

ORIGINAL ARTICLE

The species-rich assemblages of tintinnids (marine planktonic protists) are structured by mouth size

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Many microbial taxa in the marine plankton appear super-saturated in species richness. Here, we provide a partial explanation by analyzing how species are organized, species packing, in terms of both taxonomy and morphology. We focused on a well-studied group, tintinnid ciliates of the microzooplankton, in which feeding ecology is closely linked to morphology. Populations in three distinct systems were examined: an Eastern Mediterranean Gyre, a Western Mediterranean Gyre and the California Current. We found that species abundance distributions exhibited the long-tailed, log distributions typical of most natural assemblages of microbial and other organisms. In contrast, grouping in oral size-classes, which corresponds with prey-size exploited, revealed a geometric distribution consistent with a dominant role of a single resource in structuring an assemblage. The number of species found in a particular oral size-class increases with the numerical importance of the size-class in the overall population. We suggest that high species diversity reflects the fact that accompanying each dominant species are many ecologically similar species, presumably able to replace the dominant species, at least with regard to the size of prey exploited. Such redundancy suggests that species diversity greatly exceeds ecological diversity in the plankton.

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Introduction

Hutchinson's paradox of the plankton, 'How can so many species coexist in a relatively homogenous environment?', is now over 50 years old. (Hutchinson, 1961) To date no explanation (including his own) is generally accepted, and new mechanisms, or twists, continue to be proposed (Shoresh *et al.*, 2008; Fox *et al.*, 2010; Martin, 2012). The paradoxically high diversity of the plankton described by Hutchinson was based on microscopic observations, and this diversity is now known to be dwarfed by that revealed through sequencing the DNA of natural plankton communities. Considering only eukaryotic protists, genetic data suggests that there are thousands of species in a few liters of seawater (for example, Brown *et al.*, 2009; Edgcomb *et al.*, 2011). Such an astounding diversity is difficult to explain, and raises the question of how such species diversity translates into ecological diversity? Complicating any attempt

to address the question is the fact that in many groups of protists phylogeny, morphology and ecology are not clearly related to one another. For example, among the dinoflagellates, gymnodinid dinoflagellates can be benthic, planktonic, phototrophic, mixotrophic, grazers or parasites (see Taylor, 1987; Gomez 2012). In contrast to many microbial taxa, tintinnid ciliates represent an exceptionally coherent group.

Tintinnid ciliates are a single suborder of the Choreotrichidae, characterized by the possession of a shell or lorica whose architecture forms the basis of classic taxonomic schemes. About 1200 species have been described (Agatha and Strüder-Kypke, 2012), virtually all 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 and Brownlee, 1986); analogous to gape-size, it is related to the size of the food items ingested. The largest prey ingested is about half the LOD in longest dimension, and a given species feeds most efficiently on prey about 25% of its LOD in size; the overwhelming majority of described species have an LOD between 20 µm and 60 µm, indicating a typical prey size range of 5–15 µm (Dolan, 2010). LOD is also positively related to lorica volume (Dolan, 2010), as well as specific growth rate (Montagnes, 2012), reflecting

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the common relationship between cell size and maximum growth rate. Because LOD is a conservative taxonomic character, the morphological diversity of an assemblage, in terms of different sizes of LODs, is closely related to taxonomic diversity (Dolan *et al.*, 2006).

Tintinnids are generally a minority component in the microzooplankton (<5% of cells) compared with other taxa, such as oligotrich ciliates or heterotrophic dinoflagellates. In offshore waters they commonly occur in concentrations of less than 100 per liter (McManus and Santoferrara, 2012), and most have maximum clearance rates of less than $10\ \mu\text{l h}^{-1}$ (Montagnes, 2012). Consequently, tintinnids rarely directly control the concentration or composition of their prey, as their aggregate feeding activity usually equates to clearing a maximum of 1–2% per day of the surface layer waters they occupy. Thus, they are not only a phylogenetically, morphologically and ecologically coherent group, but also are unlikely to significantly change their own environment. This is in contrast to taxa, which can, for example, deplete an important resource, thereby altering the environment, such as when a particular taxon of phytoplankton blooms, thereby changing the phytoplankton assemblage with the result of altering the entire food web. Organisms which can alter their environment (for example, depleting or monopolizing a resource) considerably complicate the study of diversity, as dynamics likely change with distinct scales of time and space. The general lack of feedback effects concerning tintinnids, or large effects on their own food web, simplifies the study of diversity in the group.

We examined how species diversity relates to ecological diversity by comparing large scale or metapopulation characteristics in the traditional terms of species, and in terms of 'ecotypes', or defined here as species of similar feeding ecology. We sampled geographically separate populations in distinct systems: an oligotrophic gyre in the Eastern Mediterranean, an oligotrophic gyre in the Western Mediterranean, and the productive California Current in the eastern Pacific. In each system a set of seven stations at least 30 km distant from one another was sampled providing 2000–3000 individuals for the analysis of the characteristics of each assemblage.

We examined how the species in the assemblages were organized in terms of species and in terms of 'ecotypes'. Observed patterns of species abundance distribution were 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. For the three populations, the size-class abundance distributions of the ecologically significant characteristic of LOD were analyzed in similar fashion by substituting size-class of oral diameter for 'species'.

Materials and methods

Sampling and sample analysis

Material for enumeration and identification of tintinnids was obtained during two oceanographic studies, BOUM (Biogeochemistry from the Oligotrophic to the Ultraoligotrophic Mediterranean in the Mediterranean) in June–July 2008 and the LTER (Long Term Ecological Research) CCEP0810, 'A-Front Study' cruise in the Pacific in October 2008. In the Mediterranean our data is from seven stations sampled in oligotrophic gyres in the eastern and western basins around Stations 'A' and 'C'; for detailed descriptions of the biological and physical characteristics of the gyres see Christaki *et al.* (2011) and Moutin and Prieur (2012). In the Eastern Pacific, seven stations were sampled in the productive California Current System following drogues tracking upwelled water; for drogue deployment locations and summary biological characteristics of the study see Landry *et al.* (2012).

In the Mediterranean gyres six discrete depth samples, usually 10 l each, were obtained at each of the stations between the surface and depth of the chlorophyll maximum. In the upwelled California Current waters, two discrete depth samples of the surface layer were taken (see Table 1 for summary data for the three sites). At each station, the 5–10 l volumes of sample from each depth, obtained using Niskin bottles, were concentrated to 20 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. We have found that using a 20 μm concentrator yields higher numbers of tintinnids than settling whole-water samples, in agreement with Pierce and Turner (1994), and have used the method in several previous studies (Dolan *et al.*, 2006, 2009; Dolan and Stoeck, 2011). Concentrated water samples were fixed with Lugol's solution (2% final conc.). Aliquots (2–10 ml) of concentrated sample were settled in sedimentation chambers and the entire surface of the chamber was examined using an inverted microscope at $\times 200$ total magnification. Thus, all material from all the samples was examined. It should be noted that the sampling was designed to obtain coverage of a large geographic area, not to determine conditions in which particular species occur, and individual samples often contained few cells. Consequently, our data are not well-suited for multivariate data analysis.

Data analysis

We examined the patterns of both species abundance distribution and the abundance distributions of LOD size-classes of 4 μm intervals (for justification of interval size see Dolan *et al.*, 2006) using data pooled from the seven locations for each assemblage. We first made log-rank abundance curves by calculating relative abundance for each species and ranking species from highest to lowest and plotting

Table 1 Summary data for the three sites sampled

Site	Ctd #	Lat, long	Date	Depths (m)	# samples	vol ex (l)	# cells	# spp	Chl a
West Med Gyre C	19	33.47°N, 32.77°E	6/25/2008	5 125	6	60	356	41	0.16
	22	33.47°N, 32.59°E	6/25/2008	5 125	6	60	318	42	0.15
	25	33.62°N, 32.59°E	6/25/2008	5 125	6	60	255	39	0.15
	28	33.62°N, 32.77°E	6/26/2008	5 125	6	60	389	37	0.14
	47	33.63°N, 32.64°E	6/27/2008	5 145	6	55	248	40	0.20
	55	33.68°N, 32.63°E	6/28/2008	5 120	6	55	307	38	0.18
Totals	66	33.71°N, 32.65°E	6/29/2008	3 138	6	60	331	34	0.18
						410	2206	61	
East Med Gyre A	131	39.02°N, 5.25°E	7/12/2008	5 125	6	60	423	39	0.12
	134	39.17°N, 5.25°E	7/12/2008	5 125	6	60	462	38	0.14
	137	3.17°N, 5.44°E	7/12/2008	5 125	6	60	327	42	0.17
	140	39.02°N, 5.29°E	7/12/2008	4 126	6	60	765	39	0.12
	162	39.12°N, 5.30°E	7/14/2008	5 130	6	70	415	36	0.15
	170	39.11°N, 5.19°E	7/15/2008	5 130	6	55	391	39	0.12
Totals	181	39.22°N, 5.15°E	7/16/2008	4 130	6	60	483	36	0.15
						430	3266	59	
Cal Cur	12	34.02°N, 120.80°W	10/5/2008	15 35	2	20	471	25	0.326
	18	33.62°N, 120.76°W	10/8/2008	5 20	2	20	121	19	1.623
	32	32.21°N, 123.87°W	10/14/2008	10 50	2	20	1378	19	0.25
	40	34.06°N, 121.72°W	10/17/2008	5 15	2	20	940	21	0.86
	51	33.60°N, 121.20°W	10/21/2008	10 25	2	20	139	21	1.1
	59	32.83°N, 120.65°W	10/23/2008	8 15	2	20	173	19	1.7
Totals	75	32.57°N, 120.39°W	10/27/2008	20 50	2	20	259	19	0.33
						140	3491	37	

Each station corresponded to a CTD Niskin Bottle cast (Ctd #) as in the cruise databases: Gyres C and A: <http://mio.pytheas.univ.amu.fr/BOUM/> and the California Current (Cal Cur): <http://cce.lternet.edu/data/cruises/ccep0810/>. Material was examined from large volumes of water (vol ex in liters). For each station the number of cell enumerated and identified (# cells) and the number of species (# spp) is given. The average integrated concentration of chlorophyll a in $\mu\text{g l}^{-1}$ throughout the portion of the water column sampled (depths) is also given. Totals represent the pooled volume of water examined, number of cells enumerated and the number of species encountered for each of the three sites.

$\ln(\text{relative abundance})$ versus. 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 (Dolan *et al.*, 2007, 2009; Raybaud *et al.*, 2009; Claessens *et al.*, 2010; Doherty *et al.*, 2010; Dolan and Stoeck, 2011).

The observed rank abundance distributions were compared with the hypothetical models using a Bayesian approach: an Akaike Goodness of fit calculation (19). Using this approach, an Akaike Information Criterion was determined as the natural logarithm of the mean (sum divided by S) of squared deviations between observed and predicted $\ln(\text{relative abundance})$ 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 Akaike Information Criterion value, the better the fit. A difference of 1 in Akaike Information Criterion corresponds roughly to a 1.5 evidence ratio; we considered differences of less than 1.0 in Akaike Information Criterion to represent indistinguishable fits following Burnham and Anderson (2002). We used simple correlation analysis of log-transformed values to test the relationship between the portion of individuals in a given size class and the portion of

the species pool contained within that same LOD size-class.

Results and discussion

A total of 80 species were encountered, of which relatively few could be characterized as rare, that is found at only one or two stations. Most species were found in several stations and in at least two of the three populations sampled (Figure 1). Seven species occurred in all of the 21 stations sampled, and ~a third of the species were found in all three populations. Occupation of a wide number and variety of sites has been equated with broad niche breadth in diatoms (Soininen and Heino, 2007), and this appears to characterize many tintinnid species.

Although the assemblages of the three systems were all species-rich, with 37–61 species (Table 1), they were all also highly dominated. In the Eastern Mediterranean seven species accounted for over 50% of the total cells, in the Western Mediterranean six species, and in the California Current three species represented over 50% of individuals. There was some overlap in the identities of the dominant species among the three populations with, for example, the occurrence of two species among the dominants of all three assemblages, albeit in different rank positions (Figure 2). The abundant forms defined the dominant size-classes of the

particular assemblage. In each assemblage the numerically dominant species were of distinct LOD size. For example, in the Western Mediterranean the two most abundant species were *Salpingella curta* with an LOD of about 15 μm and *Steenstrupiella steenstrupi* with an LOD of about 30 μm (Figure 2).

Species rank abundance distributions (Figure 3a and Table 2) were the long-tailed distributions with

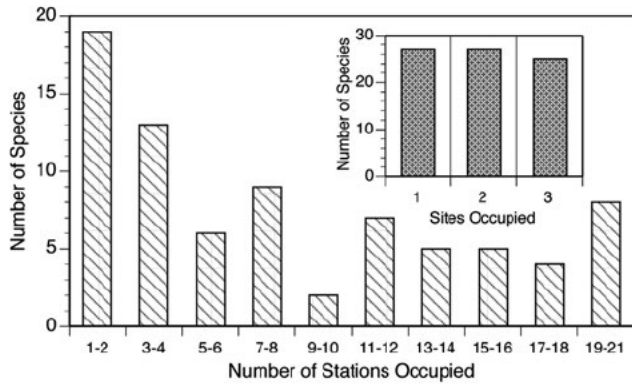


Figure 1 Frequency of species occurrence. The number of the species found in the total number of stations sampled, pooling all three sites (the Eastern Mediterranean, Western Mediterranean and California Current totaling 21 stations), binned in intervals. Note that only about 25% of the species were found in, but, 1 or 2 locations. Inset graph shows the total number of species found at 1, 2 or all 3 of the sites sampled (seven stations for each site).

large numbers of relatively rare species, commonly observed for most natural assemblages (McGill *et al.*, 2007). Notably such distributions commonly characterize rank abundance curves of planktonic protists determined using molecular techniques (for example, Brown *et al.*, 2010; Edgcomb *et al.*, 2011). The tintinnid distributions were best fit among modeled distributions by a log-series distribution. 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 in the case of a metapopulation in the case of log-series (that is, Hubbell, 2001). In contrast, ordering the populations by the sizes of LOD, rather than species identities, revealed a distinctly different distributional pattern best fit by a geometric model (Figure 3b and Table 1).

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 (for example, Whittaker, 1972). This distribution is also thought to characterize assemblages of low species richness or severe environments (Wilson, 1991) and has, for example, been found to describe the species abundance distribution of the entire planktonic ciliate community in Antarctic waters (Wickham *et al.*, 2011). In the tintinnid populations, the geometric distribution of LOD size-class abundance is most

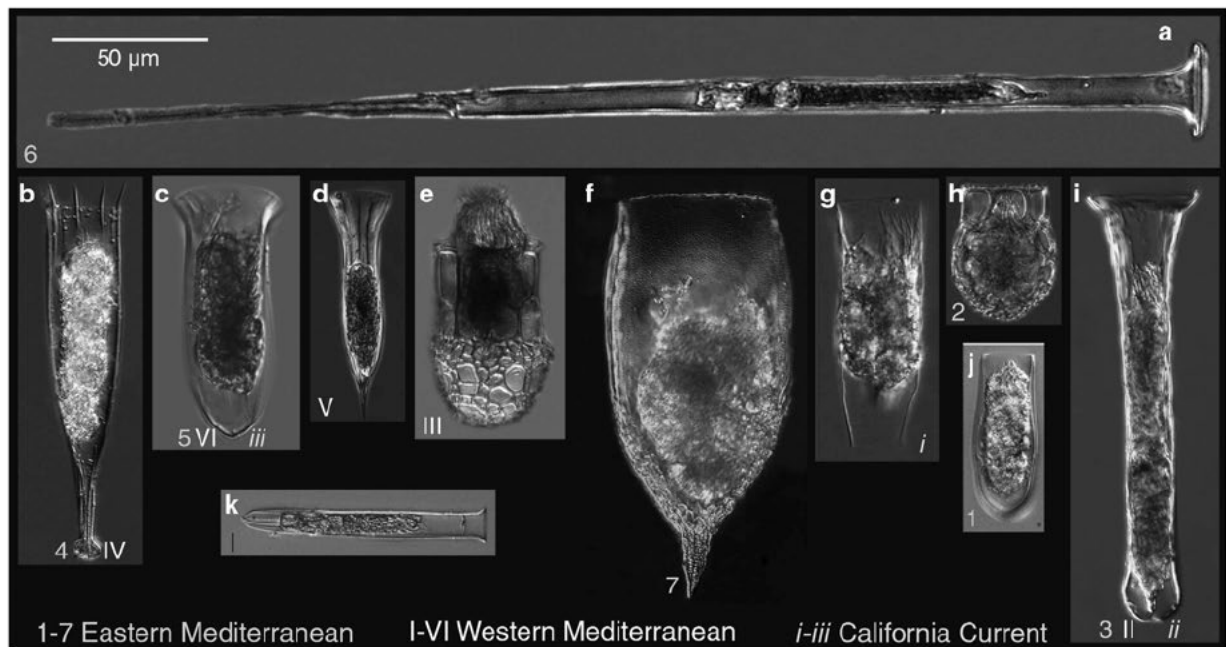


Figure 2 The species accounting for the majority of individuals in the three systems, and their relative abundance ranks. The arabic numerals indicate the abundance rank in the Eastern Mediterranean, capital roman numerals, the rank in Western Mediterranean and italic lower case roman numerals, the rank in California Current samples. Note the size differences in LOD (the open upper end of the lorica or shell) between the number one and two species in each system. The 50 μm scale bar is for all images. Species names: (a). *Salpingella attenuata*, (b). *Dadayiella ganymedes*, (c). *Amphorides quadrilineata*, (d). *Dadayiella pachtoecus*, (e). *Dictyocysta elegans*, (f). *Epiplocytilis blanda*, (g). *Eutintinnus apertus*, (h). *Dictyocysta mitra*, (i). *Steenstrupiella steenstrupii*, (j). *Undella clevei*, (k). *Salpingella curta*.

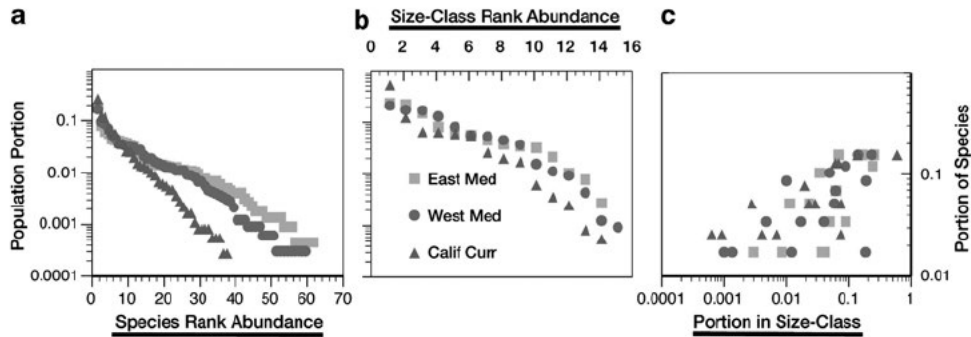


Figure 3 The species rank abundance distributions (a) appear to be the common long tailed log normal or log series distributions, and were best fit among modeled distributions by a log series distribution. In contrast, the size class rank abundances (b) were best fit by a geometric distribution except for the Calif Curr, for which there was no best fit (see Table 1.) There was a positive relationship between the portion of individuals in a size class and the number of species within the size class (c). About half the total species pool is in the 3–5 most populous size classes, those of the dominant species. Regression statistics for the relationships of (log) portion in a size class: individuals vs species pool: East Med $n = 14$, $r = 0.72$, $P = 0.004$; West Med $n = 15$, $r = 0.58$, $P = 0.042$; Calif Curr $n = 14$, $r = 0.64$, $P = 0.030$.

Table 2 Results of the analysis of tintinnid species abundance distributions and LOD size class abundances

	AIC Values		
	Log normal	Geometric	Log series
<i>Species abundance distribution fits</i>			
East Med	1.0	3.4	0.2
West Med	1.8	2.7	1.3
Calif Current	2.8	3.0	1.2
<i>LOD abundance distribution fits</i>			
East Med	1.3	0.8	0.9
West Med	2.0	0.6	1.7
Calif Current	2.7	3.1	2.7

Abbreviation: LOD, lorica oral diameter.

For each species assemblage of size class assemblage the observed log rank abundance curve was compared with model derived log normal, geometric, and log series (series) curves using the Akaike information criterion (AIC) test. The values in bold denote the lowest AIC value, indicating the closest fits. A difference of 1 unit indicates a significant difference.

simply attributable to the availability of prey concentration and size given the close relationship between LOD size and prey exploited by tintinnids (Dolan, 2010).

Notably, the relative importance of an LOD size-class was correlated with the portion of the species pool contained within it (Figure 3c). The relationships was significant in each population, but was strongest for the Eastern Mediterranean population, the most species-rich. (East Med $n = 14$, $r = 0.72$, $P = 0.004$; West Med $n = 15$, $r = 0.58$, $P = 0.042$ and Calif Curr $n = 14$, $r = 0.64$, $P = 0.030$). In each population, the numerically dominant species, rather than forming exclusive, mono-specific size-classes, were accompanied by several other species of similar LOD size, ecologically similar species in terms of feeding ecology. Roughly half the total species pool (18–30 species) occurs in 3–5 of the 16

size-classes, those of the numerically dominant species.

The high species diversity found in a relatively small component of the zooplankton, tintinnid ciliates, exists despite the fact the assemblages are highly dominated by a few species. Most of the species pool consists of forms distinctly similar to dominants in terms of the diameter of the mouth end of the lorica and in most cases (43 out of 48 species), these nondominants were not cogenetic with the dominant in their size-class. Most size-classes were populated with distinct genera.

In some assemblages species that occur in low abundances are ‘occasional’, and have ecological requirements different from the abundant species (Magurran and Henderson, 2003). However, common and rare species can be ecologically similar (Gaston, 2012), and the species-rich assemblages of tintinnids provide an example. That many of the non-dominant species can become dominant is suggested by the fact that some, rare in one assemblage, were dominant in another assemblage. For example, in the California Current population *Undella clevei* and *Dictyocysta mitra* were minor species in their respective size-classes. However, these same two species were dominants in the Eastern Mediterranean (see Supplementary data).

We know that microbial populations are largely resilient in overall structure as communities subjected to large, but temporary disturbances can return to their initial state quickly (for example, Shade et al., 2012). We also know that rare species can change in abundance rapidly (for example, Orsi et al., 2012). What we know little about is how one species can replace another in time and space scales that permit the coexistence of seemingly similar species.

There are likely many mechanisms responsible for provoking changes in abundance ranks. Obvious candidates are density-dependent mortality

mechanisms, for example, the 'killing the winner' model pointing out the probable importance model of viral-mortality in competition among planktonic prokaryotes (Thingstad and Lignell, 1997). Interestingly, parasitism is known in tintinnids, but its ecological importance has received relatively little attention (Coats and Bachvaroff, 2012). At present then we know that in the species-rich plankton a few species are abundant, while most are present in very low concentrations, perhaps waiting for an opportunity to become abundant.

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References

- Agatha S, Strüder-Kypke MC. (2012). Reconciling cladistic and genetic analyses in choreotrichid ciliates (Protists, Spirotrichea, Oligotrichea). *J. Euk. Microb* **59**: 325–350.
- Brown MV, Philip GK, Bunge JA, Smith MC, Bissett A, Lauro FM *et al.* (2009). Microbial community structure in the North Pacific ocean. *ISME J.* **3**: 1374–1386.
- Burnham KP, Anderson DR. (2002). *Model selection and multi model inference: a practical information theoretic approach*. Springer: New York, Springer.
- Christaki U, Van Wambeke F, Lefevre D, Lagaria A, Prieur L, Pujo-Pay M *et al.* (2011). The impact of anticyclonic mesoscale structures on microbial food webs in the Mediterranean Sea. *Biogeosciences* **8**: 1839–1852.
- Claessens M, Wicjham SA, Post AF, Reuter M. (2010). A paradox of the ciliates? High ciliate diversity in a resource-poor environment. *Mar. Biol.* **157**: 483–494.
- Coats DW, Bachvaroff TR. (2012). Parasites of tintinnids. In Dolan JR, Montagnes DJS, Agatha S, Stoecker DK (eds) *The Biology and Ecology of Tintinnid Ciliates: Models for Marine Plankton*. Wiley-Blackwell: Oxford, pp 146–170.
- Doherty M, Tamura M, Costas BA, Ritchie ME, McManus GB, Katz LA. (2010). Ciliate diversity and distribution across an environmental and depth gradient in Long Island Sound, USA. *Environ. Microbiol.* **12**: 886–898.
- Dolan JR, Stoeck T. (2011). Repeated sampling reveals differential variability in measures of species richness and community composition in planktonic protists. *Environ Microbiol. Rep* **3**: 661–666.
- Dolan JR. (2010). Morphology and ecology in tintinnid ciliates of the marine plankton: correlates of lorica dimensions. *Acta Protoz* **49**: 235–244.
- Dolan JR, Jacquet S, Torretón J-P. (2006). Comparing taxonomic and morphological biodiversity of tintinnids (planktonic ciliates) of New Caledonia. *Limnol. Oceanogr.* **51**: 950–958.
- Dolan JR, Ritchie ME, Tunin-Ley A, Pizay M-D. (2009). Dynamics of core and occasional species in the marine plankton: tintinnid ciliates of the N.W. Mediterranean Sea. *J. Biogeogr.* **36**: 887–895.
- Dolan JR, Ritchie ME, Ras J. (2007). The neutral community structure of planktonic herbivores, tintinnid ciliates of the microzooplankton, across the SE Pacific Ocean. *Biogeosciences* **4**: 297–310.
- Edgcomb V, Orsi W, Bunge J, Jeon S, Christen R, Leslin C *et al.* (2011). Protistan microbial observatory in the Cariaco Basin, Caribbean. 1. Pyrosequencing vs Sanger insights into species richness. *ISME J.* **5**: 1344–1356.
- Fox JW, Nelson WA, McCauley E. (2010). Coexistence and the paradox of the plankton: quantifying selection from noisy data. *Ecology* **91**: 1774–1786.
- Gaston KJ. (2012). The importance of being rare. *Nature* **487**: 46–47.
- Gomez F. (2012). A quantitative review of the lifestyle, habitat and trophic diversity of dinoflagellates (Dinoflagellata, Alveolata). *Syst Biodivers* **10**: 267–275.
- Hubbell SR. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press: Princeton, USA, Princeton.
- Hutchinson GE. (1961). The paradox of the plankton. *Amer. Nat.* **95**: 137–145.
- Landry MR, Ohman MD, Goericke R, Stukel MR, Barbeau KA, Bundy R *et al.* (2012). Pelagic community responses to a deep-water front in the California Current Ecosystem: overview of the A-Front Study. *J. Plankton Res.* **34**: 739–748.
- Laval-Peuto M, Brownlee DC. (1986). Identification and systematics of the Tintinnina (Ciliophora): evaluation and suggestion for improvement. *Ann. Inst. Océanogr. Paris* **62**: 69–84.
- Magurran AE, Henderson PA. (2003). Explaining the excess of rare species in abundance distributions. *Nature* **422**: 714–716.
- Martin A. (2012). The seasonal smorgasbord of the seas. *Science* **337**: 46.
- McGill BJ, Etienne RS, Gray JS, Alonso D, Anderson MJ, Benecha HK *et al.* (2007). Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.* **10**: 995–1015.
- McManus GB, Santoferrara LF. (2012). Tintinnids in microzooplankton communities. In Dolan JR, Montagnes DJS, Agatha S, Stoecker DK (eds) *The Biology and Ecology of Tintinnid Ciliates: Models for Marine Plankton*. Wiley-Blackwell: Oxford, pp 198–213.
- Montagnes DJS. (2012). Ecophysiology and behavior of tintinnids. In Dolan JR, Montagnes DJS, Agatha S, Stoecker DK (eds) *The Biology and Ecology of Tintinnid Ciliates: Models for Marine Plankton*. Wiley-Blackwell: Oxford, pp 85–121.
- Moutin T, Prieur L. (2012). Influence of anticyclonic eddies on the Biogeochemistry from the Oligotrophic to the Ultraoligotrophic Mediterranean (BOUM cruise). *Biogeosciences* **9**: 3827–3855.
- Pierce RW, Turner JT. (1994). Plankton studies in Buzzards Bay, Massachusetts, USA. IV. tintinnids, 1987–1988. *Ecol Prog Ser* **112**: 235–240.
- Orsi W, Song YC, Hallam S, Edgcomb V. (2012). Effect of oxygen minimum zone formation on communities of marine protists. *ISME J* **6**: 1586–1601.

- Raybaud V, Tunin-Ley A, Ritchie ME, Dolan JR. (2009). Similar patterns of community organization characterize distinct groups of different trophic levels in the plankton of the NW Mediterranean Sea. *Biogeosciences* **6**: 431–438.
- Shade A, Read JS, Youngblut ND, Fierer N, Knight R *et al*. (2012). Lake microbial communities are resilient after a whole-ecosystem disturbance. *ISME J.* **6**: 2153–2167.
- Shoresh N, Hegreness M, Kishony R. (2008). Evolution exacerbates the paradox of the plankton. *Proc Nat Acad Sci USA* **105**: 12365–12369.
- Soininen J, Heino J. (2007). Variation in niche parameters along the diversity gradient of unicellular eukaryotic assemblages. *Protist* **158**: 181–191.
- Taylor FJR. (1987). *The Biology of Dinoflagellates*. Blackwell: Oxford.
- Thingstad TF, Lignell R. (1997). Theoretical models for the control of bacterial growth rate, abundance, diversity and carbon demand. *Aquat. Microb. Ecol.* **13**: 19–27.
- Whittaker RH. (1972). Evolution and measurement of species diversity. *Taxon* **21**: 213–251.
- Wickham SA, Steinmair U, Kamennaya N. (2011). Ciliate distributions and forcing factors in the Amundsen and Bellinghousen Seas (Antarctic). *Aquat. Microb. Ecol.* **62**: 215–230.
- Wilson WJ. (1991). Methods for fitting dominance/diversity curves. *J. Veg. Sci.* **2**: 35–46.

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