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Benthic protists: the under-charted majority

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Abstract

Marine protist diversity inventories have largely focused on planktonic environments, while benthic protists have received relatively little attention. We therefore hypothesize that current diversity surveys have only skimmed the surface of protist diversity in marine sediments, which may harbour greater diversity than planktonic environments. We tested this by analyzing sequences of the hypervariable V4 18S rRNA from benthic and planktonic protist communities sampled in European coastal regions. Despite a similar number of OTUs in both realms, richness estimations indicated that we recovered at least 70% of the diversity in planktonic protist communities, but only 33% in benthic communities. There was also little overlap of OTUs between planktonic and benthic communities, as well as between separate benthic communities. We argue that these patterns reflect the heterogeneity and diversity of benthic habitats. A comparison of all OTUs against the Protist Ribosomal Reference database showed that a higher proportion of benthic than planktonic protist diversity is missing from public databases; similar results were obtained by comparing all OTUs against environmental references from NCBI's Short Read Archive. We suggest that the benthic realm may therefore be the world's largest reservoir of marine protist diversity, with most taxa at present undescribed.

Introduction

Molecular studies of marine plankton have uncovered an enormous diversity of protists, many of which could not be assigned to any accession in taxonomic reference databases (*e.g.*, de Vargas *et al.* 2015). Planktonic studies have thus found a very large pool of unknown marine protist species. However, initial molecular studies unveiled highly diverse protist communities from marine benthic habitats which exhibit key ecosystem functions and whose diversity may even exceed that of planktonic protists. Most of these benthic studies were conducted in hydrothermal vent systems (Edgcomb *et al.* 2002; López-García *et al.* 2003; López-García, Vereshchaka and Moreira 2007) and anoxic sediments (Dawson and Pace 2002; Stoeck and Epstein 2003; Takishita *et al.* 2005), both of which environments emerged as hotspots of protist biodiversity. More recently, similarly high diversity was reported from deep-sea and coastal sediments, with many genetic signatures only distantly related to taxonomically described protists (Scheckenbach *et al.* 2010; Pawlowski *et al.* 2011; Bik *et al.* 2012; Gong *et al.* 2015). At least for the three major protist lineages of ciliates, diatoms and foraminifera, the existing species inventories of morphologically delineated species support a higher and distinctively different diversity of benthic compared to planktonic species (Patterson, Larsen and Corliss 1989; Mann and Evans 2007; Pawlowski, Holzmann and Tyszka 2013).

Marine benthic studies, though, remain scarce and limited compared to the considerably larger amount of planktonic studies. Based on the sparse and locally restricted amount of data, no consensus has been reached on the extent of microbial eukaryotic diversity in marine sediments (Epstein and López-García 2007; Fierer 2008; Bik *et al.* 2012). Methodological difficulties are a partial explanation for this undersampling. The clean extraction of nucleic acids from environmental marine sediment samples is challenging (Hurt *et al.* 2001) and extensive amounts of extracellular DNA may severely bias the environmental sequencing studies (Dell'Anno and Danovaro 2005). Furthermore, specific techniques and expensive equipment are required to access these physically remote environments (Orcutt *et al.* 2011). Published benthic studies of protists are thus not only restricted in geographic scope, but also in their comparisons to the overlying planktonic protists. Despite our limited knowledge of benthic protists, there is strong agreement among microbial ecologists that marine coastal sediments play a pivotal role for the diversity and dynamics of overlying plankton communities by acting as seedbanks (Marcus and Boreo 1998). The benthic species reservoir consists of both truly active benthic species and resting stages of dormant planktonic species. Most of the latter occur in low abundances, but blooms can be initiated in response to environmental changes (Marcus and Boreo 1998). Furthermore, studies on microfossil protists have suggested that several planktonic lineages have evolved from benthic ancestors, which have colonized the pelagic realm on different occasions (Leckie 2009).

In this study, we used previously published data from Massana *et al.* (2015) that surveyed protist diversity in European coastal waters and sediments from Norway to Bulgaria using the V4 region of the 18S rRNA. Massana *et al.* (2015) provided a general taxonomic overview of planktonic and benthic protists, with particular attention on examining differences in size-fractionated planktonic protist communities and comparing results obtained from DNA and RNA templates. Building upon this initial study, here we focus on a more detailed comparison of benthic and planktonic protist diversity, with a special emphasis on the richness and phylogenetic novelty contained in marine benthic protist assemblages, two topics that were not covered by Massana *et al.* (2015). Our results not only support previous notions of more diverse benthic than planktonic protist communities, but also present clear indications of a higher degree of novelty in genetic signatures within benthic communities.

Methods

Sampling, pyrosequencing and data processing

In the framework of the BioMarKs project (Dunthorn *et al.* 2014a; Logares *et al.* 2014; Massana *et al.* 2015), water samples from the surface and deep chlorophyll maximum (DCM) layer, and sediment samples were collected from six different European coastal sites including the Skagerrak, the English Channel, the Atlantic Ocean, the Mediterranean Sea and the Black Sea (Table 1). For details on sampling protocols, nucleic acid extraction, 454-pyrosequencing of the hypervariable V4 18S rDNA region and data processing see Massana *et al.* (2015). Briefly, RNA from benthic samples was extracted from 2.5 g of surficial sediment using the Power Soil RNA kit (MoBio, Carlsbad, United States). RNA from planktonic samples was extracted with the NucleoSpin RNA kit (Macherey-Nagel, Düren, Germany) from filters of DCM and surface water samples collected with Niskin bottles. Both extraction kits are specifically optimized to gain high RNA yields from the respective samples and are routinely used in environmental high-throughput sequencing (HTS) studies. Because of the difficulties in RNA extractions from sediment samples (Hurt *et al.* 2001), using an optimized kit for the recovery of nucleic acids from benthic samples was especially important. By targeting environmental (e)RNA rather than environmental (e)DNA we minimized potential biases induced by accumulation and preservation of extracellular eDNA in sediments (Dell'Anno and Danovaro 2005; Stoeck *et al.* 2007). The effect of extracellular eDNA is less critical when only water samples are analyzed (Logares *et al.* 2014), but relevant for a comparison of water with sediment samples. Extracted RNA was then transcribed to cDNA for further processing.

Targeted amplification of the hypervariable V4 18S rDNA region was performed with the eukaryotic primer pair TAReuk454FWD1 and TAReukREV3 (Stoeck *et al.* 2010). This primer pair, though, does not cover Foraminifera and several excavate lineages that are important contributors to benthic protist communities but whose taxonomy is not very well delineated by the V4 region (Pawlowski *et al.* 2011; Lax and Simpson 2013). In contrast to other barcode genes, the V4 region does allow for better comparisons with published full-length 18S rRNA Sanger sequencing studies and has a better database coverage for taxonomic assignment (Stoeck *et al.* 2010; Dunthorn *et al.* 2012). Pyrosequencing of the amplified PCR product was conducted on a 454 GS FLX Titanium system (454 Life Sciences, USA). Resulting 454 reads were subject of a strict quality filtering, including two steps of chimera checking in UCHIME (Edgar *et al.* 2011) and ChimeraSlayer (Haas *et al.* 2011). All quality sequences were then clustered into OTUs using USEARCH (Edgar 2010) on a 97% sequence similarity value. In a second step of quality filtering, one representative of each OTU was subject to a BLASTn analysis against NCBI's nucleotide database release 183.0. All OTUs assigned to Bacteria, Archaea, Metazoa, Embryophyta and OTUs with less than 80% similarity to database entries were removed from the dataset. The final dataset included 430 894 V4 18S RNA sequences, which clustered into 12 438 distinct OTUs. The complete BioMarKs sequencing dataset is available at the European Nucleotide Archive under the study accession number PRJEB9133.

Taxonomic assignment of OTUs

To search for the best hit of each OTU to a described organism, we conducted a local BLASTn analysis (using default settings) against the protist reference database PR^2 (Guillou *et al.* 2012). Additionally, we compared our environmental data against reference data of previous environmental HTS diversity surveys of protists using a similar BLASTn analysis. To build this environmental reference database, we manually screened NCBI's Short Read Archive (SRA) for studies that at least partially included protist data of the eukaryotic 18S gene (according to the experiment's descriptions in the SRA). After downloading the respective data, we removed all references shorter than 100 bp. The final customized SRA reference database consisted of 11 708 385 references from 167 datasets (Supplemental Table S1).

Statistical analyses and diversity measures

All statistical and diversity analyses were performed in R Studio (version 2.15.1, http://r-project.org). Following recommendations of previous studies (Dunthorn *et al.* 2014b) we relied on incidence-based rather than abundance-based data to avoid biases induced by uneven gene copy numbers among different protist taxa. Species richness was estimated with the incidence-based coverage estimator (ICE) as implemented in the 'fossil' package (Vavrek 2011). ICE appropriately estimates asymptotic species richness from datasets containing many rare species (Colwell *et al.* 2012), which we expect in benthic protist communities. Additional species richness estimations in CatchAll (Bunge *et al.* 2012) are provided as supplemental material (Supplemental Fig. S2). Non-metric multidimensional scaling (NMDS) using (binary-) Jaccard distances as a measure of β-diversity was performed with the 'vegan' package (Oksanen *et al.* 2015). Non-parametrical, two-sided Kolmogorov-Smirnov tests (KS-tests) using 1000 bootstrap replicates were used to assess the significance of sequence divergence distribution from planktonic and benthic datasets in the package ‘Matching’ (Sekhon 2011).

Results

Comparison of planktonic and benthic protist diversity

The number of quality filtered sequences among the three habitats differed: 206 602 from the surface, 184 192 from the DCM, and 40 100 from the sediment (Table 1). Despite these differences, the sequences clustered into similar numbers of OTUs: 5747 in the surface, 5685 in the DCM, and 5616 in the sediment. However, ICE-based richness estimates predicted a difference in the number of total OTUs between the plankton and the sediment: 7763 from the surface, 8140 from the DCM, and 16 652 from the sediment (Fig. 1A). The proportion of OTUs thus not detected through our sequencing effort was 26% in surface, 30.2% in the DCM, and 66.3% in the sediment. Richness estimations based on abundance data revealed similar trends but predicted even more undetected OTUs (Supplemental Fig. S2). The observed trends on OTU richness were further congruent with rarefaction results of sequencing data, which were closer to saturation for water column than for sediment samples (Supplemental Fig. S3). Differences in community composition between plankton and benthos were first shown by the number of shared and exclusive OTUs (Fig. 1B). Of 7729 non-singleton OTUs observed in total, only 708 (9.2%) were shared among all three habitats. This low number is, in part, explained by the low number of co-occurring OTUs in plankton and benthos: the plankton had 4368 non-singleton OTUs not found in the benthos, of which 701 were exclusively found in the surface and 762 were exclusively found in the DCM; the benthos had 2364 non-singleton OTUs not found in the plankton.

NMDS analysis further demonstrated the partitioning of the observed diversity patterns in plankton and benthos (Fig. 2). Since differentiation in size fractions was only possible for planktonic samples and beyond the scope of this work, we pooled planktonic data of different size fractions from the same sampling events. In this analysis, surface and DCM samples clustered closely together, indicating a higher similarity in community composition among plankton samples than among benthos samples. Sediment samples were separated from the water communities in the analysis. In contrast to the narrow cluster of surface and DCM samples, the sediment samples were more widely distributed, indicating high dissimilarity in community composition between individual samples. This also applied to sediment samples from the same sampling site taken in consecutive years, as shown by the large distances between both samples from Naples and both samples from Oslo.

Taxonomic affiliation of plankton and benthos OTUs

Most OTUs in each habitat were assigned to the groups of Alveolata, Stramenopiles and Rhizaria (Fig. 3). While the Alveolata dominated the planktonic communities (3281 OTUs in surface, 3638 OTUs in DCM samples), rhizarian OTUs of the phylum Cercozoa dominated the benthic communities (1566 of 1622 benthic rhizarian OTUs). Approximately the same proportion of OTUs was assigned to Stramenopiles in all three habitats. The number of OTUs from the Amoeboza, Apusozoa, Opisthokonta (predominantly fungi), and Picozoa were notably higher in the benthos than in the plankton. In contrast, Archaeplastida and Hacrobia were more diverse in planktonic (238 and 309 OTUs in surface samples; 175 and 264 OTUs in DCM samples) than in benthic communities (50 and 179 OTUs).

On a lower taxonomic level, we observed a higher OTU richness in benthic samples for 10 of the 19 most abundant groups (Fig. 4). In seven of these groups, the OTUs detected in the benthos accounted for more than 70% of the OTUs. These groups comprised the Apicomplexa (Alveolata), Apusomonadidae (Incertae Sedis), Centrohelida (Hacrobia), Discosea and Tubulinea (both Amoebozoa), as well as the previously mentioned Cercozoa and Fungi. Further groups mainly detected in the benthos included Ciliophora (Alveolata), Bacilliarophyceae and Labyrinthulomycetes (both Stramenopiles). Dinoflagellates, however, as the taxonomic group with highest OTU richness in total, were predominantly detected in planktonic samples. Acantharea (Rhizaria), MAST (Stramenopiles) and MALV (Alveolata) are three other taxonomic groups with heterotrophic members that were distinctively more often detected in planktonic than in benthic samples. Similar observations were made among the predominantly phototrophic groups Chlorophyta (Archaeplastida), Chrysophyceae and Dictyochophyceae (both Stramenopiles), and Haptophyta (Hacrobia). Supplemental figures S4 and S5 provide a closer look on the occurrence and distribution of phototrophic taxa and show that Cryptophyta and Rhodophyta were also mostly found in planktonic samples, while more diatoms were found in the benthos (677 OTUs) than in the plankton (445 OTUs).

Database coverage and genetic divergence of plankton and benthos OTUs

To assess how well the observed diversity of OTUs matched previously collected data, we calculated their degree of genetic similarity to reference sequences of the taxonomically curated PR^2 database and to environmental reference sequences of earlier protist diversity inventories deposited in NCBI's SRA (Fig. 5). In both BLAST analyses, the novelty profile was much higher for benthic OTUs, while surface and DCM OTUs exhibited an almost identical profile. Moreover, the genetic similarity of BioMarKs OTUs to PR^2 references (Fig. 5A) was significantly lower (p<0.001) than to environmental references of the SRA database (Fig. 5B).

Considering that 71.8% of the planktonic OTUs in our study can be assigned on a 97%-sequence similarity value to references in PR^2, this database misses 28.2% of the potentially detectable plankton species (conservative estimate, see discussion). Among benthic protist communities 74.4% of the OTUs did not retrieve a taxonomically assigned hit in PR^2 at the same threshold of 97% similarity. Regarding the SRA BLAST results, 78.6% of the planktonic OTUs in our study (n=8988 OTUs) were at least 97% similar to previously deposited environmental references, compared to only 42.7% of the OTUs from benthic samples (n=2400 OTUs). These numbers illustrate that the vast majority of planktonic OTUs had already been detected in previous environmental diversity surveys. This, however, was not the case for benthic OTUs. Thus, BioMarKs benthos analyses contributed a high proportion of novel OTUs to the environmental reference database.

On closer examination of the PR^2 BLAST results, the mean sequence divergence of OTUs detected in surface and DCM samples from references of the taxonomic reference database was 2.6% (Fig. 6). By contrast, the mean sequence divergence of OTUs from sediment samples to PR^2 accessions was 6.6%, indicating that the benthic compartment contains protist species more distantly related to previously deposited taxa than the planktonic compartment. Specifically among the Alveolata, Hacrobia, Opisthokonta, Rhizaria and Stramenopiles, the difference in divergence between plankton and benthos was statistically significant (p<0.001). For example, while the mean sequence divergence of OTUs assigned to Rhizaria from PR^2 references was 3.5% in both the surface and DCM, the averaged divergence was 8.2% in the sediment.

Discussion

High α- and β-diversity shapes coastal benthic protist communities

The α- and β-diversity patterns (Figs. 1 and 2) of protists along the European coastline support previous notions of highly diverse protist communities from different benthic habitats in the world's oceans (Dawson and Pace 2002; Edgcomb *et al.* 2002; López-García *et al.* 2003; Stoeck and Epstein 2003; Takishita *et al.* 2005; López-García, Vereshchaka and Moreira 2007; Scheckenbach *et al.* 2010; Pawlowski *et al.* 2011; Bik *et al.* 2012; Gong *et al.* 2015). A direct comparison of OTU numbers to many of these initial studies is difficult, since most relied on clone library approaches (Dawson and Pace 2002; Edgcomb *et al.* 2002; López-García *et al.* 2003; Stoeck and Epstein 2003; Takishita *et al.* 2005; López-García, Vereshchaka and Moreira 2007; Scheckenbach *et al.* 2010) that produced fewer genetic signatures than the current pyrosequencing approach. Consequently, Scheckenbach *et al.* (2010) estimated a mean OTU richness of 489 in benthic biodiversity hotspots, such as hydrothermal vents, and 1240 in abyssal sediments. These numbers would be well below the mean estimated species richness of 2776 OTUs in BioMarKs sediment samples. Other studies relying on 454 pyrosequencing detected similarly high benthic diversity (Pawlowski *et al.* 2011; Bik *et al.* 2012; Gong *et al.* 2015). One of these surveys observed between 393 and 1049 protist OTUs and estimated between 421 and 1051 OTUs in coastal sediment sites of the Yellow Sea (Gong *et al.* 2015). OTU richness in European coastal sediment samples was higher, with observed protist OTU numbers ranging from 493 to 2499 and estimated OTU numbers ranging from 721 to 3573. The BioMarKs numbers are closer to those observed in Arctic and Southern Ocean deep-sea samples (between 942 and 1756 observed OTUs) (Pawlowski *et al.* 2011).

In contrast to most previous studies, our data allowed us to analyze benthic communities in the context of planktonic communities from overlying water masses of the euphotic zone. Such data are scarcely available for protists and usually limited to specific lineages. One example is a Sanger sequencing study that focused on ciliates (Doherty *et al.* 2010), which reported little overlap between genetic signatures of benthic and planktonic communities in the Gulf of Maine and Long Island Sound. This finding corroborates our observations on whole protist communities in European coastal habitats (Fig. 1B). More data exists, however, for benthic-planktonic community comparisons of marine bacteria. Zinger *et al.* (2011) showed that bacterial OTU richness and β-diversity was much higher in coastal sediments than in coastal surface waters. Similar results were obtained in an arctic fjord HTS survey (Teske *et al.* 2011). These patterns nicely reflect those obtained in our study on protists.

Building upon the Massana *et al.* (2015) study, we targeted the question of the magnitude of benthic compared to planktonic diversity by contrasting the degree of observed richness with the degree of estimated richness (Fig. 1A). In the same context, we highlighted how much of this observed diversity likely represented novel diversity (Figs. 5 and 6), a previously unexamined topic. Furthermore, we contrasted the β-diversity among benthic and planktonic communities (Fig. 2), illustrating small overlap between benthic and planktonic diversity, but also among benthic communities in particular. Given that biodiversity is considered to be higher in coastal than in open ocean habitats (Gray 1997; Zinger *et al.* 2011), the BioMarKs data suggest that marine coastal sediments may be the world’s largest reservoir of protist diversity, much of which is still undetected and most of which is still undescribed in public databases.

One major factor that might promote high diversity in benthic protist communities is a large number of distinct benthic habitats due to horizontal and vertical gradients in both physical and chemical characteristics. Even at microscale, habitat heterogeneity in marine sediments reflects gradients in grain-sizes, oxygen concentration or organic matter content (Pedersen, Smets and Dechesne 2015). The diversity of physico-chemical microhabitats likely promotes the existence of highly specialized organisms and is probably an important driver for species-richness patterns (Hortal *et al.* 2009). We thus argue that our findings of high protist richness and heterogeneity at comparably small geographical scales represents a general trend in benthic diversity, which is well supported by previous findings, *e.g.* in the Yellow Sea, where high α- and β-diversity patterns in coastal marine sediments were unveiled (Gong *et al.* 2015). To further investigate the effect of niche partitioning, species-area relationships and distance-decay relationships on small spatial and temporal scales could be analyzed for planktonic and benthic protists at the same locales (Franzén, Schweiger and Betzholtz 2012; Zinger, Boetius and Ramette 2014). In addition to habitat heterogeneity, geological structures at the seafloor may act as biogeographical barriers. Even locally, this results in a spatial separation of protist communities (Scheckenbach *et al.* 2010). Both factors, niche partitioning and allopatric speciation processes may work *in concerto* to generate and maintain a high diversity of protists in sediments. In direct comparison, environmental heterogeneity is surely much more pronounced in the benthos (Orcutt *et al.* 2011) than in the plankton, although the pelagic realm may create patchy distributions of protists as well (Menden-Deuer and Fredrickson 2010; Dolan and Stoeck 2011).

Additional reasons for diverging protist communities between individual benthic sites (Fig. 2) may also be of technical nature: we found that all sediment samples were severely undersampled as a result of their high diversity (Supplemental Fig. S3). Because of this undersampling, community divergence among different sediment samples may be artificially inflated. It is, however, reasonable to assume that with increasing sampling effort the proportion of OTUs that are shared between two samples and the proportion of OTUs that are unique to each of these samples would remain similar. We therefore argue that the observed high Jaccard-distance between the sediment protist communities is more due to true (biological) heterogeneity in species memberships rather than to (technical) undersampling.

Different protist taxon groups thrive in plankton and benthos

Benthic protist diversity uncovered by environmental HTS is comprised of i) resident species of truly benthic origin; ii) transient species, which spend at least part of their life cycle living actively in or on sediments; iii) non-resident species of planktonic origin present as inactive resting stages, or as recently settled cells. OTUs of resident species clearly dominated the benthic protist communities in our analyses (Fig. 1B). Though transient species are commonly found among different taxonomic groups (Garstecki *et al.* 2000), we found only little overlap between benthic and planktonic OTUs (Figs. 1B and 2). A notable fraction of this overlap was related to diatoms, Chrysophyceae and Chlorophyta (Supplemental Fig. S4). Since all of these groups include species of planktonic origin which are able to form benthic resting stages (McQuoid and Hobson 1996; Duff, Zeeb and Smol 2013), we cannot rule out that at least some of the phototrophic OTUs in sediments could correspond to phytoplankton cysts or cells that had sunk to the sea floor shortly before sampling. Genetic signatures of the planktonic diatom family Leptocylindraceae in sediment samples represent such a peculiar case (Nanjappa *et al.* 2014). However, particularly among phototrophic protists, diatoms were more often detected in the benthos than in the plankton. Indeed this group is known to harbour a larger diversity of benthic than planktonic species, especially in shallow coastal waters (Mann and Evans 2007). Regarding the small amount of shared OTUs between benthos and plankton in general, we argue that genetic signatures of dead or sinking organisms or dissolved RNA were considerably limited.

A striking difference in the community composition between planktonic and benthic protists at a higher taxonomic level is the dominance of numerous previously undescribed Rhizaria in coastal sediments. More than 95% of these rhizarian OTUs were assigned to the phylum Cercozoa (Supplemental Fig. S6), which have emerged as an abundant and diverse lineage in several other benthic protist diversity studies (summarized by Epstein and López-Garcia, 2008). This phylum comprises a large number of gliding zooflagellates, filose and often large reticulose amoebae, which are well adapted to a psammophilic lifestyle (Bass *et al.* 2009; Howe *et al.* 2011), but also occur as parasites of invertebrates, algae and stramenopiles with benthos-associated stages of their lifecycles (Hartikainen *et al.* 2014). Recent studies on cercozoans could link many previously uncultured environmental sequences to novel benthic cercozoans (Chantangsi and Leander 2010; Howe *et al.* 2011; Berney *et al.* 2013). In addition, genetically divergent benthic cercozoans, both free-living and parasitic, are common and diverse but rarely detected in eukaryote-wide environmental surveys, *e.g.* the amoebo-flagellate *Reticulamoeba* (Bass *et al.* 2012) or the parasitic *Ascetosporea* (Hartikainen *et al.* 2014). These examples further emphasize the importance of this phylum in the marine benthos.

Among the most abundant taxonomic groups we observed a trend of distinctively higher OTU richness in benthic than in planktonic communities (Fig. 4). Beside Cercozoa, this trend was especially prominent for Discosea and Tubulinea, two groups of rhizopod Amoebozoa, which are common inhabitants of coastal benthic ecosystems (Garstecki and Arndt 2000). Likewise, the detection of a high proportion of saprotrophic fungi that contribute to detritus processing in marine sediments is not surprising (Richards *et al.* 2012). Higher OTU richness in benthic samples, though less pronounced, was also observed for ciliates. This result is supported by previous morphological and molecular studies that reported higher benthic than planktonic ciliate diversity (Patterson, Larsen and Corliss 1989; Doherty *et al.* 2010). As discussed above, the situation was similar for diatoms.

We detected an inverse trend in diversity among the Acantharea, Dinoflagellata and MALV, all of which are commonly observed in planktonic communities (Guillou *et al.* 2008; Jeong *et al.* 2010; Massana 2011; Decelle *et al.* 2013). Acantharea and dinoflagellates are mostly planktonic organisms and both groups comprise mixotrophs or members with phototrophic symbionts (Gilg *et al.* 2010; Hansen 2010). MALV, on the other hand, can be found as parasites of ciliates, dinoflagellates, radiolarians and fish eggs (Massana 2011) and are known to form planktonic lifecycles (Guillou *et al.* 2008). Unicellular Archaeplastida (Chlorophyta) and Hacrobia (Haptophyta) were also largely missing from benthos samples but occurred in plankton samples. These groups mainly consist of autotrophic organisms performing carbon fixation (Vaulot *et al.* 2008; Not *et al.* 2012) and are major contributors to the pico- and nanoplankton diversity and biomass across the world's oceans (Bittner *et al.* 2013; Egge *et al.* 2015).

High degree of genetic novelty among benthic protist assemblages

The genetic divergence of benthic OTUs from reference sequences described the marine coastal benthic realm as a habitat having a vast majority of protist diversity still uncharted. This applied to both BLAST analyses, against the curated PR^2 reference database and the environmental genetic signatures of the SRA database. Thereby, the mean sequence similarity to taxonomic references (93.4%, Fig. 5A) and to environmental references (95.4%, Fig. 5B) was higher than reported from abyssal sediment communities of protists (87% similarity to taxonomic references, 89% to environmental references) (Scheckenbach *et al.* 2010). Recent advances in sequencing technologies enable the detection and assemblage of a broader diversity of genetic signatures in environmental microbial surveys than ever, but there still remains a clear discrepancy between what can be detected and what can be taxonomically assigned. This discrepancy is especially pronounced among benthic organisms, which display a much higher novelty in genetic diversity surveys than planktonic organisms (Figs. 5 and 6). A promising approach towards exploring this novel diversity is the combination of multiple SRA datasets in network analyses to screen for groups of sequences that do not have closely described relatives (Forster *et al.* 2015). Such highly divergent groups detected in independent environmental samples have a high potential to represent genuine undescribed organisms. The design of novel probes and primer-sets specifically for these groups will in turn enable the targeted recovery and identification of the respective organisms from life samples by molecular methods (Gimmler and Stoeck 2015). As our picture of protist diversity heavily depends on the coverage of available public databases (Pawlowski *et al.* 2012), increasing the efforts to isolate, cultivate and describe benthic protist species will also help to link genetic signatures obtained in environmental sequencing studies to a real biological entity with a phylogenetic context. Although the isolation of individual specimen remains a challenging task, methods exist to successfully address organisms in benthos samples. For example, even small flagellates can be isolated by quantitative centrifugation (Starink *et al.* 1994). More recently, a serial dilution method enabled the recovery of diatom spores from coastal sediment samples (Montresor *et al.* 2013). First studies on highly divergent BioMarKs sediment OTUs already led to the discovery of novel cercozoan vampirellids (Berney *et al.* 2013) and opisthokont Fonticulida (del Campo *et al.* 2015), two groups that were mostly known from soil or freshwater samples.

Regarding the divergence of benthic OTUs from publicly available reference sequences, we suppose that we are just scratching the surface of protist diversity in coastal sediments. Thus, we understand the BioMarKs data as a starting point that may guide the discovery of more novel benthic protist diversity by further taxon-specific screening.

Conclusions

Over the last 60 years, our perception of marine benthic environments has changed from being biologically inert deserts towards being highly heterogeneous habitats teeming with a multitude of microbial organisms. Even though new technologies allow for addressing this vast diversity, the results of the BioMarKs project strongly imply that the most part of benthic protist diversity remains a black box. While sampling the deep-seafloor surely imposes many challenges and restrictions that have lagged the exploration of benthic diversity, our data show that it is not mandatory to focus on such remote environments when looking for highly diverse protist communities. From a quantitative (*i.e.* OTU richness) and qualitative (*i.e.* degree of genetic divergence) point of view, coastal sediments inhabit intriguingly rich protist assemblages on local and regional scales. Increasing the efforts to explore these assemblages will be beneficial to learn more about the dispersal patterns of benthic protists, their roles in ecosystem functioning and to complement current species inventories by identifying many still unknown organisms.

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Conflict of interest

The authors declare that they have no conflict of interest.

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Table 1 Overview of BioMarKs samplings along the European coastline.

			Quality sequences per sampled habitat		
Sampling Event	**Latitude/Longitude**	**Oceanic region**	**Surface water**	**DCM**	**Sediment**
Blanes	41°40'N/2°48'E	Mediterranean Sea	16 568	n.d.	3576
Gijon	43°40'N/5°35'W	Atlantic Ocean	20 966	n.d.	n.d.
Naples 2009	40°48'N/14°15'E	Mediterranean Sea	62 250	52 114	15 739
Naples 2010	40°48'N/14°15'E	Mediterranean Sea	22 132	31 268	3159
Oslo 2009	59°16'N/10°43'E	Skagerrak	33 133	36 988	12 835
Oslo 2010	59°16'N/10°43'E	Skagerrak	19 316	24 819	3071
Roscoff	48°46'E/3°57'W	English Channel	9298	n.d.	1720
Varna	43°10'N/28°50'E	Black Sea	22 939	39 003	n.d.

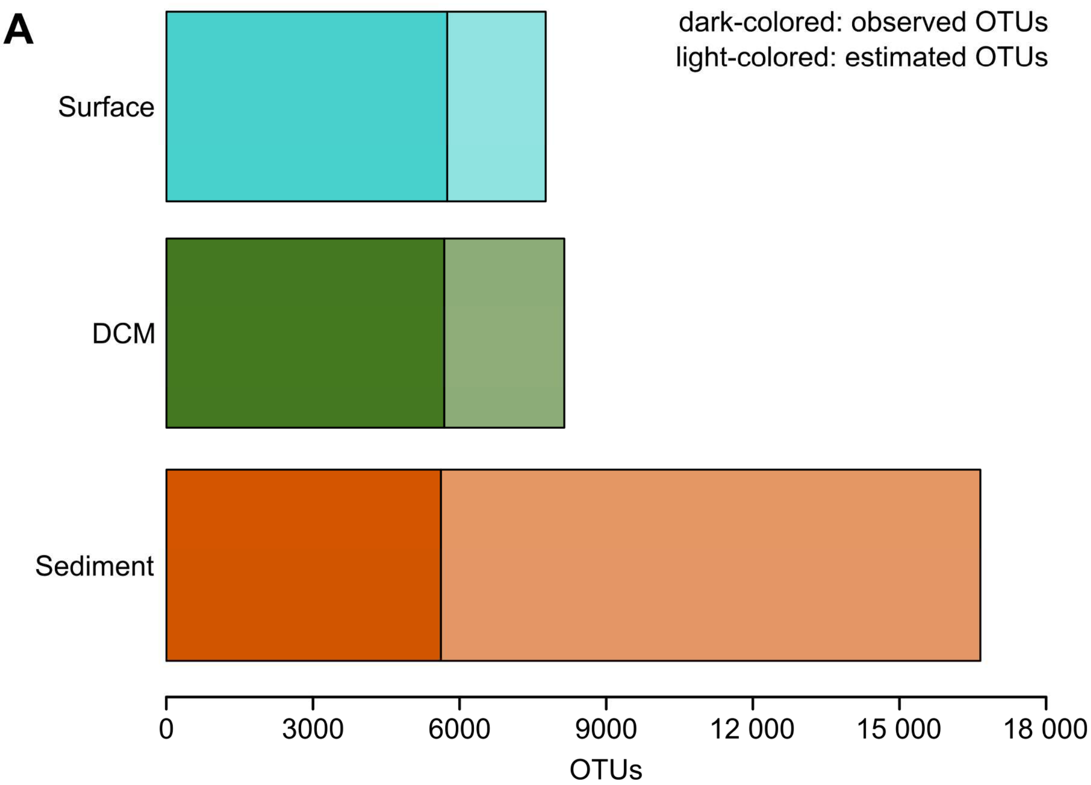
DCM, deep-chlorophyll maximum; n.d., no data available.

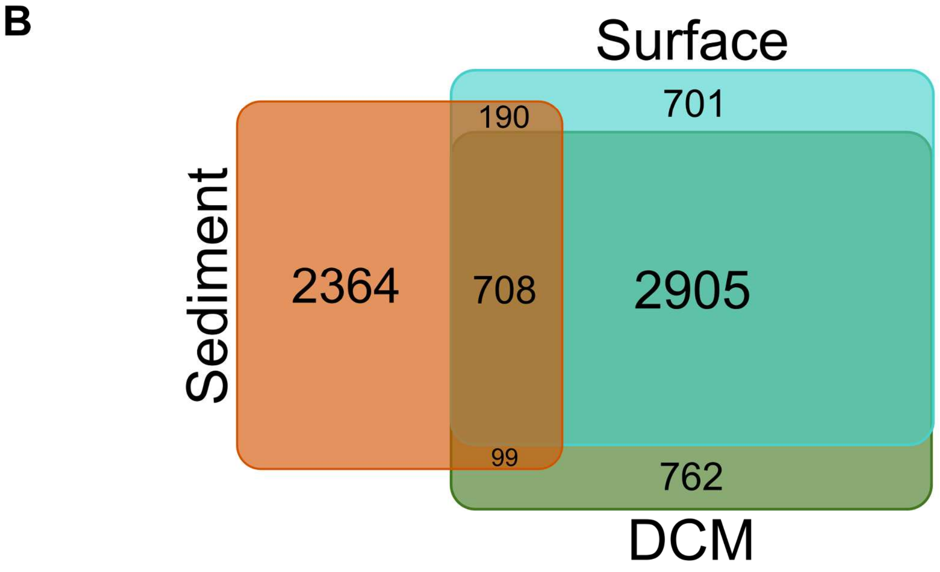
Total number of surface water quality sequences: 206 602.

Total number of DCM quality sequences: 184 192.

Total number of sediment quality sequences: 40 100.

Fig. 1 OTU richness and shared OTUs of planktonic and benthic protist communities. (A) For each habitat the bars show the number of observed (left, dark colored part) and estimated OTUs (right, lighter colored part). Estimations are based on the incidence-based coverage estimator (ICE). (B) The Venn-Diagram highlights how many non-singleton OTUs were shared between all habitats, shared between any two of the sampled habitats or exclusively detected in a single habitat. Numbers indicate the amount of OTUs which fall into the respective category. The area of each category was proportionally approximated to the number of OTUs from the respective habitat.


A
dark-colored: observed OTUs
light-colored: estimated OTUs
Surface
DCM
Sediment
0
3000
6000
9000
12 000
15 000
18 000
OTUs


B
Surface
701
190
Sediment
2364
708
2905
99
762
DCM

707

708

Fig. 2 Beta diversity analysis of single sampling events. The NMDS is based on binary-Jaccard distances between protist communities of single samples (NMDS stress level = 0.2). Colors of the data points were chosen with respect to their habitat affiliation. Data points of the same affiliation were linked and the area between the linked points was colored with respect to their habitat affiliation.

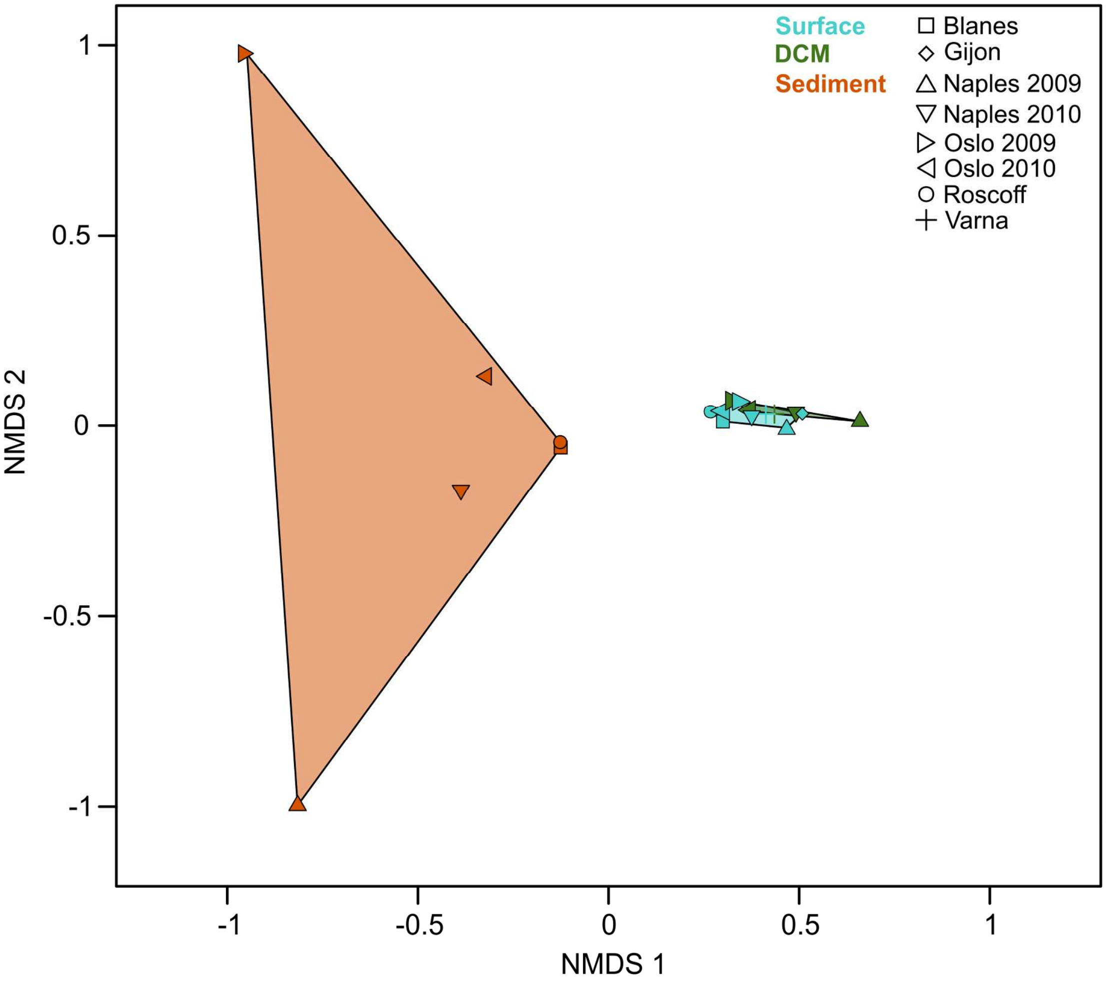


Fig. 3 Taxonomic community compositions as revealed by the PR^2 database. The pie charts reflect the distribution of OTUs within major protist groups, by pooling the data of all samples from each habitat. The surface dataset included 5747 distinct OTUs, the DCM dataset 5685 distinct OTUs and the sediment dataset 5616 distinct OTUs.

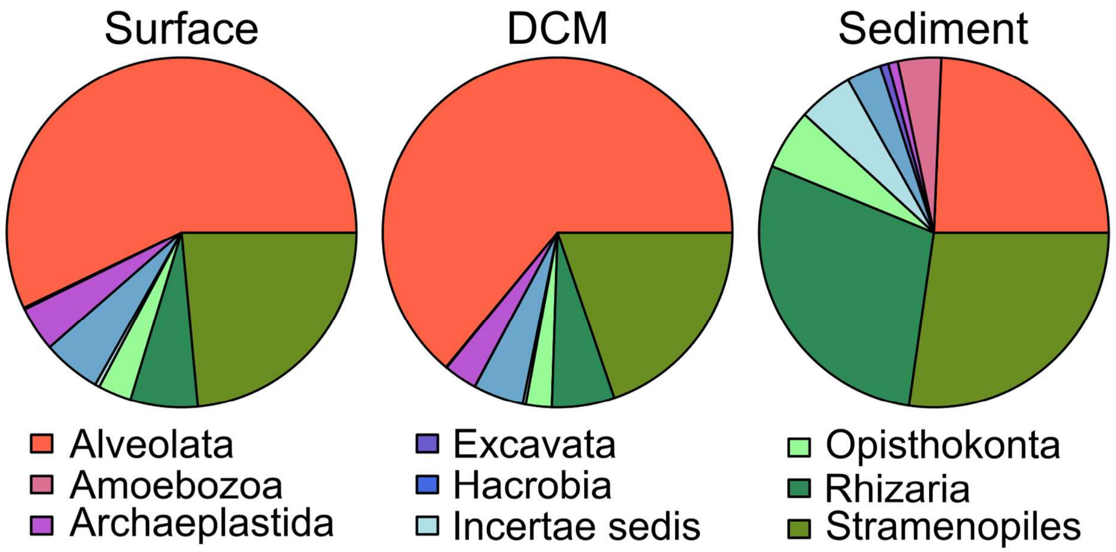


Fig. 4 Number of OTUs within taxonomic groups in planktonic and benthic samples. Only groups contributing to at least 1% of the OTU number in either surface, DCM or sediment communities were considered. Note the different scale among the two panels, to display taxonomic groups with more than 200 OTUs in total (A) or with less than 200 OTUs in total (B).

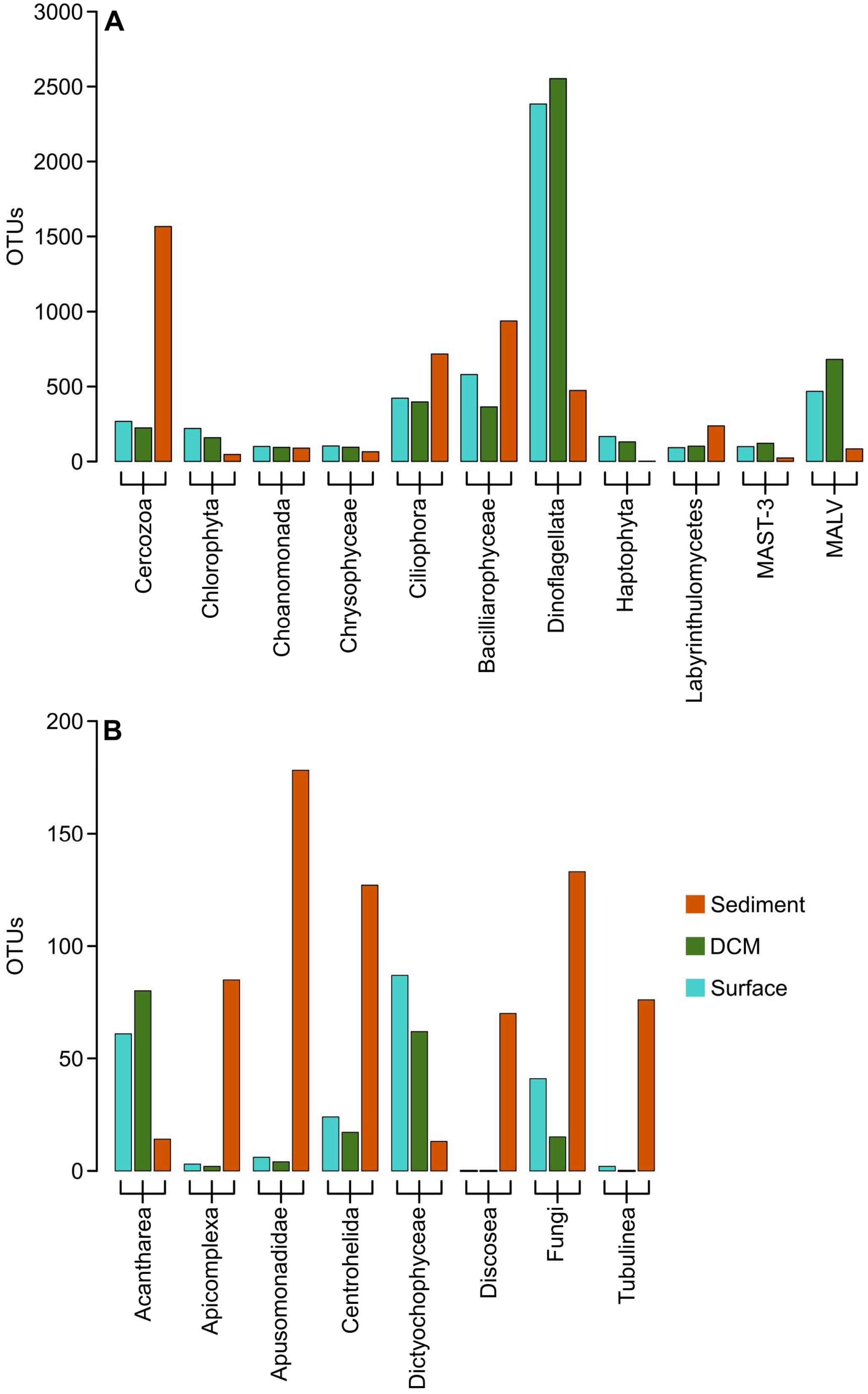

A
OTUs
3000
2500
2000
1500
1000
500
0
Cercozoa
Chlorophyta
Choanomonada
Chrysophyceae
Ciliophora
Bacilliarophyceae
Dinoflagellata
Haptophyta
Labyrinthulomycetes
MAST-3
MALV
B
OTUs
200
150
100
50
0
Acantharea
Apicomplexa
Apusomonadidae
Centrohelida
Dictyochophyceae
Discosea
Fungi
Tubulinea
Sediment
DCM
Surface

Fig. 5 Rank abundance curves displaying the sequence similarity distribution of OTUs against reference databases. Results are shown for two different BLAST queries, against the PR^2 database (A) and against a custom-built subset of NCBI's Short Read Archive (B). The curves display the number of OTUs with a given similarity with the closest match from the respective reference database. Sequence similarities are binned in 0.5 % intervals.

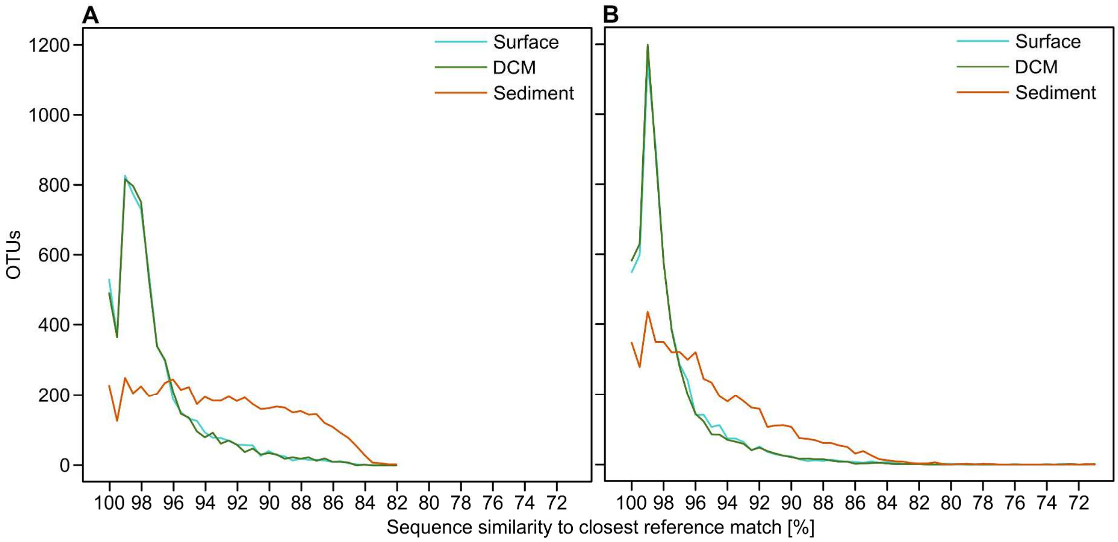
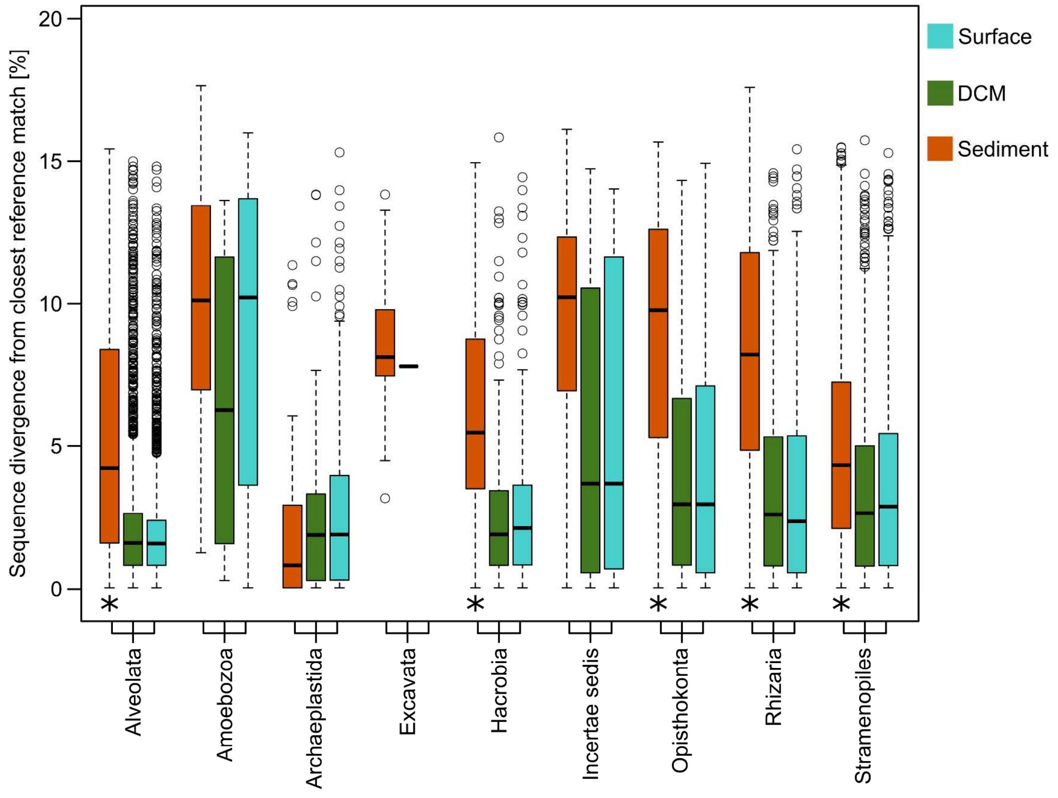


Fig. 6 Sequence divergence of OTUs to their closest taxonomic hit. Each boxplot comprises the sequence divergence values of all OTUs within a given taxonomical group from the same habitat to their closest reference in the PR^2 database. The taxonomic assignment is shown at the supergroup level. Missing boxplots indicate that the taxonomical group was not detected in the respective habitat. For each taxonomic group, differences between the distribution of sequence dissimilarity values of sediment OTUs to planktonic OTUs was tested for significance (*p*<0.001, indicated by stars). The distribution of sequence dissimilarity values was never significantly different between DCM and surface OTUs. Black bars represent the median of each boxplot, the part of the box above the median represents the upper quartile; accordingly, the part of the box below the median represents the lower quartile. Circles show the outliers of each group of data.



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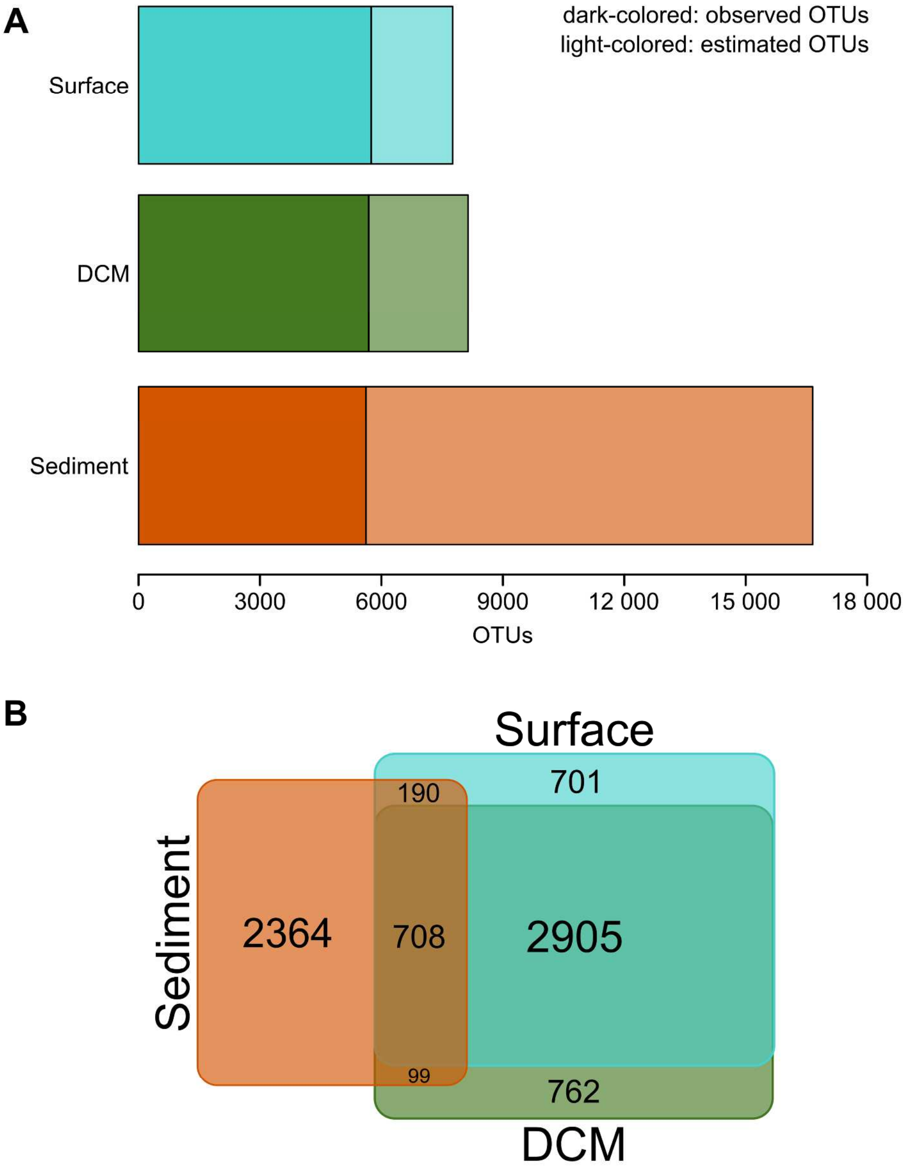

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228x290mm (300 x 300 DPI)

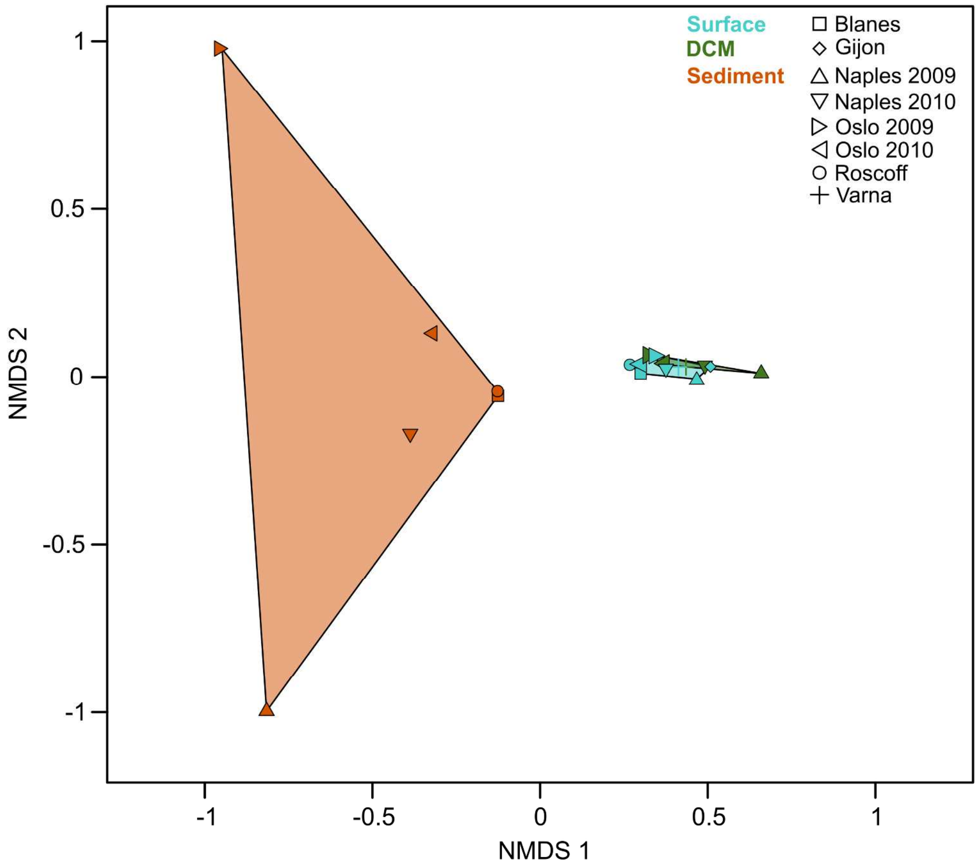

Fig. 2 Beta diversity analysis of single sampling events. The NMDS is based on binary-Jaccard distances between protist communities of single samples (NMDS stress level = 0.2). Colors of the data points were chosen with respect to their habitat affiliation. Data points of the same affiliation were linked and the area between the linked points was colored with respect to their habitat affiliation.
228x200mm (300 x 300 DPI)

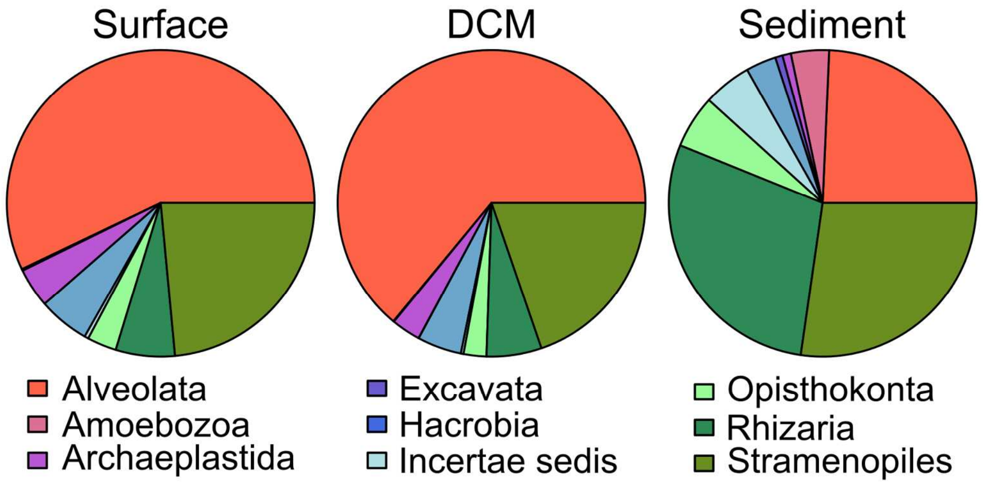

Fig. 3 Taxonomic community compositions as revealed by the PR2 database. The pie charts reflect the distribution of OTUs within major protist groups, by pooling the data of all samples from each habitat. The surface dataset included 5747 distinct OTUs, the DCM dataset 5685 distinct OTUs and the sediment dataset 5616 distinct OTUs.

160x79mm (300 x 300 DPI)

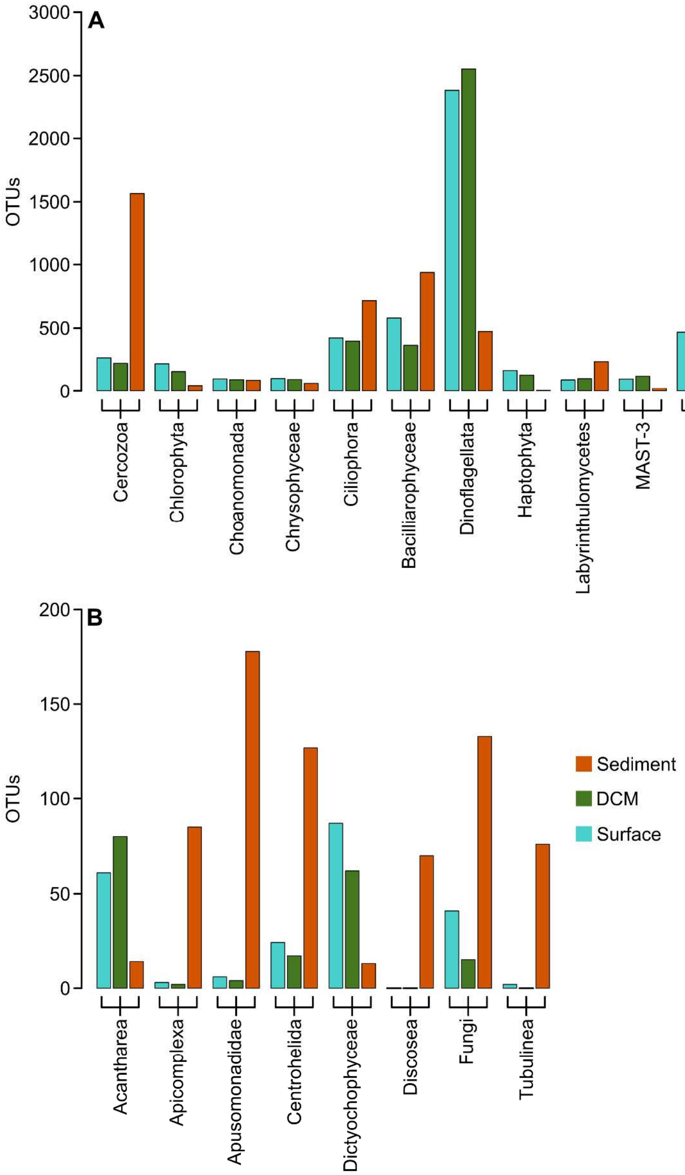

Fig. 4 Number of OTUs within taxonomic groups in planktonic and benthic samples. Only groups contributing to at least 1% of the OTU number in either surface, DCM or sediment communities were considered. Note the different scale among the two panels, to display taxonomic groups with more than 200 OTUs in total (A) or with less than 200 OTUs in total (B).
228x360mm (300 x 300 DPI)

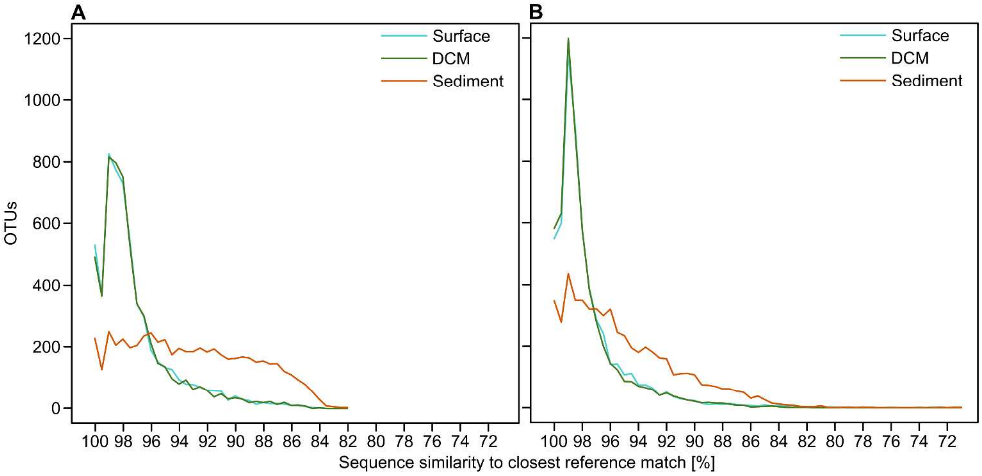

Fig. 5 Rank abundance curves displaying the sequence similarity distribution of OTUs against reference databases. Results are shown for two different BLAST queries, against the PR2 database (A) and against a custom-built subset of NCBI's Short Read Archive (B). The curves display the number of OTUs with a given similarity with the closest match from the respective reference database. Sequence similarities are binned in 0.5 % intervals.

336x169mm (300 x 300 DPI)

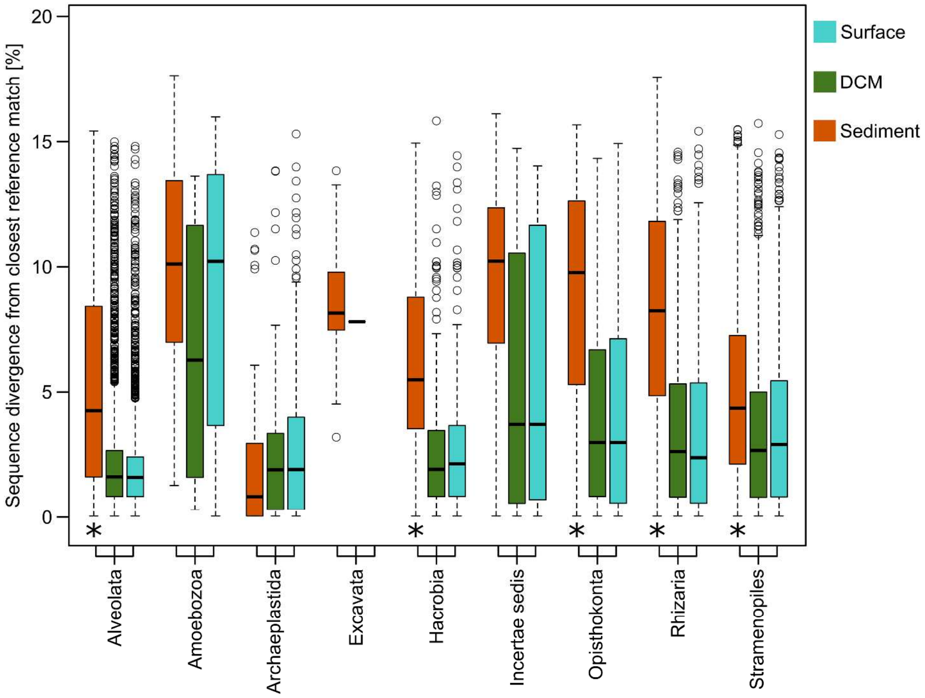

Fig. 6 Sequence divergence of OTUs to their closest taxonomic hit. Each boxplot comprises the sequence divergence values of all OTUs within a given taxonomical group from the same habitat to their closest reference in the PR2 database. The taxonomic assignment is shown at the supergroup level. Missing boxplots indicate that the taxonomical group was not detected in the respective habitat. For each taxonomic group, differences between the distribution of sequence dissimilarity values of sediment OTUs to planktonic OTUs was tested for significance ($p<0.001$, indicated by stars). The distribution of sequence dissimilarity values was never significantly different between DCM and surface OTUs. Black bars represent the median of each boxplot, the part of the box above the median represents the upper quartile; accordingly, the part of the box below the median represents the lower quartile. Circles show the outliers of each group of data.
336x250mm (300 x 300 DPI)

Benthic protists: the under-charted majority

Dominik Forster, Micah Dunthorn, Fréderic Mahé, John R. Dolan, Stéphane Audic, David Bass, Lucie Bittner, Christophe Boutte, Richard Christen, Jean-Michel Claverie, Johan Decelle, Bente Edvardsen, Elianne Egge, Wenche Eikrem, Angélique Gobet, Wiebe H.C.F. Kooistra, Ramiro Logares, Ramon Massana, Marina Montresor, Fabrice Not, Hiroyuki Ogata, Jan Pawlowski, Massimo C. Pernice, Sarah Romac, Kamran Shalchian-Tabrizi, Nathalie Simon, Thomas Richards, Sébastien Santini, Diana Sarno, Raffaele Siano, Daniel Vaulot, Patrick Wincker, Adriana Zingone, Colomban de Vargas, Thorsten Stoeck

Supplemental Table S1 Additional information of the SRA database. The table includes all 167 distinct datasets used to build our custom subset of the SRA. We screened the complete archive for protist datasets of the eukaryotic 18S gene. After downloading the respective data, we removed all sequences shorter than 100 bp. The final customized SRA reference database consisted of 11 708 385 sequences. Information in the table was downloaded directly from NCBI’s SRA platform along with the respective sequences.

Supplemental Fig. 2 Observed and estimated OTU richness calculated by abundance-based analyses. Additionally to incidence-based ICE analyses (Fig.1) we estimated OTU richness with the abundance-based CatchAll tool. In direct comparison ICE and CatchAll results show the same trends, though the estimated richness of the abundance-based analyses always exceeded the one of the incidence-based analyses. For each habitat the plot shows the amount of observed and estimated OTUs. The left, dark colored part of each bar shows the actually observed number of OTUs, the right, light colored part of each bar shows how many more OTUs were estimated to be in each dataset by extrapolation of the data.

Supplemental Fig. S3 Normalized rarefaction curves of sampled habitats. Sequence data of all single sampling events were pooled with regard to the respective habitat. Each habitat rarefaction curve was normalized to 40 100 sequences, which equals the smallest total amount of sequences found in any of the three habitats. Depicted is the amount of SSU V4 rDNA sequences in relation to the amount of resulting OTUs into which the sequences were clustered.

Supplemental Fig. S4 Community composition among phototrophic protist taxon groups. Represented are all phototrophic groups detected in BioMarKs. The upper bar shows the phototrophic OTUs exclusively found in the plankton, the middle bar the phototrophic OTUs present in both plankton and benthos and the lower bar the phototrophic OTUs exclusively found in the benthos. Dinoflagellates were not considered in the analyses.

Supplemental Fig. S5 Occurrence of each phototrophic protist taxon group in the sampled habitats. For each phototrophic taxon group, the bars indicate the fraction of OTUs which was found exclusively in the plankton, in both plankton and benthos and exclusively in the benthos. Dinoflagellates were not considered in these analyses.

Supplemental Fig. S6 Community composition across different taxonomic levels. The pie charts reflect the proportion of taxonomic groups of the total microbial eukaryote community in each habitat. The inner ring is equivalent to Fig. 4 and represents the taxonomical assignment into major protist groups (corresponding to the left part of the taxonomic legend). The outer ring represents the taxonomical assignment at the phylum level (corresponding to the right part of the taxonomic legend). Only phyla which contributed with at least 5% to the total community where considered with a specific color in the outer ring. Exact proportions are given in square brackets behind the taxonomical group names.

Experiment Accession
ERX145205
ERX145206
ERX145207
ERX145208
ERX250340
ERX250341
ERX250342
ERX250343
SRX003229
SRX006203
SRX006204
SRX037894
SRX037895
SRX037896
SRX050582
SRX050583
SRX057201
SRX057202
SRX099033
SRX154532
SRX155674
SRX155675
SRX155676
SRX155677
SRX155678
SRX155679
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SRX673677
SRX719588
SRX734515
SRX768577

Experiment Title
Gene expression during the initiation phase of growth in the dinoflagellate Alexandrium catenella (Dinophyceae)
community profiling of Mirs Bay seawater by 18S rRNA V4 amplicon 454 sequencing
community profiling of Tolo Harbor seawater by 18S rRNA V4 amplicon 454 sequencing
Pooled bacterial amplicons from 10 Arctic marine surface water samples from 2003-2009 plus 2010
Pooled archaeal amplicons from 10 Arctic marine surface water samples from 2003-2009 plus 2010
Pooled eukarya amplicons from 10 Arctic marine surface water samples from 2003-2009 plus 2010
Marine microbial eukaryote community analysis in Korea
Marine microbial eukaryote community analysis in Korea
GS_FLX sequencing for environmental diversity study using the SSU rRNA as taxonomic marker
GS_FLX_Titanium sequencing for environmental diversity study using the SSU rRNA as taxonomic marker
RN_RepliG_Sequencing
Pooled sample of 12 Arctic (Amundsen Gulf and Franklin Bay) sea ice samples from 2008
microbial diversity of ornamental fish aquarium water sample D1
microbial diversity of ornamental fish aquarium water sample E1
microbial diversity of ornamental fish aquarium water sample D2
microbial diversity of ornamental fish aquarium water sample A1
microbial diversity of ornamental fish aquarium water sample A2
microbial diversity of ornamental fish aquarium water sample E2
microbial diversity of ornamental fish aquarium water sample E1.V4
microbial diversity of ornamental fish aquarium water sample D1.V4
microbial diversity of ornamental fish aquarium water sample A1.V4
microbial diversity of ornamental fish aquarium water sample A2.V4
microbial diversity of ornamental fish aquarium water sample D2.V4
microbial diversity of ornamental fish aquarium water sample E2.V4
microbial diversity of ornamental fish aquarium water sample B2.V4
Pooled samples of protist communities at 8 depth from Lake A in May 2008
Pooled samples of protist communities at 4 depths from Lake A in August 2008
Pooled samples of protist communities at 5 depths from Lake A in July 2009
Environmental Samples from ANT-XXVI/3-NS
Partial ribosomal gene sequences Ciliates in DHABs in the Mediterranean Sea
V4 18S rRNA amplicons from cDNA prepared from different microbialite sediment samples from Highborne Cay, B
V4 amplicons (18S rRNA) of eukaryotes obtained from cDNA prepared from various microbialite samples from Sha
ANT XXVI/3 - WE
a test of 16-18s universal primers using sponge samples
Comparative Microbial Analysis to Understand Taxonomic Fingerprints of Healthy Coral Holobiont Communities at
Protistan communities of the upper Arctic Ocean
Comparative Microbial Analysis to Understand Taxonomic Fingerprints of Healthy Coral Holobiont Communities at

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Comparative Microbial Analysis to Understand Taxonomic Fingerprints of Healthy Coral Holobiont Communities a
Exp1.Ward Hunt Lake Dilution Experiment Eukaryotes RNA
Characterisation of uncultured marine eukaryotes in the Canada Basin
Chukchi Sea < 3 um Stn BS1
Chukchi Sea < 3 um Stn AN1
Chukchi Sea < 3 um Stn KS6
Chukchi Sea < 3 um Stn EC5
Chukchi Sea < 3 um Stn HLY
Chukchi Sea < 3 um Stn CC18
Chukchi Sea < 3 um Stn CN3
Chukchi Sea < 3 um Stn CN14
Chukchi Sea < 3 um Stn BCH7
Chukchi Sea < 3 um Stn IE
Chukchi Sea < 3 um Stn HSN5
Chukchi Sea > 3 um Stn BS1
Chukchi Sea > 3 um Stn AN1
Chukchi Sea > 3 um Stn KS6
Chukchi Sea > 3 um Stn CHA1
Chukchi Sea > 3 um Stn EC5
Chukchi Sea > 3 um Stn HLY
Chukchi Sea > 3 um Stn CC18
Chukchi Sea > 3 um Stn CN3
Chukchi Sea > 3 um Stn CN14
Chukchi Sea > 3 um Stn BCH7
Chukchi Sea > 3 um Stn IE
Chukchi Sea > 3 um Stn HSN5

454

Sequences from three sediments
Design and validation of four primers for next-generation sequencing to target the 18S rRNA gene of gastrointesti
Design and validation of four primers for next-generation sequencing to target the 18S rRNA gene of gastrointesti
Design and validation of four primers for next-generation sequencing to target the 18S rRNA gene of gastrointesti
454 pyrosequencing of plankton community collected from Hamilton harbour
454 pyrosequencing of plankton community collected from Nanaimo harbour

Investigating marine microbial plankon in meso-eutrophic ecosytem (Eastern English Channel)
JB121SF_DNA
JB121SF_RNA GoMA July 2010
JB121SCM_DNA GoMA July 2010
JB121SCM_RNA GoMA July 2010
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NEF512SCM_RNA GoMA July 2010
Eukaryota Arctic Ocean Survey
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Marine microbial community structure assessed from combined metagenomic analysis and ribosomal tag pyroseq
Protists in Havre-aux-Maisons Lagoon
Protists in Havre-aux-Maisons Lagoon
Protists in Havre-aux-Maisons Lagoon
Protists in Havre-aux-Maisons Lagoon
Protists in Havre-aux-Maisons Lagoon
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Protists in Havre-aux-Maisons Lagoon
Protists in Havre-aux-Maisons Lagoon
Protists in Havre-aux-Maisons Lagoon
Eukaryotic Plankton Assemblages Inhabiting Saline Lakes in the Qaidam Basin
Marine picoplankton
Deep Hypersaline Anoxic Basin sediment microbial eukaryotes
Three years diversity in the Eastern English Channel

Organism Name	Instrument
marine metagenome	454 GS FLX
marine metagenome	454 GS FLX
marine metagenome	454 GS FLX
marine metagenome	454 GS FLX
aquatic metagenome	454 GS FLX Titanium
aquatic metagenome	454 GS FLX Titanium
aquatic metagenome	454 GS FLX Titanium
aquatic metagenome	454 GS FLX Titanium
Alexandrium catenella	454 GS FLX
marine metagenome	454 GS FLX
marine metagenome	454 GS FLX
marine metagenome	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium
uncultured marine eukaryote	454 GS FLX Titanium
uncultured marine eukaryote	454 GS FLX Titanium
metagenomes	454 GS FLX
metagenomes	454 GS FLX Titanium
Rotylenchulus reniformis	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium
metagenomes	454 GS FLX
metagenomes	454 GS FLX
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metagenomes	454 GS FLX
metagenomes	454 GS FLX
freshwater metagenome	454 GS FLX Titanium
freshwater metagenome	454 GS FLX Titanium
freshwater metagenome	454 GS FLX Titanium
uncultured marine eukaryote	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium
eukaryote XCL-2011	454 GS FLX Titanium
eukaryote XCL-2011	454 GS FLX Titanium
marine metagenome	454 GS FLX
Suberites ficus	454 GS FLX Titanium
Isopora palifera	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium
Seriatopora hystrix	454 GS FLX Titanium

Montipora digitata	454 GS FLX Titanium
Porites cylindrica	454 GS FLX Titanium
Isopora palifera	454 GS FLX Titanium
Isopora palifera	454 GS FLX Titanium
Isopora palifera	454 GS FLX Titanium
Montipora digitata	454 GS FLX Titanium
Montipora digitata	454 GS FLX Titanium
Montipora digitata	454 GS FLX Titanium
Seriatopora hystrix	454 GS FLX Titanium
Seriatopora hystrix	454 GS FLX Titanium
Seriatopora hystrix	454 GS FLX Titanium
Porites cylindrica	454 GS FLX Titanium
Porites cylindrica	454 GS FLX Titanium
Porites cylindrica	454 GS FLX Titanium
aquatic metagenome	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium
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marine metagenome	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium
gut metagenome	454 GS FLX
marine sediment metagenome	454 GS FLX+
gut metagenome	454 GS FLX Titanium
gut metagenome	454 GS FLX Titanium
gut metagenome	454 GS FLX Titanium
freshwater metagenome	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium

marine metagenome	454 GS FLX Titanium
uncultured eukaryote	454 GS FLX Titanium
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uncultured eukaryote	454 GS FLX Titanium
marine metagenome	454 GS FLX+
marine metagenome	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium
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marine metagenome	454 GS FLX Titanium
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marine metagenome	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium
aquatic metagenome	454 GS FLX
marine metagenome	454 GS FLX
marine sediment metagenome	454 GS FLX Titanium
marine metagenome	454 GS FLX Titanium

Submitter	Study Accession
ESE	ERP001773
ESE	ERP001773
ESE	ERP001773
ESE	ERP001773
MPIMM	ERP002513
MPIMM	ERP002513
MPIMM	ERP002513
MPIMM	ERP002513
CNRS/UNIVERSITE MONTPELLIER 2	SRP000647
The Chinese University of Hong Kong	SRP000936
The Chinese University of Hong Kong	SRP000936
Universite Laval	SRP005272
Universite Laval	SRP005272
Universite Laval	SRP005272
Inha univ.	SRP006126
Inha univ.	SRP006126
University of Kaiserslautern	SRP003169
University of Kaiserslautern	SRP003169
Alabama A&M University	SRP008476
Universite Laval	SRP013740
MBL	SRP013874
MBL	SRP013874
MBL	SRP013874
MBL	SRP013874
MBL	SRP013874
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Université Laval	SRP014823
Université Laval	SRP014823
Université Laval	SRP014823
Alfred Wegener Institute for Polar and Marine Rese	SRP016049
University of Kaiserslautern	SRP017187
Woods Hole Oceanographic Institution	SRP017332
Woods Hole Oceanographic Institution	SRP017334
Alfred Wegener Institute for Polar and Marine Rese	SRP016049
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University of Sydney	SRP022083
Laval University	SRP022176
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Universit* Laval	SRP027540
Universite Laval	SRP029291
Université Laval	SRP029300
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AWI	SRP032538
University of Bergen	SRP033298
University of Vermont	SRP034591
University of Vermont	SRP034591
University of Vermont	SRP034591
RCEES, Chinese Academy of Sciences	SRP038053
RCEES, Chinese Academy of Sciences	SRP039005

Universite du Littoral Cote d'Opale	SRP039908
Université Laval	SRP040423
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Universite du Littoral Cote d'Opale	SRP039908
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Universié Laval	SRP043016
Universié Laval	SRP043016
Institute of Shandong River Wetlands	SRP045389
Alfred Wegener Instiute	SRP048617
Woods Hole Oceanographic Institution	SRP049010
Universite du Littoral Cote d'Opale	SRP039908

Study Title
Accuracy of protist diversity assessments: morphology compared to cloning and direct pyrosequencing of 18S rRN
Accuracy of protist diversity assessments: morphology compared to cloning and direct pyrosequencing of 18S rRN
Accuracy of protist diversity assessments: morphology compared to cloning and direct pyrosequencing of 18S rRN
Accuracy of protist diversity assessments: morphology compared to cloning and direct pyrosequencing of 18S rRN
Microbial community response during the iron fertilization experiment LOHAFEX
Microbial community response during the iron fertilization experiment LOHAFEX
Microbial community response during the iron fertilization experiment LOHAFEX
Microbial community response during the iron fertilization experiment LOHAFEX
Alexandrium catenella
Composition and genetic diversity of picoeukaryotes in subtropical coastal waters as revealed by 454 sequencing-
Composition and genetic diversity of picoeukaryotes in subtropical coastal waters as revealed by 454 sequencing-
Microbial Community Diversity Response to a Changing Arctic Ocean
Microbial Community Diversity Response to a Changing Arctic Ocean
Microbial Community Diversity Response to a Changing Arctic Ocean
Marine microbial eukaryote community analysis in Korea
Marine microbial eukaryote community analysis in Korea
Error rate of 454 GS FLX sequenced V4 and V9 PCR amplicons of various protists
Error rate of 454 GS FLX sequenced V4 and V9 PCR amplicons of various protists
Rotylenchulus reniformisGenome sequencing
Arctic sea ice Targeted Locus (Loci)
Microbial Diversity and Potential Pathogens in Ornamental Fish Aquarium Water
Microbial Diversity and Potential Pathogens in Ornamental Fish Aquarium Water
Microbial Diversity and Potential Pathogens in Ornamental Fish Aquarium Water
Microbial Diversity and Potential Pathogens in Ornamental Fish Aquarium Water
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Microbial Diversity and Potential Pathogens in Ornamental Fish Aquarium Water
Microbial Diversity and Potential Pathogens in Ornamental Fish Aquarium Water
Lake A protist communities
Lake A protist communities
Lake A protist communities
Marine eukaryotic protists Metagenome
Partial ribosomal RNA gene of DHAB Ciliates
Highborne Bay eukaryotic small subunit ribosomal RNA diversity
Shark Bay eukaryotic small subunit ribosomal RNA diversity
Marine eukaryotic protists Metagenome
Sponge metagenome
Reef-building coral species harbour Chromera velia and apicomplexan “type-N” (cf. Gemmocystis cylindrus) on the
Protistan communities of the upper Arctic Ocean (18S SSU-rRNA Targeted Locus)
Reef-building coral species harbour Chromera velia and apicomplexan “type-N” (cf. Gemmocystis cylindrus) on the

Reef-building coral species harbour Chromera velia and apicomplexan “type-N” (cf. Gemmocystis cylindrus) on the
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Reef-building coral species harbour Chromera velia and apicomplexan “type-N” (cf. Gemmocystis cylindrus) on the
Ward Hunt Lake Dilution Experiment Eukarya
Uncultured marine eukaryotes Targeted Locus (Loci)
Surface ocean Targeted Locus (Loci)
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Surface ocean Targeted Locus (Loci)
Gut content of salps Targeted Locus (Loci)
Environmental eukaryotes Metagenome
Design and validation of three primer sets to target the 18S rRNA gene of rumen protozoa.
Design and validation of three primer sets to target the 18S rRNA gene of rumen protozoa.
Design and validation of three primer sets to target the 18S rRNA gene of rumen protozoa.
454 pyrosequencing of plankton sample collected from Hamilton Harbour
Plankton sample collected from Nanaimo Harbour Targeted Locus (Loci)

Marine metagenome Targeted Locus (Loci)
Uncultured eukaryotes Targeted Locus (Loci)
Uncultured eukaryotes Targeted Locus (Loci)
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Eukaryota Arctic Ocean Survey Targeted Locus (Loci)
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Eukaryota Arctic Ocean Survey Targeted Locus (Loci)
Eukaryota Arctic Ocean Survey Targeted Locus (Loci)
Marine metagenome Targeted Locus (Loci)
Protists in Havre-aux-Maisons Lagoon, Magdalen Islands, Quebec, Canada
Protists in Havre-aux-Maisons Lagoon, Magdalen Islands, Quebec, Canada
Protists in Havre-aux-Maisons Lagoon, Magdalen Islands, Quebec, Canada
Protists in Havre-aux-Maisons Lagoon, Magdalen Islands, Quebec, Canada
Protists in Havre-aux-Maisons Lagoon, Magdalen Islands, Quebec, Canada
Protists in Havre-aux-Maisons Lagoon, Magdalen Islands, Quebec, Canada
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Protists in Havre-aux-Maisons Lagoon, Magdalen Islands, Quebec, Canada
Protists in Havre-aux-Maisons Lagoon, Magdalen Islands, Quebec, Canada
Protists in Havre-aux-Maisons Lagoon, Magdalen Islands, Quebec, Canada
aquatic metagenome Genome sequencing
Marine picoplankton Targeted Locus (Loci)
Environmental pyrotags for eukaryotes Targeted Locus (Loci)
Marine metagenome Targeted Locus (Loci)

Sample Accession	Sample Title	Total Size, Mb	Total RUNs	Total Spots	Total Bases
ERS169722	marine metagenome	23.79	1	21827	9839469
ERS169723	marine metagenome	21.43	1	23993	8082496
ERS169724	marine metagenome	18.76	1	17244	7794090
ERS169725	marine metagenome	17.47	1	19798	6666525
ERS249848		85.86	1	72440	38229935
ERS249849		102.95	1	81845	47054441
ERS249850		118.91	1	98290	53957382
ERS249851		100.9	1	88895	43788914
SRS002344		35.51	1	71986	18253824
SRS004112		61.34	1	100911	27881207
SRS004113		53.61	1	87392	24193478
SRS152378		75.57	2	74742	32439603
SRS152378		105.05	2	93195	46778615
SRS152378		190.11	2	174077	86125205
SRS182654		3.27	1	3025	1487037
SRS182654		4.98	1	4575	2292151
SRS086207		22.19	1	53155	10757013
SRS086207		14.35	1	15221	5812974
SRS265308		1523.59	1	1206043	732000297
SRS345723		115.48	1	97702	48782681
SRS346704		12.67	1	11368	6229595
SRS346705		15.56	1	14233	7736979
SRS346706		9.52	1	8332	4512789
SRS346707		11	1	9993	5429341
SRS346708		14.43	1	13015	7108579
SRS346709		17.94	1	16171	8854309
SRS346705		3.35	1	8248	1578966
SRS346704		2.99	1	7443	1424093
SRS346707		3.3	1	8032	1538044
SRS346708		3.96	1	9691	1858955
SRS346706		3.07	1	7788	1489084
SRS346709		3.29	1	8133	1555000
SRS348706		3.9	1	9538	1827278
SRS355910		86.28	1	72724	36293480
SRS355910		42.46	1	35716	17867669
SRS355910		76.54	2	66130	34180949
SRS367508		378.84	1	300582	180399874
SRS375573		540.47	1	513347	236974344
SRS377421		277.64	1	260367	120224628
SRS377419		293.83	1	273186	128190762
SRS415390		351.24	1	278116	166721838
SRS417793		4.62	1	11325	6671280
SRS418650		0.91	1	7981	1692614
SRS419165		322.41	1	273168	144033297
SRS419338		0.41	1	3871	806497

SRS419339	0.81	1	7392	1559199
SRS419340	1.04	1	11758	2445426
SRS418650	0.68	1	3132	976006
SRS418650	1.64	1	7869	2535594
SRS418650	5.82	1	21910	8789284
SRS419339	0.82	1	3714	1214580
SRS419339	1.77	1	8746	2761817
SRS419339	1.93	1	7460	2842999
SRS419338	4.94	1	18201	7310788
SRS419338	1.04	1	3904	1497539
SRS419338	0.82	1	3682	1202397
SRS419340	0.99	1	4352	1465489
SRS419340	0.91	1	4454	1311120
SRS419340	0.89	1	3886	1329835
SRS463199	196.76	2	173394	87300958
SRS474263	162.05	1	144296	73326694
SRS474328	8.68	1	7316	3910652
SRS474346	18.1	1	15303	8161494
SRS474349	15.9	1	13493	7128393
SRS474350	13.83	1	11664	6215030
SRS474351	16.15	1	13734	7262782
SRS474352	18.29	1	15517	8240291
SRS474353	11.44	1	9655	5121533
SRS474354	17.62	1	14747	7924648
SRS474356	16.06	1	13611	7207989
SRS474357	17.41	1	14939	7808117
SRS474358	9.22	1	7748	4147573
SRS474359	13.97	1	12148	6399423
SRS474360	18.17	1	15778	8326048
SRS474361	13.18	1	11435	5969057
SRS474362	8.88	1	7728	4058666
SRS474363	13.63	1	11864	6249808
SRS474364	12.67	1	11010	5797710
SRS474365	12.04	1	10497	5506280
SRS474366	14.59	1	12686	6679449
SRS474367	14.41	1	12487	6529205
SRS474368	14.11	1	12243	6426116
SRS474369	14.04	1	12182	6373006
SRS474371	9.96	1	8600	4515861
SRS498636	297.51	1	337737	130753424
SRS507106	219.12	1	860390	354289445
SRS514888	5.06	1	22051	10260945
SRS514890	2.82	1	11405	5460929
SRS514891	1.69	1	9223	3633683
SRS559023	209.76	4	1714374	329548979
SRS563175	169.38	2	789405	273242265

SRS569198	521.92	1	498945	236436763
SRS579457	11.73	1	10432	5170818
SRS579488	10.13	1	8796	4472640
SRS579489	10.83	1	9743	4774971
SRS579508	10.88	1	9487	4807091
SRS579509	10.08	1	8872	4460573
SRS579510	8.73	1	7592	3840296
SRS579511	11.39	1	10188	5037956
SRS579512	8.88	1	7740	3918258
SRS579513	11.34	1	9971	5060281
SRS579514	9.92	1	8615	4382786
SRS579515	12.26	1	10827	5479712
SRS579516	10.81	1	9410	4779994
SRS579517	11.2	1	9851	4988947
SRS579518	10.54	1	9167	4636301
SRS579519	10.48	1	9209	4650741
SRS579520	10.89	1	9398	4783119
SRS579521	11.97	1	10539	5349735
SRS579522	11.62	1	10111	5108976
SRS579523	10.54	1	9432	4725730
SRS579524	9.49	1	8300	4179958
SRS579525	11.33	1	10010	5047486
SRS579526	11.09	1	9847	4830421
SRS579527	10.63	1	9333	4732068
SRS579528	8.71	1	7578	3833004
SRS584239	9.26	1	9027	4434127
SRS584240	8.98	1	8782	4296411
SRS584241	12.45	1	12226	5973192
SRS584242	12.22	1	12079	5870832
SRS584243	9.91	1	9660	4741315
SRS584244	11.71	1	11525	5643505
SRS584245	12.91	1	12567	6203763
SRS584246	12.43	1	12097	5938216
SRS584248	18.89	1	18592	9110667
SRS584249	13.26	1	13090	6382758
SRS584251	12.93	1	12647	6195428
SRS584252	12.38	1	12162	5972069
SRS584257	10.22	1	9454	4727038
SRS584258	9.5	1	8796	4397118
SRS584324	11.74	1	10844	5394881
SRS584326	11.33	1	10463	5210335
SRS584327	11.8	1	10936	5474639
SRS584345	13.6	1	12616	6222179
SRS584346	12.56	1	11734	5854858
SRS584357	11.93	1	11028	5503305
SRS584358	13.44	1	12395	6210778

SRS584359	14.03	1	12942	6456278
SRS584360	8.6	1	7907	3955921
SRS584361	14.47	1	13365	6677072
SRS584362	12.43	1	11770	5895814
SRS584363	12.81	1	12106	6060868
SRS584364	13.81	1	13145	6534390
SRS584365	13.88	1	13345	6585414
SRS584366	7.25	1	6960	3450835
SRS584367	15.2	1	14340	7186457
SRS584368	15.66	1	14810	7397424
SRS584369	14.13	1	13423	6633286
SRS584370	14.5	1	13560	6756945
SRS584372	13.97	1	13192	6577063
SRS584373	14.7	1	13435	6832284
SRS584374	13.14	1	12472	6190537
SRS569198	2726.45	1	1135587	1033738707
SRS629197	12.05	1	10283	5062010
SRS629198	12.16	1	10368	5109882
SRS629199	8.25	1	6992	3454326
SRS629200	13.76	1	11779	5796806
SRS629201	12.28	1	10494	5171193
SRS629202	12.39	1	10538	5211005
SRS629203	13.89	1	11819	5847093
SRS629204	13.02	1	11077	5470294
SRS629205	15.87	1	13484	6676694
SRS629206	11.71	1	9963	4932541
SRS677471	193.28	1	155510	90495203
SRS715739	0.72	4	34093	1251455
SRS722944	270.9	1	229068	122310596
SRS752744	1809.99	1	1566895	865799314

FTP Path to Experiment
ftp://ftp-trace.ncbi.nlm.nih.gov/sra/sra-instant/reads/ByExp/sra/ERX/ERX145/ERX145205
ftp://ftp-trace.ncbi.nlm.nih.gov/sra/sra-instant/reads/ByExp/sra/ERX/ERX145/ERX145206
ftp://ftp-trace.ncbi.nlm.nih.gov/sra/sra-instant/reads/ByExp/sra/ERX/ERX145/ERX145207
ftp://ftp-trace.ncbi.nlm.nih.gov/sra/sra-instant/reads/ByExp/sra/ERX/ERX145/ERX145208
ftp://ftp-trace.ncbi.nlm.nih.gov/sra/sra-instant/reads/ByExp/sra/ERX/ERX250/ERX250340
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Library Name	Library Strategy	Library Source	Library Selection
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Tintinnid_ITS_lib	AMPLICON	GENOMIC	PCR
Tintinnid_SSU_lib	AMPLICON	GENOMIC	PCR
Tintinnid_ITS_lib	AMPLICON	GENOMIC	PCR
LOHAFEX library of sample day_-1	AMPLICON	METAGENOMIC	PCR
LOHAFEX library of sample day_9	AMPLICON	METAGENOMIC	PCR
LOHAFEX library of sample day_18	AMPLICON	METAGENOMIC	PCR
LOHAFEX library of sample day_36	AMPLICON	METAGENOMIC	PCR
SUBINI	EST	TRANSCRIPTOMIC	RANDOM
MB	AMPLICON	GENOMIC	PCR
TH	AMPLICON	GENOMIC	PCR
AMCEpooledBACT	AMPLICON	OTHER	PCR
AMCEpooledARCH	AMPLICON	OTHER	PCR
AMCEpooledEUK	AMPLICON	OTHER	PCR
Ciliate-specific	AMPLICON	METAGENOMIC	PCR
Eukaryote-universal	AMPLICON	METAGENOMIC	PCR
GS_FLX	AMPLICON	METAGENOMIC	PCR
GS_FLX_Titanium	AMPLICON	METAGENOMIC	PCR
Lib_RepliGRN	WGS	GENOMIC	unspecified
ASID	AMPLICON	METAGENOMIC	PCR
VS-454-MBL:assay:D1.3_Bacteria	AMPLICON	METAGENOMIC	PCR
VS-454-MBL:assay:E1.5_Bacteria	AMPLICON	METAGENOMIC	PCR
VS-454-MBL:assay:D2.4_Bacteria	AMPLICON	METAGENOMIC	PCR
VS-454-MBL:assay:A1.1_Bacteria	AMPLICON	METAGENOMIC	PCR
VS-454-MBL:assay:A2.2_Bacteria	AMPLICON	METAGENOMIC	PCR
VS-454-MBL:assay:E2.6_Bacteria	AMPLICON	METAGENOMIC	PCR
VS-454-MBL:assay:E1.V4.11_Bacteria	AMPLICON	METAGENOMIC	PCR
VS-454-MBL:assay:D1.V4.9_Bacteria	AMPLICON	METAGENOMIC	PCR
VS-454-MBL:assay:A1.V4.7_Bacteria	AMPLICON	METAGENOMIC	PCR
VS-454-MBL:assay:A2.V4.8_Bacteria	AMPLICON	METAGENOMIC	PCR
VS-454-MBL:assay:D2.V4.10_Bacteria	AMPLICON	METAGENOMIC	PCR
VS-454-MBL:assay:E2.V4.12_Bacteria	AMPLICON	METAGENOMIC	PCR
VS-454-MBL:assay:B2.V4.13_Bacteria	AMPLICON	METAGENOMIC	PCR
	AMPLICON	METAGENOMIC	PCR
	AMPLICON	METAGENOMIC	PCR
	AMPLICON	METAGENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	RNA-Seq	GENOMIC	PCR
	AMPLICON	METATRANSCRIPTOMIC	RANDOM
	AMPLICON	TRANSCRIPTOMIC	RANDOM
	AMPLICON	GENOMIC	PCR
	AMPLICON	METAGENOMIC	PCR
PRJNA193567	AMPLICON	METAGENOMIC	PCR
	AMPLICON	GENOMIC	PCR
JS_NGS176-2_short	AMPLICON	METAGENOMIC	PCR

JS_NGS60a_short	AMPLICON	METAGENOMIC	PCR
JS_NGS66-2_short	AMPLICON	METAGENOMIC	PCR
JS_NGS42a_EUK1	AMPLICON	METAGENOMIC	PCR
JS_NGS42a-EUK-A7	AMPLICON	METAGENOMIC	PCR
JS_NGS42a_bact	AMPLICON	METAGENOMIC	PCR
JS_NGS60a_EUK1	AMPLICON	METAGENOMIC	PCR
JS_NGS60a-EUKA7	AMPLICON	METAGENOMIC	PCR
JS_NGS60a_bact	AMPLICON	METAGENOMIC	PCR
JS_NGS176-2_bact	AMPLICON	METAGENOMIC	PCR
JS_NGS176-2_EUK1	AMPLICON	METAGENOMIC	PCR
JS_NGS176-2-EUK-A7	AMPLICON	METAGENOMIC	PCR
JS_NGS66-2-EUK-A7	AMPLICON	METAGENOMIC	PCR
JS_NGS66-2_EUK1	AMPLICON	METAGENOMIC	PCR
JS_NGS66-2_bact	AMPLICON	METAGENOMIC	PCR
WHL_DilEXEuk	AMPLICON	METAGENOMIC	PCR
	AMPLICON	METAGENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
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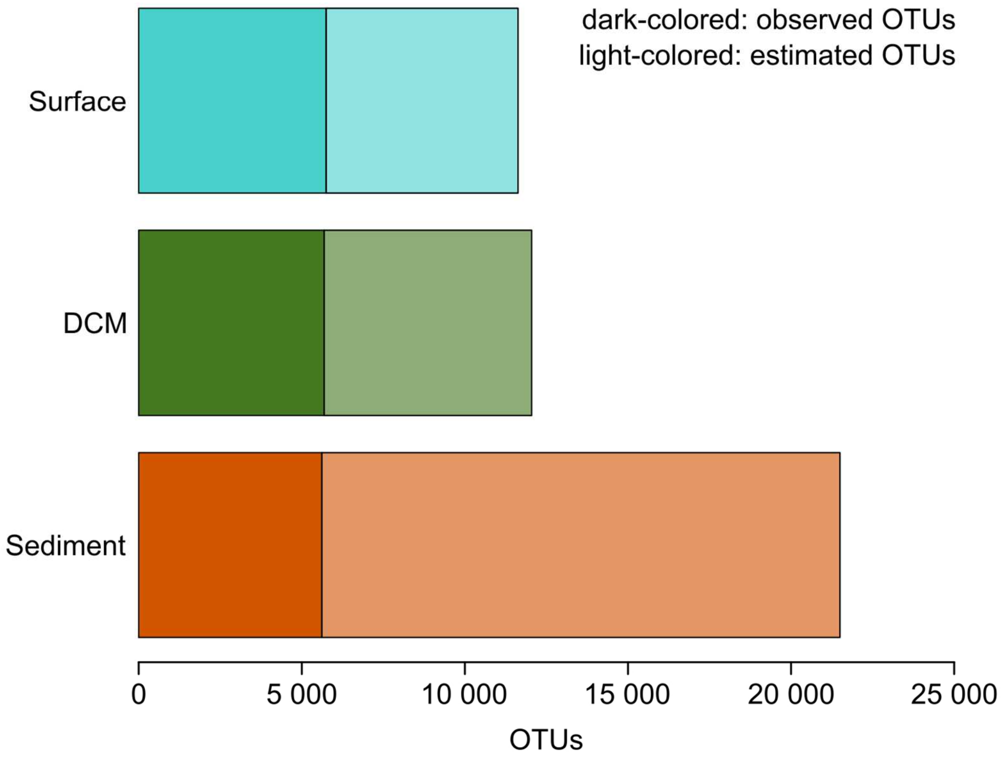
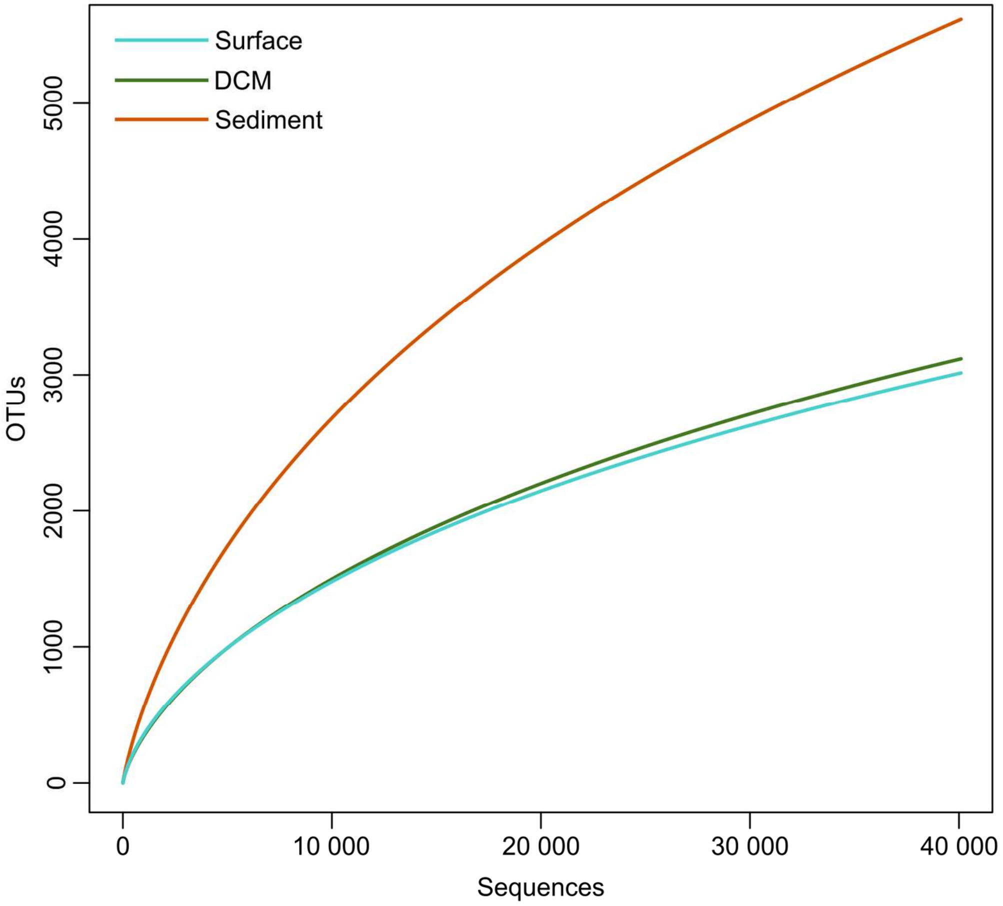
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
ThreeSeds	AMPLICON	METAGENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
Hamilton-18S_Replicate	AMPLICON	METAGENOMIC	PCR
Nanaimo plankton	AMPLICON	GENOMIC	PCR

EEC_2013	AMPLICON	GENOMIC	PCR
	AMPLICON	METAGENOMIC	PCR
JB121SF_RNA	AMPLICON	METAGENOMIC	cDNA
JB121SCM_DNA	AMPLICON	METAGENOMIC	PCR
JB121SCM_RNA	AMPLICON	METAGENOMIC	cDNA
JB700SF_DNA	AMPLICON	METAGENOMIC	PCR
JB700SF_RNA	AMPLICON	METAGENOMIC	cDNA
JB700SCM_DNA	AMPLICON	METAGENOMIC	PCR
JB700SCM_RNA	AMPLICON	METAGENOMIC	cDNA
JB601SF_DNA	AMPLICON	METAGENOMIC	PCR
JB601SF_RNA	AMPLICON	METAGENOMIC	cDNA
JB601SCM_DNA	AMPLICON	METAGENOMIC	PCR
JB601SCM_RNA	AMPLICON	METAGENOMIC	cDNA
NEC211SF_DNA	AMPLICON	METAGENOMIC	PCR
NEC211SF_RNA	AMPLICON	METAGENOMIC	cDNA
NEC211SCM_DNA	AMPLICON	METAGENOMIC	PCR
NEC211SCM_RNA	AMPLICON	METAGENOMIC	cDNA
NEF43SF_DNA	AMPLICON	METAGENOMIC	PCR
NEF43SF_RNA	AMPLICON	METAGENOMIC	cDNA
NEF43SCM_DNA	AMPLICON	METAGENOMIC	PCR
NEF43SCM_RNA	AMPLICON	METAGENOMIC	cDNA
NEF512SF_DNA	AMPLICON	METAGENOMIC	PCR
NEF512SF_RNA	AMPLICON	METAGENOMIC	cDNA
NEF512SCM_DNA	AMPLICON	METAGENOMIC	PCR
NEF512SCM_RNA	AMPLICON	METAGENOMIC	cDNA
HB_2010_710_10m_euk	AMPLICON	GENOMIC	PCR
HB_2010_710_34m_euk	AMPLICON	GENOMIC	PCR
HB_2010_699_6m_euk	AMPLICON	GENOMIC	PCR
HB_2010_699_15m_euk	AMPLICON	GENOMIC	PCR
HB_2010_709_9m_euk	AMPLICON	GENOMIC	PCR
HB_2010_709_30m_euk	AMPLICON	GENOMIC	PCR
HB_2010_745_10m_euk	AMPLICON	GENOMIC	PCR
HB_2010_745_47m_euk	AMPLICON	GENOMIC	PCR
HB_2010_706_10m_euk	AMPLICON	GENOMIC	PCR
HB_2010_706_30m_euk	AMPLICON	GENOMIC	PCR
HB_2010_706_40m_euk	AMPLICON	GENOMIC	PCR
LS_2006_301_25m_euk	AMPLICON	GENOMIC	PCR
LS_2008_303_16m_euk	AMPLICON	GENOMIC	PCR
LS_2008_303_2m_euk	AMPLICON	GENOMIC	PCR
CB_2011_314_18m_euk	AMPLICON	GENOMIC	PCR
CB_2011_314_2m_euk	AMPLICON	GENOMIC	PCR
BB_2005_131_40m_euk	AMPLICON	GENOMIC	PCR
BB_2005_131_5m_euk	AMPLICON	GENOMIC	PCR
BB_2005_100_22m_euk	AMPLICON	GENOMIC	PCR
BB_2005_100_5m_euk	AMPLICON	GENOMIC	PCR
BB_2008_108_20m_euk	AMPLICON	GENOMIC	PCR

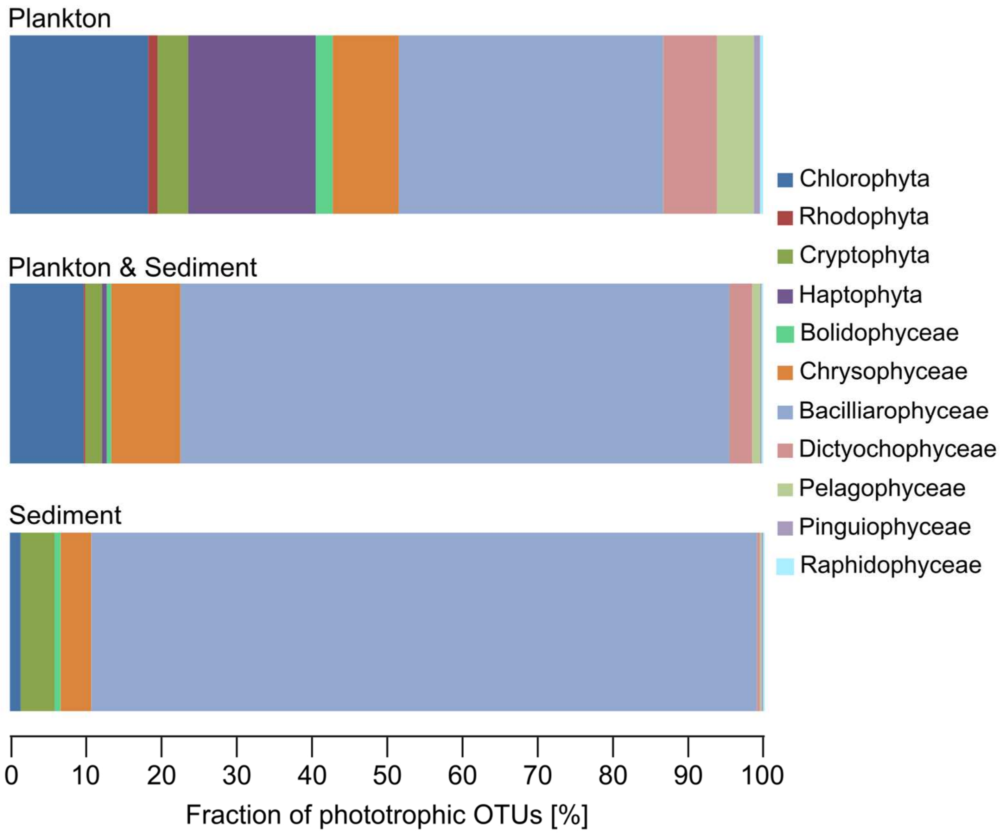
BB_2008_108_5m_euk	AMPLICON	GENOMIC	PCR
BB_2008_101_33m_euk	AMPLICON	GENOMIC	PCR
BB_2008_101_3m_euk	AMPLICON	GENOMIC	PCR
BB_2006_BA0405_40m_euk	AMPLICON	GENOMIC	PCR
BB_2006_BA0405_28m_euk	AMPLICON	GENOMIC	PCR
BB_2006_BA0405_10m_euk	AMPLICON	GENOMIC	PCR
BB_2006_123_45m_euk	AMPLICON	GENOMIC	PCR
BB_2006_123_10m_euk	AMPLICON	GENOMIC	PCR
Lv_2007_VB0603_5m_euk	AMPLICON	GENOMIC	PCR
Lv_2007_VB1007_7m_euk	AMPLICON	GENOMIC	PCR
Lv_2007_VB1607_8m_euk	AMPLICON	GENOMIC	PCR
Lv_2007_VB2107_7m_euk	AMPLICON	GENOMIC	PCR
Lv_2007_VB3807_6m_euk	AMPLICON	GENOMIC	PCR
Lv_2007_VB3807_100m_euk	AMPLICON	GENOMIC	PCR
Lv_2007_VB7207_5m_euk	AMPLICON	GENOMIC	PCR
EEC_2013_De novo	WGS	METAGENOMIC	RANDOM
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	AMPLICON	GENOMIC	PCR
	CLONE	GENOMIC	unspecified
	AMPLICON	GENOMIC	PCR
031814MPtarEuk	AMPLICON	METATRANSCRIPTOMIC	RT-PCR
	AMPLICON	METAGENOMIC	PCR



136x102mm (300 x 300 DPI)



152x138mm (300 x 300 DPI)



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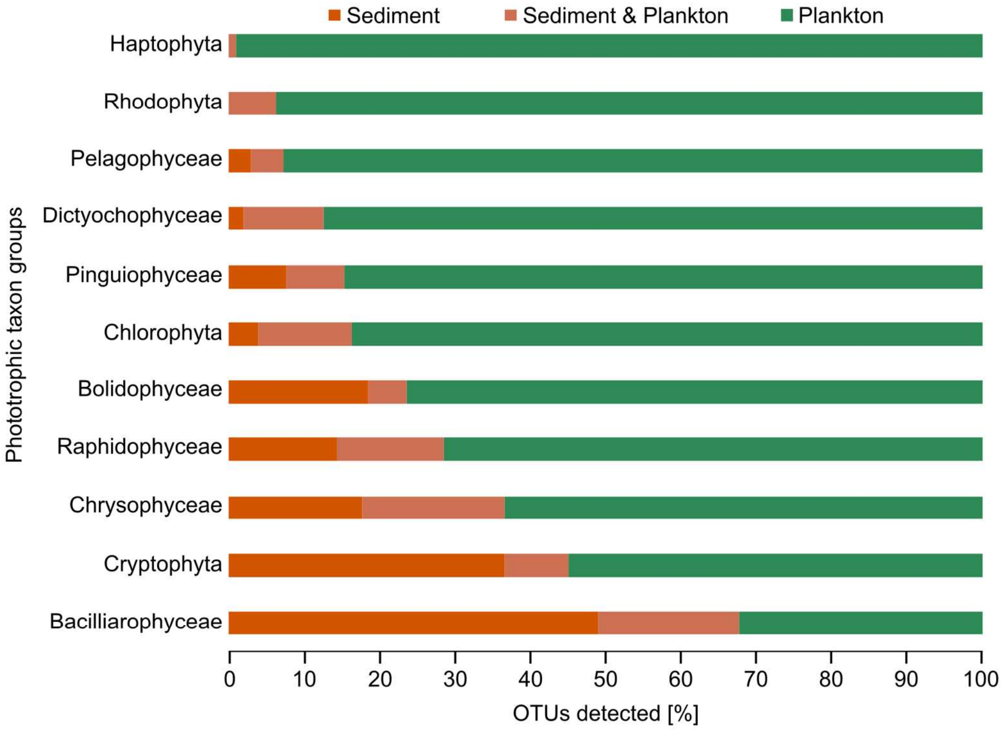
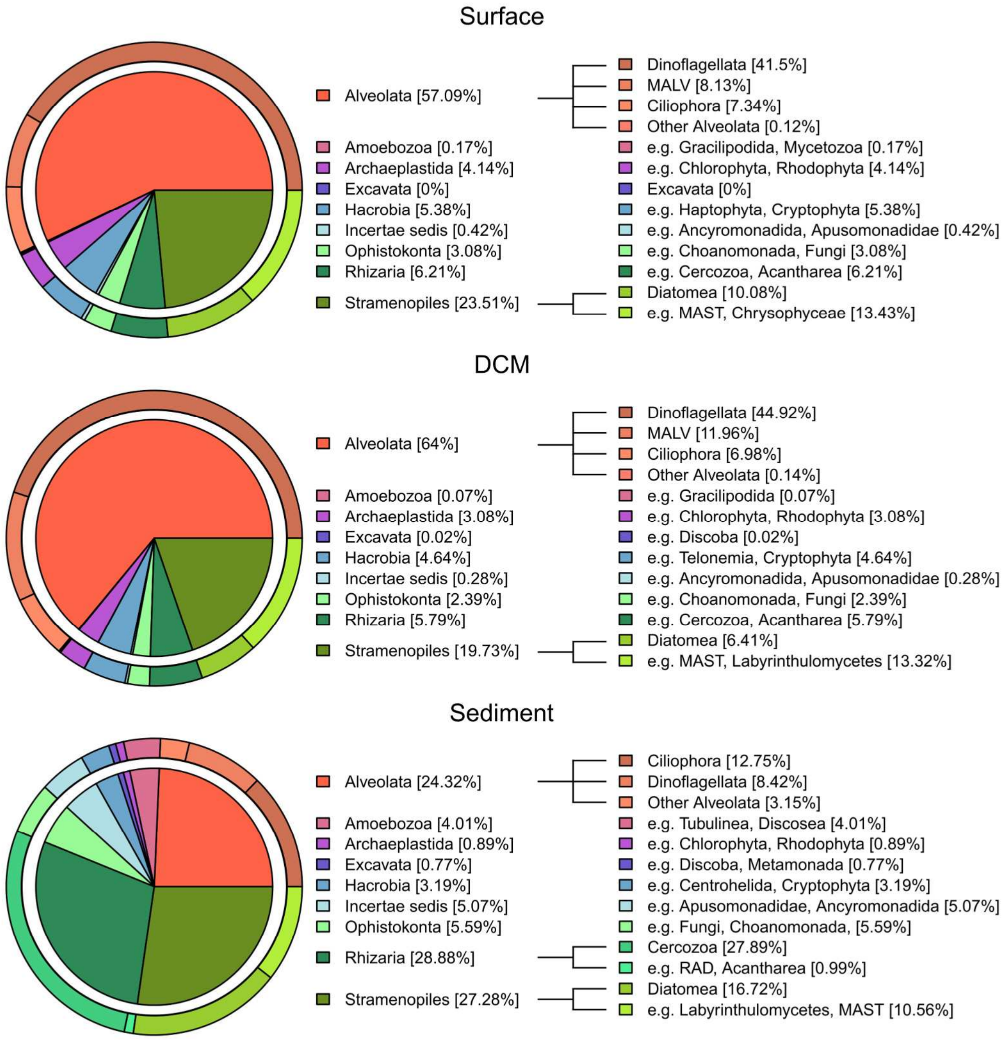


160x116mm (300 x 300 DPI)



171x178mm (300 x 300 DPI)