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Marine carbon dynamics in a coral reef ecosystem of Southern Taiwan

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Running title: pCO_2 in a coral reef ecosystem

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ABSTRACT

The ocean is the planet's largest carbon reservoir and plays a crucial role in regulating atmospheric CO_2 levels, especially in the face of climate change. In coral reef ecosystems, understanding the carbonate system is critical for predicting and mitigating the impact of ocean acidification on these vulnerable marine ecosystems, especially as atmospheric CO_2 concentrations continue to rise. This study measured pCO_2 over space and time in Nanwan Bay, a coral reef ecosystem in southern Taiwan, to identify factors that influence its variation. The results showed that mean surface water pCO_2 values varied seasonally, with values of 393.7 (±10.8), 406.3 (±16.1), 399.2 (±18.6), and 366.9 (±14.5) µatm in spring, summer, fall, and winter, respectively. These seasonal mean differences (ΔpCO_2) relative to atmospheric pCO_2 were 7.7 (±10.8), 29.3 (±16.1), 21.2 (±18.6), and -16.1 (±14.5) µatm, respectively. These findings suggest that the Nanwan Bay is a highly dynamic coral reef ecosystem, exhibiting both spatial and seasonal variability in carbon exchange. The carbonate system parameters of the surface water in this high-biodiversity, sub-tropical marine ecosystem was influenced not only by seasonal temperature variation but also by vertical mixing, intermittent upwelling, and biological effects.

Keywords: carbon sink, carbon source, coral reef, pCO_2, total alkalinity, upwelling

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1. Introduction

Understanding whether the ocean acts as a carbon dioxide (CO_2) sink or source is crucial in the context of climate change, as it directly affects climate regulation, ecosystem health, and the effectiveness of mitigation efforts. Oceans absorb about 30% of human-produced CO_2 (Ipcc, 2021). If the ocean's ability to absorb CO_2 decreases, more CO_2 will remain in the atmosphere, exacerbating global warming. CO_2 concentration in marine systems varies between region and over time (Fay et al., 2021; Sitch et al., 2015; Schimel et al., 2001). For example, high-latitude temperate regions and coastal seas act as sinks for atmospheric CO_2, while subtropical and tropical coastal seas, estuaries, and coral reefs are generally sources (Borges et al., 2005; Cai et al., 2003; Frankignoulle et al., 1998; Frankignoulle et al., 1996; Gattuso et al., 1997; Gattuso et al., 1993; Ito et al., 2005; Ohde and Van Woesik, 1999; Wang and Cai, 2004; Yan et al., 2011; Bates et al., 2001). The hydrological characteristics of coastal waters, such as temperature, salinity, upwelling, and mixing, also exhibit substantial variation, leading to differences in surface water pCO_2 even within the same continental shelf. Furthermore, upwelling areas along the coasts of California and Oman act as CO_2 sinks, whereas those along the coasts of Galicia and Oregon serve as CO_2 sources (Borges and Frankignoulle, 2002; Friederich et al., 2002; Goyet et al., 1998; Hales et al., 2005). Borges (2005) notes that when estuaries are included

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in the gas exchange process, coastal seas worldwide are sources of CO_2, but they become sinks when estuaries are excluded.

Various factors, such as temperature, tides, currents, river discharge, upwelling, vertical mixing, and biological metabolism, influence CO_2 levels in coastal areas (e.g., Dai et al., 2009; Chen et al., 2024; Ibanhez et al., 2015). For instance, temperature changes can directly affect the solubility of CO_2 in seawater, with higher temperatures generally reduce CO_2 solubility (Dai et al., 2009). Tides and currents can enhance vertical mixing, bringing CO_2-rich deep waters to the surface and increasing pCO_2 levels (Ibanhez et al., 2015; Dai et al., 2009). River discharge introduces fresh water and organic matter, which can stimulate biological metabolism and further influence CO_2 levels through respiration and decomposition processes (Chen et al., 2024; Ibanhez et al., 2015). These factors interact and help explain why seasonal variation in CO_2 levels can differ greatly across regions. For example, measurements taken at the Bermuda Atlantic Time-series station in the Northwest Atlantic from 1996 to 1998 showed that CO_2 levels were lowest in winter and highest in summer (Takahashi et al., 2002). Conversely, data collected from the Kyodo Western North Pacific Ocean Time-Series station between 1998 and 2000 indicated that CO_2 levels were lower in summer compared to winter (Takahashi et al., 2002).

Coral reef ecosystems are known for their high productivity, biomass, and

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efficient carbonate deposition rates. However, due to their structural complexity and high biodiversity, the carbon dynamics of coral reefs differ substantially from those of the open ocean. Whether coral reef ecosystems function as net carbon sources (Ware et al., 1992; Gattuso et al., 1993; Gattuso et al., 1999; Fagan and Mackenzie, 2007; Lønborg et al., 2019; Yan et al., 2018; Watanabe and Nakamura, 2019; Frankignoulle et al., 1998) or sinks (Kayanne et al., 1995; Mayer et al., 2018; Suzuki, 1998; Suzuki and Kawahata, 2004) remain uncertain due to factors like the high spatial and temporal variability within these ecosystems. Sedimentation rates and anthropogenic influences further complicate the coral reef carbon balance. Moreover, ocean acidification could reduce coral calcification rates, diminish their ability to produce CO_2, thereby buffering and reducing the pCO_2 levels in seawater (Ries, 2011; Fabry et al., 2008; Albright et al., 2016). Consequently, predicting changes in seawater carbon levels in response to oceanographic anomalies remains a challenge.

Nanwan Bay, located at the southernmost tip of Taiwan (Fig. 1), is a semi-enclosed area between Cape Moubitou and Cape Oluanpi, characterized by high-biodiversity and abundant fringing coral reefs (Yang and Dai, 1980). Previous studies of Nanwan Bay have noted that periodic upwelling causes the mixing of upper and lower seawater layers, facilitating the transfer of nutrients from the deeper waters to shallower areas (Chen et al., 2005). In most coastal upwelling regions, the ocean

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absorbs CO_2 from the atmosphere (Hales et al., 2005), a process closely tied to the increased primary production of phytoplankton in the nutrient-rich waters following upwelling. Primary productivity in marine ecosystems plays a crucial role in carbon cycling by driving the fixation of CO_2 (Dugdale and Wilkerson, 1989; Murray et al., 1995). During periods of heightened primary productivity, the increased demand for carbon can lead to greater uptake of CO_2 from seawater, potentially reducing its concentration (Chen et al., 2004). Interestingly, this phenomenon has yet to be explored within the coral reef ecosystem of Nanwan Bay.

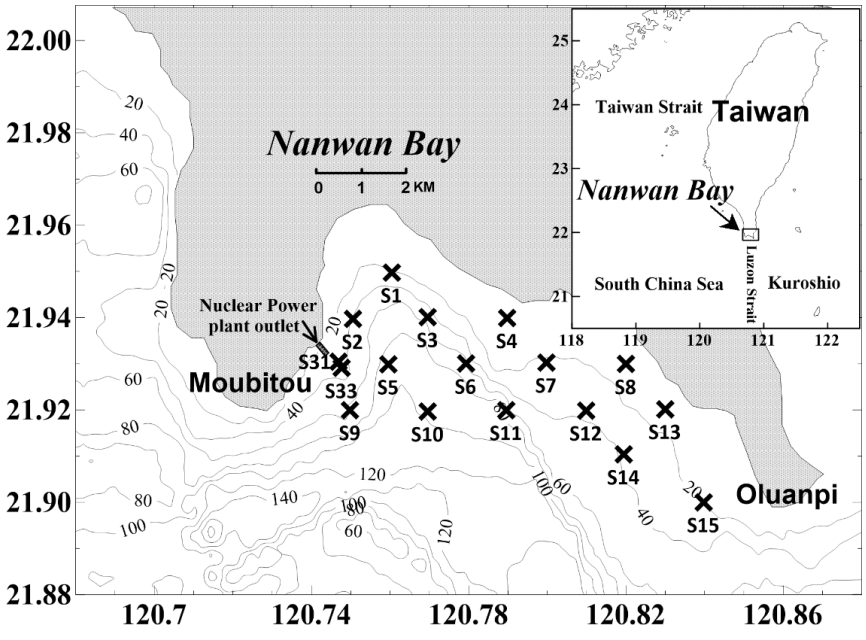

Fig. 1 Map of sampling stations (marked with "X" with the station number underneath) in Nanwan Bay, Taiwan, along with contours of depth (m).

The difference between seawater pCO_2 ($pCO_2^{seawater}$) and atmospheric pCO_2

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(pCO_2^{air}) not only serves as a metric but also determines whether a marine system functions as a source or sink of carbon. In this context, a positive difference, where $pCO_2^{seawater}$ - pCO_2^{air} > 0, indicates a carbon source, while a negative difference signifies a carbon sink. To determine whether Nanwan Bay behaves as a net carbon source or sink, this study evaluates the role of hydrological conditions and their potential influence on the carbonate system and CO_2 fluxes. To achieve this, we conducted a comprehensive analysis of the marine carbonate system across various spatial and temporal gradients.

2. Methods

2.1 Study site Nanwan Bay (Fig. 1) is flanked by the Pacific Ocean to the east, the Taiwan Strait to the west, the Luzon Strait to the south, and the South China Sea (SCS) to the southwest (Lee, 1999) and covers an area of ~30 km^2 (estimated via Google Earth Pro). Nanwan Bay is among the most diverse marine regions in Taiwan, which led to its inclusion within Kenting National Park (Meng et al., 2008). The complex seabed in Nanwan Bay encompasses diverse habitats, including: sandy beaches, rocky shores, and coral reefs. This area represents the initial point of interaction between the SCS waters and the warm, highly saline Kuroshio Current. The water is oligotrophic, and temperatures typically range from 21 to 30°C (with periodic upwelling events occurring;(Chen et al., 2005). In the course of the

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upwelling event, the surface water of Nanwan Bay can drop by >3°C, coupled with a rise in nitrate concentration exceeding 2 μM, as documented by (Chen et al., 2005). The bay hosts over 1,200 fish species and more than 200 species of reef-building coral, making it a significant research focus area for both the reefs and the anthropogenic stressor regime (Meng et al., 2007). Studies have shown that high levels of nutrients and suspended solids may have contributed to the decline in coral cover between 2001 and 2022 (Meng et al., 2008; Chen et al., 2022).

2.2 Sampling and analysis The study was conducted across four seasons: spring (31 March 2011), summer (5 July 2011), autumn (20 October 2011), and winter (22 January 2013), in the area between Nanwan Bay's two capes, Moubitou and Oluanpi. A total of 17 seawater sampling stations were established, including two (Sts. 31 and 33) located near the outlet of a nuclear power plant (Fig. 1). Temperature and salinity data were collected using an Idronaut Ocean Seven 304 CTD calibrated against an International Association for the Physical Sciences of the Ocean seawater standard. Water samples were collected using Niskin bottles with Teflon-coated inner walls. Seawater at each station was taken at two to five depths at intervals of 3 to 25 m in areas shallower than 50 m; extra samples at 65, 80 and/or 100 m were taken for stations with depths of 65-100 m. Please refer to Table S1 for details on the sampling times and sampling depths at each station. Notably, all samples were collected

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exclusively during daytime. Water samples were immediately analyzed for dissolved oxygen (DO) content using YSI 52 and YSI 5905 BOD electrodes (factory accuracy=99.9%). Other water samples were divided into different sample bottles for additional analyses, including chlorophyll *a* (Chl *a*), pH, and total alkalinity (TA). One 300-mL amber bottle was pre-inoculated with 0.2 mL of mercuric chloride to suppress biological activity that could affect TA and other carbonate system parameters.

For Chl *a* analysis, 1 L of seawater were was immediately filtered through GF/F filter paper (Whatman, 47 mm) and stored in liquid nitrogen. The Chl *a* retained on the GF/F filters was determined fluorometrically (Turner Design 10-AU-005; Parsons et al., 1984).

Seawater pH and total TA were measured using an automated titration system consisting of a Mettler-Toledo DL53 with a DG-111 electrode. Prior to measurements, the electrode was calibrated using Merck standard buffer solution (NIST) at 25°C. The calibration ranges for pH 4, 7, and 10 were set to fall within the range of 176±30 mV, 0±30 mV, and -176±30 mV, respectively (calibration slope of -56 to -59). Measured pH values were expressed on the NBS scale.

For TA measurements, 40 g of seawater were titrated with 0.1 N HCl at 25°C. Titration continued until the pH exceeded the end point (~pH 4.4) and then continued

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until ~pH 3.0, with the potential change and titration volume recorded. The consumed volume of HCl was calculated using the Gran (1952) function based on the linear relationship between titration volume and pH, and TA was obtained by plotting the consumed volume of HCl. The reference material for experimental quality control was obtained from Professor Andrew Dickson (Scripps Institute of Oceanography, USA), and the pH of the reference material was calculated by entering dissolved inorganic carbon (DIC) and TA data into CO2SYS software ver. 1.02 (Lewis and Wallace, 1998).

The pH measurement accuracy in this study was ±0.01 units and the TA accuracy was ±2.7 μmol kg^{-1} (precision=0.12%). pCO_2 and DIC were also calculated with CO2SYS from measured pH and TA. The dissociation constants of carbonic acid used were the revised K1 and K2 values from Dickson and Millero (1987) refit from the values of Mehrbach et al. (1973). Notably, the surface water pCO_2 was estimated using the average values of samples collected at depths of 1 and 3 m at each station (Table S1).

2.3 Calculation of the exchange flux of CO_2 between the ocean and the atmosphere. The formula for calculating the exchange flux of CO_2 between the ocean and the atmosphere (F_{GAS}) was as follows:

$$F_{GAS}=k \times K_H \times (pCO_2^{seawater}-pCO_2^{air})$$

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where k is the gas exchange rate of CO_2 (air-sea gas transfer rate) and K_H is the solubility of CO_2 gas in seawater. The air-sea gas transfer rate, k, was obtained from an empirical formula based on wind speed proposed by Wanninkhof (1992): $k=0.31 \times u^2 \times (Sc/660)^{-0.5}$, where u is wind speed 10 m above sea level (in m/s; data from the Central Weather Bureau's Oceanic Center-Oluanpi buoy); and Sc (Schmidt number) is a function of temperature (Wanninkhof, 1992), which can be obtained from the *in situ* sea surface temperature (T) as follows:

$$Sc = 2073.1 - 125.62 \times T + 3.6276 \times T^2 - 0.043219 \times T^3$$

The solubility of CO_2 gas in seawater (K_H), expressed in mol $L^{-1} \cdot atm^{-1}$, was calculated using the formula developed by Weiss (1974):

$$\ln K_H = -58.0931 + 90.5069\left(\frac{100}{T}\right) + 22.2940\ln\left(\frac{T}{100}\right) + S\left[0.027766 - 0.025888 + \left(\frac{T}{100}\right) + 0.0050578\left(\frac{T}{100}\right)^2\right]$$

Since we did not directly measure pCO_2^{air}, we used xCO_2 data provided by the United States National Oceanic and Atmospheric Administration (NOAA) from Dongsha Island (https://gml.noaa.gov/aftp/data/trace_gases/co2/flask/surface/txt/co2_dsi_surface-flask_1_ccgg_event.txt). Dongsha Island, located at approximately 20.70°N, is a coral atoll with a latitude similar to that of Nanwan Bay, and importantly, it shares the characteristic of being part of a coral reef ecosystem. The dry air xCO_2 values were corrected to 100% humidity, assuming atmospheric pressure of 1 atm, using the

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temperature and salinity data recorded at the time of sampling. The resulting pCO_2^{air} was 386, 377, 378, and 383 μatm on March 31, July 5, and October 18, 2011, and January 22, 2013, respectively.

The seasonal fluxes across the bay were calculated by multiplying the mean CO_2 exchange flux at all stations for each season by the bay's area of ~30 km^2.

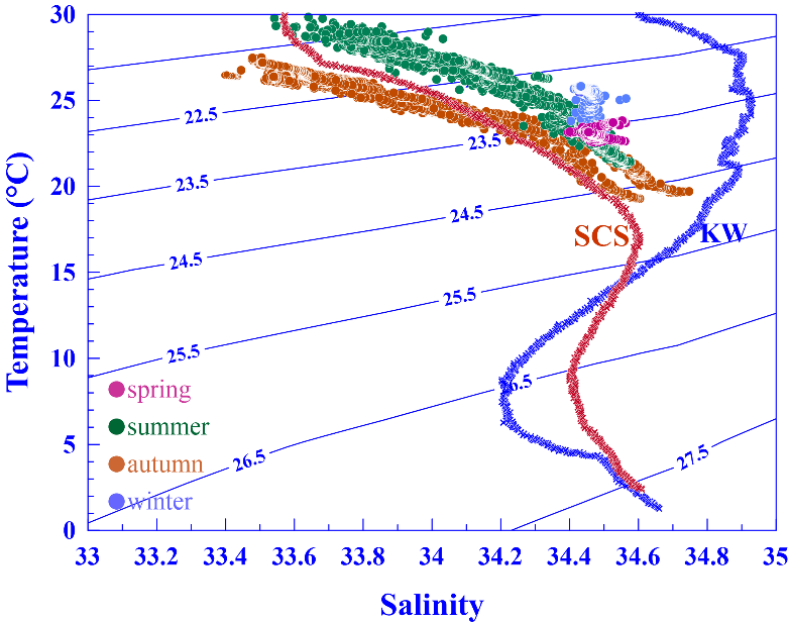

Fig. 2 Temperature vs. salinity (T-S) diagram at Nanwan Bay, Taiwan in spring, summer, autumn, and winter. SCS = South China Sea and KW = Kuroshio Waters.

3. Results and discussion

3.1 Variation in hydrological parameters. Both temperature and salinity varied over time in Nanwan Bay (Fig. 2), with the seasonal variation likely driven by both the monsoon and SCS circulation patterns as follows. The Kuroshio Current flows

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northwards along Taiwan's east coast, with a portion of the Western Philippine Sea (WPS) water following the Kuroshio and then flowing westward along the northern SCS shelf (Yuan et al., 2006). Nan et al. (2015) suggested that surface salinity of 34 or higher is characteristic of the Kuroshio, indicating potential inundation of the Kuroshio Current into Nanwan Bay during the high-salinity spring period. During summer, the southwest monsoon dominates, leading to a decrease in the Kuroshio's influence; the main circulation of the Kuroshio shifts westward to the Luzon Strait, limiting its intrusion into the northwestern SCS region (Liang et al., 2008). In the northern SCS region, the southwest-to-northeast circulation pattern prevails during the monsoon, with most seawater flowing out of the SCS through the Luzon Strait and converging with the Kuroshio axis, resulting in Nanwan Bay being dominated by the SCS water mass during the summer. An analysis of temperature and salinity data from Nanwan Bay, the SCS, and the Kuroshio Current indicates that Nanwan Bay mainly consists of the SCS water mass during summer and autumn, while during spring and winter, the water masses are intermediate between the two (Fig. 2). As such, Nanwan Bay is classified as a mixed water mass area, comprising both SCS and Kuroshio Current water masses.

During the survey period, there was a clear positive correlation between pH and temperature. Additionally, pH and TA exhibited significant correlations with salinity

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Table 1. Correlation matrix of seawater quality variables with correlation coefficients (*r*) for spring, summer, autumn, and winter. Variables include temperature, salinity, dissolved oxygen (DO), DO saturation (DO%), total alkalinity (TA), dissolved inorganic carbon (DIC), and pH.

Spring	Temperature	Salinity	DO	DO (%)	TA	DIC	pH
Salinity	0.35**						
DO	-0.23	-0.40**					
DO (%)	0.02	-0.32**	0.89**				
TA	0.04	0.03	0.19	0.11			
DIC	-0.17	-0.04	0.25*	0.11	0.92**		
pH	0.43**	0.13	-0.02	0.05	0.61**	0.27*	
pCO_2	-0.28*	-0.07	0.03	-0.02	-0.45**	-0.09	-0.96**

Summer	Temperature	Salinity	DO	DO (%)	TA	DIC	pH
Salinity	-0.96**						
DO	0.65**	-0.53**					
DO (%)	0.90**	-0.81**	0.90**				
TA	-0.82**	0.81**	-0.52**	-0.72**			
DIC	-0.91**	0.84**	-0.68**	-0.87**	0.91**		
pH	0.89**	-0.79**	0.72**	0.89**	-0.72**	-0.94**	
pCO_2	-0.22*	0.07	-0.45**	-0.38**	0.23*	0.51**	-0.64**

Autumn	Temperature	Salinity	DO	DO (%)	TA	DIC	pH
Salinity	-0.95**						
DO	0.88**	-0.85**					
DO (%)	0.95**	-0.93**	0.98**				
TA	-0.57**	0.56**	-0.51**	-0.55**			
DIC	-0.76**	0.75**	-0.66**	-0.72**	0.88**		
pH	0.79**	-0.77**	0.66**	0.73**	-0.43**	-0.80**	
pCO_2	-0.32**	0.33**	-0.22	-0.27*	0.27*	0.63**	-0.83**

Winter	Temperature	Salinity	DO	DO (%)	TA	DIC	pH
Salinity	-0.32**						
DO	0.43**	-0.26*					
DO (%)	0.78**	-0.34**	0.70**				
TA	-0.15	0.06	-0.19	-0.17			
DIC	-0.39**	0.02	-0.34**	-0.41**	0.89**		
pH	0.59**	0.06	0.39**	0.61**	-0.12	-0.56**	
pCO_2	-0.34**	-0.19	-0.33**	-0.44**	0.29**	0.67**	-0.94**

*: $p \leq 0.05$ and **: $p \leq 0.01$.

during summer and autumn, but such correlations were not evident in spring and

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winter (Table 1). It is expected that TA and salinity will covary because the charge differences between cations and anions in seawater change with salinity. Salinity generally increases with depth and is influenced by various factors such as rainfall, evaporation, and freshwater input, which can lead to changes in TA. It is worth noting that the absence of a major river nearby the study sites, as well as the absence of any

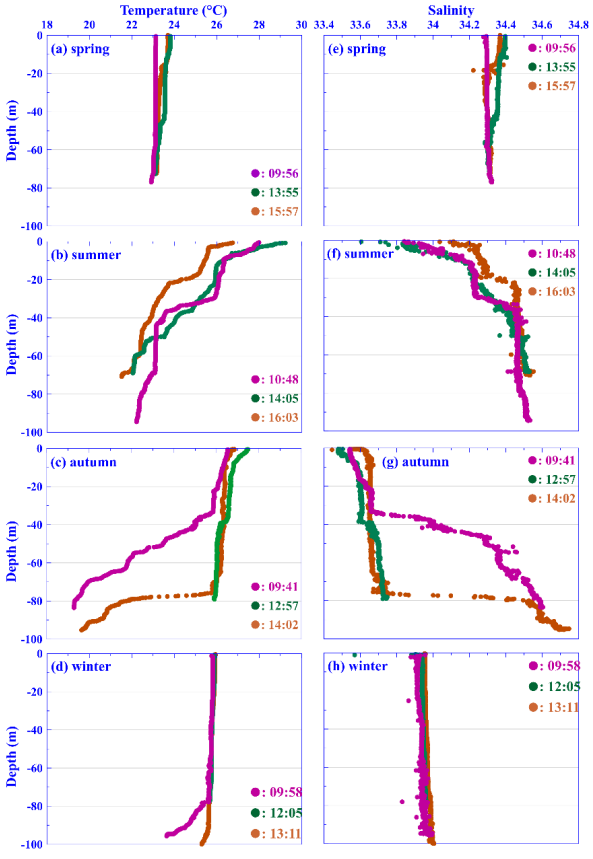

Fig. 3. Vertical profiles of temperature and salinity at station S10 in spring (a & e, respectively), summer (b & f, respectively), autumn (c & g, respectively), and winter (d & h, respectively) at three sampling times (see Table S1 for details.) as indicated in each panel.

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observed rainfall events one week prior to each survey period, strongly suggests that freshwater input did not play a significant role in altering TA within this study area. Moreover, the absence of significant correlations among salinity, TA, and pH in spring and winter implies that these relationships might be influenced by factors such as intense vertical mixing or upwelling, which could disrupt the salinity, TA, and pH vertical profiles. This supposition is further supported by the well-mixed profiles of salinity and temperature found throughout the water column at station S10 during spring and winter (Fig. 3a, d, e, & h). Additionally, seawater characterized by low temperature, low pH, and high salinity observed at station S10 during the spring suggests that this well-mixed pattern throughout the water column may be primarily associated with upwelling during this period (Figs. 3 and S1; further details can be found in the next section).

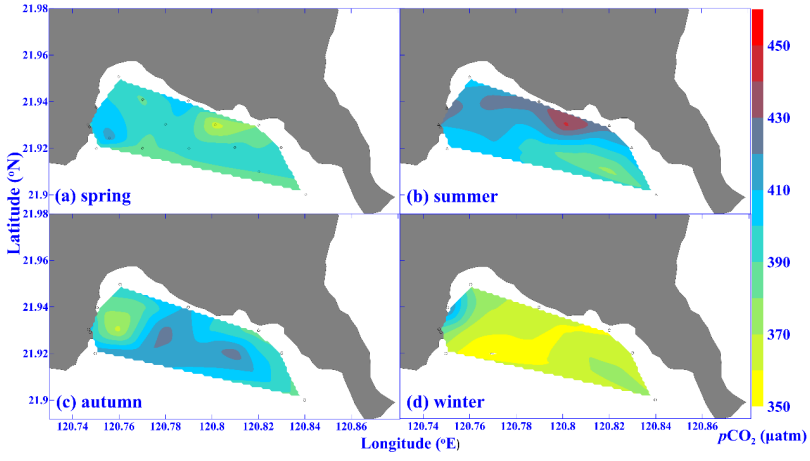

Fig. 4. Seasonal variation in sea surface pCO_2 (μatm) in Nanwan Bay, Taiwan in spring (a), summer (b), autumn (c), and winter (d).

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3.2 Changes in surface water pCO_2. Surface pCO_2 levels in Nanwan Bay ranged from 364–422, 362–448, 350–480, and 345–427 μatm in spring, summer, autumn, and winter, respectively (Fig. 4). The means values (±SD) across all stations (N = 17) for each season were 393.2 (±11.6), 411.4 (±19.0), 401.7 (±18.3), and 370 (±17.3) μatm, respectively. The mean surface seawater temperatures during these seasons were 23.4 (±0.4), 28.8 (±0.8), 27.0 (±1.0), and 26.0 (±0.6)℃, respectively. In the open ocean, pCO_2 levels are primarily influenced by temperature, horizontal transport and vertical mixing, biological processes, and gas exchange (e.g., Dai et al., 2009). Due to the mixing of different water masses by monsoons, tides, eddies, upwelling, and other ocean currents, significant variation in temperature and salinity of the water column was observed at different times at station S10 (Fig. 3) and in the carbonate parameter data (Fig. 5d & S1-S4). Similarly, significant diurnal variation in seawater pCO_2 has been reported in another coral reef ecosystem (Yan et al., 2018), suggesting that more extensive temporal and spatial sampling is needed to accurately capture the true dynamics of the carbonate system in coral reef environments. During spring and winter, pronounced mixing was evident, as demonstrated by the straight vertical profiles in temperature and salinity in Fig. 3a, d, e, and h. Conversely, in summer and autumn, mixing was less apparent.

According to Lee et al. (1997; 1999a; 1999b), cold-water upwelling occurs with

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tidal changes in Nanwan Bay, which increases vertical mixing. The temperature-salinity-pH-DO diagram of station S1 illustrates that throughout the entire upwelling

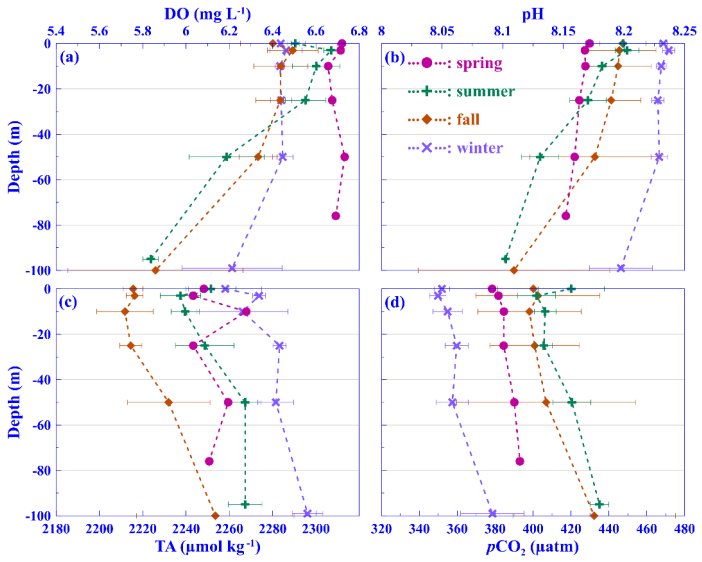

Fig. 5. Vertical profiles of mean (± SD) dissolved oxygen (DO; a), pH (b), total alkalinity (TA; c), and pCO_2 (d) at station S10 in different seasons.

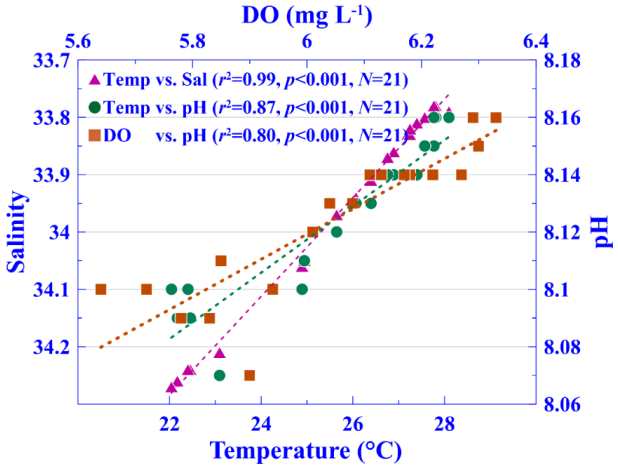

Fig. 6 Relationships amongst temperature and salinity or pH, as well as dissolved oxygen (DO) vs. pH, during multiple upwelling events at Station S1 (data from Tew et al., 2014).

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event, there is an intrusion of cold, low-DO, low-pH, and high-salinity deep-sea water into the nearshore regions of Nanwan Bay (Fig. 6). Seawater property profiles of S10 provide additional evidence of upwelling, as indicated by the presence of low temperatures (23.3±0.6℃), low pH (8.16±0.01), high salinity (34.32±0.03), and relatively low pCO_2 (385.4±5.4 μatm) across the well-mixed water column in spring (Figs. 3 & 5).

As temperature increases, CO_2 solubility decreases, causing an increase in pCO_2. To accurately isolate and understand the specific impact of temperature variations on pCO_2, it is crucial to normalize these factors. This approach allows for a clearer distinction between temperature-induced changes and those driven by other influences. Takahashi et al. (2002) proposed to evaluate the relative effects of temperature and non-temperature effects on pCO_2 changes as follows:

$$pCO_2 \text{ at } T_{obs} = (pCO_2)_{\text{Mean annual}} \times \exp[0.0423(T_{obs} - T_{mean})]$$

$$pCO_2 \text{ at } T_{mean} = (pCO_2)_{obs} \times \exp[0.0423(T_{mean} - T_{obs})]$$

pCO_2 at T_{obs} is calculated using the average pCO_2 to determine the pCO_2 value at a given temperature; pCO_2 at T_{mean} is the standardized pCO_2 value at the average temperature; and T_{mean} and T_{obs} are the annual average temperature and the measured temperature on-site, respectively. To assess the impact of temperature (T) and non-temperature (nT) effects on pCO_2, the following equations were employed:

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T effect = pCO_2 at T_{obs} - pCO_2 at T_{mean}

nT effect = pCO_2 - pCO_2 at T_{obs}

The fluctuations in the mean pCO_2 at each monitoring station over time suggest that temperature and non-temperature effects had distinct influences on the average pCO_2 at each station (Fig. 7). This means that seasonal changes in pCO_2 are influenced by both temperature and non-temperature effects (e.g., gas exchange, tides, currents, river discharge, upwelling, vertical mixing, and biological processes), with some stations showing larger changes than others. It is believed that the stations with larger pCO_2 variations are likely dominated by either temperature or non-temperature

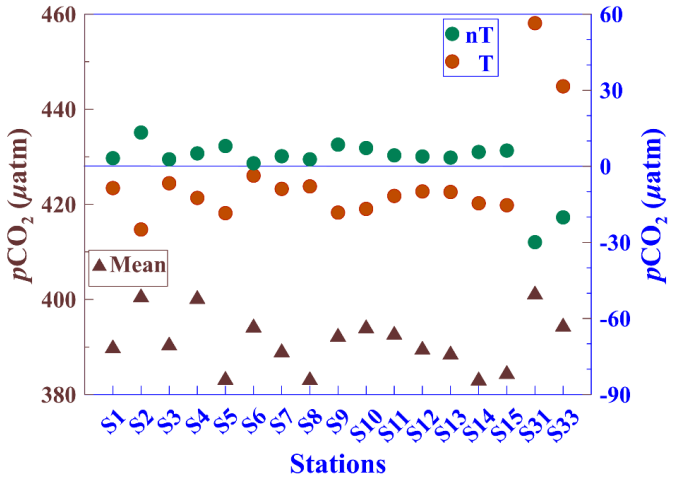

Fig. 7. Mean values and impact levels of surface water pCO_2 at each station in Nanwan Bay are presented. The "Mean" represents the average value for each station across the four seasons and is plotted on the left y-axis. The terms "nT" and "T" refer to the non-temperature and temperature effects on surface water pCO_2, respectively, and are displayed on the right y-axis for clarity.

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effects, while the smaller changes reflect the mutual offsetting of the two effects (Dai et al., 2009). For example, the variability in pCO_2 observed at S31 and S33, which are located near the Nuclear Power Plant outlet, is likely driven by temperature change, as the water temperature in this area was consistently higher and exhibited greater variability compared to the surrounding area throughout the year. In fact, we expected that temperature effects on pCO_2 would be more pronounced at these sites.

During the entire study duration, variation in surface water pCO_2 in Nanwan Bay was influenced by a combination of temperature and non-temperature factors throughout all seasons, albeit with varying degrees of influence in different seasons.

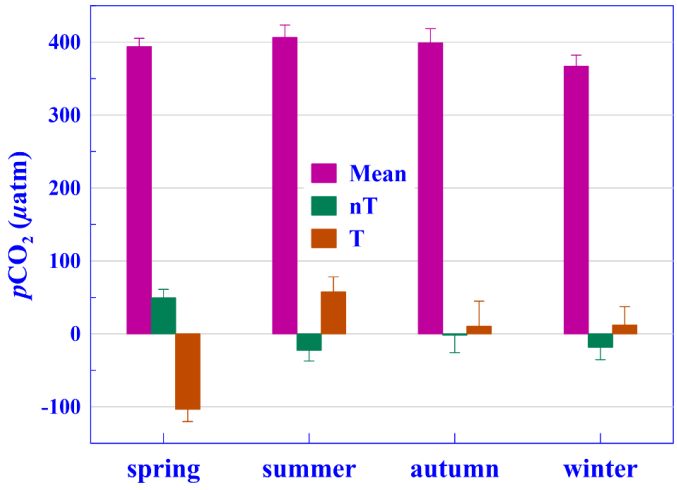

Fig. 8. Mean values and impact levels of surface water pCO_2 in Nanwan Bay during different seasons. "Mean" represents the average value across sampling stations for each season. "nT" denotes non-temperature effects on surface water pCO_2, while "T" signifies temperature effects on surface water pCO_2. Error bars represent standard deviation.

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Notably, the effect of temperature was more prominent in the spring and summer (Fig. 8). The relationship between surface water pCO_2, surface water temperature, and Chl *a* concentration revealed a significant correlation with pCO_2 and temperature in the summer ($p<0.01$; Fig. 9a), and a positive correlation between pCO_2 and Chl *a* in autumn ($p<0.05$; Fig. 9b). This suggests that temperature and Chl *a* may be the factors affecting surface water pCO_2 in summer and autumn, respectively. In general, Chl *a* affects pCO_2 by driving photosynthesis, which removes CO_2 from seawater via

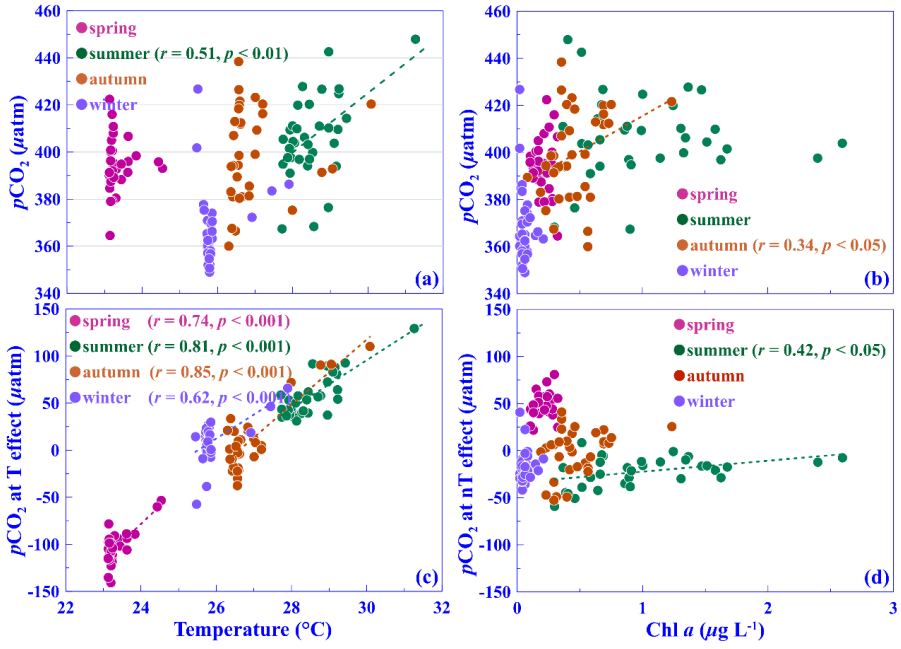

Fig. 9. Relationships between surface water pCO_2 and (a) temperature, and (b) Chl *a*, (c) the temperature (T) effect on surface water pCO_2 and temperature, and (d) the non-temperature (nT) effect on surface water pCO_2 and Chl *a* across different seasons in Nanwan Bay. The linear relationships, along with the corresponding r and p values, are provided for reference.

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phytoplankton activity (Chen et al., 2019). Higher chlorophyll levels suggest increased primary productivity, leading to greater CO_2 drawdowns during the day.

To further assess the influence of T and nT effects on surface water pCO_2 across different seasons, we compared T-driven surface water pCO_2 with temperature and nT-driven surface water pCO_2 with Chl *a* (one of the nT factors; Fig. 9c, d). Significant correlations were observed between T-driven surface water pCO_2 and temperature in all seasons (Fig. 9c), and between nT-driven surface water pCO_2 and Chl *a* during summer (Fig. 9d). Overall, the results (Figs. 8 and 9) indicate that temperature is the primary driver of seasonal pCO_2 variation, with non-temperature factors, particularly Chl *a*, also contributing. However, the lower *r* values suggest that additional, unmeasured factors may be influencing the temporal variation in pCO_2 (Fig. 9d).

As mentioned above, seawater pCO_2 levels can be influenced by phytoplankton via photosynthesis. Therefore, nutrient availability in seawater primarily affects pCO_2 levels by either promoting or limiting phytoplankton growth and consequently primary production. In the case of Nanwan Bay, like many coral reef ecosystems, its benthic environment supports nutrient regeneration through processes such as organic carbon decomposition and other processes. However, due to the high shallow water temperature and frequent stratification, regenerative nutrients cannot easily be

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transported to the shallows. This results in the shallow areas rarely becoming eutrophic (Leichter et al., 1996; Torréton, 1999; Wolanski and Pickard, 1983). Another reason for Nanwan Bay's oligotrophy is that when nutrients flow into reef areas, resident organisms may quickly utilize them (Wilkerson and Trench, 1986). Although nutrient input from outside the bay is greater than the outward flux, rapid circulation of water in Nanwan Bay leads to unused nutrients being swiftly exported out of the bay (Su, 2009). This causes oligotrophy and high benthic productivity in the area. Su (2009) reported that during spring tides, the water can be replaced in just 1.6 tidal cycles. Therefore, nutrient levels and Chl *a* may have only small influences on pCO_2 in Nanwan Bay, with temperature changes and seawater movement having a more significant impact.

3.3 Spatial and temporal variations of $\triangle pCO_2$ and CO_2 air-sea flux. The partial pressure difference between CO_2 in surface seawater and the atmosphere, denoted as $\triangle pCO_2$, indicates the direction of air-sea CO_2 exchange. When $\triangle pCO_2>0$, CO_2 in seawater is released into the atmosphere, contributing to an increase in atmospheric CO_2 concentration (i.e., a source). On the other hand, when $\triangle pCO_2<0$, CO_2 from the atmosphere enters the seawater, acting as a sink for atmospheric CO_2. In spring, the $\triangle pCO_2$ range was between -14.3 and 27.7 μatm, with an average of 7.7 (±10.8) μatm (Fig. 10a). The highest value was observed near the Nuclear Power

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Plant outlet station, i.e., St. 2. In summer, it ranged between -5.1 and 54.5 µatm, with an average of 29.3 (±16.1) µatm. The highest value was measured near station S7. In autumn, the range was between -14.6 and 51.2 µatm, with an average of 21.2 (±18.6) µatm. The highest value was observed near stations S10-S12. In winter, the range was between -33.2 and 31.3 µatm, with an average of -16.1 (±14.5) µatm. The highest value occurred near stations S2. It is important to note that pCO_2 measurements in this study were limited to daytime, when photosynthesis is actively occurring, typically resulting in lower pCO_2 levels. As reported in this study and other coral reef ecosystems (Yan et al., 2018) , significant diurnal variations in seawater pCO_2 have been observed. Therefore, it is likely that the $\triangle pCO_2$ values presented here may be underestimates due to this limitation.

Based on data from the Central Weather Bureau's Oluanpi buoy, the average sampling date wind speed during the southwest monsoon season (summer) was 1.4 (±1.0) m s^{-1}, while during the northeast monsoon seasons (spring, autumn, & winter), it was 10.6 (±0.8), 9.2 (±2.5), and 3.3 (±0.7) m s^{-1}, respectively. In other words, high wind speeds are consistently observed during the northeast monsoon, in contrast to the relatively lower wind speeds experienced during the summer season along the coast of Taiwan (Ren et al., 2022). Utilizing these wind speed values, the CO_2 air-sea exchange flux in Nanwan Bay was calculated (Figure 10b). During spring, the CO_2

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flux ranged from -19.9 to 32.6 mmol m^{-2} day^{-1} (average=8.2±12.7 mmol m^{-2} day^{-1}). In summer, the CO_2 flux ranged from 0.0 to 4.2 mmol m^{-2} day^{-1} (average=0.9±1.2 mmol m^{-2} day^{-1}). During autumn, the CO_2 flux ranged from -17.1 to 59.5 mmol m^{-2} day^{-1}, with an average of 16.0±18.4 mmol m^{-2} day^{-1}. Finally, in winter, the CO_2 flux ranged from -5.9 to 5.6 mmol m^{-2} day^{-1}, with an average of -1.8±2.4 mmol m^{-2} day^{-1}. These findings highlight that wind speed plays a crucial factor in regulating CO_2 air-sea exchange flux. Moreover, any factors that impact wind speed can significantly affect gas exchange estimates. For instance, when using daily wind speed data for the

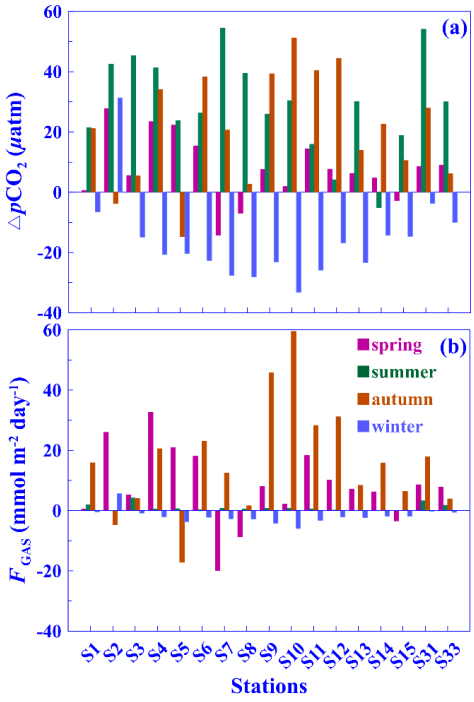

Fig. 10. Seasonal variation in (a) surface water $\triangle pCO_2$ and (b) air-sea CO_2 exchange flux (F_{GAS}) at each station. Values are presented relative to the annual mean (scaled to 0).

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sampling month, the CO_2 flux increase from 0.9 (±1.2) to 12.4 (±9.9) mmol m^{-2} day^{-1} in summer, and 16.0 (±18.4) to 29.5 (±11.9) mmol m^{-2} day^{-1} in fall (Table S2).

The area between Cape Moubitou and Cape Oluanpi, covering approximately 30 km^2 (Fig. 1), shows CO_2 fluxes of 6.2 tC, 0.7 tC, 11.9 tC, and -1.3 tC in spring, summer, fall, and winter, respectively, based on wind speeds recorded on the sampling date (Table S2). However, when using daily wind speed data for the sampling month, significant changes in CO_2 flux are observed, such as an increase from 0.7 to 9.4 tC in summer and from 11.9 to 21.9 tC in fall (Table S2). This indicates that CO_2 flux estimates are highly sensitive to wind speed variability, introducing uncertainty in determining whether Nanwan Bay's coral reef ecosystem functions as a carbon sink or source based on this limited dataset. Most coral reef areas act as atmospheric CO_2 sources, such as Bermuda (14.4 gC m^{-2} $year^{-1}$; Bates et al., 2001), Okinawa (21.6 gC m^{-2} $year^{-1}$; Ohde and Van Woesik, 1999), the Great Barrier Reef (18 gC m^{-2} $year^{-1}$; Frankignoulle et al., 1996), French Polynesia (1.2 gC m^{-2} $year^{-1}$; Frankignoulle et al., 1996; Gattuso et al., 1997; Gattuso et al., 1993), and Hawaii (17.4 gC m^{-2} $year^{-1}$; Fagan and Mackenzie, 2007). In addition to wind speed, the primary factor influencing the atmospheric carbon sink/source nature of this coral reef ecosystem is the substantial vertical mixing and upwelling observed during the spring and winter. These periods are characterized by a well-mixed water column, lower seawater

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temperatures, and reduced pCO_2 levels, particularly during the northeast monsoon, when high winds significantly enhance the CO_2 sea-air gas exchange flux. In contrast, despite high $\triangle pCO_2$ values in summer, wind speeds were relatively low, especially during the southwest monsoon, making the CO_2 sea-air flux insufficient to offset the carbon sink observed in winter. Although land-based inputs can affect nearshore environments, leading to pCO_2 variations and influencing CO_2 sea-air flux (Meng et al., 2008; De Carlo et al., 2007), the impact here is minimal, as no large river is near this coral reef ecosystem. Additionally, the wind speed data used for CO_2 flux calculations were collected from buoys within the ecosystem, providing an accurate reflection of local conditions. It is important to note that short-term and long-term wind speed fluctuations, prevailing climate conditions, and specific events can affect CO_2 flux calculations, given the nonlinear relationship between wind speed and gas exchange (Chou et al., 2011; Evans et al., 2012; De La Paz et al., 2011).

4. Conclusions

Nanwan Bay experiences notable seasonal variations in temperature and salinity, largely influenced by the South China Sea and the Kuroshio Current. These changes impact the seawater carbonate system (including pCO_2), with additional influences from vertical water movement and biological activity. Temperature emerged as the primary driver of spatio-temporal variations in pCO_2, particularly at the consistently

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warmer outlet station. Non-temperature factors also played a role during the spring, while the interaction between temperature and other factors became more prominent in the autumn and winter. During the winter, the bay absorbs more CO_2 from the atmosphere, whereas in the spring, summer, and autumn, it releases more CO_2 than it absorbs. The complex interplay of temperature, water mass origin, vertical water movement, and biological activity in Nanwan Bay significantly affects its carbon dioxide dynamics and its influence on atmospheric CO_2 levels.

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Data were submitted to Dryad for archiving (doi: 10.5061/dryad.63xsj3v7d).

6. Credit author statement

This manuscript was conceptualized by PJM and CCC; CMC and HYH conducted investigations on all cruises and collected and analyzed the initial data; PJM, ABM,

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and CCC wrote the initial draft; all authors provided comments and edits. The authors declare that they have no competing interests.

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