Planktonic food web structure at a coastal time-series site: II. Spatiotemporal variability of microbial trophic activities

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Graphical Abstract:

Highlights:

- Nutrient concentrations and microbial abundances were higher nearshore than offshore
- Rates of growth and grazing did not differ substantially among sites or seasons
- The amount of carbon consumed depended on the standing stock of the prey population
- Phytoplankton were the main carbon source nearshore and during spring and summer
- Phytoplankton and bacteria were similarly consumed offshore and during fall and winter

Abstract

The grazing activities of phagotrophic protists on various microbial assemblages play key roles in determining the amount of carbon available for higher trophic levels and for export out of the photic zone. However, comparisons of the proportion of carbon consumed from the phytoplankton (cyanobacteria + photosynthetic eukaryotes) and heterotrophic bacteria (bacteria + archaea, excluding cyanobacteria) are rare. In this study, microbial community composition, phytoplankton growth and mortality rates (total chlorophyll *a*, *Synechococcus*, *Prochlorococcus*, and photosynthetic picoeukaryotes), and bacterial mortality rates were measured seasonally from 2012-2014 at three environmentally distinct sites in the San Pedro Channel, off the coast of southern CA, USA. Higher nutrient concentrations at the nearshore site supported community standing stocks that were 1.3-4.5x those found offshore, yet average growth and grazing rates of the phytoplankton and bacterial assemblages were generally similar between sites and across seasons. Thus, the amount of carbon consumed by the grazer assemblage was largely dictated by prey standing stocks. Heterotrophic bacteria constituted an important source of carbon for microbial consumers, particularly at the two offshore sites where bacterial carbon consumed was roughly equivalent to the amount of phytoplankton carbon consumed. Carbon removal by grazers at the nearshore station was predominantly from the diatoms, which were the primary component of the photosynthetic community at that site. This study highlights the significant contribution of protistan-bacterial trophic interactions to planktonic food webs and provides unique community composition and turnover data to inform biogeochemical models.

1. Introduction

Marine microbes (bacteria, archaea, and microbial eukaryotes) are a functionally diverse group of single-celled organisms that, together with viruses, play critical roles in the global cycling of key elements (C, N, P, and S)(Karner et al. 2001, Suttle 2005, Sherr et al. 2007, Caron et al. 2012, Fuhrman et al. 2015). Oceanic primary production is overwhelmingly dominated by planktonic microbes (Field et al. 1998), and much of the organic carbon transferred to higher trophic levels or exported out of the photic zone by these species is directly mediated by the activities of microbial consumers (Sherr & Sherr 1994, Sherr & Sherr 2002, Calbet & Landry 2004, Schmoker et al. 2013). Yet, accurate descriptions of the abundances, biomasses, and trophic activities of microbial assemblages are incomplete and confounded by the extremely high biodiversity and many nutritional and life strategies of marine microbes (Caron et al. 2012, Worden et al. 2015, Caron 2016). A better understanding of these assemblages and their activities are necessary as climate change may restructure the community composition, primary productivity, trophic interactions, and export efficiency of microbial communities (Doney et al. 2012, McMahon et al. 2015).

The considerable amount of phytoplankton or bacterial carbon consumed by protistan grazers has profound implications for the biogeochemistry of an ecosystem. Food web efficiency decreases as the number of trophic interactions increases due to respiratory losses of carbon. Thus, food webs in which large amounts of primary productivity are routed through the heterotrophic bacterial assemblage (“the microbial loop”; Azam et al. 1983) tend to remineralize a substantial portion of the organic matter and are less efficient than classical phytoplankton-macrozooplankton trophic interactions at moving energy and carbon up into higher trophic levels. Nonetheless, the microbial loop is an important mechanism by which some non-living

particulate and dissolved organic carbon is salvaged (Strom 2000). The proportion of carbon flowing directly from phytoplankton into herbivorous zooplankton, relative to that passing through non-living organic matter into the heterotrophic bacteria and their consumers, therefore affects overall food web efficiency in the plankton. Direct comparisons of these key trophic connections have rarely been conducted.

We investigated the spatial and temporal variability of microbial standing stocks, community composition, and trophic interactions at a coastal ocean site in the San Pedro Channel. The region is the site of a long-term oceanographic study of plankton dynamics (the San Pedro Ocean Time-series, SPOT; <https://dornsife.usc.edu/spot/>). The SPOT station is located equidistant between the Port of Los Angeles to the northeast and Santa Catalina Island to the southwest (~45 km offshore). The Port of Los Angeles receives extensive runoff from metropolitan and industrial land development from a population of ~18 million residents. Waters adjacent to Santa Catalina Island are more oceanic and pristine in nature than near the port, lack the substantial anthropogenic impact of a large metropolitan area, and are the site of a marine protected area. Episodic wind-driven upwelling and rainfall events and mild seasonality drive changes in primary productivity in the San Pedro Channel (Nezlin et al. 2012). These changes are accompanied by distinct seasonal shifts in prokaryotic (Chow et al. 2013, Cram et al. 2014) and eukaryotic (Countway et al. 2010, Kim et al. 2014, Hu et al. 2016) community composition. The Channel provides an environmentally diverse landscape with recurrent seasonal patterns of microbial community productivity and composition in which to study seasonal and spatial drivers of microbial community structure and function.

In this study, microbial community abundances and rates of phytoplankton growth, phytoplankton mortality, and bacterial mortality were measured seasonally at the Port of Los

Angeles, the SPOT station, and near Catalina Island. Microbial community composition and standing stocks varied spatially and temporally, however, rates of growth and grazing mortality (d^{-1}) were similar among sites and seasons. Thus, differences in the amount of carbon ingested from the various prey assemblages at the different sites and seasons were largely related to differences in standing stock. Mean daily phytoplankton carbon ingested by grazers ranged from 0.18 to 18.5x the mean bacterial carbon consumed, with high values of carbon flow through herbivorous microconsumers attributable to increased diatom abundances onshore and during the spring season. The mean daily carbon consumption of the heterotrophic bacteria (bacteria + archaea, excluding cyanobacteria) and photosynthetic picoplankton (coccioid cyanobacteria + photosynthetic picoeukaryotes) by grazers was similar in magnitude at all sites. This study highlights the importance of bacteria as a food source for higher trophic levels, a trophic interaction that is often not explicitly included in ecosystem models but can be as important as the link between phytoplankton and their grazers.

2. Materials and Methods

2.1 Study site characterization and sample collection

Seasonal microbial standing stocks and trophic dynamics were examined across a range of anthropogenically affected sites spanning the San Pedro Channel: the heavily impacted Port of Los Angeles (Port of LA, ~3 km offshore within the breakwater, 33°42.75'N, 118°15.55'W), the coastal ocean San Pedro Ocean Time-series station (SPOT, ~17 km offshore, 33°33'N, 118°24'W), and a marine protected area off Santa Catalina Island (Catalina, ~45 km offshore, 33°27.17'N, 118°28.51'W) (Fig. 1). The approximate water column depths at the Port of LA, SPOT, and Catalina stations were 15 m, 900 m, and 140 m, respectively. Water collection was

conducted quarterly to assess microbial standing stocks and measure seasonal differences in microbial rate processes. Sampling occurred during the winter (January), spring (March-April), summer (July), and fall (October) of 2012-2014. Surface water (0 to 1 m depth) was collected by submerging 23 L, acid-cleaned (5% HCl), polycarbonate carboys, inverted with the spigot open, and allowing water to gently enter through the mouth of the carboy. Once full, the spigot was closed, the lid replaced underwater, and the carboy was stored in the dark onboard the ship until processing within 4 h of sampling. The collection method was carried out to reduce bubbling that damages delicate microzooplankton.

Physical and chemical parameters were measured at each site to characterize differences across the San Pedro Channel. Temperature was measured during each cruise using a YSI 63 handheld meter (Yellow Springs Instruments, Yellow Springs, Ohio) or profiling natural fluorometer (PNF) (Kiefer et al. 1989). Salinity was measured using a YSI 63 handheld meter or refractometer. Samples for inorganic nutrient measurements were collected at each site by adding 0.2 μm -filtered seawater to 20 mL plastic scintillation vials that were pre-washed with 5% HCl and rinsed three times with 0.2 μm -filtered seawater. Nutrient samples were frozen at -20°C until processed for ammonium, phosphate, nitrite (all 0.1 μM limit of detection), nitrate plus nitrite (0.2 μM limit of detection), and silicate (1.0 μM limit of detection) at the Marine Sciences Institute Analytical Lab at UCSB (<http://www.msi.ucsb.edu/services/analytical-lab>).

2.2 Community composition and biomass

The abundances of various components of the picophytoplankton (0.2-2.0 μm in size)—specifically *Synechococcus*, *Prochlorococcus*, and photosynthetic picoeukaryotes—were determined by flow cytometry. Triplicate samples were collected at the beginning of the

incubation for each site, passed through a 20 μm filter, preserved with 1% formalin (final concentration), and stored at -80°C until flow cytometric analysis. Flow cytometry was performed using a FACSCalibur flow cytometer (Becton Dickinson, San Jose, California). The autofluorescence of photosynthetic pigments and forward scatter were used to distinguish these three groups of picoplankton. Average cell abundances of these plankton categories were converted to biomasses using carbon conversion factors of 200 fg C cell⁻¹ for *Synechococcus* (Caron et al. 1995), 90 fg C cell⁻¹ for *Prochlorococcus* (Casey et al. 2013, Martiny et al. 2016), and 183 fg C μm^{-3} for photosynthetic picoeukaryotes (assuming an average picoeukaryote radius of 1 μm)(Caron et al. 1995). Bacterial abundances (bacteria + archaea) were measured by flow cytometry using a standard staining procedure (SYTO 13; ThermoFisher Scientific S7575) (del Giorgio et al. 1996). Bacterial abundance was converted to carbon biomass assuming a carbon conversion factor of 15 fg C cell⁻¹, which is a conservative estimate for bacteria characteristic of coastal regions (Caron et al. 1995, Fukuda et al. 1998, Kawasaki et al. 2011, Buitenhuis et al. 2012).

Nanoplankton abundances (photosynthetic and heterotrophic protists, 2-20 μm in size) were determined using epifluorescence microscopy on samples collected at the beginning of each experiment. Aliquots of seawater (150 mL) were preserved in 1% formalin (final concentration) for each site. Preserved aliquots (15 mL for Port of LA; 30 mL for SPOT and Catalina) were filtered down to ~ 1 mL onto 25 mm, 0.2 μm blackened polycarbonate filters and stained with 50 μL of a 1 mg mL⁻¹ working solution of 4',6'-diamidino-2-phenylindole (DAPI; Sigma D9542) for 5-10 minutes (Sherr et al. 1993). Samples were then filtered and rinsed, the filters placed onto glass slides, a drop of immersion oil placed on each filter, and a coverslip added and sealed with clear nail polish. Slides were prepared in triplicate and stored at -20°C until analyzed by

epifluorescence microscopy. Phototrophic and heterotrophic nanoplankton were differentiated by the presence or absence of chlorophyll autofluorescence when viewed with blue-light excitation. Nanoplankton biomasses were calculated from cell abundances using a carbon conversion factor of 183 fg C μm^{-3} (Caron et al. 1995), with an assumed average nanoplankton radius of 1.5 μm . Only slides prepared for March 2012, July 2012 (Port of LA only), October 2013, and all months in 2014 were included in subsequent analyses because some slides were unsuitable for counting. Nanoplankton biomass was excluded from the total phytoplankton standing stock value when calculating carbon flow to higher trophic levels (Fig. 8) in order to facilitate the comparison of all sampling dates.

Microplankton abundances were enumerated from formalin-preserved, 200 mL samples (final concentration 1%) collected at the beginning of each experiment. Aliquots of preserved samples (25-100 mL) were settled in Utermöhl chambers for 24 to 48 h and counted using an inverted light microscope at 400x magnification (Utermöhl 1958). Diatom, dinoflagellate, and ciliate abundances were recorded, and carbon biomasses were calculated using a carbon conversion factor of 0.138 ng C cell⁻¹. This value is an average value determined from the phototrophic microplankton data presented in Caron et al. (1995). Photosynthetic and heterotrophic dinoflagellates were not distinguished in this study, and therefore total dinoflagellate biomass was split evenly between these nutritional modes when assessing the composition of the phytoplankton and grazer communities.

A detailed discussion of the carbon biomass conversion factors selected for our study region can be found in Caron et al. (in revision).

2.3 Phytoplankton growth and grazing experiments

2.3.1. Experimental set-up

A modified dilution method was used to determine the growth and grazing rates of the total phytoplankton community as well as three ecologically distinct groups of picoplanktonic phototrophs: *Synechococcus*, *Prochlorococcus*, and photosynthetic picoeukaryotes (Landry & Hassett 1982, Landry et al. 1995). The dilution method allows simultaneous measurement of phytoplankton growth (μ) and mortality (m) through sequential dilution of experimental water with 0.2 μ m diluent. Whole, unfiltered seawater (WSW) from two 23 L carboys collected at each site was joined into a 50 L carboy to ensure homogeneity between treatments. Diluent was prepared from water collected at each site by filtering WSW through an acid-cleaned and rinsed Pall 0.2 μ m Acropak 1550 Capsule Filter with Supor Membrane. A five-point dilution series (100%, 80%, 60%, 40% and 20% WSW) was established in acid-washed, polycarbonate, 2.3 L bottles for each site. All treatments were prepared and incubated in triplicate, with care taken to reduce bubbling that may harm delicate microzooplankton. Bottles in the dilution series were nutrient-enriched, with 1 mL of nutrient stock (final incubation concentrations of 10 μ M NaNO₃, 1 μ M NH₄Cl, 0.7 μ M NaP₂PO₄·H₂O) added to each bottle to account for the possibility of nutrient-limited phytoplankton growth in the more-dilute treatments (Landry et al. 1995). An unenriched treatment of 100% WSW bottles (in triplicate) was prepared and compared to the enriched WSW treatment for each experiment to assess the impact of nutrient addition on phytoplankton growth rates. Also, an unenriched, <200 μ m-filtered treatment was prepared to investigate the grazing impact of the micro- and nanozooplankton in the absence of mesozooplankton. Bottles were incubated in mesh bags composed of neutral density screening (mimicking 50% incident light) and incubated *in situ* for 24 h.

2.3.2 Sample collection and analysis

Chlorophyll *a* (a proxy of total phytoplankton biomass) and cell abundances for specific picoplankton were measured initially and at the end of the incubations to calculate growth and grazing rates of the entire photosynthetic community and the three picoplankton groups according to the modified dilution method (Landry et al. 1995). Chlorophyll *a* samples were prepared by filtering 50-500 mL of WSW onto 25 mm GF/F filters and stored at -20°C until analysis within the week. Triplicate samples were analyzed for initial WSW, <200 µm filtrate, and <0.2 µm filtrate. Duplicate samples were analyzed from triplicate bottles within each treatment at the end of the incubation. Filters were extracted with 4 mL of 100% acetone at -20°C overnight in the dark, and processed on a calibrated Trilogy Laboratory Fluorometer (Turner Designs, San Jose, CA) using the non-acidification method (Welschmeyer 1994). Samples collected and preserved for flow cytometry were processed as described in section 2.2.

Net growth rates (nutrient-enriched growth (μ_n); y-intercept of the regression) and mortality rates (m ; slope of the regression) of the total phytoplankton (based on chlorophyll *a*) or specific assemblages (based on flow cytometric counts) were determined using Model I linear regressions of plots of apparent growth rate (y-axis) versus dilution factor (x-axis) assuming exponential growth of the phytoplankton (Landry & Hassett 1982). Intrinsic growth rates (μ_0) of the unenriched phytoplankton community were determined from growth in the unenriched treatment and the mortality rate (Landry et al. 1995).

The daily percentage of total phytoplankton standing stock (%SS) consumed by grazers was calculated according to the following equations,

$$\%SS = G * (100/C_0)$$

$$G = m * C_m$$

$$C_m = C_0[e^{(\mu_0 - m)t} - 1]/(\mu_0 - m)t$$

where μ_0 = the unenriched growth rate of the phytoplankton (d^{-1}), m = the mortality rate of the phytoplankton (d^{-1}), t = length of the incubation (d), C_0 = the initial Chlorophyll *a* concentration (or picophytoplankton abundance), C_m = the mean chlorophyll *a* concentration (or picophytoplankton abundance) during the incubation, and G = the grazing impact of the consumers (Landry et al. 2000, Landry & Calbet 2004).

2.4 Bacterivory by FLB disappearance

Fluorescently-labeled bacteria (FLB) were prepared from a monoculture of *Dokdonia donghaensis* according to standard protocol (Sherr et al. 1987, Caron 2001). Briefly, *D. donghaensis* was cultured in Zobell medium, harvested by centrifugation, and resuspended and incubated in 0.2 μm filtered seawater to starve the bacteria and induce shrinkage to better mimic bacterial size in natural assemblages (rod-shaped, average length = 1 μm). Bacteria were then stained with 5-(4,6-dichlorotriazin-2-yl) aminofluorescein (DTAF), heat-killed, rinsed three times, aliquoted, and stored at -80°C until the time of the experiment. FLB aliquots for the duration of the study were prepared in a single batch to ensure homogeneity across experiments.

FLB incubations were conducted in conjunction with the dilution experiments at each site beginning in July 2012. Two sets of triplicate, 2.3 L, polycarbonate bottles were completely filled with experimental water; one set received WSW to assess FLB disappearance related to grazing, while the other set received 0.2 μm filtered seawater to serve as a control for losses unrelated to grazing. The FLB stock was vortexed, filtered through a 3.0 μm polycarbonate filter to remove clumps, and added to each bottle at ~10% of the natural bacterial abundance (average T_0 FLB concentration = 1.52×10^5 cells mL^{-1} ; average natural bacterial abundance = 1.6×10^6 cells mL^{-1}). Samples (2 mL) were removed from each bottle immediately after adding FLB and

at the end of the incubations, preserved with 1% formalin (final concentration), flash frozen in liquid nitrogen, and stored -80°C until counted using flow cytometry. Changes in FLB abundances in the WSW treatment were used to calculate removal of the bacterial community due to grazing (taking non-grazing changes into account from the controls) according to the following equation,

$$g = \ln(F_t/F_0)*(-1/t)$$

where g = bacterial grazing mortality (d^{-1}), F_0 and F_t = the number of FLB at the beginning and end of the incubation, respectively, and t = length of the incubation (d) (Marrasé 1992).

2.5 Statistical analysis

All statistical analysis was carried out in R (R Core Team 2014), with a critical value of 0.05 denoting significance. Linear regression analysis (Model I) was used to relate dilution level to phytoplankton growth rate, enabling the determination of m , μ_n , and μ_0 for the phytoplankton groups. Differences in the phytoplankton growth rates between the nutrient-enriched and unenriched treatments, as well as between the WSW and <200 μm treatments were determined with a Welch Two-Sample T-Test. One-way analysis of variance (ANOVA) paired with Tukey's Honest Significant Difference Test was used to determine significant differences in mean values between sites and seasons. A median percentile bootstrap, a robust option for datasets containing tied-values, was employed to assess significant differences in the median values between sites and seasons. Spearman's rank order correlation analysis was applied to determine significant relationships between environmental variables and the population abundances, growth rates, and mortality rates of the prey populations studied.

3. Results

3.1 Environmental and biological context at the three study sites

Temperatures ranged from 13.1 to 21.6°C throughout the annual cycle, with the Port of LA values averaging ~1°C lower than those measured at the SPOT station and near Catalina on all sampling dates (Table 1). Salinity was relatively constant for all sampling dates ($\bar{x} = 32.8$ ppt), with no onshore-offshore salinity gradient observed (data not shown). Chlorophyll *a* values were consistently highest at Port of LA on all dates (range 2.06 – 15.0 $\mu\text{g L}^{-1}$). The ranges of chlorophyll *a* values at the SPOT station and Catalina were 0.24 – 5.86 $\mu\text{g L}^{-1}$ and 0.20–2.73 $\mu\text{g L}^{-1}$, respectively, and were $<1 \mu\text{g L}^{-1}$ on the majority of sampling dates (Table 1). Mean concentrations of silicate, ammonium, nitrate, nitrite, and phosphate were significantly higher at Port of LA than at the SPOT station and mean silicate, nitrite, and phosphate were significantly higher at Port of LA than Catalina ($p < 0.05$, Fig. 2).

Port of LA had consistently higher standing stocks of microbial biomass than the SPOT station or Catalina, and seasonal maxima at the latter sites were less than the seasonal minimum at Port of LA (maxima were 65 and 61 $\mu\text{g C L}^{-1}$ at the SPOT station and Catalina, respectively, versus a minimum of 73 $\mu\text{g C L}^{-1}$ at Port of LA; Fig. 3). All sites experienced seasonal maxima in biomass during the spring, but the average value at Port of LA during spring was approximately 4-fold greater than the average winter value at that site and >4-fold greater than all seasons at the other sites, primarily due to diatom blooms in the harbor (Fig. 3). In comparison, the seasonal ranges of total microbial biomass at the SPOT station and Catalina varied by less than 2-fold (range = 34–65 $\mu\text{g C L}^{-1}$). Seasonal minima in standing stocks at Port of LA and Catalina occurred during winter, whereas the SPOT station exhibited seasonal minima during summer and fall.

Heterotrophic bacteria (bacteria + archaea, excluding cyanobacteria) were a major contributor to total community biomass at all sites, however bacterial biomass at Port of LA was consistently greater (seasonal mean range = 25.9-40.3 $\mu\text{g C L}^{-1}$) than that observed at the SPOT station and Catalina (range = 14.3-26.2 $\mu\text{g C L}^{-1}$ and 15.6-27.4 $\mu\text{g C L}^{-1}$, respectively; Fig. 3). Mean bacterial biomass at Port of LA exhibited a winter minimum and fall maximum. Mean bacterial biomass also fluctuated seasonally at the SPOT station and Catalina, but exhibited winter and summer minima and spring and fall maxima. Significant positive correlations were found between chlorophyll concentration and bacterial abundance ($\rho = 0.492$) and between microzooplankton abundance and bacterial abundance ($\rho = 0.438$) when all sites and sampling dates were considered ($p < 0.05$, Fig. 4).

Diatoms were a significant proportion of the photosynthetic biomass at all sites during the spring (70-90%, Fig. 5a). Diatom abundance in the San Pedro Channel was positively correlated with phosphate concentration ($\rho = 0.343$), chlorophyll concentration ($\rho = 0.729$), and the abundance of microzooplankton grazers ($\rho = 0.563$), and negatively correlated with water temperature ($\rho = -0.583$; $p < 0.05$, Fig. 4). The taxonomic composition of the diatom community was generally conserved across sites, with *Chaetoceros spp.* and *Pseudo-nitzschia spp.* consistently dominant. *Leptocylindrus*, *Eucampia*, *Skeletonema*, *Cylindrotheca*, and *Guinardia* were also common genera found during spring. Diatoms continued to be major components of the phytoplankton community during winter and summer at Port of LA, while photosynthetic pico- and nanoeukaryotes were prominent at that site in the fall (combined ~60%, Fig. 5a). Photosynthetic picoeukaryote abundance was positively correlated with nitrate+nitrite concentration ($\rho = 0.362$), silicate concentration ($\rho = 0.597$), and chlorophyll concentration

($\rho = 0.386$; $p < 0.05$, Fig. 4). Microbial eukaryotes were the primary component of the photosynthetic community at Port of LA during all seasons.

Cyanobacteria were important constituents of phytoplankton biomass at the SPOT and Catalina stations. *Synechococcus* and *Prochlorococcus* collectively comprised ~50% of the phytoplankton biomass in the summer and fall months at those sites, and 30-40% of the phytoplankton biomass during the winter (Fig. 5a). *Synechococcus* abundance positively correlated with temperature ($\rho = 0.727$) and chlorophyll concentration ($\rho = 0.524$), while *Prochlorococcus* abundance positively correlated with temperature ($\rho = 0.548$) and negatively correlated with chlorophyll concentration ($\rho = -0.540$) and microzooplankton abundance ($\rho = -0.465$; $p < 0.05$, Fig. 4). *Synechococcus* biomass surpassed *Prochlorococcus* biomass at all sites. *Prochlorococcus* was nearly absent from the phytoplankton community at all sites during the spring and during all seasons at Port of LA. The photosynthetic pico- and nanoeukaryotes attained maximal contributions to phytoplankton biomass at the SPOT and Catalina stations during the fall (40-45%), when diatom abundances were minimal (Figs. 3 & 5a).

Dinoflagellates were minor contributors to phytoplankton biomass at all sites and seasons, never exceeding 5% of the biomass of the photosynthetic community (Fig. 5a).

The combined biomass of the heterotrophic grazer community ranged from 3-16% of the total microbial biomass among all sites and seasons ($\bar{x} = 9\%$; Fig. 3). Microbial grazer biomass was dominated by heterotrophic nanoplankton across all sites and sampling dates (65-98% of the grazer community, Fig. 5b). Microzooplankton (ciliates, dinoflagellates) comprised approximately one-third of the grazer community biomass at all sites during the spring and at Port of LA during the fall. Ciliate biomass exceeded dinoflagellate biomass at the SPOT and

Catalina stations (except in the spring), while dinoflagellate biomass consistently surpassed ciliate biomass at Port of LA.

3.2 Growth and grazing mortality of the photosynthetic community

Community growth and grazing mortality rates of the total phytoplankton community and distinct components of the picoplankton size class (*Synechococcus*, *Prochlorococcus*, photosynthetic picoeukaryotes) were carried out in four seasons throughout the 3-year study (Table 1 and 2, respectively). Rates were assessed by site (all seasons included) and by season (all sites included), with the goal of identifying spatial and seasonal trends in microbial rate processes.

3.2.1 Phytoplankton growth rates

Unenriched growth rates (μ_0 = intrinsic growth rate) of the total phytoplankton community ranged from -1.36 to 1.53 d⁻¹ ($\bar{x}$ = 0.36 d⁻¹; Table 1). Corresponding ranges and averages of μ_0 for *Synechococcus*, *Prochlorococcus*, and photosynthetic picoeukaryotes were -0.09 to 2.56 d⁻¹ ($\bar{x}$ = 0.42 d⁻¹), -1.94 to 2.5 d⁻¹ ($\bar{x}$ = 0.06 d⁻¹), and -1.08 to 3.03 d⁻¹ ($\bar{x}$ = 0.25 d⁻¹), respectively (Table 2). No significant differences in median or mean values of μ_0 were observed for the total phytoplankton community when the sites (all seasons included) or seasons (all sites included) were compared (Fig. 6). However, median values of μ_0 trended higher at Port of LA (0.44 d⁻¹) than at the SPOT (0.27 d⁻¹) or Catalina stations (0.32 d⁻¹) for the total phytoplankton community (Fig. 6a). Seasonally, higher median values of μ_0 were observed during the spring and fall for the total phytoplankton community, and the lowest median value occurred during winter (Fig. 6b).

No significant differences in median or mean values of μ_0 were observed for the specific picoplankton groups when compared by site (all seasons included, Fig. S1). Higher median values, albeit not significantly, were observed at Port of LA for *Synechococcus* and photosynthetic picoeukaryotes than at the SPOT or Catalina stations (Fig. S1). Conversely, median μ_0 for *Prochlorococcus* was lowest for Port of LA, with negative growth rates in 5 of 10 experiments. When seasons were compared, all picoplankton groups exhibited their highest median μ_0 values during summer (median growth rates were 0.46 d^{-1} , 0.24 d^{-1} , and 0.38 d^{-1} for *Synechococcus*, *Prochlorococcus*, and photosynthetic picoeukaryotes, respectively) (Fig. S2). Overall, negative values of μ_0 for *Prochlorococcus* were obtained for 12 of 30 picoplankton dilution experiments (Table 2).

Nutrient-enriched growth rates (μ_n) of the total phytoplankton community were significantly higher than the corresponding unenriched growth rates (μ_0) at each site ($p < 0.05$, all seasons included), and during the spring, summer, and fall seasons ($p < 0.05$, all sites included; Table S1). However, nutrient addition did not consistently enhance the growth rates of *Synechococcus*, *Prochlorococcus*, or the photosynthetic picoeukaryotes, thus, averaged μ_0 and μ_n for those assemblages were not significantly different when grouped by season or site. No environmental parameters were found to correlate significantly with unenriched growth rates of the total phytoplankton or the picoplankton groups ($p < 0.05$, Fig. 4).

3.2.2 Phytoplankton grazing mortality rates

Grazing mortality rates (m) of the total phytoplankton community ranged from -0.76 to 1.31 d^{-1} throughout the study period, with an overall average of 0.38 d^{-1} across 33 experiments (Table 1). Ranges and averages for mortality rates of *Synechococcus*, *Prochlorococcus*, and

photosynthetic picoeukaryotes were 0 to 2.84 d⁻¹ ($\bar{x}$ = 0.51 d⁻¹), 0 to 2.22 d⁻¹ ($\bar{x}$ = 0.44 d⁻¹), and -0.62 to 2.89 d⁻¹ ($\bar{x}$ = 0.40 d⁻¹), respectively (Table 2).

Median grazing mortality rates for the total phytoplankton community were generally greater at Port of LA (0.59 d⁻¹) than at the SPOT (0.21 d⁻¹) and Catalina (0.29 d⁻¹) stations, but no significant differences in the mean or median values were detected when data were grouped by sites (Fig. 6c). The lowest median mortality rates for the total phytoplankton community were observed in the winter, significantly lower than mortality rates observed during the summer ($p < 0.05$, Fig. 6d). Total phytoplankton grazing mortality rate was positively correlated with chlorophyll concentration ($\rho = 0.497$, $p < 0.05$, Fig. 4).

Median grazing mortality rates for *Synechococcus* and photosynthetic picoeukaryotes were generally greater at Port of LA than the other two sites, but grazing mortality was lowest at Port of LA for *Prochlorococcus* (Fig. S1). The mean and median grazing mortality rate of *Synechococcus* was significantly higher at Port of LA than the SPOT station (mean of 0.87 d⁻¹ vs. 0.36 d⁻¹) and Catalina (median 0.70 d⁻¹ vs. 0.27 d⁻¹), respectively ($p < 0.05$). Neither the mean nor median grazing mortality rates for *Prochlorococcus* or photosynthetic picoeukaryotes were significantly different when data were grouped by sites.

Highest median grazing mortality rates were observed for all groups during the summer, but no significant differences in mean or median mortality rates were detected for *Synechococcus* or photosynthetic picoeukaryotes when data were grouped by season (Fig. S2). However, *Prochlorococcus* mean grazing mortality rate was significantly higher in the summer than in the spring, and *Prochlorococcus* median grazing mortality rate was significantly higher in the winter than the spring ($p < 0.05$).

Synechococcus grazing mortality rate was positively correlated with silicate concentration ($\rho = 0.407$), chlorophyll concentration ($\rho = 0.454$), and heterotrophic nanoplankton abundance ($\rho = 0.528$; $p < 0.05$, Fig. 4), while the mortality rate of *Prochlorococcus* was negatively correlated with microzooplankton abundance ($\rho = -0.375$). No significant correlations were found between environmental parameters and photosynthetic picoeukaryote mortality rate.

Comparison of the net changes in phytoplankton growth rates between the treatment with mesozooplankton and microzooplankton (WSW) and the treatment containing only microzooplankton (<200 μm filtrate) yielded no significant differences for either the total phytoplankton community or the three picoplankton groups. Mean apparent growth rate of total phytoplankton for all dates was -0.041 and -0.039 d^{-1} for the <200 μm and WSW treatments, respectively, indicating no apparent effect of mesozooplankton removal (or a compensatory effect by the microzooplankton).

3.3 Bacterial grazing mortality

Rates of grazer-related bacterial mortality averaged 0.34 d^{-1} for all experiments, with a range of 0.00 to 0.72 d^{-1} (Fig. 7). Median bacterial mortality rates grouped by study site were slightly higher at Port of LA (0.39 d^{-1}) and Catalina (0.38 d^{-1}) than at the SPOT station (0.24 d^{-1}), but no significant differences among the mean or median bacterial grazing rates were detected between sites (Fig. 7a). The mean or median bacterial mortality rates were not significantly different between seasons, but lower median values were observed during the winter (0.23 d^{-1}) and higher median values during the summer (0.51 d^{-1} ; Fig. 7b), a similar trend to that observed for total phytoplankton grazing mortality.

3.4 Carbon flow to higher trophic levels

Daily removal rates of phytoplankton and bacterial standing stocks by grazers were calculated in order to compare the amount of carbon grazed daily from each constituent of the assemblage (Table 3). Photosynthetic nanoplankton biomasses were excluded from total phytoplankton standing stock calculations due to limited data, as explained section 2.2. This exclusion may have reduced the total phytoplankton standing stock calculations by an average of $7.7\% \pm 6\%$, which would proportionately underestimate the amount of daily phytoplankton carbon grazed.

Mean values for the amount of phytoplankton standing stock grazed per day (all sampling dates included) were 75.8, 8.78, and $8.27 \mu\text{g C L}^{-1} \text{d}^{-1}$ for Port of LA, the SPOT station, and Catalina, respectively, while mean values for bacterial standing stock removal per day were 10.9, 4.83, and $5.47 \mu\text{g C L}^{-1} \text{d}^{-1}$ for each site. More phytoplankton carbon than heterotrophic bacterial carbon was consumed daily by grazers during all seasons at Port of LA (1.3-18.5x; gray columns: Fig. 8a,b). Phytoplankton standing stocks and daily carbon removal were also higher than that of the heterotrophic bacteria during the spring and summer at the SPOT station and Catalina, although the magnitude of the difference between food sources was smaller (1.6-3.7x; gray columns: Fig. 8c-f). During the winter, similar amounts of phytoplankton and bacterial carbon were grazed at the SPOT station, whereas the amount of bacterial carbon grazed was 5.3x higher than the phytoplankton carbon grazed at Catalina. More bacterial carbon was grazed daily at the SPOT station than phytoplankton carbon during the fall (2.3x higher), while daily removal of phytoplankton and bacterial carbon was similar at Catalina during this season (gray columns: Fig. 8c-f).

The standing stock of the heterotrophic bacteria was the largest of the picoplankton groups at all sites, exceeding the standing stock of the other groups by up to two orders of magnitude (Table 4). The amount of carbon grazed daily from the heterotrophic bacteria (10.9, 4.83, and 5.47 $\mu\text{g C L}^{-1} \text{ d}^{-1}$ for Port of LA, the SPOT station, and Catalina, respectively) was approximately equal to that grazed from the three picophytoplankton groups combined (13.49, 7.53, and 6.59 $\mu\text{g C L}^{-1} \text{ d}^{-1}$ for Port of LA, the SPOT station, and Catalina, respectively). The average percentage of carbon grazed within a picoplankton group (mean daily carbon grazed divided by mean standing stock) ranged from 25-59% of the total standing stock of that group (Table 4).

4. Discussion

4.1 Microbial growth and grazing rates were similar among sites

Despite differences in microbial community composition and standing stocks, rates of phytoplankton growth and mortality revealed few statistically significant differences between the three study sites. The sole significant difference between sites was a greater *Synechococcus* grazer-related mortality rate at the Port of LA, yet this relationship was not highly robust as it depended on the metric used to evaluate statistical significance (i.e. mean or median). These findings were surprising as they indicated that microbial communities of different composition and standing stocks exhibited similar overall turnover rates. In our study, significantly higher mean nutrient concentrations at the Port of LA supported microbial community standing stocks that were 2-4.5x those found at the SPOT station or Catalina (Figs. 2 & 3). Also, environmental differences between sites (Fig. 2) supported dominance of different phytoplankton onshore and offshore (Figs. 3 & 5a). Photosynthetic microbial eukaryotes (picoeukaryotes, nanoeukaryotes,

diatoms, and dinoflagellates) comprised 77-99% of the phytoplankton biomass during all seasons at the Port of LA (Fig. 5a), while coccoid cyanobacteria constituted ~50% of the total phytoplankton biomass at the SPOT and Catalina stations (with the exception of the spring season in which diatoms dominated the communities at all sites). Bray Curtis community dissimilarity results from a parallel molecular survey of microbial eukaryotic diversity and activity corroborate our findings, demonstrating that the Port of LA clustered separately from the SPOT and Catalina stations (Hu et al. 2016). The predominance of larger phytoplankton in the Port of LA presumably reflects more nutrient replete conditions there, whereas the smaller phytoplankton dominance offshore may reflect the lower half-saturation constants and greater diffusive efficiency characteristic of minute phytoplankton (Williams & Follows 2011).

Similar growth and grazing rates within our geographically constrained study region (~45km across, all at 118°W) are not surprising given that comparable findings have been reported along longitudinal gradients spanning ~10°. In the California Current Ecosystem (CCE), standing stocks between coastal and offshore waters varied up to 30-fold, yet the rates of phytoplankton growth and microzooplankton grazing did not differ substantially among locations (Landry et al. 2009). Similarly, no significant differences in phytoplankton growth and mortality rates were detected between a coastal river plume and Kuroshio current waters in the East China Sea (Zheng et al. 2015), a gradient that spans ~7° longitude. Decreasing trends in phytoplankton and picoplankton growth and grazing mortality rates have been reported along onshore-offshore gradients in the North Atlantic Subtropical Gyre and East China Sea, however, those trends were either not significant (Gutiérrez-Rodríguez et al. 2011) or the significance was not reported (Guo et al. 2014). Our study, taken together with these findings, suggests that the biological

productivity of a given location does not necessarily dictate the rates of phytoplankton growth and mortality, at least at small spatial scales.

Rates of grazer-mediated bacterial mortality were also not significantly different between stations when all seasons were included (Fig. 7a). This finding is not surprising because bacterial abundances did not vary markedly between locations (Fig. 3). To our knowledge, we are the first study to address bacterial mortality rates across an onshore-offshore gradient. Our study suggests that bacterial mortality rates, like phytoplankton growth and mortality rates, are not necessarily linked to the biological productivity of an area at small spatial scales.

The microbial abundances and rates of growth and mortality reported in this study are in good accordance with other microbial rate studies in the waters off California. In the San Pedro Channel, we found phytoplankton growth rates and grazing mortality rates averaging 0.36 d^{-1} and 0.38 d^{-1} , respectively. These averages are similar to averages of growth (0.44 and 0.48 d^{-1}) and grazing mortality rates (0.2 and 0.5 d^{-1}) reported in the CCE (Landry et al. 2009, Pasulka et al. 2015), as well as the median growth (0.53 d^{-1}) and grazing mortality rates (0.36 d^{-1}) reported for coastal Pacific regions in a meta-analysis (Schmoker et al. 2013). The average *Synechococcus* growth rate (0.42 d^{-1}) in the San Pedro Channel agreed well with other averages reported from the CCE and at Scripps Pier (range 0.44 - 0.66 d^{-1}), but our average mortality rate (0.51 d^{-1}) was approximately double that found at those sites (range 0.14 - 0.33 d^{-1}) (Worden & Binder 2003, Worden et al. 2004, Pasulka et al. 2015). Conversely, *Prochlorococcus* and photosynthetic picoeukaryote average growth rates (0.06 and 0.25 d^{-1} , respectively) were less than those reported in the CCE and at Scripps Pier (range 0.33 - 0.99 and 0.40 - 0.99 d^{-1}). Average grazing mortality rates of *Prochlorococcus* (0.44 d^{-1}) and the photosynthetic picoeukaryotes (0.40 d^{-1}) were within the range of mean values reported for the CCE and at Scripps Pier (range 0.36 - 0.49

and 0.39-0.45 d⁻¹, respectively). The average bacterial standing stock removal (28% d⁻¹) in our study was less than the reported range from Santa Monica Bay (43-82% d⁻¹)(Fuhrman & Noble 1995), but it was consistent with an average of 29% d⁻¹ reported by a seasonal study in the NW Mediterranean (Boras et al. 2009). Our average bacterial mortality rate is also in agreement with bacterial doubling times of ~5 days calculated for the SPOT station (Cram et al. 2014).

4.2 Microbial growth and grazing rates revealed low seasonality in the San Pedro Channel

Relatively constant rates of growth and mortality across seasons were observed in our study, which is consistent with the narrow range of environmental factors observed in the San Pedro Channel (Table 1; Fig. 2). Increases in phytoplankton and bacterial mortality rates in the summer (Figs. 6, 7b, & S2), albeit non-significant for the bacteria, *Synechococcus*, or the photosynthetic picoeukaryotes, suggest temperature may explain the somewhat elevated grazing rates observed during the summer months. However, similarly high temperatures in the fall were accompanied by lower grazing rates, confounding our ability to determine whether temperature is an important driver of protistan grazing in our region (Fig. 4).

Relatively constant growth and mortality rates between seasons were documented despite seasonal shifts in the community composition. Several molecular studies have shown distinct seasonality in bacterial community composition (Chow et al. 2013, Cram et al. 2014) and eukaryotic community composition (Countway et al. 2010, Kim et al. 2014, Hu et al. 2016) in the surface waters of the San Pedro Channel. Changes in the relative abundance of key microbial groups between seasons were also documented in this study; for example, diatoms dominated the photosynthetic community in the spring season, coincident with an increase of microzooplankton in the heterotrophic grazer community (Fig. 5). Similar average growth and mortality rates

measured for seasonally distinct communities may reflect a tight coupling between the progression of prey populations and their predator populations.

The seasonality of microbial rate processes has been shown to be stronger in truly temperate and high-latitude regions than at our temperate-to-subtropical, coastal ocean site. Forcing factors that vary with season include changes in light availability and day length, wind and weather patterns, upwelling and nutrient availability, and temperature. The Southern California Bight appears to function at the intersection of a subtropical and temperate regime: a narrow temperature range and permanently stratified water column persist year-round (Caron et al. in revision), yet episodic wind-driven upwelling in the spring and enhanced rainfall and stormwater discharge in the winter drive seasonal fluctuations in community biomass and rate processes characteristic of temperate regions (Nezlin & Li 2003, Nezlin et al. 2012). The episodic nature of our region was reflected in the amount of variability observed for phytoplankton growth and mortality rates within a season, between seasons, and between years. That is, intraseasonal variability—the variability observed in phytoplankton growth or mortality rates within a season at all sites—demonstrated the highest level of variability (i.e. COV of 93% for μ_0 and 113% for m in winter) as the timing of rainfall or upwelling events can vary between years. Interseasonal variability—the variability observed between the average phytoplankton growth and mortality rates for each season (all sites included)—was moderate (COV of 59% for μ_0 and 52% for m), distinguishing each season from one another yet reflecting the mild seasonal shifts experienced in our region. Interannual variability—the variability observed between the average phytoplankton growth or mortality rates for each year (all sites included)—was the lowest (COV of 10% for μ_0 and 21% for m), indicating a relatively consistent seasonal signature

between years (at least during this 3-year study) and reflecting the significance of episodic events in the Southern California Bight as drivers of plankton biology.

Studies conducted in more northerly temperate environments have shown strong seasonal trends in microbial growth and grazing rates. In Narragansett Bay, Rhode Island, USA, phytoplankton growth and mortality rates peaked during the summer season, primarily due to increased temperature, but also potentially due to changes in phytoplankton community composition (Lawrence & Menden-Deuer 2012). Summer rates of phytoplankton growth and mortality were also significantly higher in the East China Sea than those recorded in the winter at that site, and paralleled increases in picoplankton abundance and temperature (Zheng et al. 2015); similar increases in picoplankton growth and mortality rates were documented, though the significance of the relationship was not reported (Guo et al. 2014). Bacterial mortality was also strongly affected by temperature in Vineyard Sound, Massachusetts, with the percentage of FLB consumed steadily increasing from 3 to 41% per day from December to June (Marrasé 1992). Conversely, bacterial mortality rates measured monthly in the NW Mediterranean (temp range 15-25°C) showed no seasonal pattern (Boras et al. 2009). Therefore, the mild seasonal shifts in growth and mortality rates observed in our study appear to reflect the temperate-to-subtropical nature of the San Pedro Channel.

4.3 Community carbon flow differed between sites and seasons

The combination of our community biomass data and protistan grazing measurements facilitated a unique comparison of carbon turnover rates between key prey populations. Our measurements revealed that phytoplankton and heterotrophic bacteria (bacteria + archaea, excluding *Synechococcus* and *Prochlorococcus*) were both important carbon sources to higher

628 trophic levels in the San Pedro Channel. Phytoplankton were the predominant carbon source for
629 protistan grazers at all three sites during the spring and summer seasons, when phytoplankton
630 standing stocks were highest (Fig. 8). However, carbon flow through the bacteria and
631 phytoplankton were of similar magnitude in the winter and fall seasons. Within the
632 picoplanktonic size class, the mean daily carbon consumption of the heterotrophic bacteria
633 equaled that of the photosynthetic component at all sites (*Synechococcus*, *Prochlorococcus*,
634 photosynthetic picoeukaryotes combined; Table 4).

635 Experiments investigating the removal rates of both the bacteria and phytoplankton are
636 rare and have generally been conducted using the dilution method to estimate growth and
637 mortality rates of all microbial groups (Putland 2000, Pearce et al. 2008, Pearce et al. 2011,
638 Pasulka et al. 2015). However, filtration processes can alter metabolite and organic matter
639 composition, and thereby impact bacterial growth rates unevenly across the dilution series
640 (Pasulka et al. 2015, Pree et al. 2016). For this reason we estimated bacterial mortality by the rate
641 of FLB disappearance. Bacterial mortality measurements based on fluorescently-labeled prey
642 also have caveats (Caron 2001), although we note that our measured bacterial mortality rates
643 were in good accordance with calculated bacterial production rates in the region (noted in section
644 4.1; Cram et al. 2014).

645 Our study did not directly address other sources of mortality such as viral lysis (Brum et
646 al. 2014), therefore, estimates of community turnover rates, particularly for the bacteria, are
647 conservative estimates. No statistical difference was found between our microzooplankton
648 (<200µm) and micro- + mesozooplankton (WSW) treatments, indicating that mesozooplankton
649 grazing impact was small during our study period.

4.4 Implications of group-specific carbon turnover for biogeochemical models

Comparisons of the standing stocks and carbon turnover of key microbial prey groups are necessary for the construction of biogeochemical models. Despite our understanding of heterotrophic bacteria as a fundamental part of microbial food webs (Azam et al. 1983, Ducklow 1983), only a few ecosystem models have explicitly represented bacterial biomass when investigating ecosystem dynamics (Hasumi & Nagata 2014, Xiu & Chai 2014, Weitz et al. 2015). Our study highlights the importance of bacteria as a major, and sometimes dominant, source of carbon to higher trophic levels, and our coincident measurements of bacterial biomass and bacterial mortality enable their inclusion in model formulations. In addition, our study supports the appropriateness of size-structured biogeochemical models (Ward et al. 2012, Ward et al. 2014), indicating a small range of mean turnover rates among the different picophytoplankton populations (27%, 12%, and 9% at Port of LA, the SPOT station, and Catalina Island, respectively; Table 4). The average standing stock removal for picophytoplankton in the San Pedro Channel was $42.3\% \text{ d}^{-1}$, which corresponds to a turnover time of 2-3 days. Our results agree with research showing comparable grazing susceptibility amongst small phytoplankton groups (0.45-4.0 μm) in the Eastern Pacific (Taniguchi et al. 2014).

Modeling zooplankton dynamics requires the construction of mathematical relationships between explanatory environmental parameters and grazing pressure. Ideal parameters are those that provide high predictive power but are relatively easily collected, such as temperature and chlorophyll concentration, but these parameters were only marginally important in the present study. Several studies have shown a strong positive relationship between temperature and microbial growth rates or grazing rates (Marrasé 1992, Rose & Caron 2007, Lawrence &

Menden-Deuer 2012, Schmoker et al. 2013, Taniguchi et al. 2014). Strong temperature dependence was not detected in our study (Fig. 4), ostensibly due to the narrow annual temperature range at our study site (13.1-21.6°C). Elevated (but non-significant) grazing rates on all microbial assemblages during the summer suggest that temperature plays only a minor role in the San Pedro Channel (Figs. 6, 7, & S2). We were able to detect a significant positive correlation between the initial chlorophyll *a* concentration and phytoplankton mortality rate as well as *Synechococcus* mortality rate (Fig. 4), a relationship that has been reported in other studies (Verity 1986, Schmoker et al. 2013). However, chlorophyll concentration has not been a consistent predictor of protistan grazing rates in the literature as bulk chlorophyll does not represent species composition, prey palatability, or predator-prey interactions (Menden-Deuer & Fredrickson 2010, Lawrence & Menden-Deuer 2012, Guo et al. 2014, Zheng et al. 2015). Integrating species composition, both of the grazers and the prey, into future studies of microbial rate processes may help better elucidate spatiotemporal patterns and environmental predictors of growth and grazing rates generally, and especially at our study site.

5. Conclusion

An investigation of microbial community composition and trophic activities across three years, three sites, and four seasons in the San Pedro Channel revealed similar averages in microbial rate processes across seasonal and spatial scales, despite differences in standing stocks and the relative abundance of key microbial assemblages. Microbial communities with substantially different standing stocks had similar rates of turnover. Comparisons of carbon flow through several microbial prey assemblages highlighted the importance of heterotrophic bacteria as a food source for protistan grazers. Carbon consumption from the heterotrophic bacteria was

of similar magnitude to the picophytoplankton in all seasons and similar to the total phytoplankton community in some locations and seasons. The narrow annual range of environmental parameters and episodic nature of the Southern California Bight precluded the detection of meaningful relationships between many environmental factors and microbial growth and mortality rates. The carbon fluxes reported in this study, combined with the detailed community biomass values of Caron et al. (in revision), facilitate the creation and parameterization of biogeochemical models at coastal ocean sites.

Acknowledgements:

This work was supported by the National Science Foundation [grant number OCE-1136818]. Authors would like to thank the Captain and Crew of the Harmony and the Sundiver Express, members of the Fuhrman Lab (especially Cathy Roney-Garcia and Erin Fichot), and the Wrigley Institute for Environmental Studies for fieldwork support. Authors would also like to thank Laura Gómez-Consarnau for providing the *Dokdonia donghaensis* culture used to prepare the fluorescently-labeled bacteria.

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Table 1. Temperature (T_0 temp) and chlorophyll a (T_0 chl a) measurements at the beginning of the experiments, and growth and mortality rates for the total phytoplankton community (estimated from chlorophyll a) for each study date and site. Grazing rates (m) and nutrient-enriched growth rates (μ_n) were calculated using Model I Linear Regressions. Unenriched growth rates (μ_0) were calculated from μ_n values to determine intrinsic population growth rates.

Experiment	T_0 temp ($^{\circ}\text{C}$)	T_0 chl a ($\mu\text{g L}^{-1}$)	m (d^{-1})	μ_n (d^{-1})	μ_0 (d^{-1})
Port of Los Angeles					
13-Mar-12	13.1	8.03	0.54**	0.74	0.82
15-Jul-12	16.0	4.67	1.31**	1.74	1.21
19-Oct-12	20.0	2.06	0.31**	1.10	0.81
9-Jan-13	14.5	2.86	0.24**	0.38	0.42
24-Apr-13	14.5	12.70	0.59**	0.65	0.38
15-Jul-13	18.0	5.00	0.59**	0.92	0.32
16-Oct-13	17.2	4.53	1.11**	0.89	0.82
7-Jan-14	15.4	2.20	ns	0.29	0.32
8-Apr-14	13.2	15.04	0.87**	1.00	0.62
14-Jul-14	18.4	3.23	0.87**	1.92	0.44
6-Oct-14	20.4	2.81	0.20**	0.84	0.01
San Pedro Ocean Time-series					
13-Mar-12	13.6	5.86	0.74**	0.75	0.72
15-Jul-12	18.0	0.45	-0.76**	0.58	-1.36
19-Oct-12	20.6	0.24	ns	0.63	0.27
9-Jan-13	15.2	1.29	0.21*	1.31	0.07
24-Apr-13	15.7	0.63	0.34**	0.94	0.17
15-Jul-13	19.9	0.29	0.93*	1.04	0.4
16-Oct-13	19.6	0.24	0.21**	1.03	0.59
7-Jan-14	16.7	0.22	ns	0.27	0.11
8-Apr-14	15.2	0.79	0.48**	1.87	0.51
14-Jul-14	21.4	0.34	0.22*	0.41	-0.31
6-Oct-14	21.6	0.24	ns	1.12	0.78
Catalina Island					
13-Mar-12	13.6	1.28	0.76**	2.20	1.53
15-Jul-12	19.0	0.78	ns	2.09	-0.45
19-Oct-12	20.6	0.20	ns	0.88	0.06
9-Jan-13	14.1	2.73	0.15*	0.53	-0.03
24-Apr-13	15.9	1.02	0.20**	0.77	-0.01
15-Jul-13	20.0	0.38	0.47**	1.13	0.36
16-Oct-13	19.4	0.68	0.58**	1.20	0.44
7-Jan-14	17.5	0.64	ns	0.42	0.18
8-Apr-14	15.4	0.37	0.38**	2.17	0.32
14-Jul-14	21.0	0.34	0.73**	1.64	0.73
6-Oct-14	21.5	0.24	0.37**	1.10	0.77

ns= not significant, *= significant at 0.05, **= significant at 0.01

m : grazing mortality, μ_n : nutrient-enriched growth, μ_0 : unenriched growth

899 Table 2. Growth and mortality rates of three groups of photosynthetic picoplankton for each study date and site. Grazing rates (m) and
 900 nutrient-enriched growth rates (μ_n) were calculated using Model I Linear Regressions. Unenriched growth rates (μ_0) were adjusted
 901 from μ_n values to calculate intrinsic population growth rates.

Experiment	<i>Synechococcus</i>			<i>Prochlorococcus</i>			Photosynthetic picoeukaryotes		
	m (d ⁻¹)	μ_n (d ⁻¹)	μ_0 (d ⁻¹)	m (d ⁻¹)	μ_n (d ⁻¹)	μ_0 (d ⁻¹)	m (d ⁻¹)	μ_n (d ⁻¹)	μ_0 (d ⁻¹)
Port of Los Angeles									
15-Jul-12	2.84**	1.12	2.56	2.22**	2.38	2.50	2.89**	1.51	3.03
19-Oct-12	0.69**	0.51	0.56	0.42**	0.11	0.06	0.67**	0.83	0.87
9-Jan-13	0.40**	0.22	0.24	ns	0.08	0.12	0.36**	0.13	0.10
24-Apr-13	0.71**	0.33	0.50	ns	-0.12	-0.36	0.73**	0.57	0.58
15-Jul-13	0.84**	0.45	0.46	ns	0.32	0.05	0.75**	0.72	0.46
16-Oct-13	0.63**	0.27	0.30	0.97**	-0.18	-0.05	0.68**	0.73	0.77
7-Jan-14	0.43**	0.37	0.39	0.52**	-0.21	-0.11	ns	0.13	0.04
8-Apr-14	0.71**	0.16	0.20	ns	-0.69	-1.04	0.32**	0.29	0.04
14-Jul-14	1.02**	0.56	0.58	ns	1.01	-1.94	0.75**	0.83	0.29
6-Oct-14	0.44**	0.42	0.52	0.55**	0.40	0.07	ns	0.22	-0.14
San Pedro Ocean Time-Series									
15-Jul-12	0.49**	0.38	0.67	0.65**	0.24	0.57	ns	0.20	0.19
19-Oct-12	0.58**	0.41	0.22	0.55**	0.12	-0.10	0.45**	0.19	0.04
9-Jan-13	0.28**	0.19	0.18	0.36**	-0.01	0.03	0.54*	-0.19	-0.22
24-Apr-13	0.32**	0.42	0.11	ns	-0.08	-0.31	ns	-0.18	-0.41
15-Jul-13	0.92**	0.27	0.37	1.49**	0.05	0.23	0.99**	0.52	0.47
16-Oct-13	0.40**	0.37	0.42	0.32**	0.06	0.06	0.79**	0.58	0.68
7-Jan-14	0.13**	0.07	0.06	0.40**	0.21	0.31	ns	-0.30	-0.30
8-Apr-14	0.49**	0.47	0.49	ns	0.30	0.14	ns	0.95	0.97
14-Jul-14	ns	0.15	0.15	1.09**	-1.01	-0.86	ns	-0.28	-0.21
6-Oct-14	0.18*	0.38	0.29	ns	0.44	0.32	ns	-0.13	-0.34
Catalina Island									
15-Jul-12	ns	-0.21	-0.29	ns	-0.58	-0.55	ns	0.33	-0.02
19-Oct-12	0.28*	0.22	0.23	ns	0.02	-0.01	ns	0.27	-0.10
9-Jan-13	ns	-0.09	-0.09	0.70**	0.24	0.49	ns	-0.57	-1.08
24-Apr-13	0.21**	0.21	0.02	ns	-1.08	-0.93	0.61**	0.25	0.40
15-Jul-13	0.76**	0.36	0.43	0.85**	0.01	0.15	0.60**	0.29	0.38
16-Oct-13	0.40**	0.45	0.58	0.17**	-0.04	-0.11	0.68**	0.58	0.40
7-Jan-14	0.26**	0.22	0.28	0.44**	0.13	0.28	ns	0.14	0.09
8-Apr-14	0.48**	0.51	0.69	ns	0.61	0.29	-0.62**	-0.08	-0.56
14-Jul-14	0.24**	0.56	0.76	0.71**	0.95	0.91	0.53**	0.80	0.87
6-Oct-14	0.29**	0.60	0.61	0.64**	1.37	1.44	0.28**	0.33	0.31

ns= not significant, *= significant at 0.05, **= significant at 0.01

m: grazing mortality, μ_n : nutrient-enriched growth, μ_0 : unenriched growth

902 Table 3. Daily standing stock removal by grazers (for calculation, see Materials and Methods)

903 for the total phytoplankton community (based on changes in chlorophyll *a*), picoplankton groups

904 (from flow cytometric measurements), and heterotrophic bacteria (from fluorescently-labeled

905 bacteria).

Experiment	Total chl <i>a</i>	Daily Standing Stock Removal (%)			Bacteria
		<i>Synechococcus</i>	<i>Prochlorococcus</i>	<i>P. picoeukaryotes</i>	
Port of Los Angeles					
13-Mar-12	63.0	-	-	-	-
15-Jul-12	125	247	257	310	-
19-Oct-12	40.2	64.7	35.3	74.2	32.4
9-Jan-13	26.3	37.0	0.00	31.7	24.3
24-Apr-13	53.0	63.8	0.00	67.6	28.7
15-Jul-13	51.6	69.8	0.00	65.0	43
16-Oct-13	96.2	53.6	60.5	71.2	45.3
7-Jan-14	0.00	42.1	38.3	0.00	21.9
8-Apr-14	77.5	56.4	0.00	28.1	39.8
14-Jul-14	71.0	82.9	0.00	60.4	50.7
6-Oct-14	18.2	45.8	43.7	0.00	17.4
San Pedro Ocean Time-series					
13-Mar-12	73.2	-	-	-	-
15-Jul-12	0.00	53.6	62.5	0.00	-
19-Oct-12	0.00	49.0	40.9	37.2	26.5
9-Jan-13	19.6	26.7	30.8	38.1	28.5
24-Apr-13	31.2	28.8	0.00	0.00	21.4
15-Jul-13	71.8	70.4	83.9	76.8	45
16-Oct-13	25.5	40.4	28.2	74.9	10.7
7-Jan-14	0.00	12.5	38.2	0.00	10.7
8-Apr-14	48.7	49.0	0.00	0.00	42.5
14-Jul-14	17.1	0.00	48.9	0.00	16.3
6-Oct-14	0.00	19.0	0.00	0.00	20.8
Catalina Island					
13-Mar-12	118	-	-	-	-
15-Jul-12	0.00	0.00	0.00	0.00	-
19-Oct-12	0.00	27.3	0.00	0.00	35.9
9-Jan-13	13.8	0.00	63.3	0.00	19
24-Apr-13	18.1	19.2	0.00	55.1	0.5
15-Jul-13	44.4	64.4	60.6	53.7	38.3
16-Oct-13	54.0	43.9	14.8	59.2	34.4
7-Jan-14	0.00	26.3	40.6	0.00	11.4
8-Apr-14	36.9	53.5	0.00	0.00	32.7
14-Jul-14	-	31.5	78.6	63.1	24.2
6-Oct-14	45.6	34.2	98.5	28.4	31.8

906 Table 4. Means (and ranges) of the total standing stock ($\mu\text{g C L}^{-1}$) and daily carbon removal by grazing ($\mu\text{g C L}^{-1} \text{d}^{-1}$) for heterotrophic
907 bacteria and three photosynthetic picoplanktonic assemblages (all seasons included). The percentage of daily carbon grazed (mean
908 daily carbon grazed divided by mean standing stock) within a given picoplankton group is provided in parentheses in the ‘Daily
909 Carbon Grazed’ column.

	Port of Los Angeles		San Pedro Ocean Time-series		Catalina Island	
	Standing Stock ($\mu\text{g C L}^{-1}$)	Daily Carbon Grazed ($\mu\text{g C L}^{-1} \text{d}^{-1}$)	Standing Stock ($\mu\text{g C L}^{-1}$)	Daily Carbon Grazed ($\mu\text{g C L}^{-1} \text{d}^{-1}$)	Standing Stock ($\mu\text{g C L}^{-1}$)	Daily Carbon Grazed ($\mu\text{g C L}^{-1} \text{d}^{-1}$)
Heterotrophic bacteria	33.1 (16.4 – 45.3)	10.9 (5.13 – 20.4) (33%)	19.1 (9.31 – 28.8)	5.88 (1.47-11.7) (25%)	20.2 (6.53 – 28.7)	5.47 (1.96 – 9.89) (27%)
<i>Synechococcus</i>	4.74 (0.226 – 14.3)	2.81 (0.215 – 9.24) (59%)	9.75 (1.43 – 38.8)	4.74 (0 – 27.3) (48%)	8.23 (0.286 – 24.5)	3.13 (0 – 15.6) (38%)
<i>Prochlorococcus</i>	0.536 (0.0243 – 1.64)	0.174 (0 – 0.628) (32%)	2.97 (0.0205 – 13.3)	1.31 (0 – 5.08) (44%)	2.09 (0.0344 – 5.87)	0.648 (0 – 2.38) (31%)
P. picoeukaryotes	19.7 (3.58 – 45.4)	10.5 (0 – 27.4) (53%)	4.16 (1.11-9.10)	1.48 (0 – 6.82) (36%)	7.03 (1.32 – 19.5)	2.81 (0 – 11.5) (40%)

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Figure Legends:

Figure 1. Study location in the San Pedro Basin, off southern California, USA, in the eastern North Pacific. The three sites were located in the Port of Los Angeles (Port of LA, 33°42.75'N, 118°15.55'W), central San Pedro Channel at the San Pedro Ocean Time-series station (SPOT, 33°33'N, 118°24'W), and adjacent to Santa Catalina Island (Catalina, 33°27.17 N, 118°28.51'W).

Figure 2: Nutrient concentrations at the Port of Los Angeles (Port of LA), San Pedro Ocean Time-series station (SPOT), and Santa Catalina Island (Catalina) sampling sites. Measured nutrients included silicate (SiO_4^{2-}), ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-), and phosphate (PO_4^{3-}). Values represent the means of all seasons and error bars represent the standard error of the mean. Values below the limit of detection were included in the calculations as 0 μM . Significant differences in the mean values between Port of LA and SPOT (☆) and Port of LA and Catalina (◆) are marked on their corresponding pair ($p < 0.05$).

Figure 3. Average seasonal biomasses of the microbial assemblages ($\mu\text{g C L}^{-1}$) at the Port of Los Angeles (Port of LA), San Pedro Ocean Time-series (SPOT), and Santa Catalina Island (Catalina) sampling sites. Carbon conversions from microbial abundances are described in the Materials and Methods. Microbial assemblages include: BACT (bacteria + archaea), SYN (*Synechococcus*), PRO (*Prochlorococcus*), PEUK (photosynthetic picoeukaryotes), PNANO (photosynthetic/mixotrophic nanoplankton), HNANO (heterotrophic nanoplankton), DIATOM

939 (diatoms), DINO (dinoflagellates), and CILIATE (loricate/aloricate ciliates).

940 Figure 4. Spearman's rank correlation coefficients (ρ) between environmental factors and
941 population abundances, unenriched growth rates, and grazing mortality rates of the total
942 phytoplankton and major picoplankton groups. Significant correlations are marked by a * ($p <$
943 0.05). Abbreviations represent: BACT (heterotrophic bacteria + archaea), SYN
944 (*Synechococcus*), PRO (*Prochlorococcus*), PEUK (photosynthetic picoeukaryotes), DIATOM
945 (diatoms), HNANO (heterotrophic nanoplankton), MICROZ (microzooplankton: ciliates +
946 dinoflagellates), PHYTO (total phytoplankton), and T₀ Chl (chlorophyll concentration at the
947 beginning of the experiments).

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949 Figure 5. Average seasonal percent contribution of major taxonomic groups to (a) total
950 phytoplankton biomass, and (b) total heterotrophic grazer biomass at the Port of Los Angeles
951 (Port of LA), San Pedro Ocean Time-series (SPOT), and Santa Catalina Island (Catalina)
952 sampling sites. Phytoplankton assemblages include: SYN (*Synechococcus*), PRO
953 (*Prochlorococcus*), PEUK (photosynthetic picoeukaryotes), PNANO
954 (photosynthetic/mixotrophic nanoplankton), DIATOM (diatoms), and DINO (dinoflagellates).
955 Grazer assemblages include: HNANO (heterotrophic nanoplankton), DINO (dinoflagellates),
956 and CILIATE (loricate/aloricate ciliates).

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958 Figure 6. Unenriched growth rates (μ_0) (a,b) and grazing mortality rates (m) (c,d) of the total
959 phytoplankton community (based on chl *a*) for the three study sites (Port of Los Angeles (Port of
960 LA), San Pedro Ocean Time-series station (SPOT), and Santa Catalina Island (Catalina)) (a,c)
961 and the four seasons (b,d). Values at each site include all seasons, and values in each season

include all sites. Outliers (black points) were identified by *R* according to the Boxplot Rule (Wilcox 2011). Pairs with significantly different mean values (▲) or median values (✱) are marked above the corresponding pair ($p < 0.05$).

Figure 7. Heterotrophic bacterial grazing mortality rates (d^{-1}) grouped (a) spatially (including all seasons), and (b) seasonally (including all sites). No significant differences in the mean or median values were identified by site or season ($\alpha = 0.05$). Outliers (black points) were identified by *R* according to the Boxplot Rule (Wilcox 2011).

Figure 8: Average seasonal standing stock ($\mu g\ C\ L^{-1}$; black columns, left axis) and daily carbon grazed ($\mu g\ C\ L^{-1}\ d^{-1}$; gray columns, right axis) for the phytoplanktonic (a,c,e) and heterotrophic bacterial (b,d,f) assemblages at the Port of Los Angeles (Port of LA, a,b), San Pedro Ocean Time-series station (SPOT, c,d), and Catalina Island (Catalina, e,f). Note the breaks in the y-axes and subsequent change of scale.

Figure S1. Unenriched growth rates (μ_0) and grazing mortality rates (m) of *Synechococcus* (SYN), *Prochlorococcus* (PRO), and photosynthetic picoeukaryotes (PEUK) for the three study sites: Port of Los Angeles (Port of LA), San Pedro Ocean Time-series station (SPOT), and Catalina Island (Catalina). Values at each site include all seasons. Outliers (black points) were identified by *R* according to the Boxplot Rule (Wilcox 2011). Sites with significantly different mean values (▲) or median values (✱) are marked above each site in the pair ($p < 0.05$).

992 **Figure 1:**

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