kong documented that low light contributes to limit productivity in these coral

communities (McIlroy et al., 2019), along with limiting the distribution of coral assemblages (Cybulski et al., 2020; Yeung et al., 2021). This suggests that, unlike other reef communities where NEP is reduced during the winter, but elevated during summer (Falter et al., 2012; Stoltenberg et al., 2020), in Hong Kong it is negative year-round. This worrying trend may be enhanced in the future as an increase in cloud cover and a corresponding decrease in surface solar radiation have been observed in Hong Kong over the past decades (Hong Kong Observatory, 2022). It must be noted that attempts to fit a photosynthesis–irradiance (PI) relationship to the observed NEP data were unsuccessful, as NEP did not approach saturation with increasing PAR at any site. The absence of a discernible P_{max} suggests that the ambient light regime in these Hong Kong coral communities remained below saturating levels for photosynthesis throughout the study period. This pattern is consistent with chronic light limitation, likely driven by high turbidity that has been shown to limit community productivity in other light-limited environments (Law and Huang, 2023).

More pronounced net respiration was evident in the wet season compared to the dry season, with negative NEP more than double during the wet (NEP_{mean}= -0.49 ± 4.83 mmol O_2 m^{-2} hr^{-1}) than dry (NEP_{mean}= -0.21 ± 0.85 mmol O_2 m^{-2} hr^{-1}). This suggests that seasonal environmental changes in the wet season may enhance respiration rates at a greater pace than increasing production, despite higher PAR in the wet season that may increase photosynthesis. One of these seasonal changes that could lower NEP in the wet season is lower salinity. Lower salinity in the wet season (Table S3, Table S4) driven by higher rainfall has been shown to induce physiological stress on coral communities in Hong Kong (Xie et al., 2020), possibly reducing their ability to maintain higher productivity. DO was also lower during the wet season, which could have decreased NEP values as well; however, low oxygen conditions have been shown to inhibit both photosynthesis and respiration of corals (Nelson and Altieri, 2019), so further studies investigating the role of low DO conditions on NEP rates over more coral habitats are needed. Finally, higher water temperatures during the wet season likely increased respiration rates of corals (Parry et al., 2025), and other respiring organisms (Nilsson et al., 2010; Tran and Johansen, 2023), in the community, further decreasing NEP in the wet season versus the dry season.

Weather patterns could also have had a role in changing community-scale organic carbon cycling. Specifically, higher rainfall in the wet season could also have contributed to the lower and more variable NEP values. While rainfall did not significantly differ during the specific deployment short-term periods between seasons, the rainfall was significantly higher during the wet season than the dry season when averaged over the entire season (Wet; Apr-Oct 2022, Dry; Nov 2021-Mar 2022). Increased rainfall can lead to several changes in the local environment of the coral communities that could increase the variability in NEP, such as increased terrestrial runoff leading to increased organic matter input (Haapkyla et al., 2011) or increased stratification of the water column due to freshwater intrusion (Goodkin et al., 2011; Zhou et al., 2012). Future studies should investigate in more detail, utilizing in-situ sensors with increased temporal resolution, what factors influence the relative level of both chemical and physical stratification in the water column to better elucidate the impact rainfall or other sources of runoff may have on strength of stratification. During periods of strong stratification, the gradient flux may not be an appropriate method to measure NEP (Takeshita et al., 2016) due to the assumptions of the GF method being violated and an overprediction of the respiration signal due to reduced vertical flux across the benthic boundary layer (Coogan et al., 2022).

The effect of the temperature gradient on NEP rates was monitored and assessed to account for this possible methodological artefact in our dataset. The strength of temperature stratification varied spatiotemporally between sites and seasons (Figure S7, Figure S8) but did not exceed > 0.5°C at any time during the deployment, therefore it was not considered to significantly affect the metabolism measurements of this study. However, we recommend future studies utilizing the gradient flux technique in strongly stratified waters to measure the salinity at both the top and bottom depth to better account for the influence of stratification on metabolism measurements.

The gradient flux method also cannot be used during periods of intense water column mixing due to the lack of a steady state boundary layer and the deterioration of a present law-of-the-wall relationship in the velocity profile with respect to the substrate. An illustration of this in our dataset was during the wet season Tung Ping Chau deployment, on Oct 17, Typhoon Nesat impacted Hong Kong coastal waters, causing intense water mixing. Following this storm event, until the end of the deployment time (Oct 18-21), NEP rates could not be calculated due to the water velocity at the bottom height (z_2 = 8 cm) being consistently greater than the velocity at the top height (z_1= 124cm), violating this assumption necessary for GF NEP calculations. Accordingly, retained NEP estimates represent periods when gradient-flux assumptions were satisfied and should be interpreted as high-resolution estimates under suitable boundary-layer and flow conditions, rather than as continuous deployment-scale averages across all hydrodynamic states experienced by the communities. Future studies should include analysis of weather conditions during deployment periods to reveal periods where intense stratification or water column mixing may be occurring, especially studies done during seasons with increased storm frequency such as the wet season in Hong Kong (Hong Kong Observatory, 2025).

4.1.3 Spatial patterns in NEP

Sham Wan displayed the lowest diurnal and seasonal variability and ranges in NEP during our study. The minimal diurnal variation in NEP likely reflects the relatively low density of metabolically active benthic organisms at this rock-dominated site (Figure 4) compared to the two other sites dominated by hard coral.

Additionally, the deeper deployment depth, which was chosen due to the lack of coral assemblages at shallower depths where a steep rocky wall borders the shore, likely contributed to reduced NEP due to lower light levels and lower water temperatures found in a couple of meters deeper water. The observations at Sham Wan highlight the likelihood that, as coral abundance and overall diversity decline westward across Hong Kong (Duprey et al., 2016, 2020; McIlroy et al, 2024), the metabolic activity of the benthic community likely decreases. Lower abundance communities, similar to Sham Wan, likely encapsulate the declines in coral community NEP expected with westward movement across Hong Kong as both water quality and coral abundance decline.

However, improved water quality and high coral cover does not uniformly equate to positive rates of productivity (Takeshita et al., 2016; Shamberger et al., 2018; Khrizman et al., 2025) if other local environmental variables act to suppress NEP. Despite TPC being described as one of Hong Kong's most diverse and abundant coral communities (Chui and Ang, 2017), NEP values here were net respiring during this study. Nighttime respiration processes (Nighttime NEP_{mean} = -1.35 ±

1.90 (mmol O_2 m^{-2} hr^{-1}) outweighed the daytime productivity (Daytime NEP_{mean} = 0.46 ± 1.90 mmol O_2 m^{-2} hr^{-1}) occurring at this site. Coral bleaching was also recorded at Tung Ping Chau in July and August, due in large part to the warm temperatures seen during the summer of 2022 (Zhao et al., 2023). Following bleaching events, community NEP may be suppressed and may shift systems to net respiration (Hughes and Grottoli, 2013; Courtney et al., 2018; Khrizman et al., 2025). But community-scale responses to bleaching are variable and context dependent, with several studies reporting little to no change in NEP rates following bleaching events (McMahon et al., 2019; Pisapia et al., 2019; Lantz et al., 2022). Additionally, most corals were recorded as recovered with minimal mortality by November 2022 (AFCD, 2022), which is in agreement with a recent review study that shows that coral communities with persistently low NEP has increased potential for recovery from disturbance events such as bleaching as a result of an increased baseline reliance on heterotrophic processes (Allgeier, 2024). Bleaching is only one of several local variables likely to act in combination to suppress NEP at this site, including low-light and potentially external nutrient input stimulating respiration.

While Tung Ping Chau exhibited consistently net-respiring conditions, Sharp Island was the only site to average net productivity, doing so in both the dry season (NEP_{mean} = 0.12 ± 1.28 mmol O_2 m^{-2} hr^{-1}) and in October in the wet season (NEP_{mean} = 0.15 ± 9.38 mmol O_2 m^{-2} hr^{-1}). However, this site also showed significantly greater metabolic variability than the other two sites, with greater productivity signals during the day but also large respiration signals at night. During the wet season, nighttime oxygen depletion was so extreme that during certain hours, periods of moderate to severe hypoxia (61-92 µmol kg^{-1}) (Pezner et al., 2023), reaching levels as low as 70.98 µmol kg^{-1}, occurred, and persisted for up to several hours at a time (Figure S3b,c). This oxygen depletion at Sharp Island could be a result of upwelling of oxygen-depleted water from offshore, as was seen in the CTD cast conducted at Sharp Island, or from in-situ respiration processes occurring within the community. Regardless, hypoxic conditions measured in the benthic water at Sharp Island warrant further investigation as they are a cause for a concern for coral at the site, with prolonged exposure to low oxygen conditions shown to have negative effects on coral physiology and function (Pezner et al., 2023).

4.2 Future directions to sustain Hong Kong coral communities

Hong Kong coral communities live under marginal local environmental conditions and have been subjected to a mix of anthropogenic and natural stressors that have contributed to their strong resilience and persistence (Goodkin et al., 2011), while also reducing their structural complexity and spatial coverage (Cybulski et al., 2020). This study demonstrates that these communities are net respiring across the east-west gradient yet still persist. These findings suggest that persistence in this system may rely on mechanisms other than high net autotrophic production.

Therefore, Hong Kong corals may offer a glimpse into how coral communities may change in response to marginal environmental conditions that are expected to prevail more widely in the future (Camp et al., 2018). Corals have already begun shifting their distributions poleward (Price et al., 2019) as the equatorial tropics pass thermal limits for coral survival (but see Huang et al.,2024, as this may be a cryptic species artefact rather than increased poleward migration). Additionally, as coastal

areas become increasingly influenced by the effects of urbanization (Hugo, 2011), studying how sub-tropical, urbanized corals are persisting under already marginal environmental conditions is a critical area of research (Schoepf et al., 2023).

By gathering empirical data on NEP rates at high temporal resolution over coral communities around Hong Kong, this study improves our understanding of which local conditions influence the degree of marginality that corals are subjected to within a larger highly urbanized marine ecosystem, such as hydrodynamics (Grimaldi et al., 2023), depth (Page et al., 2019; Cyronak et al., 2020), benthic composition (Page et al., 2017), or nutrient levels (Becker et al., 2021). There is still a need for further characterization of NEP across a wider range of reef environments to gain a better understanding of what specific local factors influence the balance between net respiration and net production of coral communities (Khrizman et al., 2025), as it still not clear how this metabolic balance will shift under future climate change.

While NEP provides critical information on organic carbon cycling, future work may benefit from pairing NEP with NEC (net ecosystem calcification) measurements to determine whether net respiration is associated with reduced calcification, enhanced dissolution, or altered carbonate balance (Shamberger et al., 2011; DeCarlo et al., 2017). Measuring coral community metabolism in terms of both NEP and NEC in this type of environment can provide critical insights into what environmental drivers assist the overall community (not just corals) to persist even with net respiration and possibly low community calcification rates, and how these drivers may change over space and time. This includes all metabolically active organisms contributing to enhanced biodiversity found in coral habitats, such as fishes, algae, and bioeroders like urchins and other bivalves. These have been reported as an overlooked but vital part of the community that can directly influence coral growth rates in Hong Kong (Yeung et al., 2021).

Future studies looking aiming to measure in-situ community NEP in Hong Kong and similar environments may also consider utilizing an approach with pair flux quantification. Recent studies have begun to utilize paired gradient flux-aquatic eddy covariance deployments (Coogan et al., 2022; Khrizman et al., 2025; Boles et al., 2026) in order to quantify NEP at higher temporal resolution and fill in time gaps where gradient flux assumptions are frequently violated. This approach also allows for a comparison of the flux measurements between the gradient flux and eddy covariance to ensure higher confidence in the calculated flux rates.

Paired NEP–NEC measurements could also help future studies evaluate whether sites with low or negative NEP differ in calcification, dissolution, or carbonate balance, and thereby provide a stronger basis for assessing restoration potential. However, the present study does not measure NEC and therefore cannot determine whether these communities are accreting, dissolving, or suitable for restoration on the basis of carbonate balance. Our results instead suggest that even coral communities with moderate to high coral cover in eastern Hong Kong can experience low or negative short-term community-scale NEP. Future restoration assessments in Hong Kong would therefore benefit from integrating NEP, NEC, benthic composition, hydrodynamics, light availability, and longer-term ecological monitoring, particularly at locations where restoration projects have already been carried out, such as Tolo Harbour (World Wildlife Fund, 2025), Bluff Island (ARCHIREEF, 2025) and Hoi Ha Wan (AFCD, 2019).

5 Conclusions

Even under marginal environmental conditions, the environmental conditions associated with community-scale organic carbon cycling vary markedly seasonally and in response to small-scale variations in local conditions. Within the periods suitable for gradient-flux calculation, this study demonstrated such variability in NEP signals over coral communities persisting under a suite of local stressors in Hong Kong. NEP rates were negative or only slightly positive for all sites and both seasons, demonstrating overall suppressed productivity at a community scale. Wet season NEP was lower and more variable than the dry season at all three study sites. These suppressed NEP rates indicate that coral communities across Hong Kong have persisted with moderate to high coral cover despite low or negative short-term community-scale NEP, likely reflecting a combination of chronic low-light limitation, external organic matter input stimulating heterotrophic feeding, benthic respiration and seasonal variability.

More studies investigating metabolic patterns of coral communities subject to highly variable and marginal environmental conditions will increase the data available to model and predict future changes in coral ecosystem functioning in response to climate change and local stressors. Furthermore, such data and models can help to identify marine environments that are more suited for management efforts and restoration projects, or conversely unlikely to support functioning coral communities in the future. We advocate for more widespread collection of concurrent high-temporal-resolution, in-situ biophysical and metabolic data over coral communities across the globe to further our knowledge of community-level organic metabolism under marginal conditions likely to dominate coastal habitats in the future.

Data availability

Environmental water quality data around Hong Kong can be obtained from the Environmental Protection Department (EPD; https://cd.epic.epd.gov.hk/EPICRIVER/marine/?lang=en), while weather observations are provided by Hong Kong Observatory (HKO; https://www.hko.gov.hk). Environmental and community composition data collected during this study have been archived at PANGAEA (https://www.pangaea.de/).

Supplement link

Supplementary Information attached.

Author contributions

T.B.K.: Conceptualization (equal), Data curation (lead), Formal Analysis (lead) Investigation (lead), Methodology (lead), Project Administration (supporting), Validation (lead), Visualization (lead), Writing – Original Draft Preparation (lead), Writing – Review & Editing (lead). **Y-D.P.:** Formal Analysis (supporting), Investigation (supporting), Methodology

(supporting), Project Administration (supporting), Writing – Review & Editing (supporting). **J.B-W.:** Investigation (supporting), Project Administration (supporting), Writing – Review & Editing (supporting). **A.S.J.W.:** Conceptualization (equal), Data curation (supporting), Funding Acquisition (lead), Investigation (supporting), Methodology (supporting), Project Administration (lead), Resources (lead), Supervision (lead), Writing – Original Draft Preparation (supporting), Writing – Review & Editing (supporting).

Competing interests

The authors have declared no competing interests.

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