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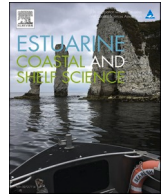
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In-situ measurements reveal alkalinity release from cold-temperate seagrass meadows

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ABSTRACT

Understanding the carbon sequestration potential of blue carbon ecosystems is important to inform climate policies and to guide restoration and protection efforts. Alkalinity generation is an often overlooked carbon sequestration mechanism, especially in seagrass meadows. Here, we quantified total alkalinity (TA) and dissolved inorganic carbon (DIC) fluxes in two cold-temperate *Zostera marina* seagrass meadows in Sweden using 24-h in-situ chamber incubations at the end of the high-productivity season. The seagrass meadows were similar net sources of TA ($16 \pm 45 \text{ mmol m}^{-2} \text{ d}^{-1}$ in Smalsund, $17 \pm 16 \text{ mmol m}^{-2} \text{ d}^{-1}$ in Bökevik), whereas DIC fluxes were highly variable ($34 \pm 59 \text{ mmol m}^{-2} \text{ d}^{-1}$ in Smalsund, $-43 \pm 35 \text{ mmol m}^{-2} \text{ d}^{-1}$ in Bökevik). Fluxes followed a diurnal cycle consistent with photosynthesis-respiration cycles. As a result, seagrass meadows ameliorated ocean acidification locally during the day, but not during the night. The large CO_2 uptake provided higher buffering levels compared to mangroves and saltmarshes. The TA fluxes were comparable to those reported for Mediterranean and tropical seagrass meadows, but 16-times lower than in mangrove forests and 5-times lower than in saltmarshes. Alkalinity generation in these cold-temperate seagrasses exceeded soil organic carbon stocks accumulation by fourfold, potentially contributing to their carbon sequestration potential and warranting inclusion in seagrass meadow carbon budgets.

1. Introduction

Blue carbon refers to the carbon stored in the world's oceans, which is becoming increasingly acknowledged as a tool for mitigating climate change (Lovelock and Duarte, 2019; Nellemann et al., 2009). Blue carbon ecosystems, i.e. mangrove forests, saltmarshes, and seagrass meadows, naturally sequester large amounts of organic carbon in their sediments per area compared to terrestrial ecosystems acting as a global CO_2 sink (McLeod et al., 2011). While they occupy only $\sim 0.5\%$ of the ocean floor, blue carbon ecosystems accumulate almost half of the organic carbon in all marine sediments (Macreadie et al., 2021). In order to resolve the presently uncertain climate benefits of blue carbon ecosystems it is essential to account for all relevant coastal carbon sources,

sinks, and transport pathways (Oschlies et al., 2025; Williamson and Gattuso, 2022). Since blue carbon was first described (Nellemann et al., 2009), much research has focused on organic carbon burial in sediments of blue carbon ecosystems, and other components of the coastal carbon cycle have been overlooked. Recently, inorganic carbon has gained larger attention as an important component in blue carbon budgets (Santos et al., 2021). Production of total alkalinity (TA), a major component of dissolved inorganic carbon (DIC), represents a long-term atmospheric CO_2 sink (Middelberg et al., 2020). Therefore, it is important to quantify TA and DIC fluxes and assess their underlying drivers in coastal ecosystems to close blue carbon budgets (Santos et al., 2021).

Previous research efforts on alkalinity production in coastal ecosystems have focused primarily on mangrove forests and saltmarshes,

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yielding global estimates of TA and DIC fluxes (Reithmaier et al., 2023). While many studies have explored organic carbon accumulation and burial in seagrass meadows (Graversen et al., 2025), research on inorganic carbon fluxes remains comparatively limited. Local case studies performed in Mediterranean and tropical seagrass meadows suggest that they can act as a TA source (Barrón et al., 2006; Champenois and Borges, 2021; Chou et al., 2025; Fan et al., 2024; Majtényi-Hill et al., 2023; Smith et al., 1991). Alkalinity production under cold-temperate conditions, where light and temperature are reduced and species differ, remains understudied (Mazarrasa et al., 2015; Soissons et al., 2018).

Photosynthesis consumes and respiration releases CO_2 , thus impacting DIC concentrations (Ganguly et al., 2017). TA-producing sedimentary processes such as denitrification and sulfate reduction can lead to additional CO_2 uptake if reoxidation of reduced metabolic products does not occur (Reithmaier et al., 2023). Dissolution of sedimentary calcium carbonate (CaCO_3) generates TA and consumes CO_2 , while the reverse occurs from formation of calcium carbonate (Van Dam et al., 2021). Though global trends remain uncertain, carbonate cycling could lead to either additional carbon uptake or emission from seagrass meadows, potentially representing a large part of the seagrass carbon budget (Van Dam et al., 2021). The relative proportions of the components within the marine DIC equilibrium ($[\text{CO}_2] + [\text{HCO}_3^-] + [\text{CO}_3^{2-}]$) are critically important for the ecosystem's capacity to absorb atmospheric CO_2 and buffer ocean acidification locally (Middelberg et al., 2020).

Inorganic carbon dynamics not only shape the potential of seagrass meadows to act as carbon sinks but also play a key role in determining habitat quality for associated species. Increasing CO_2 intensifies ocean acidification (OA) resulting in lower pH and CaCO_3 saturation in marine systems (Doney et al., 2009). Seagrass meadows have the potential to modulate seawater carbonate chemistry and ameliorate ocean acidification through net CO_2 uptake and TA production, enhancing the seawater buffering capacity compared to adjacent unvegetated habitats (Ricart et al., 2021). Short-term alterations of pH driven by changing TA and DIC ratios are primarily determined by aerobic community metabolism as a result of diel CO_2 release and uptake patterns (Buapet et al., 2013). These changes to the carbonate system are important for residing organisms such as calcifying algae and bivalves (Saderna et al., 2019). Previous studies have reached mixed conclusions that meadow ecosystems provide either refugia from acidification or drive a lower pH (Hendriks et al., 2014; Van Dam et al., 2021). Additional observations are needed to resolve how factors such as climate, species and hydrodynamics impact the seawater buffering capacity.

This study adds to the growing body of research on inorganic carbon dynamics and their underlying drivers in seagrass meadows, presenting new observations from two cold-temperate *Zostera marina* meadows on

the west coast of Sweden. We hypothesised that cold-temperate seagrass meadows will act as weaker TA sources than seagrass meadows in warmer climates due to lower temperatures and light availability reducing photosynthesis and soil carbon accumulation. Our results were put into perspective by (1) comparing acidification proxies to local offshore waters and other blue carbon ecosystems, (2) comparing inorganic carbon fluxes to other components of the local carbon budget, and (3) comparing TA and DIC fluxes to available information from seagrass sites in warmer climates as well as to other blue carbon ecosystems.

2. Methods

2.1. Site descriptions

This study was conducted in two cold-temperate seagrass meadows in the Gullmar fjord on the Skagerrak coast of Sweden close to the Kristineberg Centre for Marine Research and Innovation (Fig. 1). The mouth of the fjord is surrounded by an archipelago of small islands and bays. The upper water body of the fjord, where the seagrass meadows are located, typically has a salinity of 18–30 (Lindahl and Hernroth, 1988). Salinity variations arise from the fjord's circulation, which is influenced by a mixture of brackish Baltic outflow and marine waters from the Skagerrak and Kattegat, as well as freshwater input from the Örekil river at the fjord head and land runoff (Svansson, 1975). The study area is an open bay near the fjord mouth exposed to waves and easterly winds (Björk et al., 2021; Dahl et al., 2023).

The two sites, Smalsund ($58^\circ 15' 6.41''\text{N}$, $11^\circ 26' 37.14''\text{E}$) and Bökevik ($58^\circ 14' 56.00''\text{N}$, $11^\circ 27' 15.62''\text{E}$) (Fig. 1) are dominated by eelgrass (*Zostera marina*) meadows. Both sites are permanently submerged, as the tidal range in the Gullmar Fjord is only ~ 0.3 m (Kristiansen and Aas, 2015), preventing exposure during low tide. Bökevik is exposed to more wind directions than Smalsund, which is sheltered towards the predominating westerly winds. The sediment is mainly sandy, with a significant mud content of 50 % and 35 % at Smalsund and Bökevik, respectively (Dahl et al., 2018). The mean ($\pm$ SD) seagrass shoot density and shoot height were similar in the two sites (270 ± 70 shoots m^{-2} , 65 ± 9 cm in Smalsund and 240 ± 70 shoots m^{-2} , 72 ± 9 cm in Bökevik). The organic carbon content is on average 3–4 % in the top 50 cm of sediment (Dahl et al., 2023).

2.2. Sample collection and measurement

An in-situ chamber experiment was conducted from the 5th to the September 9, 2024. At each site, 24-h time series were performed using six chambers to resolve diel changes in DIC and TA fluxes. The chambers

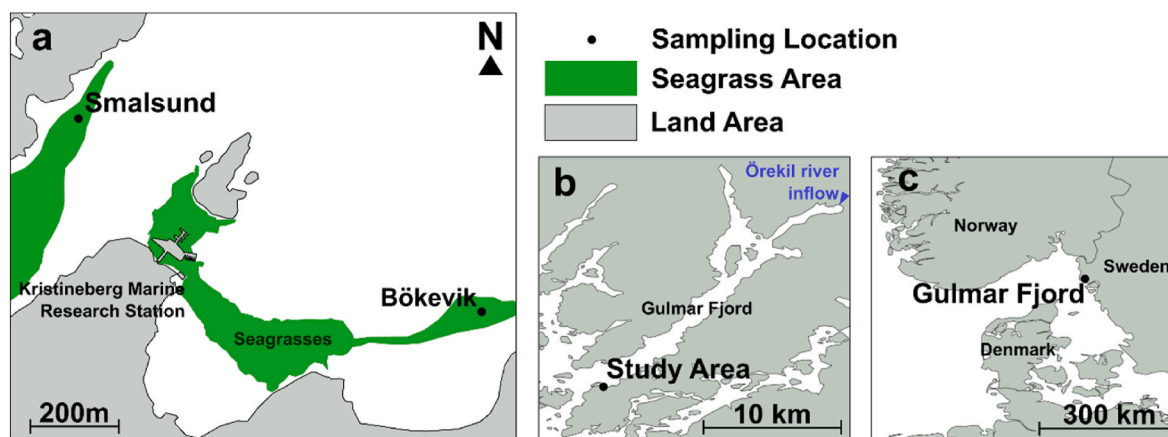


Fig. 1. Study site map showing seagrass meadows and individual study sites (Smalsund and Bökevik) next to Kristineberg Center for Marine Research and Innovation, in the Gullmar Fjord (a). The study area is situated in the mouth of the Gulmar Fjord (b) on the west coast of Sweden (c). Seagrass areas, in green, are modified from Staveley et al. (2019) and Henriksson et al. (2024).

were designed to isolate a water mass from the sediment to the water surface using flexible plastic tubes (16 cm diameter) adjusted to depth (Fig. S2). The flexible walls allowed internal mixing of the enclosed water due to external water movements. Enclosed volumes ranged from 20 to 37 L depending on the depth. The chambers remained sealed from both the surrounding water column and the atmosphere, except for a gas pocket of ~0.5 L. Chambers were deployed using SCUBA diving in two rows of increasing water depth (from 0.6 m to 1.5 m) at each site over *Zostera marina* meadows (Fig. 1).

Water samples were collected at seven time points during incubations: 11:00, 13:00, 16:00, 19:00, 23:00, 6:00 and 11:00. Nighttime lasted for approximately 10 h, with sunset at 20:00 and sunrise at 06:30. After flushing, two plastic 60 ml syringes were filled with water from each of the six chambers. Loggers were deployed adjacent to each chamber to develop consecutive time series of physiochemical parameters at each site. Light intensity was measured by Odyssey PAR loggers, indicating that the chosen sampling intervals captured key light transitions. Dissolved oxygen (DO) was measured with HOBO Dissolved Oxygen Data Loggers. Temperature, salinity and water depth were measured with YSI EXO 2 sondes. Every logger recorded at 15 min intervals. Sediment porewater samples were taken next to the chambers 1, 3 and 5 at the start and end of both time series, using a metal tube sipper with holes along the bottom to extract porewater between 5 cm and 15 cm sediment depth (Bansal et al., 2023). Porewater samples were collected 30 cm from the chambers to avoid disturbance from chamber deployment.

For DIC analysis, water samples were filtered by syringe through 0.7 µm GF/F filters into 12 ml exetainers, stored in darkness at 4°C and analysed within a week after sampling. The DIC measurements were performed using an Apollo SciTech AS-C5 multiport DIC Analyser with a precision of better than 0.05 %. Calibration was performed using certified reference material in seawater (CRM batch #216) provided by Dr. Andrew Dickson at Scripps Institution of Oceanography. For TA analysis, water samples were filtered by syringe through 0.7 µm GF/F filters into 50 ml falcon tubes, stored in darkness at 4°C and measured within two weeks after sampling. Analysis was performed by Gran titration using 0.01 M HCl with an 888 Titrando and calibrated using certified reference material (CRM, batch #216). Precision was better than 5 µmol kg⁻¹. Temperature during titration was 20–22°C. The salinity of each TA sample was measured using a handheld HACH IntelliCAL conductivity probe.

2.3. Calculations

All calculations were conducted in R (version 4.5). TA and DIC fluxes were calculated:

$$\text{Flux} = \frac{\text{TA}_n - \text{TA}_{\text{lag}}}{t_n - t_{\text{lag}}} * \frac{\text{Volume}}{\text{Area}} \quad (1)$$

where $\text{TA}_n - \text{TA}_{\text{lag}}$ is the change in total alkalinity from one time point to another. The exact volume of each respective chamber was determined by mixing 60 ml of 3 g per 1L sodium fluorescein ($\text{C}_{20}\text{H}_{10}\text{Na}_2\text{O}_5$) for 15 min with the water and measuring absorbance at 490 nm (PerkinElmer Lambda 25, UV/VIS spectrophotometer) (Reis et al., 2024). Volume was calculated with the molar absorption coefficient for sodium fluorescein of 76,900 M⁻¹ cm⁻¹ at pH 8. Area refers to the chamber area of 201 cm². Volume removed during sampling (100 ml) was accounted for during calculations. At each timepoint, averages and standard deviations were calculated across the six chambers for each site. Flux values were calculated between consecutive sampling times and plotted at the midpoint of each interval to reflect the average rate of change over that period. Daily fluxes were estimated by summing day- and night-time fluxes, which were obtained by multiplying the mean daytime flux by 14 h and the mean night-time flux by 10 h, corresponding to the respective lengths of day and night.

The partial pressure of CO₂ ($p\text{CO}_2$), pH, Ω Aragonite (Ω_{Arag}), Revelle factor, and buffer factor beta H (β_{H}) were calculated using the seacarb package with the input parameters temperature, salinity, TA and DIC. The used K_0 (solubility coefficient of CO₂ in seawater) was determined by Weiss (1974). Chosen K_1 and K_2 (dissociation constants of carbonic acid in seawater) were determined by Mojica and Millero (2002). Since calculated $p\text{CO}_2$ does not account for organic alkalinity, reported values are likely underestimated (Kerr et al., 2021). Oxygen saturation was calculated with the Marelac R package using the equation from Weiss (1970). Apparent oxygen utilisation (AOU) was then calculated as the difference between the saturation and the measured concentration. For comparison with our data, TA, DIC, temperature and salinity at the mouth of the Gullmar Fjord during the sample period were obtained from Copernicus Marine Service (2025).

3. Results

3.1. Trends and drivers of inorganic carbon dynamics

Biogeochemical parameters displayed similar trends and ranges at Smalsund and Bøkevik (Fig. 2). Diurnal patterns for DIC and TA fluxes were observed (Fig. 2a and b). TA (mean ± sd, range: 1996 ± 21, 1962–2059 µmol kg⁻¹) was lowest in the evening and highest in the morning. DIC (1798 ± 38, 1699–1899 µmol kg⁻¹) was ~10 % lower than TA and followed the same trend. $p\text{CO}_2$ was undersaturated (265 ± 51, 146–382 µatm; Fig. 2c and d) and pH ranged from 8.1 to 8.4 (Fig. 2e and f). Dissolved oxygen saturation (112 ± 10, 87–129 %) was highest in the afternoon (~16:00) and decreased throughout the night, being lowest in the early morning (Fig. 2c and d). Salinity was nearly constant ranging from 18 to 19 (Fig. 2e and f). The average water temperature (Fig. 2g and h) was 19°C, with a range of 18.2–19.2°C. PAR (Fig. 2g and h) was highest at 13:00, with a peak of 564 µmol m⁻² s⁻¹. CO₃²⁻ concentrations peaked in the evening while HCO₃⁻ declined correspondingly (Fig. S1).

Assessing TA:DIC ratios gives insights about biogeochemical processes driving inorganic carbon dynamics. TA and DIC showed a strong positive relationship at both sites (Fig. 3a). The slope of the TA versus DIC regression was 0.28 at Smalsund and 0.19 at Bøkevik. The TA:DIC ratio was weakly negatively correlated with the AOU, which was predominantly negative, underlining the importance of photosynthetic activity (Fig. 3b). TA:DIC ratios were always above one with higher values during the day (1.13 ± 0.02) than during the night (1.10 ± 0.01) suggesting that seagrasses mainly increase the local seawater pH (Cai et al., 2021).

We evaluated different proxies to examine the capacity of seagrass meadows to ameliorate ocean acidification. Ω_{Arag} , which is saturation state of aragonite (CaCO₃), was always above one (mean ± sd, day: 2.7 ± 0.4, night: 2.3 ± 0.2) indicating oversaturation and thus favourable conditions for calcifying organisms (Fig. 4a). Compared to waters outside the Gullmar fjord, the seagrass meadows had a 13 % higher Ω_{Arag} during the day and 10 % lower Ω_{Arag} during the night. Similarly, TA minus DIC (Fig. 4b), which reflects the relative changes between CO₃ and CO₂, was higher than offshore waters during daytime (226 ± 31 µmol kg⁻¹) and lower during nighttime (174 ± 21 µmol kg⁻¹). The Revelle factor, which is a measure to quantify the response of seawater to a change in $p\text{CO}_2$, was 14 % lower than offshore waters during the day (11 ± 0.8) and 1 % lower during the night (13 ± 0.8), indicating a better or similar capacity to buffer changes in atmospheric CO₂ uptake (Fig. 4c). The buffer factor β_{H} , which quantifies the change in seawater acidity due to a change in hydrogen ion concentration, indicated increased buffering during the day (0.5 ± 0.04) and decreased buffering during the night (0.4 ± 0.03) compared to offshore waters (Fig. 4d).

Porewater TA (2256 ± 246, 1864–2669 µmol kg⁻¹) and DIC (2595 ± 553, 1874–3470 µmol kg⁻¹) were higher than in surface water (Table 1). There was a higher enrichment in DIC (44 %) than in TA (13 %) in porewater relative to surface waters. TA:DIC ratios were ~1 or

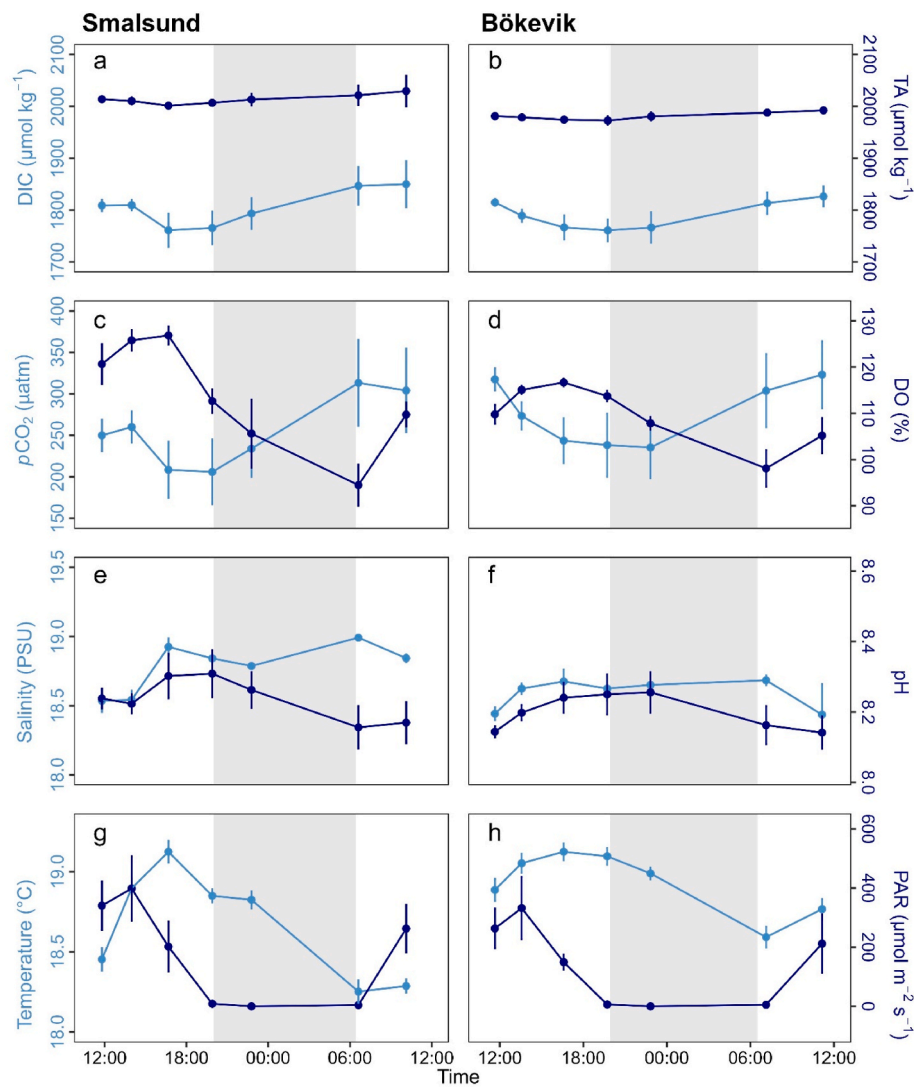


Fig. 2. Diurnal trends of dissolved inorganic carbon (DIC; a, b), total alkalinity (TA; a, b), $p\text{CO}_2$ (c, d), dissolved oxygen (DO; c, d), salinity (e, f), pH (e, f), temperature (g, h) and photosynthetically active radiation (PAR; g, h). Data shown as averages with standard deviation bars ($n = 6$) for each time point. The grey background represents the nighttime.

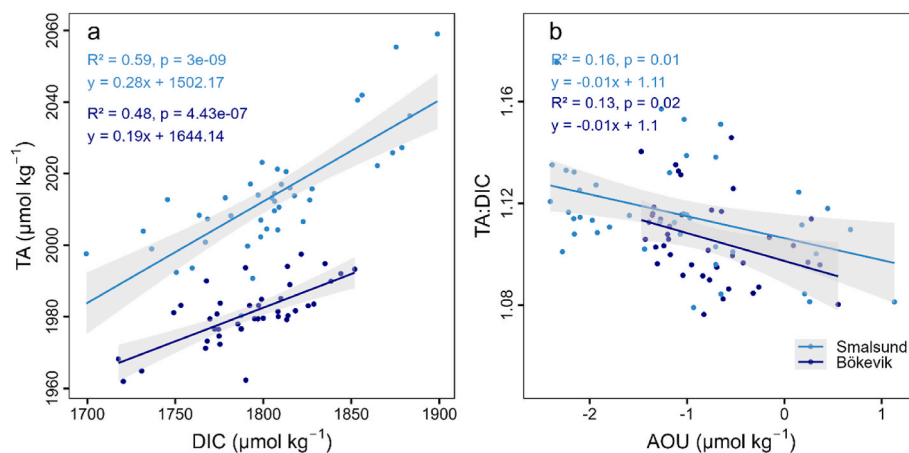


Fig. 3. Linear regressions for DIC versus TA (a) and TA:DIC ratio versus apparent oxygen utilisation (AOU, b). R^2 and p -values of linear regressions are shown with grey areas indicating the 95 % confidence intervals.

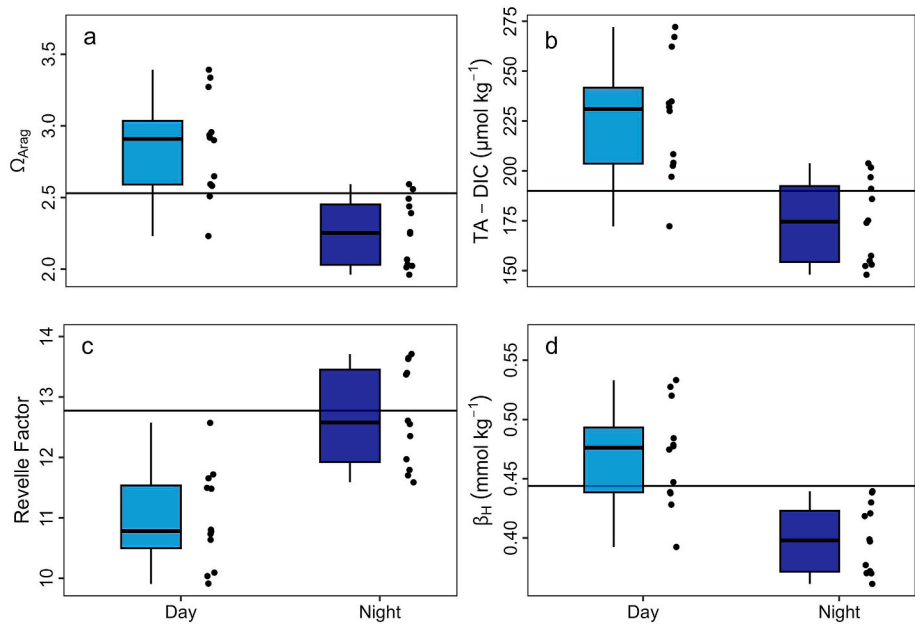


Fig. 4. Different proxies for investigating the seagrass acidification buffering, including aragonite saturation (Ω_{Arag}) (a), TA minus DIC (b), the Revelle factor (c) and buffer factor β_H (d). Black horizontal lines represent regional values from the mouth of the Gullmar fjord (58.1894N, 11.3496E) on the September 6, 2024 (Ω_{Arag} : 2.53, TA-DIC: 190 $\mu\text{mol kg}^{-1}$, Revelle factor: 12.78, β_H : 0.44) (Copernicus Marine Service, 2025).

lower. Ω_{Arag} was below 1 in all but one chamber, indicating under-saturation of aragonite.

3.2. Flux dynamics of total alkalinity and dissolved inorganic carbon

Both sites showed similar trends and ranges of TA and DIC fluxes (Fig. 5). TA fluxes ranged from -13 to $10 \text{ mmol m}^{-2} \text{ h}^{-1}$ and DIC from -50 to $22 \text{ mmol m}^{-2} \text{ h}^{-1}$. Overall, seagrass meadows were a net source for TA, with a daily mean between chambers of $16 \pm 45 \text{ mmol m}^{-2} \text{ d}^{-1}$ in Smalsund and $17 \pm 16 \text{ mmol m}^{-2} \text{ d}^{-1}$ in Bökevik. In contrast, DIC was more variable, with net flux in the chambers ranging from -98 to $106 \text{ mmol m}^{-2} \text{ d}^{-1}$. Smalsund was a net source ($34 \pm 59 \text{ mmol m}^{-2} \text{ d}^{-1}$) and Bökevik a net daily sink ($-43 \pm 35 \text{ mmol m}^{-2} \text{ d}^{-1}$). Both fluxes indicate sinks in the afternoon, becoming sources from nighttime until the end of the incubation. Compared to TA, the fluxes of DIC were two-fold higher at Smalsund and three-fold higher at Bökevik.

4. Discussion

Our results show that cold-temperate seagrass meadows act as net sources of TA during the most productive season, while DIC fluxes were more variable in direction and magnitude. Buffering against ocean

acidification was strongest during the day, following a clear diurnal pattern linked to photosynthesis and respiration. These findings highlight the dynamic role of seagrass meadows in coastal carbon cycling and their potential contribution to local acidification mitigation.

4.1. Implications for coastal acidification

The capacity of cold-temperate seagrass meadows to ameliorate ocean acidification varies over short temporal scales. We observed a stronger buffering capacity during the day as a response to photosynthesis (Fig. 4). Similarly, Buapet et al. (2013) found stronger daytime buffering by a seagrass meadow compared to the mouth of the bay in which our sites are situated (Buapet et al., 2013). The lower Ω_{Arag} supersaturation, lower buffering, and higher sensitivity to acidification during the night relates to the release of CO_2 during respiration. The use of these proxies is validated by TA minus DIC (Fig. 4b), which is linearly correlated with pH (Xue and Cai, 2020). This trend is in agreement with studies of seagrass meadows in warmer climates where diel trends were consistently observed (Challener et al., 2016; Hendriks et al., 2014; Kwiatkowski et al., 2016; Miller and Kelley, 2021; Wallace et al., 2021). During the experiment, Ω_{Arag} never dropped below 1.96 (Fig. 4a). Since calcification is impacted only below 1.4 (Bednaršek et al., 2014), calcifying organisms, such as bivalves, are unlikely to be affected by diel variations (Fig. 4a).

Comparing our data to meadows in warmer climates and other blue carbon ecosystems reveals that cold-temperate seagrasses may provide stronger OA amelioration. Worldwide observations of mangrove forests and saltmarshes displayed lower mean TA:DIC ratios (1.02) and lower mean β_H in surface waters (0.36 in mangroves and 0.30 in saltmarshes) compared to our measurements (Figs. 3 and 4d) (Reithmaier et al., 2023). In mangroves and saltmarshes, porewater DIC input is a key driver of acidification (Reithmaier et al., 2023). The influence of porewater in our study area (Table 1) is likely weak due to the subtidal setting and low tidal range (Henriksson et al., 2024) inhibiting effective advective transport related to tidal pumping in large intertidal zones typical of mangrove and saltmarsh habitats. Therefore, differences in OA buffering between blue carbon ecosystems are likely explained by habitat characteristics. Similar to mangroves and saltmarshes, the

Table 1
Porewater measurements of DIC and TA at the start and end of the incubations.

Site	Chamber	Time	DIC ($\mu\text{mol kg}^{-1}$)	TA ($\mu\text{mol kg}^{-1}$)	TA:DIC ratio	Ω_{Arag}
Smalsund	C1	start	3425	2475	0.72	0.06
	C1	end	2659	2400	0.9	0.19
	C3	start	3264	2361	0.72	0.06
	C3	end	3470	2669	0.77	0.08
	C5	start	2688	2130	0.79	0.07
	C5	end	2888	2599	0.9	0.2
Bökevik	C1	start	1909	1953	1.02	0.92
	C1	end	2227	2164	0.97	0.42
	C3	start	1874	2009	1.07	1.83
	C3	end	2221	2111	0.95	0.29
	C5	start	1960	1864	0.95	0.26
	C5	end	2559	2340	0.92	0.21

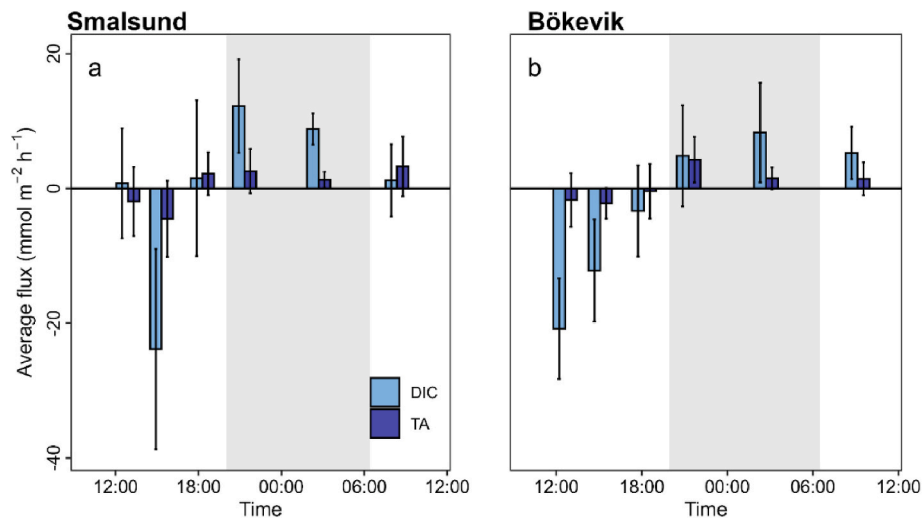


Fig. 5. Fluxes of TA and DIC at Smalsund (a) and Bøkevik (b). Data shown as averages with standard deviation bars ($n = 6$) for each time point.

seagrass porewater TA:DIC ratio was predominantly <1 , whereas TA:DIC was mostly >1.1 in the water column (Cai et al., 2021). In agreement with our results, a comparison of carbonate chemistry between a subtropical seagrass meadow and a nearby saltmarsh showed that the seagrasses had a significantly stronger buffering capacity than the saltmarsh (Wallace et al., 2021). The range of the Revelle factors reported for subtropical seagrass meadows (10–16) is similar to that of our cold-temperate meadows (10–14, Fig. 4c) (Wallace et al., 2021).

4.2. Drivers of inorganic carbon fluxes in seagrass meadows

The observed diel pattern of both TA and DIC fluxes (Fig. 5) suggests that photosynthesis and respiration are dominant drivers of inorganic carbon dynamics in the water column. DIC fluxes were most negative during peak PAR, indicating photosynthetic uptake, and shifted to positive values under low PAR, reflecting respiration (Fig. 2g and h). Temperature (Fig. 2g and h) varied by less than 2°C over the incubation period and may have had a minor influence. Physical drivers such as water movement are unlikely to have affected the results due to the hydrodynamically isolated conditions inside the chambers further supported by the nearly constant salinity and weak tidal currents in these microtidal embayments (Fig. 2e and f). The low TA:DIC regression slopes (0.19 and 0.28, Fig. 3a) at our study sites further indicate a dominance of photosynthesis and respiration, since typical slopes are -0.2 for metabolism (photosynthesis/respiration), 0.8 for denitrification, 1.0 for sulfate reduction, and 2.0 for calcium carbonate precipitation/dissolution (Sippo et al., 2016; Zeebe and Wolf-Gladrow, 2001). The mirror pattern between CO_3^{2-} and HCO_3^- (Fig. S1) reflects photosynthetic CO_2 uptake driving pH increases and shifting carbonate speciation, rather than CaCO_3 dissolution. The secondary processes driving additional TA generation might be a combination of denitrification, sulfate reduction and calcium carbonate formation/dissolution (Burdige, 2011).

The release of CO_2 from respiration can enhance the dissolution of CaCO_3 during the night, creating a diel pattern of TA fluxes (Barrón et al., 2006; Champenois and Borges, 2021; Chou et al., 2021; Fan et al., 2024). While Ω_{Arag} values in porewater (Table 1) suggest conditions favourable for dissolution, the low carbonate content ($<15\%$) and sandy, silicate-dominated sediments (Dahl et al., 2024) indicate limited contribution from abiotic carbonate cycling. In cold-temperate seagrass meadows, low inorganic carbon content in sediments is likely due to less epiphytic- or free-living calcifying algae compared to warmer regions (Dahl et al., 2020).

Organic alkalinity has been reported at significant levels in various coastal environments (Kerr et al., 2021). Seagrass meadows export dissolved organic carbon (DOC), therefore, organic acids may contribute to net alkalinity generation (Barrón et al., 2014). The observed diurnal cycle could be caused by different DOC transformation processes during day and night, e.g., remineralization and photooxidation (Kerr et al., 2021). Whether DOC-derived organic alkalinity contributes to carbon sequestration depends on its fate; labile fractions are rapidly remineralized, while recalcitrant fractions may contribute to long-term storage (Krumhansl et al., 2025). In seagrasses, further research is needed to distinguish between labile and recalcitrant fractions of exported organic alkalinity.

4.3. Contribution of total alkalinity generation to carbon sequestration

Comparing inorganic carbon fluxes to other carbon components at our study site highlights the significance of studying alkalinity generation in cold-temperate seagrass meadows. The magnitude of CO_2 uptake associated with TA fluxes depends on the dominant production pathway, with anaerobic metabolism contributing more directly to sequestration than carbonate dissolution (Zeebe and Wolf-Gladrow, 2001). However, TA generated in seagrass sediments persists in the ocean for decades to centuries and thus represents a permanent atmospheric carbon sink (Middelberg et al., 2020).

TA fluxes at both sites (Table 2) were four-fold higher than local carbon accumulation rates ($4 \pm 1 \text{ mmol m}^{-2} \text{ d}^{-1}$) (Dahl et al., 2023), demonstrating the overlooked potential of TA production contributing to blue carbon sequestration. Carbon accumulation in our site is half as high as the global average within seagrass meadows (4 vs. $10 \text{ mmol m}^{-2} \text{ d}^{-1}$) (Eyre et al., 2023). This is in contrast to our TA flux, which is 3-fold higher than the global median TA flux (16/17 vs. $5 \text{ mmol m}^{-2} \text{ d}^{-1}$), highlighting that cold-temperate seagrass meadows could be globally significant carbon sinks even if their carbon burial rates are low.

Methane emissions to the atmosphere offset local sediment carbon sequestration by less than 2% year-round (Henriksson et al., 2024). Additionally, late-summer methane water-air flux in the meadows was equivalent to 0.06% and 0.13% of carbon sequestration by TA production, based on Sustained-Flux Global Warming Potentials of methane for 100- and 20- years, respectively (Neubauer and Magonigal, 2019). Presently, fluxes of particulate organic carbon and dissolved organic carbon are unquantified in this study area. Overall, alkalinity generation seems to play a major role in the local blue carbon budget.

Table 2

Summary of studies that quantify DIC and TA fluxes in seagrass meadows. Fluxes are presented in $\text{mmol m}^{-2} \text{d}^{-1}$. A mean of Dongsha Atoll numbers was used in global mean (median) $\pm$ SD (range) calculations.

Site name	Species	Climate	Season	Method	TA Flux	DIC Flux	Citation
Smalsund Sweden	<i>Z. marina</i>	Cold-temperate	Late summer	Chamber incubations	16 $\pm$ 45	34 $\pm$ 59 (–47 to 106)	This study
Bökevik, Sweden	<i>Z. marina</i>	Cold-temperate	Late summer	Chamber incubations	17 $\pm$ 16 (–5 to 43)	–43 $\pm$ 35 (–98 to –1)	This study
Magalluf Bay, Spain	<i>P. oceanica</i>	Mediterranean	Annual	Chamber incubations	4 $\pm$ 21 (–29 to 55)	3 $\pm$ 42 (–73 to 62)	Barrón et al. (2006)
Dongsha Atoll, China	<i>T. hemprichii</i> , <i>C. rotundata</i>	Tropical	Late summer	Chamber incubations	76 $\pm$ 82	119 $\pm$ 144	Fan et al. (2024)
Dongsha Atoll, China	<i>T. hemprichii</i> , <i>C. rotundata</i>	Tropical	Winter	Chamber incubations	70 $\pm$ 41	107 $\pm$ 76	Fan et al. (2024)
Kenting, Taiwan	<i>T. hemprichii</i> , <i>H. uninervis</i>	Tropical	Wet/Late summer	Chamber incubations	1 $\pm$ 1	–0.02 $\pm$ 0.07	Chou et al. (2025)
Bay of Portlrigat, Spain	<i>P. oceanica</i>	Mediterranean	Late summer	Cross-shore transects	5 $\pm$ 6	114 $\pm$ 61	Majtényi-Hill et al. (2023)
Tomales Bay, CA, USA	<i>Z. marina</i>	Mediterranean	Annual	Hydrographic transects	5 $\pm$ 3 (–7.1 to 24.6)	–0.8 $\pm$ 1.7 (–7.3 to 9.5)	Smith et al. (1991)
Global mean (median) $\pm$ SD (range)					17 (5) $\pm$ 23 (1–73)	31 (3) $\pm$ 56 (–43 to 114)	

4.4. Contrasting seagrass meadows to other blue carbon ecosystems

Estimates of DIC and TA fluxes in seagrass meadows remain relatively scarce (Barrón et al., 2006; Chou et al., 2025; Fan et al., 2024; Majtényi-Hill et al., 2023; Smith et al., 1991). Cold-temperate seagrass meadows act as net sources of TA and as either sources or sinks of DIC with flux magnitudes comparable to those reported in warmer climates (Table 2). Reported DIC export fluxes from other seagrass systems range from –0.8 to 119 $\text{mmol m}^{-2} \text{d}^{-1}$, while our site exhibited similarly variable fluxes from –34 to 43 $\text{mmol m}^{-2} \text{d}^{-1}$. TA export fluxes in the literature range from 1 to 76 $\text{mmol m}^{-2} \text{d}^{-1}$, with a mean of $18 \pm 28 \text{ mmol m}^{-2} \text{d}^{-1}$, comparable to our observed fluxes of 16 ± 45 and $17 \pm 16 \text{ mmol m}^{-2} \text{d}^{-1}$ for Smalsund and Bökevik, respectively. Only fluxes for tropical Dongsha Atoll, which is characterized by carbonate-rich sediments, was an order of magnitude higher (Fan et al., 2024).

Compared to other blue carbon ecosystems, seagrass meadows have slightly lower TA and DIC export rates. Global median DIC export from seagrasses is 27-times lower than export from mangroves forests ($81 \pm 47 \text{ mmol m}^{-2} \text{d}^{-1}$; $n = 26$) and 19-times lower than export from saltmarshes ($57 \pm 104 \text{ mmol m}^{-2} \text{d}^{-1}$; $n = 14$) (Reithmaier et al., 2023). Global TA export from seagrasses is proportionally higher than DIC, being 16-times lower than export from mangrove forests ($81 \pm 55 \text{ mmol m}^{-2} \text{d}^{-1}$; $n = 17$) and 5-times lower than export from saltmarshes ($25 \pm 11 \text{ mmol m}^{-2} \text{d}^{-1}$; $n = 6$) (Reithmaier et al., 2023). Similarly, Fakhræe et al. (2023) estimated that alkalinity enhancement through restoration of mangroves and saltmarshes is an order of magnitude higher than from seagrasses. In subtidal seagrass meadows, diffusion and advection dominate porewater transport, resulting in lower TA and DIC export compared to mangroves and saltmarshes, where tidal pumping enhances porewater release (Cabral et al., 2021). This difference, along with lower soil carbon and anaerobic activity, might explain the generally lower carbon fluxes from seagrass systems.

Presently, the number of studies on inorganic carbon fluxes in seagrass meadows is much smaller than mangroves and saltmarshes. Research on seagrass DIC fluxes is hence needed to better resolve global estimates of TA and DIC production and export, while using consistent approaches to build confidence in comparisons. The methods employed are chamber incubations (Barrón et al., 2006; Chou et al., 2025; Fan et al., 2024), stochastic modelling (Fakhræe et al., 2023), spatial transects (Majtényi-Hill et al., 2023; Smith et al., 1991), and the boundary layer method (McGillis et al., 2011; Takeshita et al., 2016). There is no clear difference between methodologies, potentially due to the lack of direct comparisons at the same site and period.

5. Conclusion

This study provides insights into DIC and TA fluxes within two cold-temperate seagrass meadows. Diel patterns of DIC and TA flux were observed. The meadows act as net source of TA, while DIC fluxes were more variable. Photosynthesis and respiration were the primary drivers. Compared to other blue carbon ecosystems, the studied seagrasses show a stronger resistance to ocean acidification and ameliorate acidification during the day but not during the night. Seagrass meadows appear to export an order of magnitude less inorganic carbon than mangrove forests and saltmarshes. This is driven primarily by lower anaerobic carbon degradation and slow transport of porewater due to a lack of tidal pumping. TA flux was four times higher than soil carbon accumulation in our meadows, indicating that cold-temperate seagrass meadows have an overlooked potential to sequester carbon. The TA flux in this study was also similar to seagrass meadows in warmer climates, demonstrating that cold-temperate meadows warrant future consideration when evaluating the carbon sequestration potential of blue carbon ecosystems.

Future research should resolve inorganic carbon horizontal transport into adjacent systems and across distinct geomorphologies to better account for spatial variation and the contribution of underlying drivers.

Seasonality should also be investigated to determine seagrass TA fluxes during less productive periods of the year, particularly in cold-temperate regions where seasonal variation is pronounced. The contribution of organic alkalinity should also be quantified, with future work distinguishing between labile and recalcitrant fractions to assess whether DOC-derived alkalinity is rapidly remineralized or contributes to long-term carbon sequestration potential. Expanding studies across different climatic regions and geomorphic contexts will be essential to resolve global estimates of seagrass-driven DIC and TA generation.

CRedit authorship contribution statement

Samuel Scott-Askin: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Isaac R. Santos:** Writing – review & editing, Resources, Funding acquisition, Formal analysis. **Gerli Albert:** Writing – review & editing, Project administration, Methodology, Investigation, Conceptualization. **Maria E. Asplund:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Diana Deyanova:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Sara C. Forsberg:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Aurora M. Ricart:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Martin Gullström:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Mats Björk:** Writing – review & editing, Project administration, Conceptualization. **Gloria M.S. Reithmaier:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of generative AI in scientific writing

During the preparation of this work the authors used ChatGPT (OpenAI) in order to support grammar refinement and R code troubleshooting. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Gloria Reithmaier reports financial support was provided by Swedish Research Council Formas. Isaac Santos reports financial support was provided by Swedish Research Council Vetenskapsrådet. Martin Gullström reports financial support was provided by Swedish Research Council Formas. Aurora M. Ricart reports financial support was provided by LaCaixa Foundation. Aurora M. Ricart reports financial support was provided by Spanish Ministry of Science and Innovation. Maria E. Asplund reports was provided by Baltic Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2025.109550>.

Data availability

The full dataset is available on Figshare: https://figshare.com/articles/dataset/Alkalinity_release_from_seagrasses_Scott-Askin_et_al_Figshare_xlsx/30164122?file=58090567.

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