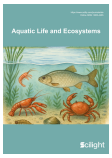
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Phytoplankton Dynamics in Contrasting Coastal Embayments of South Australia: Implications for Bivalve Aquaculture

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Abstract: This study investigated seasonal phytoplankton communities in two contrasting oyster-growing embayments, Coffin Bay and Franklin Harbour (Eyre Peninsula, South Australia), to assess how environmental conditions influence food availability across the full phytoplankton size spectrum. In both embayments, nutrient availability was a major driver of phytoplankton dynamics during summer, while seasonal changes in physical conditions coincided with a shift in the phytoplankton community from oligotrophic to mesotrophic assemblages. In Coffin Bay, the community was dominated by picoplankton (<2 µm), accounting for more than 50% of total biomass for over 8 months of the year. In contrast, Franklin Harbour was dominated by larger phytoplankton (>20 µm). Productivity in outer Coffin Bay was primarily supported by inflowing shelf waters, which sustained peak picoeukaryote biomass (44.27 µg C L^{-1}), and was further enhanced by a late-summer upwelling event in the eastern Great Australian Bight. However, productivity in Franklin Harbour was primarily generated internally, with the highest picoeukaryote biomass (68.15 µg C L^{-1}) in the southern end. This study provides new insights into phytoplankton dynamics across the full spectrum in two contrasting embayments. The findings demonstrate how variations across the phytoplankton size spectrum can inform assessments of coastal productivity and carrying capacity, with implications for the sustainable management of bivalve aquaculture in temperate coastal regions.

Keywords: phytoplankton community; seasonal pattern; picophytoplankton; food availability; oyster aquaculture

1. Introduction

Coastal ecosystems are among the most productive environments supporting a substantial proportion of global aquaculture production. Due to increased seafood demand, aquaculture has expanded rapidly and by 2014 already supplied approximately half of the world's seafood production, with filter feeders such as oysters, mussels and clams accounting for 30.8% of total farmed production [1]. Commercial bivalve production largely relies on natural food availability that is closely associated with primary production, nutrient cycling and trophic interactions within coastal ecosystems [2]. Meanwhile, nutrient inputs from rivers, run-off and episodic upwelling can also trigger rapid shifts in large phytoplankton biomass and community composition [3]. Therefore, understanding the ecological processes that regulate the availability and dynamics of these food resources is essential for maintaining ecosystem health, improving aquaculture productivity and supporting sustainable resource management [4–6].

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A key concept underpinning bivalve aquaculture is the ecosystem's carrying capacity, which requires accurate characterisation of food availability, primary productivity, species trophic dynamics, and the physical and oceanographic processes that regulate these factors across space and time [4,5,7]. Since oceanographic and biological conditions can vary remarkably over relatively small spatial and temporal scales [8–11], it can be challenging to estimate the carrying capacity in coastal environments. Bivalves acquire nutrition by filtering suspended particulate matter from the water column, including both organic and inorganic particles [12–16]. Although microphytoplankton (>20 μm) generally represent the dominant food source [17,18], bivalves can also effectively retain and assimilate nanoplankton (2–20 μm), picophytoplankton (<2 μm), and even virus-like particles (VLP) [17,19–21]. A comprehensive assessment of ecosystem productivity and carrying capacity should therefore consider the quantity, size structure and composition of suspended particulate matter.

Previous studies of coastal phytoplankton have focused primarily on larger taxa because conventional microscopy has limited capacity to identify the smaller planktonic organisms [22–24]. Moreover, many picophytoplankton lack distinctive morphological characteristics, further restricting taxonomic identification. As a result, the ecological significance of picoplankton communities has often been underestimated, even though they provide substantial contribution to primary production, particularly in oligotrophic marine environments [25,26]. Picoplankton communities typically comprise picophytoplankton like the cyanobacterial genera *Prochlorococcus* sp. and *Synechococcus* sp., together with diverse picoeukaryotes, virus-like particles (VLP) and heterotrophic bacteria [27–29]. These tiny microorganisms form fundamental components of microbial food webs, nutrient regeneration and biogeochemical cycling, thereby influencing ecosystem productivity across different spatial and temporal scales [30–32]. Therefore, to incorporate these microbial size classes into ecological assessments is critical for accurately estimating primary productivity and developing realistic carrying-capacity models for coastal ecosystems.

In South Australia (SA), the Pacific oyster *Crassostrea gigas* is the major cultivated bivalve species, with aquaculture areas extending from the Eyre Peninsula to Kangaroo Island along the extensive mid-latitude continental shelf [33,34]. Although surface waters across this region are generally characterised by relatively low primary productivity, intermittent upwelling and nutrient-enrichment events can enhance local phytoplankton production [35,36]. In Spencer Gulf and Gulf St Vincent, seasonal circulation is characterized by density-driven outflows during summer and inflows of shelf waters during winter [37–39]. This results in pronounced temporal variability in nutrient availability and biological productivity, influencing the quantity and composition of food resources available to suspension-feeding bivalves [25,40]. Despite the economic importance of oyster aquaculture in SA, ecological datasets describing phytoplankton community structure, nutrient dynamics and hydrodynamic variability remain limited for many oyster-growing embayments [41–45], including the major oyster-growing areas in Coffin Bay and Franklin Harbour.

Coffin Bay consists of several shallow and interconnected bays that are separated from shelf waters by a spit of land forming a narrow channel for water exchange between the inner Port Douglas Bay and the eastern Great Australian Bight (GAB) [46]. Franklin Harbour consists of two interconnected bays that are joined to the upper Spencer Gulf by a narrow channel characterised by strong tidal currents and efficient seasonal mixing [47]. Previous studies have shown that pico- and nanoplankton contribute substantially to estuarine food webs in Coffin Bay [36], while episodic upwelling from the eastern GAB enhances nutrient availability and phytoplankton productivity [48]. However, the annual succession of phytoplankton communities, particularly the dynamics of picophytoplankton and associated microbial components, has not been studied in detail. There is also limited ecological information for Franklin Harbour, despite its contrasting nutrient regime and environmental conditions. Together, these two contrasting embayments provide an ideal natural system for investigating how environmental variability shapes phytoplankton communities within South Australia's oyster-growing ecosystems.

Therefore, this study was conducted over a complete annual cycle with monthly sampling of phytoplankton dynamics in Coffin Bay and Franklin Harbour. Flow cytometry was combined with conventional environmental measurements to quantify the full phytoplankton size spectrum and associated microbial communities. The aims of the research were to (1) identify the environmental variables driving picoplankton dynamics; (2) determine temporal and spatial variation in phytoplankton community structure and food webs; and (3) evaluate the available food sources of full spectrums in the ecosystem with great potentials for local bivalve aquaculture.

2. Materials and Methods

2.1. Study Areas

Coffin Bay is an inverse estuary located at the southern tip of the Eyre Peninsula, South Australia (Figure 1a). Commercial oyster aquaculture zones are located within Port Douglas Bay on both the eastern and western sides of the main flow channel on shallow, sandy bottom with sparse seagrass meadows.

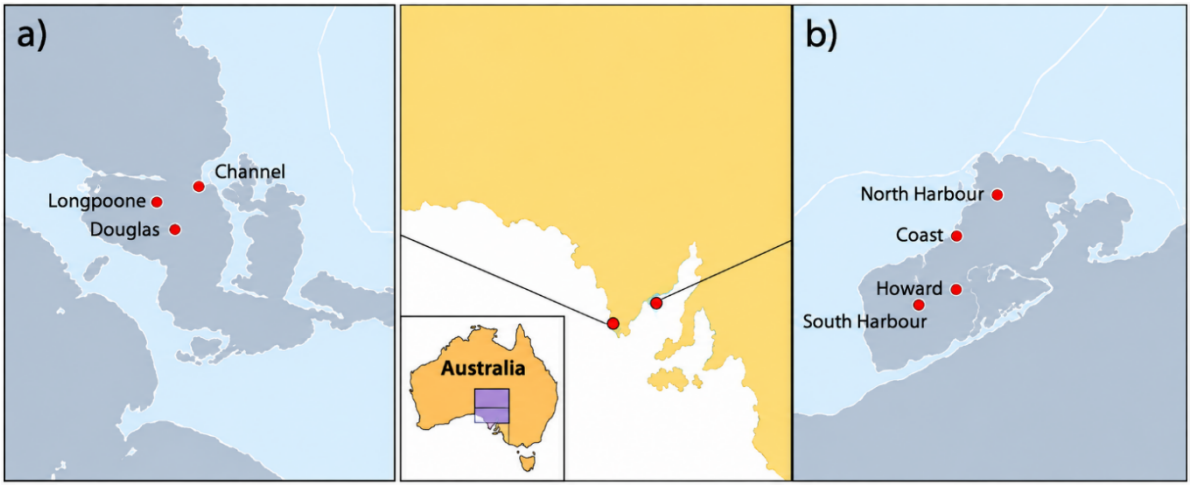


Figure 1. The study sites in (**a**) Coffin Bay: the sites of Douglas (34°33′27.79″ S, 135°21′40.90″ E) and Longnose (34°32′21.48″ S, 135°20′48.16″ E) were located within the oyster farming zone, and the Mouth site (34°31′46.78″ S, 135°22′28.74″ E) was located in the deepest area of the narrowest part of the connecting channel between Port Douglas Bay and the eastern GAB; and (**b**) Franklin Harbour: the North Harbour site (33°41′35.66″ S, 136°56′46.10″ E), and South Harbour site (33°44′52.44″ S, 136°53′57.95″ E) were located in the northern and middle of the southern bay. The Coast site (33°42′49.14″ S, 136°55′3.36″ E) and the Howard site (33°44′28.50″ S, 136°55′3.68″ E) were within the oyster aquaculture zone.

Franklin Harbour is a smaller inverse estuary located on the eastern side of the Eyre Peninsula (Figure 1b) with coastal wetlands of national significance [49]. The bay is bordered by extensive mangrove habitats, especially around the entrance to the harbour and a substantial portion of the water entering the southern bay passes through the mangrove mudflats. Commercial oyster aquaculture zones are located on the shallow edges of the southern bay on a range of sandy-bottom and seagrass meadows.

Sampling at each site was conducted monthly from April 2017 to April 2018. Water samples were collected from a depth of >1 m or from the middle of the remaining water column in the event of low tide. Water was pumped into three 5 L dark bottles and kept cool and dark until sub-sampling in the laboratory. Temperature and dissolved oxygen (DO) data were collected at each site using an OxyGuard Handy Polaris 2 and salinity was sampled using a WTW pH/Cond 340i.

2.2. Nutrient Measurement

Triplicate 100 mL subsamples of water were collected from separate composite sample bottles, pre-filtered through 0.45 µm (Minisart RC, Sartorius, Göttingen, Germany) using a bonnet syringe, and then stored at −20 °C until further analysis. Nitrate and nitrite (NO_X^-), ammonium (NH_4^+) and silicate (SiO_2) were measured using flow injection analysis in a QuikChem QC8500 Automated Ion Analyser (Lachat Instruments, Loveland, CO, USA) using the Lachat method 31-107-04-1-D, 31-107-06-1-B, 31-115-01-1-G and 31-114-27-1-A, respectively. Detection limits were 0.071 µM for NO_X^- and NH_4^+ and 0.33 µM for SiO_2.

2.3. Particulate Matter Determination

Triplicate 2 L sub-samples of water were filtered through pre-combusted (450 °C for 4 h) and pre-weighed glass-fibre filters (Whatman GF/F), rinsed with 60 mL milli-Q water, and stored at −20 °C. Total particulate organic matter (POM) was determined gravimetrically by drying the filters for 48 h and weighing them, followed by combustion at 450 °C for 4 h and reweighing.

2.4. Pigment Analysis

The concentrations of chlorophyll *a* (*Chl a*) and accessory pigments in water samples were analysed using high-performance liquid chromatography (HPLC, Agilent 1200), but only for the samples collected from the Douglas site in Coffin Bay and the Howard site in Franklin Harbour. One 2 L sub-sample of water was filtered as above, and the wrapped filters were frozen in liquid nitrogen and stored at −80 °C. Samples were analysed using the gradient elution procedure [50] on an HPLC. The analytical assessments were conducted in the environmental chemistry laboratory at South Australian Research and Development Institute (SARDI). The derived pigment data

were used for analysing phytoplankton community with size structure into three size classes: microplankton (>20 μm), nanoplankton (2–20 μm) and picoplankton (<2 μm) [51].

2.5. Picoplankton Analysis

In order to improve the size class estimation, flow cytometric analysis (FACS-Canto II, Becton Dickinson with a 488 nm laser) was employed to identify picoeukaryotes, picophytoplankton, VLPs and bacteria in three replicate 1 mL sub-samples of seawater. The samples were subsequently fixed with glutaraldehyde (electron microscopy grade) at final concentrations of 0.5% and 0.25%. All samples were fixed in the dark for 15 min, then frozen in liquid nitrogen and stored at −80 °C. Then, these samples were thawed at 37 °C, diluted 10-fold in Tris EDTA (pH = 8.0, Sigma-Aldrich), stained with SYBR Green I (a 0.5×10^{-4} dilution of commercial stock, Molecular Probes) in the dark at 80 °C for 10 min [52]. For picoeukaryotes, VLP's and bacteria analyses, 0.75 μm fluorescent beads (Molecular Probes) were added as an internal standard, whereas 1 μm beads (Molecular Probes) were used for picophytoplankton assessment. FACS acquisition was run for 2 min at a flow rate of 30 μL min^{-1} for VLP's and bacteria analyses, but it was run for 3 min at a flow rate of 60 μL min^{-1} for picophytoplankton readings. Picophytoplankton groups were discriminated into cyanobacteria groups of *Prochlorococcus* sp. and *Synechococcus* sp., and picoeukaryotes with two size groups of P1 and P2, based on red and orange autofluorescence of chlorophyll, the pigment phycoerythrin, and light scatter properties of side-angle light scatter (SSC) and forward-angle light scatter. Bacteria and viruses were separated on plots of SSC and green (SYBR I) fluorescence and SSC and red (chlorophyll *a*) fluorescence [53].

To quantify the carbon biomass of these picoplankton groups, the average cell sizes of *Prochlorococcus*, *Synechococcus* and picoeukaryotes were assumed to be 0.7, 0.9 and 2.0 μm respectively [28]. Carbon conversion factor of 34, 76 and 1000 fg C $cell^{-1}$ were applied to the respective picophytoplankton groups based on previous literature [54]. However, for non-photosynthetic picoplankton, an approximate carbon conversion of 0.2 fg C $cell^{-1}$ was used for VLP [55], and a conversion of 12 fg C $cell^{-1}$ was applied to bacteria [30].

2.6. Statistical Analysis

Results were expressed as mean ± standard deviation (SD). Variables were analysed using a two-way ANOVA with two factors (sites and months). Where a significant effect of site, month and/or the interaction was observed, main effects were compared monthly. Picoplankton group relationships to each other and the environmental variables were further analysed using Pearson's correlation coefficient. ANOVA and correlation analyses were conducted in IBM SPSS Statistics 20. The relationship between picoplankton and the environmental variables was further explored in the Primer + PERMANOVA v6 software package (Primer-E, Plymouth, UK). Picoplankton biomass results were log10(x + 1) transformed and compared to the normalised environmental variables using a stepwise distance-based linear model (DistLM). A distance-based redundancy analysis was also conducted to visualise the relationships across the study period. The significance value for all tests was set at $p < 0.05$.

3. Results

3.1. Physicochemical Variation

3.1.1. Coffin Bay

Water temperatures at Coffin Bay sites ranged from 11.9 to 24.1 °C during the study period, reflecting a typical pattern of seasonal variation in SA (Figure 2a). These temperatures were largely consistent between the sites within Coffin Bay. DO was in the range of 6.4–8.8 mg L^{-1}, and the peak value was observed in May at the Mouth and Douglas sites (Figure 2a, $p < 0.01$). And then DO was slowly declining through spring and summer but increased in March, when the Longnose site had a higher level ($p < 0.01$). Salinity increased from September through the summer months. The highest salinity level was detected in February and April at 38.7 at the Douglas site (Figure 2a). POM was significantly higher at the Mouth site in May ($p < 0.01$), reaching the top level of 12.1 mg L^{-1}. After this, there was no difference between sites over the year, with POM concentrations of 1.9–4.0 mg L^{-1} in the water, but the lowest concentration was detected in February (Figure 2a).

NH_4^+ fluctuated in Coffin Bay from 0.05 to 1.21 μM over the year, but the top level was recorded at the Douglas site in February (Figure 3a). In the comparison with Longnose and the Mouth sites, the Douglas site had higher NH_4^+ levels in April 2017, June, December and February ($p < 0.05$). The concentration of NO_X^- experienced large fluctuations, showing the lowest level close to 0.1 μM at all sites in September and then increasing to different degrees across three sites. The higher levels of NO_X^- were detected at Longnose in May and March, and at Douglas in May ($p < 0.01$). There was also a fluctuation in SiO_2 concentration among the three

sites. The peak level was detected at Douglas with 4.4 μM in January, above the concurrent values at the Mouth and Longnose sites ($p < 0.01$). However, the lowest values (0–0.5 μM) were also recorded at Douglas between September and December, below the values at the other two sites ($p < 0.05$). In May, Longnose had a higher SiO_2 concentration than both Douglas and the Mouth ($p < 0.05$).

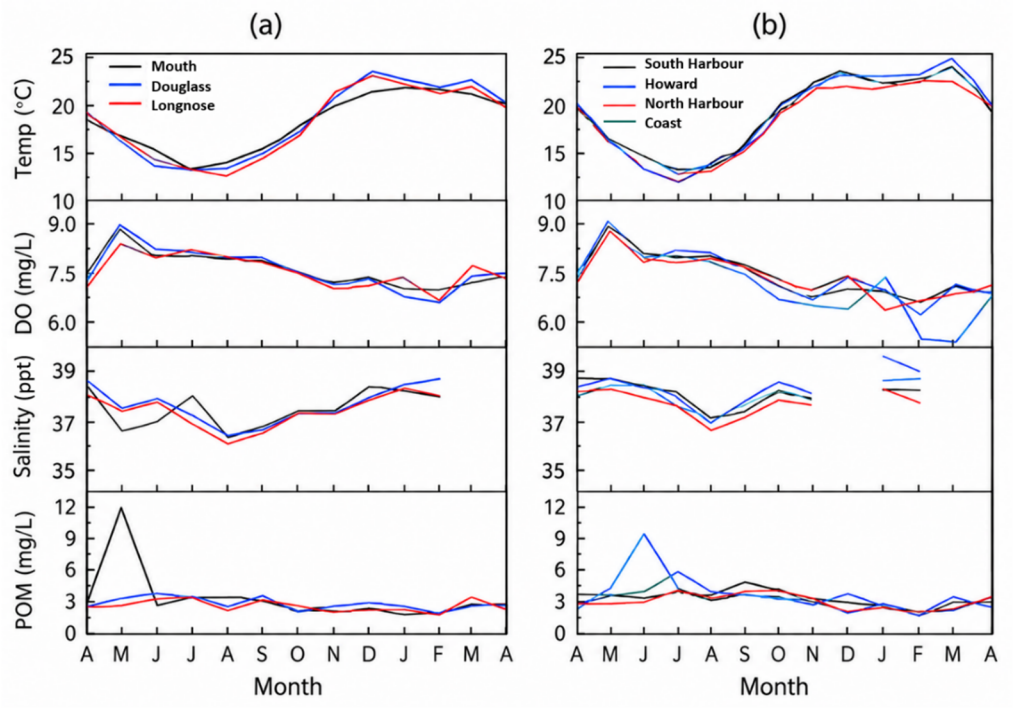


Figure 2. Mean physical properties of temperature (Temp °C), dissolved oxygen (DO mg L^{-1}), salinity and particulate organic matter (POM, mg L^{-1}) detected in **(a)** Coffin Bay and **(b)** Franklin Harbour during the study period.

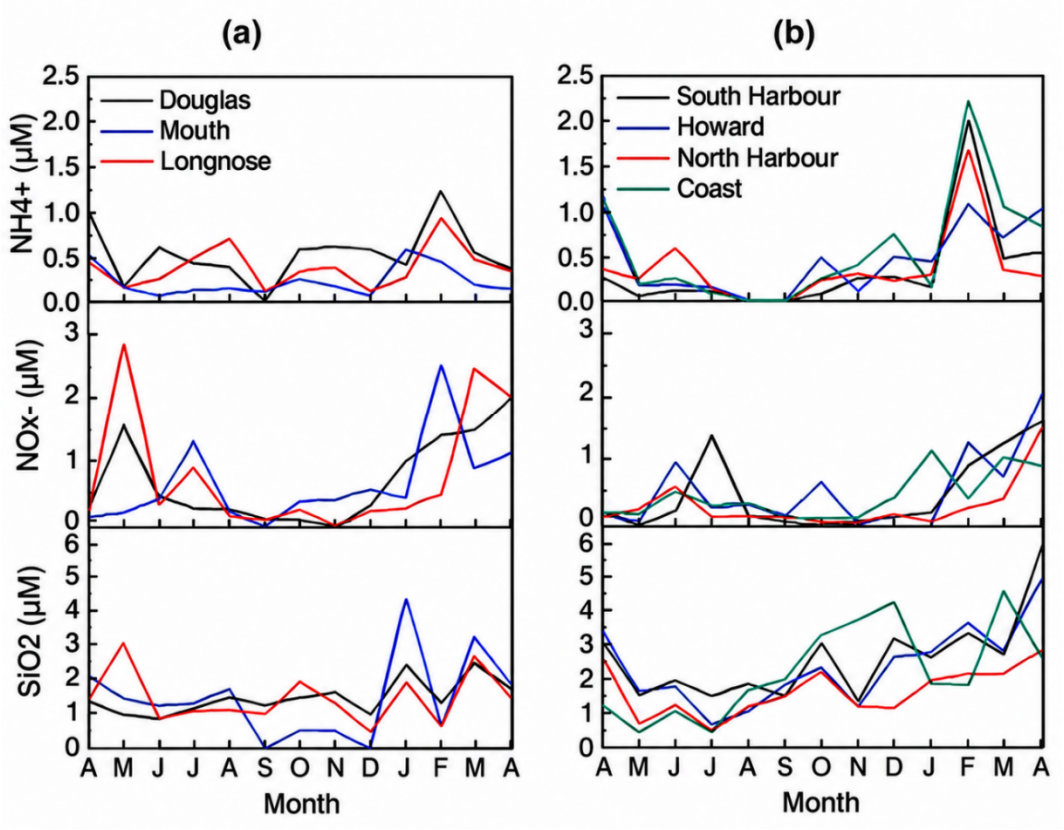


Figure 3. Mean values of ammonium (NH_4^+), nitrate + nitrite (NO_X^-) and silicate (SiO_2) in **(a)** Coffin Bay and **(b)** Franklin Harbour over a year.

Although *Chl a* was detected only at the Douglas site, it showed substantial variation over the year (Figure 4a). Overall, it was maintained between 0.11 and 0.82 μg L^{-1} most of the time, but peaked at 1.5 μg L^{-1} in February. Based on the pigment assessment, the phytoplankton community was dominated by pico- sized cells for most of the year (Figure 5a). Likely, a bloom of nanoplankton occurred in June and September, while microplankton cells dominated in February.

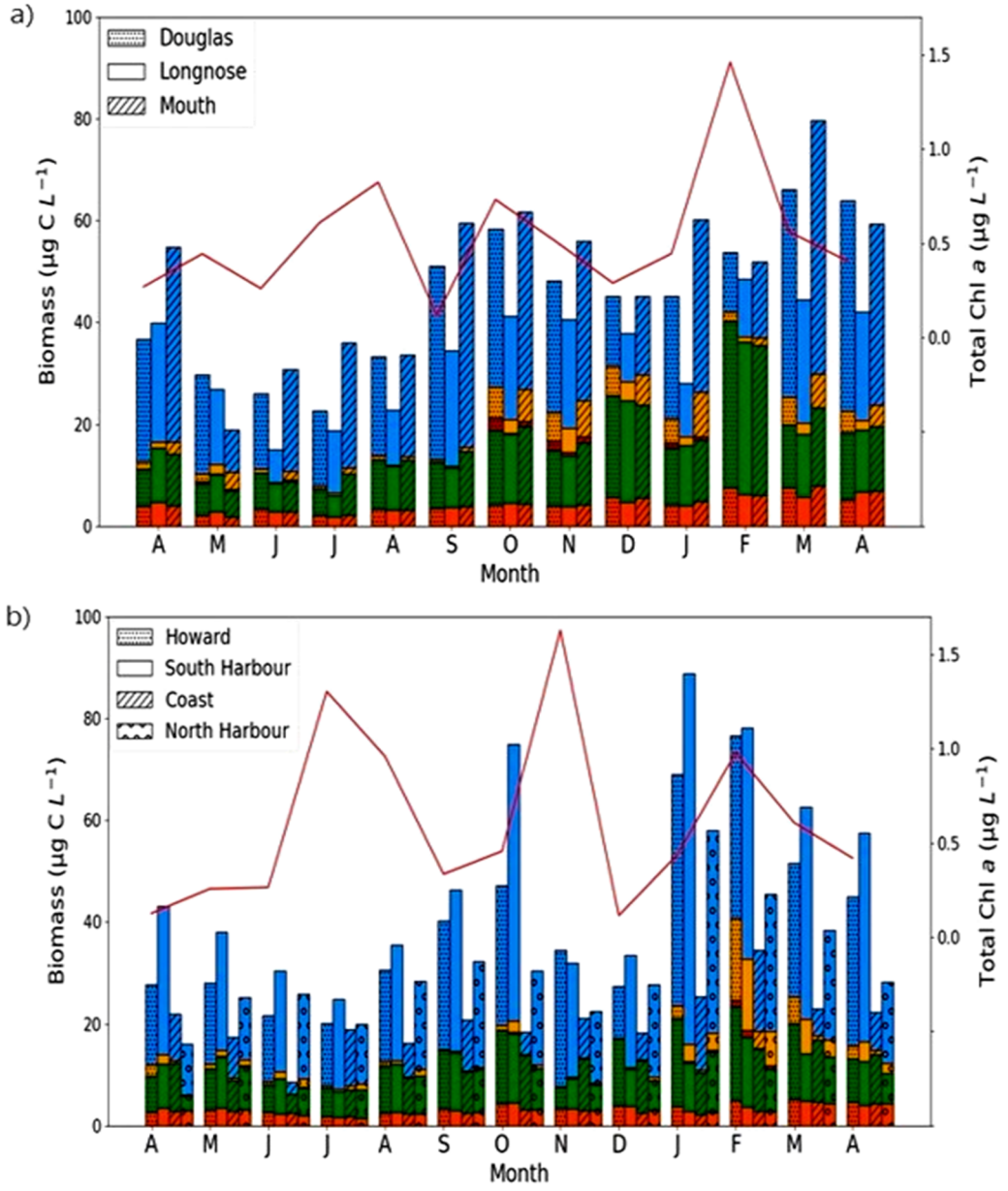


Figure 4. Mean contributions of picoplankton biomass and total chlorophyll *a* concentration (red line) in (**a**) Coffin Bay and (**b**) Franklin Harbour. On bars: virus-like particles (VLP, orange), Bacteria (green), *Prochlorococcus* sp. (dark red), *Synechococcus* sp. (yellow) and picoeukaryotes (blue).

3.1.2. Franklin Harbour

The water temperature in Franklin Harbour showed a seasonal pattern between 11.0 and 25.7 °C across the year (Figure 2b). And the temperature was similar across four sites. Salinity ranged from 36.6 to 39.7 ppt throughout the year. The level of DO was consistent between sites, showing an increase from April 2017 to a maximum value of 8.9 mg L^{-1} in May. And then the values decreased through the year, and lowest readings were recorded at the Coast in February and March 2018 which was less than at the other sites ($p < 0.01$). The remaining salinity data showed that the North Harbour has significantly lower salinity than the South Harbour and Howard sites ($p < 0.05$) and lower than the Coast in all months except April and July 2017. POM was relatively stable

across the four sites after August, with a relatively low level of 1.6 mg L^{-1} in February. There was a fluctuation of POM at the Coast site, exhibiting a significant increase to the highest level of 9.9 mg L^{-1} in June (Figure 2b, $p < 0.01$).

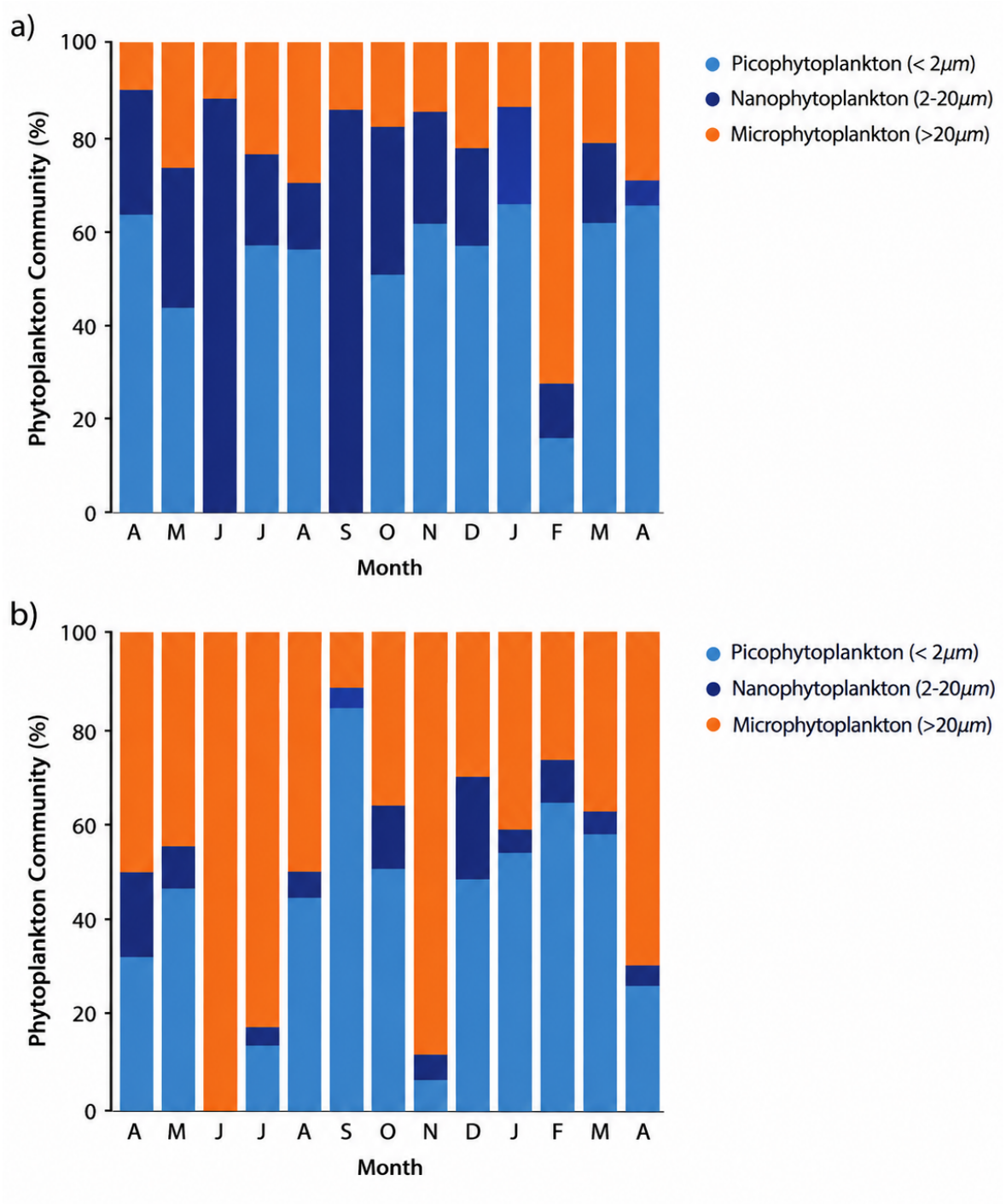


Figure 5. Proportion of phytoplankton size fractions in (**a**) Coffin Bay and (**b**) Franklin Harbour over the study period.

NH_4^+ values showed a similar pattern to Coffin Bay, but with a slightly higher range of 0.07 to 2.1 µM (Figure 3b). The peak level was recorded at the Coast and South Harbour sites in February. The concentration of NO_X^- fluctuated from 0.02 to 2.0 µM with a general increasing trend from summer to autumn. There was also a significant fluctuation in SiO_2. SiO_2 was higher at the sites of Howard and South Harbour between April and June in 2017 ($p < 0.01$). The Coast site had lower SiO_2 initially, but picked up and exceeded other sites around November. The South Harbour and Howard sites recorded the maximum values in April 2018 of 5.8 µM and 4.9 µM respectively.

The *Chl a* was detected at the Howard site only, increasing from 0.17 to 1.3 µg L^{-1} from April to July in 2017 (Figure 4b). It started decreasing after July and stabilising through September to October and then reaching a maximum level of 1.6 µg L^{-1} in November. In the pigment assessment, the percentage of the phytoplankton community >20 µm

remained >50% until August 2017, when an increase in picoplankton was observed (Figure 5b). There was an increase in the proportion of larger phytoplankton in November but picophytoplankton became dominant afterwards.

3.2. Structure of Picoplankton Biomass

In this study, four groups were identified in the picoplankton community: picoeukaryotes, cyanobacteria, marine bacteria and VLP.

3.2.1. Picoeukaryotes

The picoeukaryotes were divided into two size classes: smaller picoeukaryotes (P1) and larger picoeukaryotes (P2) (Figure 6).

In Coffin Bay, biomass was significantly different among sites ($p < 0.05$), but all sites exhibited a similar pattern (Figure 6a). P1 biomass ranged from 5.02 to 44.27 µg C L^{-1} over the study period, dominating the total picoeukaryote biomass over the year. The Douglas site closely followed the pattern in the Mouth with a decrease in biomass over winter and then an increase in spring. After February, all sites experienced a sharp increase in P1 biomass in April 2018. Longnose exhibited a similar pattern in P1 biomass but at a lower magnitude than at the Douglas site. This relationship between sites was consistent with the P2 class, albeit at a lower range of 0.76–8.18 µg C L^{-1}. At the Mouth site, P2 increased twice in July and September in 2017. P2 recorded lower values in late spring and into summer, peaking again in February (Figure 6b).

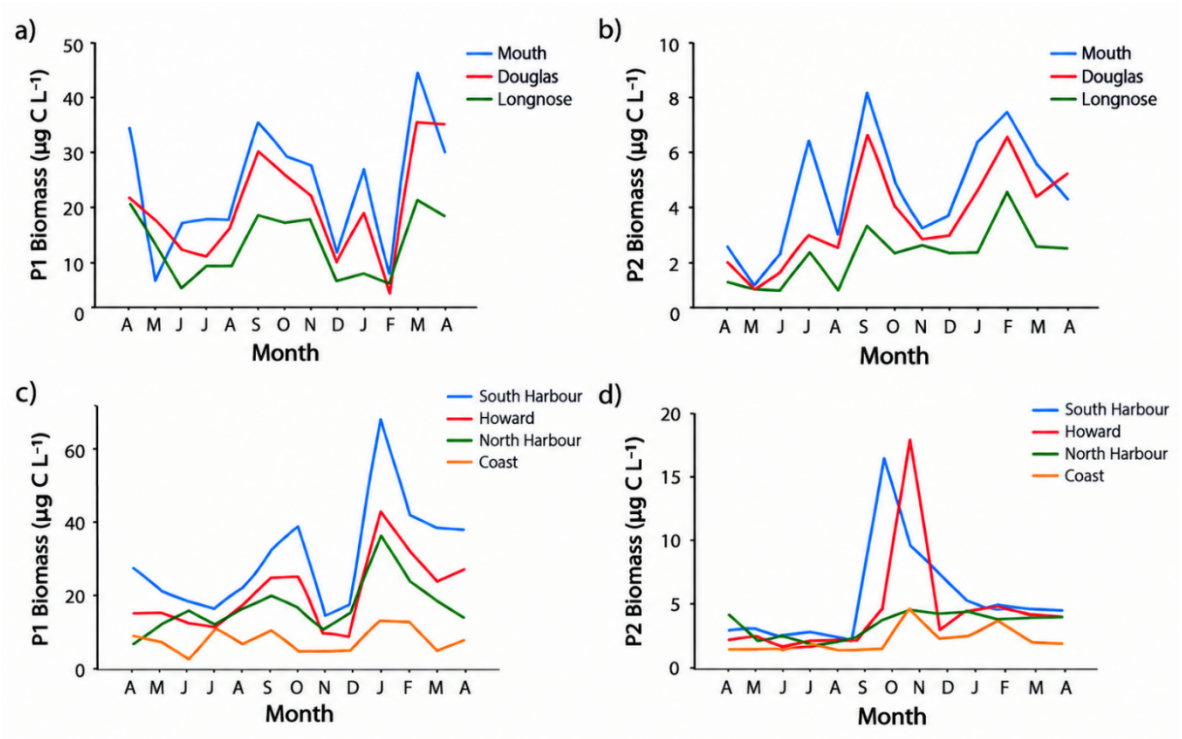


Figure 6. Picoeukaryote biomass of two differentiated size classes (**a**) P1 and (**b**) P2 in Coffin Bay; and (**c**) P1 and (**d**) P2 in Franklin Harbour over the study period. Flow cytometry analysis, mean value.

In Franklin Harbour, there was also a significantly different biomass pattern at each site ($p < 0.05$), which was largely recorded in the P1 size fraction where the South Harbour site experienced the highest P1 biomass followed by similar patterns at the Howard and North Harbour sites with lower biomasses at the Coast (Figure 6c). P1 biomass again dominated the overall picoeukaryote biomass, ranging from 3.89 to 68.15 µg C L^{-1} throughout the study period. The Coast site had the lowest P1 biomass, with only moderate increases in the summer months. Biomass increased at all other sites in the spring months from stable levels over the winter period. P2 biomass ranged from 3.49 to 17.50 µg C L^{-1}. A peak at the other sites was reached in October, then decreased sharply in November and December (Figure 6d). At the Howard site, the maximum value was recorded in November, with a similar peak in biomass in the South Harbour in October. Overall P2 biomass was slightly elevated in summer compared to winter.

3.2.2. Cyanobacteria—*Synechococcus* sp. and *Prochlorococcus* sp.

In Coffin Bay, *Synechococcus* sp. biomass ranged from 0.25 to 8.69 μg C L^{-1} throughout the study period (Figure 4a), and biomass differed significantly among sites ($p < 0.05$). During autumn and winter, the Mouth had significantly higher values than the other two sites ($p < 0.05$). From September onward, the Mouth and Douglas sites followed the same pattern. The Longnose site exhibited a similar pattern, albeit at a lower magnitude ($p < 0.05$) from 0.25 to 4.79 μg C L^{-1}. In contrast, *Prochlorococcus* sp. biomass was not consistently present in Coffin Bay. Biomass was higher in the Mouth than at the aquaculture zone sites, and it increased slightly in May and continued the trend in June ($p < 0.05$). In spring, all sites experienced an increase in biomass to a maximum level of 1.14 μg C L^{-1}, which then declined in December and reappeared in January at the Mouth and Douglas sites.

In Franklin Harbour, neither *Synechococcus* sp. nor *Prochlorococcus* sp. was not present at substantial abundance in this study (Figure 4b). *Synechococcus* sp. biomass ranged from 0.06 to 16.07 μg C L^{-1} remaining very low at all sites until January, and it increased to a maximum of >14 μg C L^{-1} in February at the South Harbour and Howard sites. The same pattern to a lesser magnitude was observed at the North Harbour and Coast sites and *Synechococcus* sp. biomass appeared more at all sites through March and April 2018. The *Prochlorococcus* sp. biomass was low in May and June at both Harbour sites and at the South Harbour in October. A maximum biomass of >1.4 μg C L^{-1} was recorded at the South Harbour and Howard sites in February, following an increase at all sites similar to the pattern observed in *Synechococcus* sp. It had disappeared by March.

3.2.3. Marine Bacteria

In Coffin Bay, no significant difference in bacterial biomass was observed between sites ($p > 0.05$, Figure 4a). The lowest biomass (<4.5 μg C L^{-1}) was recorded in July, then increased through spring and summer. Bacterial biomass reached a maximum value of 32.62 μg C L^{-1} in February and then rapidly decreased in autumn.

However, in Franklin Harbour, there was a significant difference between sites ($p < 0.05$) despite lower biomasses (Figure 4b). From August to October, higher bacterial biomasses were observed at the South Harbour and Howard sites. In November, bacterial biomass was low at all sites except the Coast. Bacterial biomass remained consistent over the spring-summer period with a small peak in February-March. All other sites experienced increases in bacterial abundance in summer, with the most significant value at the Howard site reaching >18 μg C L^{-1} in February.

3.2.4. Virus-Like Particles (VLP)

The VLP biomass pattern was consistent between sites in Coffin Bay. There were significant monthly differences in VLP biomass ($p < 0.05$; Figure 4a). Minimum VLP biomass of ~1.8 μg C L^{-1} was seen in May and July, increasing through spring and summer. In February and March, there was a dramatic increase in VLP biomass at the Douglas and Mouth sites, reaching >7.5 μg C L^{-1}. Longnose also increased, but to a lesser extent until April 2018.

Although the overall VLP loading in Franklin Harbour was low over the year, the pattern was consistent at all sites. The minimum value of <1.5 μg C L^{-1} was recorded in July, increasing through spring into October with a significant increase at Howard and South Harbour sites (Figure 4b). After a 3-month decrease, a sharp increase occurred at the Howard site during February and March, with a maximum value above 5.2 μg C L^{-1}.

3.3. Patterns of Picoplankton Variation and Physiochemical Parameters

In Coffin Bay, the pattern of physiochemical variables and the succession of phytoplankton groups were complex throughout the study period. Picoeukaryote cell groups (P1 and P2) were positively correlated with each other (Table 1). VLP biomass was positively correlated with all other groups except for *Prochlorococcus* sp. Bacteria were correlated with *Synechococcus* sp. and P2, and *Prochlorococcus* sp. was only correlated with *Synechococcus* sp. and P1. *Synechococcus* sp. was correlated with P1 and P2. The percentage of picophytoplankton was related to changes in major accessory pigments (Figure 7a). However, *Chl a* alone was only positively correlated with bacterial biomass (Table 1, $r > 0.7$, $p = 0.01$).

The relationships between the phytoplankton community and physicochemical parameters were further investigated using a multivariate linear regression and a distance-based redundancy analysis. In Coffin Bay, the community structure was closely related to changes in temperature, DO and nutrients, accounting for more than 47% of the total variation (Figure 8a). In winter, the community was primarily affected by temperature and DO. This corresponded with DO negatively correlating with VLP, bacteria and *Synechococcus* sp. but positively correlated with P2 (Table 1). As water temperature increased throughout the year, the effects of other environmental variables became apparent. In January, the increase in SiO_2 was associated with the rise of *Synechococcus* sp. and

P1 (Figure 8a). Subsequently, their relationships shifted, driven by increases in NO_X^- and NH_4^+, toward a community dominated by larger phytoplankton such as diatoms.

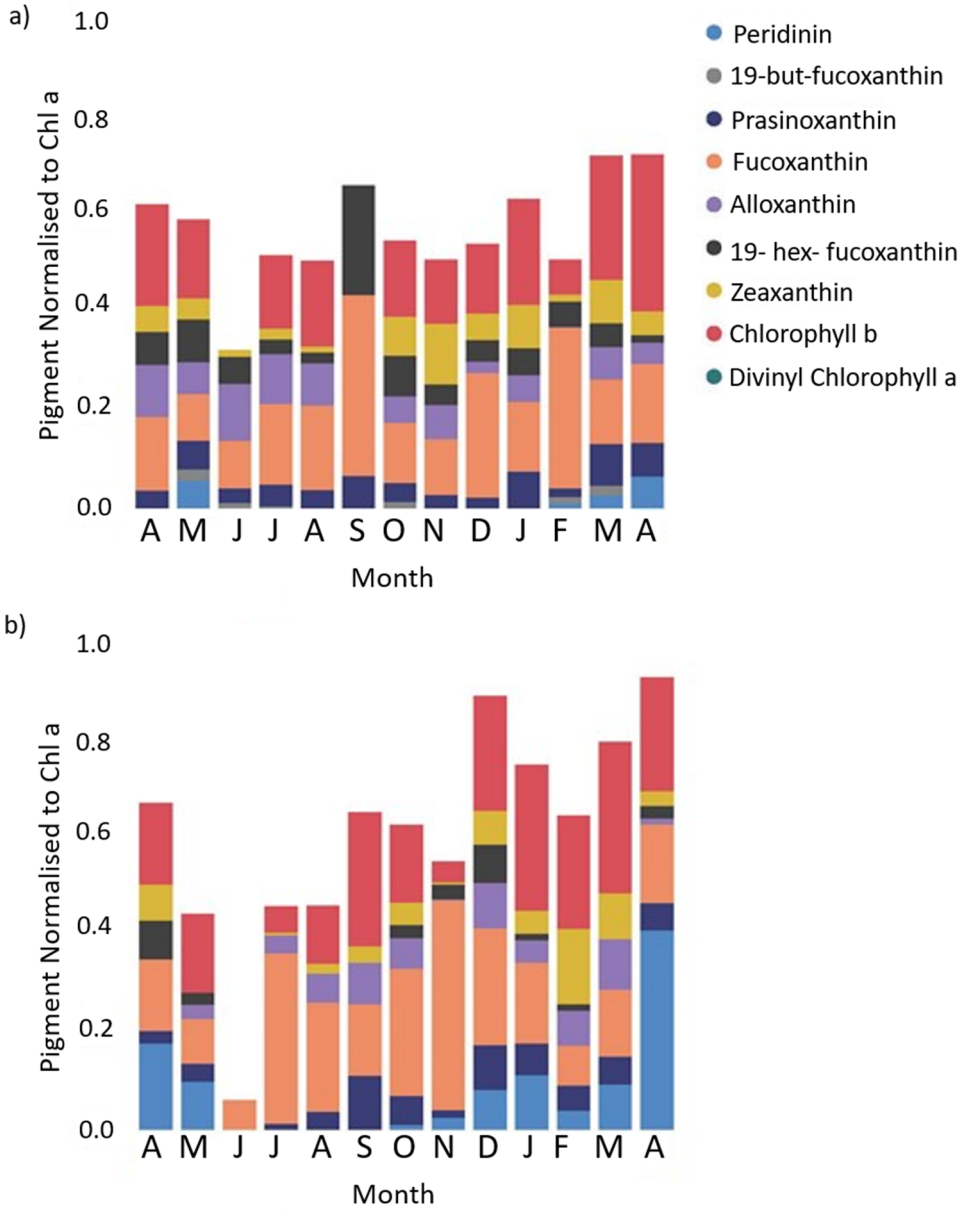


Figure 7. Normalised accessory pigments of the dominant phytoplankton based on chlorophyll *a* in (**a**) Coffin Bay and (**b**) Franklin Harbour over the year.

In Franklin Harbour, the biomass of VLP, *Prochlorococcus* sp. and P1 was positively correlated with all other phytoplankton groups (Table 2). P2 cells were positively associated with VLP, *Prochlorococcus* sp. and P1 only. *Chl a* was positively correlated with P2 only. These correlations coincided with their increases in October and November (Figures 4b and 6d). Changes in the community structure of phytoplankton in the Harbour sites and at the Howard aquaculture zone were also strongly related to variations in temperature, DO and the nutrients, showing more than 41% of the total variation (Figure 8b). In contrast, the phytoplankton community at the coast site was coincident with the changes in temperature, DO, POM, SiO_2 and NO_X^- nutrients, with over 70% of the total variation (Figure 8c). In winter, variation was driven mainly by low DO, which showed a significantly negative correlation with all picophytoplankton groups except P1 (Table 2). Warmer temperature and an increase in SiO_2 in November and December, and again in March, drove increased productivity at the Coast site (Figure 8c). Throughout spring, there was a pattern of increase starting with picophytoplankton P1 group at the South Harbour which shifted to a significant increase in P2. This process was accompanied by an increase in fucoxanthin in November (Figure 7), indicating that algae containing such pigments, such as golden-brown algae could be

responsible for this change. These observations were significantly correlated with SiO_2 concentrations (Table 2). The increase in *Chl a* and a shift to P2 at both the South Harbour and Howard sites were observed in the following months. Nutrients were the main driver of the presence of cyanobacteria *Synechococcus* sp. and *Prochlorococcus* sp. in late summer and autumn in the South Harbour and at the Howard site (Figure 8b).

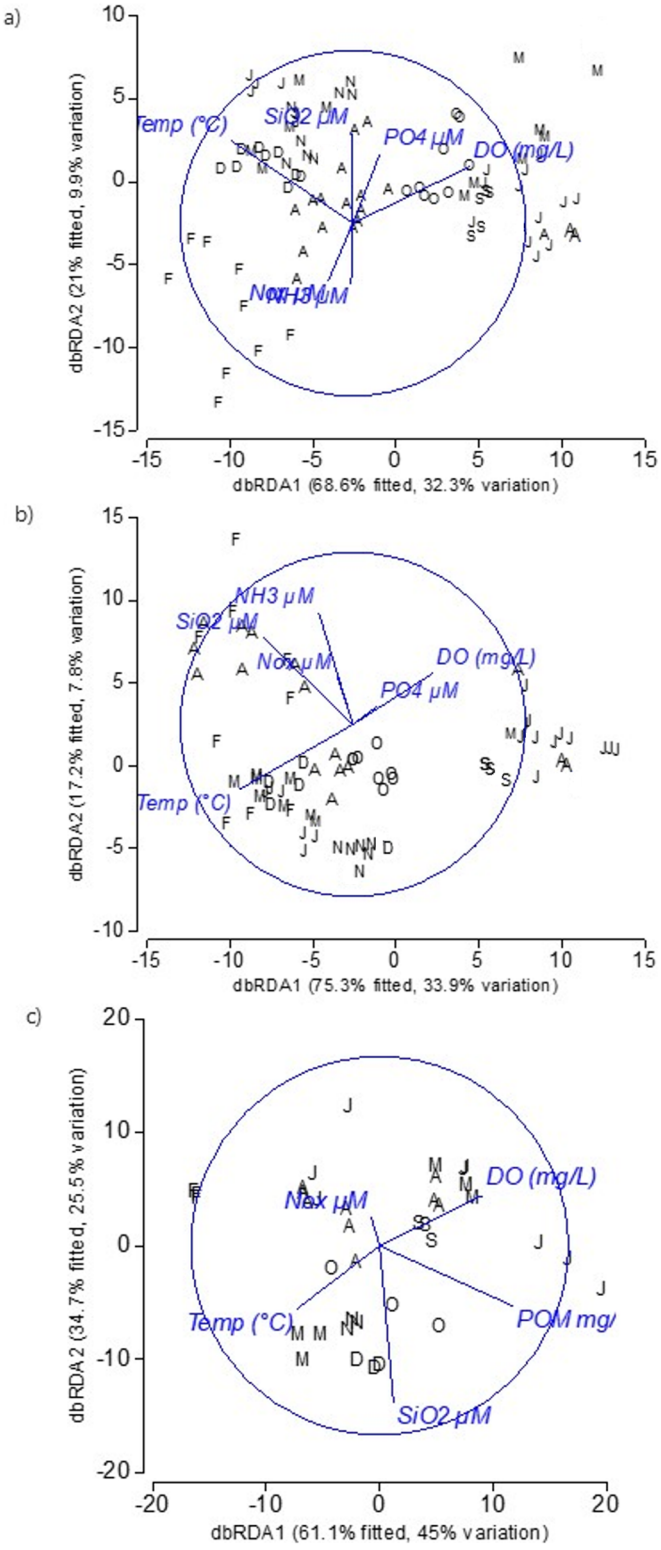


Figure 8. Distance-based redundancy plot of phytoplankton biomass in (**a**) Coffin Bay, (**b**) combination of North Harbour of Howard and South Harbour sites and (**c**) Coast site in Franklin Harbour. Vectors indicate the influence of environmental variables on monthly biomass distribution.

Table 1. Correlation matrix for the picoplankton groups in Coffin Bay: virus-like particles (VLP), Bacteria, *Prochlorococcus* sp. (Pro), *Synechococcus* sp. (Syn), small picoeukaryotes (P1) and large picoeukaryotes (P2); and physicochemical parameters: total chlorophyll *a* (*Chl a*), temperature (Temp), dissolved oxygen (DO), salinity (Sal), particulate organic matter (POM), ammonium (NH_4), nitrate + nitrite (NO_X) and silicate (SiO_2); in Coffin Bay. R values denoted * are significant at $p < 0.05$ and denoted ** are significant at $p < 0.01$.

	VLP	Bacteria	Pro	Syn	P1	P2
Bacteria	0.695 **					
Pro	−0.108	−0.048				
Syn	0.387 **	0.214 *	0.645 **			
P1	0.273 **	−0.177	0.225 *	0.439 **		
P2	0.396 **	0.496 **	0.051	0.243 **	0.380 **	
Chl a	0.516	0.706 **	0.094	−0.009	−0.423	0.326
Temp	0.683 **	0.594 **	0.125	0.615 **	0.114	0.206 *
DO	−0.678 **	−0.681 **	−0.117	−0.401 **	−0.118	0.374 **
Sal	0.431 **	0.359 **	−0.025	0.210 *	−0.045	0.174
POM	−0.330 **	−0.326 **	−0.055	−0.089	−0.131	−0.227 *
NH_4	0.247 **	0.375 **	−0.078	−0.080	−0.192 *	0.130
NO_x	0.344 **	0.265 **	−0.244 **	−0.065	−0.128	0.065
SiO_2	0.131	−0.223 *	0.082	0.246 **	0.348 **	−0.011

Table 2. Correlation matrix for the picoplankton groups in Franklin Harbour: virus-like particles (VLP), Bacteria, *Prochlorococcus* sp. (Pro), *Synechococcus* sp. (Syn), small picoeukaryotes (P1) and large picoeukaryotes (P2); and physicochemical parameters: total chlorophyll *a* (*Chl a*), temperature (Temp), dissolved oxygen (DO), salinity (Sal), particulate organic matter (POM), ammonium (NH_4), nitrate + nitrite (NOx) and silicate (SiO_2); in Franklin Harbour. R values denoted * are significant at $p < 0.05$ and denoted ** are significant at $p < 0.01$.

	VLP	Bacteria	Pro	Syn	P1	P2
Bacteria	0.574 **					
Pro	0.206 **	0.452 **				
Syn	0.398 **	0.503 **	0.887 **			
P1	0.286 **	0.458 **	0.425 **	0.539 **		
P2	0.341 **	0.690	0.182 *	0.115	0.269 **	
Chl a	−0.227	−0.240	0.238	0.161	−0.143	0.629 *
Temp	0.592 **	0.414 **	0.254 **	0.386 **	0.226 **	0.379 **
DO	−0.420 **	−0.394 **	−0.288 **	−0.346 **	−0.147	−0.292 **
Sal	0.416 **	0.341 **	0.204 *	0.267 **	0.214 *	0.119
POM	−0.280 **	−0.319 **	−0.301 **	−0.357 **	−0.229 **	−0.167
NH_4	0.228 **	0.313 **	0.465 **	0.493 **	0.074	0.028 *
NO_x	0.333 **	0.063	0.166 *	0.344 **	0.108	−0.109
SiO_2	0.577 **	0.426 **	0.197 **	0.336 **	0.282 **	0.133

4. Discussion

This study highlights the importance of the seasonal dynamics of the phytoplankton community within two contrasting oyster-growing embayments in SA, and expands the knowledge of coastal phytoplankton ecology in these systems. It also presents the first detailed seasonal dataset of picophytoplankton and VLP in Franklin Harbour. Despite their geographical proximity, Coffin Bay and Franklin Harbour exhibited different phytoplankton community structures and seasonal dynamics, reflecting differences in environmental conditions and hydrodynamic regimes.

4.1. Phytoplankton Community Characteristics

Similar to the previous estimation of phytoplankton size [51], picophytoplankton dominated the community in Coffin Bay for most of the year, whereas Franklin Harbour was characterised by a greater contribution from microphytoplankton. However, both systems showed similar seasonal shifts associated with changes in water temperature, indicating that temperature is a key regulator of phytoplankton succession.

In Coffin Bay, seasonal variability reflected alternation between two functional food-web states. Under baseline conditions, productivity was primarily sustained by a microbial food web dominated by picophytoplankton. During

periods of nutrient enrichment, the community shifted towards larger microphytoplankton, indicative of a more classical grazing food web [36]. This transition was accompanied by an increase in the abundance of P2 picoeukaryotes, especially at the Mouth site. This indicates the phytoplankton productivity is related to oceanic exchange and hydrodynamic connectivity in the outer estuary.

Similar seasonal patterns at the aquaculture sites further indicate strong hydrodynamic connectivity within the outer estuary. This also suggests that productivity near the estuary entrance is impacted by episodic inputs from adjacent shelf waters. Previous studies have documented that intermittent nutrient enrichment and picophytoplankton blooms are associated with upwelling on the eastern GAB shelf [36,43,44,56]. In this study, the elevated abundances of *Synechococcus* and *Prochlorococcus* observed in October and November are consistent with either offshore nutrient inputs or favourable seasonal environmental conditions. As cyanobacterial growth is strongly driven by warm temperatures [23,57,58], this study further supports the view that these taxa respond rapidly to environmental change and may represent early exploiters of newly available resources [24].

In contrast, Franklin Harbour showed a more "isolated" seasonal cycle, consistent with its longer residence time and weaker exchange with shelf waters. During late summer and early autumn, cyanobacterial abundance increased substantially in the South Harbour and Howard sites. This was coincident with elevated temperature and salinity and a decline in picoeukaryote biomass. This pattern aligns with the competitive advantage of cyanobacteria under warm and saline conditions [59,60]. Unlike Coffin Bay, the food web in Franklin Harbour was more dominated by picophytoplankton throughout the year, with a larger phytoplankton bloom in the South Harbour.

This long residence time of the estuary likely promotes stable summer stratification and limits external nutrient exchange with Spencer Gulf [47]. This could allow internal processes to regulate phytoplankton succession with booms and busts throughout the year, as demonstrated by the picophytoplankton abundances and *Chl a* concentration in this study. Coupled with increased solar irradiation and nutrient availability, seasonal water-column mixing during autumn and winter can promote phytoplankton blooms [61,62]. In addition, nutrient inputs from tidal exchange with mangrove habitats and sediment resuspension may further enhance internal nutrient recycling in summer [47]. As a result, subsequent succession towards larger taxa, such as diatoms and golden-brown algae, in spring is consistent with the increased P2 biomass detected in the Howard aquaculture zone.

Overall, Coffin Bay appears to function as a more open coastal system and is strongly influenced by oceanic forcing and shelf-water exchange. However, Franklin Harbour behaves as a more self-contained estuarine system where internal nutrient cycling and residence time regulate phytoplankton succession. These contrasting dynamics would represent different food availability conditions for filter-feeding bivalves. Meanwhile, this discovery highlights the importance of regional variability in phytoplankton size structure and microbial productivity when assessing ecological carrying capacity for oyster aquaculture.

4.2. Nutrient Effect on Phytoplankton Dynamics

Although nutrient availability is a key regulator of primary productivity in oligotrophic environments [63], the present study indicates that it was not the primary driver of picoplankton dynamics. Instead, temperature and DO play a greater role in regulating community succession, shifting from picoplankton-dominated communities towards larger phytoplankton. This pattern was particularly evident in Franklin Harbour, where a significant increase in NH_4^+ in February extended from the Coast site into both the South Harbour and Howard sites. This enrichment is likely associated with organic matter decomposition in adjacent mangrove systems [47,64], as the elevated temperature and reduced dissolved oxygen can enhance microbial remineralisation and then provide additional inorganic nutrients for phytoplankton populations. Therefore, the concurrent nutrient enrichment and increased cyanobacterial abundance represent an interaction of nutrient supplement and local hydrodynamics in structuring phytoplankton communities.

Seasonal nutrient regeneration may also explain the recurring blooms of *Prorocentrum* spp. in autumn (Clinton Wilkinson, pers. comm.), coincident with the elevated concentration of peridinin (dinoflagellate marker pigment) in this study. As *Prorocentrum* spp. has a preference for ammonium nutrient [65], the seasonal NH_4^+ pulse likely promotes its bloom formation. These findings highlight that short-term nutrient inputs can rapidly change phytoplankton communities, resulting in potential variation of food availability to aquaculture systems.

4.3. Upwelling Influence in the Coffin Bay System

Previous work identified a limited linkage between eastern GAB upwelling and Coffin Bay during early summer [36]. However, this study suggests episodic connectivity during late summer 2018, when a short-lived increase in fucoxanthin indicated a diatom bloom in outer Coffin Bay. This event followed a slight decrease in temperature and a spike in SiO_2 concentrations in January. As previously hypothesised in the region during summer

periods [36,48], this trend is closely associated with the advection of nutrient-enriched waters from the eastern GAB shelf into outer Coffin Bay. Diatoms are known to be a regular component of summer phytoplankton communities in Coffin Bay [48], and this study suggests that their dominance may be temporary and closely associated with intermittent offshore enrichment events rather than sustained local production. The rapid return to a picoplankton-dominated system by autumn further highlights the intermittent nature of shelf–estuary coupling in this system.

4.4. Relationship between Chl a and Phytoplankton Groups

In both embayments, measurements of *Chl a* were consistent with increases of nano- and microphytoplankton biomass, indicating a transition from oligotrophic to more mesotrophic conditions. However, in Franklin Harbour, elevated *Chl a* in February was closely related to the increase in larger microphytoplankton only. These findings suggest that *Chl a* alone does not fully represent food availability for suspension-feeding bivalves, particularly in systems where picoplankton dominate a substantial fraction of the food web [20]. Under low-chlorophyll conditions, picoplankton contribute substantially to biomass, but they are not consistently captured by chlorophyll-based assessments. However, they are still an important food source making a substantial contribution to bivalve nutrition [21]. Therefore, it is critical to explore the specific dynamics of picoplankton communities in the regional coastal system.

4.5. Implication for Bivalve Food Resources

During summer bloom periods, the phytoplankton community was dominated by microplankton in both embayments. Although this indicates that diatoms and dinoflagellates likely represent key nutritional resources for bivalves [17,18,66], both ecosystems were dominated by microbial food webs supported by picoplankton for much of the year.

It is well known that bivalves have a high degree of plasticity for their food particle size selection [15]. Pacific oyster *C. gigas* can ingest a wide size range of particles, including picoplankton [21]. As one substantial but underappreciated component of the food source, the persistence of picoplankton dominance in both embayments suggests that oyster productivity in both Coffin Bay and Franklin Harbour is supported by a broader spectrum of food resources than traditionally assumed. These results are consistent with recent calls to re-evaluate the role of small particles in bivalve nutrition, particularly in environments with a large fraction of seston in the <2 μm size range [67]. Therefore, it is pivotal to incorporate full seston size spectra into assessments of food availability and aquaculture carrying capacity especially in oligotrophic and mesotrophic coastal systems [42,68].

5. Conclusions

Effective management of coastal bivalve aquaculture requires consideration of the full phytoplankton size spectrum rather than reliance on quantification of *Chl a* alone. This study demonstrates that picoplankton constitutes a substantial and persistent component of available food resources in both embayments, with great potential implications for oyster nutrition and productivity. The contrasting dynamics between Coffin Bay and Franklin Harbour highlight the importance of hydrodynamic setting in regulating phytoplankton succession and food-web structure. Integrating picoplankton seasonal dynamics into ecosystem models will facilitate the estimation of ecosystem carrying capacity valid to bivalve aquaculture activity. Overall, an ecosystem-based approach that incorporates both picoplankton and classical food-webs is essential for sustainable oyster aquaculture management in SA coastal waters.

Author Contributions

SH: conceptualization, methodology, data analysis, writing—original draft preparation; M.A.R: investigation, methodology; P.D.v.R: data validation, editing, funding acquisition; X.L: conceptualization, supervision, funding acquisition; Y.L: supervision, writing, validation and research administration. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement

The study was conducted according to the guidelines of the Australian Code for the Care and use of Animals for Scientific Purposes, 8th edn, 2013 (the Code), with the approval from the Flinders University Animal Ethics Committee (AEC) before the commence of experiments.

Informed Consent Statement

Not applicable.

Data Availability Statement

The data supporting the results of this study can be obtained from the corresponding author upon reasonable request.

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Conflicts of Interest

The authors declare no conflict of interest

Use of AI and AI-Assisted Technologies

No AI tools were utilized for this paper.

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