Insights into the structure of the pelagic microbial food web in the oligotrophic tropical Western Pacific: Examining trophic interactions and relationship with abiotic variables

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ABSTRACT

Microbial food webs (MFW) play an indispensable role in marine pelagic ecosystem, yet their composition and response to abiotic variables were poorly documented in the oligotrophic tropical Western Pacific. During winter of 2015, we conducted a survey to examine key components of MFW, including *Synechococcus*, *Prochlorococcus*, picoeukaryotes, heterotrophic prokaryotes (HP), heterotrophic/pigmented nanoflagellates and ciliates, across water column from surface to 2000 m. Each MFW component exhibited unique vertical distribution pattern, with abundance ratio varying over six and three orders of magnitude across Pico/Microplankton ($1.6 \pm 1.0 \times 10^6$) and Nano/Microplankton ($3.2 \pm 2.8 \times 10^3$), respectively. Furthermore, HP was main component for MFW in the bathypelagic (>1000 m) zone. Multivariate biota-environment analysis demonstrated that environmental variables, particularly temperature, significantly impacted MFW composition, suggesting that bottom-up control (resource availability) dominated the water column. Our study provides benchmark information for future environmental dynamics forcing on MFW in the oligotrophic tropical seas.

1. Introduction

Microbial food webs (MFW) play a critical role in ocean biogeochemical cycles by generating most of the primary production consumed by upper trophic levels or exported to the seafloor (Falkowski et al., 2004). They are mainly comprised of viruses, *Synechococcus* (SYN), *Prochlorococcus* (PRO), picoeukaryotes (PEUK), heterotrophic prokaryotes (HP), heterotrophic/pigmented nanoflagellates (HNF/PNF) and ciliates (CTS) with body-size ranging from 0.2 to 200 μm in the marine ecosystem (Di-Poi et al., 2013; Giannakourou et al., 2014; Li et al., 2020; Sugai et al., 2023). Simultaneously, they dominate several trophic linkages at the base of the traditional classical food web (from mesozooplankton to fish) (Azam et al., 1983; Landry, 2002; Pavés and González, 2008), and conduct the cycling process of marine carbon and nutrients (Herndl and Weinbauer, 2003; Seymour et al., 2017). While empirical studies related to MFW have provided unambiguous insight into the species diversity and activities of MFW largely through genetic approaches (e.g., DeLong and Karl, 2005; Caron, 2009; Shao et al., 2023), accurate descriptions of the abundances, biomasses, and trophic level interactions of each MFW component in the oligotrophic tropical seas (Ducklow and Doney, 2013) are still incomplete.

The Pacific Ocean boasts the largest oligotrophic sea area worldwide. In the oligotrophic tropical Western Pacific (Dai et al., 2023), the mixed surface layer is typically considered a typical low-nutrient-low-chlorophyll area (Ma et al., 2019; Dai et al., 2020, 2022), and the MFW are characterized by a stable metabolic state (Ducklow and Doney, 2013) and a microbe-dominated ecosystem (e.g., small heterotrophs and phototrophs) (Zhao et al., 2020). Although the community compositions

and trophic interactions of MFW have been studied in the Mediterranean Sea (Tanaka and Rassoulzadegan, 2002; Di-Poi et al., 2013; Gianna-kourou et al., 2014; Šolić et al., 2010, 2018; Trombetta et al., 2020; Dinasquet et al., 2022), Southern Ocean (Christaki et al., 2008, 2014, 2020), Arctic Ocean (Franzè and Lavrentyev, 2017; Jacquemot et al., 2022) and coastal waters worldwide (Nakano et al., 2004; Pavés and González, 2008; Chen and Liu, 2010; Latorre et al., 2018; Meddeb et al., 2018; Sugai et al., 2023), studies in the oligotrophic tropical Western Pacific have been scarce. Despite discrete MFW components (viruses, picoplankton, flagellates and ciliate) being studied in the oligotrophic tropical Western Pacific in different surveys (Sohrin et al., 2010; Wang et al., 2019, 2021, 2023; Zhao et al., 2020), their underlying trophic interactions between each MFW component, which ultimately affect the marine food web structure, remains unclear.

In the marine pelagic ecosystem, variations in MFW structure and their role in biogeochemical processes were determined by environmental factors (e.g., Cotner and Biddanda, 2002; Berglund et al., 2005; Šolić et al., 2010; Archibald et al., 2022). For instance, temperature can directly affect marine organisms through metabolic processes (Archibald et al., 2022), when nutrients concentrations can directly affect primary productivity, which are the vital material basis for phytoplankton and HP growth, and their concentrations can directly affect primary productivity (Šolić et al., 2010; Song, 2011; Ma et al., 2020). The quantity and quality of Chlorophyll a (Chl a, food supply, through lipid unsaturation) can directly determine compositions of pelagic micro-/mesozooplankton (Šolić et al., 2010; Våge and Thingstad, 2015; Holm et al., 2022). Therefore, it is reasonable to conclude that environmental factors control the composition and dynamics of MFW, which ultimately alter the classical food web through predator–prey interactions (Azam et al., 1983; Azam, 1998). Despite the significant differences in environmental variables from epipelagic to bathypelagic zones in the oligotrophic tropical Western Pacific (Sohrin et al., 2010; Ma et al., 2020), our understanding of the responses of MFW to environmental parameters in this region is still very limited.

In this study, we hypothesize that composition of each MFW component and their response to environmental parameters will vary from epipelagic to bathypelagic zones of the oligotrophic tropical Western Pacific. Through examining variations in MFW composition (SYN, PRO, PEUK, HP, HNF, PNF, CTS) and their relationships with environmental factors (depth, temperature, salinity, Chl a and nutrients) from epipelagic to bathypelagic zones, we aim to gain insight into: 1) the interactions in each trophic level, and 2) uncover the impact of abiotic conditions in the oligotrophic tropical seas. Our results will provide a fundamental baseline for understanding the composition and dynamics of MFW in the oligotrophic tropical seas, and variations in the future can serve as indicator for environmental change.

2. Materials and methods

2.1. Field sampling

Sampling was conducted aboard *R.V.* "KEXUE" in the tropical Western Pacific Ocean (11–21°N, 126–136°E) from 10 to 22 December 2015 (Transect D) (Fig. 1; Table A.1). A total of 12 stations (St.) were occupied along a transect (D1–D12) with bottom depth deeper than 3000 m (Table A.1). Vertical profiles of temperature and salinity were determined at each station from surface (3 m) to 2000 m using a SBE911-conductivity-temperature-depth (CTD) unit. The MFW component (SYN, PRO, PEUK, HP, HNF, PNF, CTS) and environmental variables (temperature, salinity, chlorophyll a [Chl a], ammonium [NH_4^+], nitrate [NO_3^-], nitrite [NO_2^-], orthophosphate [PO_4^{3-}], orthosilicate [Si$(OH)_4$]) were sampled at depths of 3 m, 15 m, 30 m, 50 m, 75 m, DCM (deep Chl a maximum layer), 150 m, 200 m, 300 m, 500 m, 1000 m and 2000 m.

Chl a: Chl a concentration was processed by filtering 1 L of seawater through a Whatman GF/F glass fiber filter (0.7 μm). The filtered samples were stored in the dark at −20 °C for further measurement.

Nutrients: Seawater samples (250 mL) were collected from each sampling layer filtered through a 47 mm diameter glass-fiber filter (Whatman GF/F), collected in a polythene bottle, and fixed with chloroform (final concentration 2 ‰). All samples were stored at −20 °C for nutrient analysis (NH_4^+, NO_2^-, NO_3^-, PO_4^{3-}, Si$(OH)_4$).

Picoplankton (0.2–2 μm): Subsamples (5 mL) of picoplankton (SYN, PRO, PEUK, HP) were fixed onboard with paraformaldehyde (final concentration 1 %), kept at room temperature for at least 10 min, freeze-trapped and stored in liquid nitrogen. A total of 429 water samples were collected for picoplankton analysis.

Nanoplankton (2–20 μm): Subsamples (20 mL) of nanoplankton (HNF, PNF) were filtered onto 0.2 μm pore size black polycarbonate membrane filters with Hg pressure lower than 100 mm. After 1 mL sample remained in the funnel, the vacuum pump was turned off and the sample was stained with DAPI for 10 min. The pump was then turned on
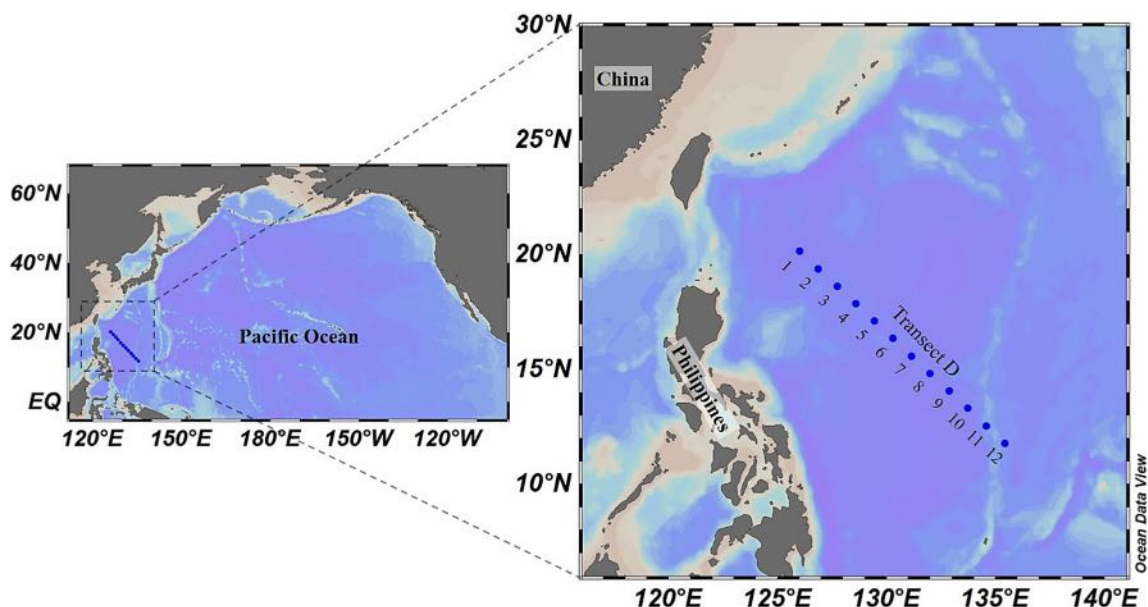

Fig. 1. Survey stations in the tropical Western Pacific Ocean.

again to allow the residual liquid pass through the membrane filter completely. The sample slide was immediately stored in the dark at −20 °C. A total of 143 water samples were collected for nanoplankton analysis.

Microplankton (20–200 μm): Subsamples (1000 mL) of microplankton (CTS) were fixed with acid Lugol's (1 % final concentration) and stored in darkness at 4 °C during the cruise. A total of 143 water samples were collected for planktonic ciliate analysis.

2.2. Sample analysis in the laboratory

Chl *a*: Plankton retained on the filter in each subsample was extracted in 90 % (vv^{-1}) acetone. Fluorescence was measured using a Turner Trilogy fluorometer Model 10, following the Joint Global Ocean Flux Study (JGOFS) protocol (Knap et al., 1996).

Nutrients: Subsamples of each water layer were analyzed using a nutrient automatic analyzer (SEAL QuAAtro). The concentrations of NH_4^+, NO_2^-, NO_3^-, PO_4^{3-} and $Si(OH)_4$ were determined with detection limits of 0.01, 0.01, 0.02, 0.01 and 0.01 μM, respectively. Meanwhile, the precision of analysis was determined using China's national standard references and all nutrients met the required precision (better than 3 %) and recoveries (97.2–103.5 %).

Picoplankton: Subsamples (5 mL) of picoplankton were analyzed using a BD FACSJazz flow cytometer (Becton Dickinson). Autotrophic picoplankton (SYN, PRO and PEUK) were distinguished based on their scatter and autofluorescence. HP were stained with SYBR Green I before analysis and then resolved based on their side scatter and green fluorescence. Flow cytometric data were collected and analyzed with BD FACS™ Sorware Sorter software and Summit v4.3 software, respectively.

Nanoplankton: Nanoflagellates were counted using an epifluorescence microscope (Olympus BX 53) at 1000× magnification. PNF were distinguished from HNF based on the presence of red fluorescence in the former using a blue excitation laser set (Tsai et al., 2005). At least 30 fields of view were examined. The length (L) and width (W) of a nanoflagellate cell were measured on photomicrographs using software Image-Pro Plus. At least 60 cells per sample were measured.

Microplankton: Each water sample was concentrated to approximately 200 mL by siphoning off the supernatant after settling the sample for 60 h in the laboratory. After two rounds of settling and siphoning process, a final volume of 25 mL was settled in a Utermöhl counting chamber (25 mL) (Utermöhl, 1958) for at least 24 h. CTS were counted using an Olympus IX 73 inverted microscope (100× or 400×).

2.3. Data processing

Picoplankton abundance was converted to carbon biomass using constant conversion factors: 250, 49, 671 and 15 fg C cell^{-1} for SYN, PRO, PEUK and HP, respectively.

Nano volumes were estimated according to the following form (Girault et al., 2013):

$$V = \frac{W^2 \times L \times \pi}{6}$$

where V (μm^3) was the cell volumes, W and L were the width and length (μm) of a nanoplankton cell. The cell volumes of nanoflagellates were converted to carbon biomass using a conversion of 220 fg C/μm^3.

Microplankton (CTS) volumes were estimated according to their appropriate geometric shapes (cone, ball, and cylinder). Carbon biomass of each individual was estimated by the equation (Verity and Lagdon, 1984):

$$C = V_i \times 0.053 + 444.5$$

where C (pg C) was the carbon biomass of individual tintinnid, V_i (μm^3) was the lorica volume. As for aloricate ciliates, we used a conversion

factor (0.19 pg/μm^3) for calculating their carbon biomass (Putt and Stoecker, 1989). The unit of biomass was converted into μg C/L in the manuscript. Classification of mixotrophic (including SYN, PRO, PEUK, PNF) and heterotrophic (including HP, HNF, CTS) planktons were referring to Li et al. (2020). Classification of epipelagic (0–200 m)/mesopelagic (200–1000 m)/bathypelagic (≥1000 m) zones in whole waters was referring to Zhao et al. (2020).

3. Results

3.1. Hydrography and abundance and biomass of each MFW component

All environmental variables (except for NH_4^+ and NO_2^-) showed a clear delamination pattern from surface to 2000 m layers (Fig. 2). A thermocline (16–24 °C) was presented steadily at depths ranging from 100 to 300 m, with higher salinity occurring at depths ranging from 100 to 200 m (Fig. 2; Fig. A.1). Chl *a* concentrations were relative high in waters shallower than 150 m, with the DCM occurring at approximately 100 m (Fig. A.1). Nutrient patterns indicated that productivity in surface waters at the study site were typically and consistently N-limited and P-limited (Fig. 2; Fig. A.2). In the euphotic zone, high concentrations of NH_4^+ and NO_2^- occurred at DCM in several stations (Fig. 2; Fig. A.1). The concentrations of NO_3^-, PO_4^{3-}, $Si(OH)_4$ were lower than the detection limits at surface waters, and then gradually increased to 2000 m (Fig. 2). Generally, different environmental variables exhibited three vertical distribution patterns in the tropical Western Pacific: 1) temperature showed a surface-peak pattern, 2) salinity, Chl *a*, NH_4^+ and NO_2^- showed a DCM-peak pattern, and 3) NO_3^-, PO_4^{3-} and $Si(OH)_4$ exhibited a 2000 m-peak pattern (Fig. A.2).

Each MFW component exhibited various distribution characteristics in vertical profiles (Fig. 3; Fig. A.3). The abundances of SYN, PRO, PEUK, HP, HNF, PNF and CTS were 0.0–2.1 × 10^3, 0.0–1.4 × 10^5, 0.0–3.0 × 10^3, 0.1–5.5 × 10^5, 14.8–622.4, 0.0–385.3 cells/mL and 2–443 ind/L, respectively. Their biomass were 0.0–0.2, 0.0–7.5, 0.0–4.6, <0.1–6.6, <0.1–1.0, 0.0–1.5 and <0.1–0.8 μg C/L, respectively. High total abundance and biomass of MFW occurred mainly in waters shallower than 150 m (epipelagic zone), and decreased to 2000 m (bathypelagic zone) (Fig. 2; Fig. A.1). Horizontally, there were few variations of each MFW component at each sampling layers of each station. Based on the abundance and biomass in vertical profiles, different MFW components were categorized into three types: 1) SYN, HP, HNF and PNF showed a surface-peak type, 2) PRO and PEUK showed a DCM-peak type, and 3) CTS showed a bimodal-peak (surface- and DCM-peaks) type (Figs. A1 and A3).

3.2. Composition of MFW component

Abundance and biomass compositions of each MFW component varied with depths (Fig. 3; Fig. A.3). HP was the most dominant group in the MFW, accounting for >69.3 % at each depth (69.3–99.5 %, average 92.8 ± 9.1 %) in terms of abundance. The highest value of PRO occurred at the DCM with a relative abundance of 29.6 % to MFW (Fig. 3a). As for biomass, HP was the dominant group in the MFW at all depths except for the DCM. At surface and 15 m layers, PEUK was the second dominant group in the MFW, while at 30, 50, 75, and 150 m, the second dominant group in the MFW shifted to PRO. In waters deeper than 200 m, HNF was the second dominant group in the MFW (Fig. 3b), indicating a distinct MFW composition in different water columns. To understand the regulation of HP and HNF by resource (bottom-up control) and/or predation (top-down control) (Gasol, 1994), the relationship between HP and HNF abundance was examined (Fig. A.4). Most of HNF (sampled from epipelagic to mesopelagic zones) fell above the MRA (mean realised abundance) line (Fig. A.4), suggesting stronger bottom-up control on HNF. However, for sampling points below the MRA line especially at epipelagic zone (Fig. A.4), the top-down control on HNF played the main role.
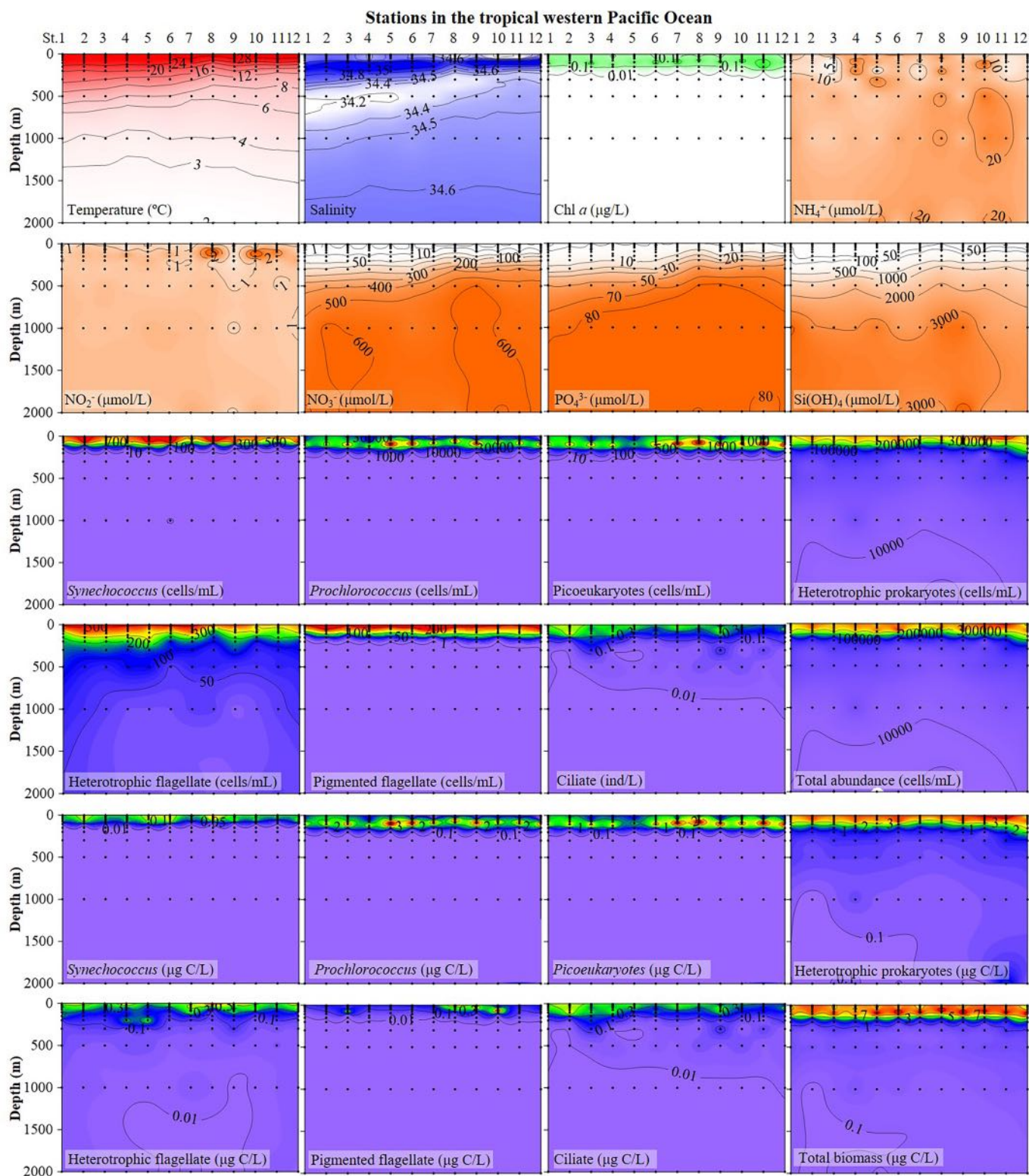
Fig. 2. Vertical distribution of environmental variables (Temperature, salinity, Chlorophyll *a* [Chl *a*], ammonium [NH_4^+], nitrate [NO_3^-], nitrite [NO_2^-], ortho-phosphate [PO_4^{3-}], orthosilicate [$Si(OH)_4$]), and each microbial food web component (abundance and biomass of *Synechococcus*, *Prochlorococcus*, picoeukaryotes, heterotrophic prokaryotes, heterotrophic/pigmented nanoflagellate, ciliate) from surface to 2000 m depth in the tropical Western Pacific Ocean. Black dots are sampling depths.

The picoplankton (0.2–2 μm), nanoplankton (2–20 μm) and microplankton (20–200 μm) sized-plankton exhibited different vertical distribution patterns in all stations. Both picoplankton and microplankton showed bimodal-peak (surface- and DCM-peaks) pattern, with their highest average abundance and biomass occurring at DCM and surface layers, respectively. Nanoplankton showed a surface-peak pattern with the highest average abundance and biomass at surface waters (Fig. 3c and d). The relative abundance ratio ranged from 0.4 to 5.0 × 10⁶
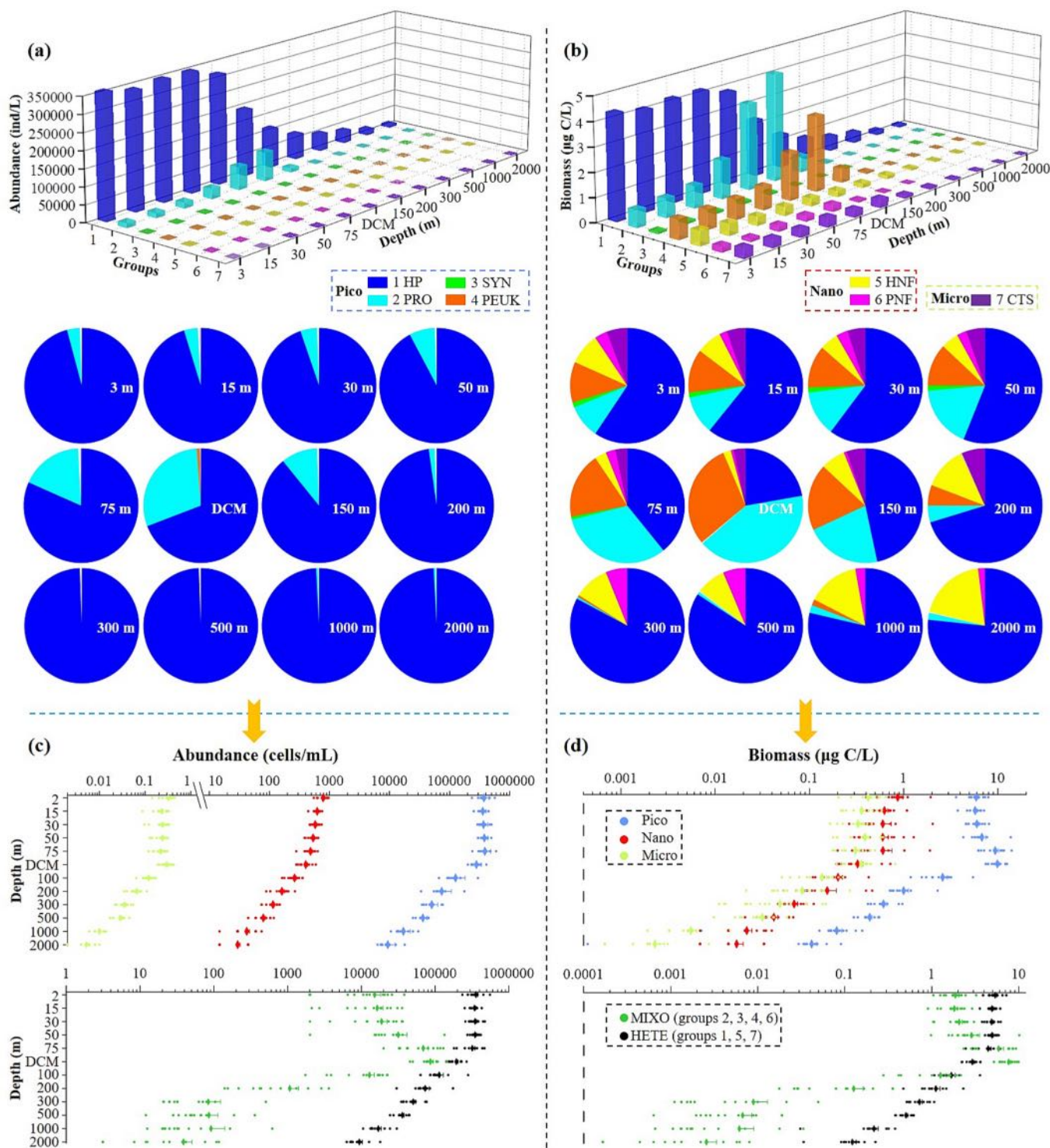
Fig. 3. Representation for vertical distribution of each microbial food web component abundance/biomass and its abundance/biomass proportion (a and b), and vertical distribution patterns of Pico/Nano/Micro sized-plankton and heterotrophic (HETE)/mixotrophic (MIXO, including autotroph and mixotroph) plankton abundance and biomass (c and d).

(average $1.6 \pm 1.0 \times 10^6$) for pico/microplankton and $0.8–22.2 \times 10^3$ (average $3.2 \pm 2.8 \times 10^3$) for nano/microplankton at all sampling depths. The relative biomass ratio ranges from 2.2 to 169.6 (average 28.5 ± 26.1) for pico/nanoplankton and 0.4–49.1 (average 2.9 ± 4.6) for nano/microplankton (Fig. A.5). In terms of different sampling depths, the relative abundance ratio for both pico/microplankton and nano/microplankton were lowest at the DCM layers (average $1.0 \pm 0.4 \times 10^6$ and $1.4 \pm 0.4 \times 10^3$, respectively), then increased to 2000 m

(average $2.5 \pm 1.6 \times 10^6$ and $8.5 \pm 7.2 \times 10^3$, respectively) (Fig. A.5). The highest values for relative biomass ratio for both pico/microplankton and nano/microplankton occurred at 2000 m layers (average 67.0 ± 53.2 and 14.1 ± 16.8, respectively), while their lowest values occurred at different layers (pico/microplankton at the surface [average 15.5 ± 6.0], while nano/microplankton at the DCM [average 1.1 ± 0.8]) (Fig. A.5).

Mixotrophic and heterotrophic plankton showed distinctive vertical

distribution patterns (Fig. 3) with DCM-peak and surface-peak, respectively (Fig. 3c and d). With respect to ratios between Mixotrophic/heterotrophic plankton at different layers, both their abundance and biomass showed an increasing trend from the surface to the DCM, followed by a decrease to 2000 m (Fig. A.6). The relative abundance of mixotrophic plankton at each depth were lower than 30.5 % (Fig. A.6a), while the relative biomass of mixotrophic plankton at 75 m and DCM layers were higher than 50 % when compared to the percentage of each group (Fig. A.6b).

3.3. Relative biomass of each MFW component to HP

The biomass values of the MFW components (SYN, PRO, PEUK, HNF, PNF and CTS) were normalized by HP as described by Li et al. (2020). The relative biomass trends of different MFW components showed

significant variations (Fig. 4a). The relative biomass of SYN, PNF, HNF and CTS were <1 at all depths, while PRO and PEUK were >1 at the DCM layer (Fig. 4; Fig. A.7). For both picoplankton and microplankton, their relative biomass first increased from the surface to the DCM layers, then decreased to 2000 m (Fig. 4; Fig. A.7). In contrast, the relative biomass of nanoplankton remained steady from the surface to 2000 m layers (Fig. A.7). With respect to mixotrophic and heterotrophic planktons, their relative biomass exhibited a DCM-peak and bimodal-peak (surface- and DCM-peaks) patterns, respectively (Fig. 4; Fig. A.7).

3.4. Relationship between MFW components and environmental variables

The relationship between the MFW components (PRO, SYN, PEUK, HP, HNF, PNF, CTS) and environmental variables (temperature, salinity, Chl a, NH_4^+, NO_2^-, NO_3^-, PO_4^{3-}, $Si(OH)_4$) were clearly different (Fig. 5a).
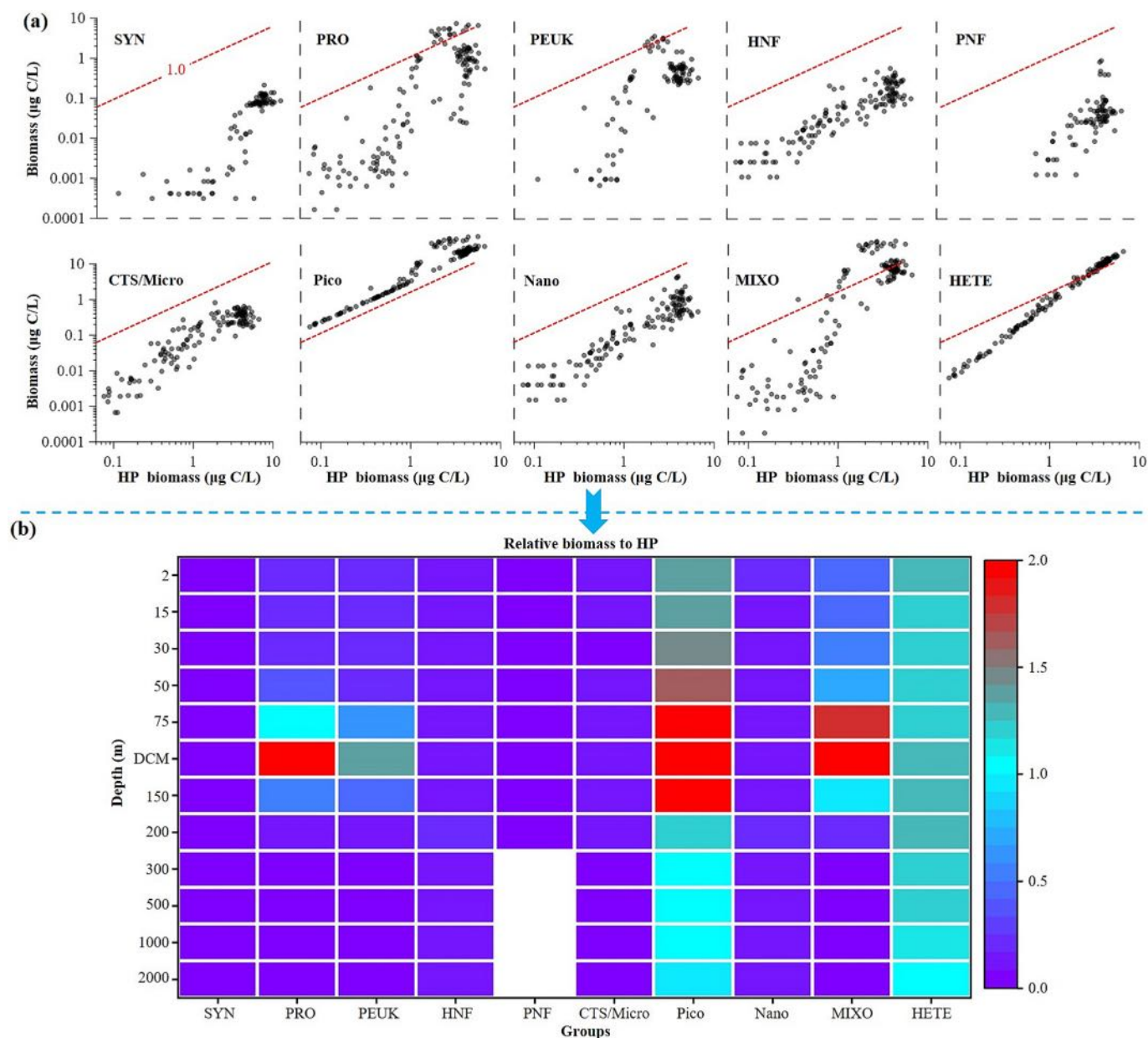
Fig. 4. Variations of microbial food web component biomass relative to HP biomass (a) and heatmap representation for their average relative biomass value at each depth. HP, heterotrophic prokaryotes; PRO, *Prochlorococcus*; SYN, *Synechococcus*; PEUK, phototrophic picoeukaryotes; HNF, heterotrophic nanoflagellates; PNF, pigmented nanoflagellates; CTS (or Micro, microplankton), ciliate; Pico, picoplankton (HP, PRO, SYN, PEUK); Nano, nanoplankton (HNF, PNF); MIXO, autotrophic and mixotrophic organisms (PRO, SYN, PEUK, PNF), HETE, heterotrophic organisms (HP, HNF, CTS).
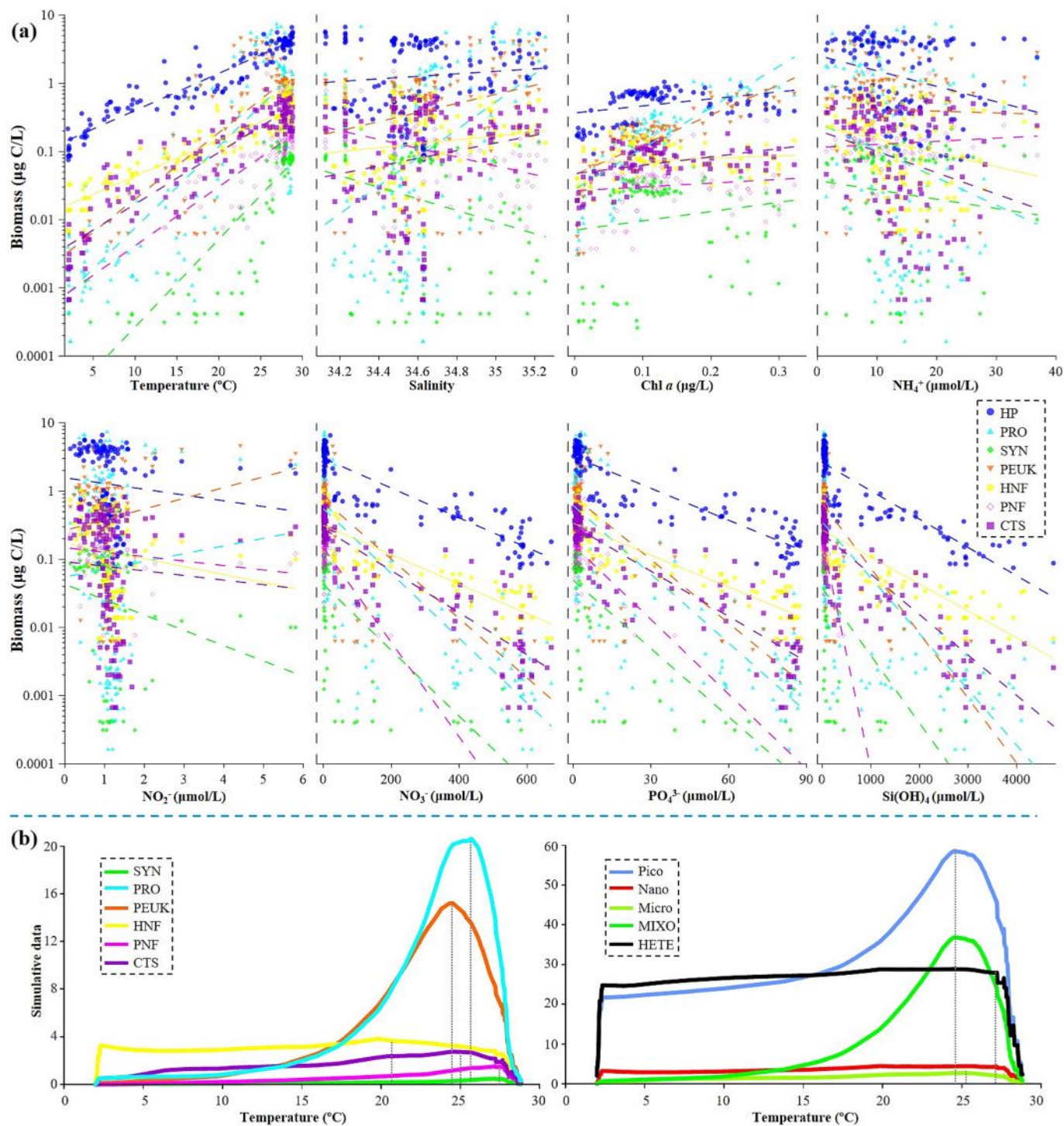
Fig. 5. Variations of different MFW component biomasses to environmental variables (a), and simulative curve based on each relative biomass of MFW component to HP and temperature (b) in the tropical Western Pacific Ocean. Pico/Nano/Micro, Pico/Nano/Microplanktons; MIXO, mixotrophic plankton; HETE, heterotrophic plankton.

High biomass of each MFW component occurred at relatively high temperatures and Chl *a* levels, and relatively low NH_4^+, NO_3^-, PO_4^{3-} and $Si(OH)_4$ levels (Fig. 5a). The suitable NO_2^- range for each MFW component was 0.2–1.5 μmol/L. Among MFW components, PRO, PEUK, HP, HNF and CTS showed relative higher biomass in higher salinity environment, while PNF and SYN exhibited the opposite pattern (Fig. 5a). Additionally, variations in the highest ratio of MFW component to HP and temperature revealed that they had different suitable growing habitats with particular temperature environment (Fig. 5b).

To compare variations in environmental sensitivities, we performed Mantel tests between the MFW components and environmental variables (Fig. 6a). Biomass of each MFW component was strong significantly correlated to temperature ($p < 0.01$). Additionally, SYN, PRO, PEUK and HP were strong significantly correlated to Chl *a*, PO_4^{3-} and NO_3^- ($p < 0.01$). In contrast, both HNF and CTS were strong significantly correlated to depth, PO_4^{3-}, NO_3^- and $Si(OH)_4$ ($p < 0.01$) (Fig. 6a). In addition, SYN, PRO, PEUK, HP and CTS were significantly correlated to $Si(OH)_4$, NO_2^-, depth, NH_4^+ and Chl *a*, respectively ($p < 0.05$) (Fig. 6a).
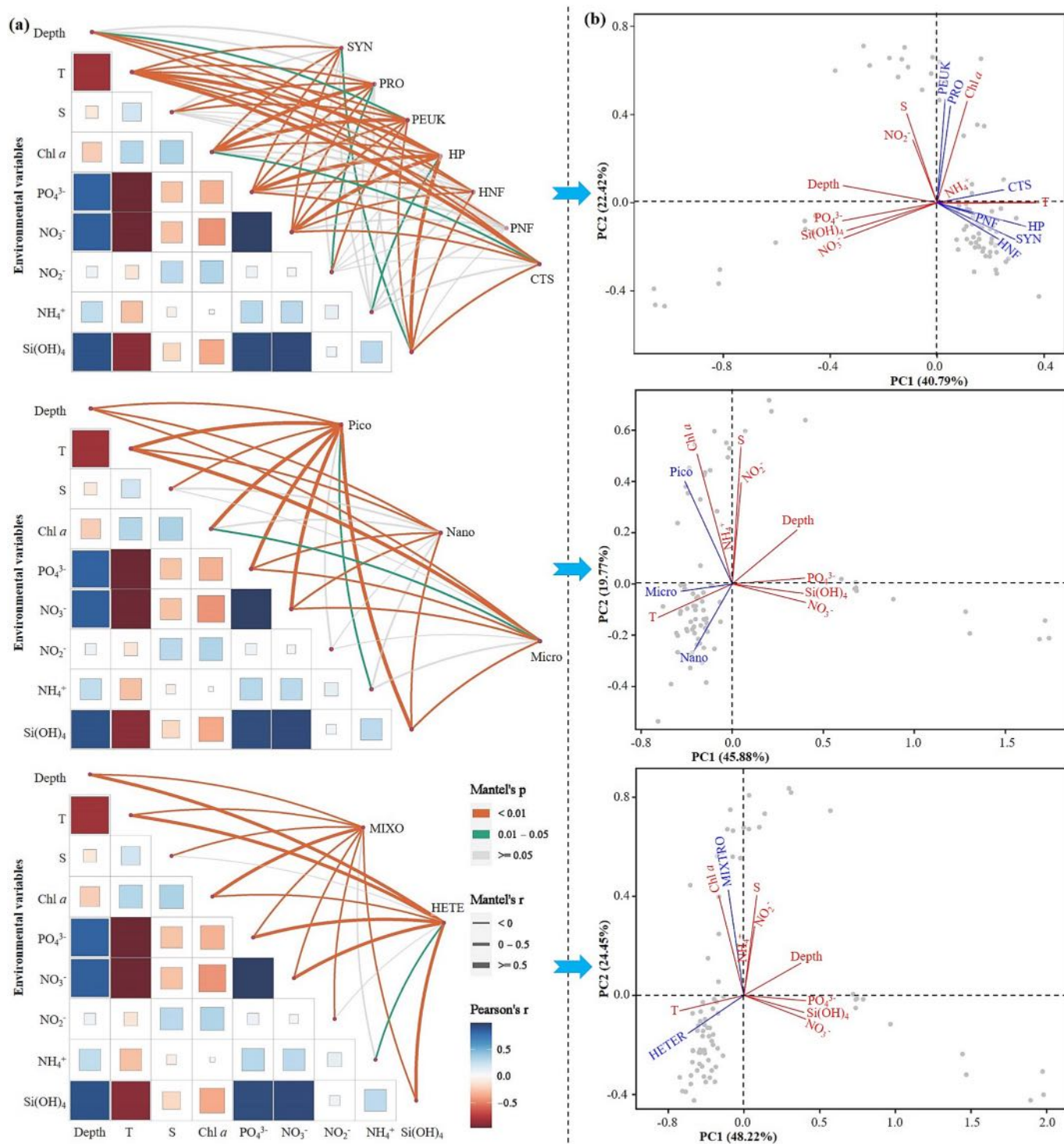
Fig. 6. Relationships between different microbial food web component and environmental variables by partial Mantel tests (a) and Principal component analysis (PCA) (b) in the tropical Western Pacific Ocean. Edge width corresponds to the Mantel's r statistic for the corresponding distance correlations, and edge color denotes the statistical significance based on 9999 permutations. The x-axis is the first PCA axis, and the y-axis is the second PCA axis. Environmental variables and microbial food web component are indicated by red lines and blue lines, respectively. Pico/Nano/Micro, Pico/Nano/Microplanktons; MIXO, mixotrophic plankton; HETE, heterotrophic plankton. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

With respect to pico/nano/microplanktons, their biomasses were strong significantly correlated to depth, temperature, PO_4^{3-}, NO_3^- and $Si(OH)_4$ ($p < 0.01$). Additionally, picoplankton was strong significantly correlated to salinity and Chl a ($p < 0.01$), and significantly correlated to NH_4^+ ($p < 0.05$) (Fig. 6a). Both mixotrophic and heterotrophic planktons were strong significantly correlated to depth, temperature, Chl a, PO_4^{3-}, NO_3^-

and $Si(OH)_4$ ($p < 0.01$). Except that, mixotrophic plankton was strong significantly correlated to salinity and NO_2^- ($p < 0.01$), while heterotrophic plankton was significantly correlated to NH_4^+ ($p < 0.05$) (Fig. 6a).

Principal component analysis was conducted to examine the contribution of the environmental variables to the MFW components at

all stations (Fig. 6b). Two principal components discriminated the environmental conditions in different water layers. These components explained large proportions of the variance in each MFW component (63.21 %), pico/nano/microplanktons (65.65 %), and heterotrophic/mixotrophic planktons (72.67 %), respectively. The first principal component was closely related to temperature, depth, PO_4^{3-}, NO_3^-, Si $(OH)_4$, five MFW components (CTS, HP, PNF, SYN, HNF) or microplankton, nanoplankton or heterotrophic plankton. Among them, CTS (microplankton) and heterotrophic plankton had strongly positive correlation with temperature, but strongly negative correlation with depth, PO_4^{3-}, NO_3^- and $Si(OH)_4$ (Fig. 6b). In addition, the second principal component was closely related to Chl *a*, salinity, NO_2^-, NH_4^+, two MFW components (PEUK, PRO) or picoplankton or mixotrophic plankton (Fig. 6b).

4. Discussion

To our knowledge, our study is the first comprehensive investigation of all the major components of the MFW simultaneously, from HP to CTS and the first to estimate the biological carbon flux at vertical dimension (from surface to 2000 m) in the oligotrophic tropical Western Pacific. Overall, the microbial abundances and biomasses reported at epipelagic zone in this study are consistent with those reported by Sohrin et al. (2010). The environmental variables (except NH_4^+ and NO_2^-) in seawater showed obvious delamination from surface to 2000 m, with little variations compared to other seasons at neighboring seas (Gómez, 2007; Dai et al., 2020; Ma et al., 2021a, 2021b), suggesting that the results on MFW structures are applicable to other times of year. Moreover, our analysis of MFW structure (abundance, biomass, vertical distribution patterns and trophic linkage) and abiotic conditions from the tropical Western Pacific were consistent with studies carried out in the oligotrophic ocean, where picoplankton-dominated in marine pelagic ecosystem, contribution of small forms (picoplankton and nanoplankton) was higher than 90 %, and rapid attenuation of each MFW component abundance and biomass occurred at around 100 m with strong positive correlation to temperature and Chl *a* (Landry, 2002; Thingstad, 2005; Sohrin et al., 2010; Christaki et al., 2011; Chiang et al., 2014; Kormas et al., 2014; Selph et al., 2018). In addition to these similarities, our study revealed more interactions between each MFW component and their relationship with abiotic variables in the oligotrophic tropical Western Pacific were discovered.

4.1. The dynamics of MFW component in the vertical dimension

MFW organisms are the fundamental base of pelagic ecosystems and support the entire marine food web (Trombetta et al., 2020). Understanding the ecological function of MFW components in marine ecosystems requires information on their vertical distribution. Therefore, researchers have focused on the vertical characteristics of each MFW component to uncover their trophic level interactions in various seas (e.g., Tarran et al., 2001; Landry, 2002; Tanaka and Rassoulzadegan, 2002; Christaki et al., 2008, 2011, 2014, 2020; Sohrin et al., 2010; Kormas et al., 2014; Caron et al., 2017). Empirical studies have found that the abundance ratios between pico(prokaryotes)/nano(HNF)/microplanktons(CTS) were approximately $10^6/10^3/1$ at discrete sampling depths in the Mediterranean Sea (Tanaka and Rassoulzadegan, 2002) and the North tropical Pacific (Sohrin et al., 2010). Our results in the oligotrophic tropical Western Pacific from epipelagic to bathypelagic zones (Fig. 3c) were in accordance with mentioned-above seas. Meanwhile, we further uncovered the variations of discrete trophic linkage in different sampling depths.

The oceanic water in the oligotrophic tropical Pacific is relatively homogenous, and vertical distribution patterns of each MFW component remain relatively steady (Sohrin et al., 2010; Zhao et al., 2020). The high abundance and biomass of top grazer (CTS) in the MFW at surface water was supported by SYN, HP, HNF and PNF (surface-peak pattern), while

at DCM water, it was supported by PRO and PEUK (DCM-peak pattern). The existence of these components can determine the balance between resource limitation (bottom-up control) and strong predation (Top-down control) in the marine food web (Calbet et al., 2001). Regarding the trophic coupling between microbial heterotrophs, we found a one-order-of-magnitude increase in biomass ratio of both pico/nano-plankton and nano/microplankton in bathypelagic zones (Fig. 3d; Fig. A.5), similar to the Mediterranean Sea (Tanaka and Rassoulzadegan, 2002). This phenomenon suggests that the prey biomass at deep water is controlled more by resource than by predation. However, in waters shallower than 150 m, the CTS grazing process (Top-down control) may play a key role in controlling HNF/PNF and HP community, as suggested by previous studies (Gonzalez et al., 1990; Hall et al., 1993; Ayo et al., 2009; Šolić et al., 2010; Di-Poi et al., 2013; Nakajima et al., 2017; Meddeb et al., 2018; Selph et al., 2018; Rekik et al., 2021).

Plankton size spectra were used to indicate their ecological functions through prey-predator interactions in marine ecosystem (Vandromme et al., 2012; Wang et al., 2023a). For instance, ciliates (top grazer of the MFW), play important role in determining numerous physiological and ecological processes (e.g., metabolism, carbon flux, turnover and food web dynamics), as their body size is an important factor influencing the predation of *meso*−/macro-zooplankton (Turner, 2002; Brown et al., 2004; García-Comas et al., 2016; Liu et al., 2023; Wang et al., 2023a). Generally, the method of molecular biological biomarkers for describing the MFW through the relative abundance (DeLong and Karl, 2005; Caron, 2009; Shao et al., 2023), but it cannot reveal the real abundance and interaction between each trophic level in the marine ecosystem. Therefore, our results can fill in gaps of 16S/18S rRNA gene-based surveys.

4.2. Relative biomass of each MFW component and their function

The relative biomass variations of different MFW components (SYN, PRO, PEUK, HNF, PNF, CTS) exhibited different trends compared to the increase in HP biomass (Fig. 4), suggesting the variation of the MFW in vertical dimension of the oligotrophic tropical Western Pacific. Previous studies have shown that the relative biomass of each MFW component to HP in surface water was <1 at all seasons in oceanic water of the Arabian Sea (Garrison et al., 2000) and coastal water of the Sanggou Bay (China) (only occurred in spring and winter) (Li et al., 2020). Our results for the relative biomass of each MFW component to HP in surface water was consistent with these findings. At DCM layers, the relative biomasses of both PRO and PEUK were >1, indicating significant variations in their ecological roles compared to surface water.

Regarding mixotrophic and heterotrophic planktons, their relative biomass (mixotrophic: heterotrophic plankton) first increased from the surface (unproductive water) to the DCM (relatively productive water) layers, then decreased to 2000 m (Fig. A.6). This phenomenon was in accordance with Gasol et al. (1997), who first proposed that unproductive and productive waters were characterized by high and low relative heterotrophic plankton biomass, respectively. Previous studies considered that biomass ratio of HP: autotrophic plankton = 1 as a boundary index for indicating a pelagic ecosystem living in the oligotrophic (>1, HP dominant) or eutrophic (<1, phytoplankton dominant) conditions (Li et al., 1993). Our results revealed that the oligotrophic tropical Western Pacific in winter was living with a HP dominant state throughout the water column except 75 m and DCM layers, which is consistent with Duarte et al. (2013).

4.3. The MFW structure associated with the environmental parameters

The MFW structure and its contribution to carbon fluxes rely significantly on the abiotic (e.g., temperature, salinity, Chl *a*, nutrients, Fe, pH) factors, as each MFW component is highly reactive to environmental changes (Fitter and Hillebrand, 2009; Christaki et al., 2014; Sala et al., 2016; Zander et al., 2017; Trombetta et al., 2020). Thus, abiotic

environmental variations play a crucial role in determining the community structure of marine pelagic ecosystems. Among the majority environmental variables, temperature has a direct effect on marine organisms through intrinsically temperature-dependent metabolic processes (Archibald et al., 2022). The statistically significant upward or downward trend for each MFW component was established, exhibiting a strong significant correlation with temperature (Fig. 6). Simultaneously, the HNF/HP and CTS/HP ratios increased with temperature (Fig. 5b), which suggests a strong bottom-up control of bacteria dominance (Šolić et al., 2018) in layers ranged from 2000 m to DCM (around 100 m). Additionally, our results revealed that heterotrophic plankton was more abundant than mixotrophic plankton at relative higher temperature environments (27.5–28.8 °C) in the oligotrophic tropical Western Pacific (Fig. 5b). This phenomenon may be attributed to the higher temperature sensitivity processes (growth/grazing rate) of heterotrophic than mixotrophic plankton (Parain et al., 2016; Connell et al., 2017; Šolić et al., 2018; Archibald et al., 2022).

Nutrients (e.g., N, P, Si) have strong impacts on the MFW composition in the marine ecosystem (Šolić et al., 2010; Song, 2011; Dai et al., 2023). For example, P is an essential element for synthesizing ribosomes, DNA, and cell membranes (Muscarella et al., 2014), while Si plays a key role in maintaining the dominance of diatoms. Through osmotrophs by bacteria and phytoplankton (Lignell et al., 2013), nutrients were transported to the MFW trophic linkage, and their enrichment would lead to high abundance/biomass of each MFW component (Berninger et al., 1991; Šolić et al., 2010). Our results showed that the small phytoplankton fraction (SYN, PEUK, PRO) dominated the total phytoplankton community in waters shallower than 150 m, accompanied by low nutrient environment in the oligotrophic systems. The high abundance of small-sized phytoplankton in the oligotrophic tropical Western Pacific is attributed to their higher affinity for inorganic nutrients (Button, 1986) and lower energetic costs compared to larger phytoplankton (Neidhardt et al., 1990). However, there was a mismatch between low abundance/biomass of each MFW component and high nutrients in waters deeper than 200 m, which could be due to the extreme pressure and low temperature environment in those depths.

4.4. Potential responses of MFW to rapid global warming

The rapid global warming has led to more frequent occurrences of anomaly events (e.g., El Niño and La Niña) (McPhaden et al., 2006; Cai et al., 2021; Geng et al., 2023), which are expected to alter water column biogeochemical processes of oligotrophic tropical ecosystems in the near future (Archibald et al., 2022). Marine phytoplankton and microzooplanktons under rapid global warming progress have shown a tendency towards miniaturization in the shelf seas (Wang et al., 2023), Arctic Ocean (Zhuang et al., 2021; Wang et al., 2022) and Southern Ocean (Fitch and Moore, 2007; Beans et al., 2008; Mendes et al., 2013; Wang et al., 2023b). The variations in community structure of MFW might be responsible for this trend. To better understand their response to global warming, future studies should integrate species composition of both producers (prey) and consumers (predators) of MFW. Previous studies have shown that warming benefits heterotrophs more than autotrophs, especially for small-sized organisms (Brown et al., 2004; Daufresne et al., 2009; Zander et al., 2017; Šolić et al., 2018; Trombetta et al., 2020; Archibald et al., 2022). Therefore, HP may play a more important role in future oligotrophic tropical seas under rapid global warming. Our results indicate that each MFW component has a unique thermal tolerance (compared to HP), and the MFW will cascade when temperature exceeds 29 °C (Fig. 5b). This finding is in accordance with Trombetta et al. (2020).

Predicting the response of food webs to environmental variations requires an understanding of how trophic levels react to global warming under different abiotic and biotic conditions. Among the MFW components, lower trophic levels are expected to react faster than higher trophic levels, as they typically consist of smaller-bodied species with higher reproductive rates (Zander et al., 2017; Trombetta et al., 2020; Archibald et al., 2022). This response could lead to a mismatch to trophic levels, in which predators and prey will respond differently to changing abiotic conditions (Parain et al., 2016). To accurately identify key species among the MFW, future research needs to develop novel theories that can rapidly assess their biodiversity and function.

5. Conclusion

We examined the microbial community composition from epipelagic to bathypelagic zones of the oligotrophic tropical Western Pacific and compared each MFW prey assemblages. Our findings highlighted the importance of heterotrophic bacteria as a dominant component for MFW, particular in the bathypelagic zone. We also observed a significant increase in the biomass of mixotrophic plankton (SYN, PRO, PEUK, PNF) with increasing temperature, indicating their great potential as an additional carbon biomass that can be transported to higher trophic levels at waters shallower than 150 m. The abundance comparison between HNF and HP suggests that the bottom-up control of HNF (resource availability) played a key role throughout the water column. Our results contribute to a better understanding of carbon flux in the tropical Western Pacific MFW, and will help assess and predict future changes in marine pelagic food web of oligotrophic tropical seas under the influence of the rapid global warming.

CRediT authorship contribution statement

CW, LZ and WZ involved in the investigation. CW, WZ and TX designed the experiments. CW and LZ finished species identification and counting. CW, YW, ZX and YZ contributed to data analyses. CW, LZ, ZX and WZ wrote the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2023.115772.

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Supplemental figures
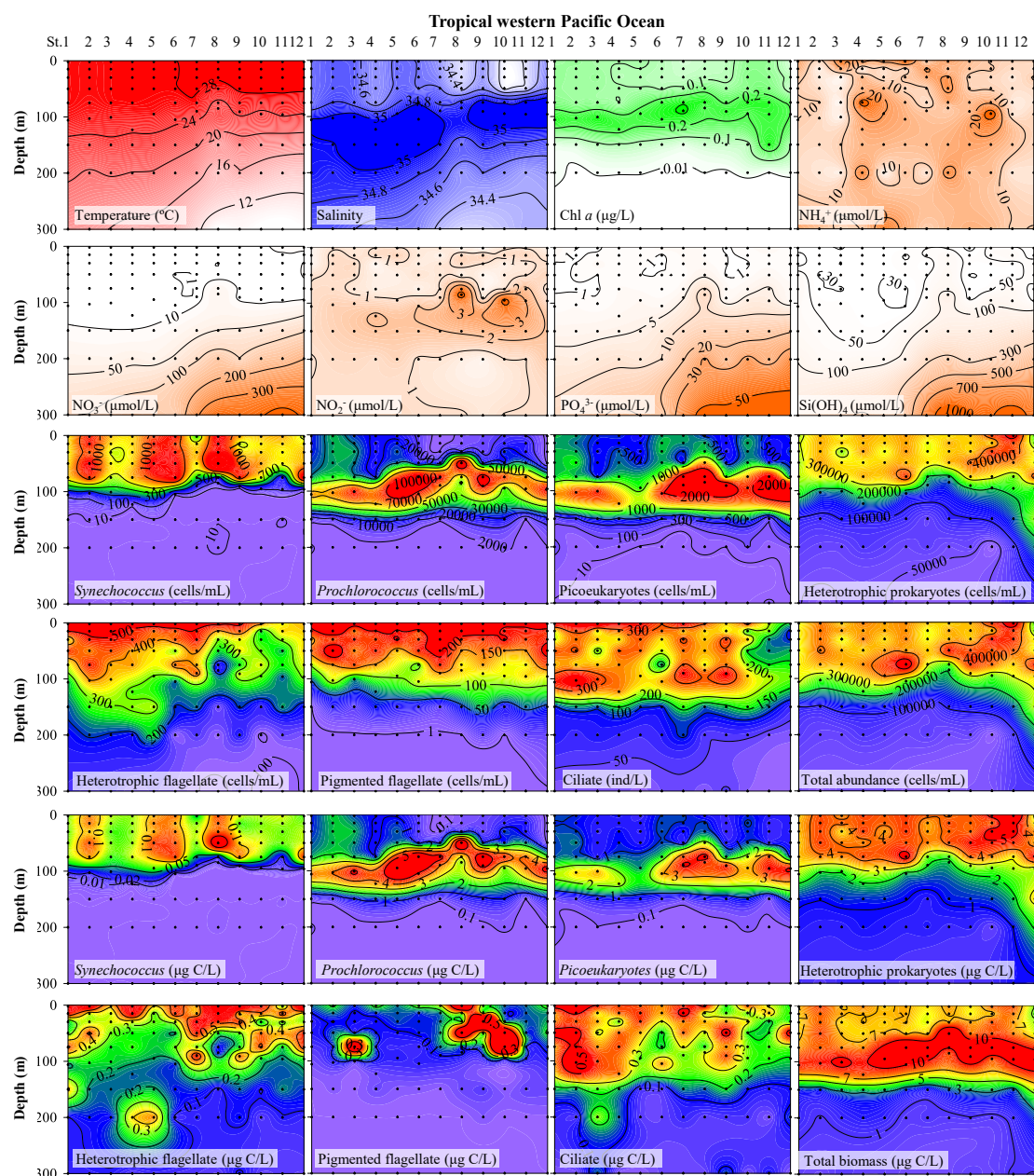


Fig. A.1. Vertical distribution of environmental variables (Temperature, salinity, Chlorophyll *a* [Chl *a*], ammonium [NH$_4^+$], nitrate [NO$_3^-$], nitrite [NO$_2^-$], orthophosphate [PO$_4^{3-}$], orthosilicate [Si(OH)$_4$]), and each microbial food web component (abundance and biomass of *Synechococcus*, *Prochlorococcus*, picoeukaryotes, heterotrophic prokaryotes, heterotrophic/pigmented nanoflagellate, ciliate) from surface to 300 m depth in the tropical Western Pacific Ocean.
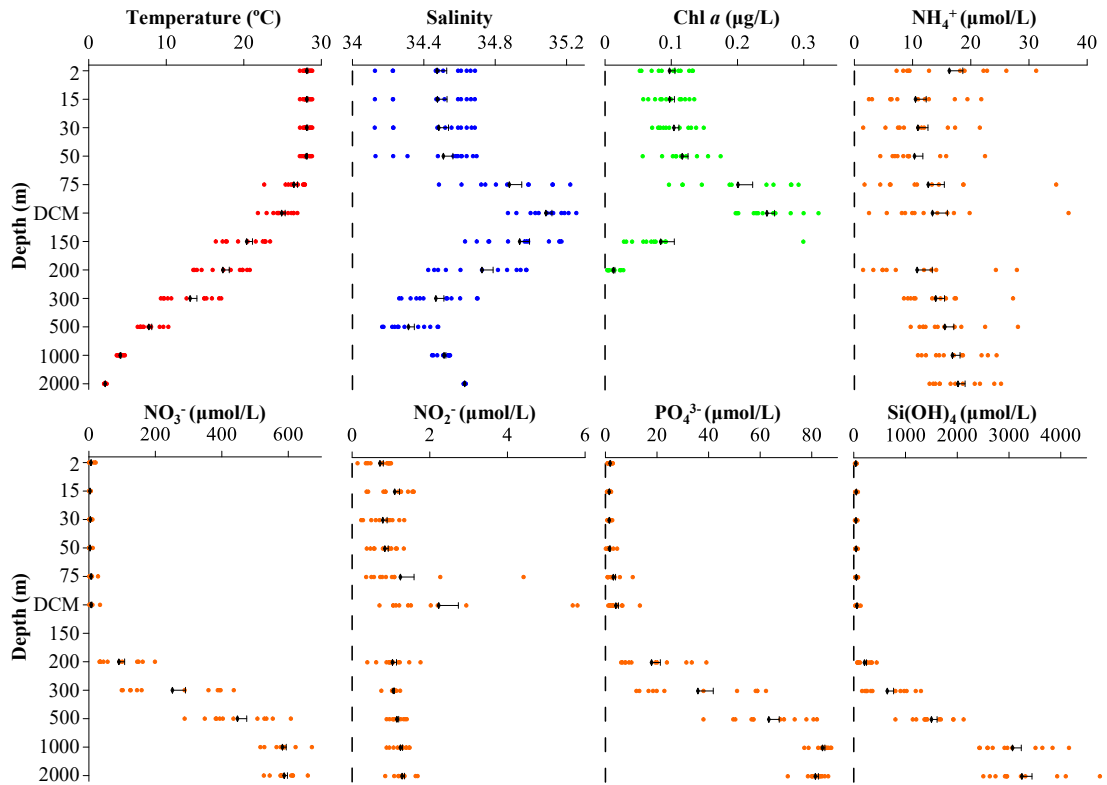
Fig. A.2. Vertical distribution patterns of environmental variables from surface to 2000 m depth.
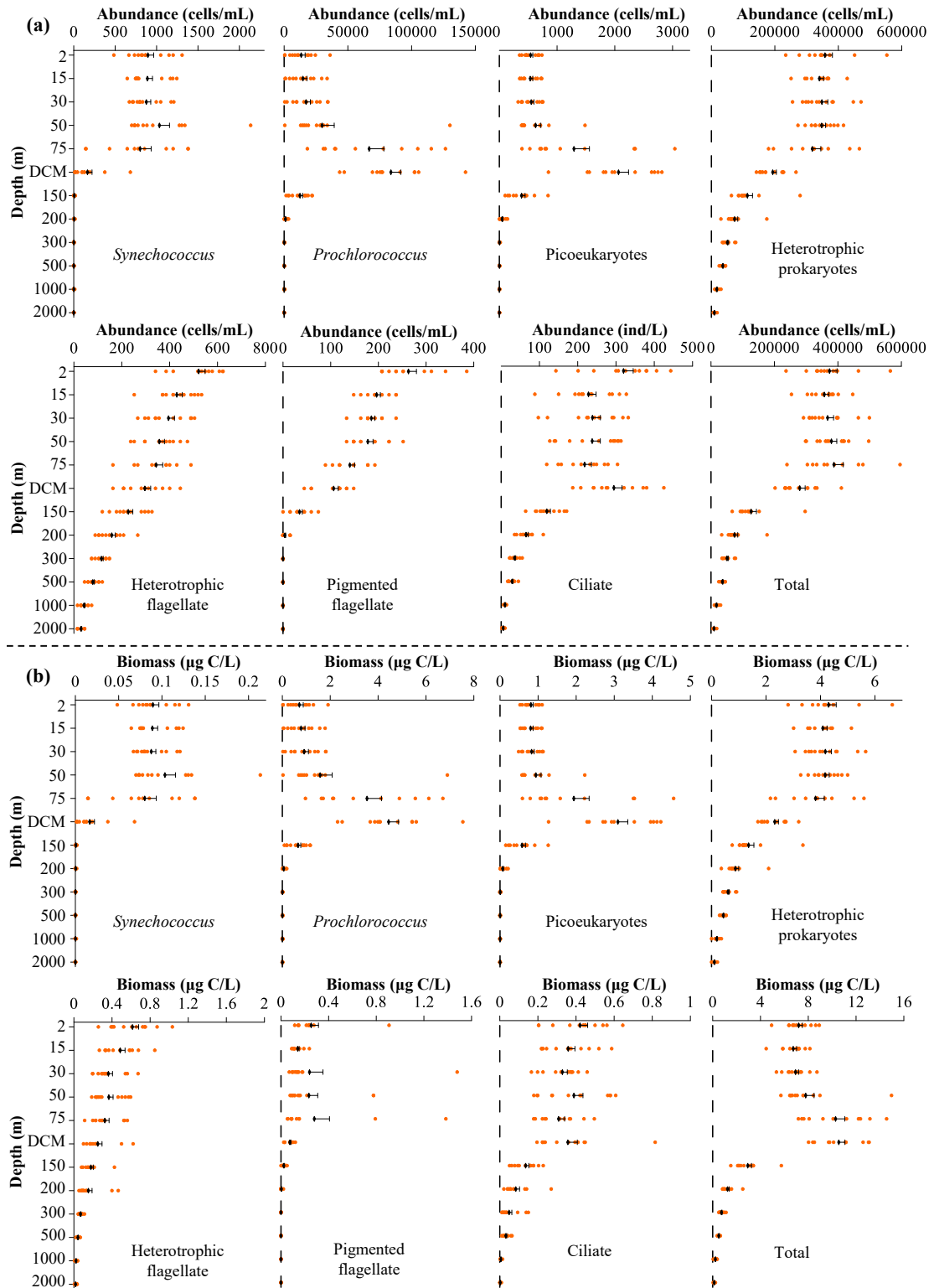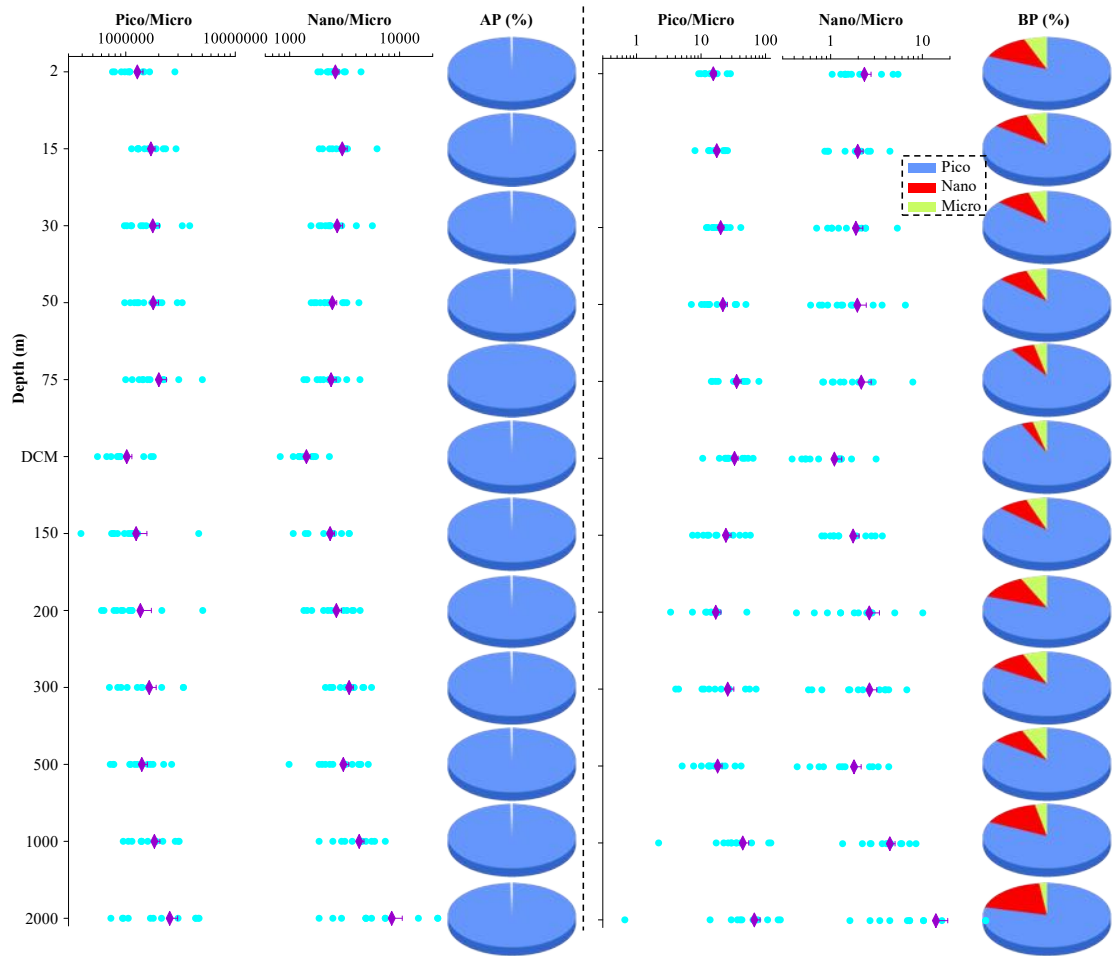
Fig. A.3. Vertical distribution patterns of each microbial food web component (abundance and biomass) from surface to 2000 m depth.
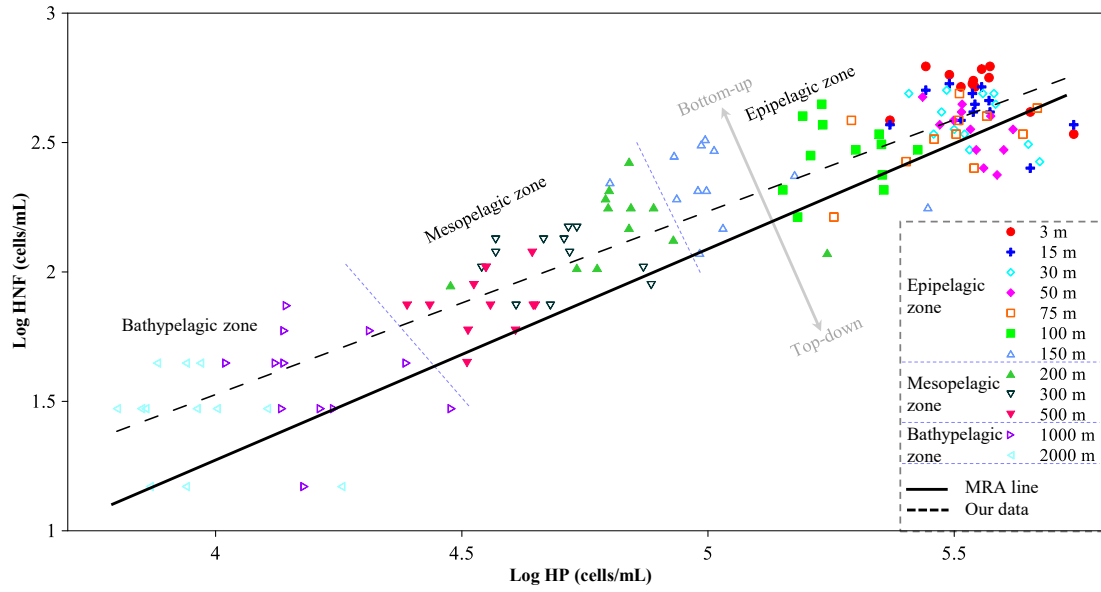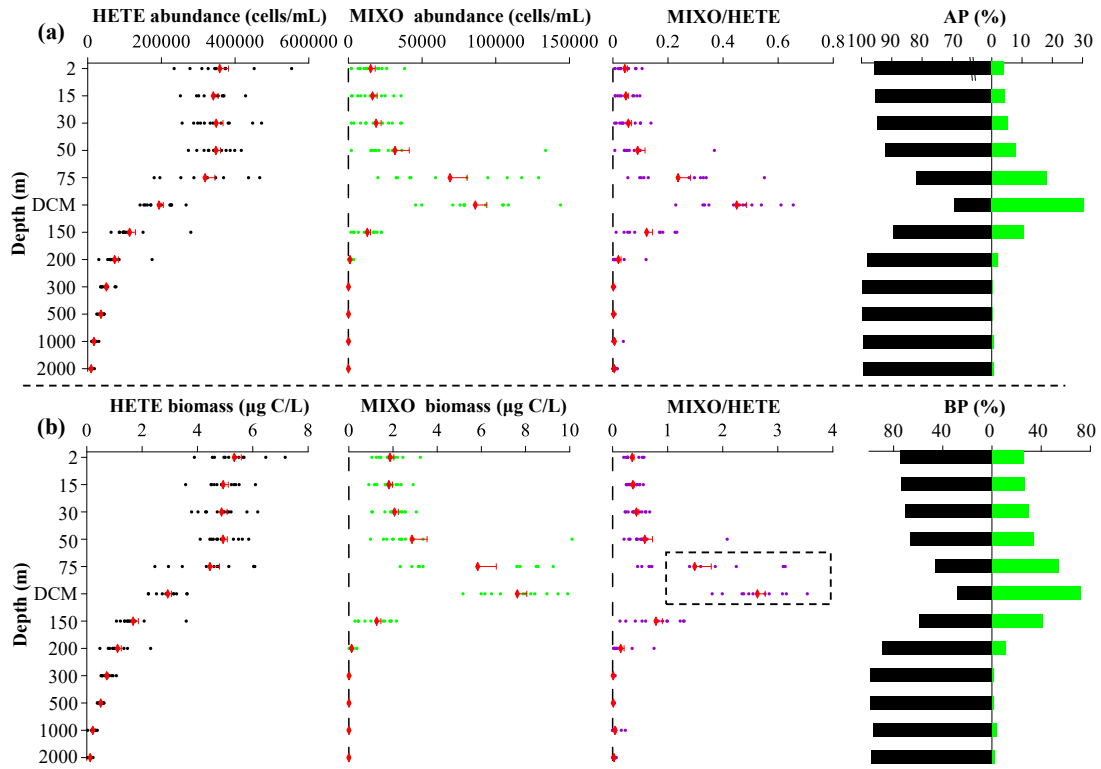
Fig. A.4. Relationship between bacterial and HNF abundance from epipelagic zone to mesopelagic zone at study stations. The data of MRA (mean realised abundance) originated from Gasol (1994).

Fig. A.5. Relative abundance and biomass ratio between Pico- or Nano- and Micro-plankton, and its abundance/biomass proportion (A/BP) at each depth of the tropical western Pacific.

Fig. A.6. Vertical distribution patterns of mixotrophic (MIXO) and heterotrophic (HETE) organisms (abundance and biomass), ratio between MIXO and HETE, and their abundance/biomass proportion (A/BP) at each depth of the tropical western Pacific.
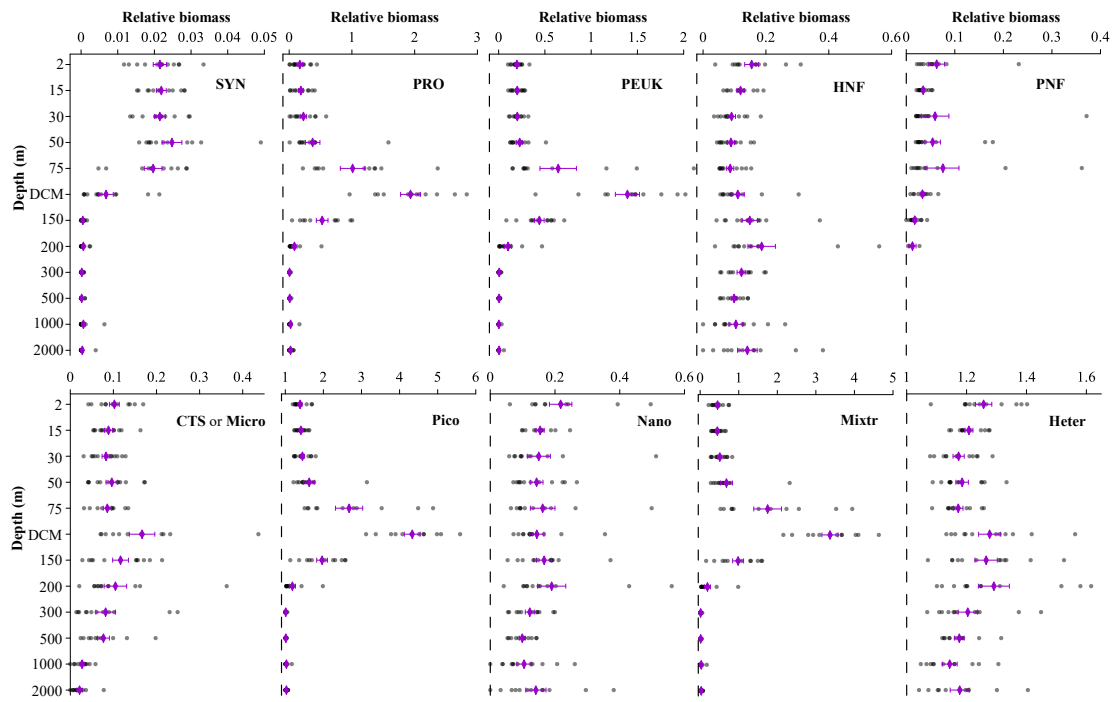
Fig. A.7. Relative biomass variations between each microbial food web component (except HP, heterotrophic prokaryotes) and HP at each depth of the tropical western Pacific.

Supplemental tables

Table A.1. List of stations with date sampled in the tropical Western Pacific

Stations	Date sampled	Longitude (°E)	Latitude (°N)	Depth (m)
D12	10/12/2015	126°00′29.52″	20°09′49.32″	4765
D11	13/12/2015	126°51′51.84″	19°24′07.38″	3286
D10	14/12/2015	127°43′14.16″	18°38′25.48″	5160
D9	14/12/2015	128°34′36.12″	17°52′43.54″	5840
D8	15/12/2015	129°25′58.44″	17°07′01.63″	5609
D7	16/12/2015	130°17′20.76″	16°21′19.69″	5364
D6	17/12/2015	131°08′43.08″	15°35′37.79″	6592
D5	18/12/2015	132°00′05.40″	14°49′55.85″	5241
D4	19/12/2015	132°51′27.72″	14°04′13.94″	5492
D3	20/12/2015	133°42′49.68″	13°18′32.00″	5023
D2	21/12/2015	134°34′12.00″	12°32′50.10″	5377
D1	22/12/2015	135°25′34.32″	11°47′08.16″	6158