



1 Hydro-biogeochemical processes govern inorganic nitrogenous
2 nutrient dynamics in a subtropical semi-enclosed mariculture bay:
3 nitrogen-carbon coupling
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5 Aiqin Han^{a,b,*}, Zhenzhen Zheng^{c,#}, Rong Fu^{a,c}, Lili Lang^b, Shuh-Ji Kao^c, Yuanbiao
6 Zhang^a, Yasong Li^b

7 ^a Third Institute of Oceanography, Ministry of Natural Resources, Xiamen, China

8 ^b Fujian Key Laboratory of Water Cycling and Eco-Geological Processes, Institute of
9 Hydrogeology and Environmental Geology, CAGS, Xiamen, China

10 ^c State Key Laboratory of Marine Resource Utilization in South China Sea, School of
11 Marine Science and Engineering, Hainan University, Haikou, China

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13 ***Corresponding author:** Aiqin Han, Third Institute of Oceanography, Ministry of

14 Natural Resource, Xiamen, China, 361005, email: hanaiqin@tio.org.cn,

15 [Tel:+86-592-2195219](tel:+86-592-2195219)

16 **#Co-Corresponding author:** Zhenzhen Zheng, State Key Laboratory of Marine

17 Resource Utilization in South China Sea, School of Marine Science and Engineering,

18 Hainan University, Haikou, China, email: zzz@hainanu.edu.cn

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22 Abstract

23 Semi-enclosed bays are ideal for mariculture, but this activity modifies dissolved
24 inorganic nitrogen (DIN: NH_4^+ , NO_2^- , NO_3^-) pools through organic matter enrichment,
25 remineralization, nitrification (ammonia/nitrite oxidation, AO, NiO), and ammonium,
26 nitrite, nitrate uptake (AU, NiU, NaU), converting coastal waters into biogeochemical
27 reactors regulating N dynamics. This study examines seasonal DIN variation in
28 Sansha Bay, the world's largest *Larimichthys crocea* farming zone, influenced by
29 river runoff and coastal water masses. A two end-member mixing model revealed
30 persistent net DIN accumulation in the main channel in winter and summer; western
31 mariculture areas with more prolonged water residence showed contrasting
32 characteristics: winter DIN accumulated alongside lower particulate organic carbon
33 (POC) concentrations and lighter isotopic signature $\delta^{13}\text{C}_{\text{DIC}}$; summer showed NH_4^+
34 loss, NO_2^- generation, bidirectional NO_3^- variation, higher POC and heavier $\delta^{13}\text{C}_{\text{DIC}}$.
35 ^{15}N incubation assays revealed suppressed winter N uptake and nitrification,
36 consistently high AU and AO, sustained by NH_4^+ released via intense remineralization.
37 High NiO converted NO_2^- to NO_3^- , while weak NaU led to net NO_3^- accumulation.
38 Strong vertical stratification governed summer N transformations. In surface layers,
39 dominant AU and moderate NaU partially consumed NH_4^+ and NO_3^- , with minor NiU
40 yielding NO_2^- surplus. At depth, nitrification outpaced weak NiU and NaU, causing
41 low NH_4^+ but NO_2^- and NO_3^- buildup. This study reveals the regulation of DIN
42 dynamics coupled to C and N biogeochemistry via interactions between water mass
43 exchange and mariculture, and clarifies the controls exerted by N uptake and



44 nitrification on DIN conditions and eutrophication risk in intensive mariculture

45 coastal systems.

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47 **Keywords:** Inorganic nitrogen dynamics; Nitrogen-carbon coupling; Nitrogen uptake;

48 Nitrification; Fish mariculture

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66 **Introduction**

67 Nitrogen (N) is an indispensable biogenic nutrient modulating diverse metabolic
68 biogeochemical processes within aquatic ecosystems. Driven by intensified
69 anthropogenic activities, the flux of reactive N (Nr) to coastal waters has risen sharply,
70 with riverine runoff serving as the dominant transport pathway delivering Nr into
71 coastal embayments (Jickells, 1998; Liu et al., 2010). Water mass exchange with
72 offshore waters further complicates N cycling dynamics across coastal zones (Jickells,
73 1998; Liu et al., 2010). Unlike naturally derived Nr in undisturbed coastal systems,
74 intensive mariculture releases massive exogenous N loads into adjacent nearshore
75 waters. Owing to low feed assimilation efficiency (only 20%-25% for finfish
76 mariculture), substantial unutilized feed N is discharged into ambient seawater (Dong
77 et al., 2000; Hu et al., 2012). As the world's leading mariculture producer, China
78 annually discharges up to 324.3 kilotons of N from coastal mariculture operations
79 (Cui et al., 2023). Excess aquaculture-derived N frequently leads to eutrophication,
80 harmful algal blooms, and hypoxia within embayment ecosystems, posing a severe
81 threat to coastal fishery resources and ecological integrity as well as generating
82 negative climate feedbacks (Dai et al., 2023). Semi-enclosed bays, although
83 geographically suitable for mariculture, feature limited water exchange capacity that
84 extends hydraulic residence time inside the bay (Lin et al., 2017; Souvermezoglou and
85 Anagnostou, 2025). Such prolonged water retention generates complex dissolved
86 inorganic nitrogen (DIN) transformation processes that remain insufficiently
87 constrained by existing research.



88 Numerous prior studies have assessed the environmental footprint of
89 mariculture by constructing mass N budgets to quantify N influxes and effluxes
90 (Islam, 2005; Luo et al., 2018; Jiao et al., 2022; Liu et al., 2026). Nevertheless,
91 mariculture expansion reshuffles the concentrations and interconversion of all Nr
92 pools, including particulate organic nitrogen (PN), ammonium (NH_4^+), nitrite (NO_2^-),
93 and nitrate (NO_3^-), which further complicates DIN turnover pathways such as
94 remineralization of organic matter (OM), nitrification, and phytoplankton nutrient
95 uptake (Hargreaves, 1998; Gruber, 2008). Distinct N species perform different
96 biogeochemical functions; therefore, evaluating the magnitude of pollution and
97 associated ecological risks solely via total N measurements cannot capture nuanced
98 biogeochemical responses. For instance, PN, the primary particulate N reservoir,
99 decomposes and releases low- $\delta^{15}\text{N}$ ammonium into seawater during microbial
100 remineralization, leaving residual particulate organic material enriched in heavy ^{15}N
101 due to N isotopic fractionation (Sigman et al., 2009). Analogously, particulate organic
102 carbon (POC), the dominant particulate carbon pool, undergoes remineralization
103 accompanied by C isotope fractionation such that lighter ^{13}C is released into the water
104 column, while heavier ^{13}C is retained within residual particles (Lamb et al., 2006). As
105 a bioavailable reduced N substrate, NH_4^+ is rapidly assimilated by phytoplankton and
106 can be sequentially oxidized to NO_2^- via ammonia oxidation. Subsequently,
107 nitrite-oxidizing bacteria convert NO_2^- to NO_3^- . Both NH_4^+ and NO_3^- fuel
108 phytoplankton photosynthesis and concurrent CO_2 consumption is characterized by
109 lighter ^{13}C . Remineralization processes govern substrate ($\text{NH}_4^+/\text{NO}_2^-$) availability for



110 nitrification, a pivotal pathway that mitigates excess N accumulation (Nixon, 1981;
111 Álvarez-Salgado et al., 1997). Notably, nitrifiers compete directly with phytoplankton
112 for shared NH_4^+ and NO_2^- substrates. NO_3^- also acts as a key N source supporting
113 primary production and biological C export.

114 Furthermore, marine N cycling is tightly coupled to the interplay of autotrophic
115 and heterotrophic metabolic processes, as well as N-C stoichiometry and biological
116 pump efficiency. Against this backdrop, there is growing research interest in
117 disentangling DIN dynamics (speciation and concentration gradients) modulated by
118 remineralization, nitrification and phytoplankton uptake within coastal environments.
119 Stable carbon ($\delta^{13}\text{C}_{\text{DIC}}$, $\delta^{13}\text{C}_{\text{POC}}$) and nitrogen isotopes ($\delta^{15}\text{N}_{\text{PN}}$, $\delta^{15}\text{N}_{\text{NH}_4}$, $\delta^{15}\text{N}_{\text{NO}_2}$,
120 $\delta^{15}\text{N}_{\text{NO}_3}$) have been widely adopted to qualitatively and quantitatively resolve
121 individual or coupled biogeochemical transformations (Lamb et al., 2006; Sigman et
122 al., 2009; Alling et al., 2012; Xu et al., 2022). While isotopic investigations have been
123 extensively documented in coastal waters, targeted research focusing specially on
124 intensive mariculture semi-enclosed bays remains scarce (Yokoyama et al., 2006; Han
125 et al., 2017; Han et al., 2024; 2026). For instance, a suite of estuarine and coastal
126 systems prone to seasonal hypoxia, including Chesapeake Bay, the Pearl River
127 Estuary, the East China Sea and the the Laptev and East Siberian Seas, have utilized
128 $\delta^{13}\text{C}_{\text{DIC}}$ signatures to qualitatively trace POM remineralization (Alling et al., 2012; Su
129 et al., 2019; Zhao et al., 2020). Combined $\delta^{13}\text{C}_{\text{POC}}$ and $\delta^{15}\text{N}_{\text{PN}}$ signatures have also
130 been applied to apportion multiple N sources and quantify the impacts of
131 anthropogenic N loading on coastal bay POM pools (Rožič et al., 2014; Samanta et al.,



2019; Ming et al., 2023). Given the antagonistic activity of nitrifiers and phytoplankton, $\delta^{15}\text{N}$ isotope pulse labeling techniques enable efficient quantification of concurrent N transformation rates, including rates of ammonia oxidation (AO) and nitrite oxidation (NiO), and phytoplankton ammonium/nitrite/nitrate uptake (AU/NiU/NaU) (Gruber, 2008; Xu et al., 2017). This approach has been successfully deployed in the Pearl River Estuary, Changjiang Estuary, Amazon and Pará Estuaries, the Bay of Bengal, and the Southern Ocean) (Wang et al., 2018; Chen et al., 2020; Mdutyana et al., 2020; Xu et al., 2022; Choisnard et al., 2024; Priyanka et al., 2024; Hou et al., 2025). Yet few studies have systematically unraveled the mechanistic controls over DIN dynamics, including N production via OM remineralization, its accumulation through nitrification, and biological removal via phytoplankton assimilation, within semi-enclosed embayments hosting intensive finfish mariculture (Jiang et al., 2020; Maxey et al., 2026, and references therein).

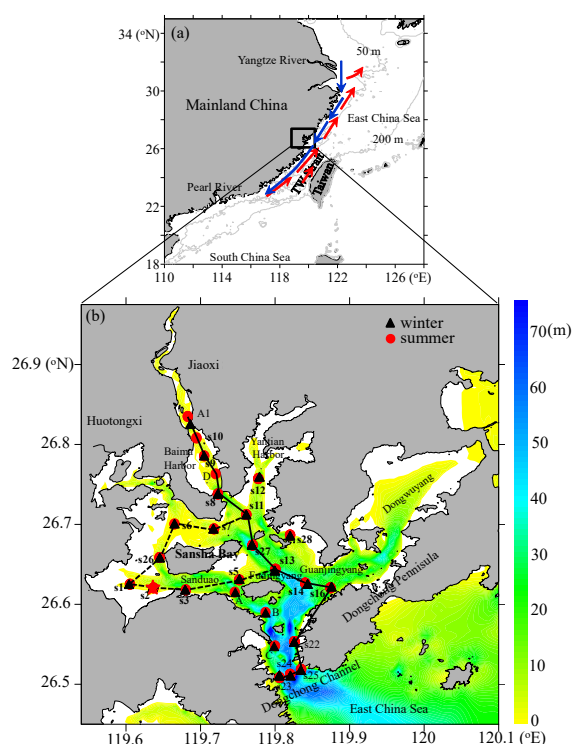
To fill this research gap, two comprehensive field cruises were conducted in Sansha Bay, the world's largest large yellow croaker (*Larimichthys crocea*) mariculture base. As a typical semi-enclosed mariculture bay, Sansha Bay receives substantial Nr inputs from fluvial runoff, offshore seawater exchange, and dense mariculture facilities, rendering it a representative study site of mariculture-dominated coastal embayments globally (Han et al., 2021). To the best of our knowledge, this study represents one of the pioneering attempts to integrate N-C elemental coupling, dissolved inorganic C/N pools, and particulate organic C/N fractions to explore internal N cycling mechanisms (OM remineralization, nitrification rates, and



154 phytoplankton uptake rates). This study helps to elucidate the impact on external N
155 addition/removal behaviors in a complex coastal embayment simultaneously
156 influenced by riverine inputs, adjacent coastal seawater, and intensive mariculture. By
157 elucidating the control of N over the ecology and corresponding climatic feedback in
158 estuaries, this study delivers actionable insights for N pollution abatement and
159 ecological risk evaluation along the mariculture-intensive river-coastal continuum.
160 Finally, the nutrient transformation rates measured in this study provide vital
161 benchmarks for the calibration of coastal biogeochemical models.

162 2. Materials and methods

163 2.1. Site description



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165 **Figure 1.** Map showing the location of Sansha Bay and sampling stations during the



166 December 2013 (winter) and August 2014 (summer) field cruises. (a) Schematic
167 illustrating the seasonal surface circulation offshore Sansha Bay: the China Coastal
168 Current (CCC, blue arrows) prevails in winter, while the South China Sea Warm
169 Current (SCSWC, red arrows) dominates summer flow patterns (Hu et al., 2000; Naik
170 and Chen, 2008; Han et al., 2013). (b) Sampling stations are marked with filled black
171 triangles (winter cruise) and solid red circles (summer cruise). Shaded color contours
172 denote bay bathymetry, modified from Lin et al. (2017). The red star at Station S2 (b)
173 indicates the location of ^{15}N incubation assays.

174 Sansha Bay (Fig. 1), a semi-enclosed coastal embayment in southeast China,
175 hosts the world's largest mariculture base for *Larimichthys crocea*. The Jiaoxi River
176 provides the primary freshwater input to the bay, with an average discharge of ~ 365
177 $\text{m}^3 \text{s}^{-1}$ in summer and $\sim 64 \text{ m}^3 \text{s}^{-1}$ in winter (Han et al., 2021). Sansha Bay connects to
178 the East China Sea (ECS) through the narrow ($\sim 3 \text{ km}$ wide, Lin et al., 2017)
179 Dongchong (DC) Channel. The north-south corridor extending from Baima Harbor to
180 the DC channel is defined as the main channel. Seasonal monsoon patterns drive
181 distinct offshore current regimes. Southwesterly winds prevail in summer, steering the
182 northward South China Sea Warm Current (SCSWC) toward the outer bay, whereas
183 northeasterly winter winds push the Chinese Coastal Current (CCC) southward
184 beyond the DC channel. Over 2.2×10^5 fish mariculture cages are distributed
185 predominantly in the western portion of the bay, away from the main channel
186 (hereafter referred to as the off-main channel, Fig. 1; Zhu et al., 2013). Annual organic
187 inputs derived from mariculture feeding are substantial, reaching $2.3 \times 10^7 \text{ kg y}^{-1}$ of



188 formulated fish feed and 1.5×10^9 kg y^{-1} of raw trash fish scraps (Han et al., 2021).

189 **2.2. Sampling and analysis**

190 Two field surveys were conducted in winter (December 28-30, 2013) and
191 summer (August 6-8, 2014) to resolve seasonal variations in N biogeochemical
192 dynamics. Temperature and salinity were acquired via conductivity-temperature-depth
193 (CTD) sensors: Citadal (RDI Co., USA) was deployed during the winter cruise, and
194 Idronaut (S.r.l. Co., Italy) during the summer cruise. Discrete water samples were
195 collected for post-cruise salinity calibration using a portable salinometer (Portasal
196 8410A, Guildline Co., Canada) to correct raw CTD salinity readings. Seawater
197 samples for chemical analysis were retrieved using Niskin bottles mounted on the
198 CTD rosette.

199 All seawater subsamples for DIN (NO_3^- , NO_2^- , and NH_4^+) were immediately
200 filtered onboard through 0.45 μm cellulose acetate membranes. For NH_4^+
201 quantification, a 250 mL filtrate was preserved with 1-2 mL chloroform and stored at
202 4°C. An additional 250 mL filtrate aliquot was frozen at -20°C for subsequent NO_3^-
203 and NO_2^- spectrophotometric measurements using a Technicon AA3 continuous-flow
204 autoanalyzer (Bran-Lube, GmbH) (Han et al., 2012). Total $NO_3^- + NO_2^-$ concentrations
205 were determined via copper-cadmium column reduction, while NO_2^- alone was
206 measured using the standard pink azo dye spectrophotometric method (Han et al.,
207 2012). NH_4^+ concentrations were quantified following the indophenol blue
208 spectrophotometric protocol (Pai et al., 2001). Method detection limits were 0.1 μmol
209 L^{-1} for $NO_3^- + NO_2^-$, 0.04 $\mu mol L^{-1}$ for NO_2^- , and 0.5 $\mu mol L^{-1}$ for NH_4^+ . Filters retained



210 for POC analysis were wrapped in aluminum foil and frozen at -20°C immediately
211 after filtration until laboratory processing. In the laboratory, filters were de-carbonated
212 via acidification with 1 mL of 1 N HCl, oven-dried at 60°C for 48 h, and sectioned for
213 parallel elemental and isotopic measurements. POC and $\delta^{13}\text{C}_{\text{POC}}$ analysis was
214 conducted using a continuous flow elemental analyzer (Vario PYRO cube, Germany)
215 coupled to an isotope ratio mass spectrometer (Isoprime 100, EA-IRMS) (Kao et al.,
216 2012). PN and $\delta^{15}\text{N}_{\text{PN}}$ samples were analyzed using a gasbench-isotope-ratio mass
217 spectrometer (GB-IRMS) (Thermo Delta V Advantage, Germany) using the denitrifier
218 method outlined in Xu et al. (2017). $\delta^{13}\text{C}_{\text{DIC}}$ was determined via acidification with
219 H_3PO_4 followed by analysis on a Thermo Fisher Finnigan Delta V IRMS coupled with
220 a GasBench II preparation module for trace gas samples. The analytical precision was
221 better than 0.2‰ (Yin et al., 2020; Han et al., 2026).

222 Both winter and summer POC, PN, and $\delta^{13}\text{C}_{\text{DIC}}$ values were derived from Han et
223 al. (2001, 2004, 2026) and reprocessed in the present study. Summer $\delta^{13}\text{C}_{\text{POC}}$ and
224 $\delta^{15}\text{N}_{\text{PN}}$ datasets were sourced from Han et al. (2024) and reanalyzed herein, whereas
225 winter $\delta^{13}\text{C}_{\text{POC}}$ and $\delta^{15}\text{N}_{\text{PN}}$ data were unavailable. Chlorophyll *a* (Chl *a*)
226 concentrations were determined fluorometrically using a Turner Trilogy fluorometer
227 following the protocol of Welschmeyer (1994), and were replotted from Han et al.
228 (2021, 2004, 2006).

229 2.3. Two end-member conservative mixing model

230 A two end-member mixing model was employed to characterize the water mass
231 mixing behavior between riverine freshwater plumes and nearshore coastal water



within Sansha Bay, as validated by carbonate system vs. salinity relationships established in Han et al. (2026). The riverine end-member featured elevated DIN concentrations, whereas the coastal seawater endmember (imported via the DC Channel) exhibited minimal DIN concentrations. A strong linear correlation between DIN species and salinity confirmed that two end-member mixing is the primary driver of distributions across the bay (Fig. 2).

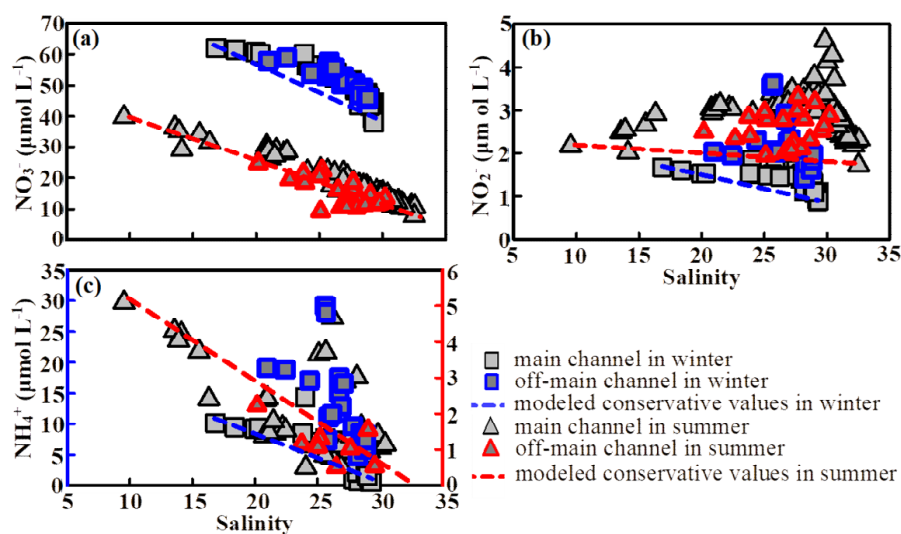


Figure 2. Linear relationships between dissolved inorganic nitrogen DIN (nitrate, NO_3^- , nitrite, NO_2^- , and ammonium, NH_4^+) concentrations and salinity (S) in Sansha Bay during winter and summer.

Salinity was adopted as a conservative tracer (Álvarez-Salgado et al., 1997).

Mass balance equations for fractional water mass contributions are defined as:

$$F_{\text{RI}} + F_{\text{SW}} = 1 \quad (1)$$

$$S_{\text{RI}}F_{\text{RI}} + S_{\text{SW}}F_{\text{SW}} = S_{\text{meas}} \quad (2)$$

where S_{meas} represents the in situ measured salinity; the subscripts RI and SW denote



247 riverine and coastal seawater end-members, respectively; F_{RI} and F_{SW} represent the
248 fractional contributions of each end-member. The following fractions were used to
249 calculate theoretical conservative mixing concentrations of NO_3^- ($NO_3^-_{cons}$), NO_2^-
250 ($NO_2^-_{cons}$), and NH_4^+ ($NH_4^+_{cons}$):

$$251 \quad NO_3^-_{cons} = NO_3^-_{RI}F_{RI} + NO_3^-_{SW}F_{SW} \quad (3)$$

$$252 \quad NO_2^-_{cons} = NO_2^-_{RI}F_{RI} + NO_2^-_{SW}F_{SW} \quad (4)$$

$$253 \quad NH_4^+_{cons} = NH_4^+_{RI}F_{RI} + NH_4^+_{SW}F_{SW} \quad (5)$$

254 where $NO_3^-_{RI}$, $NO_3^-_{SW}$, $NO_2^-_{RI}$, $NO_2^-_{SW}$, $NH_4^+_{RI}$, and $NH_4^+_{SW}$ are the respective DIN
255 concentrations of the two end members.

256 Deviations from conservative mixing (Δ) quantify net biological production
257 (positive Δ values) or removed (negative Δ values) of each N species:

$$258 \quad \Delta NO_3^- = NO_3^-_{in situ} - NO_3^-_{cons} \quad (6)$$

$$259 \quad \Delta NO_2^- = NO_2^-_{in situ} - NO_2^-_{cons} \quad (7)$$

$$260 \quad \Delta NH_4^+ = NH_4^+_{in situ} - NH_4^+_{cons} \quad (8)$$

261 where $NO_3^-_{in situ}$, $NO_2^-_{in situ}$, and $NH_4^+_{in situ}$ represent field-measured DIN
262 concentrations.

263 **2.4. Onboard incubation experiments**

264 Stable ^{15}N isotope tracer assays were conducted to quantify N transformation
265 rates. $^{15}NH_4^+$ and $^{15}NO_2^-$ tracers were amended to measure ammonium uptake (AU),
266 nitrite uptake (NiU), ammonia oxidation (AO), and nitrite oxidation (NiO), whereas
267 $^{15}NO_3^-$ was added for nitrate uptake (NaU). Full methodological details are provided
268 in Xu et al. (2017).



269 All incubations for AU, NiU, NaU, AO, and NiO were carried out on deck in
270 temperature-controlled incubators. Incubation temperatures matched in situ surface
271 water conditions; i.e., $\sim 12^{\circ}\text{C}$ for winter and $\sim 27^{\circ}\text{C}$ for summer, which were
272 maintained via circulating ambient seawater. At each sampling depth, seawater was
273 subsampled into 500 mL polycarbonate (PC) bottles, which received separate gradient
274 additions of pre-prepared $^{15}\text{NH}_4^+$, $^{15}\text{NO}_2^-$, and $^{15}\text{NO}_3^-$ stock solutions. Tracer
275 amendment volumes were adjusted according to ambient DIN concentrations (Figs. 2
276 and 3). Final enriched substrate concentrations were set to $0.4\ \mu\text{mol L}^{-1}$ (winter) and
277 $0.8\text{--}4.0\ \mu\text{mol L}^{-1}$ (summer) for both $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_2^-$; final $^{15}\text{NO}_3^-$ concentrations
278 were $2.0\ \mu\text{mol L}^{-1}$ in winter and $4.0\ \mu\text{mol L}^{-1}$ in summer. Immediately after tracer
279 spiking, for AU assays, 200 mL of water from the $^{15}\text{NH}_4^+$ addition bottle were filtered
280 through a pre-combusted Whatman GF/F glass fiber filter $0.22\ \mu\text{m}$ particle retention
281 size, and particulate samples were collected in a 50 mL centrifuge tube as the AU t_0 .
282 The residual seawater in each 500 mL PC bottle was redistributed evenly into 500 mL
283 PC bottles to perform incubations with exposure to Prime 52 HD full-spectrum LED
284 lights mimicking natural solar irradiance. Incubations were terminated (t_1) after a 3
285 h-incubation period, and particulate filters were collected following the identical t_0
286 sampling protocol. For AO assays, a 15 mL aliquot from each 500 mL bottle was
287 filtered through a 10 mL-disposable syringe with $0.22\ \mu\text{m}$ polyethersulfone (PES)
288 filters, and the filtrate was retained as described for the AO (t_0) sample. The remaining
289 seawater subsamples were wrapped with black plastic bags for dark incubation.
290 Incubations were terminated after 3 h and 6 h to collect t_1 and t_2 samples, respectively,



291 via filtration. All collected filters and filtrates were frozen at -20°C prior to laboratory
292 analysis.

293 **2.5. Rate estimates**

294 The N isotope ($\delta^{15}\text{N}$) of NO_x^- (the combined pool of NO_3^- and NO_2^- , the end
295 product of AO and NiO), were analyzed via the denitrifier method (Sigman et al.,
296 2001; Casciotti et al., 2002; Xu et al., 2017). Briefly, NO_x^- was quantitatively
297 converted to N_2O by denitrifying bacteria, and its isotopic signature was measured
298 with a Gasbench-II (Thermo Fisher) coupled to a Delta V Advantage isotope-ratio
299 mass spectrometer (Thermo Fisher). For PN derived from N uptake, samples were
300 first oxidized to NO_3^- using potassium persulfate, followed by $\delta^{15}\text{N}_{\text{PN}}$ quantification
301 via the same denitrifier method.

302 Nitrogen transformation rates, including oxidation (AO, NiO) and uptake (AU,
303 NiU, and NaU), were calculated from the increase in ^{15}N abundance within product
304 pools over the incubation period using Eq. (9):

$$V = \frac{r_t \times [P_t] - r_0 \times [P_0]}{T_i} \times \frac{[^{14}\text{N}]}{[^{15}\text{N}]} \quad (9)$$

306 where V represents the N transformation rate ($\text{nmol L}^{-1} \text{ h}^{-1}$). r_t and r_0 stand for ^{15}N
307 atom % of the product pool (PN for uptake assays, NO_x^- for oxidation assays) at
308 incubation termination and initiation, respectively. P_t and P_0 are the product pool
309 concentrations at the end and start of incubation, respectively, and T_i is the incubation
310 duration. $[^{14}\text{N}]$ and $[^{15}\text{N}]$ represent the initial substrate ($\text{NH}_4^+/\text{NO}_2^-/\text{NO}_3^-$)
311 concentrations of ^{14}N and ^{15}N immediately after tracer amendment.

312 **3. Results**



313 3.1. Hydrography

314 Seasonal hydrographic conditions in Sansha Bay have been systematically
315 described in our previous study (Han et al., 2021); the bay is characterized by
316 pronounced seasonal and spatial variation in water temperature (T) and salinity (S)
317 (Figs. 3a, b, 4a, b). In winter, the main channel stretching from Baima Harbor to the
318 DC Channel was dominated by cold, well-mixed water masses, with T ranging from
319 ~13.3°C to 14.9°C and S from ~17.2 to ~29.2. The western off-main channel zone
320 exhibited even cooler waters at ~12.2°C-13.2°C, with a moderate S of ~25-27, a
321 pattern attributed to limited tidal exchange and prolonged hydraulic residence time (>
322 30 d) within this semi-enclosed sub-basin (Lin et al., 2017). Vertical transect
323 observations indicate a fully mixed water column across the bay in winter (Figs. 5a, b,
324 6a, b). Temperature and S gradually rise along the north-south main channel, whereas
325 the western off-main channel remains persistently colder (~13.5°C-14.5°C) and
326 fresher (S ~21.5-24).

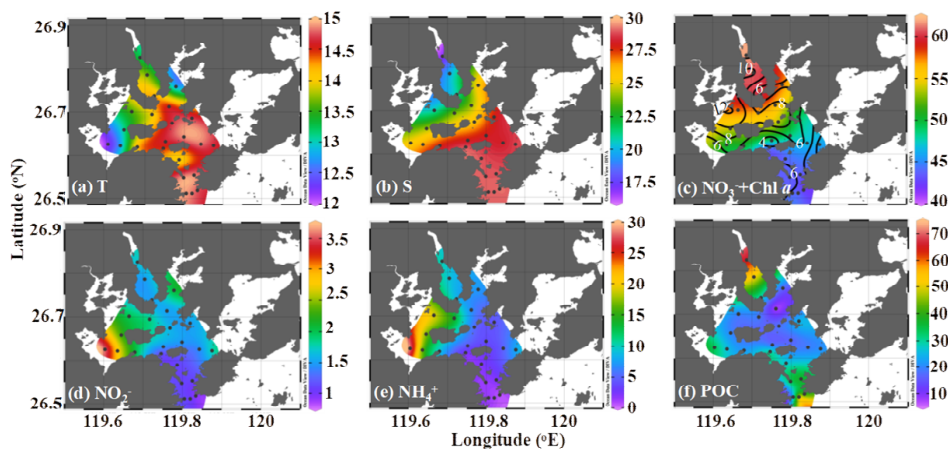
327 Summer water temperatures were substantially higher than those in winter. Warm
328 riverine discharge (~29.6°C) from Baima Harbor mixes with cooler offshore seawater
329 (~27.2°C) entering via the DC Channel. Concurrent elevated freshwater runoff
330 drastically lowers basin-wide salinities, with values ranging from ~9.6 to ~31.2 along
331 the main channel. The western off-main channel maintains an elevated T of ~29.4°C
332 to 30.8°C and moderate S of ~25-27, again driven by sluggish water exchange and
333 extended residence time (Lin et al., 2017). Distinct thermal stratification develops
334 along the main channel in summer, where low-density riverine plumes at the surface



335 overlay denser saline bottom waters (Fig. 7a, b). In contrast, weaker stratification
336 occurs across the western off-main channel due to the shallower bathymetry, with
337 clear mixing observed between riverine freshwater and intruding coastal water (Fig.
338 8a, b).

339 **3.2. Spatial distribution of biogeochemical variables**

340 **3.2.1. Surface distribution**

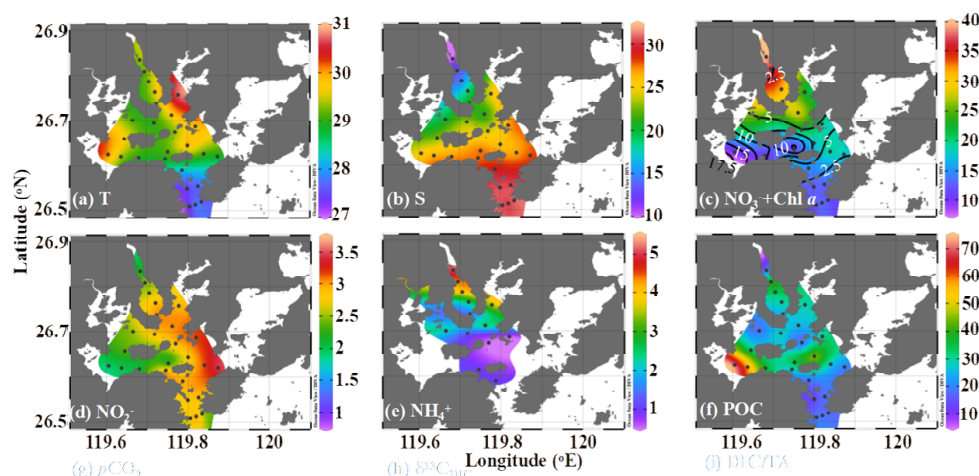


341 **Figure 3.** Surface distribution of temperature (a, T, °C), salinity, S (b), nitrate
342 concentrations (c, NO₃⁻, μmol L⁻¹) overlaid with chlorophyll *a* (Chl *a*, mg m⁻³)
343 contours with values in white, nitrite (d, NO₂⁻, μmol L⁻¹), ammonium (e, NH₄⁺, μmol
344 L⁻¹), and particulate organic carbon (f, POC, μmol L⁻¹) in Sansha Bay in winter 2013.
345 Winter Chl *a* and POC datasets were extracted and replotted from Han et al. (2021,
346 2026), while S data were replotted according to Han et al. (2026).

348 In winter, surface DIN exhibits spatial gradients tightly coupled to the baywide
349 hydrography (Fig. 3c-e), which was reflected in the total DIN distributions in Han et
350 al. (2021). As shown in Figure 3, NO₃⁻ concentrations generally declined from ~62.0



351 $\mu\text{mol L}^{-1}$ inside Baima Harbor to $\sim 42.0 \mu\text{mol L}^{-1}$ near the DC Channel, with
352 intermediate values of ~ 45.0 to $55.0 \mu\text{mol L}^{-1}$ in mid-bay. Markedly elevated NO_3^-
353 levels of ~ 50.4 – $53.0 \mu\text{mol L}^{-1}$ were detected in the western off-main channel. NO_2^-
354 and NH_4^+ followed an identical along-channel decreasing trend but displayed a
355 narrower concentration range, i.e., NO_2^- varied from ~ 1.7 to $\sim 0.9 \mu\text{mol L}^{-1}$, and NH_4^+
356 ranged between $\sim 10.1 \mu\text{mol L}^{-1}$ and ~ 0.6 – $1.6 \mu\text{mol L}^{-1}$. POC and Chl *a* peaked within
357 Baima Harbor, reaching $\sim 65.6 \mu\text{mol L}^{-1}$ and $\sim 7.3 \text{ mg m}^{-3}$, respectively. The PN
358 distribution covaried closely with that of POC, with peak concentrations of $\sim 6.2 \mu\text{mol}$
359 L^{-1} (Fig. 4g in Han et al., 2021). $\delta^{13}\text{C}_{\text{DIC}}$ reached a minimum value of -2.6‰ in the
360 harbor zone (Fig. 3h in Han et al., 2026). Mid-bay POC and Chl *a* concentrations
361 dropped to ~ 6.7 – $16.4 \mu\text{mol L}^{-1}$ and ~ 6.4 – 9.2 mg m^{-3} , respectively. Toward the DC
362 channel, POC increased to ~ 15.9 – $62.5 \mu\text{mol L}^{-1}$ and was paralleled by a moderate rise
363 in $\delta^{13}\text{C}_{\text{DIC}}$ to -0.8‰ – -1.4‰ , consistent with intrusion of the CCC (Han et al., 2013).
364 The western off-main channel featured striking NO_2^- and NH_4^+ accumulation at
365 ~ 2.8 – $3.6 \mu\text{mol L}^{-1}$ and ~ 16.1 – $29.2 \mu\text{mol L}^{-1}$, respectively. Surface Chl *a* remained
366 relatively high at ~ 5.0 – 7.4 mg m^{-3} , while POC (~ 26.2 – $33.9 \mu\text{mol L}^{-1}$), PN (~ 2.4 – 3.1
367 $\mu\text{mol L}^{-1}$), and $\delta^{13}\text{C}_{\text{DIC}}$ ($\sim -2.1\text{‰}$ – -2.6‰) reached basin-wide minima here (Fig. 4g in
368 Han et al., 2021; Fig. 3h in Han et al., 2026).



369

370 **Figure 4.** Surface distribution of T (a, °C), S (b), NO_3^- (c, $\mu\text{mol L}^{-1}$) overlaid with Chl
371 a (mg m^{-3}) contours, NO_2^- (d, $\mu\text{mol L}^{-1}$), NH_4^+ (e, $\mu\text{mol L}^{-1}$), and POC (f, $\mu\text{mol L}^{-1}$) in
372 Sansha Bay in summer 2014 (parameters as in Fig. 3). Summer Chl a and POC were
373 replotted from Han et al. (2024); S data for plotting derived from Han et al. (2026).

374 In summer, the horizontal DIN distribution is again shaped by mixing between
375 the riverine freshwater plume and low-nutrient adjacent coastal seawater, whose N
376 pools are far depleted relative to winter CCC inputs (Fig. 4c-e). Baima Harbor
377 exhibited elevated NO_3^- (~ 35.2 - $39.8 \mu\text{mol L}^{-1}$) and NH_4^+ (~ 4.0 - $5.1 \mu\text{mol L}^{-1}$), while
378 NO_2^- remained relatively stable at ~ 2.2 - $2.6 \mu\text{mol L}^{-1}$. Corresponding surface POC,
379 Chl a , and $\delta^{13}\text{C}_{\text{DIC}}$ ranged from ~ 16.4 to $32.3 \mu\text{mol L}^{-1}$, ~ 2.0 to $2.6 \mu\text{mol L}^{-1}$, and $\sim$
380 -3.2‰ to -2.0‰ (Fig. 4h in Han et al., 2026). Mid-bay NO_3^- concentrations decreased
381 to ~ 17.6 - $28.9 \mu\text{mol L}^{-1}$, while NH_4^+ concentrations fell to $\sim <0.5$ - $2.4 \mu\text{mol L}^{-1}$, and
382 NO_2^- remained relatively uniform at ~ 2.8 - $3.0 \mu\text{mol L}^{-1}$. The mid-bay POC and PN
383 concentrations ranged ~ 25.6 - $47.2 \mu\text{mol L}^{-1}$ and ~ 1.8 - $3.8 \mu\text{mol L}^{-1}$, with $\delta^{13}\text{C}_{\text{DIC}}$
384 shifting to -0.2‰ - -1.3‰ . The western off-main channel exhibited extremely depleted



DIN pools in summer, particularly that of NO_2^- ($\sim 1.9\text{--}2.0 \mu\text{mol L}^{-1}$) and NH_4^+ ($<0.5 \mu\text{mol L}^{-1}$), associated with low NO_3^- concentrations ($\sim 9.2\text{--}10.6 \mu\text{mol L}^{-1}$). By contrast, particulate nutrient pools and phytoplankton biomass surged at $\text{POC} \sim 58.0\text{--}71.3 \mu\text{mol L}^{-1}$, $\text{PN} \sim 3.4\text{--}8.3 \mu\text{mol L}^{-1}$, and $\text{Chl } a \sim 14.8\text{--}16.6 \text{ mg m}^{-3}$, with $\delta^{13}\text{C}_{\text{DIC}}$ reaching a light range of $-0.1\text{‰}\text{--}0.5\text{‰}$ (Han et al. 2024, 2026).

3.2.2. Vertical transect distributions

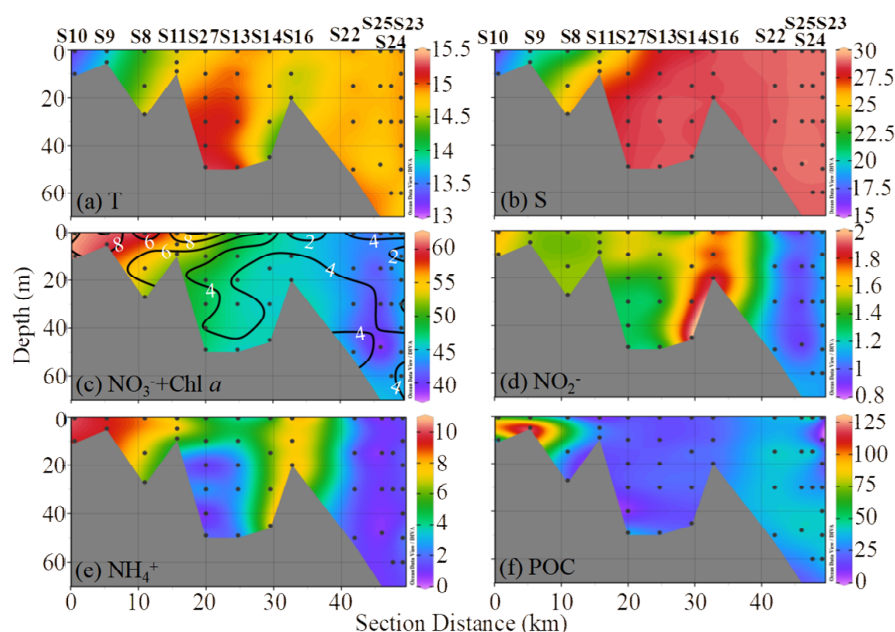
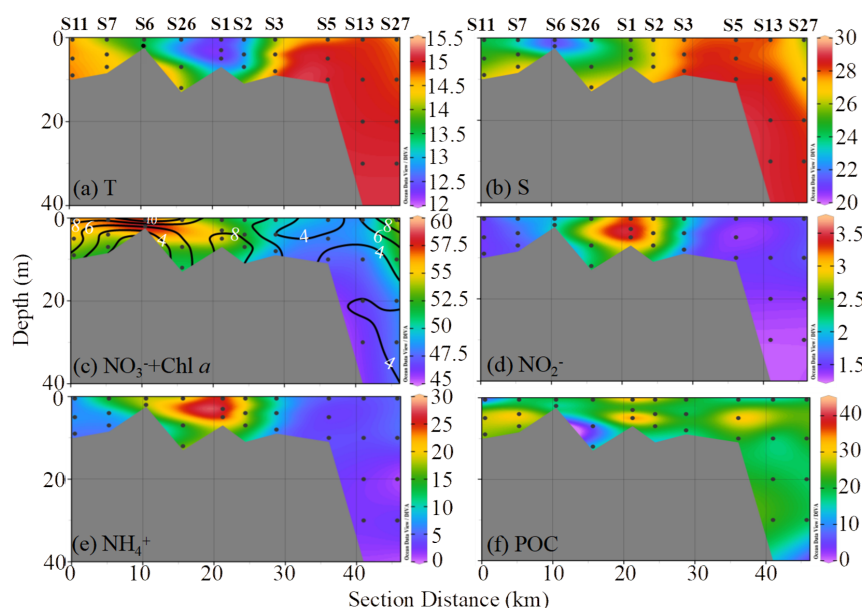


Figure 5. Vertical profiles of T (a, $^{\circ}\text{C}$), S (b), NO_3^- (c, $\mu\text{mol L}^{-1}$) overlaid with $\text{Chl } a$ (mg m^{-3}) contours, NO_2^- (d, $\mu\text{mol L}^{-1}$), NH_4^+ (e, $\mu\text{mol L}^{-1}$), and POC (f, $\mu\text{mol L}^{-1}$), along the main channel in Sansha Bay in winter 2013 (parameters as in Fig. 3). $\text{Chl } a$ and POC in winter were redrawn from Han et al., 2021, 2026; T and S were sourced from Han et al., 2026.

Vertical transects across the main channel and western off-main channel reveal a fully mixed water column consistent with winter convective cooling (Fig. 5). In the



399 slightly seaward Baima Harbor, NO_3^- peaked at $\sim 52.4\text{--}62.0 \mu\text{mol L}^{-1}$ and gradually
400 declined toward the DC channel ($\sim 38.2\text{--}44.4 \mu\text{mol L}^{-1}$). NH_4^+ followed this spatial
401 pattern, decreasing from $\sim 6.1\text{--}10.1 \mu\text{mol L}^{-1}$ in the inner Baima Harbor to $\sim 0.6\text{--}2.1$
402 $\mu\text{mol L}^{-1}$ near the bay mouth. Mid-bay NO_2^- concentrations remained vertically
403 homogeneous at $\sim 1.3\text{--}1.5 \mu\text{mol L}^{-1}$. Notable NO_2^- ($\sim 1.4\text{--}2.0 \mu\text{mol L}^{-1}$) and NH_4^+
404 ($\sim 4.7\text{--}8.2 \mu\text{mol L}^{-1}$) enrichment occurred at stations S14 and S16, driven by intensive
405 mariculture in the Guanjingyang and Dongwuyang semi-enclosed coves (Fig. 1). POC
406 concentrations peaked at $\sim 125.0 \mu\text{mol L}^{-1}$ inside Baima Harbor, declined sharply to
407 $\sim 16.4\text{--}25.3 \mu\text{mol L}^{-1}$ in mid-bay, and rebounded to $\sim 31.2\text{--}62.5 \mu\text{mol L}^{-1}$ adjacent to the
408 DC Channel. Full vertical Chl *a* and $\delta^{13}\text{C}_{\text{DIC}}$ profiles are shown in our prior studies
409 (Fig. 12d in Han et al., 2021, and Han et al., 2026, their Fig. S2g), as Chl *a* declined
410 seaward from $\sim 10.6 \text{ mg m}^{-3}$ to $\sim 1.2\text{--}5.6 \text{ mg m}^{-3}$, while $\delta^{13}\text{C}_{\text{DIC}}$ gradually increased
411 from -2.6‰ to -0.8‰ along the channel axis.

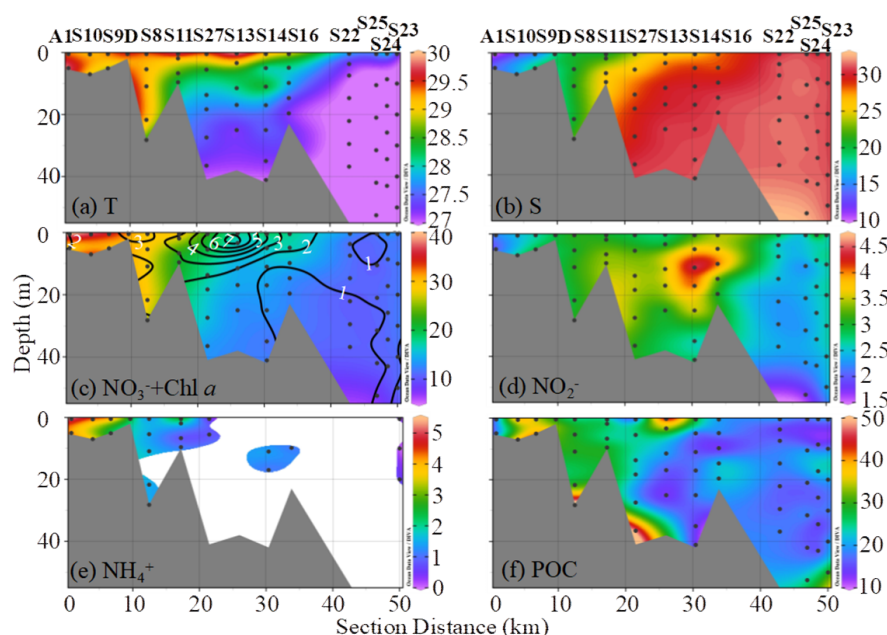


412



413 **Figure 6.** Vertical profiles of T (a, °C), S (b), NO_3^- (c, $\mu\text{mol L}^{-1}$) overlaid with Chl *a*
414 (mg m^{-3}) contours in black, NO_2^- (d, $\mu\text{mol L}^{-1}$), NH_4^+ (e, $\mu\text{mol L}^{-1}$), and POC (f, μmol
415 L^{-1}), along the western off-main channel in Sansha Bay in winter 2013 (parameters as
416 in Fig. 3). POC data in winter were sourced from Han et al., 2026; T and S were
417 redrawn from Han et al., 2026.

418 Distinct biogeochemical vertical gradients emerge in the western off-main
419 channel, that are tightly coupled to the local hydrographic regime (Fig. 6). Northern
420 stations with $S < 25.8$ were dominated by riverine inputs, featuring high NO_3^-
421 concentrations ($\sim 54.3\text{--}59.0 \mu\text{mol L}^{-1}$), elevated Chl *a* ($\sim 5.0\text{--}11.8 \text{ mg m}^{-3}$), and light
422 $\delta^{13}\text{C}_{\text{DIC}}$ ($\sim -1.9\text{‰}$ to -2.6‰). Southern stations influenced by relatively saline CCC
423 intrusions ($S > 29.0$) showed depleted NO_3^- ($\sim 47.7\text{--}48.9 \mu\text{mol L}^{-1}$), low Chl *a*
424 ($\sim 2.6\text{--}4.9 \text{ mg m}^{-3}$), and heavy $\delta^{13}\text{C}_{\text{DIC}}$ ($\sim -1.5\text{‰}$ to -1.6‰). Stations S26-S3 represent
425 hotspots of biogeochemical transformation, characterized by extremely high NO_2^- ($\sim$
426 $3.6 \mu\text{mol L}^{-1}$), high NH_4^+ ($\sim 29.2 \mu\text{mol L}^{-1}$), abundant POC and PN ($\sim 44.5 \mu\text{mol L}^{-1}$
427 and $\sim 4.4 \mu\text{mol L}^{-1}$, respectively), light $\delta^{13}\text{C}_{\text{DIC}}$ ($\sim -2.6\text{‰}$) and elevated Chl *a* (~ 11.8
428 mg m^{-3}), accompanied by weakened carbonate buffering capacity (Han et al., 2026).
429 These signals point to massive OM accumulation and subsequent heterotrophic
430 remineralization. Collectively, these geochemical tracers confirm amplified
431 heterotrophic activity within the western off-main channel, sustained by the extended
432 hydraulic residence time and mariculture-derived OM loading.



433

434 **Figure 7.** Vertical profiles of T (a, °C), S (b), NO_3^- (c, $\mu\text{mol L}^{-1}$) overlaid with Chl *a*
 435 (mg m^{-3}) contours, NO_2^- (d, $\mu\text{mol L}^{-1}$), NH_4^+ (e, $\mu\text{mol L}^{-1}$), and POC (f, $\mu\text{mol L}^{-1}$),
 436 along the main channel in Sansha Bay in summer 2014 (parameters as in Fig. 3).
 437 Summer Chl *a* and POC distributions reconstructed from Han et al. (2024); T and S
 438 datasets sourced from Han et al. (2026). The blank areas in (e) represent NH_4^+
 439 concentrations $< 0.5 \mu\text{mol L}^{-1}$.

440 Vertical biogeochemical distributions along the main channel mirrored the strong
 441 summertime thermohaline stratification (Fig. 7). Buoyant riverine plumes occupy the
 442 upper 20 m from Baima Harbor to mid-bay, with the following range of
 443 biogeochemical variables: $\text{NO}_3^- \sim 39.8\text{-}12.6 \mu\text{mol L}^{-1}$, $\text{NH}_4^+ \sim 5.1\text{-} <0.5 \mu\text{mol L}^{-1}$,
 444 POC $\sim 43.0\text{-}12.0 \mu\text{mol L}^{-1}$, and $\delta^{13}\text{C}_{\text{DIC}} \sim -3.2\text{‰}$ to -0.24‰ . Maximal Chl *a* ($\sim 7.8 \text{ mg}$
 445 m^{-3}) and POC ($\sim 47.2 \mu\text{mol L}^{-1}$) occurred within the mid-bay plume. Beneath the



buoyant freshwater layer, the water column was dominated by nutrient-poor SCSWC coastal seawater, with uniformly lower biogeochemical values ($\text{NO}_3^- \sim 15.8\text{--}10.2 \mu\text{mol L}^{-1}$, $\text{NH}_4^+ < 0.5 \mu\text{mol L}^{-1}$, $\text{POC} \sim 20.9\text{--}13.0 \mu\text{mol L}^{-1}$, and $\delta^{13}\text{C}_{\text{DIC}} \sim -0.2\text{‰}\text{--}0.3\text{‰}$) (Han et al., 2026, their Fig. S3g). Unlike other DIN compounds, NO_2^- was vertically homogeneous across the entire bay and far more concentrated in summer ($\sim 3.5 \mu\text{mol L}^{-1}$) relative to that winter.

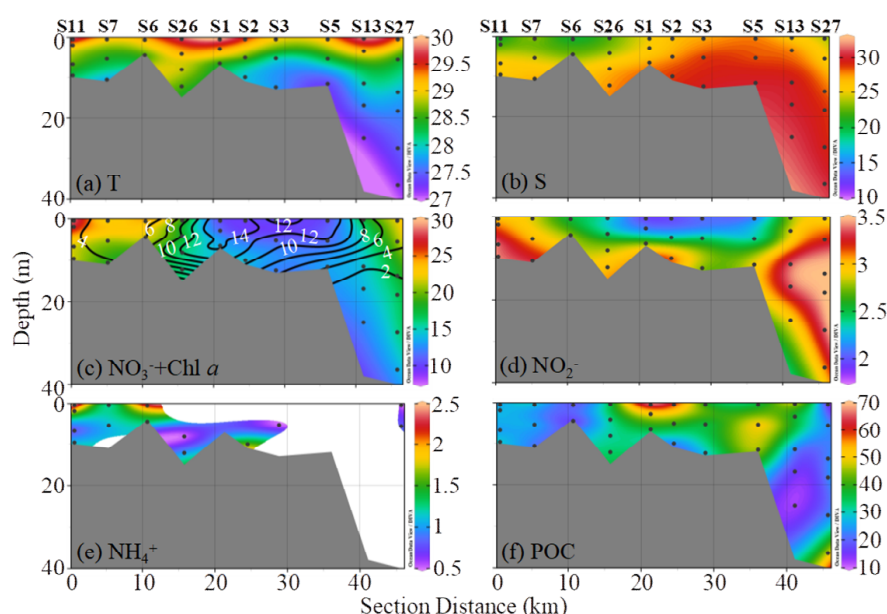


Figure 8. Vertical profiles of T (a, °C), S (b), NO_3^- (c, $\mu\text{mol L}^{-1}$) overlaid with Chl *a* (mg m^{-3}) contours, NO_2^- (d, $\mu\text{mol L}^{-1}$), NH_4^+ (e, $\mu\text{mol L}^{-1}$), and POC (f, $\mu\text{mol L}^{-1}$), along the western off-main channel in Sansha Bay in summer 2014 (parameters as in Fig. 3). Chl *a* and POC in summer were replotted from Han et al., 2024. T and S were redrawn from Han et al., 2026. The blank areas in (e) represent NH_4^+ concentrations $< 0.5 \mu\text{mol L}^{-1}$.

The western off-main channel receives minimal riverine influence in summer



(Fig. 8). Freshwater plumes are confined to the top in 5 m of northern stations ($S < 24.0$). Surface NO_3^- and NH_4^+ plumes reached $\sim 24.7 \mu\text{mol L}^{-1}$ and $\sim 2.2 \mu\text{mol L}^{-1}$, respectively, i.e., higher concentrations than those in the bottom layer (~ 18.5 – $22.4 \mu\text{mol L}^{-1}$ for NO_3^- and $< 1.2 \mu\text{mol L}^{-1}$ for NH_4^+). NO_2^- concentrations were lower in the surface plume ($\sim 2.5 \mu\text{mol L}^{-1}$) and rose to $\sim 3.4 \mu\text{mol L}^{-1}$ in bottom waters.

In contrast to the vertically stratified DIN pool, Chl *a*, POC, and $\delta^{13}\text{C}_{\text{DIC}}$ displayed weak vertical variation across northern off-main channel stations (Fig. 4c, f in Han et al., 2024, and Han et al., 2026, their Fig. S4g). Stations S26 and S3 exhibited unique summertime biogeochemical signatures, including depleted NO_3^- ($\sim 9.2 \mu\text{mol L}^{-1}$), low NO_2^- ($\sim 1.9 \mu\text{mol L}^{-1}$), negligible NH_4^+ ($< 0.5 \mu\text{mol L}^{-1}$), and extremely high Chl *a* ($\sim 16.6 \text{ mg m}^{-3}$), abundant POC ($\sim 71.3 \mu\text{mol L}^{-1}$), and heavy $\delta^{13}\text{C}_{\text{DIC}}$ ($\sim -0.1\text{‰}$). These sites also featured an elevated $\delta^{13}\text{C}_{\text{POC}}$ ($\sim -17\text{‰}$) and moderately light $\delta^{15}\text{N}_{\text{PN}}$ ($\sim 8.1\text{‰}$) (Fig. 4g, h in Han et al., 2024).

Our observations demonstrate that dense summertime phytoplankton productions drive the massive DIN uptake within this semi-enclosed bay system, where the geomorphology prolongs water residence time. OM and CO_2 generated by primary production carried isotopic signatures enriched in heavy C and N isotopes, converting the western off-main channel into a strong DIN sink throughout the summer. Intense primary production evidently alleviates the risk of N buildup within the mariculture bay. Nevertheless, variation in nutrient concentrations alone cannot definitively verify whether nitrification proceeds concurrently with DIN removal, which would increase the hypoxia risk in this intensively cultured semi-enclosed embayment.



3.3. Qualitative relationships between NO_2^- , NH_4^+ , POC, and $\delta^{13}\text{C}_{\text{DIC}}$

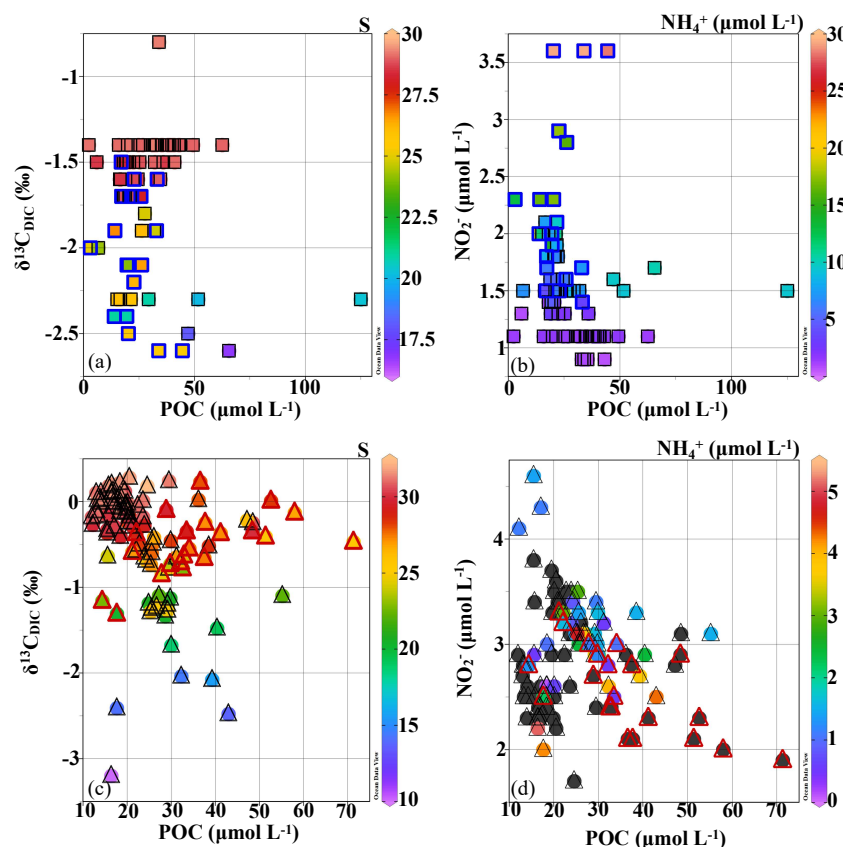


Figure 9. Scatter plots showing the relationship between particulate organic carbon, POC and the stable C isotopic signature $\delta^{13}\text{C}_{\text{DIC}}$ vs. salinity, S, and POC and nitrite, NO_2^- vs. ammonium, NH_4^+ in Sansha Bay during winter (a, b) and summer (c, d). Black squares and triangles denote samples from the main channel in winter and summer, respectively; blue squares and red triangles represent off-main channel measurements in winter and summer, respectively. POC and $\delta^{13}\text{C}_{\text{DIC}}$ in summer were sourced from Han et al., 2024 and 2026.

Correlations among POC, $\delta^{13}\text{C}_{\text{DIC}}$, NO_2^- , and NH_4^+ , exhibit pronounced seasonal



492 differences throughout Sansha Bay (Fig. 9). In winter, POC concentrations within
493 high S water masses spanned a broad range of $\sim 0.5\text{--}62.5\ \mu\text{mol L}^{-1}$, accompanied by
494 relatively enriched $\delta^{13}\text{C}_{\text{DIC}}$ values ranging from $\sim -1.7\text{‰}$ to -0.8‰ . Only isolated
495 riverine plume samples showed high POC levels (maximum of $\sim 65.6\ \mu\text{mol L}^{-1}$) with
496 distinctly light $\delta^{13}\text{C}_{\text{DIC}}$ signatures approximating -2.6‰ . For moderately saline waters
497 occupying the western off-main channel, most stations showed substantial POC
498 depletion with an average concentration $\sim 25.0\ \mu\text{mol L}^{-1}$ and exceptionally light
499 $\delta^{13}\text{C}_{\text{DIC}}$, ranging from -2.6‰ to -1.5‰ (Fig. 9a). This covariation is consistent with
500 heterotrophic respiration in the water column, a metabolic process that consumes POC.
501 This biogeochemical pathway has been quantified via $\delta^{13}\text{C}_{\text{DIC}}$ stoichiometric
502 calculations in our companion study (Han et al., 2026). For summer samples (Fig. 9c),
503 high-S water masses along the main channel yielded extremely low POC
504 concentrations ($\sim 12.2\text{--}48.5\ \mu\text{mol L}^{-1}$), with $\delta^{13}\text{C}_{\text{DIC}}$ clustered between -0.5‰ and
505 0.3‰ . By contrast, low-S water masses strongly influenced by riverine freshwater
506 plumes featured elevated POC levels, with a maximum concentration range of ~ 55.2
507 $\mu\text{mol L}^{-1}$ and $\delta^{13}\text{C}_{\text{DIC}}$ as light as -3.2‰ . Most notably, the western off-main channel
508 exhibited exceptionally high POC levels (up to $\sim 71.3\ \mu\text{mol L}^{-1}$) alongside enriched
509 $\delta^{13}\text{C}_{\text{DIC}}$ signatures ($\sim 0.2\text{‰}$). The coupled high POC and heavy $\delta^{13}\text{C}_{\text{DIC}}$ observed
510 within this western sub-basin indicate intense phytoplankton primary production, as
511 corroborated by paired $\delta^{13}\text{C}_{\text{POC}}\text{--}\delta^{15}\text{N}_{\text{PN}}$ isotopic datasets ($\sim -16.94\text{‰}$ for $\delta^{13}\text{C}_{\text{POC}}$ and
512 $\sim 7.2\text{‰}$ for $\delta^{15}\text{N}_{\text{PN}}$) and $\delta^{13}\text{C}_{\text{DIC}}$ stoichiometric analysis reported in our prior studies
513 (Han et al., 2024, 2026). Collectively, covariation between POC and $\delta^{13}\text{C}_{\text{DIC}}$ acts as



514 reliable tracer for both autotrophic organic C synthesis and heterotrophic OM
515 remineralization.

516 It is noteworthy that a characteristic winter signal emerges within the western
517 off-main channel. Stations with depleted POC consistently showed elevated NO_2^-
518 ($\sim 1.4\text{--}3.6 \mu\text{mol L}^{-1}$) and NH_4^+ ($\sim 3.3\text{--}28.2 \mu\text{mol L}^{-1}$) (Fig. 9b). This coupling again
519 points to intense heterotrophic respiration, which consumes POC, releases regenerated
520 inorganic N, and drives $\delta^{13}\text{C}_{\text{DIC}}$ toward lighter values independent of river-coastal
521 water mass mixing (Álvarez-Salgado et al., 1997; Han et al., 2026). Summer
522 observations indicate the opposite pattern in the western zone (Fig. 9d). Extremely
523 high POC coincides with decreased NO_2^- (as low as $\sim 1.9\text{--}3.3 \mu\text{mol L}^{-1}$) and NH_4^+ ($<$
524 $0.5 \mu\text{mol L}^{-1}$), consistent with intense photosynthetic assimilation that removes DIN to
525 fuel algal production. By contrast, the main channel maintains lower POC alongside
526 relatively higher NO_2^- and NH_4^+ concentrations, resulting from OM remineralization
527 as indicated by lighter $\delta^{13}\text{C}_{\text{DIC}}$ (Fig. 6b in Han et al., 2026), thus differing sharply
528 from conditions in the off-main mariculture zone.

529 The above combined observations confirm that N biogeochemistry in Sansha
530 Bay is tightly coupled to POC standing stocks and $\delta^{13}\text{C}_{\text{DIC}}$ signatures. However, these
531 seasonal shifts arise from intertwined physical and biogeochemical drivers, i.e.,
532 mixing between riverine freshwater and intruding adjacent coastal seawater, as well as
533 autotrophic-heterotrophic metabolic cycling. Such multi-factor complexity highlights
534 the critical value of two-endmember mixing models. This modeling framework
535 enables quantitative separation of physical mixing signals from biologically mediated



transformations, including N regeneration, nitrification and phytoplankton N uptake rates. Resolving these competing drivers is essential to fully understand seasonal shifts in bay-scale ecosystem biogeochemical functioning.

4. Discussion

4.1. End-member selection and model validation

The distribution of DIN across Sansha Bay is primarily governed by conservative mixing between two distinct water mass end-members: riverine inflow (RI) and adjacent coastal seawater (SW). This two-endmember mixing framework has been validated via carbonate system parameter analysis in a previous study (Fig. 2 in Han et al., 2026). Deviations above and below theoretical conservative mixing lines signal superimposed biogeochemical transformations, which are strongly modulated by intensive mariculture operations. The latter substantially alter POC pools as well as C and N isotopic signatures, including $\delta^{13}\text{C}_{\text{DIC}}$, $\delta^{13}\text{C}_{\text{POC}}$, and $\delta^{15}\text{N}_{\text{PN}}$ (Han et al., 2021, 2024, 2026).

Linear correlations between DIN (NO_3^- , NO_2^- , and NH_4^+) and S in both winter and summer (Fig. 2) confirm robust two end-member mixing dynamics between RI and SW (Han et al., 2026). Distinct chemical signatures of the two end-members reflect inherent water mass geochemistry as well as seasonal shifts in biological transformation rates. Clear end-member differentiation is evident under winter conditions. The RI end-member (Station S10) exhibited elevated DIN concentrations ($\text{NO}_3^- \sim 62.0 \mu\text{mol L}^{-1}$, $\text{NO}_2^- \sim 1.7 \mu\text{mol L}^{-1}$, and $\text{NH}_4^+ \sim 10.2 \mu\text{mol L}^{-1}$) at a S of ~ 16.76 and $\delta^{13}\text{C}_{\text{DIC}}$ of $\sim -2.6\text{‰}$, whereas the SW end-member (Station S25) was characterized



558 by depleted N pools ($\text{NO}_3^- \sim 40.1 \mu\text{mol L}^{-1}$, $\text{NO}_2^- \sim 0.9 \mu\text{mol L}^{-1}$, and $\text{NH}_4^+ \sim 0.7 \mu\text{mol}$
559 L^{-1}) at ~ 29.2 S and $\delta^{13}\text{C}_{\text{DIC}}$ of $\sim -1.4\text{‰}$. Notably, the western off-main channel
560 experienced substantial DIN accumulation (maxima of $\sim 55.7 \mu\text{mol L}^{-1}$ for NO_3^- , ~ 3.6
561 $\mu\text{mol L}^{-1}$ for NO_2^- , and $\sim 28.2 \mu\text{mol L}^{-1}$ for NH_4^+) (Fig. 2), accompanied by highly
562 depleted $\delta^{13}\text{C}_{\text{DIC}}$ ($\sim -2.6\text{‰}$, Fig. 6b in Han et al., 2026). This leads to a shift from
563 conservative mixing points to strong in situ heterotrophic biogeochemical cycling.
564 Summer values indicated contrasting end-member biogeochemistry. In summer, the
565 SW end-member sampled at the DC Channel mouth exhibited low DIN levels (NO_3^-
566 $\sim 7.8 \mu\text{mol L}^{-1}$, $\text{NO}_2^- \sim 1.7 \mu\text{mol L}^{-1}$, and $\text{NH}_4^+ < 0.5 \mu\text{mol L}^{-1}$) with enriched $\delta^{13}\text{C}_{\text{DIC}}$
567 (up to $\sim 0.2\text{‰}$, Fig. 6 in Han et al., 2026) at a S of ~ 32.49 . By comparison, the RI
568 end-member featured far higher DIN loads ($\text{NO}_3^- \sim 39.8 \mu\text{mol L}^{-1}$, $\text{NO}_2^- \sim 2.2 \mu\text{mol L}^{-1}$,
569 and $\text{NH}_4^+ \sim 5.1 \mu\text{mol L}^{-1}$) and an extremely light $\delta^{13}\text{C}_{\text{DIC}}$ (-3.2‰) at a S of ~ 10.0 .
570 Conversely, the western off-main channel experienced net DIN removal, with
571 depleted NO_3^- ($\sim 9.2 \mu\text{mol L}^{-1}$), NO_2^- ($\sim 1.9 \mu\text{mol L}^{-1}$), and NH_4^+ ($< 0.5 \mu\text{mol L}^{-1}$)
572 alongside elevated $\delta^{13}\text{C}_{\text{DIC}}$ (maximum $\sim 0.2\text{‰}$). End-member properties are
573 summarized in Table 1.

574 **Table 1.** Summary of seasonal physical and biogeochemical end-member
575 characteristics.

Season	End-member	Salinity	NO_3^- ($\mu\text{mol L}^{-1}$)	NO_2^- ($\mu\text{mol L}^{-1}$)	NH_4^+ ($\mu\text{mol L}^{-1}$)
Winter	River plume	S10-0.5m	16.76	62.0	1.7
	Coastal water	S25-all	29.20	40.1	0.9
Summer	River plume	A1-0.5m	10.02	39.8	2.2
	Coastal water	S25-50m	32.49	7.8	1.7

576

577 Stations S10 and A1 are designated as the river plume end-members, and Station S25



578 represents the adjacent coastal seawater end-member (water depth is indicated). The
579 end-member extrapolation scheme is fully documented in Han et al., 2026.

580 Using these well-constrained end-member nutrient values and S-derived water
581 mass mixing fractions, we calculated theoretical conservative DIN concentrations
582 ($\text{NO}_3^-_{\text{cons}}$, $\text{NO}_2^-_{\text{cons}}$, and $\text{NH}_4^+_{\text{cons}}$) using Eqs. 1-5). The propagated uncertainty in
583 mixing fraction calculations induced by end-member S selection was quantified in
584 Han et al., 2026. Thus, deviations between measured in situ DIN concentrations and
585 conservative mixing predictions (ΔNO_3^- , ΔNO_2^- , and ΔNH_4^+ , Eqs. 6-8) were
586 subsequently computed to quantify the magnitude of net non-conservative
587 biogeochemical processes throughout Sansha Bay (Fig. 2).

588 **4.2. Seasonal non-conservative cycling of DIN (ΔNO_3^- , ΔNO_2^- , and ΔNH_4^+)**

589 **4.2.1. Seasonal NO_3^- divergence between the main and western off-main channels**

590 Along the main channel, net NO_3^- production exhibited moderate seasonal
591 differences, as winter ΔNO_3^- ranged from $\sim 0.4 \mu\text{mol L}^{-1}$ to $\sim 11.3 \mu\text{mol L}^{-1}$ (mean: 4.9
592 $\mu\text{mol L}^{-1}$), while summer net NO_3^- accumulation dropped to ~ 0.6 - $5.0 \mu\text{mol L}^{-1}$ (mean:
593 $2.8 \mu\text{mol L}^{-1}$) (Fig. 2a). The western off-main channel yielded contrasting seasonal
594 NO_3^- responses. Maximal net NO_3^- accumulation ($\sim 8.8 \mu\text{mol L}^{-1}$) occurred in winter,
595 whereas substantial net NO_3^- removal reaching $\sim 9.0 \mu\text{mol L}^{-1}$ and net NO_3^-
596 accumulation attaining $\sim 2.8 \mu\text{mol L}^{-1}$ occurred in summer (Fig. 2a). This seasonal
597 dichotomy arises from two competing biological processes shaped by mariculture
598 organic loading and prolonged hydraulic residence time. Winter mariculture-derived
599 OM fuels heterotrophic remineralization and subsequent net NO_3^- enrichment,
600 although potential NO_3^- assimilation in this region remains unquantified. In contrast,



601 intense summertime phytoplankton primary production drives pronounced NO_3^-
602 drawdown, while the rate of NO_3^- accumulation via NiO remains poorly constrained.

603 **4.2.2. Persistent net NO_2^- production with reversed seasonal spatial gradients**

604 In this study, NO_2^- maintained positive non-conservative offsets across the bay in
605 both seasons (Fig. 2b), while the spatial NO_2^- vs. S distribution exhibited seasonal
606 reversal. Main channel ΔNO_2^- reached $\sim 0.1\text{--}1.0 \mu\text{mol L}^{-1}$ (mean $\sim 0.4 \mu\text{mol L}^{-1}$) in
607 winter, with extreme NO_2^- accumulation confined to the western off-main channel
608 ($\sim 0.5\text{--}2.5 \mu\text{mol L}^{-1}$, mean $\sim 1.2 \mu\text{mol L}^{-1}$). This suggests that the stagnant
609 hydrodynamic conditions in the western off-main channel facilitate intense OM
610 remineralization, which probably retains NO_2^- as a dominant nitrification intermediate
611 under limited removal pathways. However, the potential contribution of NO_2^-
612 assimilation toward NO_2^- consumption in this bay region remains unknown. In
613 summer, the net range of NO_2^- production along the main channel was $\sim 0.4\text{--}2.9 \mu\text{mol}$
614 L^{-1} (mean $\sim 1.2 \mu\text{mol L}^{-1}$), yet NO_2^- buildup within the western mariculture zone
615 declined markedly (to $\sim 0.1\text{--}1.5 \mu\text{mol L}^{-1}$, mean $\sim 0.7 \mu\text{mol L}^{-1}$). Elevated ambient T
616 likely enhances water-column nitrification, thereby raising background NO_2^-
617 concentrations throughout the main channel. By contrast, the western off-main
618 channel showed a weaker NO_2^- accumulation signal, presumably because active NO_2^-
619 uptake by phytoplankton partially counterbalances in situ NO_2^- production, although
620 the exact assimilation rates remain unknown. Combined isotopic evidence from
621 $\delta^{13}\text{C}_{\text{DIC}}$ ($\sim 0.2\text{‰}$), $\delta^{13}\text{C}_{\text{POC}}$ ($\sim -16.9\text{‰}$) and $\delta^{15}\text{N}_{\text{PN}}$ ($\sim 7.2\text{‰}$) signatures (Han et al.,
622 2024, 2026) also confirms concurrent NO_2^- production and consumption processes.



623 The persistent net positive ΔNO_2^- in the western bay further demonstrates that NO_2^-
624 production dominates over removal processes, indicative of robust NiO .

625 **4.2.3. Spatially differentiated NH_4^+ cycling across seasons**

626 NH_4^+ non-conservative dynamics also showed pronounced seasonal and spatial
627 heterogeneity (Fig. 2c). Winter was characterized by net NH_4^+ regeneration ($\sim 0.3\text{--}8.5$
628 $\mu\text{mol L}^{-1}$) along the main channel with mean values of $\sim 2.4 \mu\text{mol L}^{-1}$ to $\sim 1.8\text{--}25.7$
629 $\mu\text{mol L}^{-1}$ in western zones of the bay with an average of $\sim 11.0 \mu\text{mol L}^{-1}$ driven by
630 heterotrophic mineralization. Summer exhibited mixed NH_4^+ signals along the main
631 channel, with coexisting zones of net production ($\sim 0\text{--}1.5 \mu\text{mol L}^{-1}$, mean $\sim 0.5 \mu\text{mol}$
632 L^{-1}) and removal ($\sim 0\text{--}3.2 \mu\text{mol L}^{-1}$, mean $\sim 0.9 \mu\text{mol L}^{-1}$). Within the western off-main
633 channel, summertime NH_4^+ frequently fell below detection limits and remained lower
634 than conservative mixing predictions ($\sim 0.1\text{--}2.2 \mu\text{mol L}^{-1}$, mean $\sim 1.0 \mu\text{mol L}^{-1}$). It is
635 unclear whether NH_4^+ removal is driven solely by phytoplankton assimilation or is
636 partially coupled with AO that promotes NO_2^- accumulation. Further quantitative rate
637 analysis (see Section 4.4), is required to disentangle these concurrent processes. By
638 comparison, the main channel was consistently controlled by OM remineralization in
639 both seasons, with regenerated NH_4^+ showing in situ concentrations above
640 conservative values. Meanwhile, NH_4^+ assimilation was also stimulated along the
641 main channel in summer. This spatial contrast reveals simultaneous heterotrophic
642 degradation, autotrophic assimilation, and possible nitrification unique to the
643 semi-enclosed mariculture sub-basin.

644 **4.3. Hydrological connectivity and coupled N-C biogeochemical controls on**



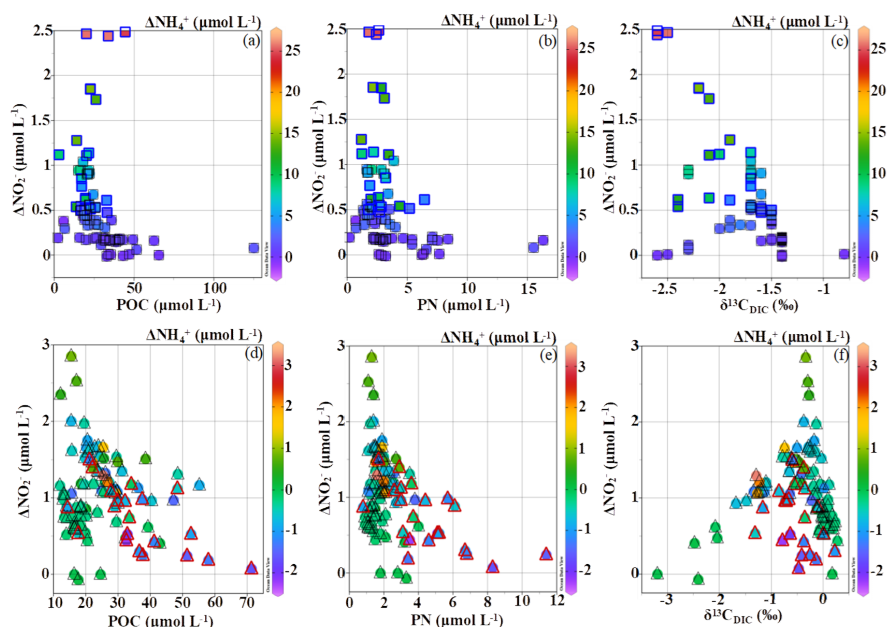
inorganic N dynamics

Stoichiometric coupling between offset DIN variation, and POC, PN, and $\delta^{13}\text{C}_{\text{DIC}}$ provides mechanistic insights into winter N cycling (Fig. 10). A prior study validated Redfield-type OM remineralization across the bay, marked by widespread POC and PN depletion ($\sim 10\text{-}50\ \mu\text{mol L}^{-1}$ and $\sim 1.0\text{-}7.5\ \mu\text{mol L}^{-1}$, respectively) and depleted $\delta^{13}\text{C}_{\text{DIC}}$ ($\Delta\delta^{13}\text{C}_{\text{DIC}} \sim 0.0\text{‰}$ to -0.7‰ , mean -0.2‰) in winter (Table 2, Han et al., 2026). Along the transport gradient from the main channel toward the western off-main channel, POC and PN gradually declined (from $50\ \mu\text{mol L}^{-1}$ to $25\ \mu\text{mol L}^{-1}$ for POC and from $7.5\ \mu\text{mol L}^{-1}$ to $2.5\ \mu\text{mol L}^{-1}$ for PN, respectively) and $\delta^{13}\text{C}_{\text{DIC}}$ showed much greater C depletion ($\Delta\delta^{13}\text{C}_{\text{DIC}} \sim -0.1\text{‰}$ to -1.0‰ , mean -0.4‰) (Table 2, Fig. 10a-c), accompanied by extremely elevated ΔNO_2^- and ΔNH_4^+ in western waters. These signals confirm that heterotrophic aerobic respiration drives concurrent NH_4^+ and NO_2^- production superimposed on physical mixing gradients, thus explaining the observed winter DIN enrichment patterns (see Section 4.2).

Table 2. Deviations (mean and range) from conservative mixing of biogeochemical parameters measured in Sansha Bay in winter and summer (see text).

Seasons	Area	Biogeochemical parameters							
		ΔNO_3^-		ΔNO_2^-		ΔNH_4^+		$\Delta\delta^{13}\text{C}_{\text{DIC}}$	
		Ranges	Mean	Ranges	Mean	Ranges	Mean	Ranges	Mean
Winter	Main channel	+0.4 to +11.3	+4.9	+0.1 to +1.0	+0.4	+0.3 to +8.5	+2.4	0.0‰ to -0.7‰	-0.2‰
	Western off-main channel	+2.9 to +8.8	+6.5	+0.5 to +2.5	+1.2	+1.8 to +25.7	+11.0	-0.1‰ to -1.0‰	-0.4‰
Summer	Main channel	+0.6 to +5.0	+2.8	+0.4 to +2.9	+1.2	0 to +1.5	+0.5	-0.02‰ to -1.0‰	-0.3‰
	Western off-main channel	+0.1 to +2.8	+1.2	+0.1 to +1.5	+0.7	0 to -3.2	-0.9	0.02‰ to 0.2‰	+0.1‰
		-0.7 to -9.0	-3.6			-0.1 to -2.2	-1.0	-0.02‰ to -0.5‰	-0.2‰
								0.1‰ to 0.4‰	+0.2‰

Note: for ΔNO_3^- , ΔNO_2^- , and ΔNH_4^+ ‘+’ indicates DIN production, and ‘-’ indicates DIN removal. For $\Delta\delta^{13}\text{C}_{\text{DIC}}$ ‘+’ indicates that $\delta^{13}\text{C}_{\text{DIC}}$ is heavier, and ‘-’ indicates that $\delta^{13}\text{C}_{\text{DIC}}$ is lighter; $\Delta\delta^{13}\text{C}_{\text{DIC}}$ values were sourced from Han et al., 2026.



666

667 **Figure 10.** Scatter plots of the relationship among POC ($\mu\text{mol L}^{-1}$), ΔNO_2^- ($\mu\text{mol L}^{-1}$),
668 and ΔNH_4^+ in Sansha Bay during winter (a) and summer (d). PN ($\mu\text{mol L}^{-1}$) and
669 ΔNO_2^- ($\mu\text{mol L}^{-1}$) plots, overlaid with ΔNH_4^+ ($\mu\text{mol L}^{-1}$) in Sansha Bay during winter
670 (b) and summer (e). Plots of $\delta^{13}\text{C}_{\text{DIC}}$ (‰) vs. ΔNO_2^- ($\mu\text{mol L}^{-1}$), overlaid with the
671 ΔNH_4^+ ($\mu\text{mol L}^{-1}$) in Sansha Bay during winter (c) and summer (f). Δ : deviations in
672 nutrient concentrations from conservative mixing. Sampling stations are categorized
673 by season and location using the symbols: blue squares (winter, western off-main
674 channel), red triangles (summer, western off-main channel), black squares (winter,
675 main channel), and black triangles (summer, main channel). POC, PN, and $\delta^{13}\text{C}_{\text{DIC}}$
676 were sourced from Han et al 2024 and 2026.

677 Summer biogeochemical regimes between the main channel and western
678 off-main channel are decoupled. Along the main channel, residual OM degradation
679 sustained moderate nitrification and weak net inorganic N production. Corresponding



680 water column nutrient profiles showed gradually decreasing POC and PN
681 concentrations (from ~ 50.0 to ~ 10.0 $\mu\text{mol L}^{-1}$ and from ~ 4.0 to ~ 1.0 $\mu\text{mol L}^{-1}$,
682 respectively) paired with lighter $\delta^{13}\text{C}_{\text{DIC}}$ values ($\Delta\delta^{13}\text{C}_{\text{DIC}} \sim -0.02\text{‰}$ to -1.0‰ , mean
683 -0.3‰ , Table 2, Fig. 10a-c) and $\delta^{13}\text{C}_{\text{POC}}$ ($\sim -21.5\text{‰}$ to -24.5‰ , Fig. 6b in Han et al.,
684 2024), further supporting the occurrence of persistent aerobic N regeneration within
685 the channel.

686 The western mariculture zone in Sansha Bay shifts to autotrophic dominance in
687 summer, as evidenced by substantial POC and PN production (~ 20.0 - 70.0 $\mu\text{mol L}^{-1}$
688 and ~ 2.0 - 8.0 $\mu\text{mol L}^{-1}$, respectively) and enriched C isotopic signatures ($\Delta\delta^{13}\text{C}_{\text{DIC}} \sim$
689 0.1‰ to 0.4‰ , mean 0.2‰ (Table 2); and $\delta^{13}\text{C}_{\text{POC}} \sim -20.0\text{‰}$ to -16.8‰ , Fig. 6b in
690 Han et al., 2024; Han et al., 2026). Markedly reduced ΔNO_2^- and ΔNH_4^+ in this region
691 of the bay reflect intense phytoplankton consumption of regenerated DIN, which
692 reverses the winter DIN enrichment pattern described in Section 4.2.

693 Synthesizing observations across the entire bay, OM remineralization acts as the
694 primary driver of inorganic N accumulation in both seasons. This remineralization
695 derived N loading is partially offset in summer by two autotrophic processes,
696 including widespread phytoplankton assimilation of NO_3^- , NO_2^- , and NH_4^+ , and robust
697 in situ OM production that enriches $\delta^{13}\text{C}_{\text{DIC}}$ and $\delta^{13}\text{C}_{\text{POC}}$ within the western
698 off-channel sector of the bay. Collectively, these spatial and seasonal biogeochemical
699 gradients illustrate complex interactions between physical water mass transport and
700 biologically mediated N transformations within this coastal mariculture ecosystem.

701 4.4. Quantification of the rates of N cycling in the western embayment zone



702 As mentioned above, the collective seasonal variation in ΔNO_3^- , ΔNO_2^- , and
703 ΔNH_4^+ indicated persistent OM remineralization across the mariculture system in both
704 seasons, accompanied by concurrent nitrification and N assimilation. The western
705 off-main channel, acting as an active “N reactor” modulated by intensive fish
706 mariculture activities, exhibited particularly pronounced N transformation signals.
707 Notably, non-conservative “ Δ ” values only represent net changes in DIN
708 concentrations, yielding purely qualitative constraints on biogeochemical processes.
709 Such net signals may mask individual DIN oxidation and assimilation pathways,
710 while the corresponding transformation rates for different DIN species cannot be
711 resolved using the two end-member mixing model. Accordingly, ^{15}N tracer
712 incubations were performed to quantify in situ DIN uptake and oxidation rates under
713 ambient environmental conditions. Sampling was conducted at Station S2 in the
714 western off-main channel zone, an area characterized by intensive mariculture activity
715 and prolonged water residence time during winter 2024 (January 28) and summer
716 2023 (August 6). We here acknowledge that the rate incubation experiments and the
717 mapping cruises were conducted separately. Nevertheless, the proportional
718 contribution of individual DIN species to total DIN at the incubation stations were
719 highly consistent with those measured during the mapping cruises (Table S1): NH_4^+
720 accounted for 17.6%-23.2% in winter and 0%-8.0% in summer; NO_2^- ranged from
721 4.0% to 5.6% in winter and 16.1% to 29.5% in summer; NO_3^- ranged from 71.8% to
722 76.7% in winter and 67.8% to 83.9% in summer. Accordingly, the incubation-derived
723 transformation rates can reasonably interpret the DIN dynamics within the western



off-main channel.

Table S1. Concentrations and percentages of individual dissolved inorganic nitrogen (DIN) species at Station S2 (see Fig. 1) from incubation experiments and mapping cruises in Sansha Bay during winter and summer

Seasons	Depth (m)	NH_4^+ ($\mu\text{mol L}^{-1}$)	NO_2^- ($\mu\text{mol L}^{-1}$)	NO_3^- ($\mu\text{mol L}^{-1}$)	NH_4^+ proportion (%)	NO_2^- proportion (%)	NO_3^- proportion (%)
Winter-incubation cruise	0.5	9.6	2.7	37.5	19.2	5.4	75.4
	5	8.9	2.8	38.6	17.6	5.6	76.7
	19	9.9	2.8	38.4	19.4	5.5	75.1
Summer-incubation cruise	0.5	2.1	10.1	25.8	5.5	26.6	67.8
	8	1.3	8.5	21.3	4.1	27.4	68.4
	15	0.5	7.7	17.8	2.0	29.5	68.5
Winter-mapping cruise	0.5	16.1	2.8	50.4	23.2	4.0	72.8
	4	15.0	2.9	51.6	21.6	4.2	74.2
	7	17.5	2.9	52.1	24.1	4.1	71.8
Summer-mapping cruise	0.5	<0.5	2.0	10.6	0	16.1	83.9
	5	<0.5	2.3	11.6	0	16.2	83.8
	10	1.6	3.2	14.6	8.0	16.5	75.4

4.4.1. Elevated ammonium and nitrate uptake mitigate N accumulation

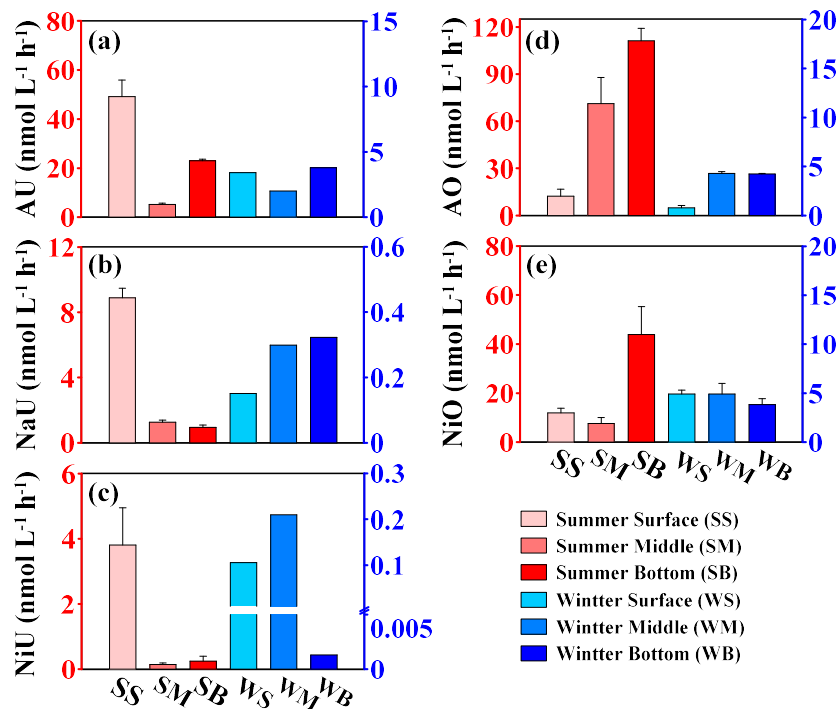


Figure 11. Rates of dissolved inorganic nitrogen (DIN) uptake (NO_3^- , NaU; NO_2^- ,



732 NiU; NH_4^+ , AU) and nitrification rates (NH_4^+ , AO; NO_2^- , NiO) in the western
733 off-main channel (station S2) of Sansha Bay. Blue and red borders indicated winter
734 and summer, respectively. NaU, NiU, and AU represent the uptake rate of nitrate,
735 nitrite and ammonium, respectively.

736 In winter, AU rates remained uniformly low throughout the entire water column ,
737 with values of $\sim 3.4 \text{ nmol L}^{-1} \text{ h}^{-1}$, $\sim 2.0 \text{ nmol L}^{-1} \text{ h}^{-1}$, and $\sim 3.8 \text{ nmol L}^{-1} \text{ h}^{-1}$ at surface,
738 mid-water, and bottom layers, respectively (Fig. 11a). NiU increased gradually with
739 depth but remained consistently below $\sim 0.21 \text{ nmol L}^{-1} \text{ h}^{-1}$ (Fig. 11b). Among all
740 measured DIN uptake pools, NiU was the weakest compared to AU and NaU, a
741 finding consistent with observations in other estuaries (Moneta et al., 2014; Xu et al.,
742 2022). NaU vertical profiles were analogous to those of NiU exhibiting the same
743 order of magnitude, ranging from $\sim 0.2 \text{ nmol L}^{-1} \text{ h}^{-1}$ at the surface to $\sim 0.3 \text{ nmol L}^{-1} \text{ h}^{-1}$
744 near the bottom (Fig. 11c). Relatively low NaU and NiU may be explained by the
745 known inhibitory effect of high NH_4^+ on NO_3^- uptake (Dugdale et al., 2007; Glibert et
746 al., 2016).

747 In summer, AU peaked at the surface ($\sim 49.2 \text{ nmol L}^{-1} \text{ h}^{-1}$) and declined sharply
748 downward to $\sim 5.2\text{--}23.0 \text{ nmol L}^{-1} \text{ h}^{-1}$ in mid- and bottom waters, respectively (Fig.
749 11a). Surface NiU reached only $\sim 3.8 \text{ nmol L}^{-1} \text{ h}^{-1}$ (Fig. 11b), far lower than surface
750 AU (i.e., by a factor of 13). Consistent with the winter pattern, NiU ($\sim 0.3 \text{ nmol L}^{-1} \text{ h}^{-1}$
751 at depth) represented a minor uptake pathway compared to AU and NaU (Moneta et
752 al., 2014; Xu et al., 2022), in agreement with results in the Gulf of Aqaba (Mackey et
753 al., 2011). In contrast, NaU displayed pronounced vertical stratification, with surface



754 rates ($\sim 8.9 \text{ nmol L}^{-1} \text{ h}^{-1}$) markedly higher than those at mid- and bottom depths (~ 1.0
755 $\text{nmol L}^{-1} \text{ h}^{-1}$) (Fig. 11c). Higher uptake rates of NH_4^+ and NO_3^- in surface waters
756 during summer reasonably account for the signatures indicating net removal of NH_4^+
757 and NO_3^- (Fig. 2a, c). The weak uptake of NO_2^- explains the net production rather than
758 removal of NO_2^- (Fig. 2b). The overall nutrient uptake in winter is markedly lower
759 (nearly 13-fold difference) than that in summer (Fig. 11), which logically results in
760 the accumulation of the entire DIN pool in winter (Han et al., 2021).

761 **4.4.2. Nitrification regulates ammonium removal and nitrite net production**

762 Winter ammonia oxidation (AO) rates and nitrite oxidation (NiO) rates showed
763 comparable magnitudes throughout the water column (except at the surface where AO
764 $\sim 0.8 \text{ nmol L}^{-1} \text{ h}^{-1}$), with values of $\sim 4.3 \text{ nmol L}^{-1} \text{ h}^{-1}$ for AO and $\sim 3.8\text{--}4.9 \text{ nmol L}^{-1} \text{ h}^{-1}$
765 for NiO, respectively (Fig. 11d, e). The oxidation rates align with measurements from
766 the Jiulong River Estuary (Yan et al., 2019) and other comparable mid-salinity coastal
767 estuaries (Xu et al., 2022; Hou et al., 2025).

768 In contrast to the sluggish winter cycling, N transformation pathways exhibited
769 drastically enhanced biogeochemical activity in summer. Both AO and NiO were
770 suppressed in surface waters (minimum of $12.29 \text{ nmol L}^{-1} \text{ h}^{-1}$ and $11.91 \text{ nmol L}^{-1} \text{ h}^{-1}$),
771 whereas mid- and bottom waters became hotspots of intensive nitrification, with AO
772 and NiO reaching maxima of $111.21 \text{ nmol L}^{-1} \text{ h}^{-1}$ and $43.91 \text{ nmol L}^{-1} \text{ h}^{-1}$, respectively.

773 Elevated surface AU likely depletes NH_4^+ regenerated from mariculture-derived
774 OM, and planktonic NH_4^+ assimilation outcompetes ammonia oxidizers for shared
775 substrates (Xu et al., 2022). With increasing depth, light attenuation relieves



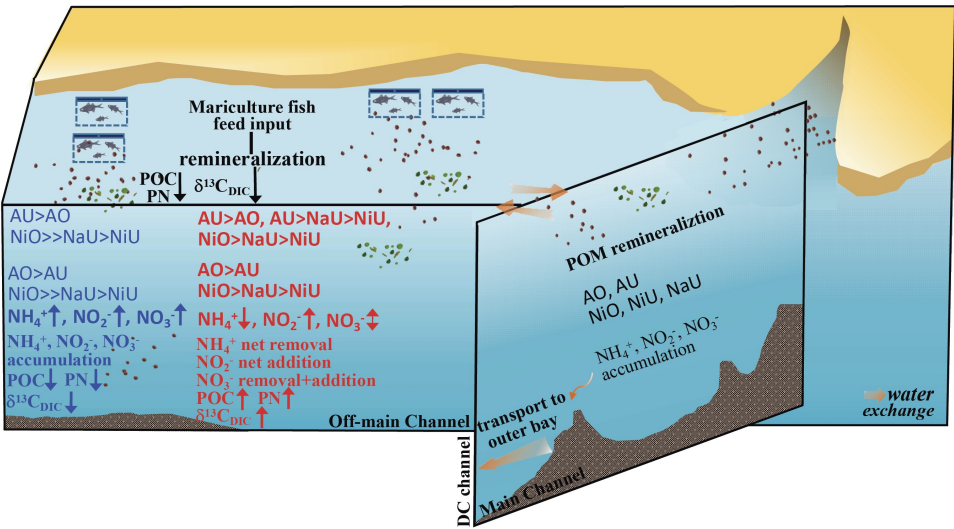
776 photoinhibition of nitrifying microbial populations. Sustained OM remineralization
777 exported from the euphotic zone continuously supplies NH_4^+ substrate to deeper
778 waters, while phytoplankton-mediated competition for reduced N declines with depth.
779 Additionally, weakly oxygenated subsurface environments provide
780 thermodynamically and kinetically favorable conditions for ammonia- and
781 nitrite-oxidizing microbial consortia. Collectively, these depth-dependent regulatory
782 factors drive the prominent upward increase of AO and NiO from surface to bottom
783 layers.

784 In summary, winter AU and AO are uniformly elevated, fueled by ample NH_4^+
785 regenerated via intense remineralization. Despite robust AO, net NH_4^+ buildup
786 persists, yielding large ΔNH_4^+ values. Winter NiU remains depressed, whereas NiO
787 increases by an order of magnitude. This disparity signals rapid conversion of NO_2^- to
788 NO_3^- and minimal NO_2^- storage, consistent with the finding that ΔNO_2^- is substantially
789 smaller than both ΔNH_4^+ and ΔNO_3^- . NaU is roughly an order of magnitude lower
790 than NiO; therefore, this uptake capacity is inadequate to fully scavenge the NO_3^-
791 produced during nitrification, resulting in net NO_3^- accumulation. Summer is
792 characterized by strong vertical stratification in AO metrics. AU peaks within surface
793 waters, while AO dominates midwater and bottom layers. Enhanced AO across the
794 water column drives rapid NH_4^+ turnover and effectively strips NH_4^+ from the water
795 column, nearly erasing the NH_4^+ surplus and accounting for pronounced drawdown in
796 ΔNH_4^+ . Concurrently, vigorous AO likely generates substantial NO_2^- intermediates
797 and intensive NiO promotes transient NO_3^- production, yet benthic NaU remains weak,



798 fostering NO_3^- buildup at depth. By contrast, surface waters exhibit efficient NaU that
799 partially relieved NO_3^- pools. In summary, the NO_3^- pool undergoes concurrent
800 production and biological removal across the water column (Fig. 2).

801 **5. Conclusion**



802
803 **Figure 12.** Conceptual schematic illustrating the DIN (nitrate, NO_3^- , nitrite, NO_2^- , and
804 ammonium, NH_4^+) dynamics in Sansha Bay affected by intensive fish mariculture and
805 under the influence of both river nutrient inputs and those from adjacent coastal
806 waters (see text for explanation).

807 A conceptual framework was proposed to describe DIN dynamics in Sansha Bay,
808 representative of embayments affected by intensive fish mariculture as illustrated in
809 Fig. 12. Along the main channel during winter and summer, DIN levels showed net
810 additions into the bay, where OM remineralization and/or N regeneration dominated
811 over N removal. Instead, in the western off-main channel, a zone of intensive fish
812 mariculture and longer water residence time, $\text{AU} > \text{AO}$ and $\text{NiO} \gg \text{NaU} > \text{NiU}$ were



813 observed in the upper water column in winter; while nitrification (AO and NiO)
814 dominated in the bottom layer, thus N accumulation occurs in winter, leading to
815 “excess” DIN in the bay as reported in Han et al., 2021. In summer, OM-associated N
816 uptake and nitrification rates were far higher than those in winter. The co-occurrence
817 of N uptake and nitrification alters the removal and accumulation patterns of various
818 N species such that AU dominates in the upper water layer. Elevated AU and NaU
819 mitigate N accumulation and reduce NH_4^+ and NO_3^- concentrations. With increasing
820 water depth, substantial nitrification rates surpass N uptake rates, leading to the
821 buildup of NO_2^- and NO_3^- .

822 Collectively, our observations in Sansha Bay demonstrate that water residence
823 time is a key driver of spatial heterogeneity in DIN cycling within intensive finfish
824 mariculture semi-enclosed bays. The contrasting biogeochemical regimes between the
825 well flushed main channel and the stagnant western bay highlight that hydrodynamics
826 can modulate the relative importance of nitrification and phytoplankton assimilation,
827 thereby controlling net DIN accumulation or depletion in aquaculture impacted
828 coastal waters. Although this study is based on a single representative mariculture bay,
829 the mechanistic framework derived here can be broadly applicable to other
830 semi-enclosed coastal systems subject to intensive finfish farming. These findings
831 advance our mechanistic understanding of how human driven nutrient inputs interact
832 with physical hydrodynamic conditions to regulate inorganic nitrogen dynamics,
833 which is critical for assessing eutrophication risk in comparable mariculture -
834 dominated coastal environments worldwide.



835 **Declaration of Competing Interest**

836 The authors declare that they have no conflict of interest.

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849 with sample collection.

850 **Author Contribution Statement**

851 **Aiqin Han:** Designing of the research, funding, performing the research (inorganic
852 nitrogen dynamics, nitrogen uptake, and nitrification), methods (nutrient autoanalyzer,
853 GB-IRMS, etc.), analyzing data, and writing the manuscript. **Zhenzhen Zheng:**
854 Designing of the research, performing the research (nitrogen uptake, and nitrification),
855 methods (GB-IRMS, etc.), analyzing data, and writing the manuscript. **Rong Fu, Lili**
856 **Lang:** Performing the research (inorganic nitrogen dynamics, nitrogen uptake, and



857 nitrification), methods (GB-IRMS, etc.), analyzing data, and writing the manuscript.

858 **Shuh-Ji Kao:** Designing of the research, methods (GB-IRMS, etc.), analyzing data,

859 and writing the manuscript. **Yuanbiao Zhang, Yasong Li:** Designing of the research,

860 analyzing data, and writing the manuscript.

861 **Data Availability Statement**

862 The data that support the findings of this study are available from the corresponding

863 author upon reasonable request.

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