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Phaeogromids of the mesopelagic marine plankton: temporal variability of concentrations and observations of feeding structures of 4 species from the mesopelagic in the Mediterranean Sea.

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ABSTRACT

Challengerids, phaeogromids rhizarian protists, are emblematic protists of the deep sea but are also enigmatic as they occur in very low concentrations. In previous studies, we reported on temporal changes in abundance at a near-shore mesopelagic site, but only as part of sampling of the entire microplankton assemblage, not well suited for examining phaeogromids. Consequently, we turned to using a closing plankton net to provide material from large volumes of seawater thus allowing for more robust estimates of concentrations and material for observations of living cells, to our knowledge the first made. Here we report our results on the four most commonly occurring species: *Challengeranium diadon, Challengereron willemoesii, Challengeria xiphodon* and *Euphysetta lucani*. In contrast to our previous report, we found that changes in concentrations were not related to water column stratification, and the four species roughly co-varied with time. Observations of live cells revealed that all four species deploy tentacle-like pseudopods and also very large unstructured webs of fine pseudopods. The similarities in feeding webs suggest similar prey are exploited, and the similar temporal changes in abundances, suggest a common factor or factors (unknown at this time) govern their concentrations. Films of live cells are provided in supplementary files.

Keywords: Challengerids, Rhizaria, Cercozoa, deep sea, water column structure, microzooplankton

INTRODUCTION

The first phaeogromid rhizarian protist was described in 1856, and is now known as *Lirella baileyi* (Nakamura & Suzuki 2015). It was found in material recovered from deep water soundings in the Bering Sea by Jacob Bailey, and noted as "Infusoria, Rhizopoda?" (Bailey 1856). Similar forms were found by George Wallich and he described a new genus, *Protocytis*, from material recovered from soundings in the North Atlantic (Wallich 1869). Several years later, these rhizarians became famous as deep sea protists because of the Challenger Expedition (1872-1876). They were found in material collected using tow nets attached to deep sea dredges, or trawl lines. John Murray, in his preliminary report on the expedition (Murray 1876), called them "Deep-Sea Rhizopods". He stated that they are new forms, "*universally distributed in deep water ... for the sake of convenience we have been accustomed to call the organisms Challengeridae*" (Fig. 1a). Charles Wyville Thompson (1877) more formally described them as an order with the type genus *Challengeria*, calling them a group of beautiful minute forms, similar to but differing from, known radiolaria. Presciently, he stated that their zoological position, rather than allied with radiolaria, may not be far from such forms as *Gromia*. Nonetheless, they were originally classified by Ernst Haeckel as radiolaria, given their own order, Phaeogromia, one of 4 orders of the 'legion' Phaeodoraria (Haeckel 1879). Based on molecular data (e.g., Polet et al. 2004), the phaeogromid rhizarians are today in the phylum Cercozoa as is *Gromia* (Adl et al. 2019). Within the Cercozoa, phaeogromids are placed in the class Thecofilosa, as the family Phaeogromia in the order Phaeodarea (Adl et al. 2019). Their remarkable morphologies were presented to the general public by Haeckel in the first plate of the first issue in 1899 of his classic *Kunstformen der Natur* (Haeckel 1899-1904). The plate of Challengerids, as art form of nature, included some of the forms illustrated by Murray (Fig. 1b) and by depicting them in the first plate of the first issue, Haeckel gave them considerable importance.

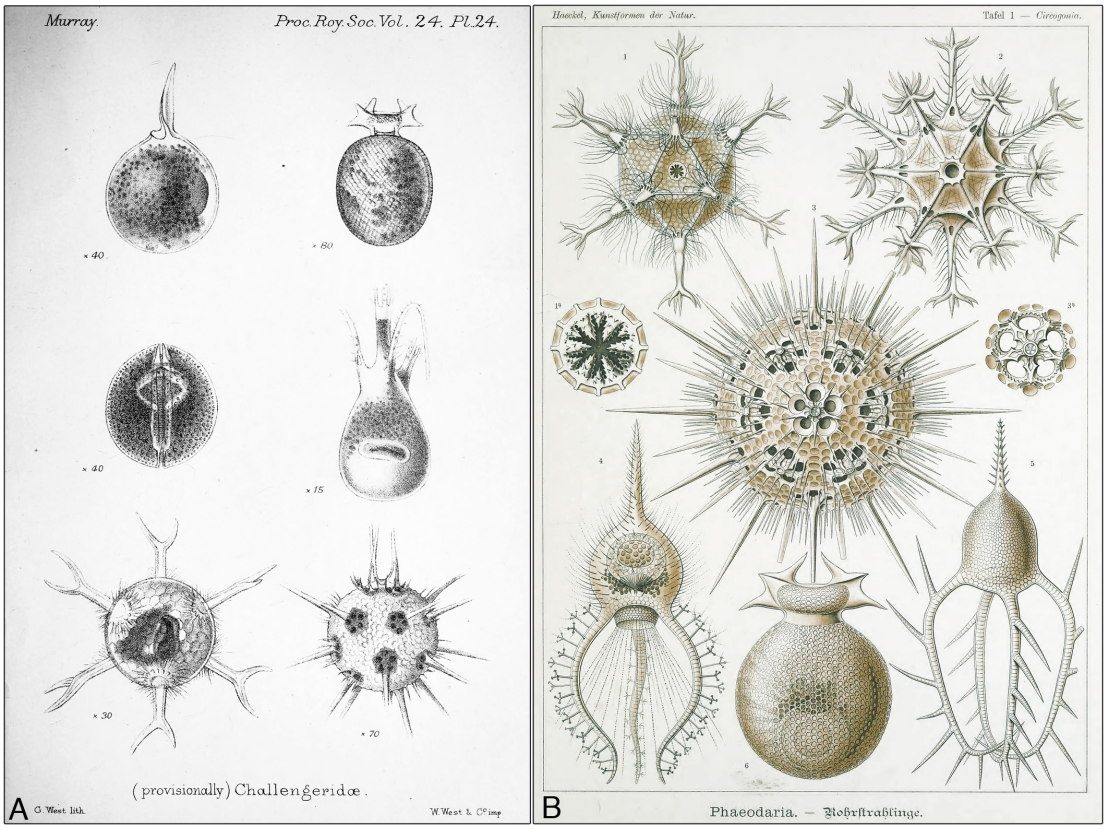

Fig. 1. A. The illustrations of phaeogromids as deep sea protists from Murray's preliminary report of the results of the Challenger Expedition (Murray 1876). B. The first plate in the first issue of Haeckel's *Kunstformen der Natur* (Haeckel 1899-1904) featured some of Murray's 'challengerids' as art forms of nature, introducing them to the general public over one hundred years ago.

Despite such a very notable historical heritage, the ecology of the challengerids (*sensu* Murray), have received little attention beyond many scattered records of occurrences (reviewed in Nakamura and Suzuki 2015). Our knowledge of their biology is limited to Gowing's very admirable studies of food vacuole contents (e.g., Gowing 1986, 1933, Gowing & Bentham 1994; Gowing & Garrison 1992) and that of Gonzalez (1992). Thus, we know that phaeogromids are found in the deep layers of nearly all seas and their food vacuoles contain a large variety of both prokaryotic and eukaryotic prey. What is largely unknown is how concentrations of individual species may vary with time, and how they capture prey. With regard to feeding behavior, there is but a single study documenting the behavior of a living phaeogromid phaeodarian, that of Nakamura et al. (2018) reporting that *Gazelletta kashiwaensis*, found in the surface waters of the Philippine Sea, deployed large webs of pseudopods to capture prey.

In previous studies (Dolan et al. 2019a,b) we presented data on the temporal variability of a variety of protist taxa, including phaeogromids from a site in the

mesopelagic Mediterreanean Sea. To our knowledge, these were the first reports based on high-frequency (≈ weekly) sampling of a deep water site. We suggested that different phaeogromid species, specifically, *Challengeranium diadon*, *Challengeron willemoesi* and *Challengeria xiphodon* were all lowest in concentration in winter when the water column is mixed, but otherwise varied in concentration independently of one another. However, in our previous studies, material from *ca*. 100 l were from discrete depth water samples, filtered through a 20 µm net. The technique was largely adequate for enumerating tintinnid and oligotrich ciliates, but not ideal for estimating phaeogromid concentrations. Raw cell counts of phaeogromids were often only 1or 2 cells, and on most dates some of the species were apparently absent, or more precisely, undetectable. Consequently, we turned to a sampling technique that provides material from large volumes of water, a 70 cm diameter Nansen closing plankton net of 52 µm mesh size. The Nansen net (Nansen 1915) has long been used to sample specific depth strata of the water column.

Here we report the results from our plankton net tows, from a depth of 275 m to 225 m, conducted at near weekly intervals from June 2020 through July 2021 providing material from about 75 cubic meters for each date. Sample material was adequate to provide robust estimates of concentrations of the four most common species from a preserved portion of the sample. These species were *Challengeranium diadon*, *Challengeron willemoesi*, *Challengeria xiphodon* and *Euphysetta lucani*. We also had material permitting observations of living cells, and, to our knowledge, ours are the first observations of living cells of the species. We found that the four, differing considerably in size, displayed roughly similar patterns of temporal changes in abundance, independent of both water column stratification and surface layer chlorophyll concentration. Observations of living specimens revealed that all 4 produce webs of fine pseudopods resembling those reported by Nakamura et al. (2018) for *Gazelletta kashiwaensis.* The shared feeding modes support a view that all four species may exploit similar prey. We conclude that the similar temporal changes in abundances suggest that the four species are controlled by a common factor. However, we found that the controlling factor(s) is not related in a simple fashion to seasonal changes in water column stratification or to surface layer phytoplankton concentrations and thus remains to be identified.

MATERIALS AND METHODS

Sampling

The site sampled is a near shore deep water site, 'Point C' (Fig. 2A), a SOMLIT coastal monitoring site, described in detail in Dolan et al. (2019a,b). Briefly, the site is approximately 1 km off shore with a total depth of over 300 m. Water column profiles of salinity, temperature and conductivity were obtained at near

weekly intervals. In the winter, mixis of the water column characterises the North West Mediterranean Sea with no gradient of temperature separating near surface waters from deep waters (e.g., Copppola et al. 2018). For our sampling point, salinity and temperature profile data were used to characterize water column structure in terms of an index of stratification as given in Dolan et al. (2019a,b). The stratification index is based on potential density difference between 10 and 300 m calculated following Dave and Lozier (2010) and Lozier et al. (2011). While no chlorophyll data is available for Point C, it is located about 1 km from the main, shallow water monitoring site, 'Point B' (80 m total depth) at which chlorophyll concentrations are measured at 0 and 50 m depth during the same weekly monitoring. We present the chlorophyll data (sampling and analytical methods given in Pedrotti et al. (2017) for Point B, as a reasonable proxy for the chlorophyll concentrations in the surface waters of our nearby sampling site.

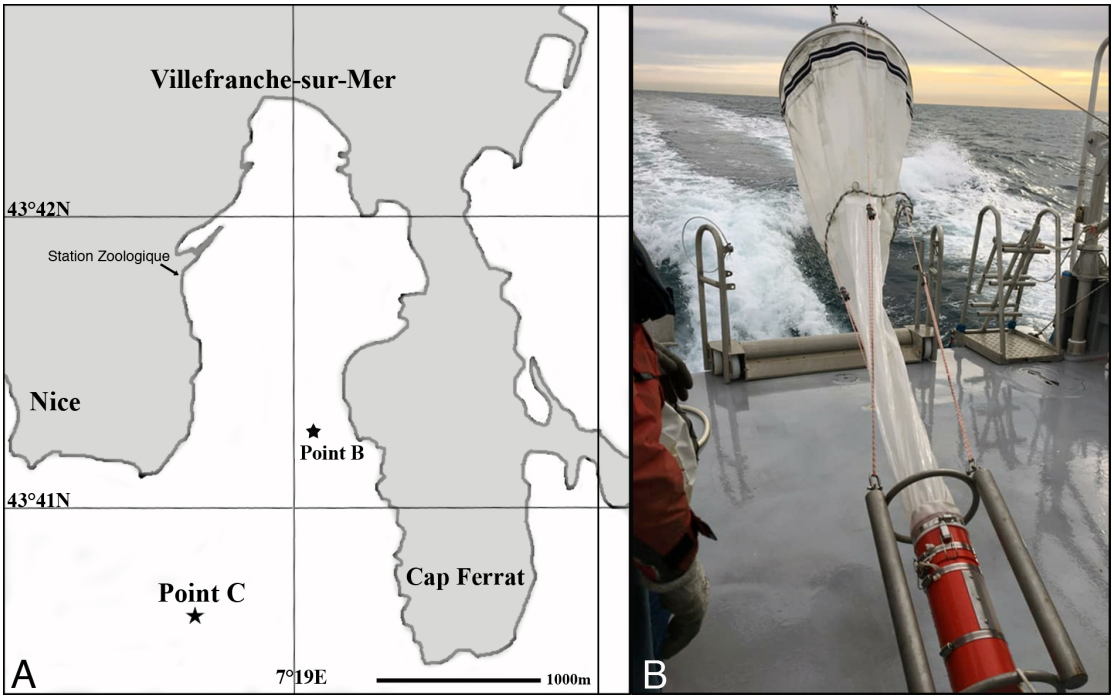

Fig. 2. A. Map showing our deep water sampling site on the N.W. coast of the Mediterranean Sea, Point C, and the site Point B where samples for chlorophyll *a* determinations are taken on the same sampling days. B. The Nansen Closing Net used to sample the depth 275 - 255 m depth strata.

Our sampling was conducted using the research vessel *Sagitta 3* at roughly weekly intervals from June 02, 2021 to 26 July, 2022. Exceptions occurred due to Covid-19 confinement protocols, bad weather, or ship unavailability (because of mechanical problems, or maintenance). These events accounted for 10 missed samples. We sampled the depth strata of 275 - 225 m using a Nansen Closing Net of net mouth size of 70 cm dia., 3 m total length, with a mesh size of 52 µm (Fig.

2B), supplied by Hydro-Bios (Attenholz, Germany). To sample, the net was lowered to 275 m, brought up at a speed of 0.5 m s^{-1} to 225 m and then closed with a messenger-triggered choke line. The closed net was then brought up at a speed of 0.8 m s^{-1}. Aliquots from the 500 ml sample in the collector were fixed immediately on board with Lugol's Solution (2% final concentration) and portions reserved for examination of living cells in the laboratory. The elapsed time from the net closure at 225 m depth and return to the laboratory in the Station Zoologique was approximately 30 minutes. Sampling with the net ended when the net was damaged beyond repair while being hauled onboard.

Laboratory Observations

Observations of fixed material were employed to estimate *in situ* concentrations. Multiple aliquots (1-10 ml) of net tow material totaling 46 to 296 ml for each sampling date, representing material from 7,000-46,000 liters, were examined in settling chambers. A flow meter was not used on the net but the small amounts of material in the cod end collector indicate that net clogging did not occur. Abundance data presented here concerns only the four species of phaeogromids shown in Fig. 2 found to be present in nearly all samples *Challengeranium diadon*, *Challengeria xiphodon*, *Challengeron willemoesi* and *Euphysetta lucani.* For theses species, different generic and/or species names appear in the literature. The following useful summaries of taxonomic descriptions, indicating common synonyms, was prepared largely by Yasuhide Nakamura (National Museum of Nature and Science, Tsukuba, Japan).

Challengeranium diadon was originally described by Haeckel (1887) as *Challengeron diodon*, it was given its own genus, *Challengeranium* by Haecker (1906) who also synominized it with the forms described as *Challengeron nathorsti* by Cleve (1899) and *Challengeron heteracanthum* by Jörgensen (1900). The species is found commonly in the literature under the names of both *Challengeron diadon* and *Challengeranium diadon*. Most recently, a new genus was erected for the species, *Kozohashetta,* (Dumitrica 2016). However, to date no subsequent publications have appeared using *Kozohashetta diadon*. Here we use then the commonly employed *Challengeranium diadon*. *Challengeria xiphodon* was originally described by Haeckel (1887) as *Challengeria xiphodon*, the species of the genus were transferred by Borgert (1901) to the genus *Protocystis* Wallich (1869) and thus many, but not all reports, subsequently used *Protocystis xiphodon*. *Challengeron willemoesii* was originally described by Heackel (1887) and was synonymized with the following forms by Takahashi & Honjo (1981): *Challengeron rottenburgi* Borgert, 1892, *Challengeron armatum* Borgert, 1901 *Challengeron gracile* Borgert, 1908, *Challengeron gracillimum* Borgert, 1908 and *Challengeron walwini* Wolfenden, 1902. *Euphysetta lucani* was originally described by Borgert (1892) and was synonymized with a form described as *Euphysetta mediterranea* by Lohmann (1899) by Borgert (1901). The species

was also synonymized by Haecker (1908) with a form described as *Euphysetta rara* by Borgert (1902).

Observations of living cells were made in the laboratory by pipetting a 1 ml aliquot of net tow material into a 3 ml volume Utermöhl chamber, diluted with 2 ml 0.2-µm filtered seawater, and then examined with an Olympus IX71 inverted microscope equipped with differential interference contrast optics, and imaged using a Canon Eos 5D Mark II digital camera. The settling chamber was scanned at low magnification (100 x total magnification), and occasionally living cells removed with a micropipette, placed into an Utermöhl chamber filled with 0.2-µm filtered seawater and imaged using the digital camera.

RESULTS

Temporal changes in abundance

Summary data on the occurrences and average abundance over the study period of the four species (shown in Figure 3) are provided in Table 1. All four species were found on most of the dates sampled (44 to 47 of the 47 dates sampled) and occurred in similar concentrations (average concentrations of 6 to 18 cells m^3). Temporal changes in concentrations of each species, along with an index of water column stratification, and a proxy of food concentration in the surface layer (chlorophyll a concentration at the near-by Pt B monitoring station), are shown in Fig. 4. Abundances of all four species roughly co-varied. Statistical relationships are given in Table 2 and scatter plots of each species pairs are given in a supplementary file. Casual inspection suffices to show that shifts in abundance were not directly relatable to changes in water column stratification of Point C nor to shifts in chlorophyll concentrations in the nearby surface waters of Point B.

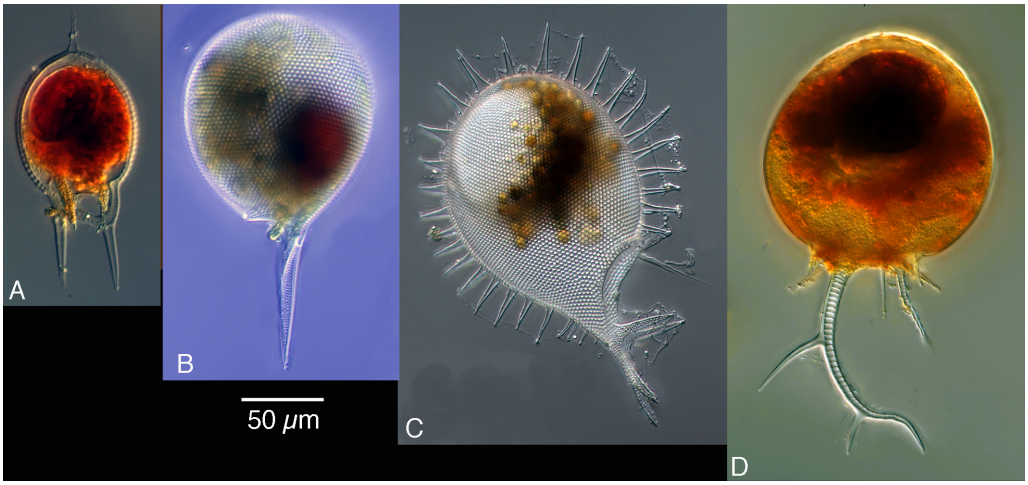

Fig. 3. Typical examples of Lugol's preserved specimens of the four species reported upon in this study: A. *Challengeranium diadon*, B. *Challengeria xiphodon*, C. *Challengeron willimoesii*, D. *Euphysetta lucani*.

Table 1. Summary occurrence and abundance data. Occurrence given as % of dates found out of the 47 dates (#%dates). Abundance given as average given as cells per m^3 with standard deviation for the 47 dates.

Species	Fig 1	% dates	avg conc cells ± sd
Challengeranium diodon	A	98	9±9.8
Challengeria xiphodon	B	96	14±12.8
Challengeron willemoesi	C	100	18±18,6
Euphysetta lucani	D	94	6±6.9

Table 2. Correlation coefficients of abundance among the species (r^2 values of correlation coefficients of log +1 transformed data, n= 47, df =45, p-values in parentheses). All values were positive, significant values are shown in bold. Scatter plots of the relationships are given in the supplementary files.

	Challengeranium diadon	*Challengeria xiphodon*	*Challgeron willemoesi*	*Euphysetta liucani*
Kozohashetta diadon		**0.252** (.05)	0.200 (ns)	0.136 (ns)
Challengeria xiphodon	**0.252** (.05)		0.234 (ns)	**0.365** (.025)
Challgeron willemoesi	0.200 (ns)	0.234 (ns)		**0.533** (.005)
Euphysetta liucani	0.136 (ns)	**0.365** (.025)	**0.533** (.005)	

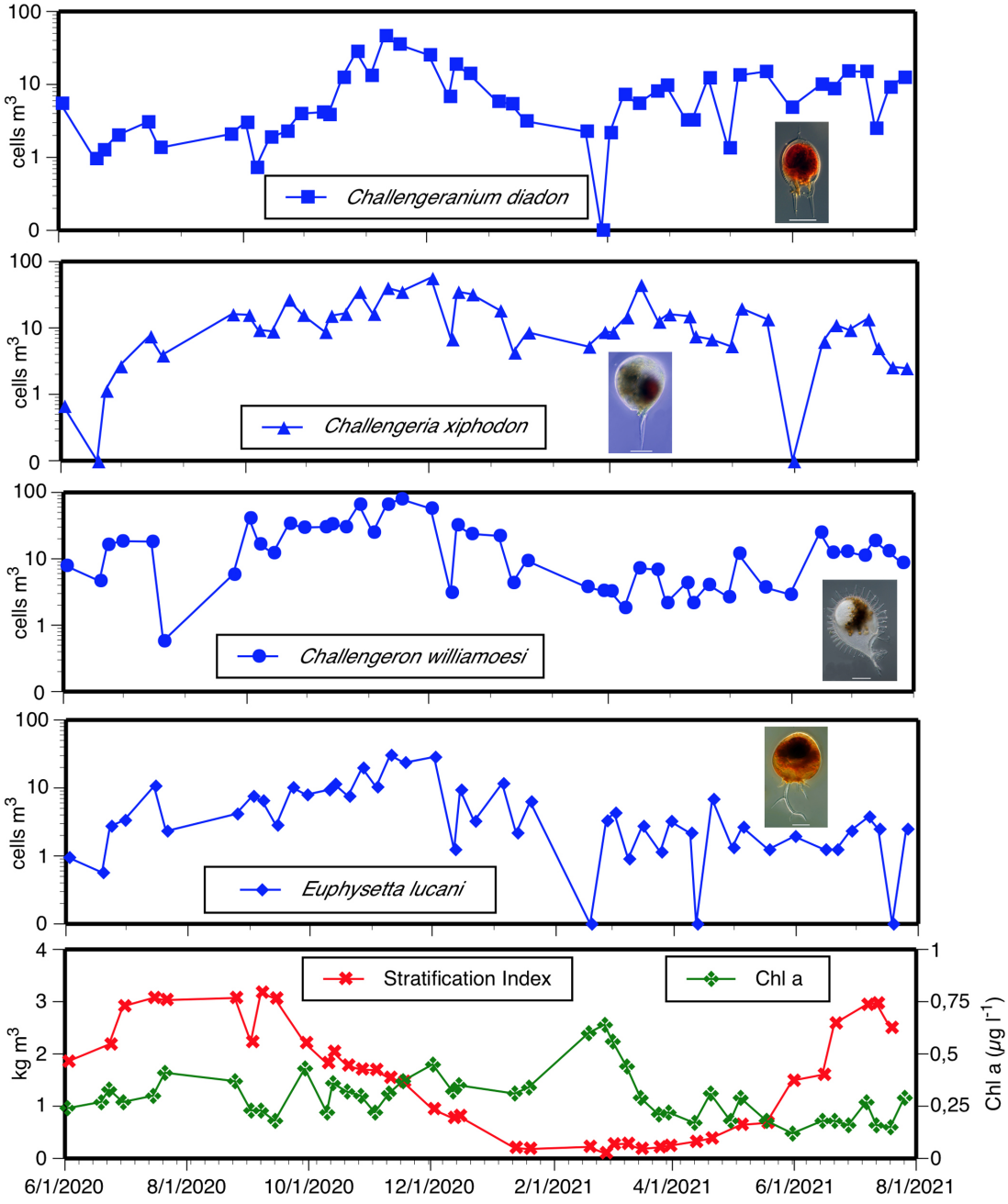

Fig. 4. Temporal changes in the concentrations of the four species and an index of water column stratification at the sampling site, Point C, along with surface layer chlorophyll a concentrations from the near-by Point B. The stratification index, when greater than 1, indicates a mixed layer down to 300 m for our sampling point water column mixis. Note the roughly similar temporal trends of all four species without any clear relationship with water column stratification or chlorophyll a concentrations.

Observations of living cells

Surprisingly, all four species were observed to use pseudopods in two distinct fashions. The cell either extended a single relatively thin pseudopod resembling a fishing line, or created a large web (extending out over several shell lengths of

the cell) of irregularly tangled fine pseudopods. Both types were seen in all four species. Examples are shown in the image of Figure 5 and in the supplementary video files. The videos are also available through Figshare (doi: 10.6084/m9.figshare.21778940). We cannot exclude the possibility that single pseudopod extension is simply the first stage in creating the extended pseudopod web. It was not possible to observe a cell over an extended period of time as they perished after about 30 minutes under the microscope. It is also should be noted that observations were made of cells the cells lying on a glass surface rather than being suspended in water as they would be in situ. Nonetheless, there was a clear similarity among the species in their uses of pseudopods, at least in vitro.

Fig. 5. Images of living cells. Scale bar represents 50 µm. A. *Challengeranium diadon* with a network of filamentous pseudopods. B. *Challengeron xiphodon* extending one thick and one thin pseudopod. C. *Challengeria willemoesii* extending several thin filaments and forming a sheet of sorts to the right of the cell. D. *Euphysetta lucani* deploying a large net of pseudopods. Films given in the supplementary files show each species appears to be capable of the different types of pseudopod use, from a single filament to forming a large extensive web.

DISCUSSION

The occurrence and abundance data derived from analysis of the net samples from tows between 275 and 225 m depth (Table 1), differed somewhat from the data reported previously (i.e., Dolan et al. 2019a,b) using a different protocol. In the earlier studies, whole water samples from 250 m depth were filtered on board through a 20 µm mesh net and detection of the phaeogromid species focused upon here was sporadic, ranging from presence in only 18% of the samples (*Euphysetta lucani*) to 76% of the samples (*Challengeranium diadon*). However, in the earlier study, the average abundances of the species reported upon here ranged from 2 to 26 cells m^3, similar to the data from the net samples given here of 6 to 18 cells m^3. It also should be noted that in the previous studies,

the data on the individual species of phaeogromids was not specifically mentioned in the paper, rather the data allowing calculations of occurrences and average abundances were given in the supplementary data file of Dolan et al. 2019b.

Abundance data is known to be very sparse for phaeodarian taxa (Gowing 1993). Nearly all the reports are derived from sediment samples or sediment trap material and often do not distinguish empty shells from entire remains nor report data for individual phaeodarian species. To our knowledge, there are actually only two reports, other than our previous study, giving data on the abundances in the water column for the phaeodarian species examined in our study and neither reported on temporal changes. The first was in a study of the tintinnid ciliate fauna of the Adriatic that mentioned, only in passing, that *Challengeranium diadon* (as *Challegeron diadon*) and *Challengeron willemoesii* were found in peak abundances of, respectively, 40 cells m^3 and 30 cells m^3, in the mesopelagic in October of 1985, without any further mention (Krsinic 1988, pg. 427). The other report concerned radiolarian distributions in waters surrounding Japan and included a graph showing stocks of living *Challengeranium diadon* (as *Challengeron diadon*) ranging from 10 to 150 $cells^{-1}$ m^3 as a function of salinity and temperature (Ishitani & Takahashi 2007, fig. 12). Several studies have reported data on temporal patterns for pooled species of phaeodarians (e.g. Boltovskoy et al. 1993 and references therein) but, to our knowledge, the only comparative data available concerning temporal changes in abundances of individual species is that of our previous reports.

In contrast to our previous reports, we found no evidence of abundances declining during periods of water column mixis or successional patterns among species. Rather, the four species appeared to roughly co-vary in concentration. The differences found with our previous study may be to due to inter-annual differences. However, we are more inclined to favor the explanation of the net sampling as having provided more robust estimates of abundance. This is based on the fact that in our previous studies, in most of the samples some of the species were not found and apparent absence cannot be distinguished from presence below the detection limit. In our previous studies the detection limit was presence in material examined from 100's of liters compared to material examined from 1000's of liters in the present report.

Here, in contrast to our previous report, we found no obvious simple relationship of changes in species abundances with water column structure nor with phytoplankton concentrations, as indicated by chlorophyll *a* concentrations in a nearby site (i.e., Fig. 4). Our observation that the species roughly co-varied in abundance leads us to assume a common factor or factors acts upon all four species. Given the apparent lack of a relationship with the typical 'bottom-up'

factor of phytoplankton concentration, we are inclined to hypothesize that the 'top-down' factor of predation may yield temporal changes in abundance. Unfortunately we lack any data allowing us to test the hypothesis of temporally variable predation pressure. The typical predators of microzooplankton are large copepods. There are studies that have examined community structures (e.g., Kaiser et al. 2018), latitudinal patterns (e.g., Bode et al. 2018) and feeding behaviour of mesopelagic copepods (e.g. Sano et al. 2013). However, to our knowledge, there are no data on seasonal patterns of the abundance of the typical predators of microzooplankton, large copepods, in the mesopelagic of the Mediterranean Sea or elsewhere.

Our observation on living cells of *Challengeranium diadon*, *Challengeron willemoesi*, *Challengeria xiphodon* and *Euphysetta lucani* are the first for these species. We follow the first report documenting behaviour of a living phaeodarian of Nakamura et al. (2018) on *Gazelletta kashiwaensis*. Our observation are in accordance those of Nakamura et al. (2018) as we found that all four species deployed large "protoplasmic webs" of fine pseudopods and retractable tentacles (see supplementary film files). The protoplasmic webs seen were sometimes of a rough diameter equal to several times the shell length. As remarked upon by Nakamura et al., (2018), the apparent feeding mode of the planktonic phaeodarians is distinct from that known in nasselarians and spumellarians and enlarges the known feeding strategies of planktonic rhizaria.

CONCLUSION

We found that the four most common phaeodarian species of the mesopelagic plankton in the Mediterranean Sea roughly co-varied in abundance together and produced similar large protoplasmic webs, presumably to feed. Given their low abundances, averaging approximately 10 cells m^3, interaction among individuals are likely rare. We tentatively favor the hypothesis that similar changes in abundance among the four species results from changes in temporal rates of mortality due to predation, by default, as changes in abundance appeared unrelated to shifts in phytoplankton stocks in surface waters, the presumed ultimate source of prey for the phaeodarians.

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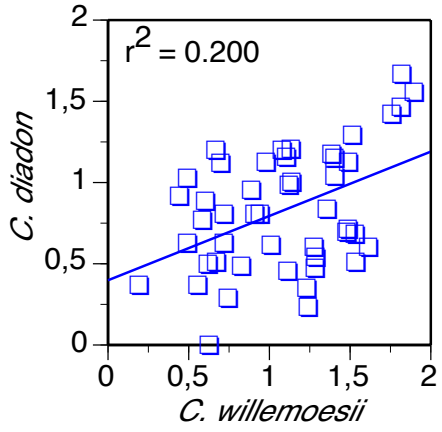
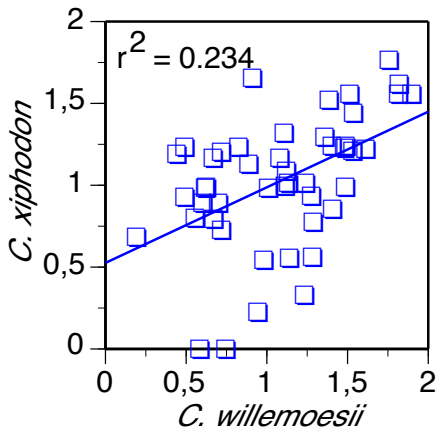
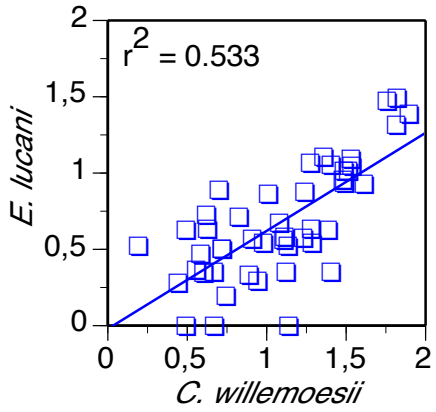
SUPPORTING INFORMATION

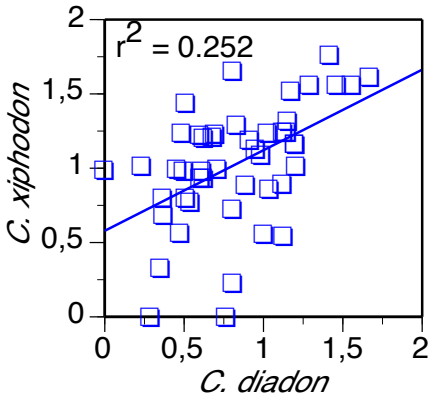
Additional supporting information, an excel file containing the count data for each date and films of live cells may be found online in the Supporting Information section at the end of the article. Films are also available via FigShare: doi:10.6084/m9.figshare.21778940

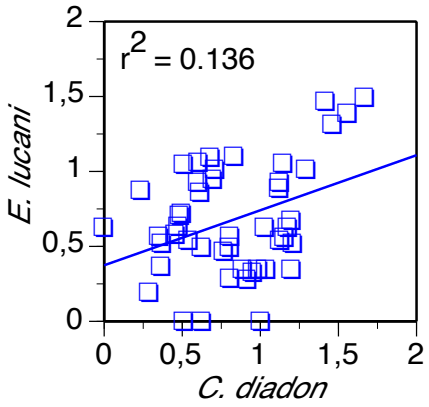
S1. PhaeodarianCountsSuppDataFile.xlsx
S2. Scatterplots of species correlations
S3.CdLargeWeb.mov
S4.CdLittleTentacle.mov
S5. CwHugeFdgWeb.mov
S6. CwHugeNet2.mov
S7. CwilThinFilamBranching.mov
S8. CwilThinFilamentSlo.mov
S9. CwLineFishing.mov
S10. CwNetTentacle.mov
S11. CwParticleFilament.mov
S12. CwRetractClaw.mov
S13. CwThickFilamSlow.mov
S14. CxCastgClawNo.mov
S15. EiSmallTentacle.mov
S16. ElFWeb.mov

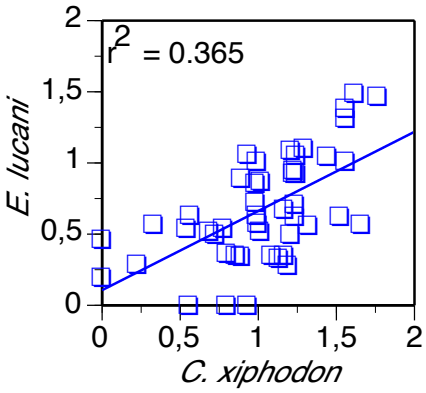












Scatterplots of species abundances with one another. See Table 2 for details.