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ABSTRACT
Transient 'hot spots' of phytoplankton productivity occur in the generally oligotrophic Southern Pacific Ocean and we hypothesized that the population structure of tintinnid ciliates, planktonic grazers, would differ from that of a typical oligotrophic sites. Samples were collected over a 1 week period at each of two sites between Fiji and Tahiti: one of elevated chlorophyll *a* concentrations and primary productivity with an abundance of N-fixing cyanobacteria *Trichodesmium*, and a distant oligotrophic site. Tintinnid abundance differed between the sites by a factor of 2. A single species (*Favella* sp.), absent from the oligotrophic site, highly dominated the 'hot spot' site. However, total species richness was identical (71 spp) as well as short-term temporal variability (2-4 days). At both sites species abundance distributions most closely fit a log-series or log-normal distribution and the abundance distributions of ecological types, forms of distinct lorica oral diameter, were the typical geometric. Morphological diversity was only slightly lower at the high productivity site. We found that communities of these plankton grazers in 'hot spots' of phytoplankton productivity in oligotrophic systems differ little from surrounding oligotrophic areas.

Keywords: biogeography, biodiversity, plankton, species abundance distribution, Choreotrichia, *Trichodesmium*

TINTINNIDS are loricate ciliates of the marine microzooplankton which groups heterotrophic or mixotrophic planktonic organisms ranging in size from 20 to 200 µm. Microzooplankton are thought to account for the consumption of most of the primary production in the world ocean (Calbet & Landry 2004). While microzooplankton is usually numerically dominated by ciliates and heterotrophic dinoflagellates, it is actually a very heterogenous group taxonomically, ecologically, and morphologically (e.g., Beers 1982). It commonly includes many other protist taxa such as acantharia and radiolaria as well as the larval forms of metazoan taxa. Within this heterogeneous group, tintinnid ciliates are a species-rich group, coherent in terms of phylogeny, ecology and morphology, and are also relatively well studied (Dolan 2013).

Tintinnids are characterized by the possession of a shell or lorica into which the ciliate cell contracts when disturbed. Morphology and structure of the lorica is classically the basis for distinguishing species and grouping higher-level taxa, although its utility has been regularly disputed (e.g., Agatha et al. 2013; Santoferrara et al. 2016). The aperture through which the ciliate cell extends when swimming and feeding, termed the lorica oral opening, is a taxonomically conservative characteristic of the lorica (Laval-Peuto & Brownlee 1986). It is also a key ecological character because the size of the opening, the lorica oral diameter (LOD), is related not only to the maximum prey size ingested, but also the optimum prey size in terms of maximum clearance rate, and the maximum rate of cell division (Dolan 2010; Montagnes 2013). Tintinnid species of similar LOD are then ecologically similar in terms of feeding characteristics and maximum growth capacity. Not surprisingly perhaps, assemblages of tintinnids appear to be organized by mouth size (Dolan et al. 2009; 2013).

The structure of tintinnid populations has been studied in a wide variety of marine systems. In species-rich assemblages (tropical, subtropical and temperate systems), species abundance distributions resemble a long-tailed lognormal or log-series distribution, as is the case for most species-rich communities (e.g. Magurran 1974). Grouping organisms by the size of the LOD, rather than species identity, reveals a geometric distribution. The most densely populated LOD size-classes contain not only the dominant tintinnid species but generally several other species as well, species of apparently similar ecological characteristics, ecological redundant or stand-in species, accompanying the dominants. This pattern has been found in tropical and subtropical assemblages (Dolan et al. 2007; Dolan et al. 2013; Sitran et al. 2007). In contrast, the relatively species-poor assemblages of high latitudes (i.e., polar and sub-polar) do not show the same pattern. Species richness, as well as species redundancy, is markedly lower and dominant species are alone in their size classes. This pattern was been reported for assemblages in both the Southern (Santoferrara & Alder 2012) and the Northern Hemisphere (Dolan et al. 2016). While the patterns appear coherent among similar systems, little is known with regard to temporal variability over short time-scales or responses to transient changes in the environment. To our knowledge only the sub-tropical N.W. Mediterranean tintinnid assemblages have been studied in this regard. The assemblages were found to be fairly stable over a period of 4 weeks. There was an invariant set of dominant core species accompanied by their redundants, and a variable assemblage of transient species (Dolan et al. 2009). However, the study site was also quite stable in terms of the hydrology and most biological parameters (Anderson et al. 2009). Variability is perhaps of most interest in tropical assemblages with the twin puzzling characteristics of high species richness and low abundances (Kofoid 1930).

Once thought to be stable ‘desert areas’ of the world ocean, tropical oligotrophic gyres are now known to be subject to transient phytoplankton blooms, many associated with blooms of the N-fixing cyanobacteria *Trichodesmium* (Westbury & Siegel 2006; Wilson & Qiu 2008). While *Trichodesmium* itself is apparently subject to low grazing rates (Capone et al. 1997), field experiments have shown that a large portion (up to 47%) of the nitrogen fixed by *Trichodesmium* may be transferred to co-occurring primary producers thus fueling blooms of other species (e.g., Mulholland et al. 2014). Consequently, *Trichodesmium* blooms are considered to be likely of considerable importance in overall budgets of energy and matter in the oligotrophic gyres (Dore et al. 2008).

The OUTPACE cruise was designed specifically to sample a variety of trophic conditions across a large zone in the SE Pacific Ocean in which blooms of *Trichodesmium* have been reported. Here we present data from sampling at two contrasting stations separated by 500 km between Fiji and Tahiti (Fig. 1), each occupied for a one-week period. To our knowledge these are first data on microzooplankton in a *Trichodesmium* bloom and the first data on short-term temporal variability in tropical oceanic waters. We hypothesized that the tintinnid assemblage in the *Trichodesmium* bloom station, with relatively high concentrations of food resources, would support a larger population but of reduced diversity, based on observations from the SE Pacific (Dolan et al. 2007). Data from a wide range of conditions encountered across the SE Pacific overall suggested that tintinnid diversity was negatively related to chlorophyll concentration and positively related to chlorophyll dispersion as the depth of the chlorophyll maximum layer (Dolan et al. 2007). We predicted then that the 'hot spot' of productivity would show lower species richness, and lower species turnover compared to the assemblage in a typical oligotrophic site.

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MATERIALS AND METHODS

Sampling and sample analysis

Sampling was conducted through the oceanographic project 'OUTPACE'. The program was centered around observing variability in water column processes at sites across the South West Pacific by sampling stations between New Caledonia and Tahiti (https://outpace.mio.univ-amu.fr/spip.php?rubrique26). Here we report data from two 'long' stations, each occupied for a 7 day period in March 2015: Station "B" 18.24 °S, 170.8 °E and approx. 500 km distant, Station "C" 18.42 °S, 165.94°E. Analysis of satellite images preceeding, throughout the cruise, and shortly after were compiled to allow assessment of the short-term history of the study areas (De Verneil, in prep.). Samples were obtained on days 1, 3, & 5; On each day 6 depths were sampled between the surface and the bottom of the chlorophyll maximum depth (based on data from a CTD equipped with a fluorescence probe) using 20 l Niskin bottles. For each discrete-depth sample, a 10 l volume was concentrated to 50 ml by slowly and gently pouring the water through a 20 µm mesh Nitex screen fixed to the bottom of a 10 cm dia. PVC tube. Concentrated water samples were fixed with Lugol's solution (2 % final conc.), 2-3 ml aliquots were settled in sedimentation chambers and examined using an inverted microscope at 200x total magnification. Thus for each date, material from 60 l of water was examined, yielding a total of over 1,000 tintinnids for each of the stations. To assess the abundance and composition of the entire ciliate community, whole water samples from same Niskin bottles sampled on days 1 & 5 were fixed with Lugol's (2 % final conc.); 100 ml aliquots were settled in sedimentation chambers and examined using an inverted microscope at 200x total magnification. Phytoplankton composition was assessed in a single surface water sample from each station. A 50 ml aliquot of Lugol's-fixed whole water was settled and examined using an inverted microscope at 200x total magnification. Abundance and lengths of *Trichodesmium* filaments were determined along with abundances of dinoflagellates and diatoms. All microscopic examinations employed an Olympus inverted microscope, model IX51 equipped with DIC optics, an Olympus DP71 digital camera and Olympus Cell Sense Image Analysis software (Olympus, Rungis, France) used for cell measurements and imaging. For data reported here as average water column concentrations we employed a trapezoidal integration from the surface to the lowest depth sampled.

Tintinnid identifications were made based on lorica morphology and following Kofoid & Campbell (1929; 1939), Marshall (1934) and Hada (1938). Species of certain tintinnid genera are known to display different lorica morphologies (e.g., Laval-Peuto, 1983; Bachy et al. 2013; Kim et al. 2013; Santoferrara et al. 2015). However, only a few of the species encountered in this study appeared variable and may or may not represent single species (e.g. *Dadayiella ganymedes-acuta-bulbosa*). We adopted a 'conservative diversity' approach, considering very similar 'species' of the same genus and near identical LOD to be a single taxon. Empty lorica were not enumerated. Morphological categories consisted of size-classes of lorica oral diameter (LOD). Each species was assigned the average dimensions reported in Kofoid & Campbell (1929, 1939) and Marshall (1969). Size-class diameters were binned over 4 µm intervals beginning with the overall smallest diameter (12 µm) and continuing to the largest diameter encountered in a given sample.

Data Analysis

Taxonomic diversity was estimated for each sample as the Shannon index (ln-based, e.g., Magurran, 2004) and species richness. Morphological diversity was estimated by placing species into size-classes of lorica oral diameter (LOD). For each sample, morphological diversity was estimated as the number of size-classes and a Shannon index of morphological diversity calculated using numbers and proportional importance of different size classes (ln-based).

Using the pooled data set from the three sampling dates, we constructed log-rank abundance curves for the tintinnid assemblages by calculating relative abundance for each species and ranking species from highest to lowest and plotting ln(relative abundance) vs. rank. In parallel we also examined the abundance distributions of morphological categories by substituting the category 'species x' with 'LOD size-class x'. For both species and LOD size-classes, we constructed hypothetical log-rank abundance curves that could fit the data by using parameters of the particular assemblage. We constructed curves for three different models of community organization: geometric series, log-series, and log-normal, as in several previous studies (Raybaud et al. 2009; Claessens et al. 2010; Doherty et al. 2010; Dolan et al. 2007, 2009, 2013, 2016; Dolan & Stoeck 2011).

A geometric series distribution represents the result of the priority exploitation of resources by species arriving sequentially in a community (Whittaker, 1972), and is modeled by assuming that each species' abundance is proportional to a fixed proportion p of remaining resources. Thus the relative abundance of the ith species is (1-p)pi-1. For the tintinnid samples we used the relative abundance of the most abundant species to estimate p.

A log-series distribution represents the result of random dispersal from a larger community, a metacommunity in Hubbell's neutral theory (Hubbell, 2001). In a community exhibiting a log-series distribution, species having abundance n occur with frequency $\alpha x^n/n$, where x is a fitted parameter and α is Fisher's alpha, a measure of species diversity that is independent of total community abundance. For a given community with N total individuals and S species, x can be found (Magurran, 2004) by iteratively solving the following equation for x: $S/N = -\ln(1-x)(1-x)/x$ and then finding Fisher's alpha as $\alpha = N(1-x)/x$. For the tintinnid assemblages, we simply used the observed S and N for each sample to calculate x and α.

Log-normal species abundance distributions are thought to result from either a large number of species of independent population dynamics with randomly varying (in either space or time) exponential growth. Consequently, $N(i) \propto e^{r_i}$ where r_i is a random variable. Since N(i) is a function of an exponential variable, ln(N(i)) should be normally distributed (May 1975). Species in a community that are limited by multiple factors that act on population size in a multiplicative fashion should also exhibit a lognormal distribution of abundances. We calculated the expected log-normal species abundance distribution for each tintinnid sample by calculating the mean and standard deviation of ln(abundance) and using these parameters to generate expected abundance distributions for the S species in the sample using the NORMSINV function in an Excel® spreadsheet. We then calculated the mean abundance for each species, ranked from highest to lowest, and then calculated relative abundance. For each of the model distributions we also examined the abundance distributions of morphological categories by substituting the category 'species x' with 'LOD size-class x'.

For the assemblages from the two stations, the observed rank abundance distributions were compared to the hypothetical models using a Bayesian approach: an Akaike Goodness of fit test (Burnham & Anderson, 2004). In this test, an Akaike Information Criterion (AIC) was determined as the natural logarithm of the mean (sum divided by S) of squared deviations between observed and predicted ln(relative abundance) for all ranked S species plus an additional term to correct for the number of estimated parameters, k (1 for geometric series and 2 each for log-series and log-normal distributions): $(S + k)/(S-k-2)$. The lower the calculated AIC value, the better the fit. A difference of 1 in AIC corresponds roughly to a 1.5 evidence ratio. Following Burnham and Anderson (2002) we consider differences in AIC of less than 1 to represent indistinguishable fits among modeled distributions.

Chlorophyll Determinations

Seawater samples from 6 depths were collected from the Niskin bottles of the rosette sampler. Volumes between 5.6 and 1 L (depending on the trophic conditions) were filtered onto 25mm GF/F filters, and the filters stored in liquid nitrogen at −80° C until analysis on land. The samples were extracted in 3mL methanol for a minimum of 1 h, with filter disruption by ultra-sonication. The clarified extracts were injected onto an Agilent Technologies 1100 series High Performance Liquid Chromatography (HPLC) system equipped with a refrigerated auto sampler and a column thermostat, according to a modified version of the method described by Van Heukelem and Thomas (2001). Separation was achieved within 28 min during a gradient elution between a Tetrabutylammonium actetate: Methanol mixture (30:70) and 100% methanol. The chromatographic column, a Zorbax-C8 XDB (3×150 mm) was maintained at 60° C. Chlorophyll a, divinyl chlorophyll a and derived products were detected at 667 nm and the other accessory pigments at 450 nm using a diode array detector. (Detection limits for chlorophyll a were 0.0001 $\mu g\ l^{-1}$, injection precision was 0.4%). The different pigments were identified using both their retention times and absorption spectra. Quantification involved an internal standard correction (Vitamin E actetate) and a calibration with external standards provided by DHI Water and Environment (Denmark).

Primary production

Carbon fixation estimates followed the experimental protocol recommended by France-JGOFS-P.F.O. (1988) and given in detail in Moutin and Raimbault (2002). Description of the full experimental protocol and all of the in situ incubations conducted throughout the cruise will appear elsewhere (Gimenez, in prep.); here only data from two of the long stations (B & C) are reported. Briefly, samples were obtained with 12-l Niskin bottles at 9 depths chosen according to the CTD fluorescence profiles. Each sample (320-ml polycarbonate bottle, 3 light and one dark sample per depth) was collected before sunrise, inoculated with 150 µl of the 14C working solution just before sunrise, and then incubated in situ on a mooring line for 24 hours. After incubation, the samples were filtered on GF/F filters to measure net absorption (AN mg C m-3). Filters were immediately covered with 500 µl of HCl 0.5 M and stored for subsequent analysis in the laboratory. Before each incubation, 3 samples were filtered immediately after inoculation and 250 µl of sample was taken at random from 3 bottles and stored with 250 µl of ethanolamine to determine the quantity of added tracer (Qi). In the laboratory, samples were dried for 12 h under and extractor hood, 10 ml of Ultimagold-MV (Packard) were added to the filters and samples then analysed using a Packard Tri carb 2100 TR liquid scintillation counter. Data reported here are average integrated primary production, a trapezoidal integration from the surface to 110 m depth.

RESULTS

Station Phytoplankton Characteristics

Station B was located in an area of high surface layer chlorophyll as shown in satellite images (Fig. 1.). Analysis of satellite images preceding and throughout the cruise showed the bloom developed in mid-February and disappeared in late March (De Verneil, in prep.). The March 15th surface sample (from 6 m) contained a dense population of filaments and tufts of *Trichodesmium* c.f. *erythraeum* (Fig. 2). Filaments ranged in length from 40 - 1500 µm with a total concentration, in linear terms, equal to about 2 m of *Trichodesmium* filament l^{-1}. Also present were dinoflagellates, dominated by small cells (20 µm dia.) found in abundances of about 2000 l^{-1} and large diatoms (> 50 µm), approx. 500 cells l^{-1}. Chlorophyll concentrations were maximal near the surface with a second peak at about 75m depth (Fig. 3). Primary production averaged 4.0 µg C l^{-1} d^{-1} (Table 1).

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Station C was located in an area of very low surface layer concentrations of chlorophyll (Fig. 1). The chlorophyll maximum layer was located at about 150 m depth (Fig. 3). The surface sample from Station C, taken on March 27 (from 6.5 m), contained few *Trichodesmium* filaments with a total concentration, in linear terms, equal to about 0.2 m of *Trichodesmium* filaments l^{-1}. Compared to Station B, dinoflagellates and diatoms were found in lower concentrations of about 1000 l^{-1} and 100 l^{-1}, respectively. Primary production averaged 2.0 µg C^{-1} l^{-1}, half the rate found at Station B (Table 1).

Ciliate Abundances & Vertical Distributions

At Station B average water column concentrations of both tintinnids, and all planktonic ciliates, ranged narrowly: 9.0-11.0 tintinnids l^{-1} and 570-710 total ciliates l^{-1}. However vertical distributions were quite irregular either comparing days or groups (Fig. 3). At Station C average water column concentrations also ranged narrowly: 5.7- 6.2 tintinnids l^{-1} and 670-730 total ciliates l^{-1}. In contrast to Station B, vertical distributions were similar between groups and with time (Fig. 3). The marked differences in the vertical distributions suggest that Station B populations were dynamic compared to the apparent steady state of Station C populations. For both Station B and Station C there were no clear differences in the species composition of the tintinnid assemblages with depth in accordance with findings from previous studies (e.g., Dolan 2000; Dolan et al. 2009). Water column profiles of temperature, salinity and density were nearly invariant and identical at the 2 stations (data not shown) supporting the hypotheses that variability in vertical distributions found in Station B populations reflected biological interactions rather than physical dynamics.

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Tintinnid Assemblages

At Station B the assemblage was highly dominated (about 30% of total cells) by a single species, *Favella* sp. (Fig. 4a), not found in Station C, and it alone accounted for about half of the twofold difference in the overall abundance of tintinnids comparing the two stations (Table 1). In contrast, the most abundant species at the oligotrophic Station C, *Steenstrupiella steenstrupii* (Fig. 4b) accounted for only 12% of the population. At both stations the species richness was high, ranging from day to day from 46 to 54 at Station B and 43 to 56 at Station C. Numbers of 'trace species', found as one cell in the 60 l examined for each day, were also of similar magnitude at the two sites ranging from 7 to 16 and 7 to 17, respectively, at Stations B and C. Total species richness at the two sites was numerically identical at 71 species. Metrics of morphological diversity, H' values of LOD size-classes, and the numbers of size-classes found, were only slightly lower in the Station B assemblage (Table 1). Analysis of abundance distribution patterns (Table 2 & Fig. 5) indicated similar population structure in Stations B and C. Species abundance distributions were lognormal or log-series (i.e., not significantly different fits) and the size-class abundance distributions were both best modeled by a geometric distribution. However, there were some differences in the two assemblages other than the presence of a relatively dense population of *Favella* sp. at Station B.

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=> Insert Here Table 1 and Table 2.

There were differences in the size-structure of the two assemblages. In the Station C assemblage, the number of species in an LOD size-class was positively related to the number of cell in the size class. In the Station B assemblage, there was no significant relationship between the number of species in a given size-class of LOD and the number of cells in that size class. This was the case both with and without including the Favella sp. data (Fig. 6). The species inventory also differed in composition between the two sites. There were 13 species found in Station B absent from Station C, and 23 species found in Station C absent from Station B. There were interesting similarities in the characteristics of the species found in one site only. The 'one site only' species were mostly those with an LOD size close to that of the Station B dominant *Favella* sp. (Fig. 7). Most of the species found with *Favella* at Station B, but not at Station C, had an LOD close to that of the *Favella* sp. Similarly, the species found in Station C, but absent from the *Favella*-dominated assemblage, have an LOD close to that *Favella*. Thus most of the difference in the species inventories of the high producitivity and oligotrophic sites concerned forms with of an LOD close to the *Favella* sp. of the high productivity site. The tintinnid data by date is provided in a Supplemental File.

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DISCUSSION

We expected to find distinct differences between the population structure of a tintinnid assemblages in a 'hot spot' of productivity site compared to a typical oligotrophic site. Specifically, we expected the high productivity site to harbor a larger population but of lower species richness and show lower variability in the total species inventory from day to day. These expectations were based on the patterns found in the SE Pacific where across a large gradient of stations tintinnid diversity was negatively related to average chlorophyll concentration and positively related to the depth of the chlorophyll maximum layer (Dolan et al. 2007). It is unclear exactly what mechanism is behind the relationship. The two parameters, depth of the maximum concentration of chlorophyll and average water column concentration, are themselves usually strongly and inversely related. The depth of the surface mixed layer often, but not always, corresponds with the depth of the chlorophyll maximum layer (Cullen 1982). The large-scale pattern of diversity in planktonic foraminfera has been related to the depth of the surface mixed layer. In planktonic forminifera assemblages diversity increases with the depth of the surface mixed layer; high diversity corresponding with a mixed layer of a larger volume (Rutherford et al. 1999). Regardless of the mechanism behind the large-scale geographic pattern relating depth of the chlorophyll maximum layer and diversity, our data show that a site with a shallow chlorophyll maximum (St B) can harbor high species diversity.

Our comparison of communities from sites differing in primary productivity, chlorophyll concentration, and chlorophyll vertical distribution revealed some differences. The variability in the vertical profiles of both total ciliates and tintinnids (Fig. 3) suggested that the microzooplankton overall was highly dynamic in St. B compared to St. C. The 'hot spot' of productivity had a tintinnid community highly dominated by one species. The two populations differed in abundance by about a factor of 2, roughly corresponding to the differences in rates of primary productivity (pooled data, Table 1). There were also differences in the temporal variability of vertical distributions (Fig. 3), species inventories, and the strength of size-structuring in the assemblages i.e., the relation ship of species richness of an LOD size-class and the number of cells in the size-class (Fig. 6). Overall however the populations were largely similar in terms of species richness, patterns of abundance distributions (Fig. 4) and showed the same turn over or temporal variability in species inventories. Furthermore the metrics of morphological diversity were quite similar as well (Table 1). The overall characteristics of both assemblages were very much like those found in the oligotrophic sites in the SE Tropical Pacific (Dolan et al. 2007). Specifically the sites in the SE Tropical Pacific with deep (> 150 m) chlorophyll maximum layers and low chlorophyll concentrations were found to harbor assemblages of 21-41 spp with Shannon Index values of 2.6 -3.2, values quite similar to those reported here (Table 1). Furthermore, there were no obvious differences in the communities of non-tintinnid ciliates; at both stations the numerically dominant form was a small (15 µm dia.) oligotrichid form. Our results suggest that tropical microzooplankton populations do not change dramatically in a transient period of high primary productivity.

The effects of transient phytoplankton blooms on other components of the planktonic food web have been investigated as part of large-scale iron fertilization experiments. However data are quite sparse with regard to effects on microzooplankton. The experiments mostly have been conducted in high latitude sites in both the southern and northern hemispheres. These studies have yielded contradictory results with regard to effects on other components of the plankton. In the EIFEX experiment in the Antarctic circumpolar current, the experimentally induced bloom yielded large shifts in the protozooplankton assemblage, including tintinnid assemblages (Assmy et al. 2014). However, during the EisenEx experiment in the Southern Ocean no major changes occurred in the composition of the bacterial community based on phylogenetic signatures (Arrieta et al. 2004). Similarly, in the LOHAFEX iron fertilization experiment in the South Atlantic, while chlorophyll concentrations increased by a factor of 3, the prokaryote populations were "remarkably constant" (Thiele et al. 2012) as was the composition of eukaryotic nanoplankton (Thiele et al. 2014). In the Subarctic Pacific, iron enrichment in the SERIES study, in NE Subarctic Pacific, resulted in little change in the community composition of the mesozooplankton (Sastri & Dower 2006). In the SEEDS experiment, in the western Subarctic Pacific, the only notable shift in the microzooplankton was an increase in the abundance of heterotrophic dinoflagellates (Saito et al. 2005).

Our findings of overall similarity in assemblages of tropical tintinnids in a productivity 'hot spot', compared to a non-hot spot, may reflect the fact that the productivity of the 'hot spot' we sampled was not sufficiently elevated compared to the reference site to provoke a marked change in the tintinnid assemblage other than the development of a single species. Alternatively perhaps as the bloom was relatively old when we were sampling, having begun about a month earlier, the tintinnid assemblage was in transition towards typical oligotrophic site assemblage. Cleary it would be desirable to sample more stations and survey populations throughout the occurrence of a phytoplankton bloom. Unfortunately, oceanographic expeditions are complex, costly and infrequent limiting severely our access to natural populations in remote sites of oligotrophic tropical systems. We can only hope that future expeditions will provide additional opportunities to investigate these fascinatingly diverse assemblages.

CONCLUSIONS

We examined the characteristics of tintinnid ciliate assemblages in the South West Pacific Ocean. We analyzed 2 assemblages, comparing one found in a site with high primary productivity associated with a bloom of the nitrogen-fixing cyanobacterium *Trichodesmium* with the assemblage found in a typical oligotrophic site. Tintinnid abundance differed between the sites by a factor of 2 and a species absent from the oligotrophic site, highly dominated the 'hot spot' site. Despite some differences in the species inventories of the two assemblages, total species richness was identical. Both morphological diversity and temporal variability were similar as well. For both assemblages, the species abundance distributions were most closely fit by a log-series or log-normal distribution, and the abundance distributions of ecological types, forms of distinct lorica oral diameter, were the typical geometric as found in assemblages from other tropical and subtropical sites. Despite large differences in population size and dominance, the two populations were similar by most measures. We found that populations of these plankton grazers in 'hot spots' of phytoplankton productivity in oligotrophic systems may not differ from those in surrounding oligotrophic areas.

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FIGURE LEGENDS

Figure 1. Surface chlorophyll-a concentration during the OUTPACE cruise. The ocean color satellite products were produced by Collecte Localisation Satellites (http://www.cls.fr/en/).

Figure 2. A tuft of the N-fixing *Trichodesmium* c.f. *erythraeum* which was abundant in Station B.

Figure 3. Vertical profiles of the abundances of tintinnid ciliate and the total planktonic ciliate populations at Stations B and C plotted by date (2015); chlorophyll data were available for a single date for each site and did not include a near surface sample. Satellite data (Fig. 1) showed a surface concentration of over 1 µg chlorophyll l^{-1} for Station B (over 5 times the maximum concentration at Station C) and a surface concentration of 0.03 µg chlorophyll l^{-1} for Station C. Note the relatively irregular distributions found at the high primary productivity Station B compared to the nearly invariant and coherent distributions and abundances found in the Station C.

Figure 4. The left panel, A, shows the Station B dominant tintinnid form, *Favella* sp.; it represented over 30% of the abundant tintinnid population found in the 'hot spot' station. The form closely resembles the species depicted as *Favella azorica* by Marshall (1934) in both shape and dimensions, with an LOD of about 45 µm. However, Cleve's original description as *Undella azorica*, gave an LOD of 66 µm (Cleve 1899). Hence we term the form found in Station B *Favella* sp.. The right panel, B, shows the Station C dominant species *Steenstrupiella steenstrupii*; it represented about 12% of the Station C tintinnids.

Figure 5. Plots of the rank abundance distributions of the tintinnid assemblages from Station B (St B) and Station C (St C). Right panel shows the species rank abundance distribution. Note that with the exception of the first ranked species and size class for for St B, the distributions for St B and St C are nearly identical.

Figure 6. Size structure of the tintinnid assemblages found in Stations B and C. The tintinnid assemblages were binned in categories of lorica oral diameter. Shown are only lorica size categories which contained at least 10 cells. The upper panel, data from Station B, shows a near invariant number of species per size-class. In contrast, in the Station C assemblage, the number of cells within a size-class appears positively related to the number species in the size class. Simple linear correlation analysis confirmed these patterns. For Station C data there was a significant linear relationship between the number of cells and species in a size class: r = 0.70** n = 14. For Station B data there was no significant relationship between the number of cells in a size classs and the

number of species in the size class: r = 0.50 ns, n = 13; excluding the dominant *Favella* sp did not improve the relationship: r = 0.44 ns, n = 13.

Figure 7. Morphological characteristics (lorica oral diameter) of tintinnid species found in only one of the two sites sampled. Note that most of the 'one station only' species were of LOD sizes close to that of the Station B dominant, *Favella* sp..

SUPPORTING INFORMATION

Tintinnid Supplementary Data, Video of time-course changes in surface concentrations of chlorophyll a based on satellite image data.

Table 1. Summary data for tintinnid populations sampled and primary production. Data from discrete depth samples were pooled to yield total number of individuals encountered (∑ cells), number of species (# spp), number of species found as a single individual (# trace spp), Shannon diversity index for species (spp H'), numbers of LOD size-classes (# LODs), and Shannon diversity index of LOD size-classes present (LOD H'). Primary production (PP) in μg C l^{-1} d^{-1} average integrated for the 0-110 m segment of the water column.

population	date sampled	∑ cells	# spp	# trace spp	spp H'	# LODs	LOD H'	PP
Stat B CTD 110	Mar 15 2015	572	46	7	3.01	14	2.16	3.9
Stat B CTD 128	Mar 17 2015	578	54	12	3.25	16	2.3	4.6
Stat B CTD 146	Mar 19 2015	771	52	16	2.41	15	1.84	3.3
Stat C CTD 159	Mar 23 2015	374	43	7	3.22	14	2.24	1.4
Stat C CTD 176	Mar 25 2015	356	56	17	3.47	16	2.32	1.4
Stat C CTD 194	Mar 27 2015	337	49	17	3.33	16	2.24	1.4
Stat B Pooled	Mar 15-19	1921	71	9	2.98	17	2.14	avg. 4.0
Stat C Pooled	Mar 23-27	1051	71	11	3.51	17	2.29	avg 1.4

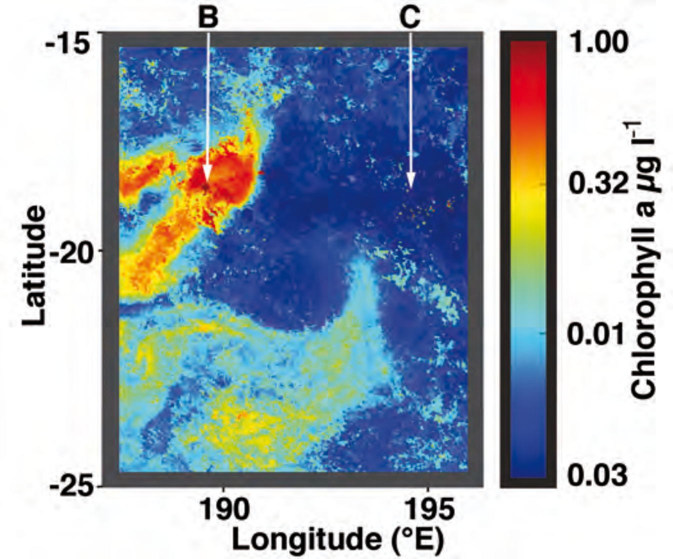
Table 2. Results of modeling abundance distribution patterns. Lowest AIC values (red) indicate the best model fit. Multiple values in red indicate indistinguishable fits (differences <1).

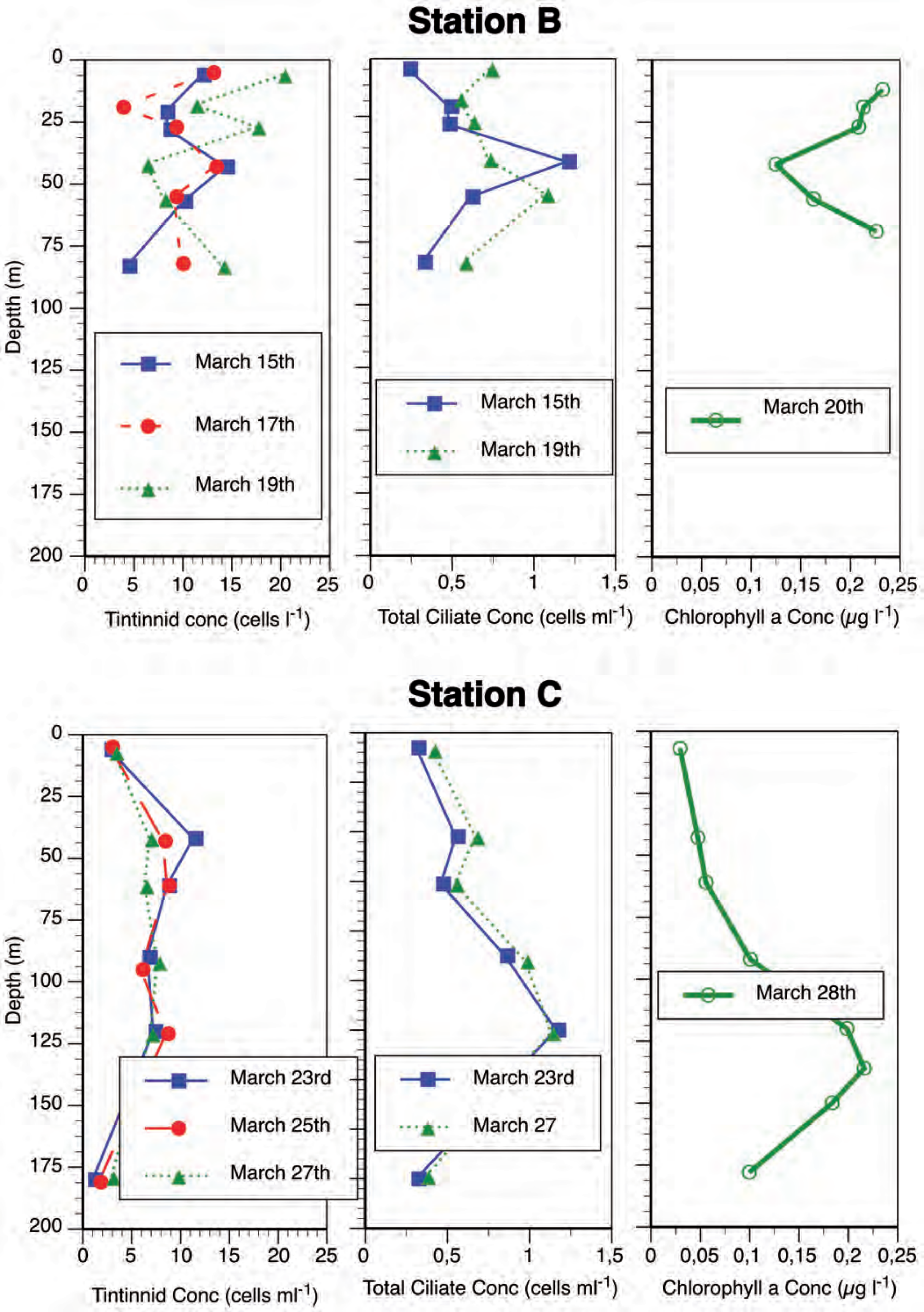
Species Abundance Distribution fits

population	Log-Normal	Geometric	Log-Series
Stat B	**1.4**	3.5	**0.1**
Stat C	**1.2**	**2.6**	**1.0**

Size-Class Abundance Distribution fits

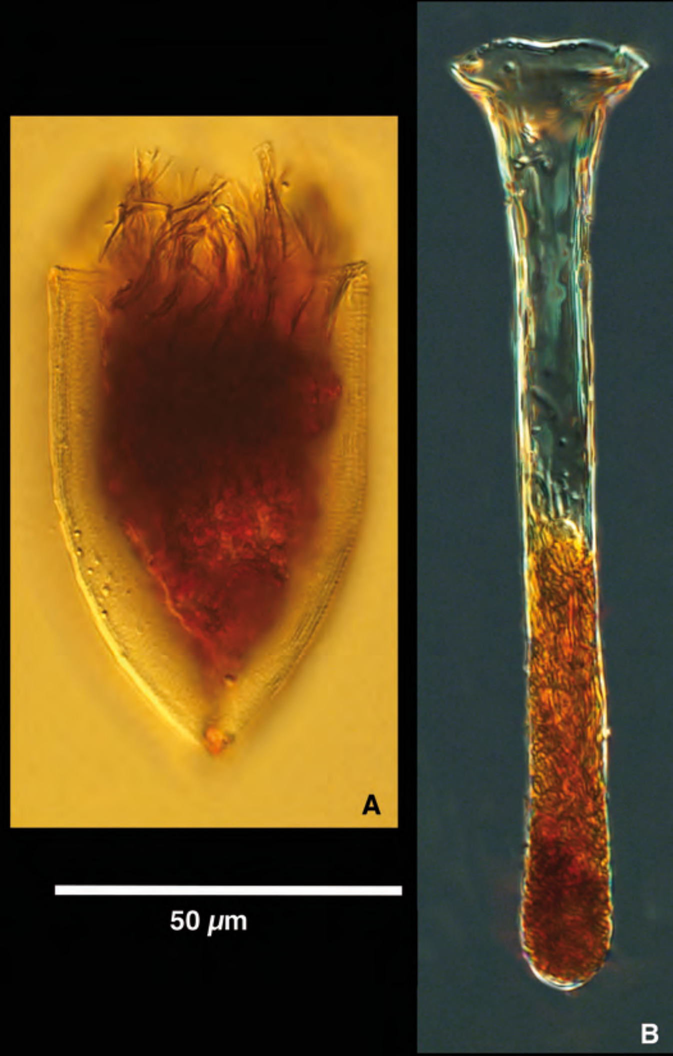
population	Log-Normal	Geometric	Log-Series
Stat B	2.4	**0.3**	2.2
Stat C	1.7	**-0.1**	1.3

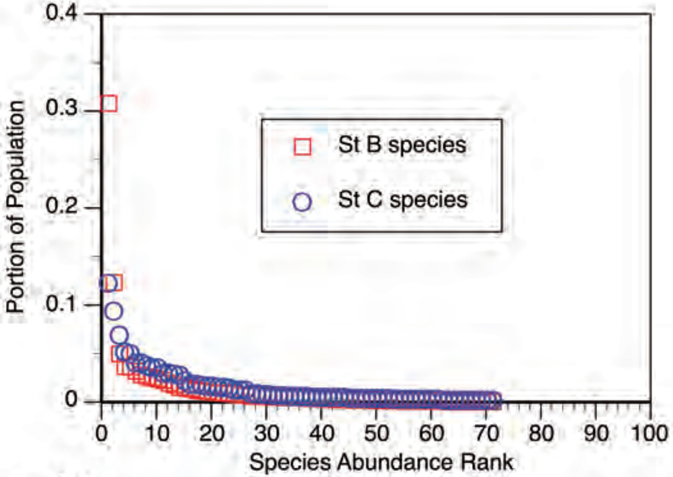

B
C
-15
-20
-25
Latitude
190
195
Longitude (°E)
1.00
0.32
0.01
0.03
Chlorophyll a $\mu g\ l^{-1}$



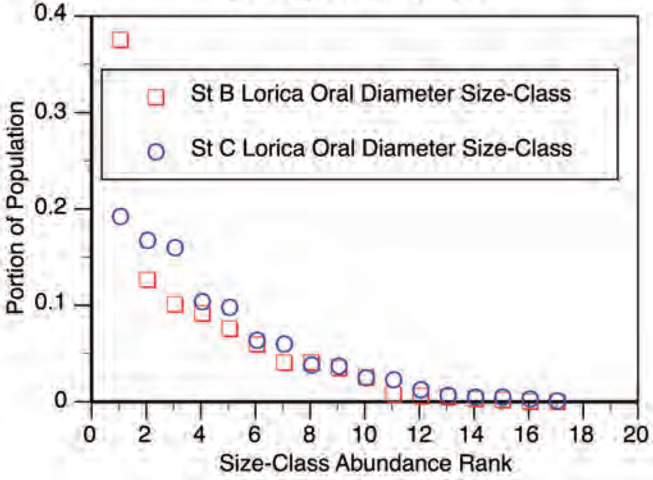
Station B
Depth (m)
Tintinnid conc (cells l-1)
Total Ciliate Conc (cells ml-1)
Chlorophyll a Conc (μg l-1)
March 15th
March 17th
March 19th
March 20th
Station C
Tintinnid Conc (cells ml-1)
March 23rd
March 25th
March 27th
March 27
March 28th


1 mm

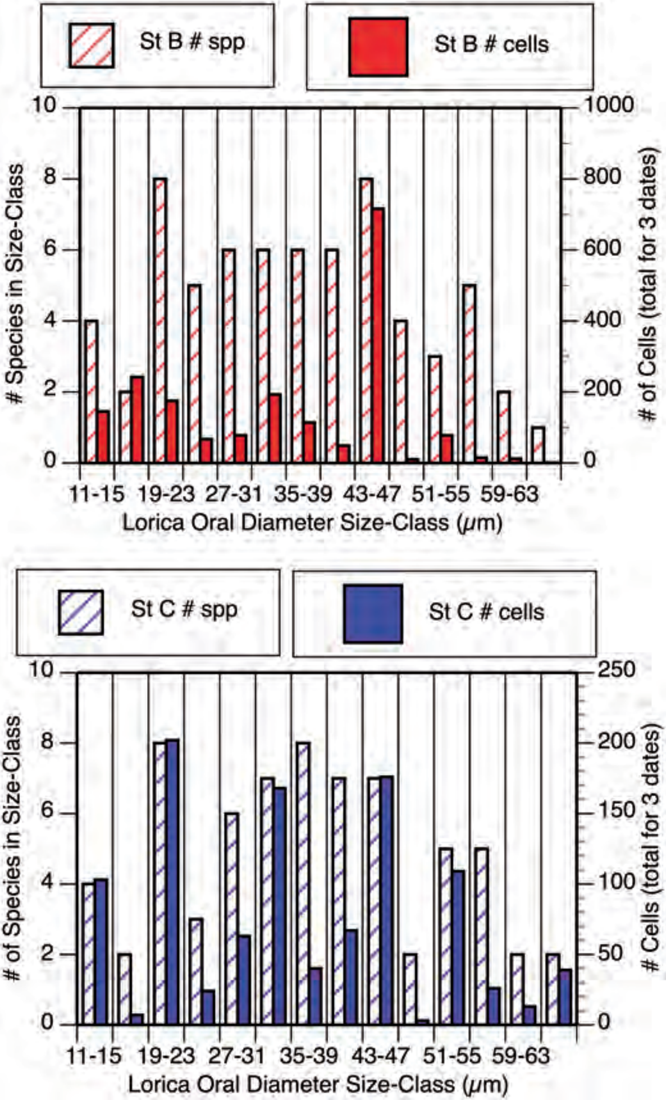

A
50 μm
B

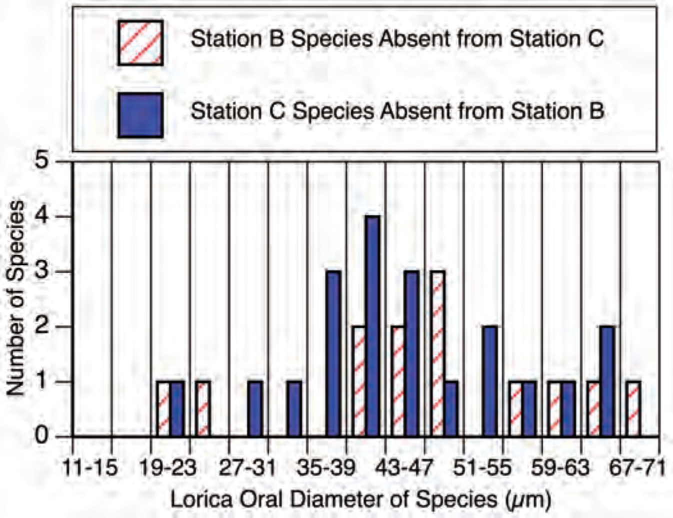


Portion of Population
Species Abundance Rank
St B species
St C species
0
0.1
0.2
0.3
0.4
0
10
20
30
40
50
60
70
80
90
100



Portion of Population
Size-Class Abundance Rank
St B Lorica Oral Diameter Size-Class
St C Lorica Oral Diameter Size-Class
0
0.1
0.2
0.3
0.4
0
2
4
6
8
10
12
14
16
18
20


St B # spp
St B # cells
Species in Size-Class
of Cells (total for 3 dates)
10
8
6
4
2
0
1000
800
600
400
200
0
11-15
19-23
27-31
35-39
43-47
51-55
59-63
Lorica Oral Diameter Size-Class (μm)
St C # spp
St C # cells
# of Species in Size-Class
Cells (total for 3 dates)
10
8
6
4
2
0
250
200
150
100
50
0
11-15
19-23
27-31
35-39
43-47
51-55
59-63
Lorica Oral Diameter Size-Class (μm)


Station B Species Absent from Station C
Station C Species Absent from Station B
Number of Species
0
1
2
3
4
5
11-15
19-23
27-31
35-39
43-47
51-55
59-63
67-71
Lorica Oral Diameter of Species (μm)