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ORIGINAL ARTICLE

Biomass and trophic structure of the plankton community in subtropical and temperate waters of the northwestern Pacific Ocean

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Abstract This study examined the biomass structure of autotrophic and heterotrophic plankton along a trophic gradient in the northwestern Pacific Ocean in an attempt to understand planktonic food web structure. Autotrophic biomass exceeded that of heterotrophic organisms in all sampling regions, but with lesser contribution to total planktonic biomass at stations of higher phytoplankton biomass, including the northern East China Sea, compared to the regions of lower phytoplankton biomass. The proportion of the biomass of heterotrophic bacteria, nanoflagellates (HNF), and dinoflagellates (HDF) relative to that of phytoplankton was all inversely related to phytoplankton biomass, but positive relationships were observed for both ciliates and mesozooplankton. Mesozooplankton biomass inclined greater than phytoplankton along the gradient of phytoplankton biomass, with biomass rise being most closely associated with ciliate and HDF biomass and, to a lesser degree, with large phytoplankton (>3 μm). Both bacteria and picophytoplankton were significantly and positively related to the biomass ratio of mesozooplankton to the sum of HDF and ciliates (i.e., proxy of mesozooplankton predation on protozoans), but no positive relationship was apparent either for HNF or for large phytoplankton. Such relationships may result from predation relief on lower food webs associated with mesozooplankton feeding on protistan plankton.

Keywords Biomass structure · Trophic cascade · Microbial food web · Northwestern Pacific Ocean · Western Pacific warm pool

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1 Introduction

Marine mesozooplankton obtain their energy from a variety of sources, with a significant fraction coming from diverse protistan plankton (Sherr et al. 1986; Stoecker and Capuzzo 1990; Landry and Calbet 2004; Yang et al. 2009; Saiz and Calbet 2011). Protistan plankton can ingest small phytoplankton and bacteria which mesozooplankton cannot directly feed on due to their small size, thus serving as a link between microbial food webs and mesozooplankton, which often increases the food quality, known as "trophic upgrading" (Klein Breteler et al. 1999; Tang and Taal 2005). As mesozooplankton composition and biomass vary along trophic (e.g., food availability and composition) and physical (e.g., temperature and salinity) gradients, their relationships with planktonic food webs can be quite variable (Gasol et al. 1997; Yamaguchi et al. 2004, 2005; Matsuno and Yamaguchi 2010). The study of biomass structure and the relationships between the major constituents of planktonic food webs along trophic gradients is important for understanding the mechanisms underlying planktonic food webs on large scales in the open ocean (Pérez et al. 2005).

A well-known example of such analyses shows the inverse relationship of the ratio of heterotrophic biomass to that of autotrophs with increasing phytoplankton biomass (Gasol et al. 1997). Such an inverse relationship suggests

differences in biomass structure and trophic dynamics between oligotrophic and eutrophic areas of the ocean (Gasol et al. 1997). It had been inferred that this phenomenon is caused by the combined effects of increased phytoplankton turnover and reduced carbon export to the subsurface layer in oligotrophic waters (Wassmann 1990; Baines et al. 1994). High turnover rates, low phytoplankton standing stock, and low carbon export require tight coupling between phytoplankton and heterotrophs, which is made most likely by more efficient grazing processes in the oligotrophic ocean than in eutrophic waters (Banse 1995; Gasol et al. 1997; Chen and Liu 2010). Meanwhile, carbon flows directly from phytoplankton to mesozooplankton, which would efficiently maintain low protozoan biomass in eutrophic waters. Such a food web structure implies that mesozooplankton size may vary along trophic gradients, small ones more abundant in the oligotrophic waters and larger ones in more productive waters.

The subtropical and temperate regions of the northwestern Pacific Ocean encompass various trophic systems from oligotrophic waters, such as parts of the western Pacific warm pool to the south, to more productive ecosystems, such as the East China Sea, which are affected by coastal upwelling and major river discharge to the north (e.g., the Changjiang River discharge). The North Equatorial Current (NEC) turns into the western boundary current that carries warm water from the tropics poleward, within the pathway of which our sampling stations in the Philippine Sea and warm pool are located. The surface layer of the western warm pool on the north of the NEC is characterized by high temperature (>29 °C), low salinity (<35), low nutrient concentration (<0.1 μM NO_3), and low chlorophyll concentration (<0.2 μg L^{-1}) (Blanchot et al. 2001). Meanwhile, on its way to the north of the western boundary current, the subsurface, southwestward countercurrent flow between the inshore edge of the Kuroshio and the East China Sea continental slope brings to the surface the water of the subsurface Kuroshio rich in nutrients, which are the main sources of the surface nutrients of the southern ECS (Chuang et al. 1993; Gong et al. 1996; Zhang et al. 2007). High phytoplankton biomass and primary productivity have been reported for eutrophic waters with net-phytoplankton (>20 μm) comprising nearly 45 % of the total concentration (Chen et al. 2004).

Such natural gradients in phytoplankton biomass and primary productivity in this continuum of oceanic waters may provide insights into how planktonic biomass and food web structure vary along such gradients. Previous studies on latitudinal changes in plankton biomass and community composition have been primarily restricted to equatorial waters (Mackey et al. 1995; Roman et al. 1995, 2002; Blanchot et al. 2001). The present study aims to describe heterotrophic and autotrophic biomass structure along a phytoplankton biomass gradient, and to examine the size distribution of mesozooplankton along the gradient in subtropical and temperate waters of the northwestern Pacific.

2 Materials and methods

Sampling was conducted from September 30 to October 16, 2007 at 16 stations in four different regions of the northwestern Pacific: the western warm pool (WP; W1–5), the Philippine Sea (PS; P1–3), the East China Sea (ECS; E1–4), and the northern East China Sea (NECS; NE1–4) (Fig. 1). Vertical temperature and salinity profiles at the sampling sites were measured using a SeaBird conductivity–temperature–depth sensor (CTD; SBE 9/11 plus; SeaBird, Bellevue, WA, USA).

Seawater samples for chlorophyll *a* (Chl*a*) and protistan plankton measurements were also collected using a Rosette sampler with 10-L Niskin bottles mounted on the CTD assembly at seven to eight water depths within 100 m during each upward cast. Water samples (1-L) for Chl*a* analysis were taken from each depth and were size-fractionated by filtering through 3-μm polycarbonate membrane filters, and the filtrate was re-filtered through Whatman GF/F filters to measure the contribution of picophytoplankton to total Chl*a* (Takahashi and Bienfang 1983; Ishizaka et al. 1994). All filtrations were performed under low vacuum pressure (<100 mmHg) or gravity pressure (when using 3-μm filter paper). Size-fractionated Chl*a* concentrations were determined using a Turner Design fluorometer (10 AU) following 90 % acetone extraction (Parsons et al. 1984). Phytoplankton carbon biomass was estimated from Chl*a* measurements using the C:Chl*a* ratio of 117 determined during the cruise (Yang et al. 2008b).

For heterotrophic bacterial enumeration and biomass measurements, formalin-fixed samples were filtered onto 0.2-μm black polycarbonate filters (Poretics, Livermore, CA, USA) within a few days and stained with the nucleic acid stain DAPI (4′, 6-diamidino-2-phenylindole) (final concentration of 1 pg mL^{-1}) (Sigma Chemical, St. Louis, MO, USA). Filters were mounted on glass slides and stored in the dark at −20 °C on the vessel and −85 °C in the laboratory until the bacteria were counted using epifluorescence microscopy. Bacterial densities were converted into biomass using a conversion factor of 6.3 fgC $cell^{-1}$ (Kawasaki et al. 2011).

For heterotrophic nanoflagellates (HNF), 200 mL of seawater were preserved with glutaraldehyde (1 % final concentration), and subsamples of 100–150 mL were filtered through black Nuclepore filters (pore size, 0.8 μm), stained with 4′-6-diamidino-2-phenylindole (DAPI; final

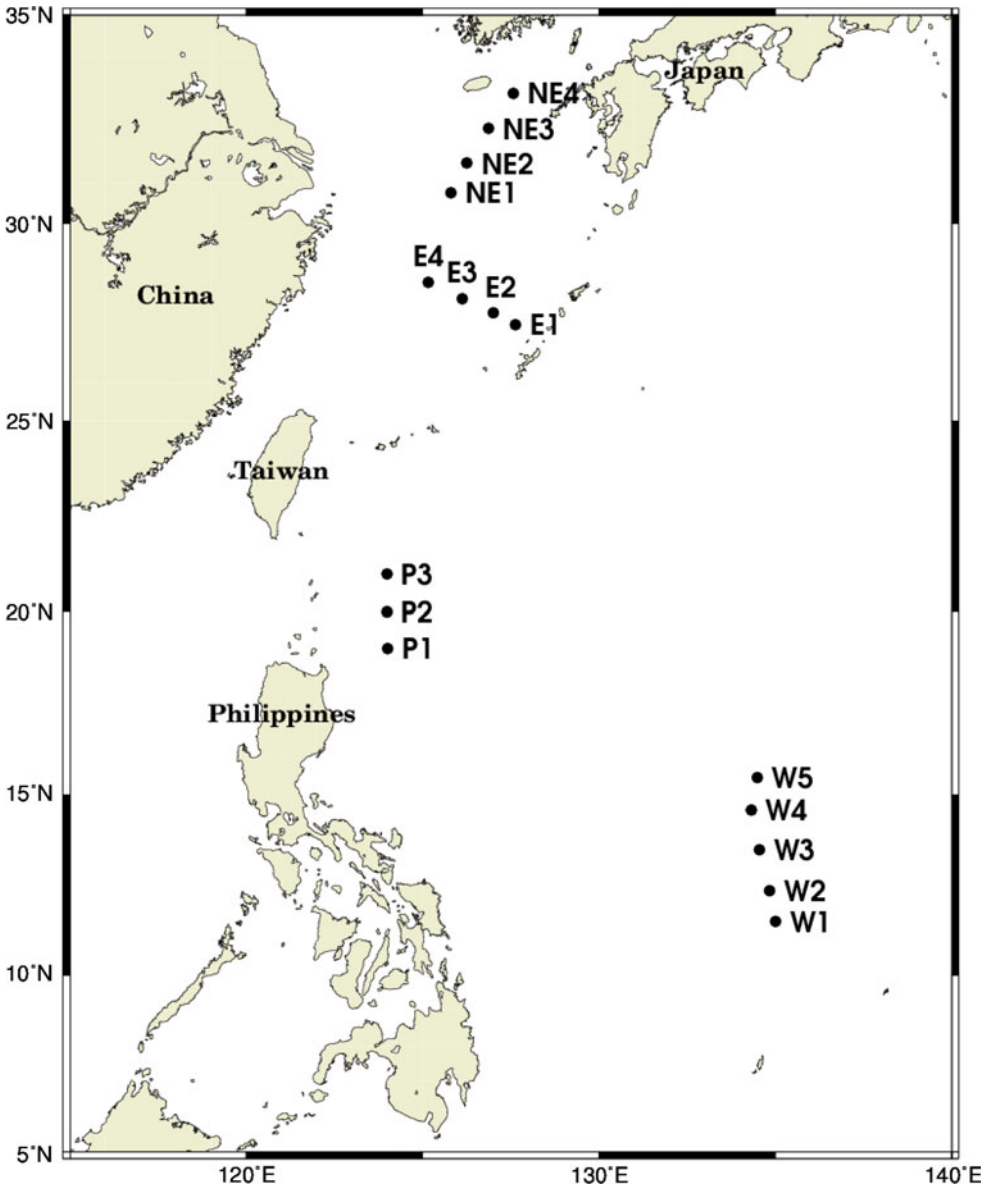

Fig. 1 Sampling stations in the four sampled regions of the North Pacific Ocean: warm pool (W1–5), Philippine Sea (P1–3), East China Sea (E1–4), northern East China Sea (NE1–4)

concentration of 5 μg mL^{-1}) and proflavin (0.33 %), and examined under an epifluorescence microscope (Nikon type 104) at a magnification of ×600–1,000. Heterotrophic flagellates were examined under both UV and blue excitation wavelengths to distinguish the autofluorescence of chlorophyll and other pigments, with cells counted in at least 50 fields for each sample. To determine the abundance of ciliates and heterotrophic dinoflagellates (HDF), 250 mL of water was preserved with acidic Lugol's iodine (5 % final concentration) and formalin (2 % final concentration), respectively (Yang et al. 2008a, 2009). The use of formalin allowed heterotrophic and autotrophic cells to be distinguished based on autofluorescence of autotrophic pigments under an epifluorescence microscope, while samples preserved with Lugol's iodine allowed better visualization of some taxa by inverted light microscopy and prevented major losses of ciliate's abundance compared to formalin (Sherr et al. 1993; Stoecker et al. 1994). Lugol's iodine preserved samples were stored in the dark and formalin preserved samples were stored at 4 °C in the dark until analysis. To determine abundances of ciliates, samples preserved in Lugol's solution were concentrated in sedimentation chambers for ≥48 h and were enumerated under an inverted microscope (Olympus IX 70) at ×200 magnification. To determine the abundance of HDF, samples preserved in formalin were concentrated in sedimentation chambers for ≥48 h in a refrigerator (4 °C), stained with DAPI (5 % final concentration), and then enumerated under an inverted epifluorescence microscope at ×200 magnification.

To estimate the carbon biomass of heterotrophic protists, cell volume was calculated by measuring cell dimensions

with an ocular micrometer in the microscope (Edler 1979). The following conversion factors and equations were used to translate cell volume into carbon biomass: 0.19 μgC μm^{-3} for naked ciliates (Putt and Stoecker 1989), carbon (pg) = 44.5 + 0.053 × lorica volume (μm^3) for loricate ciliates (Verity and Lagdon 1984), carbon (pg) = 0.216 (volume, μm^3) + 0.939 for heterotrophic dinoflagellates (Menden-Deuer and Lessard 2000), and 220 fgC μm^{-3} for heterotrophic nanoflagellates (Bøsheim and Bratbak 1987). No corrections were made for fixation-induced shrinkage as many other previous studies have done (Strom et al. 2007; Calbet et al. 2008; Yang et al. 2008a, 2009). Recent research has revealed that such a correction should apply to many other planktonic groups (Zarauz and Irigoien 2008), and yet universal factors for mixed samples containing diverse species have not been developed.

Mesozooplankton samples were collected using a "Bongo" net (mouth diameter 60 cm) fitted with 0.2-mm mesh nets equipped with a flow meter (Hydro-Bios, Kiel-Holtenau, Germany), which was towed obliquely at a depth of ~300 m to the surface at the sampling sites in the WP, the PS, and on the continental slope in the ECS. At sampling sites located on the continental shelf (<100 m in depth) in the ECS and NECS, the net was towed obliquely from near the bottom to the surface. Tow speed and duration were approximately 20 m min^{-1} and 1 h, respectively. One zooplankton sample (i.e., one cod-end bucket) was transferred to a 1-L sampling bottle and preserved with neutralized formaldehyde at a final concentration of 5–10 % (*v*/*v*) for later species identification. The other sample was used to measure the size-fractionated biomass and dry weight of each size fraction. Size fractionation was conducted on board by wet-sieving samples through nested sieves (0.5, 1.0, 2.0, and 5.0 mm), and four nominal size classes (0.2–0.5, 0.5–1.0, 1.0–2.0, and 2.0–5.0 mm, referred to as small, medium, large, and extra large zooplankton, respectively) were obtained. Each size of mesozooplankton were filtered on pre-weighed Whatman GF/C filters and rinsed twice with distilled water. The filters were frozen immediately at −20 °C. The filters were dried in the laboratory at 60 °C for 24 h, and the dry weight biomass was determined using an analytical balance (Sartorius ME235S, Goettingen, Germany) (Ara 2001). Dry weight was then converted into carbon biomass (mgC m^{-3}) using a conversion factor of 0.35 (Yamaguchi et al. 2005).

Multiple and robust linear regression analyses were conducted to examine the relationships between planktonic food web components. The errors of regression were examined for any violation of the assumptions of equal variance and normal distribution of errors. A minimal model for each regression analysis was obtained by comparing models based on Akaike's information criterion (AIC) (Akaike 1974; Venables and Ripley 2003). All statistical analyses were performed using R, an object-oriented open-source program (R Development Team 2006).

3 Results

3.1 Hydrography

Four types of water mass are found in this region (Fig. 2); Pacific Equatorial Surface Water (PESW), Subtropical Surface Water (STSW), East China Surface Water (ECSW), and North Pacific Intermediate Water (NPIW). A warmer (>28.5 °C) and less saline (<34.2) water mass is located south to 15°30′N, encompassing the area of the WP (W1–5), with a maximum salinity layer at a depth of about 150 m (Fig. 2). In both the NECS and ECS, water temperature and salinity profiles showed lower temperature and salinity, distinct from those observed in the WP and PS, suggesting that they are being affected by coastal shallow waters. Below the main thermocline, there was the NPIW of which the water temperature was below 13 °C and the salinity was less than 34.5.

3.2 Phytoplankton biomass

In the WP and PS, the depth-integrated average phytoplankton biomass was low at <15 mgC m^{-3} and fairly homogenous, but substantially increased by about 6 times to >80 mgC m^{-3} at NE1, with higher biomass found between the boundaries of the ECS and NECS (Fig. 3a).

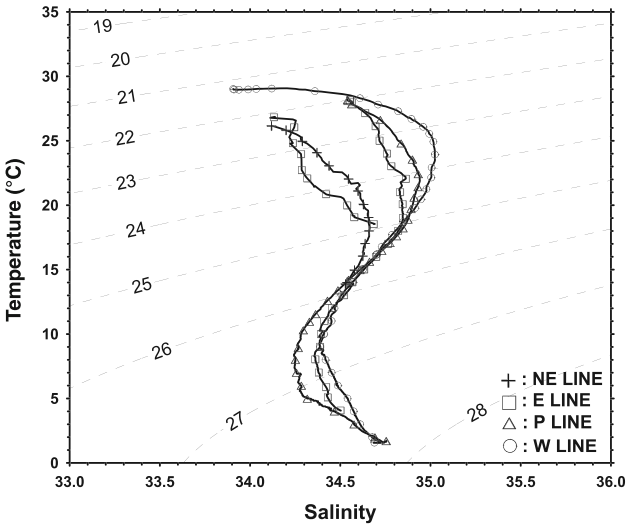

Fig. 2 Average temperature–salinity diagram of sampling stations in each sampling region showing various water masses detected during the cruise. See the text for details

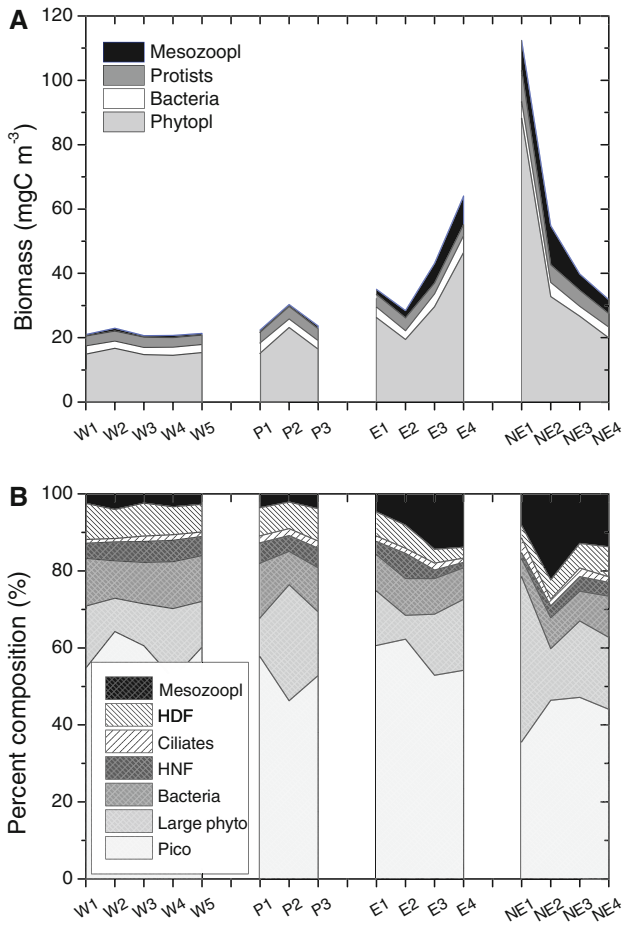

Fig. 3 Depth-integrated average biomass of autotrophic and heterotrophic plankton (**a**) and their percent composition (%) to total biomass at each sampling station (**b**)

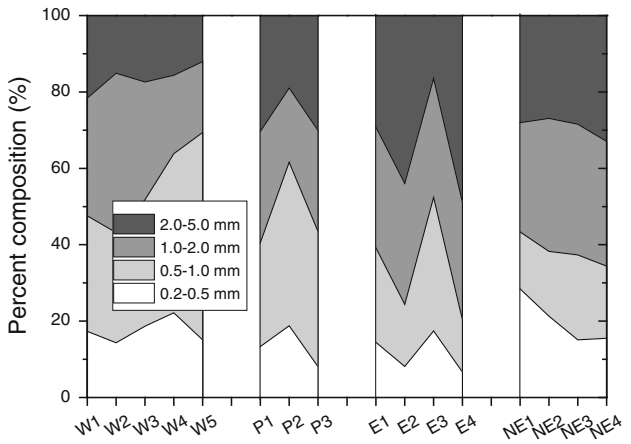

Fig. 4 Biomass composition by four different size classes of mesozooplankton (small 0.2–0.5 mm, medium 0.5–1 mm, large 1–2 mm, and extra large 2–5 mm)

Phytoplankton biomass comprised 60–80 % of total biomass measured, with higher contribution in the eutrophic waters (Fig. 3b). Within the phytoplankton, picophytoplankton dominated the phytoplankton biomass, comprising from 45 to nearly 90 % of total phytoplankton biomass (Fig. 3b), and was inversely related to phytoplankton biomass, with higher contributions in the WP and PS and the lowest contribution observed at NE1. Large phytoplankton (>3 μm) biomass exceeded that of picophytoplankton only at NE1.

3.3 Heterotrophic biomass

In most of the areas studied, heterotrophic biomass was only between 20 and 40 % of the total biomass (Fig. 3b). Both bacterial and HDF biomass dominated in oligotrophic waters (Fig. 3b), together comprising >60 % of the total heterotrophic planktonic biomass. Total heterotrophic protist biomass varied <2-fold latitudinally, ranging from 2.9 to 5.6 mgC m^{-3}. Despite having the lowest density (generally <30 cells L^{-1}) among the protistan plankton, HDF contributed the most to protist biomass due to its large size. HNF contributed the second largest amount to biomass, with ciliates comprising the lowest proportion of protist biomass. The contribution of heterotrophic protists to total planktonic biomass was generally lower in eutrophic waters than in oligotrophic waters.

Mesozooplankton biomass contributed the least to total planktonic biomass in oligotrophic waters (Fig. 3b). Its biomass contribution, however, increased substantially toward eutrophic waters and exceeded that of the protists in the ECS and NECS. The biomass of the largest size class of mesozooplankton (2–5 mm in length) comprised the lowest fraction in the WP region, whereas the medium-size class (0.5–1 mm in length) contributed the least to mesozooplankton biomass in the NECS (Fig. 4). Consequently, the fraction of the medium-size class was inversely related to increasing Chl*a* concentration ($R^2 = 0.46$, $P = 0.004$ on a log–log plot).

3.4 Biomass relationships along the trophic gradient

The biomass of all heterotrophic bacteria, ciliates, and HDF generally inclined with phytoplankton biomass, but no positive pattern was found for HNF (linear regression, slope = 0.14, $P = 0.19$ on a log–log plot; Fig. 5). Mesozooplankton biomass inclined greater than the degree of phytoplankton biomass (robust linear regression, slope = 1.96, $R^2 = 0.76$ on a log–log plot).

The biomass of total heterotrophs relative to that of autotrophs did not show any pattern with autotrophic biomass (Fig. 6a). However, examining each heterotrophic constituent showed that the ratios for bacteria, HNF, and HDF all demonstrated sharp declines with autotrophic biomass (Fig. 6b; Table 1). The ratio for both ciliates and

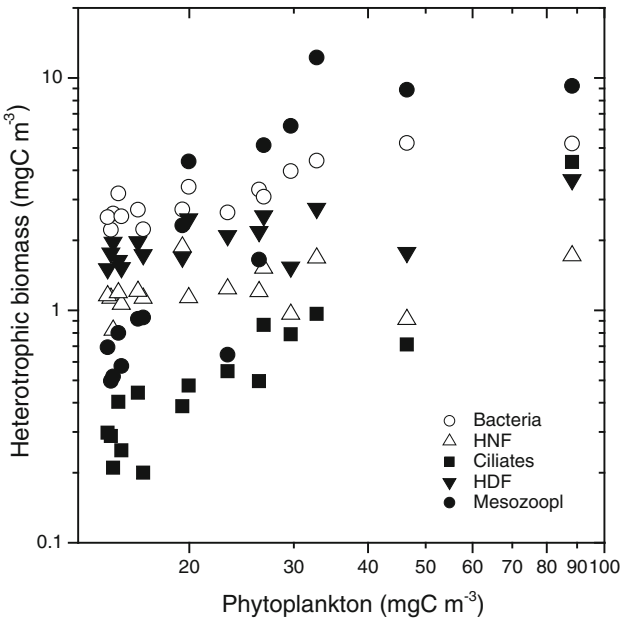

Fig. 5 Biomass relationship between phytoplankton and other heterotrophic plankton on a log–log scale. Results of the regressions are shown in Table 1

mesozooplankton, on the other hand, showed upward trends (Table 1), except for the mesozooplankton biomass in the water with the highest phytoplankton biomass (Fig. 5).

Regression analyses of potential prey showed total mesozooplankton biomass (t.mesozoopl) was associated mostly with the biomass of ciliate and HDF and to a lesser degree with large phytoplankton (lphyto), of which the linear relationship is given as

$$\mathrm{Log}_{10}(\text{t.mesozoopl}) = -1.5 + 0.13(\text{lphyto}) + 0.49(\text{HDF}) + 1.84(\text{ciliates})\left(\text{Adjusted } R^2 = 0.79, p < 0.01\right).$$

Both HDF and ciliates were positively but loosely associated with phytoplankton. HNF was not associated with either pico- or large phytoplankton ($P = 0.16$), which is most likely due to heavy predation pressure by larger protists and zooplankton, as implied in its no upward trend with phytoplankton biomass (Fig. 5).

To examine the release of protozoan grazing pressure on lower food chain constituents due to mesozooplankton predation on the protists, heterotrophic bacteria and picophytoplankton biomass were regressed onto the biomass ratio of mesozooplankton to the sum of HDF and ciliates, which is considered as a proxy for predation pressure on ciliates and HDF by mesozooplankton (*sensu* Calbet and Landry 1999). Assessed this way, both bacteria and picophytoplankton were significantly positively related to the biomass ratio of mesozooplankton to the sum of HDF and ciliates (Fig. 8a, c; $R^2 = 0.59$, $P = 0.0003$ for bacteria and $R^2 = 0.40$, $P = 0.005$ for picophytoplankton). No positive relationship was apparent for either heterotrophic nanoflagellates or large phytoplankton.

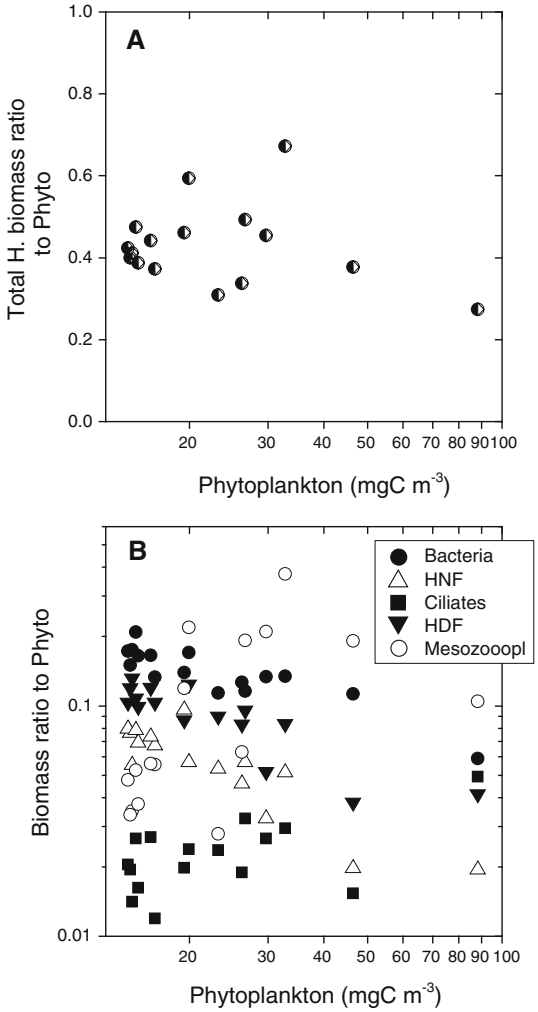

Fig. 6 Relationship between the ratio of total heterotrophic biomass to total autotrophic biomass (**a**) and the ratio of the biomass of each constituent of heterotrophic plankton to autotrophic biomass (**b**)

Table 1 Results of regression analyses of the ratio of each heterotrophic biomass to that of phytoplankton regressed onto $\log_{10}$-transformed phytoplankton biomass

Biomass ratio	Slope	R^2	P
Bacteria	−0.51	0.79	<0.001
HNF	−0.84	0.79	<0.001
HDF	−0.66	0.75	<0.001
Ciliates	0.39	0.32	0.02
Mesozooplankton	0.89	0.30	0.03

HNF heterotrophic nanoflagellates, *HDF* heterotrophic dinoflagellates

4 Discussion

Phytoplankton biomass dominated the planktonic biomass across the waters of the study regions (Fig. 3b). In oceanic environments, bacterial biomass often exceeds or is comparable to that of phytoplankton (Cho and Azam 1990; Caron et al. 1995; Gasol et al. 1997). Bacterial biomass estimates can vary considerably depending on the conversion factors used (Caron et al. 1995). In the present study, we adopted the most updated bacterial cell carbon conversion factor of 6.3 fgC cell^{-1} in the north Pacific waters (Kawasaki et al. 2011), instead of the previously widely used one of 20 fgC cell^{-1} (Lee and Fuhrman 1987), which effectively reduced bacterial biomass in the present study by two-thirds. Conversion factors as low as 2–9 fgC cell^{-1} have been reported (Christian and Karl 1994; Gundersen et al. 2002). Consequently, bacterial biomass was only 6–21 % of phytoplankton biomass, much smaller than the range of 18–60 % if the old conversion factor were used.

Inverse relationships were found between phytoplankton biomass and the ratio of heterotrophic biomass (i.e., bacteria, HNF, and HDF) relative to that of phytoplankton (Fig. 7). Our results also appear to show two exceptions to this relationship, in that neither ciliates nor mesozooplankton showed inverse patterns. Rather, the biomass ratio of both ciliates and mesozooplankton relative to phytoplankton inclined along the trophic gradient (Fig. 7). Picophytoplankton dominate the phytoplankton in nearly all regions (Fig. 3b), but they are unlikely to be a major food as they are too small for effective grazing by mesozooplankton (Johnson et al. 1979; Stoecker and Capuzzo 1990). This suggests that mesozooplankton biomass along the gradient becomes greater than the degree at which phytoplankton biomass becomes larger, and therefore mesozooplankton are likely to require food other than phytoplankton for such an upward biomass trend.

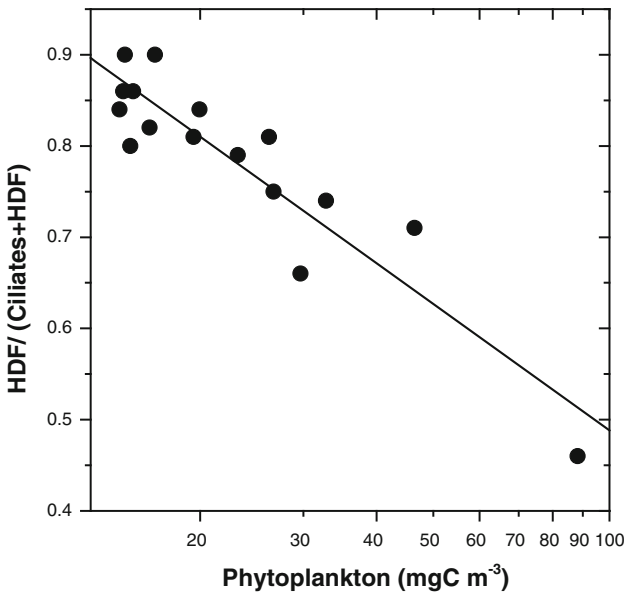

Fig. 7 The proportion of heterotrophic dinoflagellate biomass relative to the summed biomasses of ciliates and heterotrophic dinoflagellates along a trophic gradient as expressed phytoplankton biomass

Ciliates appeared to be favored over other organisms as food sources for mesozooplankton, given the much stronger response of mesozooplankton biomass to a given biomass incline of ciliates than to an incline in large phytoplankton (Table 1). Planktonic ciliates are known to consume primarily nanoplankton (Gifford 1985; Verity 1985) and picoplankton (Rassoulzadegan et al. 1988; Sherr and Sherr 2002; Jochem 2003), thus linking microbial components to mesozooplankton. For instance, daily mesozooplankton grazing on phytoplankton in the equatorial Pacific Ocean is generally <5 % of the total Chl*a* concentration where picoplankton dominate the phytoplankton, and most mesozooplankton carbon consumption derives from ciliates which apparently depend on picophytoplankton for food (Roman and Gauzens 1997).

The mesozooplankton biomass was also to some extent positively related to HDF and large phytoplankton. The relative importance of ciliates, HDF, and diatoms as food for mesozooplankton has been reviewed (Saiz and Calbet 2011). Contrary to conventional notions, analysis indicates that diatoms contribute only 8 % to copepod diets globally. HDF, despite renewed views of its role as a key component of microzooplankton (Sherr and Sherr 2007), only constitutes an important share of copepod diets in oligotrophic systems (Saiz and Calbet 2011). HDF may be in direct competition with ciliates for phytoplankton food (Fig. 7), and appear to be generally outcompeted by ciliates. HDF are likely to be more quantitatively significant consumers of large phytoplankton than of small picophytoplankton, and HDF potentially even compete with mesozooplankton for large food (reviewed in Sherr and Sherr 2007).

Although heterotrophic protists are cited as preferential food for mesozooplankton, the significant relationship between phytoplankton and mesozooplankton suggests that mesozooplankton still seem to require large phytoplankton for better growth. For instance, *Calanus sinicus*, a large and dominant calanoid copepod in the northern ECS, ingests ciliates preferentially over other components of the microplankton, and the egg production rate of female *C. sinicus* increases with ciliate standing stock. While gross growth efficiency (GGE) increases with the proportion of ciliates in the diet, the GGE of copepods fed on ciliates is only 13 % (Huo et al. 2008). These results indicate that ciliates may have higher nutrient quality than other food items, but that the diet of *C. sinicus* is nutritionally incomplete (Huo et al. 2008). Some phytoplankton may

provide an easy, digestible and rich food as indicated by their short gut transit time (Tirelli and Mayzaud 2005).

The results of fatty acid composition of *Pleuromamma* sp., an important copepod in oceanic waters in the North Pacific (Haury 1988; Ko et al. 2009), demonstrates shift in the copepod prey preference. Picophytoplankton-based food webs appear to be a major food source for the copepods in the WP and PS (Ko et al. 2009), whereas the fatty acid composition of *Pleuromamma* sp. collected in the ECS and NECS shows that the primary food of the copepod in those waters is diatoms (Ko et al. 2009). When the concentration of large diatoms is low, as in the WP and PS, the copepod may depend predominantly on microbial-loop-linked food, but switches to diatoms as a primary food as the large phytoplankton concentration becomes higher toward the NECS and ECS (Ko et al. 2009). A lack of large phytoplankton may in part explain the larger fraction of small- and medium-sized mesozooplankton (0.2–1 mm) in the WP and PS (Fig. 4) compared with their contribution to total mesozooplankton biomass in the ECS and NECS.

Top-down trophic cascade effects of predation generally lead to predation relief for intermediate trophic levels and subsequent increases in the density of lower trophic levels (Nejstgaard et al. 1997; Jens et al. 2001; Samuelsson et al. 2006; Saiz and Calbet 2011). For instance, high mesozooplankton concentrations reduce the abundance of ciliates, and this reduction in turn promotes the growth of small heterotrophic flagellates (Samuelsson et al. 2006) or phytoplankton (Nejstgaard et al. 1997; Zhang et al. 2007). In the present study, both bacteria and picophytoplankton were significantly positively related to the biomass ratio of mesozooplankton to the sum of HDF and ciliates (Fig. 8a, c). Such a relationship could arise either from predation relief of bacteria and picophytoplankton or from mesozooplankton consumption of phytoplankton over protistan plankton. Picophytoplankton dominate the phytoplankton biomass (Fig. 3b), and small phytoplankton often escapes mesozooplankton grazing, with increased biomass frequently observed during incubation experiments ("negative grazing") (Jang et al. 2010; Choi, unpublished data). The relationship observed in Fig. 8 appears to be a result of relief on bacteria and picophytoplankton from predation by ciliates and HDF (Fig. 8a, c). No positive relationship, however, was apparent for HNF or large phytoplankton, which indicates that mesozooplankton may ingest various planktonic groups including HNF, but are less likely to directly consume bacteria and picophytoplankton. Small- and medium-sized mesozooplankton (generally <1 mm in length), including adults and copepodites of genus *Oithona* spp. and other zooplankton, are known to preferentially graze on ciliates and larger protists (Jonsson and Tiselius 1990; Nakamura and Turner 1997; Turner 2004; Bollens et al. 2005; Bouley and Kimmerer 2006) and even to feed on fecal pellets of other copepods (Poulsen and Kiørboe 2006; Iversen and Poulsen 2007). However, they are also capable of feeding on nanoflagellates at rates comparable to those at which they ingest large prey (Vargas and Gonzalez 2004). HNF is likely to be a primary grazer on bacteria, and HDF and ciliates on picophytoplankton, thus the release from predation pressure on protists by mesozooplankton seems plausible only for very low trophic organisms.

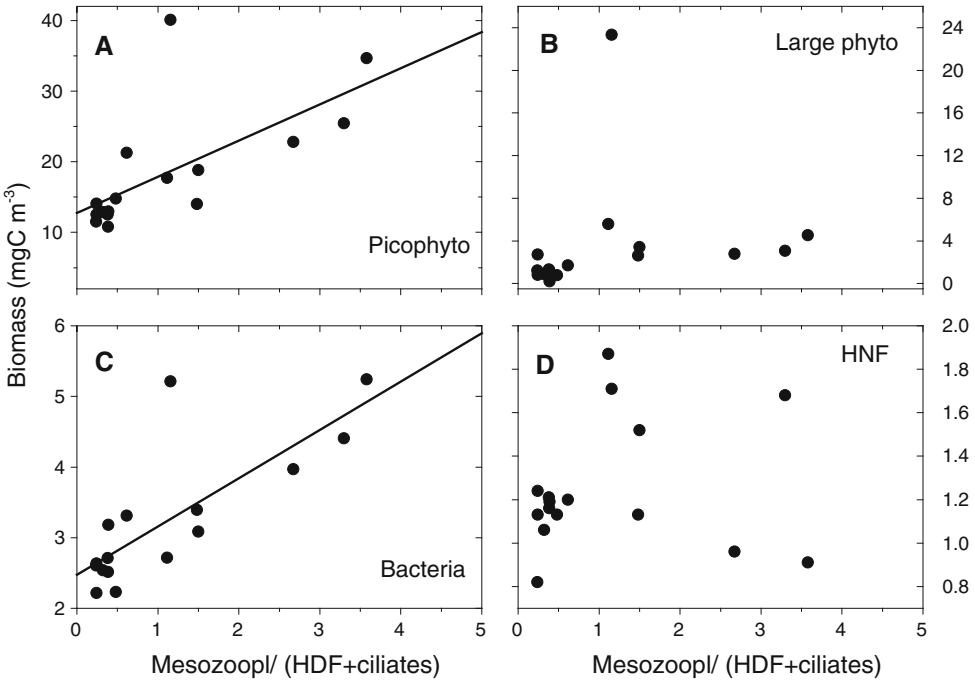

Fig. 8 Relationship between each planktonic constituent and the biomass ratio of total zooplankton to the sum of ciliates and heterotrophic dinoflagellates

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