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Protist diversity and function in the dark ocean - challenging the paradigms of deep-sea ecology with special emphasis on foraminiferans and naked protists

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Abstract

The dark ocean and the underlying deep seafloor together represent the largest environment on this planet, comprising about 80% of the oceanic volume and covering more than two-thirds of the Earth's surface, as well as hosting a major part of the total biosphere. Emerging evidence suggests that these vast pelagic and benthic habitats play a major role in ocean biogeochemistry and represent an "untapped reservoir" of high genetic and metabolic microbial diversity. Due to its huge volume, the water column of the dark ocean is the largest reservoir of organic carbon in the biosphere and likely plays a major role in the global carbon budget. The dark ocean and the seafloor beneath it are also home to a largely enigmatic food web comprising little-known and sometimes spectacular organisms, mainly prokaryotes and protists. This review considers the globally important role of pelagic and benthic protists across all protistan size classes in the deep-sea realm, with a focus on their taxonomy, diversity, and physiological properties, including their role in deep microbial food webs. We argue that, given the important contribution that protists must make to deep-sea biodiversity and ecosystem processes, they should not be overlooked in biological studies of the deep ocean.

***Keywords**:* Benthos; Ciliates; Deep-sea ecology; Flagellates; Foraminifera; History

1. Early history of deep-sea protistology

Until relatively recently, protists, and particularly the small naked taxa, were mentioned only in passing in major accounts of deep-sea biology (e.g. Menzies et al. 1973). The starting point for deep-sea studies is often given as 1873, the year the *Challenger* sailed (e.g. Wüst 1964). However, protistologists were at work on deep-sea samples long before then. Below we briefly review some of the early studies of both pelagic and benthic forms, leading up to and including the Challenger Expedition. The goal is to underline the fact that there is a long history of deep-sea protistology, perhaps forgotten in our present 'omics' era. These classical morphological approaches remain important and should be combined with those of modern molecular methods in protozoological research.

Early studies of deep-sea benthic Foraminifera

The Foraminifera d'Orbigny, 1826 were the first deep-sea protists to be discovered. The earliest record of a benthic foraminiferan from the deep sea (>300 m depth) is probably that of the renowned German microscopist Christian Gottfried Ehrenberg, who found *Grammostomum divergens* Ehrenberg, 1844 (the genus *Grammostomum* Ehrenberg, 1839 is a junior synonym of *Bolivina* D'Orbigny, 1839; see Loeblich and Tappan 1964) in a small volume of sediment collected with a sounding device at 494 m during James Ross' Antarctic expedition of 1841-1843 (Ehrenberg 1844). Subsequent papers by Ehrenberg (1854, 1858, 1861) included benthic foraminiferal species from deep Mediterranean, Atlantic and Pacific sites. Pourtales (1850) listed *Rotalina baileyi* Pourtales, 1850 (originally spelt incorrectly as *Rotulina baileyi*) in a sounding sample from 200 fathoms (366 m) depth off the east coast of North America (note that *Rotalina* d'Orbigny, 1839 is a junior synonym of *Cancris* de Montfort, 1808; see Loeblich and Tappan 1987). Later Pourtales (1853) recorded this and two other species that he assigned to *Rotalina* in soundings from 823-1920 m depth off the Atlantic coast of Florida, with *Texularia turbo* Pourtales, 1850 and *Marginulina bacheii* Bailey, 1851 (originally spelt incorrectly as *Marginulina bachei*) also occurring at 914 m and 1097 m, respectively. However, these samples were dominated by what are now known to be planktonic Foraminifera. The American microscopist Jacob Bailey (1855) analysed even deeper soundings (1975-3658 m) in the North Atlantic, but only mentioned planktonic species (Fig. 1). Another early record is that of George Wallich. He discovered two shells of '*Truncatulina lobata'* [probably *Serpula lobata* de Montfort, 1808, a synonym of *Cibicidoides lobatulus* (Walker and Jacob, 1798)] attached to small stones and 'apparently alive', in a sounding obtained during the 1860 HMS *Bulldog* cruise from 1247 m between Iceland and the Faroe Islands (p. 4 in Wallich 1862; Rice et al. 1976). *Bulldog* soundings taken off the southern tip of Greenland (198-2286 m) yielded another sessile species, later described by Wallich (1877) as *Rupertia stabilis* Wallich, 1877 [now *Rupertina stabilis* (Wallich 1877)].

Parker and Jones (1865) made the first major contribution to our knowledge of deep-sea benthic Foraminifera, based on samples (mainly soundings) from depths down to 574 m in the Arctic and, most importantly, from 42 soundings taken between 79 and 4298 m in the North Atlantic. These samples yielded 46 benthic species from depths below 300 m; 34 >1000 m, 31 >2000 m, 29 >3000 m and 18 >4000 m (Parker and Jones 1865, Table V). Soundings taken in the Mediterranean Sea (585 m), Red Sea (680-1240 m), tropical Atlantic (1975 m), South Atlantic (475-4938 m) and Indian (1646-4023 m) Oceans provided additional records (Table VII in Parker and Jones 1865).

Samples collected with dredges contributed much to our knowledge of European benthic faunas during Victorian times. In particular, members of the British Association Dredging Committee were active in sampling the seafloor around the British Isles to depths down to 100 fathoms (183 m) for several decades, starting in 1839 (e.g., Rice and Wilson 1980). Further afield, dredges were used to collect animals from as deep as 732 m during the above-mentioned James Ross expedition (Hooker 1845; Anderson and Rice 2006). However, the 1860s saw the first serious efforts to study deep-sea benthic life using dredges, which catch far more benthic organisms than small sounding samples, as well as larger species. For some years, Michael Sars and his son George Ossian had been dredging off the Norwegian coast near the Lofoten Islands, and by 1868 the elder Sars was able to list 68 species of Foraminifera from depths between 589 m and 823 m, including two that he named (but did not describe) as *Rhabdammina abyssorum* Sars, 1869 and *Saccammina sphaerica* Brady, 1871 (Sars 1868). During 1869, this work was extended to even greater depths in the Hardanger Fjord (Sars 1872), where large numbers of the same two species, and a tubular species that M. Sars called *Bathysiphon filiformis* G.O.and M. Sars in G.O. Sars, 1872 (Gooday 1988b), were recovered from 914 m. G.O. Sars (1872) lists a further 13 agglutinated and calcareous species from this site.

These Norwegian studies provided a stimulus for the British Lightening expedition of 1868, led by W.B. Carpenter and C. Wyville Thomson, to the north and west of Scotland (Mills 1983). The campaign benefited considerably from experience gained earlier by the British Association Dredging Committee. Despite often terrible weather, large numbers of ‘gigantic rhizopods’, including *R. abyssorum* and *Astrorhiza* (= *A. arenaria* Carpenter in Norman, 1877), were dredged at 968 m, and some large biloculine miliolids at the deepest station (1189 m) (Carpenter 1876; Carpenter and Thomson 1868). The abundance of life at these bathyal depths encouraged Carpenter and his colleagues to organise the ‘first great oceanographic expedition’ (p. 15 in Mills 1983), a series of three cruises during 1869 aboard HMS Porcupine (Carpenter et al. 1869). Dredge samples were obtained to the west and SW of Ireland (cruises 1 and 2) and in the Faroe-Shetland area to the north of Scotland, revisiting areas sampled by the Lightning expedition (cruise 3; Rice 1986). A particular highlight was the recovery during the second cruise of samples from 4453 m and 3822 m. These proved the existence of life at abyssal depths and finally laid to rest the curiously persistent ‘azoic theory’, proposed by Edward Forbes in the 1840s (Forbes 1844), which, despite subsequent evidence to the contrary, maintained that the deep sea was devoid of life at depths below about 550 m (Anderson and Rice, 2006). Large agglutinated foraminiferans, as well as calcareous miliolids and lageniids, were abundant in some samples and feature prominently in the expedition report (Carpenter et al. 1869). The deepest haul yielded a ‘branching flexible rhizopod’ (later described as *Rhizammina* Brady, 1879), while bathyal samples obtained on the third cruise contained immense numbers of agglutinated tubes of *Botellina* Carpenter, Jeffreys & Thompson, 1870, together with *Astrorhiza* Sandahl, 1858 and *Rhabdammina.* Carpenter (1869) gave an overview of the foraminiferans recovered during the Lightning and Porcupine cruises, and illustrated many of the species for the first time in his book ‘The Microscope and its Revelations’ (5th edition; Carpenter 1875).

The pioneering Lightning and Porcupine campaigns of 1868 and 1869 led directly to the Challenger Expedition (1872-1876) and the monumental monograph of H.B. Brady (1884), the importance of which for our knowledge of deep-sea Foraminifera cannot be over-estimated. However, other less famous cruises resulted in the discovery of species representing two very important but neglected deep-sea groups, the Komokiacea and the Xenophyophorea. *Haliphysema conferta* Norman, 1878 (now *Normanina conferta),* the first described komokiacean, was collected in the Davis Strait during the 1875 Valorous Expedition (Norman 1878). *Syringammina fragilissima* Brady, 1883*,* the first described xenophyophore, was collected in the Faroe Channel during the 1872 Triton Expedition (Brady 1883).

Early studies of planktonic deep-sea protists

In 1839 James Clark Ross set out to explore the waters of Antarctica. His ship's assistant surgeon, the later to be famous Joseph Dalton Hooker, sent samples taken from, at that time, the greatest depths sounded, to Christian Gottfried Ehrenberg. His examination of material from depths of 350–500 m revealed, in addition to the foraminiferans mentioned above, diatoms, both benthic and planktonic forms, as well as nassularian radiolarians, apparently alive at the time of sampling. He described diatoms complete with 'green ovaries', his interpretation of chloroplasts. Ehrenberg (1844) concluded, "The supposition, that in great depths, below 100 fathoms (182 m) there is no fresh nutriment for organized beings of any kind, has become untenable.", a conclusion supported by much later studies, such as those of Billett et al. (1983), Thiel et al. (1990) and Agusti et al. (2015). It also bears mentioning that in this rarely cited work, Ehrenberg listed the “protists” he found in a sample of 'atmospheric dust' deposited on the deck of the Beagle when near Cape Verde Islands off Africa, sent to him by Charles Darwin. Ehrenberg concluded that the dust was not of volcanic or meteor origin, as thought by Darwin, but most likely from a marshland in the Americas based on finding diatoms such as a *Surirella* and *Eunotia* spp. This is very likely the first evidence of long-distance atmospheric transport of terrestrial matter and protists.

A few years later, Jacob Bailey (1851) reported a rich assemblage of benthic and planktonic foraminiferans, diatoms, and silicoflagellates ("...a truly wonderful development of minute organic forms") from sounding material taken at depths down to 165 m off the New York and New Jersey (USA) coasts. Subsequently, Ehrenberg (1854) described many new species of tintinnid ciliates, radiolarians and diatoms in an article entitled "Charakteristik der neuen mikroskopischen Organismen des tiefen atlantischen Oceans" ("The systematic characteristics of new microscopic organisms of the deep Atlantic Ocean"). Unfortunately, no details were provided about the habitats sampled. For example, *Coscinodiscus profundus* is said to be "from the depths of the Atlantic Ocean 12000 feet" (3600 m) and *Cornutella profonda* was noted only as "12000 feet". As mentioned above, Bailey (1855) reported on the organisms, primarily planktonic Foraminifera, found in deep soundings (1975–3668 m) in the North East Atlantic, and gives what appears to be the first description of 'foraminiferal ooze'. His succinct report begins: "1. None of these soundings contain a particle of gravel, sand, or other recognizable unorganized mineral matter. 2. They all agree in being almost entirely made up of the calcareous shells of minute, or microscopic Foraminiferae *(Polythalamia,* Ehr.*),* among which the species of *Globigerina* greatly predominate in all the specimens, while *Orbulina universa*, D'Orb., is in immense numbers in some of the soundings, and particularly abundant in that from 1800 fathoms. 3. They all contain a few specimens of non-parasitic or pelagic Diatoms, among which *Coscinodiscus lineatus, C. excentricus,* and *C.*

radiatus of Ehrenberg, are much the most abundant." The following year, Bailey (1856) provided the first description of protists from deep-sea soundings in the North Pacific (Fig. 1), and subsequently from the subarctic Atlantic (Bailey 1857). Ehrenberg (1858) compared deep-sea forms from Eastern Mediterranean soundings to those from the North Atlantic (Ehrenberg 1854), noting that the former contained fewer foraminiferal species, but far more radiolarian species, than the latter. Later, Ehrenberg (1861) described protists in six samples from the Central Pacific at depths ranging from 3500 to 4700 m and found that the deepest samples yielded the largest number of species (Ehrenberg 1861). In 1863, the Dutch microscopist Pieter Harting considerably extended the depth limit in a long report dealing primarily with radiolarians and foraminiferans found in material taken at depths from about 1000 to 7300 m depth in the South Pacific between Australia and Malaysia (Harting 1863).

These early protistan studies, ranging geographically from Antarctica to the South Pacific to the subarctic Atlantic and the Mediterranean Sea, have been largely eclipsed by data gathered during the Challenger Expedition. This provided material for the monumental monograph of Haeckel (1887) on the planktonic Radiolaria, as well as that of Brady (1884) on Foraminifera, mentioned above. These two protist monographs are still used as standard references. However, we hope in this short summary of early works to have shown that protistologists were examining material from the deep sea long before the Challenger Expedition.

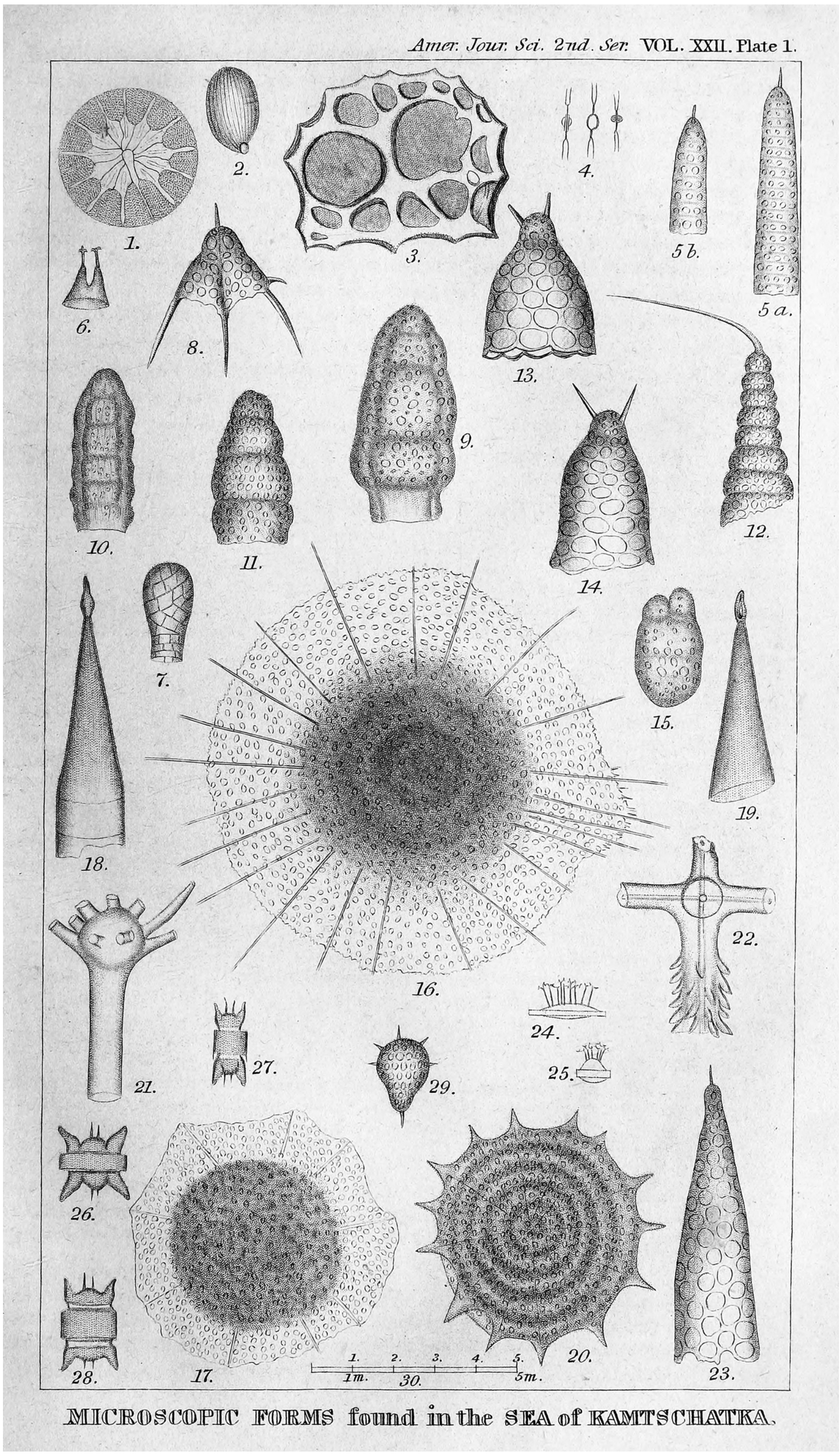

Fig. 1. Plate from Bailey (1856) illustrating 'new species' found in deep soundings from the North Pacific. 1: ***Asteromphalus brookei***, 2: *Cadium marinum*, 3: ***Ceratospyris borealis***, 4: *Chaetoceras furcillatum* (***Chaetoceros furcillatus***), 5: *Cornutella annulata*, 6: *Dicladia mitra* (***Chaetoceros mitra***), 7: *Difflugia marina*, 8: *Dictyophimus gracilipes*, 9: *Eucyrtidium aquilonaris*, 10: *Eucrytidium hyperboreum*, 11: *Eucrytidium tumidulum*, 12: *Eucrytidium cuspidatum*, 13,14: *Halicalyptra cornuta*, 15: *Lithobotrys inflatum*, 16,17: *Perichlamidium venustum*, 18,19: *Rhizosolenia hebetata*, 20: *Stylodictya stellata*, 21: *Spongolithus clavata*, 22: *Spongolithus orthogona*. Bold indicates species currently recognized as valid.

Early studies on deep-sea benthic heterotrophic flagellates and ciliates

Until the end of the last century, there were only a few morphology-based studies of deep-sea, non-testate protists. The relatively large shells of foraminiferans make it easier to investigate their diversity in comparison to other protists (e.g. ciliates, flagellates, naked rhizopods), which are small, naked, and often lack distinctive taxonomic characteristics. While being raised through the water column, these naked protists are exposed to changing environmental conditions including rising temperature and decreasing pressure, which may significantly affect their morphology and survival, making their study a challenging task.

While bacteria had been recorded in deep sea sediments as early as the 1880's (Alder and Dücker 2018; Certes 1884), the discovery of substantial densities of naked heterotrophic flagellates started only in the 1960s. Although some authors failed to find any flagellates in sediment samples from the deep-sea floor (e.g. Lighthart 1969), others reported large numbers of protists, particularly heterotrophic flagellates but also amoebae and testate forms (e.g., Alongi 1987, 1991; Burnett 1977, 1979, 1981; Snider et al. 1984; Thiel 1983), with densities as much as 10^5 cells/cm³ (Bak and Nieuwland 1997; Danovaro et al. 1998). The cultivation of samples from the deep-sea floor and marine-snow habitats in the pelagial revealed that several species of heterotrophic flagellates (at least cysts) can occur even in very deep parts of the ocean (Atkins et al. 1998, 2000; Hausmann et al. 2006; Patterson et al. 1993). In recent decades, it has become clear that a proportion of the production of organic matter in the surface waters can reach the deep seafloor at depths below 1000 m in the form of 'phytodetritus' and 'marine snow' (e.g. Alldredge and Silver 1988; Beaulieu 2002; Billett et al. 1983; Gooday 2002; Thiel et al. 1989; Turley et al. 1995), as well as other rapidly sinking particles such as *Sargassum*, faecal pellets and carcasses (e.g. Baker et al. 2018; Rowe and Staresinik 1979). Caron et al. (1982) discovered that this rapid delivery of fixed carbon from the surface waters to the deep sea via sinking particles provides a link between surface and deep-sea protist communities (Arndt et al. 2003; Patterson et al. 1993). However, whether protists from euphotic surface waters can grow under deep-sea conditions was unknown. Turley et al. (1988) were the first to report a barophilic (better growth at high pressure) bodonid flagellate in sediment contact water from 4500 m depth in the NE Atlantic, indicating an adaptation to deep-sea conditions (450 atm; 2°C). At the same site, populations of this flagellate developed only under pressure in phytodetrital aggregates collected from the sediment surface (Lochte and Turley 1988). In pressure experiments on particulate material collected at 50 m depth, also in the NE Atlantic, another flagellate (*Neobodo curvifilus* Larsen & Patterson, 1990) was shown to have a wide barotolerance with reproduction being recorded at pressures up to 300 atm, while a *Cercomonas*-like species only grew at pressures of 300 atm and above (Turley and Carstens 1991). Furthermore, Atkins et al. (1998) observed that deep-sea isolates of *Caecitellus parvulus* (Griessmann, 1913) Patterson et al., 1993 and *Rhynchomonas nasuta* (Stokes, 1888) Klebs, 1892 had a higher growth rate at higher pressures (up to 300 atm) than their shallow-water counterparts.

In more recent years, clone library and high-throughput-sequencing (HTS) studies have revealed an enormous genotypic diversity of deep-sea heterotrophic flagellates collected from the deep sea (e.g., Edgcomb et al. 2009; López-García et al. 2001; Pawlowski et al. 2011; Scheckenbach et al. 2010). Scheckenbach et al. (2005) isolated similar genotypes of heterotrophic flagellates originating from surface and deep-sea waters. However, for most genotypes it is not clear whether they originate from vital deep-sea populations or from cysts of organisms sedimented from surface waters and inactive in the deep sea. Understanding the functioning of deep-sea communities of naked protists requires a combination of ecological studies and molecular surveys. Experiments conducted to date on the pressure tolerance of different strains isolated from various marine habitats at different depths indicate that barophilic (e.g., Atkins et al. 1998; Morgan-Smith et al. 2013; Turley et al. 1988; Turley and Carstens 1991) as well as barotolerant protists may populate the deep sea (Živaljić et al. 2018, 2020a, b).

Studies conducted some 50 years ago revealed the presence of ciliates down to depths of almost 4000 m (Uhlig 1970, 1971, 1973). These included epizoic folliculinids (Uhlig 1973), subsequently also reported from hard substrates near hydrothermal vents and methane seeps (Pasulka et al. 2017; Small and Gross 1984; Van Dover et al. 1988). Cunningham and Ustach (1992) found that ciliates may outnumber foraminiferans in sediments from the Blake Outer Ridge (NW Atlantic). Abyssal ciliates belonging to the class Karyorelictea Corliss, 1974 and to the subclasses Suctoria Claparède and Lachmann, 1858 and Peritrichia Stein, 1859 have been found as epibionts on arthropods collected from the deep sea (Bartsch and Dovgal 2010; Sedlacek et al. 2013). Recently, comprehensive analyses of ciliate records from depths >1000 m using molecular techniques indicated the potential existence of a very large variety of ciliates (Schoenle et al. 2017). Nevertheless, data about ciliates living on the deep seafloor remain very scarce and mostly based on molecular studies. So far, only a few ciliates have been collected from the deep sea and cultivated successfully in laboratory conditions (Schoenle et al. 2017; Živaljić et al. 2020a, b).

Our knowledge of naked amoebae in the deep sea is even more fragmentary. Probably the first record is that of Davis et al. (1978), who found naked amoebae (*Acanthamoeba*-like) at a depth of 3090 m in the central North Atlantic. Another interesting finding was the description of a new genus of bacterivorous amoeboid protists, *Ministeria marisola* Patterson et al., 1993, from 1515 m depth, also in the North Atlantic (Patterson et al. 1993). As a sister group to choanoflagellates and metazoans, this filasterean genus occupies a key position in understanding metazoan evolution (e.g. Suga et al. 2013). Later, Moran et al. (2007) described a vannellid amoeba, *Platyamoeba oblongata* Moran et al., 2007, from a depth of 3800 m in the Ross Sea. In recent years several more species from different groups of lobose amoebae had been described from deep-sea habitats (Kudryavtsev and Pawlowski 2013; Kudryavtsev et al. 2018). Lobose amoebae have been quite frequently recorded from depths greater than 1000 m in the Meditrerranean (Arndt et al. 2003). Small naked amoebae were most probably overlooked in the past and should be considered as typical components of the pelagial and benthos of the deep sea.

2. The deep sea as a habitat for protists

The deep oceanic seafloor was long considered to be a relatively featureless habitat characterized by stable environmental conditions and low species diversity (e.g. Dayton and Hessler 1972). Nowadays, it is known that submarine canyons, deep trenches, mid-ocean ridges and fracture zones, together with smaller features such as seamounts, deep-water coral reefs, and pockmarks, form a highly complex environment at the landscape level (e.g., Devey et al. 2018; Ramirez-Llodra et al. 2010). Rather than being quiescent and depauperate, this vast and remote region is subject to episodic disturbances, including seasonally pulsed food inputs and periods of elevated current activity, and hosts highly diverse communities of benthic animals and protists (Gage 2003; Snelgrove and Smith 2002; Tyler 2003). In addition, dark inorganic carbon fixation (Herndl and Reinthaler 2013; Molari et al. 2013) and the episodic sedimentation of phytodetritus debris, including macroalgae, have changed our understanding of organic carbon available for deep-sea microbial communities (Baker et al. 2018; Boeuf et al. 2019; Duineveld et al. 2000; Lochte and Turley 1988).

The benthic deep-sea environment is divided into a number of distinctive ecological zones. The bathyal zone covers ~16% of the Earth’s surface and extends from 300 to 3500 m depth down the continental slope and rise (Watling et al. 2013) and also encompasses mid-ocean ridges (Priede et al. 2013). Abyssal plains, ranging from 3500 to 6500 m depth (Watling et al. 2013), form the largest habitat on Earth, occupying more than 50% of the submerged seafloor and characterized by temperatures of 4°C or less (Ramirez-Llodra et al.

2010). The abyss is subdivided into basins by bathyal features, such as mid-oceanic ridges (e.g. Watling et al. 2013), which may be interrupted by fracture zones that provide channels between basins. Beneath the abyss, between 6500 to almost 11000 m depth, lies the hadal zone covering only 0.24% of the Earth's surface and occupied mainly by oceanic trenches formed by the subduction of ocean crust. These are separated by abyssal areas often thousands of kilometers in extent and therefore often have island-like characteristics (Jamieson 2015; Watling et al. 2013). Large areas of the deep seafloor are covered by sediments of biological origin (Gage and Tyler 1991) with sedimentation rates depending on a number of factors, including the intensity and seasonality of biological processes, distance from sediment sources, water depth, etc. (Barron and Whitman 1981; Müller and Suess 1979; Szmytkiewicz and Zalewska 2014). For instance, under regions of high productivity, the calcareous and siliceous tests of planktonic protists, which are major deep-sea sediment components, form thicker sediment layers.

Deep-sea habitats are extremely heterogeneous at all spatial scales (Levin et al. 2001). Large-scale features, such as seamounts, submarine canyons, and cold-water coral reefs, can lead to increased productivity due to topographically modified currents and enhanced transportation of particles (Ramirez-Llodra et al. 2010). Small-scale features, such as patches of organic detritus and biogenic structures, are believed to play an important role in maintaining the high levels of species diversity that are characteristic of deep-sea sediment communities (Snelgrove and Smith 2002). Mesoscale features, including small abyssal hills and ridges, provide a source of heterogeneity that may increase regional diversity (Durden et al. 2018). Deep-sea communities are generally dependent on sinking detritus derived from surface water production (Gage 2003; Johnson et al. 2007) and are highly sensitive to variations in food supply (K.L. Smith et al. 2008). Only 1-5% of the surface primary production reaches the deep seafloor (Gooday and Turley 1990; Graf 1989) resulting in a strong food limitation shaping deep-sea communities, particularly those at abyssal depths (C.R. Smith et al. 2008).

The main exceptions to 'normal' deep-sea environments are chemosynthetic ecosystems, notably hydrothermal vents and cold seeps, where bacteria fueled by chemical energy sources act as primary producers (e.g. Orsi 2018) and form a rich food source for protists (Atkins et al. 1998, 2000; Edgcomb et al. 2002; Levin 2005). In addition, oxygen starved areas, Oxygen Minimum Zones (OMZs) (Bertagnolli and Stewart 2018; Levin 2003) and Deep Hypersaline Anoxic Basins (DHABs) can be hot spots of chemoautotrophic bacteria production (e.g. Bernhard et al. 2014; Kormas et al. 2015; Pachiadaki et al. 2014; Taylor et al. 2001), where bacteria, as well as some protists (Bernhard et al. 2012b; Koho and Piña-Ochoa 2012; Piña-Ochoa et al. 2010; Risgaard-Petersen et al. 2006), use other sources, e.g. nitrate, nitrite and sulphate, for oxidization. OMZs occur mainly along western boundaries of continents under upwelling areas. Here, deep nutrient-rich water is transported to the surface, fueling primary production and enhancing the flux of decomposing phytoplankton cells out of the photic zone, thereby increasing the demand for oxygen at depth. OMZs also occur in continental margin basins with restricted circulation due to bathymetry and stratification. The severely hypoxic Santa Barbara Basin off California, and the Cariaco Basin, a bathyal basin in the Caribbean Sea that resembles the Black Sea in being completely devoid of oxygen (i.e., anoxic) below about 250 m depth, have been important locations for intensive studies on protistan communities (e.g. Bernhard et al. 2000; Edgcomb et al. 2009, 2011). DHABs are formed on the seafloor where massive buried salt deposits, exposed to the seawater after tectonic activity, create dense anoxic brines, which are separated by a chemocline/pycnocline from the overlying oxygen-rich deep water. They have been reported from different parts of the world ocean, including the Eastern Mediterranean where there is evidence for abundant active protists within the chemocline (Bernhard et al. 2014). Protists are able to populate these various hypoxic and anoxic deep-sea habitats with the help of symbiosis with bacteria and/or the possession of hydrogenosome-like modified mitochondria. These include the euglenozoan *Calkinsia aureus* Lackey, 1960 in the Santa Barabara Basin (Yubuki et al. 2009) and ciliates (e.g. Schoenle et al. 2017).

3. Benthic Foraminiferans – classical and key deep-sea protists

Foraminifera are rhizarian protists with single-chambered (monothalamous) or multichambered (polythalamous) tests composed of organic material, calcium carbonate, or constructed from agglutinated particles (Murray 2006). Calcareous globigerinids are important members of the plankton, but they are far out-numbered in terms of species by the benthic Foraminifera that we consider here. Many deep-sea foraminiferans are small (<1 mm) and fall within the size range of meiofauna (32–300 µm) and smaller macrofauna (>300 µm), but others are considerably larger. A key defining feature of the group is the highly mobile system of fine, reticulated filopodia characterized by the bi-directional transport of particles driven by a complex microtubule cytoskeleton (Travis and Bowser 1991). This pseudopodial network is involved in many foraminiferal life processes and a major factor in their enormous success. Foraminiferal life cycles are complex and classically involve an alternation of generations that reproduce sexually (small proloculus) and asexually (large proloculus), albeit with frequent deviations from this pattern in the small proportion of species for which life cycles are known (Goldstein 1999). Reproduction in deep-sea species is poorly understood. It has been suggested that asexual reproduction is probably normal in stable deep-sea environments (p. 301 in Murray 1991), although distinguishing sexual and asexual modes based on proloculus size has proved problematic in fossil material (Schmidt et al. 2018).

Foraminifera have an outstanding fossil record. They are by far the most abundant benthic organisms preserved in deep-sea sediments and provide important proxies for reconstructing ancient oceanic environments (e.g., Gooday 2003; Jorissen et al. 2007; Murray 2006). As a result, much of the work on the ecology and distribution of modern faunas has been geologically driven and concerned the fossilizable, ‘hard-shelled’ multichambered taxa (agglutinated as well as calcareous), with little attention being paid to the delicate, often ‘soft-shelled’, monothalamids. Fortunately, the balance has been redressed to some extent since the 1970s, when deep-sea biologists began to include monothalamids, together with other foraminiferans, in quantitative studies across different size classes (Bernstein et al. 1978; Gooday 1986; Hessler 1974; Snider et al. 1984; Thiel 1983).

The deep sea encompasses different habitats and ecosystems related partly to water depth and distance from land, both of which influence the amount of food reaching the seafloor. As depth increases, the proportion of agglutinated Foraminifera, and particularly monothalamids, tends to increase at the expense of calcareous taxa (Cornelius and Gooday 2004; Phipps et al. 2012). This trend probably reflects a closer dependence of calcareous Foraminifera on inputs of fresh organic matter compared to agglutinated taxa, which seem better adapted to oligotrophic abyssal environments (Gooday 2003), combined with increasingly corrosive bottom-water (Murray 2006). Below the carbonate compensation depth (CCD: >5000 m in the Atlantic, 4000–5000 m in the Pacific), foraminiferal faunas are largely agglutinated (Saidova 1976). Here, we consider mainly, but not exclusively, the monothalamid-dominated faunas of abyssal plains. In the interests of brevity, we mention gromiids, another group of testate rhizarians that resemble organic-walled monothalamids, only in passing. Recent studies have shown these to be sometimes important components of deep-sea benthic communities (Gooday et al. 2000b; Rothe et al. 2011).

Meiofaunal Foraminifera

Foraminifera often represent 50% or more of the deep-sea meiofauna, with proportions ranging as high as 80–90% in some bathyal and abyssal areas (Gooday 2019; Thiel 1975).

Where delicate monothalamids are included, they typically make up a substantial part of the 'live' (i.e., stained with Rose Bengal) foraminiferans in fine (>32, 45 or 63 µm) sieve fractions. The proportion ranges from 27% to 58% at bathyal depths (<2000 m) in the Porcupine Seabight and Rockall Trough (NE Atlantic) (Gooday 1986; Gooday and Hughes 2002), but is higher (up to 89%) on abyssal plains (> 4000 m) in the NE Atlantic (Gooday 1996) and eastern equatorial Pacific (Gooday and Goineau 2019; Nozawa et al. 2006). Coarser fractions (>150 µm) of equatorial Pacific samples are also dominated (87–89%) by stained monothalamids (Goineau and Gooday 2017, 2019). Lower proportions (40–53%) of monothalamids were reported from three North Pacific sites (4263–5350 m), where multichambered textulariids and rotaliids were common in >32-µm fractions (Gooday et al. 2001).

These relatively small Foraminifera encompass many different morphotypes and taxa. Among those with multichambered tests, agglutinated hormosinids (mainly *Reophax* spp.) and trochamminids are often common, together with calcareous rotaliids, particularly in bathyal samples. The monothalamids include a great variety of undescribed forms (Fig. 2D–F). Small spheres are often abundant, as well as tubes (often fragmented) and fragments of Komokiacea, a group discussed further below. Other forms are difficult to categorize, even morphologically. The so-called '*Nodellum*-like' and '*Resigella*-like' species (Fig. 2E), which constitute an enigmatic group with organic-walled, tubular or segmented tests, are typically present and may be dominant at extreme hadal depths (Gooday et al. 2008; Sabbatini et al. 2002). Very fine sieve residues of abyssal sediments (32–63 or 28–63 µm) yield tiny agglutinated spheres, flasks and occasional multichambered tests, some as small as 20–30 microns (Gooday et al. 1995, 2001; Nozawa et al. 2006; Ohkawara et al. 2009). Burnett (1977, 1979, 1981) recorded even smaller testate organisms (nanobiota), interpreted as Foraminifera, in stained preparations of unsieved sediment examined under a compound microscope. These included single- and multi-chambered agglutinated structures, <10 µm to ~20 µm in size from the San Diego Trough (1200 m depth). Single-chambered Foraminifera <20 µm diameter were occasional components of the abyssal central Pacific nanobiota (Snider et al. 1984).

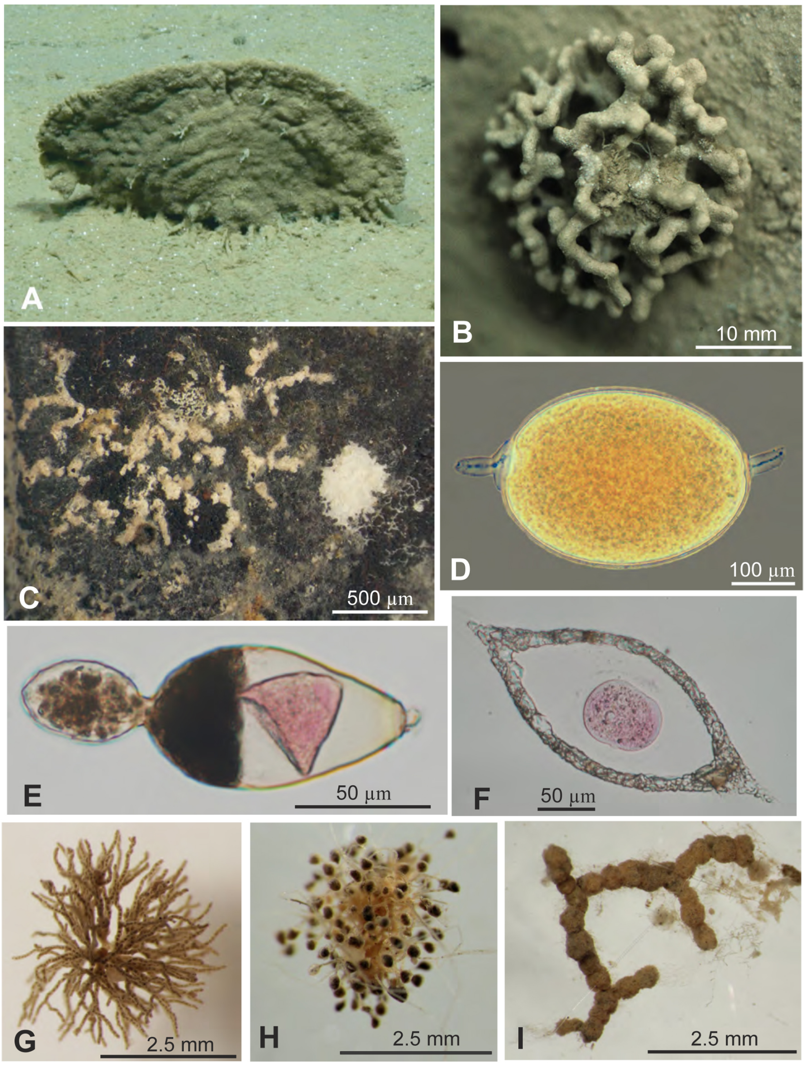

Fig. 2. Deep-sea monothalamid foraminifera from abyssal sites in the Pacific and Atlantic. Photographs are original, unless where indicated otherwise. **(A)** Large plate-like xenophyophore, width ~17 cm, photographed by the remote operated vehicle Lu'ukai in the equatorial Pacific (Area of Particular Environmental Interest 1; depth 5205 m). Photo courtesy of Craig Smith and Jennifer Durden, DeepCCZ project. **(B)** *Reticulammina* sp.; xenophyophore from the NE Atlantic (Porcupine Abyssal Plain; depth 4844 m). This photograph, taken with a hand-held camera, was previously published in Buhl-Mortensen et al. (2010 Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Marine Ecology 31**,** 21-50, Fig. 12-2E) and is reused here with permission from John Wiley and Sons. **(C)** Surface of polymetallic nodule from eastern equatorial Pacific with several different types of encrusting foraminifera (depth 4095 m); photographed under a stereo-microscope. **(D)** Organic-walled monothalamid with two tubular apertural structures from central Atlantic (BIOTRANS area; depth 4539 m); differential interference contrast illumination. **(E)** Bilocular *Resigella* sp. from eastern equatorial Pacific (4035 m depth); photo courtesy of Nina Ohkawara, unpublished PhD thesis, 2011; bright-field illumination. **(F)** *Vanhoeffenella* sp. from eastern equatorial Pacific (4035 m depth); photo courtesy of Nina Ohkawara, unpublished PhD thesis, 2011; bright-field illumination. **(G–I)** Komokiacea from the eastern equatorial Pacific; photographed under a stereo-microscope. **(G)** *Septuma* sp. (depth 4336 m). **(H)** *Normanina* sp. (depth 4080 m). **(I)** *Crambis* sp. (depth 4080 m).

Macrofaunal Foraminifera

Foraminifera >300 µm are often very abundant in deep-sea box cores and epibenthic sled samples, but since they are rarely considered as part of the macrofauna, there are no real quantitative data on their relative contribution to this size category. However, in the central North Pacific, the volume of one group, the Komokiacea, 'greatly exceeds that of all metazoans combined' (Tendal and Hessler 1977). These 'komoki' (Fig. 2G–I) were ignored for many years because they have morphologies unlike those of other Foraminifera. Around 25 species have now been established (Gooday et al. 2007a,b; Schröder et al. 1989), but many others remain undescribed. New observations have somewhat blurred the limits of the group, as defined by Tendal and Hessler (1977), leading to the distinction between 'core komoki' and 'komoki-like' forms (Gooday et al. 2007a; Kamenskaya et al. 2012). In the abyssal Pacific (5600–6000 m), the macrofauna also encompasses a rich assortment of tubes and spheres*,* together with multichambered agglutinated textulariids (Bernstein et al. 1978; Schröder et al. 1989). Assemblages in the abyssal Atlantic (4850 m) comprise a similar array of morphological and taxonomic groups, but with a greater relative abundance of certain types, such as komokiacean 'mudballs' and 'mud-walled spheres' filled with waste pellets (stercomata), as well as some large calcareous miliolids and lageniids (Gooday et al. 1992a, 1997; Shires 1994).

The foraminiferal megafauna

The tests of deep-sea agglutinated Foraminifera can reach sizes of 10 cm or more, making them large enough to appear in photographic surveys of seafloor megafauna. They include tubular species such as *Bathsiphon filiformis* Sars, 1872*,* which form dense populations on bathyal continental margins (Gooday et al. 1992b). However, the most familiar megafaunal Foraminifera are the xenophyophores (Fig. 2A,B). The first species were discovered in the late 19th century and identified as either foraminiferans or sponges, until Schulze (1907) established them as a distinct group of 'rhizopod' protists. Xenophyophores were largely forgotten during the middle decades of the 20th Century, until rescued from obscurity by the 1972 monograph of Ole Tendal, who expanded Schulze's (1907) classification to include two orders and five families (Tendal 1972). These giant protists are widely distributed in the oceans at depths below ~500 m (Tendal 1996) and are sometimes a dominant constituent of the megafauna in bathyal (Bett 2001), abyssal (Amon et al. 2016; Gooday et al. 2011; Kamenskaya et al. 2013; Simon□Lledó et al. 2019a), and extreme hadal (Gallo et al. 2015) settings. A few deep-sea gromiids also attain megafaunal size (Gooday et al. 2000b)

The phylogenetic position of xenophyophores was finally settled when the first genetic analyses showed them to be monothalamous Foraminifera (Pawlowski et al. 2003). Since then, an increasing body of genetic data has cemented their place as a monophyletic group within monothalamid Clade C (Gooday et al. 2017a,b,c, 2018; Voltski et al. 2018). Xenophyophores display an enormous variety of test morphologies, including spheres, fan-shaped plates, curved contorted plates, domes, and lumps, as well as reticulated, tubular, and segmented (pseudo-chambered) structures. In one group, the test incorporates a dense system of fine proteinaceous fibres, chemically related to silk (Hedley and Rudall 1974). Most are epifaunal and sessile species are found where hard substrates are available. They have a distinctive internal organization with dark masses of stercomata and pale strands of cytoplasm enclosed within an organic sheath that extend through much of the test (Gooday et al. 2018a). The cytoplasm is packed with heavy minerals, normally barite (Gooday and Nott 1982; Hopwood et al. 1997; Tendal 1972), although one species found in a submarine canyon accumulates titanium-rich minerals (Rothe et al. 2011).

Little is known about xenophyophore biology. Some fan-shaped species may be suspension feeders, but others probably feed either directly on the sediment or by using their morphologically complex tests to passively trap particles (Levin and Thomas 1988). A time-lapse camera recorded a ten-fold increase in the test volume of three xenophyophores over a 291-day period in the NE Atlantic, a process that involved the collection of sediment and appeared to combine growth with deposit feeding (Gooday et al. 1992a). Xenophyophore cytoplasm takes up only a few percent of the test volume (Gooday et al. 2018a), a proportion that is further diminished by the space occupied by inert intracellular crystals. Their contribution to seafloor biomass is therefore much less than their large test size would suggest (Tendal 1979). However, where they are abundant, the tests of xenophyophores and other large agglutinated Foraminifera provide an important source of habitat structure for diverse animal (Gooday et al. 1992a; Levin 1991; Levin and Thomas 1988) and foraminiferal assemblages (Hughes and Gooday 2004), and can even serve as nurseries for fish (Levin and Rouse 2020).

Hard substrates

Sessile Foraminifera are frequent colonisers of hard substrates including rocks and biogenic structures, in bathyal (Lutze and Altenbach 1988) and abyssal (Gooday and Haynes 1983) settings. Monothalamids (Fig. 2C) are typically the dominant organisms encrusting polymetallic nodules in the abyssal Pacific (Gooday et al. 2015; Mullineaux 1987; Veillette et al. 2007). Artificial hard substrates deployed in bathyal settings, including the Santa Catalina Basin (Mullineaux 1988), a Pacific seamount (Bertram and Cowen 1999), and near methane seeps (Burkett et al. 2016) and vents (Van Dover et al. 1988), have been rapidly colonised over periods of several weeks to several years by large numbers of calcareous and agglutinated foraminiferans. These hard-substrate assemblages are often diverse, and include many species that are not present in adjacent sediments.

Species diversity

Deep-sea foraminiferal assemblages are often highly diverse, with a long tail of rare species (Douglas and Woodruff 1981; Gooday 1986). Well over 100 meiofauna-sized morphospecies are typically present in the 0–1 cm layer of core samples from the abyssal NE Atlantic (Gooday et al. 1998). Surficial box-core sediments from the same area yielded comparable numbers of macrofaunal (>500 µm) species. In both cases, monothalamids represented well over half (66–82%) of the species. Similarly, high levels of morphospecies richness are reported in the abyssal Pacific (Gooday et al. 2004). For example, seven small sediment samples (3.45 cm^3 volume, >32 µm fraction) from the abyssal eastern Pacific yielded 168 morphospecies (>75% monothalamids) among 983 complete specimens, with a further 84 monothalamid species being represented by test fragments (Nozawa et al. 2006). A total of 462 stained species were picked from 11 megacore samples (78 cm^2, >150-µm fraction) obtained in a nearby area; the number increased to 546 when dead tests were included, and to 580 when fragments were included (Goineau and Gooday 2019). Five samples in which finer residues (63–150 µm) were analyzed, in addition to the >150 µm fraction (Gooday and Goineau 2019), yielded 462 morphospecies; three-quarters were monothalamids and more than a third (37%) found only in the 63–150-µm fraction.

Rough estimates suggest that the proportion of described (rather than undescribed) foraminiferal species in Atlantic deep-sea samples is much higher (generally >50%) for multichambered taxa than for monothalamids (usually <15%) (Gooday et al. 1998). Around a third of multichambered forms in abyssal Pacific samples can be easily assigned to well-known species, a proportion that will undoubtedly rise with further taxonomic study, whereas the vast majority of monothalamids (around 96%) are undescribed.

Foraminifera in deep-sea hypoxic environments

Foraminifera reach unusually high densities in bathyal OMZs (Levin 2003), where low-diversity assemblages of hypoxia-tolerant species flourish at sometimes vanishingly low oxygen concentrations (Bernhard et al. 1997, 2006; Caulle et al. 2015; Glock et al. 2012; Gooday et al. 2000a; Larkin and Gooday 2009; Mallon et al 2012; Phleger and Soutar 1973). Calcareous rotaliids and lageniids, often with flattened biserial/triserial, globular, or lenticular/planispiral morphologies, are typically common (Bernhard and Sen Gupta 1999; Koho and Piña-Ochoa 2012), but agglutinated taxa are an important faunal constituent in some OMZs (Caulle et al. 2015; Taylor and Gooday 2014) and monothalamids may also occur (Bernhard et al. 2006). There is also a record of the rotaliid *Virgulinella fragilis* Grindell and Collen, 1976 in hypoxic and sulfidic sediments of the Cariaco Basin (Bernhard 2003).

A range of morphological and physiological attributes have been suggested as possible adaptations to severe hypoxia (Bernhard and Sen Gupta 1999; Koho and Piña-Ochoa 2012). These include small, thin-walled, sometimes flattened tests (Phleger and Soutar 1973), increased test pore sizes and densities (Rathburn et al. 2019), the presence of bacterial endosymbionts and sequestered chloroplasts, and increased densities of organelles, notably mitochondria, endoplasmic reticulum, and peroxisomes (Bernhard 2003, Bernhard and Bowser 2008; Bernhard et al. 2000, 2012b). One important mechanism that has attracted considerable recent attention is the ability of many foraminiferal and gromiid species in hypoxic settings, to accumulate, store and respire nitrate rather than oxygen, a process (denitrification) that leads to the release of dinitrogen gas (Risgaard-Petersen et al. 2006; Høgslund et al. 2008, 2017; Piña-Ochoa et al. 2010; Koho and Piña-Ochoa 2012). Within the Peru margin OMZ, nitrate respiration was found to be metabolically preferable compared to oxygen respiration in nine calcareous species (Glock et al. 2019). In some cases, it appears that prokaryotic endosymbionts are responsible for denitrification (Bernhard et al. 2012a). However, the possibility that this process may be performed by foraminifera themselves (Risgaard-Petersen et al. 2006; Bernhard et al. 2012b), receives strong support from the presence of genes coding for enzymes involved in denitrification in two species of *Globobulimina,* a common genus in OMZs that does not host large numbers of bacteria (Woehle et al. 2018).

Insights from environmental genetic studies

Environmental DNA (eDNA) data supports the conclusion drawn from morphological studies that deep-sea Foraminifera are highly diverse and include a substantial proportion of undescribed monothalamids (Pawlowski et al. 2014). The majority (>70%) of ribosomal DNA sequences (OTUs = operational taxonomic units) obtained from six sediment samples collected in the Southern Ocean (1927–5338 m depth) could not be assigned to already-sequenced multichambered or monothalamous taxa, although phylogenetic analysis placed them within the monothalamid radiation, in many cases in clades comprising known environmental sequences (Pawlowski et al. 2011). DNA barcoding, based on a hypervariable region of the SSU rDNA gene unique to Foraminifera, provides a powerful tool for recognising species (Pawlowski and Holzmann 2014). Applying this approach to sediment samples collected across a wide depth range (1745–5338 m depth) in different oceans, Lecroq et al. (2011) found that reads and OTUs corresponding to monothalamids were consistently common (overall 42% and 39%, respectively), compared to the multichambered rotaliids (6.5% of OTUs) and textulariids (4.2% of OTUs). The assigned OTUs revealed considerable phylogenetic diversity, including almost all previously defined monothalamid clades. More than 200 monothalamid OTUs could not be properly assigned to a clade, suggesting that monothalamid diversity is even higher. Similarly, 74% of reads and 33% of OTUs corresponded to monothalamids in an eDNA study by Lejzerowicz et al. (2014) of samples from three sites (3966–4155 m depth) in the Southern Ocean. The samples analysed by Lecroq et al. (2011) and Lejzerowicz et al. (2014) also yielded many reads (34% and 18%, respectively) and OTUs (47.0% and 56%, respectively) that could not be assigned to any foraminiferal clade. Clearly, much remains to be learnt about the nature of deep-sea benthic foraminiferan diversity.

Biogeographic patterns

There is a general perception that deep-sea foraminiferal morphospecies, particularly those living on abyssal plains, have distributions spanning all the major oceans (Douglas and Woodruff 1981; Gooday et al. 2004; Gooday and Jorissen 2012; Holbourn et al. 2013; Murray 2006). In a few cases, genetic support exists for these wide ranges. The best example is *Epistominella exigua* (Brady, 1884)*,* populations of which are more or less identical (based on SSU rDNA sequences) in the Arctic, North Atlantic and Southern Oceans (Pawlowski et al. 2007). This conclusion was extended to the western Pacific by Lecroq et al. (2009b), who also showed that Arctic populations of a related species, *Epistominella arctica* Green, 1959, were genetically identical to those from the Antarctic.

Monothalamids are more problematic because they are (a) largely undescribed and therefore not normally recognised and (b) often rare. Among the numerous species recognised by Goineau and Gooday (2019) in the eastern Pacific, only 34 (6.2%) occur at 9–11 sites, compared to the 313 (57%) confined to one or two sites. Moreover, the widely distributed species accounted for 44% of specimens whereas the much larger number of restricted species accounted for only 17% of specimens and almost half (46.6%) were singletons. A similar picture emerges from eDNA data. Only 16 (1%) of the 1642 OTUs identified by Lecroq et al. (2011) occurred at all five sampling sites located in different oceans, whereas 1303 OTUs (~79%) were confined to one site. Yet these sixteen cosmopolitan OTUs represented a disproportionately large percentage (11.4%) of reads compared to the 1303 confined to one site (37.2%).

These kinds of observations suggest that chronic undersampling is a major hindrance to establishing the ranges of deep-sea Foraminifera, and make it almost impossible to prove endemic distributions. Nevertheless, it seems unlikely that all deep-sea foraminiferal species are cosmopolitan, even at abyssal depths. Gooday et al. (2004) and Gooday and Jorissen (2012) point to some possible examples of endemism from continental margins as well as a few from abyssal plains. Stannomid xenophyophores are common in the abyssal Pacific but represented by a single record in the Atlantic (Tendal 1996). Given the different histories and environmental characteristics of the Pacific and Atlantic, it would not be surprising if some foraminiferal species are restricted to one or other of these oceans.

Role of Foraminifera in deep-sea food webs and carbon cycling

Deep-sea foraminiferans generally feed at a low trophic level (Gooday et al. 1992a, 2008; Nomaki et al. 2008). Some species exploit pulsed inputs of fresh phytodetritus derived from surface production, using this labile food source to fuel reproduction and the rapid development of large populations (Gooday 1988a, 1993; Gooday and Hughes 2002). These predominantly calcareous opportunists, and calcareous foraminiferans in general, may be more important in the initial processing of labile organic matter on the deep seafloor than agglutinated species, particularly monothalamids, a conclusion supported by uptake experiments using ^{13}C-labelled diatoms (Enge et al. 2011; Moodley et al. 2002; Nomaki et al. 2005). Experiments by Nomaki et al. (2006) at a bathyal site (1450 m depth) off Japan utilized labelled bacteria (representing a sedimentary food source), as well as diatoms and the alga *Dunaliella* (representing a phytodetrital food source). These experiments suggested that some species feed exclusively on phytodetritus, others also select phytodetritus when it is available, but in its absence will exploit sedimentary organic matter, while a third group randomly consumes sedimentary organic matter. Nomaki et al. (2009) subsequently explored the degradation of phytodetritus at the molecular level, showing that some algal components, notably polyunsaturated fatty acids, are degraded rapidly by foraminiferans and that these protists are able to modify certain compounds (phytols and fatty acids) derived from algae and thereby influence the lipids available as food to higher trophic levels. Rapid uptake of labile dissolved organic matter (glucose) has also been demonstrated in bathyal foraminiferans (Nomaki et al. 2011).

Many monothalamids, and all gromiids, retain large quantities of stercomata containing clay minerals, and are clearly feeding in a way that is different from that of the more opportunistic calcareous taxa (Gooday et al. 2008; Tendal 1972, 1979). They may be deposit or suspension feeders that ingest sediment particles and consume associated bacteria, degraded organic matter, or organic molecules adsorbed on clay particles. The consumption of less nutritious food by stercomata-bearing monothalamids (Enge et al. 2011; Sweetman et al. 2019), and the likely sedentary life-styles of many species (suggested by complex test morphologies, large sizes, and occupancy of cryptic microhabitats), makes it likely that they are metabolically less active than calcareous species.

Foraminifera are consumed by selective and non-selective predators (Lipps 1983). Many are ingested incidentally by deep-sea deposit feeders such as holothurians, although whether they have much nutritional value is debatable (Sokolova 2000). Selective deep-sea predators include certain ascellote isopods (Gudmundsson et al. 2000; Svavarsson et al. 1993), scaphopods (Langer et al. 1995), and sipunculan worms (Heeger 1990), as well as smaller meiofaunal animals such as harpacticoid copepods (Nomaki et al. 2008). Some isopod species have powerful jaws that can crush hard foraminiferal tests, while scaphopods have a muscular stomach that functions as a gizzard (Morton 1959). Gastropods are well-known predators of hard-shelled Foraminifera in coastal settings (Culver and Lipps 2003) and possibly also in deep water (Arnold et al. 1985). Stercomata-bearing monothalamids may also be targeted. Circular holes bored through the test wall of the xenophyophore *Aschemonella ramuliformis* Brady, 1884 could be made by gastropods (Gooday et al. 2017b). Tendal (1985) showed that the monoplacophoran mollusc *Neopilina* Lemche, 1957 feeds on *Stannophyllum zonarium* Haeckel, 1889, creating shallow pits in the test similar to those seen on other Pacific xenophyophores (Gooday et al. 2017a). The remains of xenophyophores and komokiaceans are found in the guts of some deep-sea animals, including an echiurid worm, eurycopid isopods, and some holothurians and asteroids (Sokolova 2000). Thus, by linking lower and higher levels of deep-sea food webs (Lipps and Valentine 1970; Nomaki et al. 2008), benthic foraminiferans probably play an important role in carbon cycling in the deep ocean. Even the less active monothalamids could make a substantial contribution, given their shear abundance across vast tracts of abyssal seafloor.

4. Non-testate protists on the seafloor: heterotrophic flagellates, ciliates and amoebae

The possession of relatively large tests makes it easier to investigate foraminiferal diversity based on morphology. In contrast, microscopical studies may miss the majority of deep-sea protistan diversity since fragile taxa, such as tiny flagellates, amoebae and ciliates, are often disrupted during recovery through the water column, and cultivation approaches are often very selective (Arndt et al. 2003; Edgcomb et al. 2014; Schoenle et al. 2016). The establishment of in-depth culture-independent High-Throughput-Sequencing (HTS) has revolutionized our understanding of the microbial diversity that can be recorded from deep-sea samples, and millions of barcoding sequences (reads) can be obtained and compared with public reference databases. Although this very powerful technique can reveal much about non-foraminiferal protistan diversity, there are also certain limits to its interpretation (Edgcomb et al. 2014; Schoenle et al. 2016), as discussed below. It is clear from a combination of molecular studies and direct observations, that nearly all known phylogenetic groups of non-testate protists are represented in deep- sea sediments below 1000 m depth (Schoenle et al. 2016; Fig. 3).

Heterotrophic flagellates

While molecular studies indicate the presence of nearly all phylogenetic groups of flagellated protists in the deep sea, there are only a few direct observations of living specimens in samples or cultures isolated from deep-ocean habitats. While benthic and planktonic foraminiferans are largely distinct, many flagellated protists occur both on the seafloor and in the pelagial. This is due to the fact that most flagellates are in the size range 2-8 µm for which small flocs of detritus (marine snow) form a suitable habitat (Arndt et al. 2000; Caron et al. 1982). Thus, aggregate-dwelling protists like kinetoplastids and stramenopiles, as well as small naked amoebae, occur throughout the water column (Patterson et al. 1993; Arndt et al. 2003). Many of these flagellates have been shown to withstand high pressure and, therefore, are believed to remain active when they reach the seafloor via sedimentation (Živaljić et al. 2018). An extreme example is the common bicosoecid *Cafeteria burkhardae* Schoenle and Arndt, 2020, the genotype of which was recorded in samples from several abyssal plains as well as from global analyses of planktonic communities (de Vargas et al. 2015; Schoenle et al. 2020). There are certainly many barophilic flagellates that have been overlooked when using traditional sampling methods where deep-sea samples are released from pressure when brought to the surface (Edgcomb et al. 2016b). Only few studies of these barophilic flagellates currently exist (Atkins et al 1998; Turley et al. 1988; Turley and Carstens 1991; Živaljić et al. 2018). A rough estimate of deep-sea flagellate community composition can be derived from live-observations made directly after sampling, altthough some sensitive flagellate species may not survive sample recovery. Investigations at 1225 m depth in the Sporades Basin (Mediterranean; Greece) using direct microscopic analysis immediately after sampling showed that about one third of the flagellate community were euglenids, another third bodonids and the remaining part consisted of forms that are often overlooked in molecular studies (Arndt et al. 2003). Among these "overlooked" flagellate taxa were hemimastigophorans, which are thought to be rare in the environment (Lax et al. 2018) but seem to be common in bathyal sediments (Arndt et al. 2003; Arndt unpubl.). Flagellate taxa recorded from cultures or direct counts of deep-sea sediments (>1000 m depth; e.g. Arndt et al. 2003; Arndt et al. 2020; Arndt et al. unpubl., Patterson et a. 1993) include: apusomonads (*Amastigomonas*-like), filastereans (*Ministeria*-like), choanoflagellates (*Acanthocorbis*-, *Diaphanoeca*-, *Salpingoeca*-like), telonemids (*Telonema*-like), placidids (*Placidia*-, *Placilonga*-like), bicosoecids (*Bicosoeca*-, *Caecitellus*-, *Pseudobodo*-, *Cafeteria*-like), chrysomonads (*Paraphysomonas*-like), pedinellids (*Pteridomonas*-like), cercozoans (*Cercomonas*-, *Massisteria*-like, *Allantion*-, *Protaspi*s-, *Kiitoksia*-like), cryptomonads (*Goniomonas*-like), jakobids (*Jakoba*-like), percolomonads (*Percolomonas*-like, *Barbelia*-like), euglenids (*Heteronema*-, *Petalomonas*-, *Ploeotia*-, *Keelungia*-like), kinetoplastids (*Bodo-, Neobodo-, Bordnamonas-, Rhynchomonas*-, *Procryptobia*-like), ancyromonads (*Ancyromonas*-, *Fabomonas*-like), hemimastigophorans (*Spironema*-, *Hemimastix*-like), incertae sedis groups (*Meteora*-like). Since most of these taxa were not analysed in detail, and many hve not been sequenced yet, only the closest genus is given.

Ciliates

Ciliates are an abundant and ubiquitous component of deep-sea microbial food webs. Cunningham and Ustach (1992) reported abundances in fixed samples of up to 700 cells per cm^3 in surface sediments at nutrient-rich NW Atlantic stations (3833 m depth). Metabarcoding studies regularly reveal a high diversity of ciliates in most samples from the deep seafloor (for review see Schoenle et al. 2017). Representatives of nearly all major phylogenetic groups, including Karyorelictea, Heterotrichea, Spirotrichea, Armophorea, Litostomatea, Phyllopharyngea, Nassophorea, Colpodea, Prostomatea, Plagiopylea, Oligohymenophorea, have been recorded at depths of 1000–3000 m. However, only a few records exist from abyssal depths. Live observations of ciliates isolated from the deep sea are scarce (Schoenle et al. 2017; Živaljić et al. 2020a, b), possibly because they generally occur at relatively low abundances, and may be damaged by hydrostatic stress during conventional sampling. The broad spectrum of genotypes registered so far indicates that ciliates occupy diverse niches ranging from being consumers of prokaryotes, other protists and detritus, to acting as epibionts and parasites and most probably also as osmotrophs. Since most ciliates are relatively large compared to the nano-sized heterotrophic flagellates and amoebae, they have a potentially shorter generation time and their response to local accumulations of organic matter might be correspondingly slower. On the other hand, fast encystment and excystment was observed for a bacterivorous scuticociliate isolated from the deep sea. which could support the idea that ciliates can react quickly to pulsed organic matter inputs (Schoenle et al. 2017; Živaljić et al. 2020b).

Naked amoeboid protists

Since direct observations are very difficult due to low abundances, slow movement and masking by sediment particles, observations on amoebae are limited to cultivable species obtained from aliquot cultivations. Davis et al. (1978) reported an *Acanthamoeba*-like species from the North Atlantic (3090 m depth) at densities of 0.66 ind./l. Lobosean abundances (mainly vexilliferid-like and vannellid-like morphotypes) in Mediterrean deep-sea basins close to Greece reached up to 50 ind./cm^3 sediment at depths of 1225 m, considerably lower than that of flagellates although the amoebae were always present (Arndt et al. 2003). Recently, several new species have been described from deep-sea sediments, mainly representatives of paramoebid and vexilliferid amoebae (e.g. Kudryavtsev and Pawlowski 2013; Kudryavtsev et al. 2018). According to metabarcoding studies, the diversity of deep-sea amoeboid protists encompasses nearly all groups of amoebozoans, including tubulineans, evosean and discocean taxa (e.g. Rodríguez-Martínez et al. 2020).

Parasitic and symbiontic deep-sea protists

Skovgaard (2014) reviewed the great variety of marine protistan taxa that act as important parasites in the marine pelagial, observations which must also apply to deep-sea ecosystems. In a relatively early study, López-García et al. (2001) reported astonishingly high percentages of parasitic protistan genotypes (especially dinoflagellate taxa) from the deep pelagial realm (250-3000 m depth) in the Southern Ocean. Flegontova et al. (2016) pointed to the great importance in deep water of diplonemid euglenozoans, which have recently been shown to also contribute significantly to abyssal sediment communities (Schoenle 2018). It appears currently that alveolate, euglenozoan, and radiolarian genotypes are most important in the deep sea, although their specific hosts are still unknown. According to the Red Queen Principle it could be argued that these protozoan parasites potentially contribute to the high diversity of metazoans and protozoans in the deep sea.

Another important phenomenon is that of protists as symbionts. Volkova and Kudryavtsev (2017) detected *Perkinsela*-related kinetoplastids living as symbionts in deep-sea isolates of *Neoparamoeba longipodia* Volkova and Kudryavtsev, 2017 from about 5000 m depth. Symbioses between bacteria and protists have also been reported, for example, in the case of euglenozoans, allowing their survival under anaerobic conditions (e.g., Yubuki et al. 2009).

Naked protists in deep-sea hypoxic environments

Several species of heterotrophic flagellates, ciliates and amoebae, representing different phylogenetic lineages, can live as facultative anaerobes, but only a few are known to be obligate anaerobes that perform anaerobic energy metabolism (Bernard et al. 2000; Fenchel 2012). Among them are some ciliates from deep-sea sediments that possess mitochondria-derived hydrogenosomes (Stoeck et al. 2012, Schoenle et al. 2017). As in the case of foraminiferans, nitrate respiration has been recorded (Fenchel 2012), and investigations of genes expression patterns indicate that nitrate and sulphate reduction might be of importance also for anerobic protists in deep-sea hypersaline basins (DHABs; Edgcomb et al. 2016a).

Many protists have established symbioses with bacteria such as methanogens in order to reduce hydrogen tension under anaerobic conditions, while others live in symbiosis with sulfate reducers (Fenchel 2012). The euglenid *Calkinsia* is associated with ectosymbiotic bacteria at more than 500 m depth in the oxygen-depleted Santa Barbara Basin (e.g. Yubuki et al. 2009). At cold seeps, grazing by protists is believed to act as an effective process structuring bacterial and archaeal communities on the surface of the sediment, as well as influencing prokaryote community structure in deeper sediment layers (Orsi 2018). Protists in cold seeps have isotope signatures of methane-derived carbon, indicating the role of bacterivorous protists in these habitats (Orsi 2018; Pasulka et al. 2017).

Insights from environmental genetic studies

Many novel and uncultured protistan lineages from surface waters and the deep sea have been revealed by HTS, among them new superdiverse phylogenetic groups (e.g. del Campo and Massana 2011; Edgcomb et al. 2011; López-García et al. 2001; Triadó-Margarit and Casamayor 2013). Several marine stramenopile (MAST) groups seem to be restricted to planktonic communities (Massana et al. 2004), while the groups (clades) MAST-1, -9 and -12 have also been reported in significant abundances from deep-sea sediments (Takishita et al. 2007). New lineages, including several very diverse groups of marine alveolates (MALV; Groisillier et al. 2006; Guillou et al. 2008; López-García et al. 2001; Moreira and López-García 2002), have been described from the deep sea. Five independent lineages of marine alveolates (MALV group I–V) branching at the base of dinoflagellates have been discovered. One lineage (MALV II) includes sequences from described genera, among them members of the Syndiniales, which are partially or entirely intracellular parasites. It is possible that the whole MALV II group may consist of parasitic forms. On the other hand, MALV I seem to dominate permanent anoxic waters and hydrothermal ecosystems (Edgcomb et al. 2002; Groisillier et al. 2006; López-García et al. 2003). Another superdiverse deep-sea protistan group revealed by metabarcoding techniques are diplonemids belonging to the Discicristata. Although diplonemids were recorded over a decade ago (Lara et al. 2009; López-García et al. 2001), only a few sequences of cultivated and morphologically described species are currently available (Gawryluk et al. 2016; Tashyreva et al. 2018). Metabarcoding studies, however, have recently shown that diplonemids are among the most abundant and diverse lineages of marine heterotrophs in the sunlit ocean and mesopelagic waters, representing one-fifth of the eukaryotic OTUs (David and Archibald 2016; de Vargas et al. 2015; Flegontova et al. 2016). Recent molecular studies have indicated that this might also be true for abyssal deep-sea sediments (Scheckenbach et al. 2010; Schoenle 2018). The ecological roles of several of these novel and known lineages are unclear, but they could be key players in deep-ocean ecosystems and responsible for critical environmental processes. However, the activity of these different and very abundant genotypes under deep-sea conditions remains obscure.

Substrate type

Flagellates, ciliates and naked amoebae colonise all types of substrate. Generally, higher abundances are recorded from the upper sediment layers decreasing with depth due to a reduction of available food recources (Hohlfeld et al., subm.). Non-testate protists have been found to be enriched on the surface of hard substrates such as animal remains and manganese nodules (e.g., Shulse et al. 2017) most probably also supported by organic enrichment from sessile metazoans and Foraminiferans. In particular, suctorians and peritrichous ciliates have been found as epibionts on isopods, ampipods, harpacticoid copepods and other arthropods (e.g., Bartsch and Dovgal 2010; Sedlacek et al. 2013; Kniesz et al. 2018) and even on nematodes (Ingole et al. 2010) from deep-sea samples. Folliculinid ciliates may be abundant on hard substrates near vents (Van Dover et al. 1988) as well as at methane seeps, where they appear to play an important role, together with prokaryote symbionts and associates, in the biogeochemical cycling of methane-derived carbon (Pasulka et al. 2017).

Biogeographic patterns

Investigations of benthic shelf and deep-sea environments based on HTS techniques revealed distinct microbial communities within these two habitats as well as previously uncharacterized sequences indicating the existence of a specific deep-sea protist fauna (Countway et al. 2007; Edgcomb et al. 2002; López-García et al. 2001; Scheckenbach et al. 2010). Global comparisons similar to those for the eukaryotic plankton of the sunlit ocean (de Vargas et al. 2015) or the dark ocean (Giner et al. 2020; Pernice et al. 2016) are not available for the abyssal seafloor. A global survey of bathypelagic protist communities revealed an overall dominance of a few groups, although with significant differences in the relative abundance of taxa within these groups (Pernice et al. 2016). Some morphologically distinct pelagic taxa, for example, some phaeogromid cercozoans (e.g. *Challengeria*), appear cosmopolitan (e.g., Dolan et al. 2019). Multiple clades of deep-sea pelagic diplonemids showed no clear biogeographic pattern, but seemed to be vertically stratified in the dark mesopelagic realm (Flegontova et al. 2016).

Studies on deep-sea benthic protist assemblages have mainly concentrated on assumed hot spots like hydrothermal vents, cold seeps and anoxic regions, in most cases at bathyal depths (e.g. Bernhard et al. 2014; Edgcomb et al. 2011; Pasulka et al. 2017, 2019; Small and Gross 1984; Stoeck et al. 2009; Takishita et al. 2005, 2007), or have concerned only foraminiferans (see above). At hydrothermal vents in the Guyamas Basin (~2000 m depth; Pacific Ocean), mainly dinoflagellates, cercozoans and ciliates were detected as dominant groups (Pasulka et al. 2017, 2019). At Mid-Atlantic Ridge hydrothermal vents (2264 m depth) a considerable phylogenetic diversity was observed, especially within the alveolates (ciliates, MALV I, MALV II) and kinetoplastids (López-García et al. 2003). A comparison of Mid-Atlantic Ridge and Pacific (Guaymas Basin) vents showed that some protist lineages seem ubiquitous in hydrothermal areas, whereas others, notably kinetoplastid lineages, so far have been detected only in Atlantic systems (López-García et al. 2003). Ciliates and bodonids seem to be pioneers, as suggested by colonization experiments (López-García et al. 2003; Van Dover et al. 1988). The most abundant Guaymas ciliates were more likely to be represented in clone libraries from other hydrothermal, deep-sea, and/or anoxic or microaerophilic environments, supporting the hypothesis that these ciliate species are broadly distributed (Coyne et al. 2013). Moreover, taxon (OTU) richness and community structure differed among sediment habitats including different kinds of mats and in locations sometimes separated by only a few tens of centimeters. Control sediments had the greatest number of unique OTUs and the highest diversity. In general, ciliates within the Spirotrichea, Plagiopylea, Oligohymenophorea, Litostomatea, and Colpodea exhibited higher OTU richness relative to the other ciliate classes detected, with Oligohymenophorea and Litostomatea making up larger portions of the ciliate community in control sediments relative to microbial mat sediments (Pasulka et al. 2019).

Only a few studies have focused on protist life at abyssal depths (e.g. Edgcomb et al. 2002), including abyssal plains (Scheckenbach et al. 2010; Salani et al. 2012). Kinetoplastids, a group generally contributing a major part of deep-sea protistan communities (with only minor exchange with pelagic communities) showed relatively high similarities over distances of hundreds to thousands of kilometres along the SW and SE Atlantic basins (Salani et al. 2012). However, there were significant differences between Mediterranean deep-sea kinetoplastid communities, indicating the existence of spatial structure at larger scales.

Another study revealed that environmental differences between the Cape/Namibian Abyssal Plain and the Angola- and Guinea Abyssal Plains are paralleled by significant differences in the community structure of protists (Scheckenbach et al. 2010). This supports the idea of restricted distributions among at least the less opportunistic species in the abyss. The study of Zhao et al. (2017a) in the abyssal Pacific Ocean showed that benthic ciliate communities below 3800 m shared up to 78% of OTUs with those of the shallowest site (813 m depth). The abyssopelagic ciliate Pacific communities did not exhibit a horizontal distance-decay relationship, although a distinct vertical structure within the water column was observed (Zhao et al. 2017b).

Like foraminiferans (see above), most naked protist communities exhibit high diversity, but are dominated by a few very abundant species/genotypes. The majority of taxa are part of the “rare biosphere”, meaning that many species are represented by only a few individuals or sequence reads in HTS studies (Liu et al. 2015; Logares et al. 2014; Sogin et al. 2006). The “rare biosphere” serves as a reservoir of genetic and functional diversity in comparison to the dominant species (Lynch and Neufeld 2015; Pedrós-Alió 2012; Zhang et al. 2018).

Role of naked protists in deep-sea food webs and carbon cycling

The functional diversity of recorded naked protistan genotypes, and their ability to withstand high hydrostatic pressures (Fig. 3), suggests that deep-sea microbial food webs function in a very similar way as those in surface water and coastal habitats (Arndt et al. 2000; Azam et al. 1983). Barotolerant nanoprotist (<20 µm), such as bicosoecids, are known to withstand high pressure and feed on prokaryotes in porewater. Many kinetoplastids, cercozoans and amoebozoans feed on attached prokaryotes. Omnivorous grazers, such as many ciliates and some amoebae and flagellates, consume a broad spectrum of food particles including other protists (Fig. 4), while detritus is directly utilised by several protist groups. The secondary production of naked protists may vary considerably in intensity due to the locally and temporally restricted input of organic matter by sedimentation or chemosynthesis. Most protists can endure food shortages by reducing their metabolism and encysting. Finally, it is likely that protists form an important food source for metazoans. From freshwater systems it is known that protists upgrade the food quality for higher trophic levels by enrichment of essential PUFAs (Bec et al. 2006, Martin-Creuzburg et al. 2006). Stable isotope studies of abyssal communities showed that several trophic levels are missing in the transfer to macrofauna of carbon from the large quanitites of the brown algae *Sargassum* that are deposited on the deep seafloor in parts of the Atlantic (Baker et al. 2018). This probably reflects the traditional neglect of naked protists in deep-sea biology (Danovaro et al. 2020).

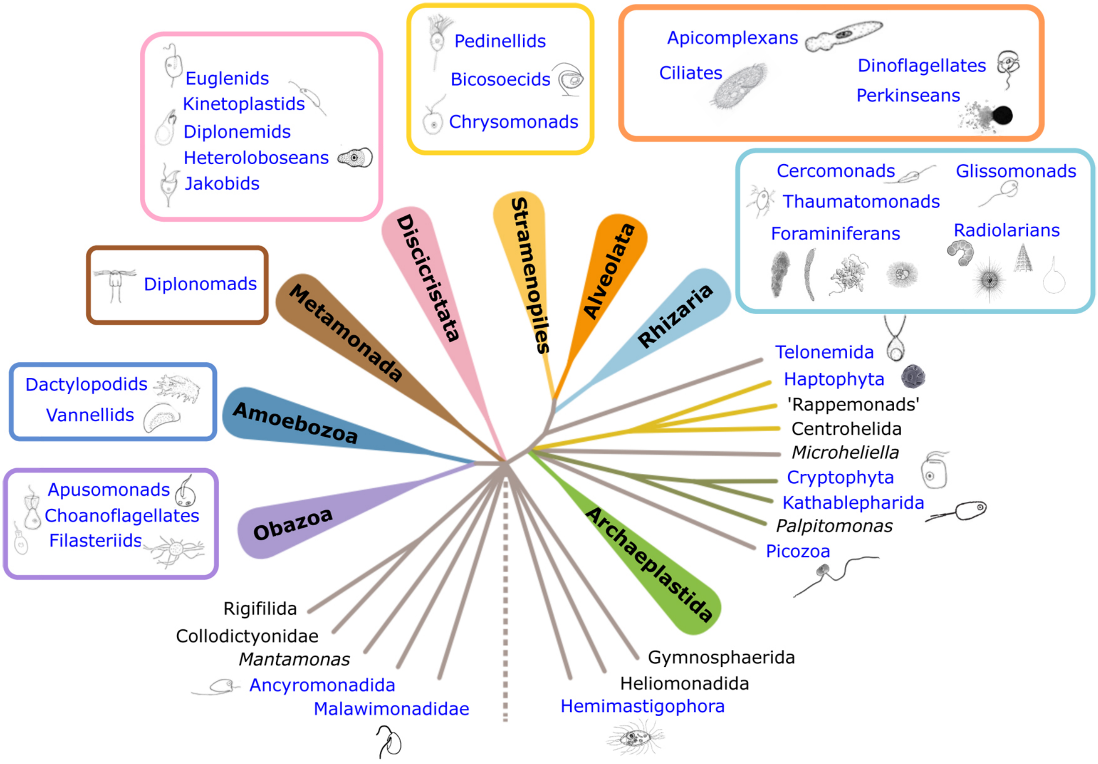

Fig. 3. Phylogenetic tree of eukaryotes highlighting protist diversity recorded from deep-sea studies (deep-sea records obtained from direct observations, cultivations and metabarcoding studies in blue). Tree adapted from Archibald et al. 2017 and Adl et al. 2019; protist schemes from different authors.

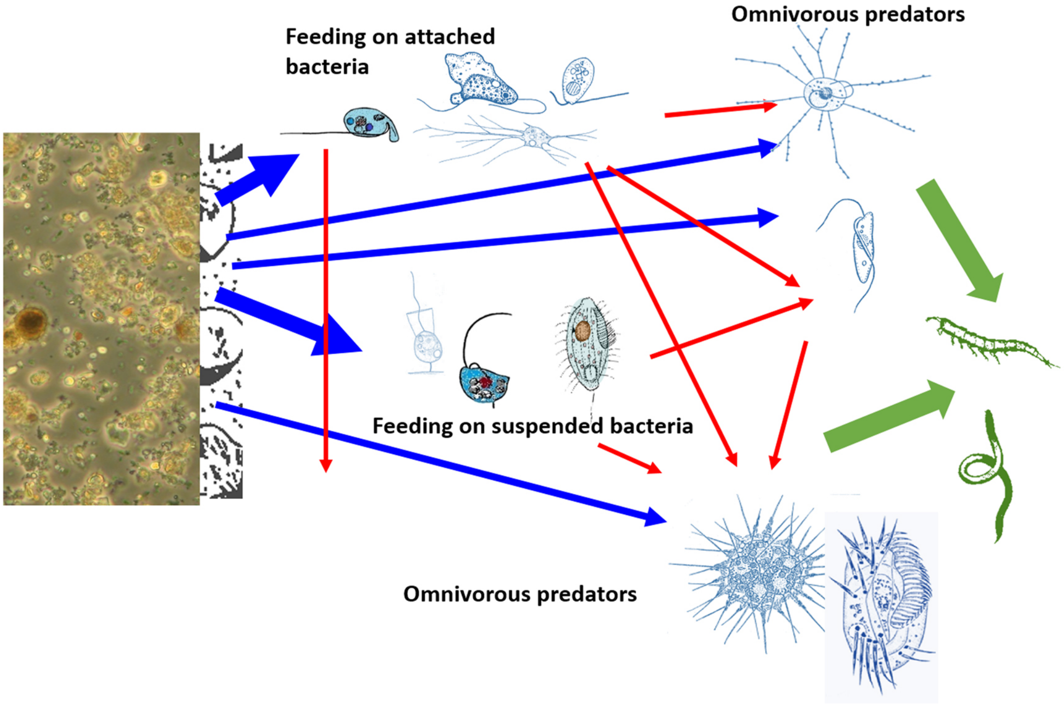

Fig. 4. Hypothetical scheme of deep-sea benthic microbial food webs with protists (several trophic levels) forming an important and essential link to higher trophic levels.

5. Methodological challenges in studying naked deep-sea protists

There are several reasons why no standardized protocol exists for the sampling and analysis of deep-sea protists. (1) Molecular HTS studies may introduce significant biases due to the selectivity of primers, incorrect and incomplete reference data bases, and the difficulty to determine whether genotypes are active. (2) Direct counts of protists in deep-sea sediments are very limited due to their low abundance (2–3 orders of magnitude lower than at littoral sites) and the masking effects of tiny sediment particles. (3) The recovery of deep-sea benthic samples occupies several hours, during which the organisms are exposed to drastic changes in hydrostatic pressures and temperature. (4) Cultivation of deep-sea protists for autecological studies is limited to species that are barotolerant.

To help overcome these and other factors hindering the adequate analysis of deep-sea protistan communities, Schoenle et al. (2016) proposed applying a multi-method approach, thereby reducing artefacts and generating a more realistic picture of community composition. Since HTS alone will certainly produce artefacts and yield little information on the autecology and morphology of target protists or their abundance, it needs to be complemented by direct observations and culture-dependent methods in order to understand the functioning of deep-sea protist biodiversity. Analyzing the functional aspects of deep-sea protist activity is especially challenging, since the handling of deep samples exposes protists to significant pressure changes and alterations of temperature, oxygen and redox conditions. Grazing experiments and molecular analyses involving deep-sea planktonic protists have shown that reliable data can only be obtained when carried out in situ, at the depth in the ocean where the organism lives (Edgcomb 2016; Edgcomb et al. 2016b; Pachiadaki et al. 2014). It is known that bacteria increase the fluidity of cell membranes by incorporation of unsaturated fatty acids as an adaptation to high hydrostatic pressures (Allen et al. 1999; DeLong and Yayanos 1985). These mechanisms need still to be investigated in the case of protists, as do biological processes such as reproduction and feeding at high hydrostatic pressure. Although at least some deep-sea protists are barotolerant (e.g., Živaljić et al. 2018, 2020b), the major part of the protistan communities is probably very sensitive and in-situ field studies are necessary to derive general conclusions.

Problems in molecular barcoding and future perspectives

HTS techniques involve several particular problems. Chimeric sequences derived from PCR amplification artifacts, random sequencing errors, varying rDNA gene copy numbers among different eukaryotes, and the restriction of ‘general’ primers to detect all protist groups, currently present substantial challenges for robust taxonomic interpretations of eukaryotic datasets (e.g. Haas et al. 2011; Kunin et al. 2010; Mahé et al. 2015; Pawlowski et al. 2012). The possibility for selective amplification needs to be considered in the interpretation of results concerning species composition and abundances (Not et al. 2007; Potvin and Lovejoy 2009). Several methods (e.g. regular incorporation of synthetic and known “mock communities” into sequencing) and different pipelines have been developed to remove, mitigate and estimate those biases and problems for downstream analyses (e.g. Yeh et al. 2018). Metabarcoding approaches based on rDNA generally recover the inactive as well as the active part of communities, including extracellular DNA (Dell’Anno 2005; Torti et al. 2015). It is uncertain if genetically detected protist communities are actually thriving on the deep seafloor or are an artifact created by cells originating from the upper water column, encysted cells, or extracellular DNA. Recent attempts to conserve the easy degradable RNA in-situ as an indicator of the active part of the community seem to be promising (Lejzerowicz et al. 2013; Rodríguez-Martínez et al. 2020).

The patchy coverage of reference databases such as GenBank, which still include many incorrectly labeled sequences, are challenging the correct assignment of HTS-obtained sequences to genus/species level (e.g., Weber and Pawlowski 2013). Thus, culturing deep-sea sediment using classical or innovative approaches is also essential to identify and better characterize the newly discovered deep-sea protist diversity and to map sequences to species. A combination of metagenomic approaches has recently been used to obtain promising results for the pelagial (Obiol et al. 2020), but studies with diverse communities on the seafloor are still pending.

Problems in the direct observation of naked protists

In contrast to foraminiferans, parallel analysis of the molecular and morphological diversity of naked protists such as nanoflagellates, ciliates or amoebae has only occasionally been attempted (Schoenle et al. 2016). As previously mentioned, a major problem is that naked protists, which are only protected by a membrane rather than a test, are easily disrupted during the transport of samples from the deep seafloor to the surface. However, promising methodological developments are allowing the recovery and study of deep-sea microbes at ambient hydrostatic pressures and the fixation of protist cells and stabilization of membranes in situ. Still, the problem remains that much morphological information gets lost during fixation. The direct observation of living cells is not only hindered by their disruption but also due to masking by sediment particles. The efforts of eight microscopists in counting a single sample in parallel on-board ship led to the identification of the first living ciliate from abyssal depths (Živaljić et al. 2020). Investigations in the deep Mediterranean Sea during winter, when surface and deep-sea water temperature were not very different (18°C and 13°C, respectively), allowed live counting and determination of deep-sea benthic protists (Arndt et al. 2003; Hausmann et al. 2002, 2006). These studies suggested that temperature increases during sample recovery may be an important factor limiting in vivo observations of naked deep-sea protists. Another possibility to observe living deep-sea protists is their cultivation in enrichments of autochthonous bacteria. Such cultures may then be used for autecological studies (Schoenle et al. 2017, 2019; Živaljić et al. 2018, 2020a, b). However, this method is currently restricted to barotolerant species. Meanwhile, live representatives of various deep-sea taxa have been reported, including choanoflagellates (Nitsche et al. 2007), kinetoplastids (e.g. Atkins et al. 1998; Scheckenbach et al. 2005) and different stramenopiles (Arndt et al. 2003; Hausmann et al. 2006; Patterson et al. 1993; Schoenle et al. 2020). In an early study, Turley et al. (1988; see also Lochte and Turley 1988) investigated the growth of a barophilic bodonid flagellate from 4500 m at ambient pressures. In-situ studies on feeding and growth rates of naked protists are of great interest for understanding their metabolic activity in the deep sea.

6. The potential role of deep-sea benthic protists

Despite the vastness of the ocean floor, our knowledge of the potential importance of protists within the deep-sea microbial food webs is scant. In the sunlit ocean, protists play a key role within the microbial food web as a link between production by different algal size classes and prokaryotes and higher trophic levels consisting of diverse metazoans. They also act as important nutrient remineralizers in biogeochemical cycles and in many cases are mixotrophs (e.g. Azam and Malfatti 2007; Landry and Calbet 2004). In the deep sea, rapidly-sinking algal detritus may be a very important direct or indirect food source for protists. Some foraminiferans are specialized on this phytodetritus, but naked protists such as flagellates, ciliates and amoebae are also able to utilize it, either directly (Posch and Arndt 1996; Scherwass et al. 2005) or by grazing on associated bacteria and cyanobacteria (Lochte and Turley 1988). Based on knowledge derived from surface waters and the results obtained by HTS studies of benthic protistan communities, we have to assume that a major part of organic carbon in deep-sea sediments is channeled via diverse assemblages of heterotrophic flagellates, ciliates and amoebae, as well as foraminiferans. Due to their ability to form resting stages, these small protists can overcome periods of food shortage (Müller and Müller 1970; Rivera et al. 1994).

Deep-sea protists are likely to form an important and essential link to higher trophic levels by providing biochemically enriched organic matter (Bec et al. 2006; Baker et al. 2018). Foraminiferans, phagotrophic flagellates, ciliates and amoebae are able to feed on suspended organic matter and prokaryotes as well as on particles attached to surfaces. At local hot spots of organic matter, pico- and nano-sized protists can reproduce relatively fast and transfer organic matter to higher trophic levels (e.g. Arndt et al. 2000, 2003). These higher trophic levels may also include (or may typically be) larger protists that follow in their population dynamics the growth of their food organisms. We recently isolated a euplotid ciliate from abyssal depth that can only survive on a flagellate food source (Živaljić et al. 2020).

Spatial patterns in biodiversity, which are shaped by the heterogeneity of deep-sea habitats at large and small spatial scales, are far from being resolved. The elucidation of biodiversity patterns at a global as well as temporal scale is the main challenge in deep-sea microbial ecology (e.g. Logares et al. 2014; Nunes-Alves 2015). Metabarcoding of ciliates has revealed the presence of all groups of nano- and micro-phagous and even predatory ciliates in the deep sea (for review see Schoenle et al. 2017). Diversity estimates derived from HTS studies suggest that the protistan components of deep-sea microbial communities are basically not very different from those found in littoral settings. However, there is a need to evaluate the relative importance of Foraminifera, compared to flagellates, ciliates and amoebae, in their use of different substrates and susceptibility to consumption by larger grazers, as well as their role, already mentioned, as denitrifiers in the global nitrogen cycle (Risgaard-Petersen et al. 2006). Although some are clearly quick-growing opportunists, the possession of a test and their relatively large size suggest that foraminiferans are more likely to be k-strategists than naked protists. The possession of a test may deter non-specialist metazoan predators of foraminiferans, or protect foraminiferans during their passage through the guts of deposit feeders such as holothurians (see above). Future in situ experiments using labelled tracers might provide an answer to this question.

7. Concluding remarks

The deep-sea floor represents the Earth's largest benthic biome, within which protists are by far the most dynamic and productive component after the prokaryotes. Analysing their potential role in the deep sea is essential in order to understand the global carbon cycle. Making progress towards this goal will involve identifying the functional importance of protistan groups and their patterns of geographical distribution. Sampling and investigating deep-sea environments and their inhabitants still present major challenges, especially in the abyss. Most of what we know about small naked deep-sea protists (flagellates, amoebae and ciliates) comes from localised settings such as hydrothermal vents, rather than the overwhelmingly larger abyssal plains. Morphological and especially molecular studies have revealed that these vast areas harbor an enormous yet undiscovered diversity of naked protists. Hence, there is an urgent need for in-situ experiments that consider, in addition to prokaryotes, the activity of small protists as the main transmitters of prokaryotic carbon and potential regulators of prokaryote activity. In Figure 4, we propose that there are several trophic levels among protists channeling sedimented carbon to higher trophic levels.

The Foraminifera represent of a special case. In addition to the usual presence of a protective test, they are typically larger, sometimes much larger, than naked protists, spanning an extraordinary size range from the nanobiota to the megafauna. In this and perhaps other respects, they may have more in common with metazoans than with small, naked protists. A large body of literature exists on deep-sea benthic foraminiferans, concentrated on the more accessible continental margins but also including abyssal plain faunas. However, much of this literature reflects a geological perspective that emphasizes 'hard-shelled', fossilizable, usually multichambered taxa rather than the delicate, often 'soft-shelled', single-chambered monothalamids, which often dominate deep-sea foraminiferal assemblages in terms of abundance and diversity, particularly on abyssal plains. An increasing number of ecological studies, notably in situ and shipboard experiments involving ^{13}C-labelled algal and bacterial food sources, are beginning to reveal something of the role of Foraminifera in deep-sea food webs. Nevertheless, much remains to be learnt, particularly regarding the monothalamids.

Understanding how protists contribute to the functioning of deep-sea ecosystems has wider societal significance in the context of climate change (Bindoff et al. 2019) and likely future human impacts, notably from seabed mining and trawling (Glover and Smith 2003; Hanson et al. 2012; Thurber et al. 2014). Large-scale studies suggest that a close link exists between benthic eukaryotic (nematode) biodiversity and ecosystem functioning, implying that the loss of biodiversity will have a negative impact on deep-sea ecosystems (Danovaro et al. 2008). This relationship is fundamental for understanding an important part of global carbon cycling. The consequences of climate change (warming, acidification, deoxygenation) will likely be profound for deep-sea ecosystems (Bindoff et al. 2019); for example, bottom-water oxygen concentration and food supply to the seafloor will probably decline (Sweetman et al. 2017) and there may be global reductions in benthic biomass (Jones et al. 2014; Yool et al. 2017). A reduced food supply to the abyss will probably favour small-sized organisms including protists (C.R. Smith et al. 2008b). Physical disturbances associated with seabed mining of polymetallic nodules, cobalt-rich crusts, and massive sulphides will also have major and long-lasting, albeit more localized, consequences for benthic communities (Washburn et al. 2019), including the loss of biodiversity (Van Dover et al. 2017) and impaired functioning (Stratmann et al. 2018). Seafloor communities have not recovered after periods of decades from experimental seabed disturbances created in 1989 in the DISCOL area of the Peru Basin and at different sites in the Clarion Clipperton Fracture Zone during the late 1970s to mid-1990s (Jones et al. 2017; Miljutin et al. 2011; Simon-Lledo et al. 2019b; Vanreusel et al. 2016). Similarly, bottom trawling has already been linked to declines in faunal biodiversity, cover and abundance caused by removing most of the benthic fauna (Pusceddu et al. 2014; Thrush and Dayton 2002). A recent review of expert opinion in the context of deep-ocean monitoring and conservation (Danovaro et al. 2020) revealed that many responding scientists considered the ecological importance of microorganisms (protozoans, bacteria and archaea) in water-column and ocean-floor ecosystems to be low compared to that of the macro- and megafauna. We argue instead that protists probably play a substantial role in deep-sea food webs and carbon cycling and should be included in assessments of how benthic communities will respond to these major environmental changes and impacts, as well as more broadly in deep-sea biological research.

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References

Adler, A., Dücker, E., 2018. When Pasteurian Science Went to Sea: The Birth of Marine Microbiology. J. Hist. Biol. 51, 107–133. https://doi.org/10.1007/s10739-017-9477-8

Agusti, S., González-Gordillo, J.I., Vaqué, D., Estrada, M., Cerezo, M.I., Salazar, G., Gasol, J.M., Duarte, C.M., 2015. Ubiquitous healthy diatoms in the deep sea confirm deep carbon injection by the biological pump. Nat. Commun. 6, 1608. https://doi.org/10.1038/ncomms8608

Alldredge, A.L., Silver, M.W., 1988. Characteristics, dynamics and significance of marine snow. Progress. Oceanogr. 20, 41–82. https://doi.org/10.1016/0079-6611(88)90053-5

Allen, E.E., Facciotti, D., Bartlett, D.H., 1999. Monounsaturated but not polyunsaturated fatty acids are required for growth of the deep-sea bacterium Photobacterium profundum SS9 at high pressure and low temperature. Appl. Environ. Microbiol. 65, 1710–1720. https://doi.org/10.1128/AEM.65.4.1710-1720.1999

Alongi, D.M., 1991. Flagellates of benthic communities: their characteristics and methods of study, in: Patterson, D.J., Larson, D.E. (Eds.), The Biology of Free-Living Heterotrophic Flagellates. Clarendon Press, Oxford, UK, pp. 57–75.

Alongi, D.M., 1987. The distribution and composition of deep-sea microbenthos in a bathyal region of the western Coral Sea. Deep Sea Res. Part Oceanogr. Res. Pap. 34, 1245–1254. https://doi.org/10.1016/0198-0149(87)90074-4

Amon, D.J., Ziegler, A.F., Dahlgren, T.G., Glover, A.G., Goineau, A., Gooday, A.J., Wiklund, H., Smith, C.R., 2016. Insights into the abundance and diversity of abyssal megafauna in a polymetallic-nodule region in the eastern Clarion-Clipperton Zone. Sci. Rep. 6. https://doi.org/10.1038/srep30492

Anderson, T.R., Rice, T., 2006. Deserts on the sea floor: Edward Forbes and his azoic hypothesis for a lifeless deep ocean. Endeavour 30, 131–137. https://doi.org/10.1016/j.endeavour.2006.10.003

Arndt, H., Dietrich, D., Auer, B., Cleven, E.-J., Gräfenhan, T., Weitere, M., Mylnikov, A.P., 2000. Functional diversity of heterotrophic flagellates in aquatic ecosystems, in: Leadbeater, B.S., Green, J.C. (Eds.), The Flagellates - Unity, Diversity and Evolution. Taylor & Francis Ltd, London, pp. 240–268.

Arndt, H., Hausmann, K., Wolf, M., 2003. Deep-sea heterotrophic nanoflagellates of the Eastern Mediterranean Sea: Qualitative and quantitative aspects of their pelagic and benthic occurrence. Mar. Ecol. Prog. Ser. 256, 45–56. https://doi.org/10.3354/meps256045

Arnold, A.J., d'Escrivan, F., Parker, W.C., 1985. Predation and avoidance responses in the foraminifera of the Galapagos hydrothermal mounds. J. Foraminifer. Res. 15, 38–42. https://doi.org/10.2113/gsjfr.15.1.38

Atkins, M.S., Anderson, O.R., Wirsen, C.O., 1998. Effect of hydrostatic pressure on the growth rates and encystment of flagellated Protozoa isolated from a deep-sea hydrothermal vent and a deep shelf region. Mar. Ecol. Prog. Ser. 171, 85–95. https://doi.org/10.3354/meps171085

Atkins, M.S., Teske, A.P., Anderson, O.R., 2000. A survey of flagellate diversity at four deep-sea hydrothermal vents in the Eastern Pacific Ocean using structural and molecular approaches. J. Eukaryot. Microbiol. 47, 400–11. https://doi.org/10.1111/j.1550-7408.2000.tb00067.x

Azam, F., Fenchel, T., Field, J.G., Gra, J.S., Meyer-Rei15, L.A., Thingstad, F., 1983. The ecological role of water-column microbes in the sea. Mar. Ecol. Prog. Ser. 10, 257–263. https://doi.org/10.3354/meps010257

Azam, F., Malfatti, F., 2007. Microbial structuring of marine ecosystems. Nat. Rev. Microbiol. 5, 782–791. https://doi.org/10.1038/nrmicro1747

Bak, R.P.M., Nieuwland, G., 1997. Seasonal variation in bacterial and flagellate communities of deep-sea sediments in a monsoonal upwelling system. Deep Sea Res. Part II Top. Stud. Oceanogr. 44, 1281–1292. https://doi.org/10.1016/S0967-0645(97)00005-2

Baker, P., Minzlaff, U., Schoenle, A., Schwabe, E., Hohlfeld, M., Jeuck, A., Brenke, N., Prausse, D., Rothenbeck, M., Brix, S., Frutos, I., Jörger, K.M., Neusser, T.P., Koppelmann, R., Devey, C., Brandt, A., Arndt, H., 2018. Potential contribution of surface-dwelling Sargassum algae to deep-sea ecosystems in the southern North Atlantic. Deep Sea Res. Part II Top. Stud. Oceanogr., Bathymetry of the Vema-Fracture Zone and Puerto Rico TRench Abyssal AtlaNtic BiodiverSITy Study (Vema-TRANSIT) 148, 21–34. https://doi.org/10.1016/j.dsr2.2017.10.002

Bailey, J.W., 1851. Microscopical examination of soundings made off the coast of the United States by the U.S. Coast Survey. Smithsonian Contrib. Knowledge, Vol. 2, Art. 3, 15 pp. + 1 pl

Bailey, J.W., 1855. Microscopical examination of deep soundings from the Atlantic Ocean. Q. J. Microsc. Sci. 3, 89–91

Bailey, J.W. 1856. Notice of microscopic forms found in the soundings of the Sea of Kamtschatka- with a plate. Amer. J. Sci. Arts, 22:1–6.

Bailey, J.W., 1857. Report upon the results of microscopic examinations of the soundings made by Lieut. Berryman of the U.S. Navy, on his recent voyages to and from Ireland in the Arctic. Amer. J. Sci. Arts, 23:153–157

Barron, E.J., Whitman, J.M., 1981. Oceanic sediments in space and time. In: Emiliani, C. (Ed.), The Oceanic Lithosphere. The Sea volume 7. John Wiley and sons, New York, Chichester, Brisbane, Toronto, Singapore, pp. 689–731.

Bartsch, I., Dovgal, I.V., 2010. A hydrothermal vent mite (Halacaridae, Acari) with a new *Corynophrya* species (Suctoria, Ciliophora), description of the suctorian and its distribution on the halacarid mite. Eur. J. Protistol. 46, 196–203.

Beaulieu, S., 2002. Accumulation and Fate of Phytodetritus on the Sea Floor, in: Atkinson, R., Barnes, M. (Eds.), Oceanography and Marine Biology, An Annual Review, Volume 40, Oceanography and Marine Biology - An Annual Review. CRC Press, pp. 171–232. https://doi.org/10.1201/9780203180594.ch4

Bec, A., Martin-Creuzburg, D., von Elert, E., 2006. Trophic upgrading of autotrophic picoplankton by the heterotrophic nanoflagellate *Paraphysomonas* sp. Limnol. Oceanogr. 51, 1699–1707. https://doi.org/10.4319/lo.2006.51.4.1699

Bernard, C., Simpson, A.G.B., Patterson, D.J., 2000. Some free-living flagellates (protista) from anoxic habitats. Ophelia 52, 113–142. https://doi.org/10.1080/00785236.1999.10409422

Bernhard, J.M., 2003. Potential symbionts in bathyal foraminifera. Science 299, 861–861. https://doi.org/10.1126/science.1077314

Bernhard, J.M., Bowser, S.S., 2008. Peroxisome proliferation in foraminifera inhabiting the chemocline: an adaptation to reactive oxygen species exposure? J. Eukaryot. Microbiol. 55, 135–144. https://doi.org/10.1111/j.1550-7408.2008.00318.x

Bernhard, J.M., Buck, K.R., Farmer, M.A., Bowser, S.S., 2000. The Santa Barbara Basin is a symbiosis oasis. Nature 403, 77–80. https://doi.org/10.1038/47476

Bernhard, Joan M, Edgcomb, V.P., Casciotti, K.L., McIlvin, M.R., Beaudoin, D.J., 2012a. Denitrification likely catalyzed by endobionts in an allogromiid foraminifer. ISME J. 6, 951–960. https://doi.org/10.1038/ismej.2011.171

Bernhard, Joan M., Casciotti, K.L., McIlvin, M.R., Beaudoin, D.J., Visscher, P.T., Edgcomb, V.P., 2012b. Potential importance of physiologically diverse benthic foraminifera in sedimentary nitrate storage and respiration. J. Geophys. Res. Biogeosciences 117, G03002. https://doi.org/10.1029/2012JG001949

Bernhard, J.M., Habura, A., Bowser, S.S., 2006. An endobiont-bearing allogromiid from the Santa Barbara Basin: Implications for the early diversification of foraminifera. J. Geophys. Res. Biogeosciences 111, G03002. https://doi.org/10.1029/2005JG000158

Bernhard, J.M., Kormas, K., Pachiadaki, M.G., Rocke, E., Beaudoin, D.J., Morrison, C., Visscher, P.T., Cobban, A., Starczak, V.R., Edgcomb, V.P., 2014. Benthic protists and fungi of Mediterranean deep hypsersaline anoxic basin redoxcline sediments. Front. Microbiol. 5, 605. https://doi.org/10.3389/fmicb.2014.00605

Bernhard, J.M., Sen Gupta, Barum K., 1999. Foraminifera of oxygen-depleted environments, in: Sen Gupta, Barun K. (Ed.), Modern Foraminifera. Springer Netherlands, Dordrecht, pp. 201–216. https://doi.org/10.1007/0-306-48104-9_12

Bernhard, J.M., Sen Gupta, B.K., Borne, P.F., 1997. Benthic foraminiferal proxy to estimate dysoxic bottom-water oxygen concentrations; Santa Barbara Basin, U.S. Pacific continental margin. J. Foraminifer. Res. 27, 301–310. https://doi.org/10.2113/gsjfr.27.4.301

Bernstein, B.B., Hessler, R.R., Smith, R., Jumars, P.A., 1978. Spatial dispersion of benthic Foraminifera in the abyssal central North Pacific. Limnol. Oceanogr. 23, 401–416. https://doi.org/10.4319/lo.1978.23.3.0401

Bertagnolli, A.D., Stewart, F.J., 2018. Microbial niches in marine oxygen minimum zones. Nat. Rev. Microbiol. 16, 723–729. https://doi.org/10.1038/s41579-018-0087-z

Bertram, M.A., Cowen, J.P., 1999. Temporal variations in the deep-water colonization rates of small benthic foraminifera: the results of an experiment on Cross Seamount. Deep Sea Res. Part Oceanogr. Res. Pap. 46, 1021–1049. https://doi.org/10.1016/S0967-0637(98)00104-6

Bett, B.J., 2001. UK Atlantic Margin Environmental Survey: Introduction and overview of bathyal benthic ecology. Cont. Shelf Res. 21, 917–956. https://doi.org/10.1016/S0278-4343(00)00119-9

Billett, D.S.M., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C., 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature 302, 520–522. https://doi.org/10.1038/302520a0

Bindoff, N.L., Cheung, W.W.L, Kairo, J.G., Aristegui, J., Guinder, V.A., Hallberg, R., Hilmi, N., Jiao, N., Karim, M.S., Levin, L., O'Donoghue, S., Purca Cuicapusa, S.R., Rinkevich, B., Suga, T., Tagliabue, A., Williamson, P., 2019. Changing ocean, marine ecosystems, and dependent commuities. In: Pörtner, H.-

O., Roberts, D.C., Masson-Delmotte, V., Zhai, P., Tignor, M., Poloczanska, E., Mintenbeck, K., Alegria, A., Nicolai, M., Okem, A., Petzold, J., Rama, B., Weyer, N.M. (Eds.), IPCC Special Report on the Ocean and Cryosphere in a Changing Climate, pp. 447–587. https://www.ipcc.ch/site/assets/uploads/sites/3/2019/11/09_SROCC_Ch05_FINAL-1.pdf

Boeuf, D., Edwards, B.R., Eppley, J.M., Hu, S.K., Poff, K.E., Romano, A.E., Caron, D.A., Karl, D.M., DeLong, E.F., 2019. Biological composition and microbial dynamics of sinking particulate organic matter at abyssal depths in the oligotrophic open ocean. Proc. Natl. Acad. Sci. 201903080. https://doi.org/10.1073/pnas.1903080116

Brady, H.B., 1883. *Syringammina,* a new type of arenaceous Rhizopoda. P. Roy. Soc. 35, 155–161.

Brady, H.B., 1884. Report on the Foraminifera dredged by H.M.S. Challenger during the years 1873–1876. *Reports on the Scientific Results of the Voyage of the H.M.S. Challenger During the Years 1873–1876, Zoology* 9, 1–814.

Burkett, A.M., Rathburn, A.E., Elena Pérez, M., Levin, L.A., Martin, J.B., 2016. Colonization of over a thousand Cibicidoides wuellerstorfi (foraminifera: Schwager, 1866) on artificial substrates in seep and adjacent off-seep locations in dysoxic, deep-sea environments. Deep Sea Res. Part Oceanogr. Res. Pap. 117, 39–50. https://doi.org/10.1016/j.dsr.2016.08.011

Burnett, B.R., 1981. Quantitative sampling of nanobiota (microbiota) of the deep-sea benthos - III. The bathyal San Diego Trough. Deep Sea Res. 28, 649–663. https://doi.org/10.1016/0198-0149(81)90127-8

Burnett, B.R., 1979. Quantitative sampling of microbiota of the deep-sea benthos. II. Evaluation of technique and introduction to the biota of the San Diego Through. Trans. Am. Microsc. Soc. 98, 233–242. https://doi.org/10.2307/3226024

Burnett, B.R., 1977. Quantitative sampling of microbiota of the deep-sea benthos—I. Sampling techniques and some data from the abyssal central North Pacific. Deep Sea Res. 24, 781–789. https://doi.org/10.1016/0146-6291(77)90500-8

Caron, D.A., Davis, P.G., Madin, L.P., Sieburth, J.McN., 1982. Heterotrophic bacteria and bacterivorous protozoa in oceanic macroaggregates. Science 218, 795–797. https://doi.org/10.1126/science.218.4574.795

Carpenter, W.B., 1869. On the rhizopodal fauna of the deep sea. Proc. Roy. Soc. London 18, 59–62.

Carpenter, W.B., 1875.The Microscope and its Revealations, 5th Edition. J and A. Churchill, London.

Carpenter, W.B., 1876. On the genus *Astrorhiza* of Sandahl, lately described as *Haeckelina* by Dr. Bessels. Q. J. Microsc. Sci. 16, 221–224, Pl. XIX.

Carpenter, W.B., Thomson C.W., 1868. Preliminary report of dredging operations in the seas to the north of the British Islands, carried on in Her Majesty's steam vessel 'Lightning'. Proc. Roy. Soc. London 17, 168–200.

Carpenter, W.B., Jeffreys, J.G., Thomson C.W., 1869. Preliminary report of the scientific exploration of the deep sea in H.M. surveying-vessel 'Porcupine', during the summer of 1869. Proc. Roy. Soc. London 18, 397–492.

Caulle, C., Mojtahid, M., Gooday, A.J., Jorissen, F.J., Kitazato, H., 2015. Living (Rose-Bengal-stained) benthic foraminiferal faunas along a strong bottom-water oxygen gradient on the Indian margin (Arabian Sea). Biogeosciences 12, 5005–5019. https://doi.org/10.5194/bg-12-5005-2015

Certes, A. 1884. Sur la culture, à l'abri des germes atmosphériques, des eaux et des sédiments rapportés par les expéditions du Travailleur et du Talisman. C. R. Hebd. Seanc. Acad. Sci., Paris, 98:690-693.

Cornelius, N., Gooday, A.J., 2004. 'Live' (stained) deep-sea benthic foraminiferans in the western Weddell Sea: trends in abundance, diversity and taxonomic composition along a depth transect. Deep Sea Res. Part II Top. Stud. Oceanogr. 51, 1571–1602. https://doi.org/10.1016/j.dsr2.2004.06.024

Countway, P.D., Gast, R.J., Dennett, M.R., Savai, P., Rose, J.M., Caron, D.A., 2007. Distinct protistan assemblages characterize the euphotic zone and deep sea (2500 m) of the western North Atlantic (Sargasso Sea and Gulf Stream). Environ. Microbiol. 9, 1219–1232. https://doi.org/10.1111/j.1462-2920.2007.01243.x

Coyne, K.J., Countway, P.D., Pilditch, C. a, Lee, C.K., Caron, D. a, Cary, S.C., 2013. Diversity and distributional patterns of ciliates in Guaymas Basin hydrothermal vent sediments. J. Eukaryot. Microbiol. 60, 433–447. https://doi.org/10.1111/jeu.12051

Culver, S.J., Lipps, J.H., 2003. Predation on and by Foraminifera, in: Kelley, P.H., Kowalewski, M., Hansen, T.A. (Eds.), Predator—Prey Interactions in the Fossil Record. Springer US, Boston, MA, pp. 7–32. https://doi.org/10.1007/978-1-4615-0161-9_2

Cunningham, J.R., Ustach, J.F., 1992. Protozoan numbers and biomass in the sediments of the Blake Outer Ridge. Deep Sea Res. Part Oceanogr. Res. Pap. 39, 789–794. https://doi.org/10.1016/0198-0149(92)90121-9

Danovaro, R., Fanelli, E., Aguzzi, J., Billett, D., Carugati, L., Corinaldesi, C., Dell'Anno, A., Gjerde, K., Jamieson, A.J., Kark, S., McClain, C., Levin, L., Levin, N., Ramirez-Llodra, E., Ruhl, H., Smith, C.R., Snelgrove, P.V.R., Thomsen, L., Van Dover, C.L., Yasuhara, M., 2020. Ecological variables for developing a global deep-ocean monitoring and conservation strategy. Nat. Ecol. Evol. 4, 181–192. https://doi.org/10.1038/s41559-019-1091-z

Danovaro, R., Gambi, C., Dell'Anno, A., Corinaldesi, C., Fraschetti, S., Vanreusel, A., Vincx, M., Gooday, A.J., 2008. Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. Curr. Biol. 18, 1–8. https://doi.org/10.1016/j.cub.2007.11.056

Danovaro, R., Marrale, D., Della Croce, N., Dell'Anno, A., Fabiano, M., 1998. Heterotrophic nanoflagellates, bacteria, and labile organic compounds in continental shelf and deep-sea sediments of the Eastern Meditteranean. Microb. Ecol. 35, 244–255.

David, V., Archibald, J.M., 2016. Evolution: Plumbing the depths of diplonemid diversity. Curr. Biol. 26, R1290–R1292. https://doi.org/10.1016/j.cub.2016.10.050

Davis, P.G., Caron, D.A., Sieburth, J.McN., 1978. Oceanic amoebae from the North Atlantic: culture, distribution, and taxonomy. Trans. Am. Microsc. Soc. 97, 73. https://doi.org/10.2307/3225685

Dayton, P.K., Hessler, R.R., 1972. Role of biological disturbance in maintaining diversity in the deep sea. Deep Sea Reserach Oceanogr. Abstr. 19, 199–204. https://doi.org/10.1016/0011-7471(72)90031-9

de Vargas, C., Audic, S., Henry, N., Decelle, J., Mahé, F., Logares, R., Lara, E., Berney, C., Le Bescot, N., Probert, I., Carmichael, M., Poulain, J., Romac, S., Colin, S., Aury, J.-M., Bittner, L., Chaffron, S., Dunthorn, M., Engelen, S., Flegontova, O., Guidi, L., Horák, A., Jaillon, O., Lima-Mendez, G., Lukeš, J., Malviya, S., Morard, R., Mulot, M., Scalco, E., Siano, R., Vincent, F., Zingone, A., Dimier, C., Picheral, M., Searson, S., Kandels-Lewis, S., Tara Oceans Coordinators, Acinas, S.G., Bork, P., Bowler, C., Gorsky, G., Grimsley, N., Hingamp, P., Iudicone, D., Not, F., Ogata, H., Pesant, S., Raes, J., Sieracki, M.E., Speich, S., Stemmann, L., Sunagawa, S., Weissenbach, J., Wincker, P., Karsenti, E., 2015. Eukaryotic plankton diversity in the sunlit ocean. Science 348, 1261605. https://doi.org/10.1126/science.1261605

del Campo, J., Massana, R., 2011. Emerging diversity within chrysophytes, choanoflagellates and bicosoecids based on molecular surveys. Protist 162, 435–448. https://doi.org/10.1016/j.protis.2010.10.003

Dell'Anno, A., Danovaro, R., 2005. Extracellular DNA Plays a Key Role in Deep-Sea Ecosystem Functioning. Science 309, 2179–2179. https://doi.org/10.1126/science.1117475

DeLong, E.F., Yayanos, A.A., 1985. Adaptation of the membrane lipids of a deep-sea bacterium to changes in hydrostatic pressure. Science 228, 1101–1103.

Devey, C.W., Augustin, N., Brandt, A., Brenke, N., Köhler, J., Lins, L., Schmidt, C., Yeo, I.A., 2018. Habitat characterization of the Vema Fracture Zone and Puerto Rico Trench. Deep Sea Res. Part II Top. Stud. Oceanogr. 148, 7–20. https://doi.org/10.1016/j.dsr2.2018.02.003

Dolan, J.R., Ciobanu, M., Coppola, L., 2019. Past President's Address: Protists of the Mesopelagic and a Bit on the Long Path to the Deep Sea. J. Eukaryot. Microbiol. 66, 966–980. https://doi.org/10.1111/jeu.12744

Douglas, R.G., Woodruff, F., 1981. Deep-sea benthic foraminifera, in: Emiliani, E. (Ed.), The Oceanic Lithosphere, The Sea. John Wiley & Sons, New York, pp. 1233–1327.

Duineveld, G.C.A., Tselepides, A., Witbaard, R., Bak, R.P.M., Berghuis, E.M., Nieuwland, G., van der Weele, J., Kok, A., 2000. Benthic–pelagic coupling in the oligotrophic Cretan Sea. Prog. Oceanogr. 46, 457–481. https://doi.org/10.1016/S0079-6611(00)00029-X

Durden, J.M., Lallier, L.E., Murphy, K., Jaeckel, A., Gjerde, K., Jones, D.O.B., 2018. Environmental Impact Assessment process for deep-sea mining in 'the Area.' Mar. Policy 87, 194–202. https://doi.org/10.1016/j.marpol.2017.10.013

Edgcomb, V.P., 2016. Marine protist associations and environmental impacts across trophic levels in the twilight zone and below. Curr. Opin. Microbiol. 31, 169–175. https://doi.org/10.1016/j.mib.2016.04.001

Edgcomb, V.P., Orsi, W., Bunge, J., Jeon, S., Christen, R., Leslin, C., Holder, M., Taylor, G.T., Suarez, P., Varela, R., Epstein, S., 2011. Protistan microbial observatory in the Cariaco Basin, Caribbean. I. Pyrosequencing vs Sanger insights into species richness. ISME J. 5, 1344–1356. https://doi.org/10.1038/ismej.2011.6

Edgcomb, V.P., Orsi, W., Leslin, C., Epstein, S.S., Bunge, J., Jeon, S., Yakimov, M.M., Behnke, A., Stoeck, T., 2009. Protistan community patterns within the brine and halocline of deep hypersaline anoxic basins in the eastern Mediterranean Sea. Extrem. Life Extreme Cond. 13, 151–167. https://doi.org/10.1007/s00792-008-0206-2

Edgcomb, V.P., Kysela, D.T., Teske, A., de Vera Gomez, A., Sogin, M.L., 2002. Benthic eukaryotic diversity in the Guaymas Basin hydrothermal vent environment. Proc. Natl. Acad. Sci. U. S. A. 99, 7658–7662.

Edgcomb, V.P., Pachiadaki, M.G., Mara, P., Kormas, K.A., Leadbetter, E.R., Bernhard, J.M., 2016a. Gene expression profiling of microbial activities and interactions in sediments under haloclines of E. Mediterranean deep hypersaline anoxic basins. ISME J. 10, 2643–2657. https://doi.org/10.1038/ismej.2016.58

Edgcomb, V.P., Taylor, C., Pachiadaki, M.G., Honjo, S., Engstrom, I., Yakimov, M., 2016b. Comparison of

Niskin vs. in situ approaches for analysis of gene expression in deep Mediterranean Sea water samples. Deep Sea Res. Part II Top. Stud. Oceanogr. 129, 213–222. https://doi.org/10.1016/j.dsr2.2014.10.020

Ehrenberg, C.G., 1844. On microscopic life in the ocean at the South Pole, and at considerable depth. Ann. Mag. Nat. Hist. 14,169–181.

Ehrenberg, C.G., 1854. Charakteristik der neuen mikroskopischen Organismen des tiefen atlantischen Oceans. Ber. Akad. Wiss. Berlin, Jahr 1854, 236–250.

Ehrenberg, C. G., 1858. Über die organischen Lebensformen in unerwartet grossen Tiefen des Mittelmeeres. K. Preuss. Akad. Wiss. Berlin, Monatsberichte, Year 1857, 538–571.

Ehrenberg C. G., 1861. Über den Tiefgrund des stil-len Oceans zwischen Californien und den Sandwich-Inseln aus bis 15600‘ Tiefe nach Lieutenant Brooke. K. Preuss. Akad. Wiss. Berlin, Monatsberichte, Year 1860, 819–833.

Enge, A., Nomaki, H., Ogawa, N., Witte, U., Moeseneder, M., Lavik, G., Ohkouchi, N., Kitazato, H., Kučera, M., Heinz, P., 2011. Response of the benthic foraminiferal community to a simulated short-term phytodetritus pulse in the abyssal North Pacific. Mar. Ecol. Prog. Ser. 438, 129–142. https://doi.org/10.3354/meps09298

Fenchel, T., 2012. Anaerobic eukaryotes, in: Altenbach, A.V., Bernhard, J.M., Seckbach, J. (Eds.), Anoxia, Cellular Origin, Life in Extreme Habitats and Astrobiology. Springer Netherlands, Dordrecht, pp. 3–16. https://doi.org/10.1007/978-94-007-1896-8_1

Flegontova, O., Flegontov, P., Malviya, S., Audic, S., Wincker, P., de Vargas, C., Bowler, C., Lukeš, J., Horák, A., 2016. Extreme diversity of diplonemid eukaryotes in the ocean. Curr. Biol. 26, 3060–3065. https://doi.org/10.1016/j.cub.2016.09.031

Forbes, E. 1844. Report on the mollucs and radiata of the Aegean Sea, and on thier distribution, considerd as bearing on geology. Rep. Thirteenth Mtg. Brit. Assoc. Adv. Sci., 130- 193.

Gage, J.D., 2003. Food utilization, carbon flow and energetics. In: Tyler, P.A. (Ed.), Ecosystems of the Deep Ocean. Ecosystems of the World volume 8. Elsevier, Amsterdam, Boston, London, New York, Oxford, Paris, San Diego, San Francisco, Singapore, Sydney, Toronto, pp. 313–380.

Gage, J., Tyler, P.A., 1991. Deep-sea biology: A natural history of organisms at the deep-sea floor. Cambridge University Press.

Gallo, N.D., James Cameron, Kevin Hardy, Patricia Fryer, Douglas H. Bartlett, Lisa A. Levin, 2015. Submersible- and lander-observed community patterns in the Mariana and New Britain trenches: Influence of productivity and depth on epibenthic and scavenging communities. Deep Sea Res. Part Oceanogr. Res. Pap. 99, 119–133. https://doi.org/10.1016/j.dsr.2014.12.012

Gawryluk, R.M.R., del Campo, J., Okamoto, N., Strassert, J.F.H., Lukeš, J., Richards, T.A., Worden, A.Z., Santoro, A.E., Keeling, P.J., 2016. Morphological identification and single-cell genomics of marine diplonemids. Curr. Biol. 26, 3053–3059. https://doi.org/10.1016/j.cub.2016.09.013

Giner, C.R., Pernice, M.C., Balagué, V., Duarte, C.M., Gasol, J.M., Logares, R., Massana, R., 2020. Marked changes in diversity and relative activity of picoeukaryotes with depth in the world ocean. ISME J. 14, 437–449. https://doi.org/10.1038/s41396-019-0506-9

Glock, N., Roy, A.-S., Romero, D., Wein, T., Weissenbach, J., Revsbech, N.P., Høgslund, S., Clemens, D., Sommer, S., Dagan, T., 2019. Metabolic preference of nitrate over oxygen as an electron acceptor in foraminifera from the Peruvian oxygen minimum zone. Proc. Natl. Acad. Sci. 116, 2860–2865. https://doi.org/10.1073/pnas.1813887116

Glock, N., Schönfeld, J., Eisenhauer, A., Hensen, C., Mallon, J., Sommer, S., 2012. The role of benthic foraminifera in the benthic nitrogen cycle of the Peruvian oxygen minimum zone. Biogeosciences Discuss. 9, 17775–17817. https://doi.org/10.5194/bgd-9-17775-2012

Glover, A.G., Smith, C.R., 2003. The deep-sea floor ecosystem: current status and prospects of anthropogenic change by the year 2025. Environ. Conserv. 30, 219–241. https://doi.org/10.1017/S0376892903000225

Goineau, A., Gooday, A.J., 2019. Diversity and spatial patterns of foraminiferal assemblages in the eastern Clarion–Clipperton zone (abyssal eastern equatorial Pacific). Deep Sea Res. Part Oceanogr. Res. Pap. 149, 103036. https://doi.org/10.1016/j.dsr.2019.04.014

Goineau, A., Gooday, A.J., 2017. Novel benthic foraminifera are abundant and diverse in an area of the abyssal equatorial Pacific licensed for polymetallic nodule exploration. Sci. Rep. 7, 45288. https://doi.org/10.1038/srep45288

Goldstein, S.T., 1999. Foraminifera: A biological overview, in: Sen Gupta, B.K. (Ed.), Modern Foraminifera. Springer Netherlands, Dordrecht, pp. 37–55. https://doi.org/10.1007/0-306-48104-9_3

Gooday, A.J., 2019. Deep-sea benthic Foraminifera, in: Cochran, J., Kirk, J., Bokuniewicz, J.H., Yager, L.P. (Eds.), Encyclopedia of Ocean Science. Elsevier, pp. 684–705.

Gooday, A.J., 2003. Benthic foraminifera (Protista) as tools in deep-water palaeoceanography: Environmental influences on faunal characteristics. Adv. Mar. Biol. 46, 1–90. https://doi.org/10.1016/S0065-2881(03)46002-1

Gooday, A.J., 2002. Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review. J. Oceanogr. 305–332.

Gooday, A.J., 1996. Epifaunal and shallow infaunal foraminiferal communities at three ahyssal NE Atlantic sites subject to differing phytodetritus input regimes. Deep Sea Res. Part Oceanogr. Res. Pap. 43, 1395–1421. https://doi.org/10.1016/S0967-0637(96)00072-6

Gooday, A.J., 1993. Deep-sea benthic foraminiferal species which exploit phytodetritus: Characteristic features and controls on distribution. Mar. Micropaleontol. 22, 187–205. https://doi.org/10.1016/0377-8398(93)90043-W

Gooday, A. J., 1988a. A response by benthic foraminifera to phytodetritus deposition in the deep sea. Nature 332, 70–73. https://doi.org/10.1038/332070a0

Gooday, A.J., 1988b. The genus *Bathysiphon* (Protista, Foraminiferida) in the NE Atlantic: revision of some species described by de Folin (1886). J. Nat. Hist. 22, 71–93. https://doi.org/10.1080/00222938800770061

Gooday, A.J., 1986. Meiofaunal foraminiferans from the bathyal Porcupine Seabight (northeast Atlantic): size structure, standing stock, taxonomic composition, species diversity and vertical distribution in the sediment. Deep Sea Res. Part Oceanogr. Res. Pap. 33, 1345–1373. https://doi.org/10.1016/0198-0149(86)90040-3

Gooday, A.J., Aranda da Silva, A., Pawlowski, J., 2011. Xenophyophores (Rhizaria, Foraminifera) from the Nazaré Canyon (Portuguese margin, NE Atlantic). Deep Sea Res. Part II Top. Stud. Oceanogr. 58, 2401–2419. https://doi.org/10.1016/j.dsr2.2011.04.005

Gooday, A.J., Bernhard, J.M., Levin, L.A., Suhr, S.B., 2000a. Foraminifera in the Arabian Sea oxygen minimum zone and other oxygen-deficient settings: taxonomic composition, diversity, and relation to metazoan faunas. Deep Sea Res. Part II Top. Stud. Oceanogr. 47, 25–54. https://doi.org/10.1016/S0967-0645(99)00099-5

Gooday, A.J., Bett, B.J., Shires, R., Lambshead, P.J.D., 1998. Deep-sea benthic foraminiferal species diversity in the NE Atlantic and NW Arabian sea: a synthesis. Deep Sea Res. Part II Top. Stud. Oceanogr. 45, 165–201. https://doi.org/10.1016/S0967-0645(97)00041-6

Gooday, A.J., Bowser, S.S., Bett, B.J., Smith, C.R., 2000b. A large testate protist, *Gromia sphaerica* sp. nov. (Order Filosea), from the bathyal Arabian Sea. Deep Sea Res. Part II Top. Stud. Oceanogr. 47, 55–73. https://doi.org/10.1016/S0967-0645(99)00100-9

Gooday, A.J., Carstens, M., Thiel, H., 1995. Micro- and nanoforaminifera from abyssal Northeast Atlantic sediments: a preliminary report. Int. Rev. Gesamten Hydrobiol. Hydrogr. 80, 361–383. https://doi.org/10.1002/iroh.19950800223

Gooday, A.J., Cedhagen, T., Kamenskaya, O.E., Cornelius, N., 2007a. The biodiversity and biogeography of komokiaceans and other enigmatic foraminiferan-like protists in the deep Southern Ocean. Deep Sea Res. Part II Top. Stud. Oceanogr. 54, 1691–1719. https://doi.org/10.1016/j.dsr2.2007.07.003

Gooday, A.J., Goineau, A., 2019. The contribution of fine sieve fractions (63–150 µm) to foraminiferal abundance and diversity in an area of the Eastern Pacific Ocean licensed for polymetallic nodule exploration. Front. Mar. Sci. 6, 114. https://doi.org/10.3389/fmars.2019.00114

Gooday, A.J., Goineau, A., Voltski, I., 2015. Abyssal foraminifera attached to polymetallic nodules from the eastern Clarion Clipperton Fracture Zone: a preliminary description and comparison with North Atlantic dropstone assemblages. Mar. Biodivers. 45, 391–412. https://doi.org/10.1007/s12526-014-0301-9

Gooday, A.J., Haynes, J.R., 1983. Abyssal foraminifers, including two new genera, encrusting the interior of *Bathysiphon rusticus* tubes. Deep Sea Res. Part Oceanogr. Res. Pap. 30, 591–614. https://doi.org/10.1016/0198-0149(83)90038-9

Gooday, A.J., Holzmann, M., Caulle, C., Goineau, A., Jones, D.O.B., Kamenskaya, O., Simon-Lledó, E., Weber, A.A.-T., Pawlowski, J., 2017b. New species of the xenophyophore genus *Aschemonella* (Rhizaria: Foraminifera) from areas of the abyssal eastern Pacific licensed for polymetallic nodule exploration. Zool. J. Linn. Soc. 182, 479–499. https://doi.org/10.1093/zoolinnean/zlx052

Gooday, A.J., Holzmann, M., Caulle, C., Goineau, A., Kamenskaya, O., Weber, A.A.-T., Pawlowski, J., 2017. Giant protists (xenophyophores, Foraminifera) are exceptionally diverse in parts of the abyssal eastern Pacific licensed for polymetallic nodule exploration. Biol. Conserv. 207, 106–116. https://doi.org/10.1016/j.biocon.2017.01.006

Gooday, A.J., Holzmann, M., Goineau, A., Pearce, R.B., Voltski, I., Weber, A.A.-T., Pawlowski, J., 2018a. Five new species and two new genera of xenophyophores (Foraminifera: Rhizaria) from part of the abyssal equatorial Pacific licensed for polymetallic nodule exploration. Zool. J. Linn. Soc. 183, 723–748. https://doi.org/10.1093/zoolinnean/zlx093

Gooday, A.J., Hori, S., Todo, Y., Okamoto, T., Kitazato, H., Sabbatini, A., 2004. Soft-walled, monothalamous benthic foraminiferans in the Pacific, Indian and Atlantic Oceans: aspects of biodiversity and biogeography. Deep Sea Res. Part Oceanogr. Res. Pap. 51, 33–53.

https://doi.org/10.1016/j.dsr.2003.07.002

Gooday, A.J., Hughes, J.A., 2002. Foraminifera associated with phytodetritus deposits at a bathyal site in the northern Rockall Trough (NE Atlantic): seasonal contrasts and a comparison of stained and dead assemblages. Mar. Micropaleontol. 46, 83–110. https://doi.org/10.1016/S0377-8398(02)00050-6

Gooday, A.J., Jorissen, F.J., 2012. Benthic foraminiferal biogeography: controls on global distribution patterns in deep-water settings. Annu. Rev. Mar. Sci. 4, 237–262. https://doi.org/10.1146/annurev-marine-120709-142737

Gooday, A.J., Kamenskaya, O.E., Cedhagen, T., 2007b. New and little-known Komokiacea (Foraminifera) from the bathyal and abyssal Weddell Sea and adjacent areas. Zool. J. Linn. Soc. 151, 219–251. https://doi.org/10.1111/j.1096-3642.2007.00326.x

Gooday, A.J., Kitazato, H., Hori, S., Toyofuku, T., 2001. Monothalamous soft-shelled foraminifera at an abyssal site in the North Pacific: a preliminary report. J. Oceanogr. 57, 377–384. https://doi.org/10.1023/A:1012447015771

Gooday, Andrew J., Levin, L.A., Linke, P., Heeger, T., 1992a. The role of benthic foraminifera in deep-sea food webs and carbon cycling, in: Rowe, G.T., Pariente, V. (Eds.), Deep-Sea Food Chains and the Global Carbon Cycle. Springer Netherlands, Kluwer Academic Publishers, Dordrecht, pp. 63–91. https://doi.org/10.1007/978-94-011-2452-2_5

Gooday, Andrew J, Levin, L.A., Thomas, C.L., Hecker, B., 1992b. The distribution and ecology of *Bathysiphon filiformis* Sars and *B. major* de Folin (Protista, Foraminiferida) on the continental slope off North Carolina. J. Foraminifer. Res. 22, 129–146. https://doi.org/10.2113/gsjfr.22.2.129

Gooday, A.J., Nott, J.A., 1982. Intracellular barite crystals in two xenophyophores, *Aschemonella ramuliformis* and *Galatheammina* Sp. (Protozoa: Rhizopoda) with comments on the taxonomy of *A. ramuliformis*. J. Mar. Biol. Assoc. U. K. 62, 595–605. https://doi.org/10.1017/S0025315400019779

Gooday, A.J., Shires, R., Jones, A.R., 1997. Large, deep-sea agglutinated Foraminifera; two differing kinds of organization and their possible ecological significance. J. Foraminifer. Res. 27, 278–291. https://doi.org/10.2113/gsjfr.27.4.278

Gooday, A.J., Sykes, D., Góral, T., Zubkov, M.V., Glover, A.G., 2018c. Micro-CT 3D imaging reveals the internal structure of three abyssal xenophyophore species (Protista, Foraminifera) from the eastern equatorial Pacific Ocean. Sci. Rep. 8. https://doi.org/10.1038/s41598-018-30186-2

Gooday, A.J., Todo, Y., Uematsu, K., Kitazato, H., 2008. New organic-walled Foraminifera (Protista) from the ocean's deepest point, the Challenger Deep (western Pacific Ocean). Zool. J. Linn. Soc. 153, 399–423. https://doi.org/10.1111/j.1096-3642.2008.00393.x

Gooday, A.J., Turley, C.M., 1990. Responses by benthic organisms to inputs of organic material to the ocean floor: a review. Philos. Trans. R. Soc. Math. Phys. Eng. Sci. 331, 119–138. https://doi.org/10.1098/rsta.1990.0060

Graf, G., 1989. Benthic-pelagic coupling in a deep-sea benthic community. Nature 341, 437–439. https://doi.org/10.1038/341437a0

Groisillier, A., Massana, R., Valentin, K., Vaulot, D., Guillou, L., 2006. Genetic diversity and habitats of two enigmatic marine alveolate lineages. Aquat. Microb. Ecol. 42, 277–291. https://doi.org/10.3354/ame042277

Guðmundsson, G., von Schmalensee, M., Svavarsson, J., 2000. Are foraminifers (Protozoa) important food for small isopods (Crustacea) in the deep sea? Deep Sea Res. Part Oceanogr. Res. Pap. 47, 2093–2109. https://doi.org/10.1016/S0967-0637(00)00013-3

Guillou, L., Viprey, M., Chambouvet, A., Welsh, R.M., Kirkham, A.R., Massana, R., Scanlan, D.J., Worden, A.Z., 2008. Widespread occurrence and genetic diversity of marine parasitoids belonging to Syndiniales (Alveolata). Environ. Microbiol. 10, 3349–3365. https://doi.org/10.1111/j.1462-2920.2008.01731.x

Haas, B.J., Gevers, D., Earl, A.M., Feldgarden, M., Ward, D.V., Giannoukos, G., Ciulla, D., Tabbaa, D., Highlander, S.K., Sodergren, E., Methé, B., DeSantis, T.Z., Consortium, T.H.M., Petrosino, J.F., Knight, R., Birren, B.W., 2011. Chimeric 16S rRNA sequence formation and detection in Sanger and 454-pyrosequenced PCR amplicons. Genome Res. 21, 494–504. https://doi.org/10.1101/gr.112730.110

Haeckel, E. 1887. Report on the Radiolaria collected by H.M.S. Challenger during the years 1873–76. pp. i–viii [= 1–8], i–clxxxviii [= 1–188], 1–1803, Pl. 1–140, in: Thomson, C. W. & Murray, J.: Report of the scientific results of the voyage of H.M.S. Challenger during the years 1873–76 under the command of Captain George S. Nares and Captain Frank Tourle Thomson. Zoology - Vol. XVIII [= 18]. London, Edinburgh, Dublin.

Hanson, C.A., Fuhrman, J.A., Horner-Devine, M.C., Martiny, J.B.H., 2012. Beyond biogeographic patterns: processes shaping the microbial landscape. Nat. Rev. Microbiol. 10, 497–506. https://doi.org/10.1038/nrmicro2795

Harting, P., 1863. Bijdrage tot de Kennis der mikroskopische Fauna en Flora van de Banda-Zee, naar aanleiding van een onderzoek van eenige door diepzeeloodingen van 990 tot 4000 vademen uit die zee opgebragte gronden (Vol. 10). CG van der Post.

Hausmann, K., Selchow, P., Scheckenbach, F., Weitere, M., Arndt, H., 2006. Cryptic species in a morphospecies complex of heterotrophic flagellates: The case study of *Caecitellus* spp. Acta Protozool. 45, 415–431.

Hedley, R.H., Rudall, K.M., 1974. Extracellular silk fibres in *Stannophyllum* (Rhizopodea: Protozoa). Cell Tissue Res. 150. https://doi.org/10.1007/BF00220384

Heeger, T., 1990. Elektronenmikroskopische Untersuchungen zur Ernährungsbiologie benthischer Foraminiferen. Berichte aus dem Sonderforschungsbereich 313 21, 1–146.

Herndl, G.J., Reinthaler, T., 2013. Microbial control of the dark end of the biological pump. Nat. Geosci. 6, 718–724. https://doi.org/10.1038/ngeo1921

Hessler, R.R., 1974. The structure of deep benthic communities from central oceanic waters, in: Miller, C.B. (Ed.), The Biology of the Oceanic Pacific. Oregon State University Press, Oregon State University, pp. 79–93.

Høgslund, S., Revsbech, N.P., Cedhagen, T., Nielsen, L.P., Gallardo, V.A., 2008. Denitrification, nitrate turnover, and aerobic respiration by benthic foraminiferans in the oxygen minimum zone off Chile. J. Exp. Mar. Biol. Ecol. 359, 85–91. https://doi.org/10.1016/j.jembe.2008.02.015

Høgslund, S., Cedhagen, T., Bowser, S.S., Risgaard-Petersen, N., 2017. Sinks and sources of intracellular nitrate in gromiids. Front. Microbiol. 6, 617, https://doi. 10.3389/fmicb.2017.00617.

Holbourn, A., Henderson, A.S., MacLeod, N., 2013. Atlas of Benthic Foraminifera. Wiley-Blackwell, West Sussex, UK.

Hooker, J.D., 1845. Notes on some marine animals brought up by deep-sea dredging during the Antarctic voyage of Captain Sir James C. Ross, R.N. Ann. Mag. Nat. Hist. 16, 238–239, DOI:10.1080/037454809495947

Hopwood, J.D., Mann, S., Gooday, A.J., 1997. The crystallography and possible origin of barium sulphate in deep sea rhizopod protists (Xenophyophorea). J. Mar. Biol. Assoc. U. K. 77, 969–987. https://doi.org/10.1017/S002531540003856X

Hughes, J.A., Gooday, A.J., 2004. Associations between living benthic foraminifera and dead tests of *Syringammina fragilissima* (Xenophyophorea) in the Darwin Mounds region (NE Atlantic). Deep Sea Res. Part Oceanogr. Res. Pap. 51, 1741–1758. https://doi.org/10.1016/j.dsr.2004.06.004

Ingole, B., Singh, R., Sautya, S., Dovgal, I., Chatterjee, T., 2010. Report of epibiont *Thecacineta calix* (Ciliophora: Suctorea) on deep-sea Desmodora (Nematoda) from the Andaman Sea, Indian Ocean. Mar. Biodivers. Rec. 3, e46. https://doi.org/10.1017/S1755267209990777

Jamieson, A., 2015. The Hadal Zone – Life in the Deepest Ocean. Cambridge University Press, Cambridge.

Johnson, N.A., Campbell, J.W., Moore, T.S., Rex, M.A., Etter, R.J., McClain, C.R., Dowell, M.D., 2007. The relationship between the standing stock of deep-sea macrobenthos and surface production in the western North Atlantic. Deep Sea Res. Part Oceanogr. Res. Pap. 54, 1350–1360. https://doi.org/10.1016/j.dsr.2007.04.011

Jones, D.O.B., Kaiser, S., Sweetman, A.K., Smith, C.R., Menot, L., Vink, A., Trueblood, D., Greinert, J., Billett, D.S.M., Arbizu, P.M., Radziejewska, T., Singh, R., Ingole, B., Stratmann, T., Simon-Lledó, E., Durden, J.M., Clark, M.R., 2017. Biological responses to disturbance from simulated deep-sea polymetallic nodule mining. PLOS ONE 12, e0171750. https://doi.org/10.1371/journal.pone.0171750

Jones, D.O.B., Yool, A., Wei, C.-L., Henson, S.A., Ruhl, H.A., Watson, R.A., Gehlen, M., 2014. Global reductions in seafloor biomass in response to climate change. Glob. Change Biol. 20, 1861–1872. https://doi.org/10.1111/gcb.12480

Jorissen, F.J., Fontanier, C., Thomas, E., 2007. Chapter seven paleoceanographical proxies based on deep-sea benthic foraminiferal assemblage characteristics, in: Hillaire–Marcel, C., De Vernal, A. (Eds.), Developments in Marine Geology. Elsevier, pp. 263–325. https://doi.org/10.1016/S1572-5480(07)01012-3

Kamenskaya, O., Gooday, A.J., Radziejewska, T., Wawrzyniak-Wydrowska, B., 2012. Large, enigmatic foraminiferan-like protists in the eastern part of the Clarion-Clipperton Fracture Zone (abyssal north-eastern subequatorial Pacific): biodiversity and vertical distribution in the sediment. Mar. Biodivers. 42, 311–327. https://doi.org/10.1007/s12526-012-0114-7

Kamenskaya, O.E., Melnik, V.F., Gooday, A.J., 2013. Giant protists (xenophyophores and komokiaceans) from the Clarion-Clipperton ferromanganese nodule field (eastern Pacific). Biol. Bull. Rev. 3, 388–398. https://doi.org/10.1134/S2079086413050046

Koho, K.A., Piña-Ochoa, E., 2012. Benthic foraminifera: inhabitants of low-oxygen environments. In: Altenbach, A.V., Bernhard, J.M., Seckbach, J. (Eds) Anoxia: Eukaryote Survival and Paleontological Strategies. Cellular Origin, Life in Extreme Habitats and Astrobiology, vol. 21, pp. 249 – 285.

Kniesz, K., Brandt, A., Riehl, T., 2018. Peritrich epibionts on the hadal isopod species *Macrostylis marionae* n. sp. from the Puerto Rico Trench used as indicator for sex-specific behaviour. Deep Sea Res. Part II Top. Stud. Oceanogr. 148, 105–129. https://doi.org/10.1016/j.dsr2.2017.10.007

Kormas, K.A., Pachiadaki, M.G., Karayanni, H., Leadbetter, E.R., Bernhard, J.M., Edgcomb, V.P., 2015. Inter-comparison of the potentially active prokaryotic communities in the halocline sediments of Mediterranean deep-sea hypersaline basins. Extremophiles 19, 949–960. https://doi.org/10.1007/s00792-015-0770-1

Kudryavtsev, A., Pawlowski, J., 2013. *Squamamoeba japonica* n. g. n. sp. (Amoebozoa): A deep- sea amoeba from the Sea of Japan with a novel cell coat structure. Protist 164, 13–23.

Kudryavtsev, A., Pawlowski, J., Smirnov, A., 2018. More amoebae from the deep-sea: Two new marine species of Vexillifera (Amoebozoa, Dactylopodida) with notes on taxonomy of the genus. Eur. J. Protistol. 66, 9–25. https://doi.org/10.1016/j.ejop.2018.07.001

Kunin, V., Engelbrektson, A., Ochman, H., Hugenholtz, P., 2010. Wrinkles in the rare biosphere: pyrosequencing errors can lead to artificial inflation of diversity estimates. Environ. Microbiol. 12, 118–123. https://doi.org/10.1111/j.1462-2920.2009.02051.x

La Cono, V., Smedile, F., Bortoluzzi, G., Arcadi, E., Maimone, G., Messina, E., Borghini, M., Oliveri, E., Mazzola, S., L'Haridon, S., Toffin, L., Genovese, L., Ferrer, M., Giuliano, L., Golyshin, P.N., Yakimov, M.M., 2011. Unveiling microbial life in new deep-sea hypersaline Lake Thetis. Part I: Prokaryotes and environmental settings: Prokaryotes in deep-sea brine Lake Thetis. Environ. Microbiol. 13, 2250–2268. https://doi.org/10.1111/j.1462-2920.2011.02478.x

Landry, M., Calbet, A., 2004. Microzooplankton production in the oceans. ICES J. Mar. Sci. 61, 501–507. https://doi.org/10.1016/j.icesjms.2004.03.011

Langer, M.R., Lipps, J.H., Moreno, G., 1995. Predation on foraminifera by the dentaliid deep-sea scaphopod *Fissidentalium megathyris*. Deep Sea Res. Part Oceanogr. Res. Pap. 42, 849–857. https://doi.org/10.1016/0967-0637(95)00025-2

Lara, E., Moreira, D., Vereshchaka, A., López-García, P., 2009. Pan-oceanic distribution of new highly diverse clades of deep-sea diplonemids. Environ. Microbiol. 11, 47–55. https://doi.org/10.1111/j.1462-2920.2008.01737.x

Larkin, K.E., Gooday, A.J., 2009. Foraminiferal faunal responses to monsoon-driven changes in organic matter and oxygen availability at 140 and 300m water depth in the NE Arabian Sea. Deep Sea Res. Part II Top. Stud. Oceanogr. 56, 403–421. https://doi.org/10.1016/j.dsr2.2008.05.037

Lecroq, B., Gooday, A.J., Cedhagen, T., Sabbatini, A., Pawlowski, J., 2009. Molecular analyses reveal high levels of eukaryotic richness associated with enigmatic deep-sea protists (Komokiacea). Mar. Biodivers. 39, 45–55. https://doi.org/10.1007/s12526-009-0006-7

Lecroq, B., Lejzerowicz, F., Bachar, D., Christen, R., Esling, P., Baerlocher, L., Osteras, M., Farinelli, L., Pawlowski, J., 2011. Ultra-deep sequencing of foraminiferal microbarcodes unveils hidden richness of early monothalamous lineages in deep-sea sediments. Proc. Natl. Acad. Sci. 108, 13177–13182. https://doi.org/10.1073/pnas.1018426108

Lejzerowicz, F., Esling, P., Pawlowski, J., 2014. Patchiness of deep-sea benthic Foraminifera across the Southern Ocean: Insights from high-throughput DNA sequencing. Deep Sea Res. Part II Top. Stud. Oceanogr. 108, 17–26. https://doi.org/10.1016/j.dsr2.2014.07.018

Lejzerowicz, F., Voltsky, I., Pawlowski, J., 2013. Identifying active foraminifera in the Sea of Japan using metatranscriptomic approach. Deep Sea Res. Part II Top. Stud. Oceanogr. 86–87, 214–220. https://doi.org/10.1016/j.dsr2.2012.08.008

Levin, L.A., 1991. Interactions between metazoans and large, agglutinating protozoans: Implications for the community structure of deep-sea benthos. Am. Zool. 31, 886–900. https://doi.org/10.1093/icb/31.6.886

Levin, L.A., 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. Oceanogr. Mar. Biol. Annu. Rev. 41, 1–45.

Levin, L. A., 2005. Ecology of cold seep sediments: interactions of fauna with flow, chemistry, and microbes. Oceanogr. Mar. Biol. Ann. Rev. 43, 1–46. https://doi: 10.1201/9781420037449.ch1

Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. Annu. Rev. Ecol. Syst. 32, 51–93. https://doi.org/10.1146/annurev.ecolsys.32.081501.114002

Levin, L.A., Rouse, G.W., 2020. Giant protists (xenophyophores) function as fish nurseries. Ecology 101. https://doi.org/10.1002/ecy.2933

Levin, L.A., Thomas, C.L., 1988. The ecology of xenophyophores (Protista) on eastern Pacific seamounts. Deep Sea Res. Part Oceanogr. Res. Pap. 35, 2003–2027. https://doi.org/10.1016/0198-0149(88)90122-7

Lighthart, B., 1969. Planktonic and benthic bacterivorous protozoa at eleven stations in Puget Bay, Australia. J. Fish. Res. Board Can. 26, 299–304. https://doi.org/10.1139/f69-030

Lipps, J.H., 1983. Biotic Interactions in Benthic Foraminifera, in: Tevesz, M.J.S., McCall, P.L. (Eds.), Biotic Interactions in Recent and Fossil Benthic Communities. Springer US, Boston, MA, pp. 331–376. https://doi.org/10.1007/978-1-4757-0740-3_8

Lipps, J.H., Valentine, J.W., 1970. The role of Foraminifera in the trophic structure of marine communities. Lethaia 3, 279–286. https://doi.org/10.1111/j.1502-3931.1970.tb01271.x

Liu, W., Yi, Z., Xu, D., Clamp, J.C., Li, J., Lin, X., Song, W., 2015. Two new genera of planktonic ciliates and insights into the evolution of the family strombidiidae (Protista, Ciliophora, Oligotrichia). PLOS ONE 10, e0131726. https://doi.org/10.1371/journal.pone.0131726

Lochte, K., Turley, C.M., 1988. Bacteria and cyanobacteria associated with phytodetritus in the deep sea. Nature 333, 67–69. https://doi.org/10.1038/333067a0

Loeblich, A.R., Tappan, H., 1964. Protista 2. Sarcodina chiefly ‘Thecamoebians’ and Foraminiferida. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, Part C, 2 vols, 1–900.

Loeblich, A. R., Tappan, H., 1987. Foraminiferal Genera and their Classification, v.1–2, Van Nostrand Reinhold, N.Y.

Logares, R., Audic, S., Bass, D., Bittner, L., Boutte, C., Christen, R., Claverie, J.-M., Decelle, J., Dolan, J.R., Dunthorn, M., Edvardsen, B., Gobet, A., Kooistra, W.H.C.F., Mahé, F., Not, F., Ogata, H., Pawlowski, J., Pernice, M.C., Romac, S., Shalchian-Tabrizi, K., Simon, N., Stoeck, T., Santini, S., Siano, R., Wincker, P., Zingone, A., Richards, T.A., de Vargas, C., Massana, R., 2014. Patterns of rare and abundant marine microbial eukaryotes. Curr. Biol. 24, 813–821. https://doi.org/10.1016/j.cub.2014.02.050

López-García, P., Philippe, H., Gail, F., Moreira, D., 2003. Autochthonous eukaryotic diversity in hydrothermal sediment and experimental microcolonizers at the Mid-Atlantic Ridge. Proc. Natl. Acad. Sci. U. S. A. 100, 697–702. https://doi.org/10.1073/pnas.0235779100

López-García, P., Rodríguez-Valera, F., Pedrós-Alió, C., Moreira, D., 2001. Unexpected diversity of small eukaryotes in deep-sea Antarctic plankton. Nature 409, 603–607. https://doi.org/10.1038/35054537

Lutze, G.F., Altenbach, A.V., 1988. *Rupertina stabilis* (Wallich), a highly adapted, suspension feeding foraminifer. Meyniana 40, 55–69.

Lynch, M.D.J., Neufeld, J.D., 2015. Ecology and exploration of the rare biosphere. Nat. Rev. Microbiol. 13, 217–229. https://doi.org/10.1038/nrmicro3400

Mahé, F., Rognes, T., Quince, C., de Vargas, C., Dunthorn, M., 2015. Swarm v2: highly-scalable and high-resolution amplicon clustering. PeerJ 3, e1420. https://doi.org/10.7717/peerj.1420

Mallon, J., Glock, N., Schönfeld, J., 2012. The Response of Benthic Foraminifera to Low-Oxygen Conditions of the Peruvian Oxygen Minimum Zone, in: Altenbach, A.V., Bernhard, J.M., Seckbach, J. (Eds.), Anoxia, Cellular Origin, Life in Extreme Habitats and Astrobiology. Springer Netherlands, Dordrecht, pp. 305–321. https://doi.org/10.1007/978-94-007-1896-8_16

Martin-Creuzburg, D., Bec, A., von Elert, E., 2006. Supplementation with sterols improves food quality of a ciliate for *Daphnia magna*. Protist 157, 477–486. https://doi.org/10.1016/j.protis.2006.07.001

Massana, R., Castresana, J., Balague, V., Guillou, L., Romari, K., Groisillier, A., Valentin, K., Pedros-Alio, C., 2004. Phylogenetic and ecological analysis of novel marine stramenopiles. Appl. Environ. Microbiol. 70, 3528–3534. https://doi.org/10.1128/AEM.70.6.3528-3534.2004

Menzies, R. J., George, R. Y., Rowe, G. T., 1973. Abyssal environment and ecology of the world oceans. New York, Wiley, 488 pp.

Mills, E.L., 1983. Problems of deep-sea biology: an historical perspective. In: Rowe, G.T. (Ed.). The Sea, Volume 8: Deep-Sea Biology. Harvard University Press, Cambridge, MA, pp. 1–79.

Miljutin, D.M., Miljutina, M.A., Arbizu, P.M., Galéron, J., 2011. Deep-sea nematode assemblage has not recovered 26 years after experimental mining of polymetallic nodules (Clarion-Clipperton Fracture Zone, Tropical Eastern Pacific). Deep Sea Res. Part Oceanogr. Res. Pap. 58, 885–897. https://doi.org/10.1016/j.dsr.2011.06.003

Molari, M., Manini, E., Dell'Anno, A., 2013. Dark inorganic carbon fixation sustains the functioning of benthic deep-sea ecosystems. Glob. Biogeochem. Cycles 27, 212–221. https://doi.org/10.1002/gbc.20030

Moodley, L., Middelburg, J., Boschker, H., Duineveld, G., Pel, R., Herman, P., Heip, C., 2002. Bacteria and Foraminifera: key players in a short-term deep-sea benthic response to phytodetritus. Mar. Ecol. Prog. Ser. 236, 23–29. https://doi.org/10.3354/meps236023

Moran, D.M., Anderson, O.R., Dennett, M.R., Caron, D.A., Gast, R.J., 2007. A description of seven antarctic marine gymnamoebae including a new subspecies, two new species and a new genus: *Neoparamoeba aestuarina antarctica* n. subsp., *Platyamoeba oblongata* n. sp., *Platyamoeba contorta* n. sp. and *Vermistella antarctica* n. gen. n. sp. J. Eukaryot. Microbiol. 54, 169–183. https://doi.org/10.1111/j.1550-7408.2007.00249.x

Moreira, D., López-García, P., 2002. The molecular ecology of microbial eukaryotes unveils a hidden world. Trends Microbiol. 10, 31–38. https://doi.org/S0966-842X(01)02257-0

Morgan-Smith, D., Garrison, C.E., Bochdansky, A.B., 2013. Mortality and survival of cultured surface-ocean flagellates under simulated deep-sea conditions. J. Exp. Mar. Biol. Ecol. 445, 13–20. https://doi.org/10.1016/j.jembe.2013.03.017

Morton, J.E., 1959. The habits and feeding organs of *Dentalium entalis*. J. Mar. Biol. Assoc. U. K. 38, 225–238.

Müller, J.A., Müller, W.P., 1970. *Colpoda Cucullus*: a terrestrial auqatic. Am. Midl. Nat. 84, 1–12.

Müller, P.J., Suess, E., 1979. Productivity, sedimentation rate, and sedimentary organic matter in the oceans—I. Organic carbon preservation. Deep Sea Res. Part Oceanogr. Res. Pap. 26, 1347–1362. https://doi.org/10.1016/0198-0149(79)90003-7

Mullineaux, L.S., 1988. The role of settlement in structuring a hard-substratum community in the deep sea. J. Exp. Mar. Biol. Ecol. 120, 247–261. https://doi.org/10.1016/0022-0981(88)90005-6

Mullineaux, L.S., 1987. Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. Deep Sea Res. Part Oceanogr. Res. Pap. 34, 165–184. https://doi.org/10.1016/0198-0149(87)90080-X

Murray, J.W., 1991. Ecology and Palaeoecology of Benthic Foraminifera. Longman Scientific and Technical, Harlow.

Murray, J.W., 2006. Ecology and Applications of Benthic Foraminifera. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511535529

Nitsche, F., Weitere, M., Scheckenbach, F., Hausmann, K., Wylezich, C., Arndt, H., 2007. Deep sea records of choanoflagellates with a description of two new species. Acta Protozool. 46, 99.

Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Kitazato, H., 2005. Species-specific ingestion of organic carbon by deep-sea benthic foraminifera and meiobenthos: In situ tracer experiments. Limnol. Oceanogr. 50, 134–146. https://doi.org/10.4319/lo.2005.50.1.0134

Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Ohkouchi, N., Ogawa, N., Kogure, K., Ikemoto, E., Kitazato, H., 2006. Different ingestion patterns of 13C-labeled bacteria and algae by deep-sea benthic foraminifera. Mar. Ecol. Prog. Ser. 310, 95–108. https://doi.org/10.3354/meps310095

Nomaki, H., Ogawa, N., Ohkouchi, N., Suga, H., Toyofuku, T., Shimanaga, M., Nakatsuka, T., Kitazato, H., 2008. Benthic foraminifera as trophic links between phytodetritus and benthic metazoans: carbon and nitrogen isotopic evidence. Mar. Ecol. Prog. Ser. 357, 153–164. https://doi.org/10.3354/meps07309

Nomaki, H., Ogawa, N., Takano, Y., Suga, H., Ohkouchi, N., Kitazato, H., 2011. Differing utilization of glucose and algal -particulate organic matter by deep-sea benthic organisms of Sagami Bay, Japan. Mar. Ecol. Prog. Ser. 431, 11–24. https://doi.org/10.3354/meps09144

Nomaki, H., Ohkouchi, N., Heinz, P., Suga, H., Chikaraishi, Y., Ogawa, N.O., Matsumoto, K., Kitazato, H., 2009. Degradation of algal lipids by deep-sea benthic foraminifera: An in situ tracer experiment. Deep Sea Res. Part Oceanogr. Res. Pap. 56, 1488–1503. https://doi.org/10.1016/j.dsr.2009.04.013

Norman, A.M., 1878. On the genus *Haliphysema*, with descriptions of several forms apparently allied to it. Ann. Mag. Nat. Hist. Series 5, 1, 265–284, pl. XVI.

Not, F., Gausling, R., Azam, F., Heidelberg, J.F., Worden, A.Z., 2007. Vertical distribution of picoeukaryotic diversity in the Sargasso Sea. Environ. Microbiol. 9, 1233–1252. https://doi.org/10.1111/j.1462-2920.2007.01247.x

Nozawa, F., Kitazato, H., Tsuchiya, M., Gooday, A.J., 2006. 'Live' benthic foraminifera at an abyssal site in the equatorial Pacific nodule province: Abundance, diversity and taxonomic composition. Deep Sea Res. Part Oceanogr. Res. Pap. 53, 1406–1422. https://doi.org/10.1016/j.dsr.2006.06.001

Nunes-Alves, C., 2015. Deep sequencing of the global oceans: Marine microbiology. Nat. Rev. Microbiol. 13, 397–397. https://doi.org/10.1038/nrmicro3509

Obiol, A., Giner, C.R., Sánchez, P., Duarte, C.M., Acinas, S.G., Massana, R., 2020. A metagenomic assessment of microbial eukaryotic diversity in the global ocean. Mol. Ecol. Resour. 00, 1–14. https://doi.org/10.1111/1755-0998.13147

Ohkawara, N., Kitazato, H., Uematsu, K., Gooday, A.J., 2009. A minute new species of *Saccammina* (monothalamous Foraminifera; Protista) from the abyssal Pacific. J. Micropalaeontology 28, 143–151. https://doi.org/10.1144/jm.28.2.143

Orsi, W.D., 2018. Ecology and evolution of seafloor and subseafloor microbial communities. Nat. Rev. Microbiol. 16, 671–683. https://doi.org/10.1038/s41579-018-0046-8

Pachiadaki, M.G., Taylor, C., Oikonomou, A., Yakimov, M.M., Stoeck, T., Edgcomb, V.P., 2016. In situ grazing experiments apply new technology to gain insights into deep-sea microbial food webs. Deep Sea Res. Part II Top. Stud. Oceanogr. 129, 223–231. https://doi.org/10.1016/j.dsr2.2014.10.019

Pachiadaki, M.G., Yakimov, M.M., LaCono, V., Leadbetter, E., Edgcomb, V.P., 2014. Unveiling microbial activities along the halocline of Thetis, a deep-sea hypersaline anoxic basin. ISME J. 8, 2478–2489. https://doi.org/10.1038/ismej.2014.100

Pasulka, A., Hu, S.K., Countway, P.D., Coyne, K.J., Cary, S.C., Heidelberg, K.B., Caron, D.A., 2019. SSU-rRNA gene sequencing survey of benthic microbial eukaryotes from Guaymas Basin hydrothermal vent. J. Eukaryot. Microbiol. 0, 1–17. https://doi.org/10.1111/jeu.12711

Pasulka, A.L., Goffredi, S.K., Tavormina, P.L., Dawson, K.S., Levin, L.A., Rouse, G.W., Orphan, V.J., 2017. Colonial tube-dwelling ciliates influence methane cycling and microbial diversity within methane seep ecosystems. Front. Mar. Sci. 3. https://doi.org/10.3389/fmars.2016.00276

Patterson, D.J., Nygaard, K., Steinberg, G., Turley, C.M., 1993. Heterotrophic flagellates and other protists associated with oceanic detritus throughout the water column in the mid North Atlantic. J. Mar. Biol. Assoc. U. K. 73, 67. https://doi.org/10.1017/S0025315400032653

Pawlowski, J., Audic, S., Adl, S.M., Bass, D., Belbahri, L., Berney, C., Bowser, S.S., Cepicka, I., Decelle, J., Dunthorn, M., Fiore-Donno, A.M., Gile, G.H., Holzmann, M., Jahn, R., Jirku, M., Keeling, P.J., Kostka, M., Kudryavtsev, A., Lara, E., Lukeš, J., Mann, D.G., Mitchell, E.A.D., Nitsche, F., Romeralo, M., Saunders, G.W., Simpson, A.G.B., Smirnov, A.V., Spouge, J.L., Stern, R.F., Stoeck, T., Zimmermann, J., Schindel, D., de Vargas, C., 2012. CBOL Protist working group: Barcoding eukaryotic richness beyond the animal, plant and fungal kingdoms. PLoS Biol. 10, e1001419.

Pawlowski, J., Fahrni, J., Lecroq, B., Longet, D., Cornelius, N., Excoffier, L., Cedhagen, T., Gooday, A.J., 2007. Bipolar gene flow in deep-sea benthic foraminifera. Mol. Ecol. 16, 4089–4096. https://doi.org/10.1111/j.1365-294X.2007.03465.x

Pawlowski, J., Fontaine, D., da Silva, A.A., Guiard, J., 2011. Novel lineages of Southern Ocean deep-sea foraminifera revealed by environmental DNA sequencing. Deep Sea Res. Part II Top. Stud. Oceanogr. 58, 1996–2003. https://doi.org/10.1016/j.dsr2.2011.01.009

Pawlowski, J., Holzmann, M., 2014. A plea for DNA barcoding of Foraminifera. J. Foraminifer. Res. 44, 62–67. https://doi.org/10.2113/gsjfr.44.1.62

Pawlowski, J., Holzmann, M., Fahrni, J., Richardson, S.L., 2003. Small subunit ribosomal DNA suggests that the xenophyophorean *Syringammina corbicula* is a foraminiferan. J. Eukaryot. Microbiol. 50, 483–487. https://doi.org/10.1111/j.1550-7408.2003.tb00275.x

Pawlowski, J., Lejzerowicz, F., Esling, P., 2014. Next-generation environmental diversity surveys of Foraminifera: Preparing the future. Biol. Bull. 227, 93–106. https://doi.org/10.1086/BBLv227n2p93

Pedrós-Alió, C., 2012. The rare bacterial biosphere. Annu. Rev. Mar. Sci. 4, 449–466. https://doi.org/10.1146/annurev-marine-120710-100948

Pernice, M.C., Giner, C.R., Logares, R., Perera-Bel, J., Acinas, S.G., Duarte, C.M., Gasol, J.M., Massana, R., 2016. Large variability of bathypelagic microbial eukaryotic communities across the world's oceans. ISME J. 10, 945–958. https://doi.org/10.1038/ismej.2015.170

Phleger, F.B., Soutar, A., 1973. Production of benthic foraminifera in three east Pacific oxygen minima. Micropaleontol., 19, 110-115.

Piña-Ochoa, E., Hogslund, S., Geslin, E., Cedhagen, T., Revsbech, N.P., Nielsen, L.P., Schweizer, M., Jorissen, F., Rysgaard, S., Risgaard-Petersen, N., 2010. Widespread occurrence of nitrate storage and denitrification among Foraminifera and Gromiida. Proc. Natl. Acad. Sci. 107, 1148–1153. https://doi.org/10.1073/pnas.0908440107

Posch, T., Arndt, H., 1996. Uptake of sub-micrometre- and micrometre-sized detrital particles by bacterivorous and omnivorous ciliates. Aquat. Microb. Ecol. 10, 45–53. https://doi.org/10.3354/ame010045

Potvin, M., Lovejoy, C., 2009. PCR-based diversity estimates of artificial and environmental 18S RNA gene libraries. J. Eukaryot. Microbiol. 56, 174–181. https://doi.org/10.1111/j.1550-7408.2008.00386.x

Pourtales, L.P.,1850. Proceedings of the American Association for the Advancement of Science. Third Meeting, held at Charleston, S.C., March 1850, 84–88

Pourtales, L.P.,1853. Notes on the specimens of the bottom of the ocean brought up in recent explorations of the Gulf Stream in connection with the coastal survey. Proceedings of the American Association for the Advancement of Science. Seventh Meeting, held at Cleveland, Ohio, July 1853, 181–184.

Priede, I.G., Bergstad, O.A., Miller, P.I., Vecchione, M., Gebruk, A., Falkenhaug, T., Billett, D.S.M., Craig, J., Dale, A.C., Shields, M.A., Tilstone, G.H., Sutton, T.T., Gooday, A.J., Inall, M.E., Jones, D.O.B., Martinez-Vicente, V., Menezes, G.M., Niedzielski, T., Sigurðsson, Þ., Rothe, N., Rogacheva, A., Alt, C.H.S., Brand, T., Abell, R., Brierley, A.S., Cousins, N.J., Crockard, D., Hoelzel, A.R., Høines, Å., Letessier, T.B., Read, J.F., Shimmield, T., Cox, M.J., Galbraith, J.K., Gordon, J.D.M., Horton, T., Neat, F., Lorance, P., 2013. Does Presence of a Mid-Ocean Ridge Enhance Biomass and Biodiversity? PLoS ONE 8, e61550. https://doi.org/10.1371/journal.pone.0061550

Pusceddu, A., Bianchelli, S., Martín, J., Puig, P., Palanques, A., Masqué, P., Danovaro, R., 2014. Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. Proc. Natl. Acad. Sci. 111, 8861–8866. https://doi.org/10.1073/pnas.1405454111

Ramirez-Llodra, E., Brandt, A., Danovaro, R., Escobar, E., German, C.R., Levin, L.A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy, B.E., Smith, C.R., Tittensor, D.P., Tyler, P.A., Vanreusel, A., Vecchione, M., 2010. Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. Biogeosciences Discuss. 7, 2361–2485. https://doi.org/10.5194/bgd-7-2361-2010

Rathburn, A.E., Willingham, J., Ziebis, W., Burkett, A.M., Corliss, B.H., 2018. A new biological proxy for deep-sea paleo-oxygen: Pores of epifaunal benthic foraminifera. Sci. Rep. 8, 9456. https://doi.org/10.1038/s41598-018-27793-4

Rice, A.L., 1986. British Oceanographic Vessels 1800–1950. The Ray Society, London

Rice, A.L., Wilson, J.B., 1980. The British Association Dredging Committee: a brief history. . In: Sears, M. (Ed.). Oceanography: the Past. Springer-Verlag, New Youk, pp. 373–385.

Rice, A.L., Burstyn, H.L., Jones, A.G.E., 1976. G.C. Wallich M.D. – megalomaniac or mis-used oceanographic genius. J. Soc. Biblphy Nat. Hist. 7, 291–319.

Risgaard-Petersen, N., Langezaal, A.M., Ingvardsen, S., Schmid, M.C., Jetten, M.S.M., Op den Camp, H.J.M., Derksen, J.W.M., Piña-Ochoa, E., Eriksson, S.P., Peter Nielsen, L., Peter Revsbech, N., Cedhagen, T., van der Zwaan, G.J., 2006. Evidence for complete denitrification in a benthic foraminifer. Nature 443, 93–96. https://doi.org/10.1038/nature05070

Rivera, F., Bonilla, P., Ramirez, E., Calderon, A., Gallegos, E., Rodriguez, S., Ortiz, R., Hernandez, D., Rivera, V., 1994. Seasonal distribution of air-borne pathogenic and free-living amoebae in Mexico City and its suburbs. Water. Air. Soil Pollut. 74, 65–87. https://doi.org/10.1007/BF01257148

Rodríguez-Martínez, R., Leonard, G., Milner, D.S., Sudek, S., Conway, M., Moore, K., Hudson, T., Mahé, F., Keeling, P.J., Santoro, A.E., Worden, A.Z., Richards, T.A., 2020. Controlled sampling of ribosomally active protistan diversity in sediment-surface layers identifies putative players in the marine carbon sink. ISME J. https://doi.org/10.1038/s41396-019-0581-y

Rothe, N., Gooday, A.J., Pearce, R.B., 2011. Intracellular mineral grains in the xenophyophore Nazareammina tenera (Rhizaria, Foraminifera) from the Nazaré Canyon (Portuguese margin, NE Atlantic). Deep Sea Res. Part Oceanogr. Res. Pap. 58, 1189–1195. https://doi.org/10.1016/j.dsr.2011.09.003

Rowe, G.T., Staresinic, N., 1979. Sources of organic matter to the deep-sea benthos. Ambio Spec. Rep. 19. https://doi.org/10.2307/25099603

Sabbatini, A., Morigi, C., Negri, A., Gooday, A.J., 2002. Soft-shelled benthic foraminifera from a hadal site (7800 m water depth) in the Atacama Trench (SE Pacific): preliminary observations. J. Micropalaeontology 21, 131–135. https://doi.org/10.1144/jm.21.2.131

Saidova, Kh. M., 1976. Benthic Foraminifera of the World Ocean: ''Nauka''Publishers, Moscow, 160 p. (in Russian)

Salani, F.S., Arndt, H., Hausmann, K., Nitsche, F., Scheckenbach, F., 2012. Analysis of the community structure of abyssal kinetoplastids revealed similar communities at larger spatial scales. ISME J. 6, 713–723. https://doi.org/10.1038/ismej.2011.138

Sars, M., 1868. Remarks on the distribution of animal life in the depths of the sea. Ann. Mag. Nat. Hist. Series 4 (3), 423–444.

Sars, G.O., 1872. Undersøgelser over Hardangerfjordens Fauna. Forhandlungen Videnskabs-Selskabs Kristiania 1871, 246–286.

Scheckenbach, F., Hausmann, K., Wylezich, C., Weitere, M., Arndt, H., 2010. Large-scale patterns in biodiversity of microbial eukaryotes from the abyssal sea floor. Proc. Natl. Acad. Sci. U. S. A. 107, 115–120. https://doi.org/10.1073/pnas.0908816106

Scheckenbach, F., Wylezich, C., Weitere, M., Hausmann, K., Arndt, H., 2005. Molecular identity of strains of heterotrophic flagellates isolated from surface waters and deep-sea sediments of the South Atlantic based on SSU rDNA. Aquat. Microb. Ecol. 38, 239–247. https://doi.org/10.3354/ame038239

Scherwass, A., Fischer, Y., Arndt, H., 2005. Detritus as a potential food source for protozoans: utilization of fine particulate plant detritus by a heterotrophic flagellate, *Chilomonas paramecium*, and a ciliate, *Tetrahymena pyriformis*. Aquat. Ecol. 39, 439–445. https://doi.org/10.1007/s10452-005-9012-4

Schmidt, D.N., Thomas, E., Authier, E., Sanders, D., Ridgwell, A., 2018. Strategies in times of crisis – insights into the benthic foraminiferal record of the Palaeocene-Eocene Thermal Maximum. Phil. Trans. Roy. Soc. A376, 20170328. http://dx.doi.org/10.1098/rsta.2017.0328

Schoenle, A., 2018. Analysis of the unique protozoan communities of the abyssal sea floors. Ph.D. Thesis, University of Cologne, 1–153.

Schoenle, A., Hohlfeld, M., Rosse, M., Filz, P., Wylezich, C., Nitsche, F., Arndt, H., 2020. Global comparison of bicosoecid *Cafeteria*-like flagellates from the deep ocean and surface waters, with reorganization of the family Cafeteriaceae. Eur. J. Protistol. 73, 125665. https://doi.org/10.1016/j.ejop.2019.125665

Schoenle, A., Jeuck, A., Nitsche, F., Venter, P., Prausse, D., Arndt, H., 2016. Methodological studies on estimates of abundance and diversity of heterotrophic flagellates from the deep-sea floor. J. Mar. Sci. Eng. 4, 22. https://doi.org/10.3390/jmse4010022

Schoenle, A., Nitsche, F., Werner, J., Arndt, H., 2017. Deep-sea ciliates: Recorded diversity and experimental studies on pressure tolerance. Deep-Sea Res. Part I 128, 55–66. http://doi.org/10.1016/j.dsr.2017.08.015

Schoenle, A., Živaljić, S., Prausse, D., Voß, J., Jakobsen, K., Arndt, H., 2019. New phagotrophic euglenids from deep sea and surface waters of the Atlantic Ocean (*Keelungia nitschei*, *Petalomonas acorensis*, *Ploeotia costaversata*). Eur. J. Protistol. 69, 102–116. https://doi.org/10.1016/j.ejop.2019.02.007

Schröder, C.J., Medioli, F.S., Scott, D.B., Schroder, C.J., 1989. Fragile abyssal foraminifera (including new Komokiacea) from the Nares Abyssal Plain. Micropaleontology 35, 10. https://doi.org/10.2307/1485535

Schultze, F.E., 1907. Die Xenophyophoren, eine besondere Gruppe der Rhizopoden. Wiss.Ergebn. dt. Tiefsee Expedit. 'Valdivia'. 11 pp. 1–55.

Sedlacek, L., Thistle, D., Fernandez-Leborans, G., Carman, K.R., Barry, J.P., 2013. First report of ciliate (Protozoa) epibionts on deep-sea harpacticoid copepods. Deep Sea Res. Part II Top. Stud. Oceanogr. 92, 165–171. https://doi.org/10.1016/j.dsr2.2013.01.033

Shires, R. 1994. The taxonomy, morphology and ecology of novel deep-sea agglutinated foraminifera in the northeast Atlantic. PhD thesis, University of Reading.

Shulse, C.N., Maillot, B., Smith, C.R., Church, M.J., 2017. Polymetallic nodules, sediments, and deep waters in the equatorial North Pacific exhibit highly diverse and distinct bacterial, archaeal, and microeukaryotic communities. MicrobiologyOpen 6, e00428. https://doi.org/10.1002/mbo3.428

Simon-Lledó, E., Bett, B.J., Huvenne, V.A.I., Köser, K., Schoening, T., Greinert, J., Jones, D.O.B., 2019b. Biological effects 26 years after simulated deep-sea mining. Sci. Rep. 9, 8040. https://doi.org/10.1038/s41598-019-44492-w

Simon-Lledó, E., Bett, B.J., Huvenne, V.A.I., Schoening, T., Benoist, N.M.A., Jones, D.O.B., 2019a. Ecology of a polymetallic nodule occurrence gradient: Implications for deep-sea mining. Limnol. Oceanogr. 64, 1883–1894. https://doi.org/10.1002/lno.11157

Skovgaard, A., 2014. Dirty tricks in the plankton: diversity and role of marine parasitic protists. Acta Protozoologica 53, 51–62. https://doi.org/10.4467/16890027AP.14.006.1443

Small, E.B., Gross, M.E., 1984. Preliminary observations of protistan organisms, especially ciliates, from the 21°N hydrothermal vent site. Biol. Soc. Wash. Bull. 6, 401–410.

Smith, C.R., Deleo, F., Bernardino, A., Sweetman, A., Arbizu, P., 2008. Abyssal food limitation, ecosystem structure and climate change. Trends Ecol. Evol. 23, 518–528. https://doi.org/10.1016/j.tree.2008.05.002

Smith, K.L., Ruhl, H.A., Kaufmann, R.S., Kahru, M., 2008. Tracing abyssal food supply back to upper-ocean processes over a 17-year time series in the northeast Pacific. Limnol. Oceanogr. 53, 2655–2667. https://doi.org/10.4319/lo.2008.53.6.2655

Snelgrove, P.V.R., Smith, C.R., 2002. A riot of species in an environmental calm: the paradox of the species-rich deep-sea floor. Oceanogr. Mar. Biol. 40, 311–342.

Snider, L.J., Burnett, B.R., Hessler, R.R., 1984. The composition and distribution of meiofauna and nanobiota in a central North Pacific deep-sea area. Deep Sea Res. Part Oceanogr. Res. Pap. 31, 1225–1249. https://doi.org/10.1016/0198-0149(84)90059-1

Sogin, M.L., Morrison, H.G., Huber, J.A., Welch, D.M., Huse, S.M., Neal, P.R., Arrieta, J.M., Herndl, G.J., 2006. Microbial diversity in the deep sea and the underexplored "rare biosphere." Proc. Natl. Acad. Sci. USA 103, 12115–12120.

Sokolova, M.N., 2000. Feeding and trophic structure of the deep-sea macrobenthos. Smithsonian Institution Press, Washington, D.C.

Sorokin, Yu.I., Paveljeva, E.B., 1972. On the quantitative characteristics of the pelagic ecosystem of Dalnee lake (Kamchatka). Hydrobiologia 40, 519–552. https://doi.org/10.1007/BF00019987

Stock, A., Breiner, H.-W., Pachiadaki, M., Edgcomb, V.P., Filker, S., La Cono, V., Yakimov, M.M., Stoeck, T., 2012. Microbial eukaryote life in the new hypersaline deep-sea basin Thetis. Extrem. Life Extreme Cond. 16, 21–34. https://doi.org/10.1007/s00792-011-0401-4

Stoeck, T., Behnke, A., Christen, R., Amaral-Zettler, L., Rodriguez-Mora, M.J., Chistoserdov, A., Orsi, W., Edgcomb, V.P., 2009. Massively parallel tag sequencing reveals the complexity of anaerobic marine protistan communities. BMC Biol. 7, 72. https://doi.org/10.1186/1741-7007-7-72

Stratmann, T., Lins, L., Purser, A., Marcon, Y., Rodrigues, C.F., Ravara, A., Cunha, M.R., Simon-Lledó, E., Jones, D.O.B., Sweetman, A.K., Köser, K., van Oevelen, D., 2018. Abyssal plain faunal carbon flows remain depressed 26 years after a simulated deep-sea mining disturbance. Biogeosciences 15, 4131–4145. https://doi.org/10.5194/bg-15-4131-2018

Svavarsson, J., Gudmundsson, G., Brattegard, T., 1993. Feeding by asellote isopods (Crustacea) on foraminifers (Protozoa) in the deep sea. Deep Sea Res. Part Oceanogr. Res. Pap. 40, 1225–1239. https://doi.org/10.1016/0967-0637(93)90135-P

Sweetman, A.K., Smith, C.R., Shulse, C.N., Maillot, B., Lindh, M., Church, M.J., Meyer, K.S., Oevelen, D., Stratmann, T., Gooday, A.J., 2019. Key role of bacteria in the short-term cycling of carbon at the abyssal seafloor in a low particulate organic carbon flux region of the eastern Pacific Ocean. Limnol. Oceanogr. 64, 694–713. https://doi.org/10.1002/lno.11069

Sweetman, A.K., Thurber, A.R., Smith, C.R., Levin, L.A., Mora, C., Wei, C.-L., Gooday, A.J., Jones, D.O.B., Rex, M., Yasuhara, M., Ingels, J., Ruhl, H.A., Frieder, C.A., Danovaro, R., Würzberg, L., Baco, A., Grupe, B.M., Pasulka, A., Meyer, K.S., Dunlop, K.M., Henry, L.-A., Roberts, J.M., 2017. Major impacts of climate change on deep-sea benthic ecosystems. Elem Sci Anth 5, 4. https://doi.org/10.1525/elementa.203

Szmytkiewicz, A., Zalewska, T., 2014. Sediment deposition and accumulation rates determined by sediment trap and 210Pb isotope methods in the Outer Puck Bay (Baltic Sea). Oceanologia 56, 85–106. https://doi.org/10.5697/oc.56-1.085

Takishita, K., Miyake, H., Kawato, M., Maruyama, T., 2005. Genetic diversity of microbial eukaryotes in anoxic sediment around fumaroles on a submarine caldera floor based on the small-subunit rDNA phylogeny. Extremophiles 9, 185–196. https://doi.org/10.1007/s00792-005-0432-9

Takishita, K., Yubuki, N., Kakizoe, N., Inagaki, Y., Maruyama, T., 2007. Diversity of microbial eukaryotes in sediment at a deep-sea methane cold seep: surveys of ribosomal DNA libraries from raw sediment samples and two enrichment cultures. Extremophiles 11, 563–576. https://doi.org/10.1007/s00792-007-0068-z

Tashyreva, D., Prokopchuk, G., Yabuki, A., Kaur, B., Faktorová, D., Votýpka, J., Kusaka, C., Fujikura, K., Shiratori, T., Ishida, K.-I., Horák, A., Lukeš, J., 2018. Phylogeny and morphology of new diplonemids from Japan. Protist 169, 158–179. https://doi.org/10.1016/j.protis.2018.02.001

Taylor, A., Gooday, A.J., 2014. Agglutinated foraminifera (superfamily Hormosinacea) across the Indian margin oxygen minimum zone (Arabian Sea). Mar. Biodivers. 44, 5–25. https://doi.org/10.1007/s12526-013-0178-z

Taylor, G.T., Iabichella, M., Ho, T.-Y., Scranton, M.I., Thunell, R.C., Muller-Karger, F., Varela, R., 2001. Chemoautotrophy in the redox transition zone of the Cariaco Basin: A significant midwater source of organic carbon production. Limnol. Oceanogr. 46, 148–163. https://doi.org/10.4319/lo.2001.46.1.0148

Tendal, O.S., 1996. Synoptic checklist and bibliography of the Xenophyophorea (Protista), with a zoogeographical survey of the group. Galathea Rep. 17, 25.

Tendal, O.S., 1985. Xenophyophores (Protozoa, Sarcodina) in the diet of *Neopilina galatheae* (Molluscs, Monoplacophora). Galathea Rep. 16, 95–98.

Tendal, O.S., 1979. Aspects of the biology of Komokiagea and Xenophyophoria. Sarsia 64, 13–17. https://doi.org/10.1080/00364827.1979.10411356

Tendal, O.S., 1972. A monograph of the Xenophyophoria (Rhizopodea, Protozoa). Galathea Rep. 12, 7–99.

Tendal, O.S., Hessler, R.R., 1977. An introduction to the biology and systematics of Komokiacea (Textulariina, Foraminiferida). Galathea Rep. 14, 165–194.

Thiel, H., 1983. Meiobenthos and nanobenthos of the deep sea, in: Rowe, G.T. (Ed.), The Sea. Wiley Interscience, New York, pp. 167–230.

Thiel, H., 1975. The size structure of the deep-sea benthos. Int. Rev. Hydrobiol. 60, 575–606.

Thiel, H., Schriever, G., Lochte, K., Gooday, A.J., Hemleben, C., Manidura, R.F.G., Turley, C.M., 1989. Phytodetritus on the deep-sea floor in a central oceanic region of the Northeast Atlantic. Biol. Oceanogr. 6, 203–239. https://doi.org/10.1080/01965581.1988.10749527

Thrush, S.F., Dayton, P.K., 2002. Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. Annu. Rev. Ecol. Syst. 33, 449–473. https://doi.org/10.1146/annurev.ecolsys.33.010802.150515

Thurber, A.R., Sweetman, A.K., Narayanaswamy, B.E., Jones, D.O.B., Ingels, J., Hansman, R.L., 2014. Ecosystem function and services provided by the deep sea. Biogeosciences Discuss. 10, 3941-3963. https://doi.org/10.5194/bg-11-3941-2014

Torti, A., Lever, M.A., Jø rgensen, B.B., 2015. Origin, dynamics, and implications of extracellular DNA pools in marine sediments. Mar. Genomics 24, 185–196. https://doi.org/10.1016/j.margen.2015.08.007

Travis, J.L., Bowser, S.S., 1991. The motility of Foraminifera, in: Lee, J.J., Anderson, O.R. (Eds.), Biology of Foraminifera. Academic Press, London, pp. 92–115.

Triadó-Margarit, X., Casamayor, E.O., 2013. High genetic diversity and novelty in planktonic protists inhabiting inland and coastal high salinity water bodies. FEMS Microbiol. Ecol. 85, 27–36. https://doi.org/10.1111/1574-6941.12095

Turley, C.M., Carstens, M., 1991. Pressure tolerance of oceanic flagellates: Implications for remineralisation of organic matter. Deep-Sea Res. 38, 403–413. https://doi.org/10.1016/0198-0149(91)90043-F

Turley, C.M., Lochte, K., Lampitt, R.S., 1995. Transformations of biogenic particles during sedimentation in the northeastern Atlantic. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 348, 179–189. https://doi.org/10.1098/rstb.1995.0060

Turley, C.M., Lochte, K., Patterson, D.J., 1988. A barophilic flagellate isolated from 4500 m in the mid-North Atlantic. Deep Sea Res. 35, 1079–1092. https://doi.org/10.1016/0198-0149(88)90001-5

Tyler, P.A., 2003. Introduction, in: Tyler, P.A. (Ed.), Ecosystems of the Deep Ocean. Ecosystems of the World volume 8. Elsevier, Amsterdam, pp. 1–3.

Uhlig, G., 1970. Untersuchungen über die Bodenmikrofauna der Tiefsee. Biologische Anstalt Helgoland, Jahresbericht 1970, 23–24.

Uhlig, G., 1971. Untersuchungen über die Bodenmikrofauna der Tiefsee. Biologische Anstalt Helgoland, Jahresbericht 1971, 17–18.

Uhlig, G., 1973. Preliminary account of meiobenthic ciliates from the deep sea. Proceedings of the IV International Congress on Protozoology, Clermont, France. Progress in Protozoology, p. 417.

Van Dover, C.L., Ardron, J.A., Escobar, E., Gianni, M., Gjerde, K.M., Jaeckel, A., Jones, D.O.B., Levin, L.A., Niner, H.J., Pendleton, L., Smith, C.R., Thiele, T., Turner, P.J., Watling, L., Weaver, P.P.E., 2017. Biodiversity loss from deep-sea mining. Nat. Geosci. 10, 464–465. https://doi.org/10.1038/ngeo2983

Van Dover, C.L., Berg, C.J., Turner, R.D., 1988. Recruitment of marine invertebrates to hard substrates at deep-sea hydrothermal vents on the East Pacific Rise and Galapagos spreading center. Deep Sea Res. Part Oceanogr. Res. Pap. 35, 1833–1849. https://doi.org/10.1016/0198-0149(88)90052-0

Vanreusel, A., Hilario, A., Ribeiro, P.A., Menot, L., Arbizu, P.M., 2016. Threatened by mining, polymetallic nodules are required to preserve abyssal epifauna. Sci. Rep. 6, 26808. https://doi.org/10.1038/srep26808

Veillette, J., Sarrazin, J., Gooday, A.J., Galéron, J., Caprais, J.-C., Vangriesheim, A., Étoubleau, J., Christian, J.R., Kim Juniper, S., 2007. Ferromanganese nodule fauna in the Tropical North Pacific Ocean: Species richness, faunal cover and spatial distribution. Deep Sea Res. Part Oceanogr. Res. Pap. 54, 1912–1935. https://doi.org/10.1016/j.dsr.2007.06.011

Volkova, E., Kudryavtsev, A., 2017. Description of *Neoparamoeba longipodia* n. sp. and a new strain of *Neoparamoeba aestuarina* (Page, 1970) (Amoebozoa, Dactylopodida) from deep-sea habitats. Eur. J. Protistol. 61, 107–121. https://doi.org/10.1016/j.ejop.2017.09.006

Voltski, I., Weiner, A.K.M., Tsuchiya, M., Kitazato, H., 2018. *Syringammina limosa* sp. nov., the first xenophyophore (Foraminifera) from the deep Sea of Okhotsk: morphological and genetic description. Deep Sea Res. Part II Top. Stud. Oceanogr. 154, 32–46. https://doi.org/10.1016/j.dsr2.2017.12.001

Wallich, G.C., 1862. The North-Atlantic sea-bed: comprising a diary of the voyage on board H.M.S. Bulldog, in 1860; and observations on the presence of animal life, and the formation and nature of organic deposits, at great depths in the ocean. John van Voorst, Paternoster Row, London, 1–160, Pls 1–5

Wallich, G.C., 1877. On *Rupertia stabilis,* a new sessile foraminifer from the North Atlantic. Ann. Mag. Nat. Hist. Series 4, 19, 423–444.

Wang, Y., Zhang, W.P., Cao, H.L., Shek, C.S., Tian, R.M., Wong, Y.H., Batang, Z., Al-Suwailem, A., Qian, P.-Y., 2014. Diversity and distribution of eukaryotic microbes in and around a brine pool adjacent to the Thuwal cold seeps in the Red Sea. Front. Microbiol. 5. https://doi.org/10.3389/fmicb.2014.00037

Washburn, T.W., Turner, P.J., Durden, J.M., Jones, D.O.B., Weaver, P., Van Dover, C.L., 2019. Ecological risk assessment for deep-sea mining. Ocean Coast. Manag. 176, 24–39. https://doi.org/10.1016/j.ocecoaman.2019.04.014

Watling, L., Guinotte, J., Clark, M.R., Smith, C.R., 2013. A proposed biogeography of the deep ocean floor. Prog. Oceanogr. 111, 91–112. https://doi.org/10.1016/j.pocean.2012.11.003

Weber, A.A.-T., Pawlowski, J., 2013. Can abundance of protists be inferred from sequence data: a case study of foraminifera. PLOS ONE 8, e56739. https://doi.org/10.1371/journal.pone.0056739

Woehle, C., Roy, A.-S., Glock, N., Wein, T., Weissenbach, J., Rosenstiel, P., Hiebenthal, C., Michels, J., Schönfeld, J., Dagan, T., 2018. A novel eukaryotic denitrification pathway in foraminifera. Curr. Biol. 28, 2536-2543.e5. https://doi.org/10.1016/j.cub.2018.06.027

Wüst, G. 1964. The major deep-sea expeditions and research vessels 1873-1960- A contribution to the history of oceanography. Prog. Oceanogr. 2, 1–52.

Yeh, Y.-C., Needham, D.M., Sieradzki, E.T., Fuhrman, J.A., 2018. Taxon disappearance from microbiome analysis reinforces the value of mock communities as a standard in every sequencing run. mSystems 3. https://doi.org/10.1128/mSystems.00023-18

Yool, A., Martin, A.P., Anderson, T.R., Bett, B.J., Jones, D.O.B., Ruhl, H.A., 2017. Big in the benthos: Future change of seafloor community biomass in a global, body size-resolved model. Glob. Change Biol. 23, 3554–3566. https://doi.org/10.1111/gcb.13680

Yubuki, N., Edgcomb, V.P., Bernhard, J.M., Leander, B.S., 2009. Ultrastructure and molecular phylogeny of *Calkinsia aureus* : cellular identity of a novel clade of deep-sea euglenozoans with epibiotic bacteria. BMC Microbiol. 9, 16. https://doi.org/10.1186/1471-2180-9-16

Zhang, W., Pan, Y., Yang, J., Chen, H., Holohan, B., Vaudrey, J., Lin, S., McManus, G.B., 2018. The diversity and biogeography of abundant and rare intertidal marine microeukaryotes explained by environment and dispersal limitation: Biogeography of intertidal benthic microeukaryotes. Environ. Microbiol. 20, 462–476. https://doi.org/10.1111/1462-2920.13916

Zhao, F., Filker, S., Xu, K., Huang, P., Zheng, S., 2017. Patterns and drivers of vertical distribution of the ciliate community from the surface to the abyssopelagic zone in the western Pacific Ocean. Front. Microbiol. 8, 2559. https://doi.org/10.3389/fmicb.2017.02559

Živaljić, S., Scherwass, A., Schoenle, A., Hohlfeld, M., Quintela-Alonso, P., Nitsche, F., Arndt, H., 2020. A barotolerant ciliate isolated from the abyssal deep sea of the North Atlantic: *Euplotes dominicanus* sp. n. (Ciliophora, Euplotia). Eur. J. Protistol. 73, 125664. https://doi.org/10.1016/j.ejop.2019.125664

Živaljić, S., Schoenle, A., Nitsche, F., Hohlfeld, M., Piechocki, J., Reif, F., Shumo, M., Weiss, A., Werner, J., Witt, M., Voss, J., Arndt, H., 2018. Survival of marine heterotrophic flagellates isolated from the surface and the deep sea at high hydrostatic pressure: Literature review and own experiments. Deep Sea Res. Part II Top. Stud. Oceanogr. 148, 251–259. https://doi.org/10.1016/j.dsr2.2017.04.022

Živaljić, S., Schoenle, A., Scherwass, A., Hohlfeld, M., Nitsche, F., Arndt, H., in press. Influence of hydrostatic pressure on the behaviour of three ciliate species isolated from the deep sea. Mar. Biol. https://doi.org/10.1007/s00227-020-3673-3