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Declines in Both Redundant and Trace Species Characterize the Latitudinal Diversity Gradient in Tintinnid Ciliates

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Abstract

The latitudinal diversity gradient is a well-known biogeographic pattern. However, rarely considered is how a cline in species richness may be reflected in the characteristics of species assemblages. Fewer species may equal fewer distinct ecological types, or declines in redundancy (species functionally similar to one another) or fewer trace species, those occurring in very low concentrations. We focused on tintinnid ciliates of the microzooplankton in which the ciliate cell is housed inside a species-specific lorica or shell. The size of lorica oral aperture, the lorica oral diameter (LOD), is correlated with a preferred prey size and maximum growth rate. Consequently, species of a distinct LOD are distinct in key ecologic characteristics while those of a similar LOD are functionally similar or redundant species. We sampled from East Sea/Sea of Japan to the High Arctic Sea. We determined abundance distributions of biological species and also ecological types by grouping species in LOD size-classes, sets of ecologically similar species. In lower latitudes there are more trace species, more size-classes and the dominant species are accompanied by many apparently ecologically similar species, presumably able to replace the dominant species, at least with regard to the size of prey exploited. Such redundancy appears to decline markedly with latitude in assemblages of tintinnid ciliates. Furthermore the relatively small species pools of the northern high latitude assemblages suggest a low capacity to adapt to changing conditions.

Keywords: biodiversity, ciliata, rare species, species packing, tintinnida

Running title: High Latitude Assemblages

Introduction

A very wide variety of taxa, both multicellular and microbial, show a latitudinal diversity gradient (Gaston & Spicer 2003). Typically, species richness peaks in the tropics, often at about 20°, dips slightly at the equator and decreases markedly with latitude both north and south. Tintinnid ciliates of the marine microzooplankton literally provide a textbook example of the pattern (Gaston & Spicer 2003). Slight variations of the pattern characterize other protist taxa of the marine plankton such as foraminifera (Rutherford et al. 1999) and *Ceratium* species of the phytoplankton (Dolan 2011). The latitudinal diversity gradient is the oldest known biogeographic pattern and the mechanisms generating it have long been debated with dozens of theories proposed, none of which have found wide acceptance (Willig et al. 2003). A universal explanation of the latitudinal diversity gradient has been termed 'The Holy Grail of Ecology' (Adams 2009). Thus, while there is little agreement as to why the gradient exists, most do acknowledge that species richness often declines with latitude (Adams 2009). The structure of species assemblages quite likely often differs with species richness but exactly how is difficult to predict. Declines in species richness can be reflected in various ways with different consequences concerning the ecological characteristics of a species assemblage.

Fewer species can represent a reduction in the overall variety or range of species within an assemblage. Less variety among species can translate into a lower capacity to respond to changes in resource compostion or predation pressure. For example, a smaller range of consumer species could have a lower capacity to exploit changes in the size or qualities of available prey items. Alternatively, lower species richness may represent only fewer forms present in very low concentrations, outside their usual habitat, members of the “accidental biosphere” (Weisse 2014). These species likely have low actual or potential ecological impact. Besides a decline in variety, lower species richness may translate into fewer presumptive redundant species (i.e., species of similar ecological characteristics) able to replace dominant species subject to a high specific mortality. Theoretically, the presence of redundant species should increase the resiliency of an assemblage, meaning its capacity to resist perturbation and survive changes in conditions (Naeem 1998).

Recent studies have re-emphasized the tremendous diversity of protists in the marine plankton (de Vargas et al. 2015). The phylogenetic diversity and extreme ecological complexity of protistan assemblages makes assessing how assemblages are structured a daunting task (e.g., Lima-Mendez et al. 2015). Among planktonic protists, tintinnids are an example of a phylogenetically and ecologically coherent group and so represent a taxon in which study of the structure of assemblages are considerably simplified. Tintinnid ciliates also represent an ideal group to examine with regard to the question of how the structure of species assemblages varies with latitude. This is because not only do they show a typical latitudinal diversity gradient but also the population structure of temperate, sub-tropical and tropical populations are well known and species of similar ecology share similar morphologies allowing identification of ecologically redundant species.

Tintinnid ciliates are characterized by the possession of a shell or lorica whose architecture and dimensions form the basis of classic taxonomic schemes (Figure 1). About 1,200 species are in the literature (Agatha & Strüder-Kypke 2012); virtually all are restricted to the marine plankton. The diameter of the mouth-end of the lorica, lorica oral diameter (LOD) is a conservative taxonomic character (Laval-Peuto &

Brownlee 1986). It does not change with development; newly divided cells form a new lorica with the same oral diameter as the fully developed organism (Agatha et al. 2013). Critically, LOD, analogous to gape-size, is related to both the size of the food items ingested and maximum growth rate. The largest prey item ingested is about 0.5 the LOD in longest dimension and a given species feeds most efficiently on prey about 0.25 of its LOD in size. LOD is negatively related to maximum growth rate. This is because LOD is positively related to the volume of the cell occupying the lorica (Dolan 2010) and tintinnids follow the common inverse relationship between cell size and maximum specific growth rate (Montagnes 2013). Tintinnid species with a similar LOD, or mouth size, are usually similar in terms of both preferred prey size and maximum growth rate; here these similarities are taken as indicating ecological redundancy.

The structure of tintinnid populations, in terms of both species abundance distributions and distributions of species grouped in size-classes, has been characterized for the species-rich assemblages of tropical, sub-tropical and temperate systems (Dolan et al. 2007; 2013). Typically in these systems, dozens of species can be found in material from 10-20 l (Dolan & Stoeck 2011). In general, species abundance distributions are log-series or log-normal distributions while grouping forms by size-classes rather than species yields a geometric distribution (Dolan et al. 2007; 2013). Assemblages are overall structured by "mouth size". Typically there are 4 to 10 abundant species and these are of mouth sizes distinct from one another. The other species, of markedly less abundance, can be divided into two groups. The first is composed of those with mouth sizes similar to one of the dominant species; these are ecologically redundant forms. The second group is formed of species in LOD size-classes distinct from those of the dominants and these species appear to be occasional, ephemeral, or rare species (Dolan et al. 2009) and are generally present in very low concentrations (Dolan et al. 2013). However, it is important to note that the categories of ‘redundant’ and trace or ‘rare’ are not exclusive. If a species found in trace concentrations is in a size-class with other species, then it is both redundant and rare while if alone in a size-class then it is not redundant but rare with ecological characteristics distinct from all the other species.

Tropical, subtropical, and temperate assemblages are characterised by high species richness reflecting both considerable species redundancy as well as the presence of species with morphologies distinct from abundant forms but found in low concentrations. In this study we address the question of how sub-arctic and arctic communities with lower species richness are structured compared to temperate communities.

We characterized communities along a latitudinal gradient of decreasing species richness. We examined large-scale or metapopulation characteristics in terms of species and in terms of 'ecotypes', defined here as species of similar feeding ecology and maximum growth rate based on LOD or mouth size. In 2012 we sampled populations of the East Sea/Sea of Japan, the North Pacific Ocean, the Bering Sea and the Chukchi Sea, and the High Arctic along a transect of over 43° of latitude and 5000 km (Figure 2). Notably the year 2012 was a year of record low sea ice extent permitting open water sampling of plankton in the High Arctic, to our knowledge for the first time. For each system 2 to 6 stations were sampled providing at least 2000 ciliate cells representing each assemblage. The parameters estimated for each of the 5 populations were species richness, number of trace species (found as a single cell), number of mouth size-classes, proportion of size-classes with multiple occupants (containing more than one species), and the number of apparently redundant species. For each assemblage the pattern of species abundance distribution was compared with modeled abundance curves constructed using parameters of the particular assemblage for three common models of community organization: geometric, log-normal and log-series. Substituting size-class of oral diameter for 'species', we also determined size-class abundance distributions.

Methods

Sampling & Sample Analysis

Data and samples were collected from onboard the Korean Research Icebreaker *Araon* from July to September in 2012. Data presented here are from 22 stations distributed between the Japan Sea and 82 °N as shown in Figure 1. Exact locations and the Korean Polar Research Station Designations are given the supplementary data file. A Niskin bottle rosette equipped with CTD probes was used to obtain temperature profile data and discrete depth samples for chlorophyll determinations. Plankton net tows were performed to assess microplankton community composition.

For chlorophyll *a* determinations, water samples of 0.3-1 l were obtained from 7-9 discrete depths between the surface and 100 m depth. Water samples were filtered through a 0.7 μm Whatman glass fiber filter (GF/F) and chlorophyll concentrations determined onboard using a Turner Designs Trilogy model fluorometer calibrated using commercial chlorophyll *a* standards.

Net tows were made with a 20μm mesh plankton net of 0.45 m diameter towed from 100 m depth to the surface, except at some shallow stations sampled from 50 or 30 m depth. A portion of the net tow material was fixed with Lugol's (2% final concentration) for direct microscopic examination. In the laboratory, multiple 1 - 2 ml aliquots of net tow material were diluted and examined in 3 ml settling chambers using an inverted microscope equipped with DIC optics. The entire surface of the settling chamber was examined at 200x total magnification. Tintinnid identifications were made based on lorica morphology and following Kofoid & Campbell (1929, 1939) and Hada (1937). We adopted a conservative approach, distinguishing all forms corresponding to species currently recognized as valid. Species names, occurrences and LOD diameters assigned are given in the supplementary data file. As previously described and justified (Dolan et al. 2006; 2007, 2009; 2013), species of similar ecology in terms of preferred prey size and maximum growth rate were grouped based on (LOD). Each species was assigned the average dimensions reported in Kofoid & Campbell (1929, 1939) and Hada (1937). Size-class diameters were binned over 4 *μ*m intervals beginning with the overall smallest diameter (11 *μ*m) and continuing to the largest diameter encountered in a given sample.

Total sample volumes examined varied, depending on the concentrations of organisms, and the dilutions employed varied according to concentrations of phytoplankton. However, multiple aliquots were examined until material from at least 100 liters filtered by the net was analyzed for each station. Nominal concentrations of organisms (given in the supplementary file) were calculated based on the volume filtered by the net (calculated from net surface area and depth of the strata sampled) and the volume of net tow material examined. It should be noted that the concentrations reported here are the average values per liter for the portion of the water column sampled, for most stations the top 100 m.

Data Analysis

Tintinnid assemblages were characterized by pooling data by system: East Sea/Sea of Japan stations 1-2; North Pacific stations 3-8; Bering Sea stations 9-12, Chukchi Sea stations A-F, and the High Arctic Sea stations G-H. The parameters estimated for each of the 5 populations were species richness, number of trace species (found as a single cell), number of mouth size-classes, proportion of size-classes containing more than one species (multiple occupants), and the number of apparently redundant species. We used simple linear correlation analysis to examine relationships across all stations between species richness and latitude, water temperature, organismal concentrations and chlorophyll a concentrations.

For each assemblage we examined the patterns of both species abundance distribution and the abundance distributions of LOD size-classes. We first made log-rank abundance curves by calculating relative abundance for each species and ranking species from highest to lowest and plotting ln(relative abundance) vs. rank. Then, we constructed hypothetical log-rank abundance curves that could fit the data by using parameters of the particular assemblage. We produced curves for three common models of community organization: geometric series, log-series, and log-normal, as in several previous studies (Claessens et al. 2010; Doherty et al. 2010; Dolan et al. 2007, 2009; 2013; Dolan & Stoeck 2011, Raybaud et al 2009).

The observed rank abundance distributions were compared to the hypothetical models using a Bayesian approach: an Akaike goodness of fit calculation (19). Using this approach, 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; we considered that a minimum difference of 1.0 between AIC values was required to represent a significantly different fit following Burnham & Anderson (2002).

Results & Discussion

The expected latitudinal decline of species richness was evident. In the East Sea/Sea of Japan species richness was much higher than in the higher latitude systems. The East Sea/Sea of Japan also had higher cell and chlorophyll *a* concentrations. However, plotting individual station data showed the decline in species richness across the 5 systems to be more closely relatable to sea surface temperature rather than latitude, and independent of the bulk characteristics of tintinnid cell or chlorophyll concentrations (Figure 3).

The dominant species in each assemblage (shown in Supplemental Figure 1) were small-mouthed species, *Proplectella expolita*, *Condonellopsis frigida*, *Acanthostomella norvegica* except in the North Pacific where the relatively large-mouthed *Ptychocylis obtusa* dominated. In each assemblage, the dominant species accounted for 45-86% of the cells encountered (Table 2). Overall, of the 31 species found most (25) were not widely distributed but rather found in only in 1 or 2 of the systems sampled. In contrast, 4 species were found in all 5 populations sampled. These widespread forms were 4 of the 6 species found in the High Arctic Sea. Thus, the few species found in the High Arctic are mostly the widely distributed forms (for details distributions of each species distributions see the supplementary data file “species data”).

Characteristics of the populations in the East Sea/Sea of Japan differed considerably from all of the high latitude assemblages (Table 1). Overall species richness was similar to that reported for stations from the California Current system in the Eastern Pacific at about the same latitude (Dolan et al. 2013). The 25 species of the East Sea/Sea of Japan assemblage were distributed in 11 size-classes, most of which were occupied by more than 1 species. Thus, a large portion of the species pool was composed of ‘ecological redundants’, species occupying a size-class along with 1 or more other species. The size class containing the largest number of species was that of the dominant species, *Proplectella expolita*, which was accompanied by three other species. The 5 rare or ‘trace’ species (those found as a single individual) were redundants with one exception. Thus only 1 rare form was distinct from all other species in terms of mouth size.

Compared to the East Sea/Sea of Japan, the North Pacific assemblage was composed of fewer species and these were distributed in fewer size-classes (Table 1). Half the size-classes contained redundants as they were occupied by more than 1 species. The dominant species, the large-mouthed *Pytchocylis obtusa*, was alone in its size-class. None of the trace species formed a distinct size-class, all appeared to be redundants. The Bering Sea assemblage resembled that of the North Pacific in species richness. The assemblage formed 9 size classes with the dominant species, *Codonellopsis frigida*, sharing a size-class with 2 redundant species. Two other redundant species shared the size class of the second most abundant species *Parafavella parumdentata*. The 2 trace species were alone in their size-class.

Low species richness characterised both Arctic assemblages (Table 1). In the Chukchi Sea the 8 species found were distributed in 7 size-classes with only the size-class of the dominant species, *Acanthostomella norvegica*, containing a redundant species. The single trace species was alone in its size-class. The High Arctic population, dominated by *Ptychocylis obtusa*, was singular in having neither rare species nor redundant species; all 6 species found were in distinct size-classes. The latitudinal decline in species richness we found from the East Sea/Sea of Japan to the High Arctic represented declines in numbers of redundant and trace species. Notably while there were many fewer species in the high latitudes, the total overall size range of LODs found in the assemblages, 11 to 75 μm, was invariant across all the assemblages.

The data reported here are from a summer time sampling as is the case for most studies of high latitude plankton. In lower latitude coastal systems seasonal changes in species richness of tintinnid assemblages are well documented and summer is usually a period of low diversity (reviewed in Dolan & Pierce 2013). Few data exist concerning seasonality in open water systems, especially in arctic and subarctic waters due to the technical difficulty of sampling in periods other than summer. The gradient we found may be more prominent in other seasons, for example when the ice cover is maximal in the Chukchi Sea and High Arctic.

Also worth noting is that rather than harboring cryptic species, some species of the high latitude assemblages have long been suspected to be polymorphic, having variable loricas, which perhaps have been designated wrongly as distinct species. Among these suspected polymorphs are *Parafavella* spp (Burkovsky 1973; Davis 1978) of which 5 are reported here (see supplemental data file). The phenomenon of cryptic species in tintinnids (i.e., Santoferrara et al. 2015) may be less common compared to polymorphism as there are species known to display different lorica morphologies, but of the same LOD, previously described as different species and/or genera (i.e., Bachy et al. 2012; Laval-Peuto, 1983; Kim et al. 2014). At present it is not clear which phenomenon is more common. Among tintinnids and foraminfera cryptic species are generally segregated either temporally or spatially (e.g. de Vargas et al. 1999; Xu et al. 2012; Santoferrara et al. 2015) whereas in polymorphic species the different morphotypes occur together (e.g. Dolan et al. 2014; 2013; 2015).

The most likely candidates for crypticism are the widespread species, those found from the East Sea/Sea of Japan to the high Arctic such as *Ptychocylis obtusa* and *Acanthostomella norvegica*. These species inhabit waters ranging in temperature from 20° to -2° C. However whether or not, for example, an East Sea/Sea of Japan population of a “species” is genetically distinct from that in the High Arctic would not change species inventories or distributions for the geographically distinct assemblages. Given that cryptic forms of tintinnids appear to be segregated either temporally, i.e., seasonally (Xu et al 2015) or spatially i.e., distinct water masses (Santoferrara et al. 2015), they are unlikely to represent hidden diversity within an assemblage. Hence, in comparing assemblages from different systems the true problematic phenomenon is polymorphism that may inflate apparent species richness of an assemblage. If the 5 *Parafavella* species distinguished here (all found in low numbers: 1-5 cells per assemblage, see supplemental data file) are revealed to be a single species, the species richness of the assemblages of the East Sea/Sea of Japan, North Pacific and Bering Sea may be slightly lower then the numbers reported here.

Besides species richness, differences between the East Sea/Sea of Japan assemblage and higher latitude populations were also evident in the structures of the assemblages. The patterns of species abundance distributions as well the abundance distributions of size-classes differed among the assemblages (Table 2 and Figure 4). Species abundance distributions of all the high latitude populations were best fit by a geometric distribution in contrast to the log-series distribution of the East Sea/Sea ofJapan. Long-tailed log or log-series distributions, with large numbers of relatively rare species, are commonly observed for most natural assemblages (McGill et al. 2007). Long-tailed distributions are typical of abundance curves of planktonic protists determined using molecular techniques (e.g., Bachy et al. 2013; Brown et al. 2009; Edgcomb et al. 2011; Orsi et al. 2012). Notably, the pattern can be partially the result of problems arising from sequencing errors and differential sequencing of different taxa, issues which require attention (e.g. de Vargas et al. 2015).

The species abundance distribution of the East Sea/Sea of Japan assemblage was best fit by a log model. Log distributions, either log-normal or log-series are associated with a multitude of factors governing relative species abundance in the case of the log-normal, or immigration and extinction from a metapopulation in the case of log-series (i.e, Hubbell 2001). Substituting size-classes for species, similar differences were evident as the log-normal distribution of the East Sea/Sea of Japan population contrasted with the mostly geometric distributions of the high latitude assemblages (Table 3). A geometric distribution represents the result of a priority exploitation of resources by individual species in a community and is classically associated with 'immature' or pioneer communities limited by a single resource such as space (e.g., Whittaker 1972). This distribution is also thought to characterize assemblages of low species richness or severe environments (Wilson 1991). In Antarctic waters, a geometric species abundance distribution was found to describe the species abundance distribution of the entire planktonic ciliate community (Wickham et al. 2011). In tintinnid assemblages, the geometric distribution of LOD size-class abundance is most simply attributable to availability of prey concentration and size given the close relationship between LOD size and prey exploited by tintinnids (Dolan 2010).

The species found in trace concentrations, just 1 individual in 100 liters, can be considered ‘rare’. The phenomenon of rare species has received a good deal of attention (e.g. Gaston 1994). Rare species have become a focus in biodiversity conservation (e.g. Lyons et al. 2005). In microbial ecology, the results from high-throughput sequencing commonly suggest the existence of very large numbers of apparently rare species, present in low concentrations (e.g., Dunthorn et al 2014). Rare species, although low in abundance, may have important roles if they possess key functional traits different from abundant species (Mouillot et al. 2013). In the protistan “rare biosphere”, rare species may be of importance because they can become abundant if conditions change favoring different species with certain characteristics (Caron & Countway 2009). Admittedly, rare species can also be of minor ecological importance, as in members of the "accidental rare biosphere" (Weisse 2014). Regardless of the nature of the rare tintinnid species we found, their numbers decreased markedly with latitude (Figure 5).

Using our non-exclusive categories, a species found as a single cell is defined as rare but if it is in the same LOD size class as another species, it is also a redundant. However, the majority of redundant species were not rare but relatively abundant, as they were found in far greater than trace concentrations. Redundants were most numerous in the size classes of the dominant species and can likely replace a dominant species, for example, one subjected to a high rate of specific mortality from a parasite or predator (i.e., Coats & Bachvaroff 2012). A species can change roles from a minor to a major role. In temperate and sub-tropical assemblages of tintinnids, a species can be dominant in one population and a redundant in another (Dolan et al. 2013). In the Bering Sea *Codonellopsis frigida* was the dominant form while in Chukchi Sea is a redundant species. It has been argued that the existence of redundant species should increase the capability of an assemblage to exploit changes in conditions (Naeem 1998). Like rare species, we found redundant species declined in relative importance with latitude (Figure 5).

Conclusion

We found the latitudinal decline in species richness of tintinnid ciliates corresponded to fewer rare species, fewer presumed redundant species, and fewer size-classes but without a reduction in the total range of size-classes present. Overall, declines were in the numbers of species accompanying the dominant forms with dominant forms remaining more or less the same set of species. The declines were then in presumed redundant species and numbers of rare species. Both categories declined with latitude to zero values in the High Arctic assemblage (Table 1 and Figure 5). The decline in species richness with latitude in the Northern hemisphere represents declines in the variety of forms in an assemblage and species redundancy. Consequently there appears to be a latitudinal gradient in the capability of assemblages to adapt to environmental changes in at least with regard to size-spectra of available prey items or the loss of a particular dominant species. The latitudinal diversity gradient in another group of planktonic protists, foraminifera, appears closely related to temperature over a wide variety of time scales (Yasuhara et al. 2012), suggesting temperature plays a preponderant role in determining species richness. If changes in species distributions occur with distributions shifted northward, Arctic assemblages may become slightly more species rich and increases in species richness would likely increase the numbers of redundant species. Theoretically, as redundancy among species increases ecosystem stability (Naeem 1998), global climate change may increase the stability of high latitude ecosystems. However, the relatively small species pools of the northern high latitude assemblages suggest a low capacity to adapt to changing conditions.

Supplementary information is available at The ISME Journal's website.

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Figure legends

Figure 1. *Salpingella acuminata.* Image of a specimen from station 10 in the Bering Sea showing the basic features of a tintinnid ciliate.

Figure 2. Locations sampled between late July and early September in 2012 ranging from the East Sea/Sea of Japan (1 & 2), across the North Pacific (3-8), the Bering Sea (9-12), the Chukchi Sea (A-F) and the High Arctic (G & H). The summer of 2012 was the year of record low sea ice extent allowing sampling in the High Arctic Sea. See supplementary data file for exact station locations and summary station data.

Figure 3. Relationship of species richness of the tintinnid assemblages to: latitude, sea surface temperature (top 10 m), average chlorophyll concentration (top 100 m), and the abundance of tintinnids. There were significant ($p < 0.01$) negative linear relationships between species richness and latitude ($r = 0.6$, $n = 21$) and sea surface temperature ($r = 0.81$, $n = 20$). ES/SJ indicates East Sea/Sea of Japan. See supplementary data file for the data.

Figure 4. Observed abundance distributions of tintinnid assemblages: species abundance distributions (spp) and size-class abundance (S-C) for pooled populations of each of the 5 systems sampled. ES/SJ indicates East Sea/Sea of Japan. See Table 3 for the results of modeling the abundance distribution shown.

Figure 5. The relationships between the average latitude sampled for each of the 5 assemblages and the portion of redundant species found (squares) and the number

trace species encountered (circles). Significant ($p < 0.01$) negative linear relationships with latitude are evident for both the % of species pool as redundants (n = 5, $r = 0.984$) and the number of trace species (n = 5, $r = 0.987$).

Table One. **Summary of data by region**. Trace species are species found as a single individual. Number of size-classes containing more than one species given as size-classes co-habitated. Number of redundant species is the number of species in excess of the number of size-classes.

Region	cells enumerated	species	Trace species	size-classes	size-classes co-habitated	redundant spp
East Sea/Sea of Japan	2203	25	5	11	7 (63%)	14
North Pacific	2566	13	4	8	4 (50%)	5
Bering Sea	2255	13	2	9	3 (33%)	6
Chukchi Sea	2038	8	1	7	1 (14%)	1
High Arctic	2496	6	0	6	0 (0%)	0

Table Two. **Identity of the Dominant species in the assemblages**. Note that dominants accounted for a large portion of the population in all 5 systems and most had a wide apparent range.

Region	Dominant species	% total cells	# other species in their size-class	Apparent range
East Sea/Sea of Japan	*Proplectella expolita*	65	3	ES/JS only
North Pacific	*Ptychocylis obtusa*	45	0	All
Bering Sea	*Codonellopsis frigida*	45	2	All but High Arctic
Chukchi Sea	*Acanthostomella norvegica*	52	1	All
High Arctic	*Ptychocylis obtusa*	86	0	All

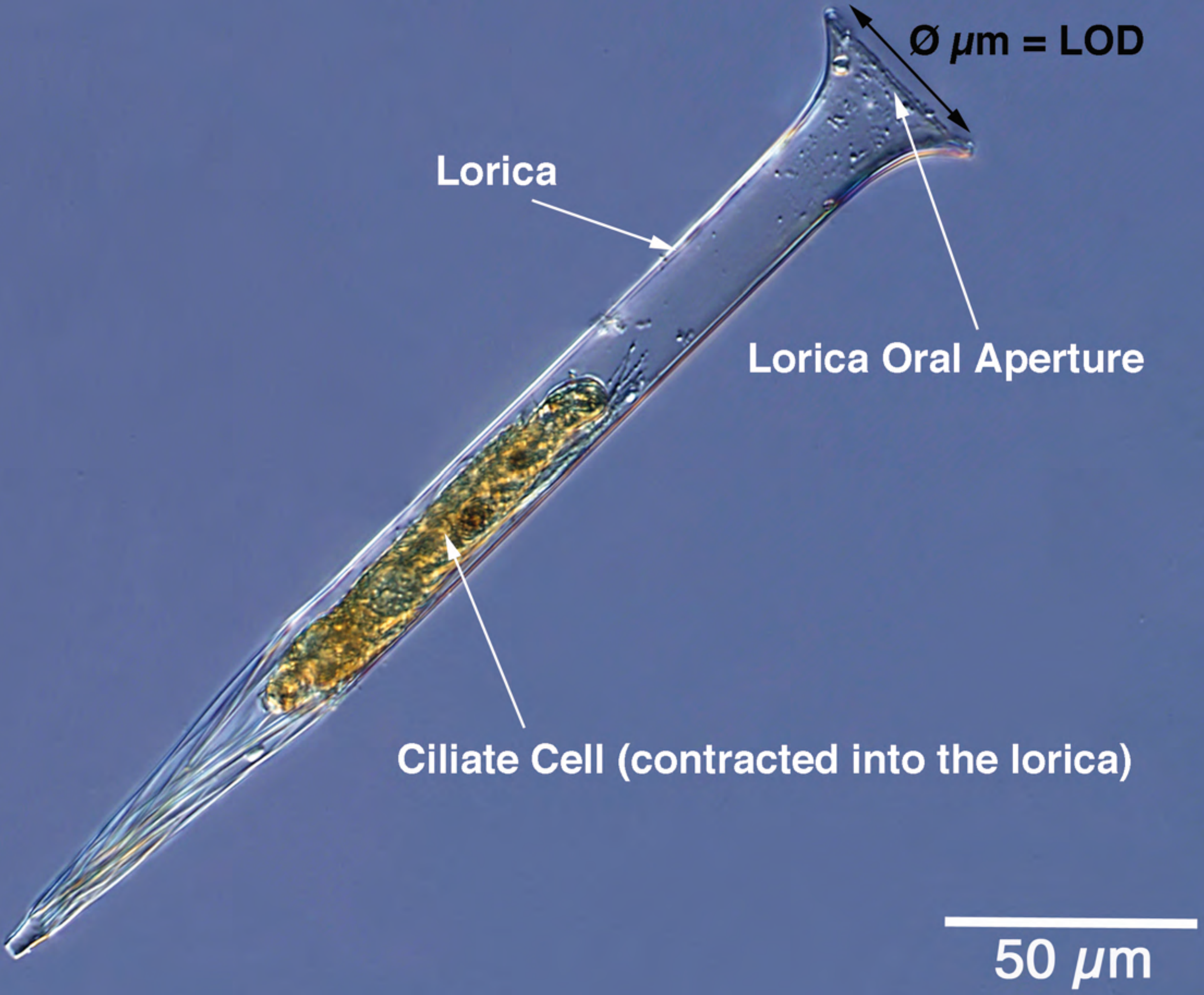
Table Three. **Results of modeling abundance distribution patterns**. Lowest AIC values (in red) indicate the best model fit. Multiple values in red indicate indistinguishable fits (differences <1).

Species Abundance Distribution fits

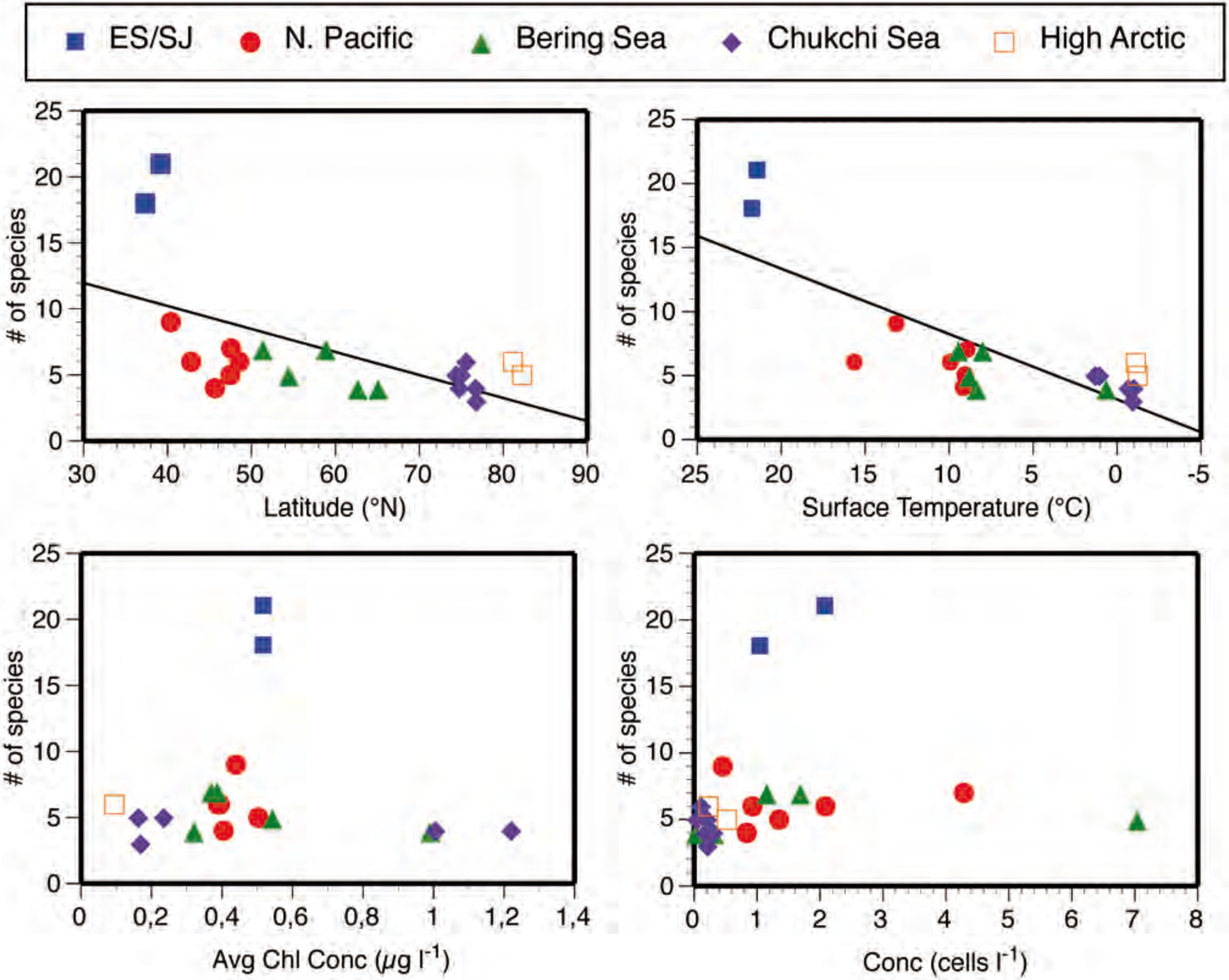
Region	Log-Normal	Geometric	Log-Series
East Sea/Sea of Japan	**3.2**	5.8	**2.7**
North Pacific	3.8	**1.9**	3.9
Bering Sea	3.3	**-0.0**	3.4
Chukchi Sea	4.0	**2.6**	4.3
High Arctic	**5.5**	**4.8**	**5.7**

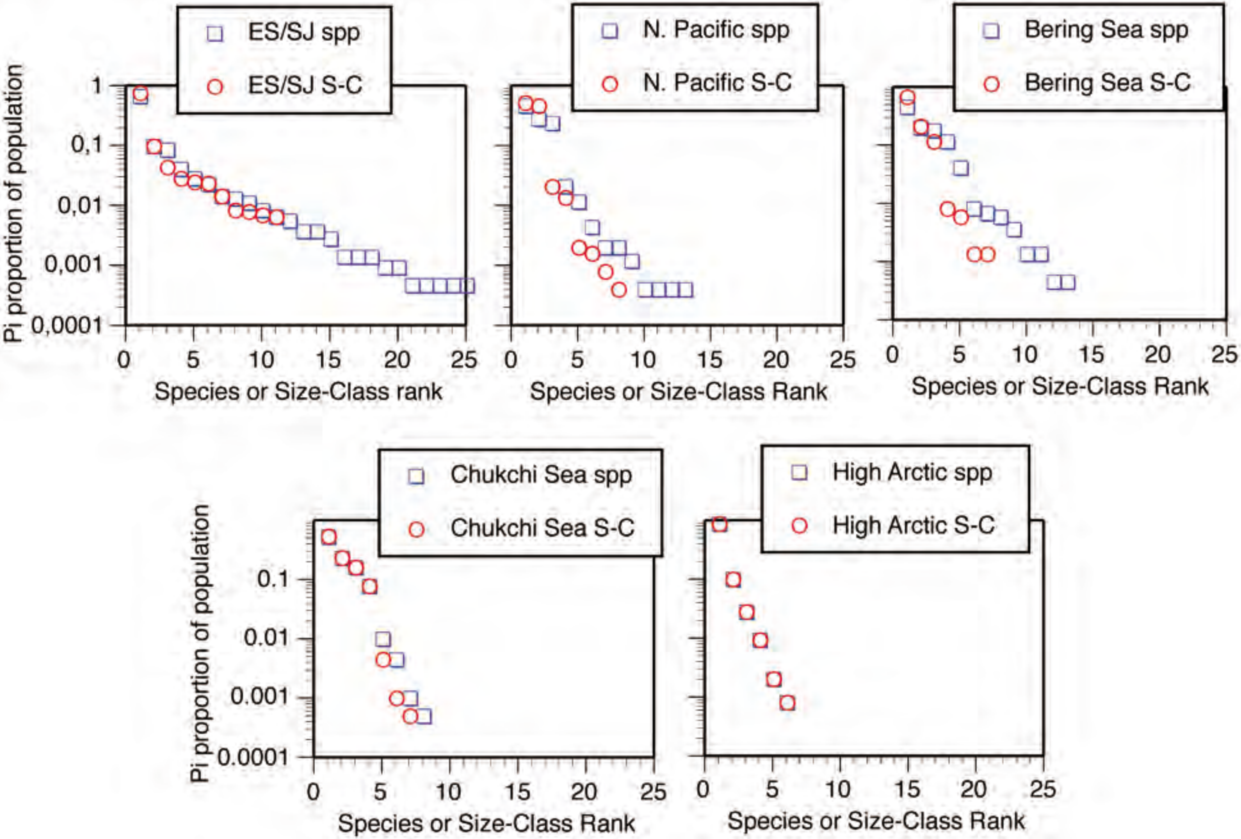
Size-Class Abundance Distribution fits

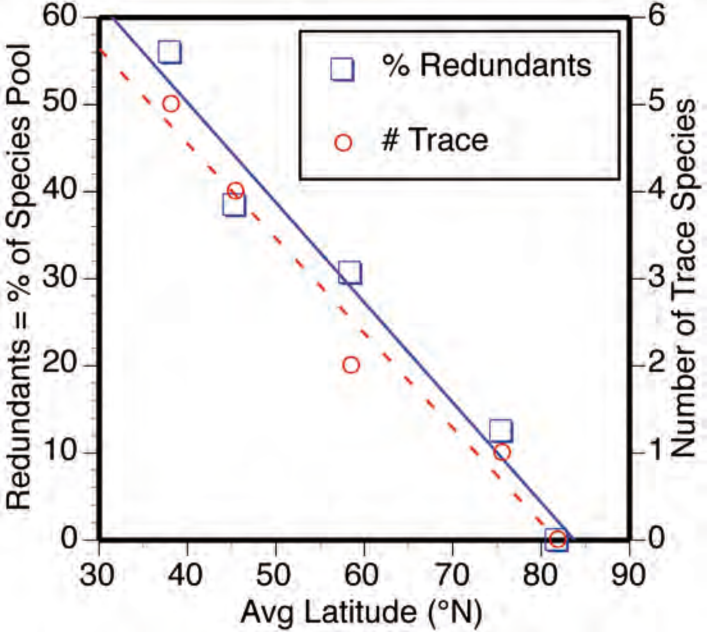
Region	Log-Normal	Geometric	Log-Series
East Sea/Sea of Japan	**1.8**	4.9	2.4
North Pacific	**4.4**	**3.7**	4.7
Bering Sea	4.4	**1.9**	4.7
Chukchi Sea	4.6	**3.8**	4.9
High Arctic	**5.5**	**4.8**	**5.7**

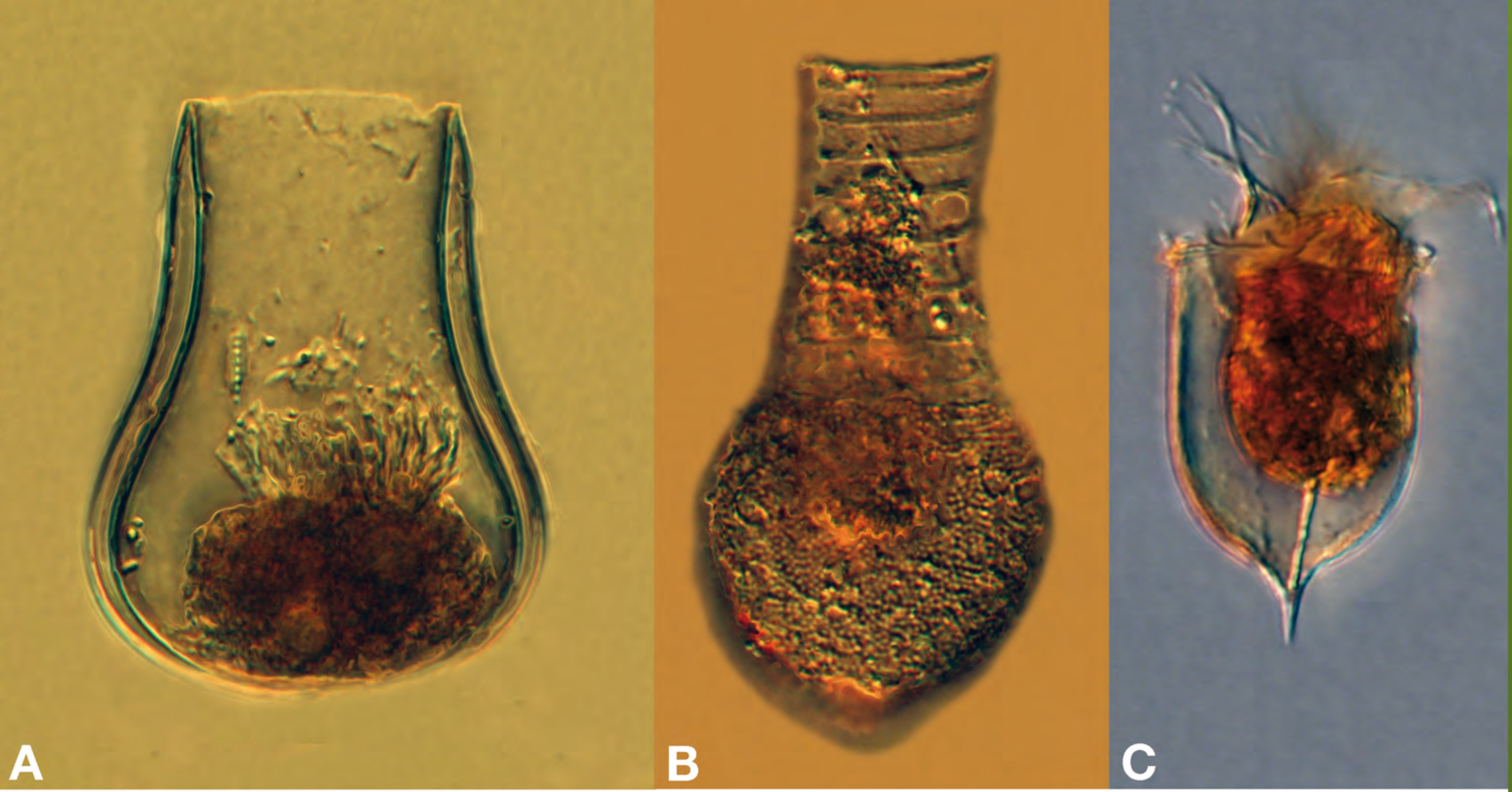

Ø µm = LOD
Lorica
Lorica Oral Aperture
Ciliate Cell (contracted into the lorica)
50 µm


180°
165°W
165°E
3
150°W
4
1
5
2
6
7
8
9
135°W
10
45°N
11
12
A
60°N
B
C
D
F
E
70°N
G
H
75°N
80° N


ES/SJ
N. Pacific
Bering Sea
Chukchi Sea
High Arctic
# of species
0
5
10
15
20
25
30
40
50
60
70
80
90
Latitude (°N)
25
20
15
10
5
0
-5
Surface Temperature (°C)
0
0,2
0,4
0,6
0,8
1
1,2
1,4
Avg Chl Conc (μg l-1)
0
1
2
3
4
5
6
7
8
Conc (cells l-1)


ES/SJ spp
ES/SJ S-C
Pi proportion of population
1
0,1
0,01
0,001
0,0001
0
5
10
15
20
25
Species or Size-Class rank
N. Pacific spp
N. Pacific S-C
Species or Size-Class Rank
Bering Sea spp
Bering Sea S-C
Species or Size-Class Rank
Chukchi Sea spp
Chukchi Sea S-C
Pi proportion of population
0.1
0.01
0.001
0.0001
Species or Size-Class Rank
High Arctic spp
High Arctic S-C
Species or Size-Class Rank


% Redundants
# Trace
Redundants = % of Species Pool
Number of Trace Species
Avg Latitude (°N)
0
10
20
30
40
50
60
30
40
50
60
70
80
90
0
1
2
3
4
5
6



Dominant Species suppl fig 1

A. *Proplectella explolita* (East Sea/Sea of Japan)
B. *Condonellopsis frigida* (Bering Sea)
C. *Acanthostomella norvegica* (Chukchi Sea)
D. *Ptychocylis obtusa* (North Pacific & High Arctic)