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Size-Fractionated Relationships Between Phytoplankton Production and Biomass

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Size-Fractionated Relationships Between Phytoplankton

Production and Biomass

Senior Thesis By

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Submitted in Partial Fulfillment
of the Requirements for
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Thesis Summary

Phytoplankton are single-celled photosynthetic algae that are the dominant primary producers in many aquatic ecosystems. They are taxonomically diverse, and differ greatly in size and shape. When studying phytoplankton and their role in nutrient cycles and food webs, scientists often split them into size categories: the picophytoplankton (0.2 - 2 μm), nanophytoplankton (2 – 20 μm), and microphytoplankton (>20-200 μm). The general idea of size fractionation is based on the principle that, usually, small organisms consume small phytoplankton, and larger organisms will consume the larger phytoplankton. Numerical models of carbon cycling through food webs, often linked to models of global climate, are based on this premise. An additional assumption made when constructing food web models is that size-fractionated biomass, i.e., the “amount” of phytoplankton in any size class, is directly proportional to corresponding rates of size-fractionated primary productivity. However, just because an organism is present doesn't necessarily mean that it is actively photosynthesizing. My thesis examined the robustness of this proportionality assumption by compiling and analyzing data on size-fractionated biomass and primary productivity from 27 studies published in the scientific literature. I found that contributions by different size-fractions to biomass should not be used to accurately infer contributions to primary productivity. Strong relationships between biomass and primary productivity were shown in only 16.6% of studies reviewed ($r^2 > 0.70$). Grazing, cell sedimentation, and changes in C:Chl *a* ratios may all contribute to the lack of consistency between biomass and production contributions. Direct measurement of size-fractionated rates of primary productivity are necessary for accurate size-based models of carbon cycling, especially if they are used to predict the response of the ocean ecosystem to future changes in climate.

Abstract

Phytoplankton are the autotrophic foundation of almost all marine ecosystems. Although represented by a myriad of different species, their relationship to ecosystem dynamics is often described by their cell size. Commonly, phytoplankton are grouped into the picophytoplankton (0.2 - 2 μm), nanophytoplankton (2 – 20 μm), and microphytoplankton (20-200 μm) size fractions. The flow of energy through an ecosystem is largely dependent how productivity moves through organisms of various sizes. For this reason, numerous studies have set out to quantify the respective contributions of these size-fractions to biomass and rates of primary production. This is done through field measurements of production or through mathematic models that infer production contributions from the easier field measured contributions to biomass. However, the accuracy of this method has been called into question. Can contributions to biomass really be used to accurately interpret contributions to production?

The purpose of this study was to evaluate this question through the analysis of past research. After comparing field measurements of production and biomass in 27 different studies, it was determined that the prediction of size-fraction contributions to production from contributions to biomass was not accurate. R² values from a linear regression of combined production and biomass data were found to be 0.512, 0.459, and 0.5271 for picophytoplankton, nanophytoplankton, and microphytoplankton respectively, implying a weak relationship between biomass and production. Individually, only 16.6% of studies reviewed showed strong relationships ($r^2 > 0.70$) between size-fractionated production and biomass. Based on these findings, direct measurement of production is recommended over the use of biomass based numerical models.

Introduction

Phytoplankton and their production dynamics are the most relevant ecological factor in the marine food web (Decembrini et al. 2009). As the autotrophic basis of almost all marine food webs, oscillations in phytoplankton production, biomass, and size-structure can have far reaching ecological effects, impacting every subsequent trophic level. Variation in phytoplankton dynamics can even be felt in humans due to effects on the fishery industry.

Size-structure, specifically, has a substantial effect on the flow of energy through the trophic levels. Size-structure refers to the size of the individual cells that comprise a phytoplankton community. Dominant cell size varies seasonally, geographically, and with depth. Typically, these sizes are fractionated based on mesh size and are commonly categorized into microphytoplankton ($>20\ \mu\text{m}$), nanophytoplankton ($20\text{-}2\ \mu\text{m}$), and picophytoplankton ($2\text{-}0.2\ \mu\text{m}$) (Hopcroft, 1990). The exact fractionation of these categories is not standardized and inconsistencies can be seen across different studies. Many studies also split phytoplankton into only two sizes. It is not uncommonly to see phytoplankton fractionated into $>2\ \mu\text{m}$ or $<2\ \mu\text{m}$ (Poulton et al. 2006) (Pérez et al. 2006) groups as well as $>5\ \mu\text{m}$ or $<5\ \mu\text{m}$ groups (Mousseau et al. 1996).

The microphytoplankton size fraction is dominated by diatoms, but also includes dinoflagellates, and larger flagellate species (Marañón, et al. 2001). Rises in microphytoplankton abundance are largely attributed to seasonal blooms of diatoms. However, depending on the location, dinoflagellate-microflagellate blooms may play a larger role in seasonal microphytoplankton dominance (Sellner et al. 1991). The nanophytoplankton size-fraction is composed of nanoflagellates, coccolithophores, and smaller diatoms and dinoflagellates. The relatively recently discovered picophytoplankton size-fraction is dominated by cyanobacteria

and picoeukaryotes such as picoflagellates (Tilstone, 2003). Two of the most common genus are *Synechococcus* (0.8 to 1.5 μm) and *Prochlorococcus* (0.8 to 1.5 μm) (Irigoien et al. 2004). These two groups are so common, that they can be found in ocean ecosystems worldwide and contribute massively to overall ocean productivity.

The microphytoplankton size fraction is more prevalent in areas of high new production in which new nitrogen enters the euphotic zone. Picophytoplankton are more commonly seen in oligotrophic zones where nutrient recycling is higher and low densities of nutrients present a disadvantage for microphytoplankton. This results in microphytoplankton being dominant in areas of nutrient inputs along the coast while picophytoplankton dominate in oligotrophic waters (Decembrini et al. 2009). Areas dominated by picophytoplankton usually have longer food webs and are characterized by microzooplankton (20-200 μm) grazing and prevalent microbial loop activity (Ceremeno et al. 2006) while areas dominated by microphytoplankton having a contrasting regime characterized by a short food web and greater trophic efficiency.

Aside from nutrient input, phytoplankton size dynamics are governed by other factors as well. Fluid dynamics play a key role in nutrient delivery and large phytoplankton sizes are favored in zones of high mixing. High mixing also prevents the sinking of large phytoplankton allowing them to remain in the euphotic zone. Differential impacts of light on phytoplankton sizes can also cause variation in production dynamics (Moreno-Ostos et al. 2011).

Due to the importance of phytoplankton to marine ecosystems, many studies have been conducted across the globe to better understand the relationship between size-fractionated biomass and production. By understanding how these dynamics are influenced and their subsequent effects, the flow of energy through an ecosystem can be better understood. Production and biomass are often measured separately. Biomass is usually measured by

quantifying the amount of chlorophyll *a* (Falkowski and Kiefer, 1985) present while production is commonly measured using the ^{14}C method (Peterson, 1980). These measurements are often taken at various depths in the water column or are integrated across the euphotic zone.

Another common method of determining the respective contributions to production and biomass by different size fractions is through field sampling of biomass and then the numerical interpretation of production. The benefit of using empirical models to estimate production comes from the fact that only biomass must be sampled. The ^{14}C methods is more difficult and comprehensive than measuring than measuring Chl *a* biomass, and relies on the assumption that photosynthesis occurs similarly in incubations as it does in the natural environment (Li and Goldman, 1981). Examples of empirical models include the ones outlined in Brush et al. (2002) and Arrigo et al. (2002). Both of these models rely on an equation incorporating Chl *a* to infer contributions to production. In Brush et al. (2002), the depth of the euphotic zone and surface irradiance are also important variables. Arrigo et al. (2002) takes the C:Chl *a* ratio with depth into account as well as the net specific biomass growth rate.

Unfortunately, the reliability of Chl *a* as an indicator of production is often called into question. In a recent study by Pommier et al. (2009) in the Northwest Atlantic, >5 μm phytoplankton were found to contribute 79% to total productivity, but only 45% to total phytoplankton biomass. In another study near Jamaica, microphytoplankton, nanophytoplankton, and picophytoplankton contributed 42%, 30%, and 28% to biomass, respectively and 27%, 30%, and 43% to total productivity (Hopcroft et al., 1990).

The goal of this study was to compare size-fractionated Chl *a* biomass and production across different study sites. Data was acquired from past studies encompassing different marine ecosystems worldwide including estuaries and open-oceanic transects. Through the

comparisons we conducted, we determined whether size-fractionated productivity can be inferred using measurements of size fractionated biomass. While some sites demonstrated similar contributions by individual size-fractions to both biomass and production, physical and environmental influences caused dramatic variation in other sites. Therefore, direct measurements of size-fractionated phytoplankton biomass and size-fractionated primary productivity are recommended for future studies.

Methods

First, a comprehensive literature search was conducted to find studies in which rates of phytoplankton biomass and primary productivity, integrated through the euphotic zone, were measured directly for different size fractions. Most commonly, studies fractionated phytoplankton into the picophytoplankton (pico), nanophytoplankton (nano), and microphytoplankton (micro) size fractions. The pico fraction was typically 0.2-2 μm , while nano were 2-20 μm and micro were >20 μm , though there was some variation in the sizes of the pico and nano fractions. The cutoff between the pico and nano sizes was 3 μm for Wang et al. (1997), Chen (2000), and Huang (1999). Many studies also gave the pico fraction different bottom limits, between 0.2 μm and 0.7 μm (here you could cite your table). Some studies only split phytoplankton into two size fractions: the Pico (<2 μm) and Net fractions (>2 μm) or the Nano (<5 or <10 μm) and Net fractions (>5 or >10 μm). We targeted studies that measured biomass as chlorophyll a, and where primary productivity experiments used the ^{14}C method were preferred due to their common usage across phytoplankton studies. However, a few experiments using the ^{13}C method were included due regional bans on the ^{14}C method.

After a large collection of studies was assembled, we created a database where we recorded the study sites, number of stations occupied, depths measured, the measurement

methods used, and the phytoplankton size ranges measured. For each entry, a table was created that displayed the raw and mean data for each site, size fraction, and depth. Standard error or standard deviation was also included. After multiple revisions, a master table was created that included all studies, 29 in total, with potentially usable sources containing both biomass and productivity data for at least two different size fractions.

For 26 of these studies (3 of the 29 were left out due to insufficient data), a plot was created comparing percent contributions to integrated biomass versus percent contributions to integrated production for the various size fractions. Many studies had already calculated percent contributions, but for those that had not, contributions by each size fraction were simply divided by the total production or biomass. If no total was reported, the different size fractions were summed. For studies in which data for the total and only one of two fractions was reported, the size-fraction data was subtracted from the total to achieve the second size-fraction. Once all the necessary data was found, a combined plot was also created that incorporated data from multiple studies that used pico, nano, and micro size fractions (Figure 1). Figure 1 displayed percent contributions to production versus biomass for these three fractions. Originally, two other graphs were created for other size-fraction groupings, but they were excluded due to low amounts of data. A list of studies, the size fractions they used, and the figures they were included in is shown in Table 1.

Unpublished data from the Richardson Phytoplankton Lab was also included in this study. This data was collected in March 2012 on a cruise of the Sargasso Sea on board the R/V *Atlantic Explorer*. Samples were collected from C2, a cyclonic eddy and from the Bermuda Atlantic Time-Series station (BATS). Before dawn, CTD casts to 200 meters were carried out to characterize the physical structure of the water column and to collect water measurements. These were used to conduct size-fractionated Chl a and primary production measurements (by

^{14}C incubations). Total (0.7-200 μm) biomass and production was found by filtering triplicate aliquots of 1 to 2 liters of 200 μm screened water onto GF/F filters. Differential filtration was then used to split the total size-fraction into picophytoplankton (0.7-2 μm), nanophytoplankton (2-20 μm), and microphytoplankton (20-200 μm). For picophytoplankton, this was accomplished by filtering triplicate aliquots of 1 to 2 liters of pre-screened water through a 2 μm Nuclepore filter (=2-200 μm) and subtracting the 2-200 μm filter from the total value. To find the nanophytoplankton's contribution, triple aliquots of pre-screened water were filtered through a 20 μm Nitex mesh then onto a GF/F filter (=0.7-20 μm). Picophytoplankton were then subtracted from the 0.7-20 μm biomass. Microphytoplankton production and biomass were then found by sampling subtracting the 0.7-20 μm fraction from the total (0.7-200 μm) fraction.

Statistical Analysis

Linear regressions were performed on size-fractionated primary productivity and Chl *a* biomass and r^2 values reported. Percent variance attributed to standard deviation was calculated using the r^2 values. Microsoft Excel 2010 was used to perform these statistical analyses. For graphs of production and biomass from individual studies, r^2 values were only calculated if there were at least three data points. Nineteen out of the twenty six studies fit this criteria.

Table 1. Table 1 displays the list of studies included in the research, the size-fractions they used, and the figures that they were included in.

	Study	Size Fractions	Figures
1	Chen Y.L. (2000)	(Pico, Nano, Micro)	Figure 1, Figure 2, Figure 3
2	Decembrini et al. (2009)	(Pico, Nano, Micro)	Figure 1, Figure 2, Figure 3
3	Decembrini et al. (2014)	(Pico, Nano, Micro)	Figure 1
4	Froneman et al. (2001)	(Pico, Nano, Micro)	Figure 1, Figure 2, Figure 3
5	Furnas M.J. (1983)	Atypical Fractions	
6	Glover et al. (1985)	(Pico and Net)	
7	Gomes et al. (1992)	(Pico, Nano, Micro)	Figure 1
8	Huang et al. (1999)	(Pico, Nano, Micro)	Figure 1, Figure 3
9	Hitchcock et al. (1987)	(Nano and Net)	
10	Hodal and Kristiansen (1990)	(Nano and Net)	
11	Hopcroft and Roff (1990)	(Pico, Nano, Micro)	
12	Iriarte et al. (2000)	(Pico, Nano, Micro)	Figure 1
13	Legrende et al. (1993)	(Nano and Net)	
14	Liu et al. (2007)	(Pico, Nano, Micro)	Figure 3
15	Malone T.C. (1971)	Atypical Fractions	
16	Marañón et al. (2001)	(Pico, Nano, Micro)	Figure 1, Figure 2, Figure 3
17	Marañón et al. (2003)	(Pico, Nano, Micro)	
18	Morán et al. (2004)	(Pico, Nano, Micro)	Figure 3
19	Mousseau et al. (1996)	(Nano and Net)	
20	Ning et al. (2004)	(Pico, Nano, Micro)	Figure 3
21	Peréz et al. (2006)	(Pico and Net)	
22	Poulton et al. (2006)	(Pico and Net)	
23	Rao and Smith (1987)	Atypical Fractions	
24	Shiomoto A. (1997)	(Pico, Nano, Micro)	Figure 1
25	Tremblay et al. (1997)	(Nano and Net)	
26	Varela et al. (1997)	(Pico, Nano, Micro)	Figure 1
27	Wang et al. (1997)	(Pico, Nano, Micro)	Figure 1
28	Weber and El-Sayed (1987)	(Pico, Nano, Micro)	
29	Wilkerson et al. (2000)	(Nano and Net)	

Results

Overall Observations

In the majority of studies where three size-fractions were measured, picophytoplankton were the most significant contributor to both biomass and production, followed by nanophytoplankton and finally microphytoplankton (Fig. 1). We generally found microphytoplankton contributed relatively more to production than biomass. The P:B ratio was found to be 0.647. Picophytoplankton contributions to production were closer to their relative contributions to biomass with a P:B ratio of 0.7186. Linear regressions revealed that for each size-fraction, phytoplankton production did not have a particularly strong relationship with biomass (Fig. 1). Picophytoplankton and microphytoplankton both had r^2 values only slightly above 0.5 (0.512 and 0.527) while nanophytoplankton only had an r^2 value of 0.459. Percent variance was less than 31% for all size fractions (residual plots, Appendix). Standard errors of regression were calculated to be 0.162, 0.129, and 0.140 for picophytoplankton, nanophytoplankton, and microphytoplankton respectively.

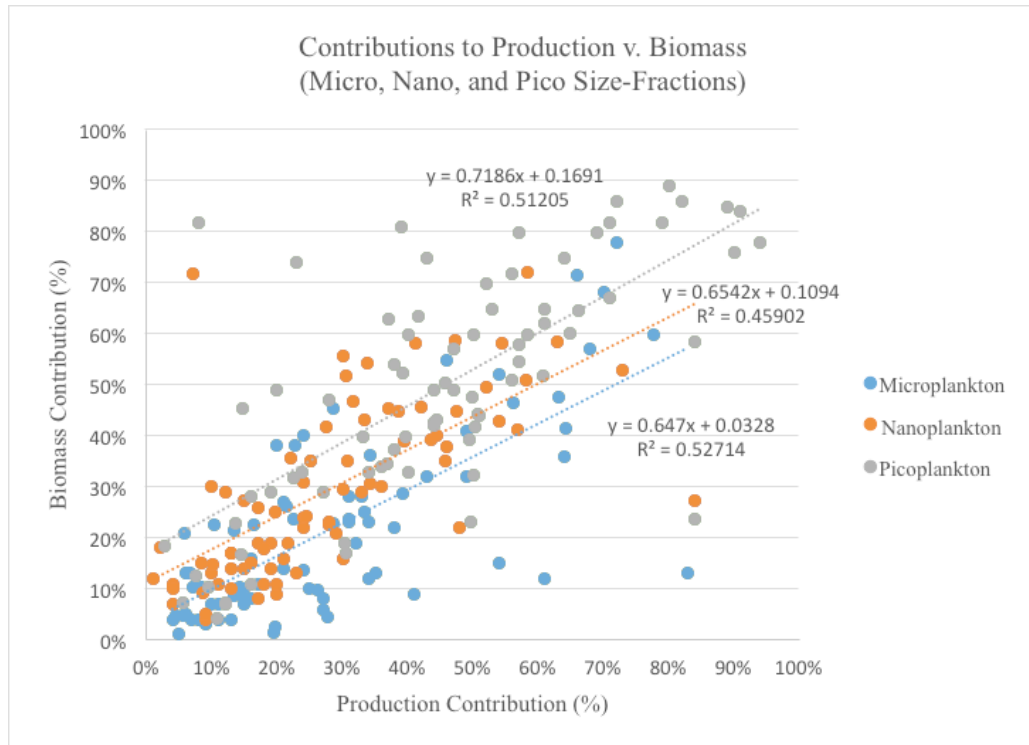


Figure 1. Figure one plots percent contributions to production against percent contributions to biomass for the Pico, Nano, and Micro size-fractions. Production and biomass measurements were taken from Decembrini et al. (2008), Decembrini et al. (2014), Marañón et al. (2001), Morán et al. (2004), Varela et al. (2002), Chen (2000), Froneman et al. (2001), Iriarte et al. (2000), Shiomoto (1997), Huang et al. (1999), Gomes et al. (2002), and Wang et al. (1997).

Specific Case Studies

Included in Figure 2 are four studies chosen for their higher relative amounts of measurements taken as well as contrasting locations. Figure 2a and 2c coastal marginal measurements while Figure 2b and 2d received their data from oceanic studies. Measurements for Figure 2a were taken in the South Tyrrhenian Sea off Italy's west coast while Figure 2c

contains data from the South East China Sea. For the open ocean studies, data for Figure 2b came from a transect from the United Kingdom to the Falkland Islands, while the data for Figure 2d came from a transect between South Africa and Antarctica. For many cases analyzed individually, picophytoplankton were shown to have larger contributions to production and biomass when compared to the other size fractions, specifically microphytoplankton, than we found for the cumulative dataset. However there were exceptions to this trend. In Figure 2d correlations between biomass and productivity were highly variable for the different size-fractions. In Figures 2a and 2b, picophytoplankton contributed roughly equally to biomass and production. Microphytoplankton dominated production in Figure 2c and biomass in Figure 2d. Nanophytoplankton contributed little to biomass and productivity in the two continental margin studies (Fig. 2b-2c). Data from the oceanic studies (Fig. 2a & 2d) depict trends consistent with the cumulative dataset (Fig. 1), where size fractionated contributions to biomass and productivity by nanophytoplankton were less than picophytoplankton but greater than microphytoplankton. Overall, regressions between biomass and productivity showed highly variable relationships between the four studies (Fig. 2). Figure 2a shows that production has little effect on determining biomass for all size-fractions compared to Figure 2c, though both studies were conducted in semi-enclosed coastal seas. Basin-wide transect studies (Figures 2b-2d) also reported differing relationships between biomass and productivity for the different size-fractions. Across all of the 19 studies in which r^2 values were calculated for the relationship between production and biomass of different size-fractions, only 16.6% of studies investigated showed strong relationships between the two measurements.

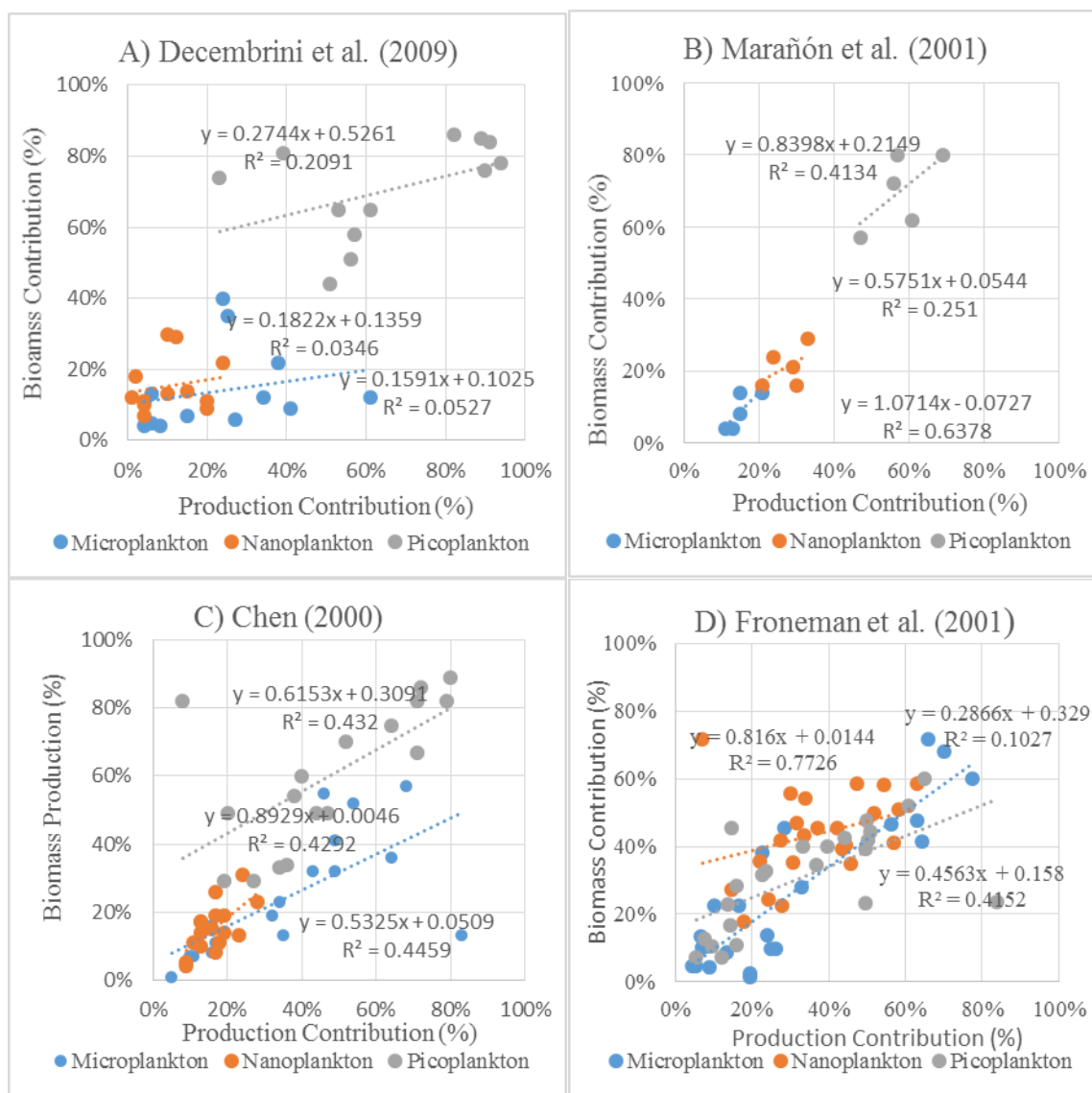


Figure 2. Figure two plots percent contributions to production against percent contributions to biomass for the Pico, Nano, and Micro size-fractions for four individual studies. Decembrini et al. (2009) (South Tyrrhenian Sea off Italy's west coast), Marañón et al. (2001) (United Kingdom to Falkland Islands), Chen (2000) (Southern East China Sea), and Froneman et al. (2001) (Southern Africa (35°S) to Antarctica (69°S)) were selected due to the comprehensive in which each study was conducted.

Observed vs. Predicted Size-fractionated Production

Individual stations from several studies with high amounts of measurements were analyzed and we found size-fractionated production determined by contributions to biomass was rarely an accurate measure (Fig. 3). For only one site investigated were predicted and measured contributions to biomass were similar (Fig. 3a). For this station measured and predicted nanophytoplankton contributions to production were identical, while contributions by the pico- and microphytoplankton varied by only 2%. Commonly, contributions by microphytoplankton to total production were noticeably underestimated by this method. While this represents a dramatic example, other studies displayed similar trends. However, Froneman et al. (2001) found microphytoplankton contributed 12.2% less to measured production than was predicted based on measurements of biomass. Often nanophytoplankton contributions to productivity were also underestimated by this method, with the exception of data from Froneman et al. (2001). Alternately, picophytoplankton production was overestimated by this method, with the exception of Froneman et al. (2001). Decembrini et al. (2009) showed the most dramatic differences between measured and predicted contributions (Fig. 3b). For this study, predicted production by microphytoplankton was only 12% of total while measured contributions were 61% (Fig. 3b), resulting in equally dramatic differences between measured and predicted productivity by the other size fractions.

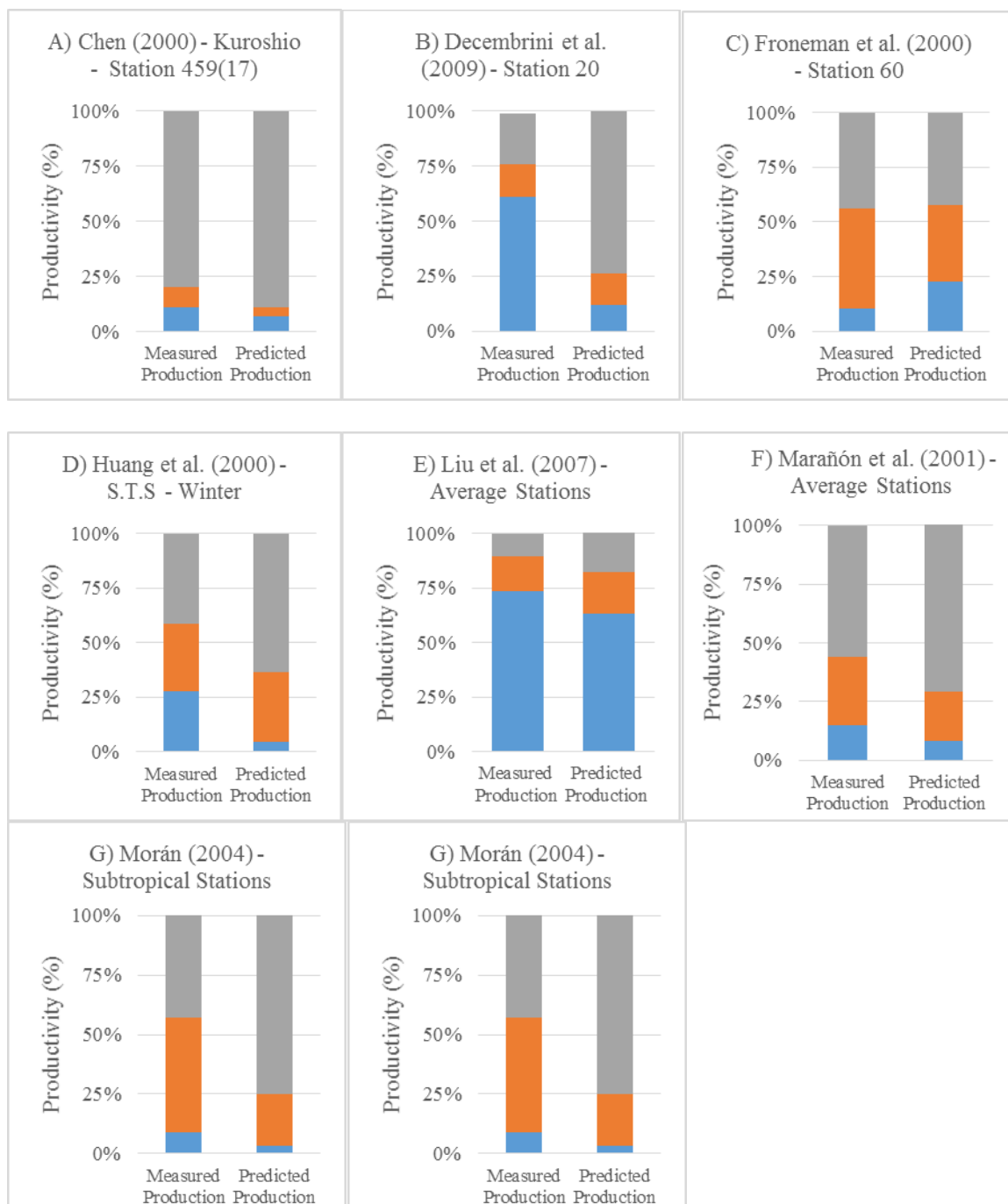


Figure 3. Percent contributions to total productivity based on measured and predicted values for the pico- (gray bars), nano- (orange bars) and microphytoplankton (blue bars) from eight studies: a) Chen (2000), b) Decembrini et al. (2009), c) Froneman et al. (2000), d) Huang et al. (2000) (Taiwan Strait), e) Liu et al. (2007) (Chukchi Sea), f) Marañón et al. (2001), g) Morán (2004) (North Atlantic Subtropical Gyre), and h) Ning et al. (2004) (South China Sea). Inferred production was calculated using percent contributions to biomass of each size fraction.

Vertical Production Profiles from Trophic-BATS study

It was more difficult to discern trends between measured and predicted production for measurements from discrete depths. At the Bermuda Atlantic Time-Series Study site (BATS) in the Sargasso Sea region of the North Atlantic, production peaked at 40 m, then decreased at subsequent depths while in the C2 eddy center, production decreased uniformly with depth (Fig. 4). Picophytoplankton dominated throughout the water column at both stations (Fig. 4). Microphytoplankton contributed relatively more to production at BATS while nanophytoplankton contributed relatively more at the center of C2. Differences in total productivity between casts could also be dramatic and were most dramatic in the center of C2; at 20 m, total productivity decreased by $2.55 \text{ mg m}^{-3} \text{ d}^{-1}$ between Cast 1 and Cast 10.

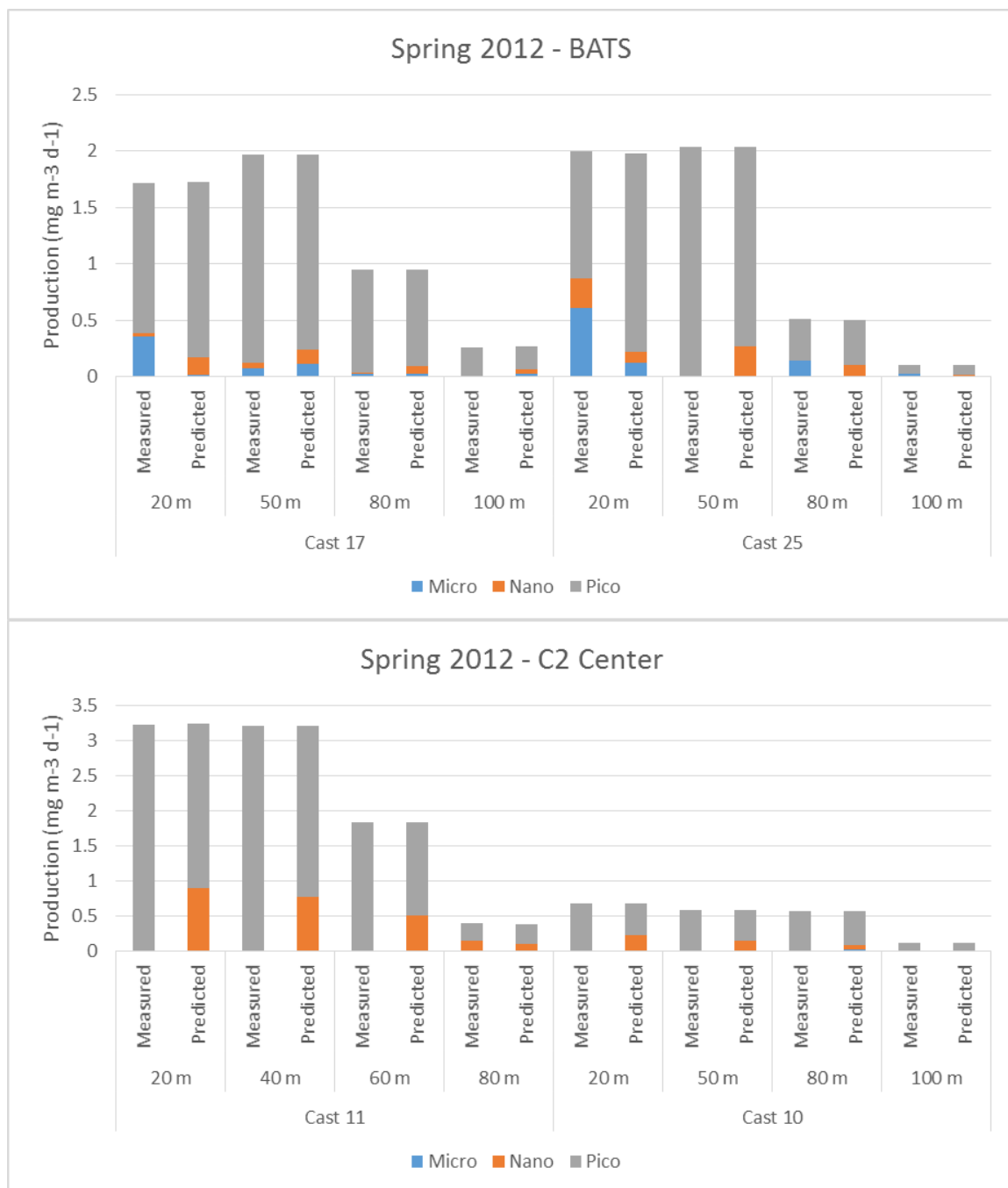


Figure 4. Figure 4 shows measured production versus predicted production at 20 m, 40 m, 60 m, and 80 m in the Sargasso Sea. The graph was made using unpublished data from the Dr. Richardson Phytoplankton Ecology Lab. predicted production was calculated using percent contributions to biomass. Production was measured using the ^{14}C and expressed as $\text{mg m}^{-3} \text{d}^{-1}$.

Discussion

From our data analyses, size-fractionated phytoplankton production inferred using measurements of size-fractionated biomass was found to provide unreliable results when compared with measurements of size-fractionated production. Although the amount of size-fractionated biomass does impact phytoplankton productivity, various other factors must be taken into account. This was apparent by our regression analyses that found weak relationships between biomass and production for the picophytoplankton, nanophytoplankton, and microphytoplankton (Fig. 1).

The variable relationship between size-fractionated biomass and production is highlighted in the Decembrini et al. (2009) study that shows an extremely weak relationship between contributions to size-fractionated production and biomass. In this case, the relationship between biomass and production was found to be very weak for the pico-, nano-, or microphytoplankton (r^2 values = 0.2091, 0.0346, and 0.0527 respectively; Fig. 2a). Linear regressions conducted on data from Chen (2000), Froneman et al. (2001), and Marañón et al. (2001) all showed stronger relationships between production and biomass. In two studies (Froneman et al., 2001 and Marañón et al., 2001) microphytoplankton exhibited a strong relationship between biomass and production ($r^2 = 0.7726$ and 0.6378 , respectively). The frequency of low r^2 values observed (only 16.6% of studies showed strong relationships) as well as the wide variability in regression analyses was consistent with our overall findings from the cumulative dataset.

Inaccuracies associated with mathematically inferring or predicting production based on measurements of biomass would often result in the underestimation of larger phytoplankton production (nano- and microphytoplankton). In some cases, predicted vs. measured production by the different size-fractions varied by over 45% (Fig. 3).

When depth was considered we found the largest differences between predicted and measured biomass occurred at the surface. Predicted and measured size-fractionated production became more similar as the depth increased. This may be due to stronger prevalence of picophytoplankton at deeper depths. Picophytoplankton exhibit higher proportional production compared to larger size-fractions in environments where irradiance is lower (Chavez, 1989) and have lower nutrient requirements. Picophytoplankton are also known to have less variable rates of production throughout the year (Mousseau et al. 1996) while microphytoplankton contributions vary incredibly and spike during the bloom season in temperate regions (Savidge, et al. 1995). In periods of blooms, microphytoplankton typically dominate biomass above the halocline while picophytoplankton dominate below (Bosak, 2012). However, since comparisons between measured and predicted size-fractionated production were made from individual casts from a small selection of studies (Fig. 3), it is difficult to extrapolate broad trends from these data.

It is a fairly common assumption that while contributions to biomass and production by different size fractions are variable, this variance is not statistically significant. Marañón et al. (2000) and Tremblay & Legendre (1994) presented research that supports this claim. However, based on our results, this does not seem to be the case in a majority of disparate studies. There are several explanations for uneven contributions to biomass and production. One involves unequal grazing pressure exerted on picoplankton. Grazing by microzooplankton-sized protists on picoplankton can account for a loss of over 80% of carbon fixed (Fernández, 2003). Calbert and Landry (2004) found that regionally averaged respiration rates for protistan grazing of picoplankton are 35-43% of daily PP. The unequal grazing pressure of microzooplankton on picoplankton could be used to explain cases in which percent contributions to production by picophytoplankton exceed percent contributions to biomass. Microzooplankton are also known

to graze on nanophytoplankton (Kamiyama, 1994), possibly producing similar effects in that size fraction.

Grazing likely exhibits an influence on the larger cell sizes as well. Ingestion by copepods (mesozooplankton) can impact phytoplankton productivity by 1% to 45% (Sarhou et al. 2005). The intense grazing pressure exhibited by copepods could produce a similar effect that protistan consumers exhibit on picophytoplankton. This would lead to an underrepresentation of microphytoplankton contributions to production if biomass was used to estimate productivity. Large differences in predicted and measured production (Fig. 4), (Decembrini et al. 2009) may occur partly due to this grazing influence.

Another mechanism includes aggregation and sedimentation, especially of diatoms, that can export entire phytoplankton communities from the euphotic zone in a period of only 24 hours. Sinking rates of diatoms vary largely with nutrient inputs; and have been shown to increase rapidly in periods of high iron or silicate inputs (Sarhou, 2005). Under increased aggregation, the combined effects of cell sinking rates also increase. A period of high Fe inputs and rapid aggregation could lead to drastically underestimated microphytoplankton productivity due to decreased rates of sinking and sedimentation.

Phytoplankton often exhibit rapid and complex responses to varying environmental conditions (Bosak, 2012) leading to fairly dramatic changes in production rates. Hydrodynamic singularities such as upwelling and transitions in vertical water column stability can influence the supply of nutrients (Tamigneauz et al. 1999) and may influence rates of assimilation. Nutrient limitation can be a major source of variability in phytoplankton biomass and production, such as we observed (Fig. 4). Studies with diatoms have shown that under nutrient stress, the ratio of organic carbon to Chl *a* increases due to a decrease in cell chlorophyll and an increase in carbon

(cite). Diatoms commonly fall into the micro size-fraction and nutrient limitation help explain differences in how the biomass and production of this size-fraction is represented.

Variation in the C:Chl *a* ratio calls into question the accuracy of using Chl *a* as a method of biomass measurement. A significant percent of difference between contributions to biomass and production may be due to cellular fluctuations of Chl *a* (de Jonge, 1980). Seasonal changes in C:Chl *a* ratios may not actually represent shifts in the community size structure, but instead, changes within the cells.

Much of the variation observed in this study may have come as a result due to the inconsistencies in methods used to collect measurements between studies such as the lack of standardization in defining the pico, nano, and micro size fractions. Most differences are found in the definition of the pico size fraction. Many studies impose a lower limit on the size fraction, commonly 0.2 μm . However, some studies define the bottom limit as 0.4 μm (Uitz et al. 2009), 0.45 μm (Robles-Jarero et al. 1993), or 0.7 μm (Pommier et al. 2009; unpublished data Richardson, pers. comm.). Variation is also commonly seen in the pico fraction's upper limit or the nano fraction's lower limit with some studies defining the limit as 3 μm (Robles-Jarero et al. 1993) or 1 μm (Savidge et al. 1995). Studies are also inconsistent with the limit between microphytoplankton and nanophytoplankton. While usually defined as 20 μm , many studies choose to define it as 10 μm (Saggiomo et al. 1998; Shiomoto, 1997; Tiera et al. 2005). If size-fractionation methods were standardized, this would eliminate much of the analytical error and allow for easier comparisons among studies.

Another source of inconsistency between studies was the depths in which production and biomass were integrated. Although, measurements were typically integrated to the bottom of the euphotic zone, the definition of this limit varied between 1% (Decembrini et al. 2009) and 0.1% (Poulton et al. 2006). The number of depths used for integration varied from 3 (Varela et

al. 2002) to 10 (Tremblay et al. 1997). There was also very little consistency in the depths sampled among different studies. The number of depths and euphotic zone definition chosen for integration were likely tailored to specific study sites, but the lack of standardization could have led to increased inaccuracy in comparisons. The use of the ^{13}C method of measuring production compared to the ^{14}C method could have also led to differences in production relationship to biomass.

Broader Implications

For the purpose of improving the understanding of ecosystems, the simplification of phytoplankton dynamics seems to be a logical first step. Already, they are commonly grouped by size fractions rather than species, when put into an ecological perspective. However, based on the results of this study, inferring production from biomass may not lead to an accurate understanding of ecosystem dynamics. Multiple factors may affect the production relative to biomass of one size-fraction leading to lower or higher relative contributions. However, this does not mean that numerical biomass based production models are still not usual tools. It is far less time and cost consuming to measure biomass than measuring both biomass and production. For many research questions, it may not be necessary to investigate production as extensively and empirical models may help eliminate unnecessary steps. However, certain means should still be undertaken in order to verify the relative contributions of each size-fraction. Through comparisons with field studies of the same regions, researchers could conjecture on the accuracy of their findings. This could also be accomplished through a brief collection of field measurements. Attempts should also be made to quantify the various influences on phytoplankton production dynamics. A model that takes note of grazing,

sedimentation, cell lysis, and changes in cell C:Chl *a* content will provide far more accurate predictions than models based only on Chl *a* biomass, irradiance,

However, as accurate as some empirical models may be, this study presents a strong case for using field measurements of production and biomass rather than inferring one from another. The direct measurement of size-fractionated biomass and production takes into account the various environmental, physiological, and biochemical factors that may influence contribution differences. The majority of problems that come with field measurements of biomass and production are rooted in the lack of standardization between studies. If greater consistency was shown between studies, it would be easier for researchers to recognize production trends and identify influences on phytoplankton ecology.

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Appendix

Figure 4. Figure 4 displays the residual plot for Microphytoplankton in Figure 1. The standard error of regression was found to be 0.140.

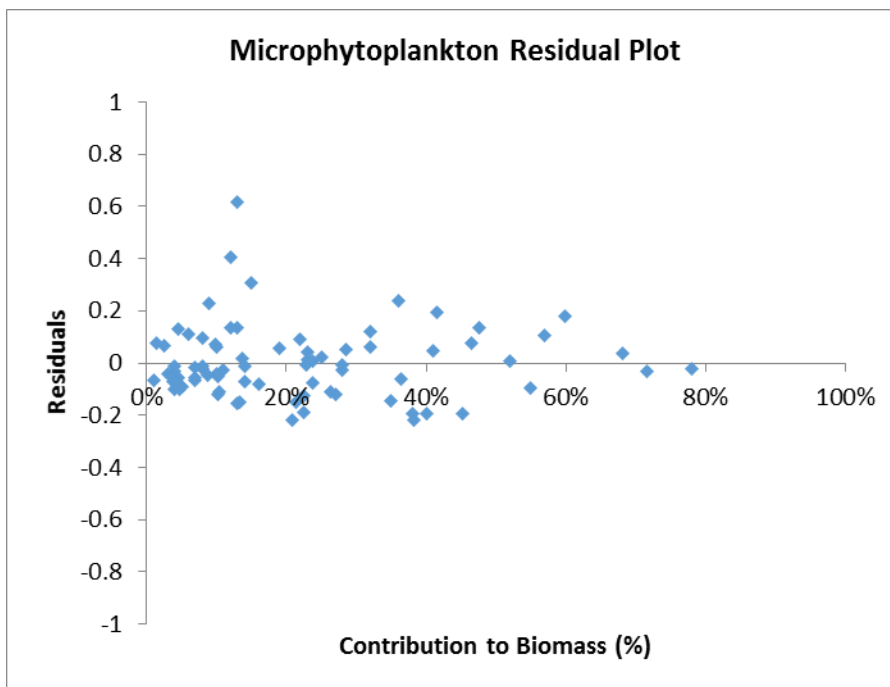
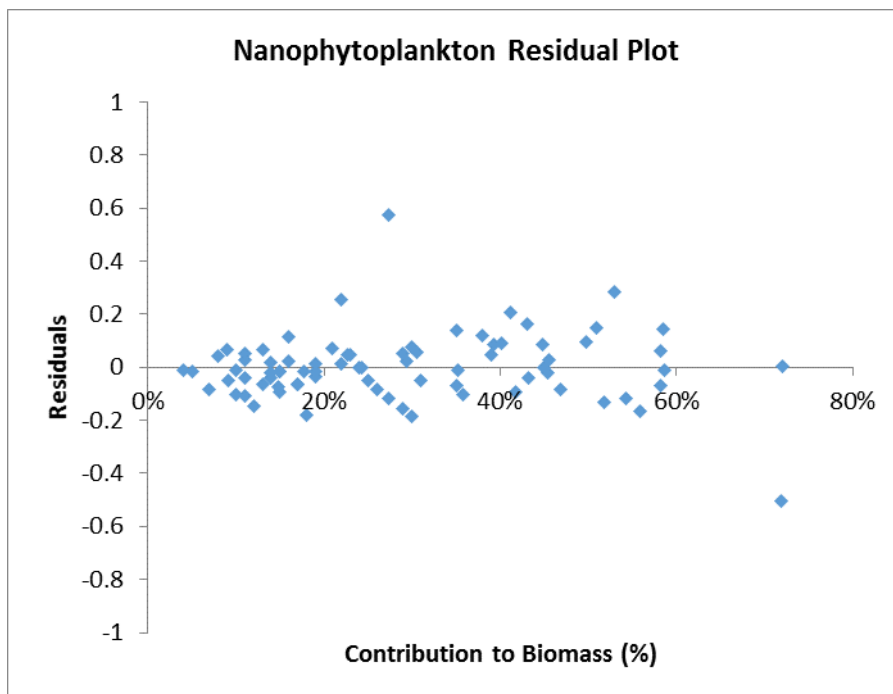


Figure 5. Figure 5 displays the residual plot for Nanophytoplankton in Figure 1. The standard error of regression was found to be 0.129.



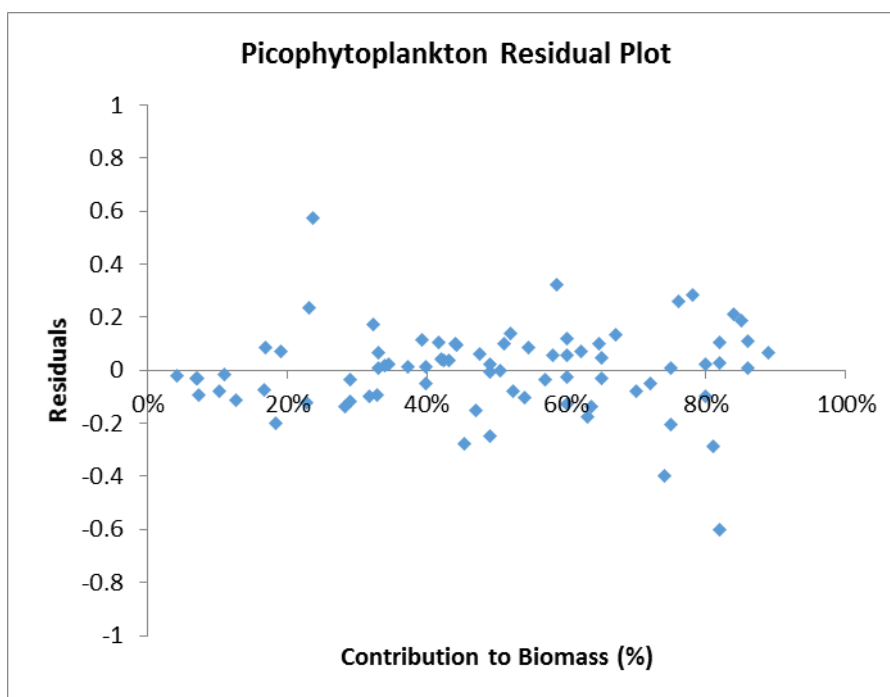


Figure 6. Residual plot of picophytoplankton from Fig. 1, and standard error = 0.162.

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