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Tintinnid and dinoflagellate variability during a neap tide sequence in the Santos Estuary

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Abstract

High-frequency sampling can resolve estuarine plankton variability that is missed by isolated observations. We examined tintinnids, dinoflagellates, hydrography and nutrients in 12 samples collected at two-hour intervals during a 22-h neap-tide sequence in the Santos Estuary, south-eastern Brazil. The net samples contained 14 tintinnid and 9 dinoflagellate taxa or morphotypes. Tintinnid counts ranged from 95 to 717 per 1-mL aliquot of net concentrate and were dominated by *Tintinnopsis campanula* (90.8% of pooled counts), with a maximum at 03:00. Dinoflagellate counts ranged from 3 to 275 per aliquot; *Tripos hircus* and *Protoperidinium* sp. contributed 49.7% and 38.6% of pooled counts and peaked at 23:00. Dinoflagellates were positively associated with recorded tidal height (Spearman ρ = 0.750), whereas tintinnids showed weaker negative associations with tidal height (ρ = −0.242) and dinoflagellates (ρ = −0.343). Nitrite and phosphate generally increased during the falling-height interval. The dinoflagellate–tide association had an unrestricted permutation p-value of 0.007 but a circular-shift value of 0.250. With only 12 rotations and one temporal sequence, these comparisons provide sensitivity checks rather than confirmatory tests of tidal control. Unknown net-filtered and concentrate volumes preclude conversion to ambient densities. The observations document marked variation in the sampled assemblage and identify hypotheses for replicated, volume-calibrated sampling across tidal and diel cycles.

1. INTRODUCTION

Estuaries are pulse-driven ecosystems in which the biological community observed at a fixed point can be reorganized within hours. Each tidal excursion moves water masses, modifies vertical structure, redistributes suspended material and nutrients, and changes the organisms delivered to the sampling station. High-frequency studies increasingly show that coastal plankton forms coherent yet short-lived states whose transitions are invisible to daily, weekly or monthly surveys (Martin-Platero et al. 2018, Gu et al. 2022, Rodier et al. 2024, Birocchi et al. 2026, Cruz et al. 2026). The ecological signal of a tidal cycle is therefore more than short-term “noise”: it is a structured component of estuarine variability and a central consideration in the design and interpretation of monitoring programmes.

Brazilian estuaries provide especially informative settings for resolving this variability because tropical and subtropical plankton develops within strong interactions among semidiurnal tides, freshwater discharge, stratification, turbidity and nutrient loading. In the Santos–São Vicente complex, phytoplankton composition changes among tidal, wind-mixing and freshwater-outflow conditions, generating contrasting dominance states within the same regional system (Moser et al. 2012). Complete-cycle observations elsewhere on the Brazilian coast have similarly shown that tidal energy, salinity structure and water movement can reorganize phytoplankton density, composition and functional traits over short intervals (Parizzi et al. 2016, Moser et al. 2017, Nascimento et al. 2021). Broader estuarine studies confirm that the relative importance of seasonal, spatial and tidal processes depends on local mixing and residence time (Santos et al. 2022, Nunes et al. 2023). These findings position high-frequency sampling to describe variation that a single monitoring value cannot resolve.

Tintinnids are loricate ciliates that transfer microbial and primary production to larger consumers while responding rapidly to hydrography and food availability. Their loricae enable routine morphological analysis and make them valuable tracers of community turnover, particularly in dynamic coastal waters. Tropical and subtropical estuaries commonly support assemblages structured by salinity, temperature, trophic state and monsoonal or seasonal forcing, often with strong contributions from *Tintinnopsis* species (Rakshit et al. 2016a, 2016b, 2017, Li et al. 2019, Durmus et al. 2023, Sathish et al. 2024). Frequent observations in Sendai Bay revealed population changes within days and showed that physicochemical and food conditions can outweigh predation pressure in organising short-term tintinnid dynamics (Kazama and Urabe, 2016). These environmental associations also support their use as indicators of eutrophication and environmental gradients (Sivasankar et al. 2018).

The distribution of tintinnids reflects the interaction between local ecological performance and water-mass history. Salinity-related differentiation has been documented from estuaries to hypersaline systems (Al-Yamani et al. 2019, Albergoli and Alder, 2024), while shelf and ocean surveys demonstrate pronounced assemblage transitions across hydrographic fronts and between neritic and oceanic waters (Yu et al. 2020, Li et al. 2021, Li et al. 2023). Community organisation also varies with vertical structure, temperature preference, lorica oral diameter and diel phase (Wang et al. 2022a, 2022b, 2023, Li et al. 2024). Studies spanning coastal lagoons, deltas and estuary–offshore continua further show that total abundance and taxonomic composition can respond differently to the same gradient (Mukherjee et al. 2018, Govindan et al. 2024, El-Tohamy and Hopcroft 2024, Wang et al. 2026a, Liu et al. 2026). A high-resolution record can therefore distinguish a stable dominant population from the rapid arrival or disappearance of less persistent taxa.

Dinoflagellates add a complementary dimension because autotrophy, heterotrophy, mixotrophy, motility and vertical positioning coexist within the group. Their distribution can respond rapidly to the balance between water-column stability, light, prey, nutrient form and advective transport. Estuarine studies have identified marked seasonal and short-term variation in dinoflagellate and mixotroph assemblages (Millette et al. 2021, Caracciolo et al. 2022, Nunes et al. 2023), and new high-resolution work shows that tidal pulses can decouple nutrient maxima from plankton biomass maxima (Cruz et al. 2026). Modelling and field observations likewise indicate that tidal modulation can govern biomass retention and export even when nutrients remain available (Wang et al. 2026b). These mechanisms predict that dinoflagellates may form a distinct tidal trajectory rather than changing in parallel with ciliates or dissolved nutrients.

Tintinnids and dinoflagellates are also connected through the microbial food web. Ciliate trophic strategies shift with the composition and size structure of phytoplankton (Haraguchi et al. 2018), and estuarine measurements show that microzooplankton grazing and phytoplankton growth can change daily to seasonal scales (Anderson et al. 2018, Anderson and Harvey 2019). Feeding experiments demonstrate taxon-specific ingestion of mixotrophic dinoflagellates by tintinnids (Yang et al. 2019), while field and experimental studies document the importance of prey identity, grazing and plastid retention to dinoflagellate performance (Busch et al. 2019; Stoecker and Pierson 2019; Ladds et al.

2024). At community scale, environmental conditions are associated with ciliate co-occurrence and productivity–diversity relationships (Trombetta et al. 2021; Liu et al. 2025; Feng et al. 2025). The temporal phase relation between the two protist groups is therefore ecologically informative even when a fixed-station sequence is used to identify patterns rather than assign a single trophic mechanism.

Here, we describe tintinnid and dinoflagellate variability during a neap-tide fixed-station sequence in the Santos estuarine channel. We examined three ecological expectations: higher dinoflagellate counts near high water; temporal separation between tintinnid and dinoflagellate maxima; and increasing nitrite and phosphate concentrations during the falling-height interval, accompanied by lower dinoflagellate counts. These expectations organize an exploratory analysis of one historical sequence. Taxon-level counts, paired surface and near-bottom measurements, and nutrient records at two-hour resolution were used to describe the sampled assemblage and its environmental context. The design cannot separate tidal exchange, diel variation and local biological processes.

2. MATERIALS and METHODS

2.1. Study area and sampling sequence

Sampling was conducted at a fixed station near the Pilot Pier in the Santos estuarine channel, São Paulo State, Brazil (approximately 23°59'S, 46°18'W). The Santos–São Vicente estuarine complex connects a densely urbanised and industrialised watershed and the Port of Santos to Santos Bay and the adjacent continental shelf. Semidiurnal tides, freshwater discharge, wind-driven circulation and channel geometry generate strong surface–bottom and estuary–coast gradients. Earlier regional observations showed that these coupled processes produce distinct plankton dominance states and rapid changes in salinity, suspended matter and phytoplankton composition (Moser et al. 2012).

The campaign aboard the R/V Danda II began on 13 March 2008 under neap-tide conditions and lasted approximately 25 h. The coordinated biological sequence comprises 12 observations collected at two-hour intervals from 19:00 on 13 March to 17:00 on 14 March, spanning 22 h. Recorded tidal height increased from 1.0 m at 19:00 to 1.6 m at 01:00, declined to 0.2 m at 13:00, and increased to 0.5 m by 17:00. Rising and falling portions refer to changes in this recorded height series. They are not measurements of flood or ebb current direction, and the 12 observations do not represent independent tidal cycles.

2.2. Hydrography, suspended material and nutrients

Surface and near-bottom temperature and salinity were measured with a YSI multiparameter instrument. Water was collected at both depths using a 2.5-L Van Dorn bottle. For dissolved nutrient analysis, 250 mL from each sample was filtered aboard the vessel through a filter with a nominal pore size of 0.45 µm. Ammonia (archived analytical label NH_3), nitrite (NO_2) and orthophosphate (PO_4) were determined colorimetrically following Parsons et al. (1984). The environmental dataset also included total phosphorus (TP), chlorophyll a, suspended matter, total organic matter and calcium carbonate.

Chlorophyll a was determined spectrophotometrically following Lorenzen (1967). Suspended matter was determined gravimetrically, organic matter by calcination at 550°C, and calcium carbonate by acid treatment.

Nutrient determinations were aligned by sampling time with the laboratory workbook. NH_3, PO_4 and TP values in the consolidated record were expressed in mg L^{-1} and converted to µg L^{-1} by multiplication by 1000; NO_2 was already expressed in µg L^{-1}. Phosphate concentrations were calculated from the mean absorbance of the available replicate readings for the same sample using the recorded calibration, C = (A − 0.0013)/7.1352, before conversion to µg L^{-1}. The surface values at 21:00 and 23:00 were 4.8165 and 4.9333 µg L^{-1}, respectively. The supplementary data retain the analytical readings and calculation provenance. The archived NH_3 label does not establish the concentration of un-ionized ammonia, and nutrient mass labels were not used to calculate N:P stoichiometry. Suspended matter is reported in g L^{-1}, and particulate organic matter and calcium carbonate as percentages.

2.3. Plankton collection, preservation and enumeration

Plankton was collected every two hours by vertical haul with a 50-µm mesh net of 40-cm mouth diameter over a nominal 8-m water column, with depth varying with tidal height. Samples were preserved in 4% neutralized formaldehyde. Tintinnids and dinoflagellates were enumerated in a 1-mL Sedgewick–Rafter chamber under a Zeiss light microscope at 100–400× magnification. Historical identifications were based on lorica and cell morphology using taxonomic literature available to the laboratory; Pierce and Turner (1992) provided ecological and morphological context.

The primary observations are integer counts in the analysed 1-mL aliquot of net concentrate, reported as counts $aliquot^{-1}$. Taxon counts were summed separately for tintinnids and dinoflagellates, and the recalculated totals matched the archived totals at all 12 times. The net-mouth area was 0.1257 m², corresponding to a nominal geometric swept volume of 1.005 m³ over 8 m. For a full-depth vertical haul, geometric volume changes by 125.66 L for each metre of depth change. The tidal reference for the nominal depth, flowmeter-derived volumes, final concentrate volumes and replicate chamber counts were not available. Consequently, the counts cannot be converted to ambient densities, and differences among aliquots may reflect variation in collection or concentration efficiency as well as assemblage variation. The 50-µm mesh selectively samples retained organisms and does not represent the complete protist community.

2.4. Taxonomic harmonisation

The dataset contained 14 tintinnid and 9 dinoflagellate taxa or morphotypes. Source names were retained in the supplementary taxonomic table and harmonised using the World Register of Marine Species (WoRMS Editorial Board, 2026). Updated combinations include *Eutintinnus fraknoii*, *Codonellopsis schabi*, *Tripos horridus*, *T. arietinus*, *T. azoricus*, *T. declinatus* and *Pyrocystis pseudonoctiluca*. The original entry “*Parundella caudata* (or *Favella* sp.)” is reported as the

Favella/Parundella morphotype. These changes concern nomenclature and spelling; they do not constitute re-identification of specimens or resolution of the ambiguous morphotype.

2.5. Statistical analysis

Analyses used the 12 observations in chronological order. Spearman rank correlations summarised the association between tidal height and each group total, and between tintinnid and dinoflagellate totals. Coefficients describe the direction and magnitude of monotonic association within this sequence. The analyses are exploratory, with one temporal sequence rather than replicated sampling of tidal regimes.

For comparison with an exchangeable-observation analysis, two-sided unrestricted permutation p-values were calculated from 100,000 label permutations, using (b + 1)/(100,000 + 1), where b is the number of absolute permuted coefficients at least as large as the observed value. Seeds were 20260729, 20260730 and 20260731 for tide–tintinnids, tide–dinoflagellates and tintinnids–dinoflagellates, respectively. Unrestricted shuffling destroys serial dependence and can overstate evidence in autocorrelated series (Yuan and Shou, 2024). A circular-shift sensitivity analysis therefore compared the observed absolute coefficient with all 12 rotations, including the unshifted alignment, of one series relative to the other. The reported circular-shift p-value is the proportion of rotations meeting or exceeding the observed absolute coefficient. Rotations retain cyclic order but join the endpoints; they do not guarantee a valid null model for a short, nonstationary record. The minimum possible value is 1/12 (0.083), so this analysis cannot attain $p < 0.05$. Lag-1 Pearson correlations described serial continuity.

Each of the eight nutrient series (four analytes at two depths) was compared with tidal height and the two group totals, yielding 24 descriptive Spearman associations and corresponding circular-shift values. Surface and near-bottom records are paired measurements from the same sequence, not independent temporal replicates. No confirmatory nutrient tests or multiplicity-adjusted significance claims were made. Calculations used Python, NumPy, pandas and SciPy. Input tables, calculation provenance, reproducible statistical code and figure code are supplied as supplementary material.

3. RESULTS

3.1. Environmental sequence

The fixed station retained a vertically structured water column throughout the sampling window (Fig. 1; Table 1). Surface salinity ranged from 28.4 to 32.6, whereas near-bottom salinity remained between 31.9 and 33.9. Bottom water was more saline at every observation, and the largest vertical difference occurred at 05:00, when surface and bottom salinity were 28.4 and 33.1, respectively. Surface temperature ranged from 24.2 to 25.4°C and increased during the final third of the sequence; bottom temperature varied within the narrower range of 24.1–24.6°C.

Surface chlorophyll a reached 0.0857 mg m^{-3} at 19:00 and was at or below 0.0231 mg m^{-3} thereafter. Near-bottom values ranged from 0 to 0.0298 mg m^{-3}. These are the recorded concentrations; zero

entries were not interpreted as proof of pigment absence because detection limits were unavailable. Surface suspended matter ranged from 0.0474 to 0.1376 g L^{-1} and peaked at 15:00, whereas near-bottom values ranged from 0.0378 to 0.1234 g L^{-1}.

Table 1
Descriptive summary of selected variables in the fixed-station sequence. Biological values are counts in the analysed 1-mL aliquot of net concentrate.

Variable	Depth	Unit	Minimum	Maximum	Mean	Time of maximum
Tidal height	—	m	0.20	1.60	0.90	01:00
Salinity	Surface	—	28.40	32.60	30.93	01:00
Salinity	Bottom	—	31.90	33.90	33.31	23:00
Temperature	Surface	°C	24.20	25.40	24.54	17:00
Temperature	Bottom	°C	24.10	24.60	24.34	19:00
Chlorophyll a	Surface	mg m^{-3}	0.0000	0.0857	0.0188	19:00
Suspended matter	Surface	g L^{-1}	0.0474	0.1376	0.0834	15:00
Tintinnids	—	counts $aliquot^{-1}$	95.0	717.0	368.4	03:00
Dinoflagellates	—	counts $aliquot^{-1}$	3.0	275.0	103.0	23:00

3.2. Nutrient phasing

All four nutrient records varied across the sequence (Fig. 2; Table 2). Surface NH_3 ranged from 52.29 to 167.05 µg L^{-1} and near-bottom NH_3 from 65.97 to 122.21 µg L^{-1}. NO_2 ranged from 13.87 to 31.91 µg L^{-1} at the surface and from 11.76 to 28.82 µg L^{-1} near the bottom. PO_4 ranged from 4.44 to 10.26 µg L^{-1} at the surface and from 3.04 to 10.61 µg L^{-1} near the bottom. TP ranged from 3.00 to 164.59 µg L^{-1} at the surface and from 12.23 to 148.43 µg L^{-1} near the bottom.

NO_2 and PO_4 generally increased as tidal height declined. The largest negative tide–nutrient coefficients were for near-bottom NO_2 (ρ = −0.935), near-bottom PO_4 (ρ = −0.869) and surface NO_2 (ρ = −0.795). The surface PO_4 coefficient was − 0.662. Surface and near-bottom NO_2 covaried negatively with dinoflagellate counts (ρ = −0.790 and − 0.748), as did near-bottom PO_4 (ρ = −0.790). Corresponding circular-shift values are reported in Table 2. These patterns describe concordant trajectories at two depths within the same sequence; they do not establish nutrient control of either plankton group.

NH_3 and TP had less consistent trajectories. Near-bottom TP was positively associated with tidal height (ρ = 0.641) and peaked at 07:00. Nutrient–tintinnid coefficients ranged from − 0.315 to 0.294. The smallest nutrient circular-shift value was 0.083, the minimum attainable with 12 rotations; none of these comparisons provides confirmatory evidence.

Table 2
Nutrient ranges and exploratory Spearman associations for 12 ordered observations. Association cells give ρ followed by the circular-shift p-value in parentheses. Analyte mass labels follow the laboratory record; they should not be used to infer nutrient stoichiometry.

Analyte	Depth	Range (μg L^{-1})	Tide ρ (p)	Tintinnids ρ (p)	Dinoflagellates ρ (p)
NH_3	Surface	52.29–167.05	-0.137 (0.750)	-0.116 (0.833)	0.179 (0.667)
NH_3	Bottom	65.97–122.21	-0.516 (0.167)	0.294 (0.417)	-0.154 (0.833)
NO_2	Surface	13.87–31.91	-0.795 (0.250)	0.217 (0.667)	-0.790 (0.083)
NO_2	Bottom	11.76–28.82	-0.935 (0.167)	0.259 (0.667)	-0.748 (0.083)
PO_4	Surface	4.44–10.26	-0.662 (0.167)	0.294 (0.333)	-0.420 (0.500)
PO_4	Bottom	3.04–10.61	-0.869 (0.250)	0.231 (0.667)	-0.790 (0.167)
TP	Surface	3.00–164.59	-0.084 (0.833)	-0.182 (0.667)	-0.105 (0.583)
TP	Bottom	12.23–148.43	0.641 (0.083)	-0.315 (0.333)	0.462 (0.417)

3.3. A *Tintinnopsis*-dominated tintinnid assemblage

Tintinnid totals ranged from 95 counts $aliquot^{-1}$ at 19:00 to 717 at 03:00, a 7.5-fold difference between aliquots separated by eight hours (Fig. 3A). *Tintinnopsis campanula* occurred in all 12 aliquots and contributed 4015 of 4421 pooled tintinnid counts (90.8%). Its maximum of 661 counts $aliquot^{-1}$ at 03:00 produced the principal group maximum, and it remained the largest contributor at subsequent observations with high tintinnid totals (Figs. 3B and 4A).

Tintinnopsis aperta reached 36 counts $aliquot^{-1}$ at 17:00, and *T. rotundata* reached 22 at 03:00. The *Favella/Parundella* morphotype occurred throughout the sequence, reached 22 counts $aliquot^{-1}$ at 19:00 and contributed 2.3% of pooled tintinnid counts. Ten other taxa made smaller contributions over the sequence. Their occurrence adds taxonomic detail to the dominance of *T. campanula*, without implying that all taxa persisted at every sampling time.

3.4. A high-water dinoflagellate pulse

Dinoflagellate totals ranged from 3 counts $aliquot^{-1}$ at 09:00 to 275 at 23:00, a 91.7-fold difference among the analysed aliquots (Fig. 3A). *Tripos hircus* occurred in every aliquot, contributed 614 of 1236

pooled dinoflagellate counts (49.7%) and reached 135 counts aliquot^{-1} at 23:00. *Protoperidinium* sp. also occurred throughout, contributed 38.6% of pooled dinoflagellate counts and reached 119 counts aliquot^{-1} at 23:00 (Figs. 3B and 4B). The dinoflagellate maximum therefore involved both dominant taxa and preceded the recorded tidal-height maximum by two hours.

Other *Tripos* taxa formed a smaller fraction of the sequence. *Pyrocystis pseudonoctiluca* occurred in nine aliquots and reached 12 counts aliquot^{-1} at 19:00. *Dinophysis caudata* was recorded at 19:00, 21:00, 01:00 and 17:00, with a maximum of 3 counts aliquot^{-1}. The four occurrences spanned both the early high-water phase and the final rising-tide observation.

3.5. Associations with recorded tidal height

Dinoflagellate counts were positively associated with tidal height (ρ = 0.750; Fig. 5B; Table 3). The unrestricted permutation p-value was 0.00699, whereas the circular-shift value was 0.250. Tidal height and dinoflagellate counts had positive lag-1 autocorrelations (r = 0.901 and 0.662). Thus, the large coefficient describes an association between serially structured records; the unrestricted permutation result is not evidence of independent replication or confirmation of tidal control.

Tintinnid counts had a weaker negative association with tidal height (ρ = −0.242; circular-shift p = 0.667; Fig. 5A). The tintinnid–dinoflagellate coefficient was also negative (ρ = −0.343; unrestricted p = 0.275; circular-shift p = 0.333). The group maxima were separated by four hours, but these coefficients do not establish antagonism or temporal niche partitioning.

Table 3
Spearman associations and randomization sensitivity analyses for one sequence of 12 ordered observations. Unrestricted permutations assume exchangeability, whereas circular shifts retain cyclic order. The circular-shift values have a lower bound of 0.083 and are descriptive sensitivity measures.

Association	n	Spearman ρ	Unrestricted p	Circular-shift p
Tidal height vs tintinnids	12	-0.242	0.4483	0.667
Tidal height vs dinoflagellates	12	0.750	0.0070	0.250
Tintinnids vs dinoflagellates	12	-0.343	0.2750	0.333

4. DISCUSSION

4.1. Plankton variability within one day

The Santos record documented contrasting temporal patterns in the net-sampled assemblage over less than one day. Dinoflagellate counts were highest at 23:00, two hours before the recorded high water, and both *Tripos hircus* and *Protoperidinium* sp. contributed to that maximum. Lower dinoflagellate counts later coincided with generally higher NO_2 and PO_4 concentrations. *Tintinnopsis campanula* dominated the

tintinnid counts throughout and peaked four hours after the dinoflagellate maximum. These are observed differences among aliquots. Assigning them to population growth, transport or trophic interactions requires additional measurements.

The timing contrasts illustrate the value of repeated sampling. Dinoflagellate counts in the 23:00 aliquot were more than 90 times those at 09:00, while tintinnid totals varied 7.5-fold. The magnitude of ambient population change cannot be estimated without volume calibration, but single-time net sampling would have yielded different descriptions of the retained assemblage. Automated observations elsewhere in Brazil have resolved tidal, diel and spring–neap periodicities over much longer records (Birocchi et al. 2026). Intensive field studies likewise document rapid plankton variability (Gu et al. 2022, Rodier et al. 2024). The present case provides a historical local example and a basis for testing recurrence across independently sampled cycles.

4.2. Dinoflagellates as a high-water assemblage

The positive dinoflagellate–height association is compatible with variation in water-mass contribution or retention within the channel. Near-bottom salinity exceeded surface salinity throughout, indicating persistent vertical hydrographic structure. However, the coincident maxima of the two dominant dinoflagellate taxa could reflect shared transport, vertical distribution or sampling efficiency. No current or transport measurements link those counts to import from Santos Bay. The coefficient of 0.750 is therefore an exploratory observation; neither its magnitude nor the unrestricted p-value demonstrates advection.

Regional studies provide plausible hydrodynamic explanations that can be tested at Santos. Phytoplankton composition in the Santos–São Vicente complex varies with tides, mixing and freshwater outflow (Moser et al. 2012). Tidal-cycle observations in Barra Grande Estuary documented changes in phytoplankton assemblages (Moser et al. 2017), while short-term plankton distributions in Babitonga Bay varied across the estuarine gradient (Nascimento et al. 2021). Dinoflagellate composition in the Paraguaçu Estuary also varied with environmental conditions (Nunes et al. 2023). These comparisons support a hydrodynamic hypothesis, but they do not identify the cause of the present count sequence.

Other studies distinguish nutrient supply from physical retention. Cruz et al. (2026) documented contrasting plankton responses to macrotidal pulses, and Wang et al. (2026b) showed in a coupled model of Xiamen Bay that physical export can outweigh biological production. Such mechanisms could contribute to temporal separation between nutrient and plankton maxima. Their relative importance at the Santos station remains unresolved because current velocity, vertical plankton distributions and production rates were not measured.

4.3. Persistence and dominance in the tintinnid assemblage

Tintinnids differed from dinoflagellates in their weaker association with recorded tidal height and their larger counts during several later observations. This pattern was dominated by *T. campanula*, which

occurred in every aliquot and contributed more than 90% of the pooled tintinnid counts. Its repeated occurrence establishes persistence in the sampled material, but does not demonstrate that the same local population remained at the station or grew there.

Dominance by *Tintinnopsis* is common in productive, salinity-variable coastal systems. Tropical estuaries in India and eutrophic waters of the Golden Horn show strong *Tintinnopsis* contributions linked to seasonal hydrography and food conditions (Rakshit et al. 2016a, 2017, Durmus et al. 2023, Sathish et al. 2024). Frequent sampling in Sendai Bay demonstrated that short-term tintinnid population change is species-specific and closely associated with physicochemical and food conditions (Kazama and Urabe, 2016). Along salinity gradients, assemblage identity may change sharply even when total abundance follows a more gradual trajectory (Li et al. 2019, Albergoli and Alder 2024). In Santos, the repeated dominance of *T. campanula* is consistent with its persistence in the net-sampled assemblage.

The *Favella/Parundella* morphotype and the later increase in *T. aperta* also contributed to temporal variation. At larger spatial scales, tintinnid composition differs among hydrographic domains (Yu et al. 2020, Li et al. 2021, 2023), and changes in water properties and diel conditions can alter ciliate assemblages (Wang et al. 2022a, 2022b, 2023, Li et al., 2024). These comparisons suggest several explanations for the Santos record. They cannot discriminate between local persistence and repeated delivery of similar assemblages.

4.4. Nutrient phase opposition

NO_2 and PO_4 concentrations generally increased during the falling-height portion at both sampled depths, while dinoflagellate counts were lower later in the record. Agreement between depths strengthens the descriptive pattern, but the paired measurements are not independent replication of tidal forcing. The inverse associations do not show that nutrients inhibited dinoflagellates or promoted tintinnids.

Temporal separation between nutrients and plankton maxima can arise when water-mass properties, light conditions, residence time and biological rates vary together. Macrotidal field observations and coupled modelling provide examples of this complexity (Cruz et al. 2026, Wang et al., 2026b). Estuarine plankton–environment relationships also vary with location and season (Parizzi et al. 2016, Mukherjee et al. 2018, Santos et al. 2022, El-Tohamy and Hopcroft 2024). At Santos, the observed sequence is compatible with changing water-mass contributions, but no nutrient-addition experiment, uptake measurement or water-mass tracer establishes nutrient limitation or its release.

NH_3 and TP had less consistent temporal patterns, including the near-bottom TP maximum at 07:00. Because analytical labels and mass units alone do not resolve nitrogen speciation or the phosphorus fractions measured, these trajectories should be compared within each analyte rather than used to calculate nutrient budgets or N:P ratios. They provide environmental context for the count sequence without identifying nutrient sources, bioavailability or causal pathways.

4.5. Temporal separation of tintinnids and dinoflagellates

The tintinnid and dinoflagellate maxima occurred four hours apart, but the negative group-level coefficient was modest (ρ = −0.343) and was not evidence of temporal niche separation. Different transport histories, diel behaviour, net retention and biological responses could all generate the observed offset. The dominance of a few taxa further limits interpretation of the group totals as uniform responses by all tintinnids or dinoflagellates.

Trophic processes remain plausible hypotheses. Ciliate feeding strategies can respond to phytoplankton composition (Haraguchi et al. 2018), tintinnid ingestion can depend on prey identity (Yang et al. 2019), and microzooplankton grazing varies on short time scales (Anderson et al. 2018; Anderson and Harvey 2019). Dinoflagellates also encompass different nutritional modes (Busch et al. 2019, Stoecker and Pierson 2019, Millette et al. 2021, Ladds et al. 2024). Nevertheless, co-occurrence patterns can arise through shared environmental responses (Trombetta et al. 2021, Liu et al. 2025). The present data contain no direct measurements of ingestion, prey availability, grazing mortality or growth that would distinguish these explanations.

The observed offset identifies specific taxa and time intervals for future process measurements. Replicated cycles combined with current profiles, prey-size spectra and grazing estimates could test whether *T. campanula* responds to a preceding prey field or follows a separate transport pathway. Consequences for other species remain an ecological hypothesis; they were not evaluated in this study.

4.6. Regional relevance and monitoring value

Monitoring in the Santos Estuary must account for an environment influenced by port activity, watershed inputs and natural circulation. The present sequence shows that sampling time can alter the composition and counts recorded in a net aliquot. It supports recording tidal height and time of day, standardizing collection effort, and distributing sampling across tidal and diel conditions. It does not establish a universally representative sampling phase or the recurrence of the observed pattern.

Tintinnids can contribute to monitoring because their morphology and environmental associations permit taxonomic comparisons across surveys (Sivasankar et al. 2018, Govindan et al. 2024). Recent studies connect tintinnid and ciliate composition with nutrient gradients and estuary–offshore transitions (Feng et al. 2025, Wang et al. 2026a, Liu et al., 2026). The repeated occurrence and dominance of *T. campanula* in these samples provide a historical taxonomic reference, provided that future comparisons account for gear, mesh size, preservation and counting effort.

Dinophysis caudata occurred in four aliquots, adding a historical occurrence record for a taxon relevant to regional surveillance. Toxigenic *Dinophysis* species have been documented in subtropical Brazilian estuaries (Tibiriçá et al. 2015). No toxin measurements or calibrated ambient densities are available here, so the observations cannot establish toxicity, bloom status or risk. Targeted water sampling and toxin analyses would be needed for those assessments.

4.7. Scope and limitations

This study describes 12 ordered observations from one 22-h sequence at a single station. Temporal autocorrelation, confounding of tidal phase with time of day, and the absence of independent cycle replication limit inference. Circular shifts enumerate possible alignments of the observed records, but their endpoint wrapping and coarse resolution do not solve the lack of replication. Non-significant shift values neither confirm a tidal mechanism nor demonstrate the absence of an association. Uncalibrated net sampling and the lack of replicate chambers further limit quantitative comparisons and uncertainty estimates.

The dissolved nutrient protocol specifies collection volume, filtration volume, pore size and shipboard filtration, but archived analytical detection limits and complete quality-control records were unavailable. Accordingly, nutrient and pigment concentrations are used as descriptive environmental measurements, with no inference from analytical zeros or calculated stoichiometric ratios. Repeated, volume-calibrated sampling across spring–neap and seasonal conditions, combined with current profiles and depth-resolved plankton samples, would allow the recurrence and physical basis of the count patterns to be tested. Replicate chamber counts, prey measurements and direct grazing assays would then address counting precision and trophic mechanisms.

5. CONCLUSIONS

Two-hour sampling documented substantial differences among tintinnid and dinoflagellate net-concentrate aliquots during a neap-tide sequence in the Santos Estuary. Dinoflagellate counts were highest before the recorded high water, while *Tintinnopsis campanula* dominated the tintinnids and peaked four hours later. Nitrite and phosphate generally increased during the falling-height interval. These observations establish a local historical sequence, with 7.5-fold and 91.7-fold count ranges for tintinnids and dinoflagellates, respectively.

The positive dinoflagellate–height coefficient and the contrasting nutrient trajectories generate hypotheses about hydrographic and biological processes. They do not establish causal tidal control, nutrient limitation, trophic interactions or general tidal periodicity. The practical implication is to combine frequent sampling with calibrated collection volumes and replication across tidal and diel conditions when evaluating estuarine plankton variability.

Declarations

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COMPETING INTERESTS

The authors declare that they have no competing financial or non-financial interests relevant to the content of this article.

AUTHOR CONTRIBUTIONS

All authors contributed to the study conception and design; Field sampling and laboratory analyses were performed by CCR and GAOM. The first draft of the manuscript was written by CCR, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

DATA AVAILABILITY

The environmental and biological tables, taxonomic summary, phosphate calculation provenance, statistical outputs, and executable statistical and figure code are provided in the Supplementary Information.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

Not applicable. This study involved planktonic protists and water-quality measurements and did not involve human participants or vertebrate animals.

CONSENT FOR PUBLICATION

All authors have reviewed the final manuscript and consent to its publication.

USE OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES

During the preparation of this manuscript, the authors used OpenAI Codex for language editing, data organization, and assistance in generating reproducible analysis and figure code. All outputs and the complete manuscript were critically reviewed and edited by the authors, who take full responsibility for the scientific content, accuracy, and integrity of the work.

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Figures

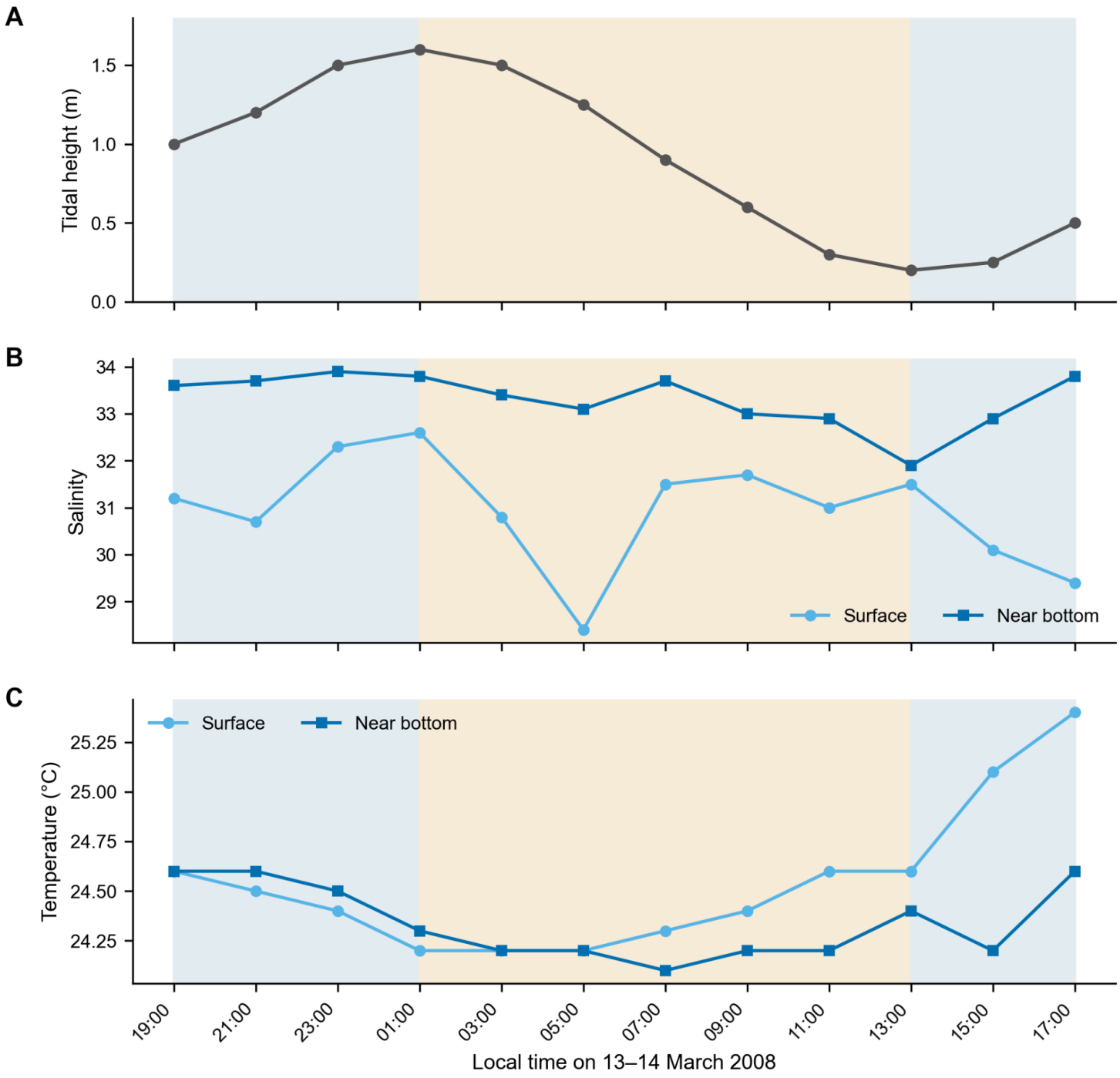

Figure 1

Recorded environmental variation during the fixed-station sequence. (A) Tidal height; (B) salinity; and (C) temperature. Surface measurements are light blue circles and near-bottom measurements dark blue squares. Grey distinguishes tidal height from the water-property series. Shading marks the rising-height intervals (blue) and falling-height interval (orange), bounded by the recorded maximum at 01:00 and minimum at 13:00. Shading does not specify current direction. Lines connect successive observations.

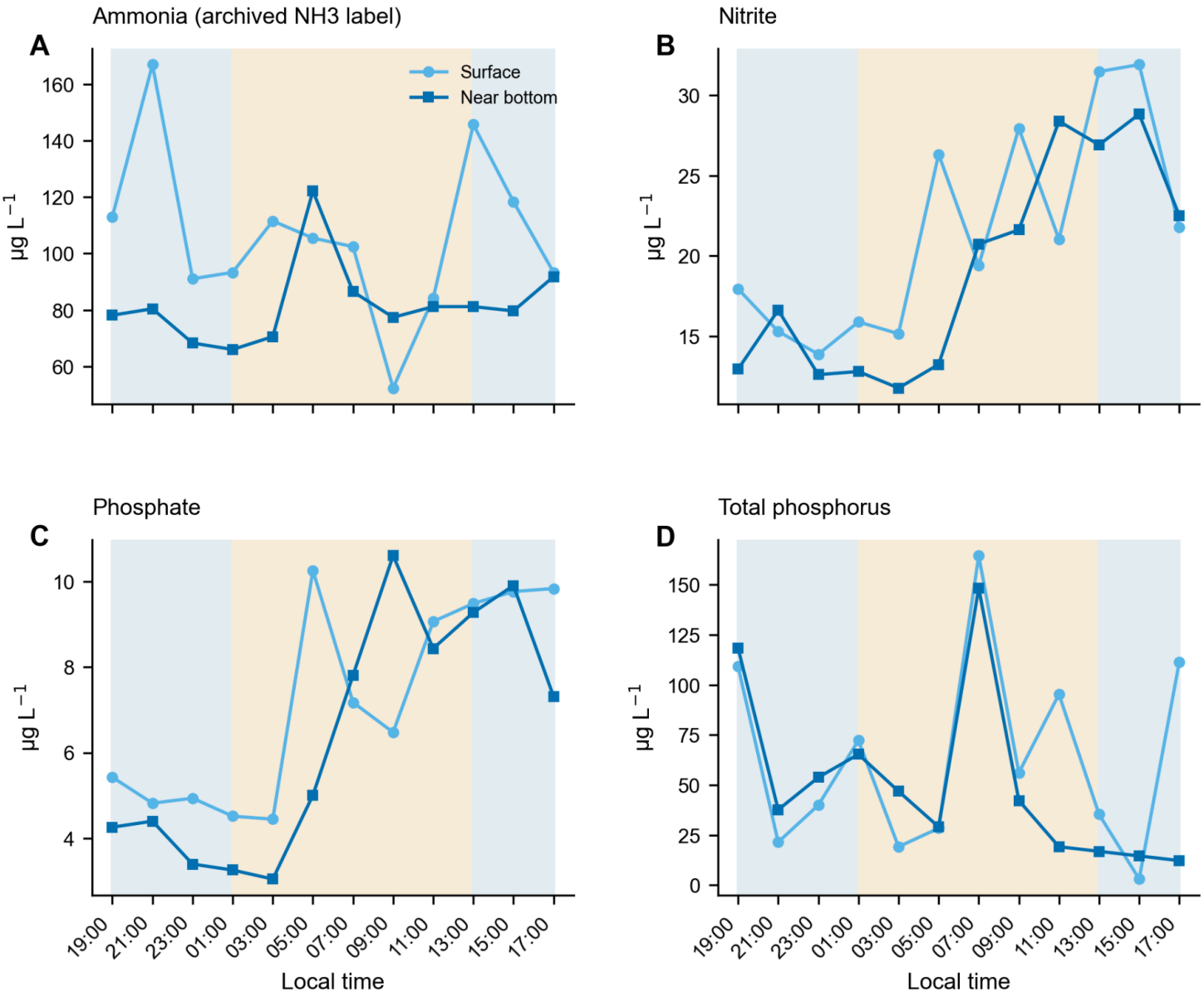

Figure 2

Nutrient concentrations at the surface (light blue circles) and near the bottom (dark blue squares). (A) Ammonia, retaining the archived NH_3 label; (B) nitrite; (C) phosphate; and (D) total phosphorus. Shading marks intervals of rising (blue) and falling (orange) recorded tidal height, as in Fig. 1. NH_3 is an analytical label and does not specify un-ionised ammonia.

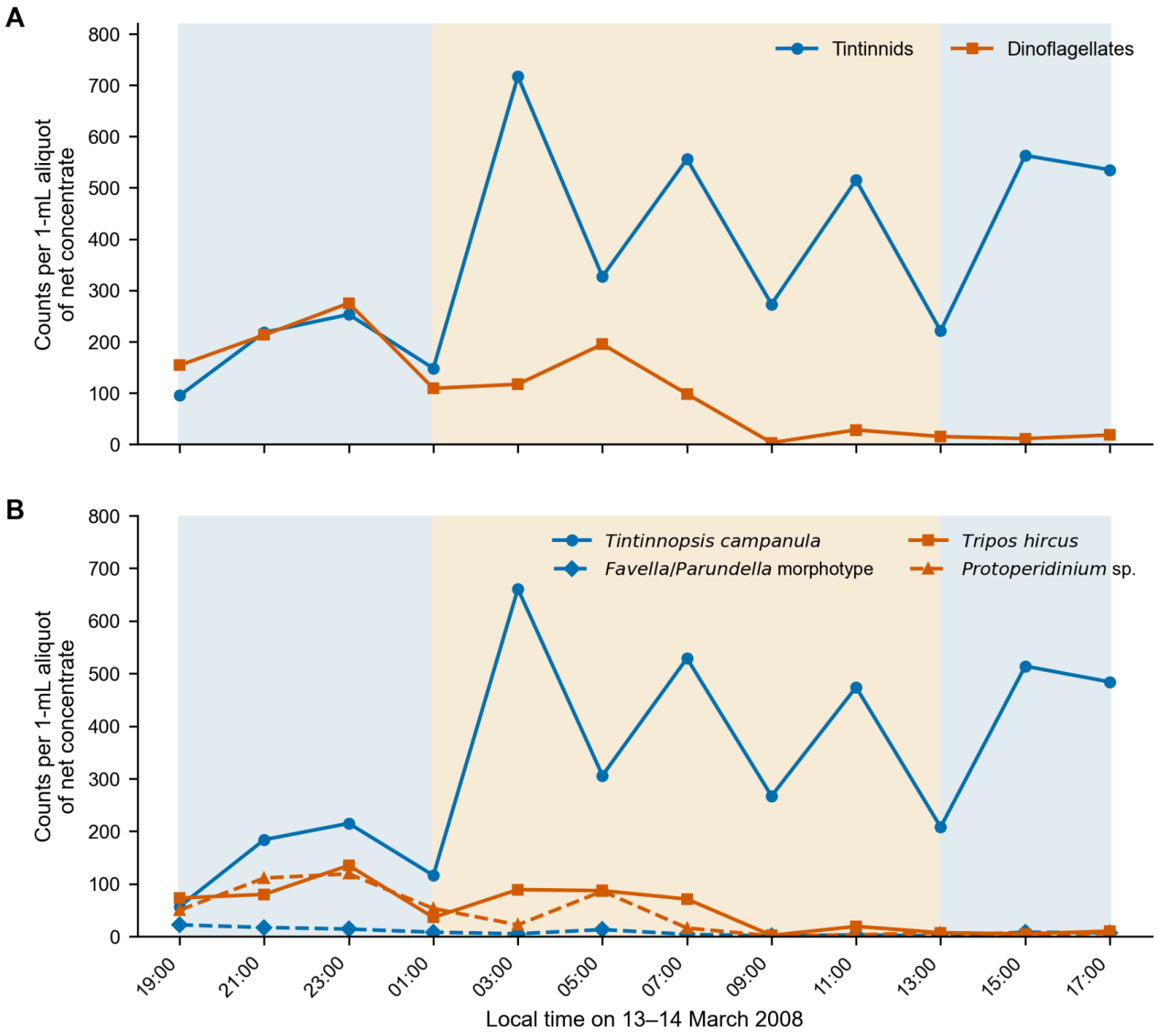

Figure 3

(A) Tintinnid and dinoflagellate totals and (B) dominant or focal taxa in the analysed 1-mL aliquots of net concentrate. Blue denotes tintinnids and orange dinoflagellates in both panels. In panel B, circles identify *Tintinnopsis campanula*, diamonds the *Favella/Parundella*morphotype, squares *Tripos hircus* and triangles *Protoperidinium* sp.; dashed lines distinguish the second taxon within each group. Shading follows Fig. 1. Counts are not ambient densities.

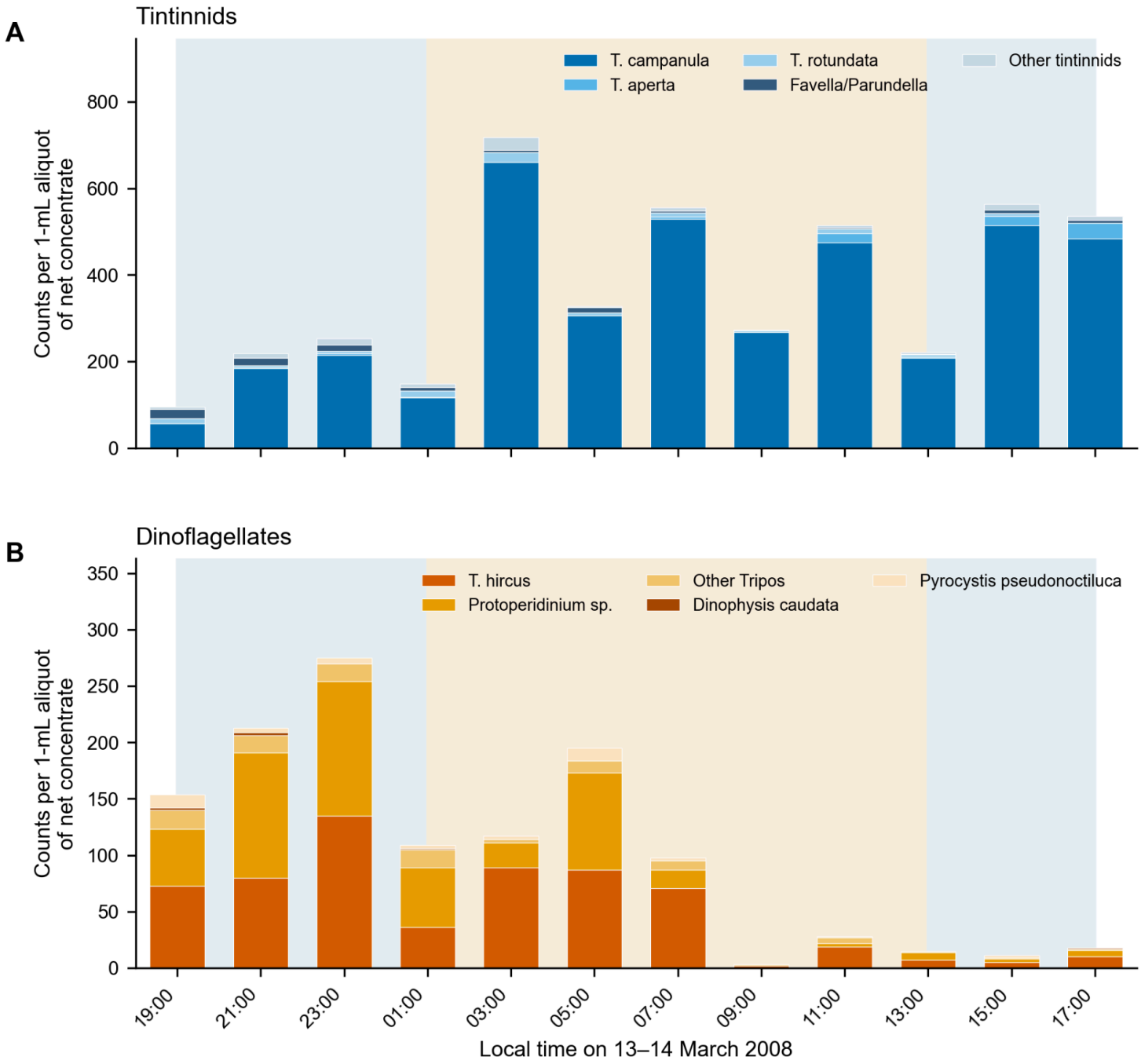

Figure 4

Taxonomic composition of the analysed net-concentrate aliquots. (A) Tintinnids, in shades of blue, and (B) dinoflagellates, in shades of orange. Bars show counts per 1-mL aliquot. Less abundant tintinnids are pooled as “Other tintinnids”, and less abundant *Tripos* taxa as “Other *Tripos*”; full counts are supplied in the supplementary data. Shading follows Fig. 1.

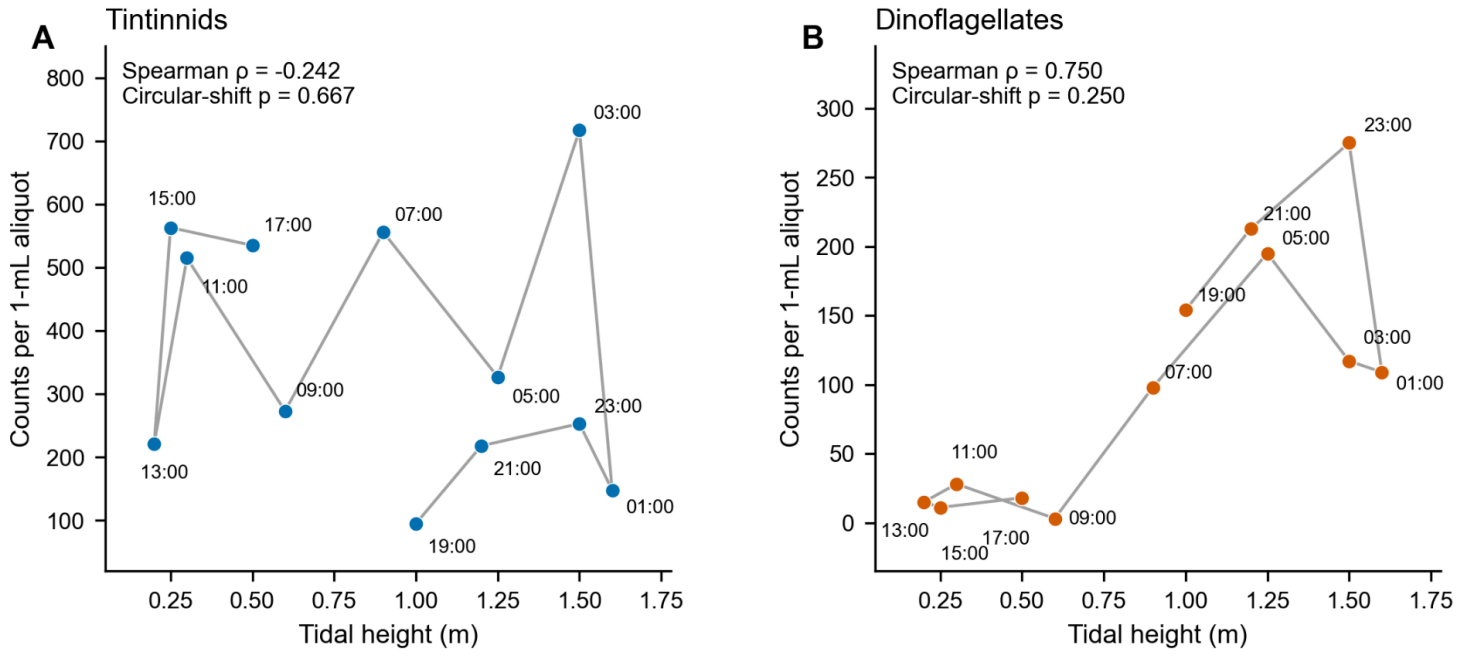

Figure 5

Recorded tidal height in relation to (A) tintinnid counts and (B) dinoflagellate counts. Points are labelled by local time and connected in sampling order. Blue denotes tintinnids and orange dinoflagellates. Spearman ρ describes the within-sequence association; circular-shift p-values summarize the 12 possible rotations and should not be interpreted as calibrated confirmatory tests for this short record.