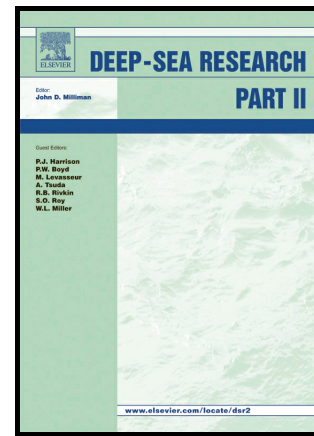


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Polychaetous annelids in the deep Nordic Seas: strong bathymetric gradients, low diversity and underdeveloped taxonomy

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Abstract

Not much is known on polychaete diversity in the deep Nordic Seas. Based on data from extensive sampling over three decades, new data on polychaetes covering depths from 550 m to 3,800 m are presently reported. On a depth gradient, the number of polychaete families gradually declined from 35 at the upper slope (500-750 m) to 11 at 3,800 m. Species diversity in eight polychaete families subjected to critical taxonomic studies showed a gradual decrease from a diverse group of slope species in the upper and middle slope (500-1,000 m) to a species poor fauna in the deepest areas (> 3,000 m), with a distinct break at about 2,000 m. Faunal changes were documented both at alpha (sample species richness) and gamma (large area species richness) scales, whereas the break at about 2,000 m was clearly from beta (turnover) species richness. Only six species (12%) in the examined families were found in the deepest areas. The slope and deep-water polychaete fauna differs substantially from west Norwegian shelf and costal fauna. Not more than 30% of the species in the examined families were recorded in coastal and shelf waters, and several presumably refer to species complexes. The strong faunal change coincides with the upper border of cold sub-zero temperature deep water at the shelf break and upper slope. Polychaete taxonomy of the deep-water fauna is generally underdeveloped, illustrated by a high proportion of recently described or undescribed species (about 40%) in the examined families. Based on the present results, we hypothesise that the cold Nordic Sea deep-water polychaete fauna differs significantly from the North Atlantic deep fauna and rather is more similar to the fauna of deep Arctic waters.

Key words Polychaeta, benthic diversity, species richness, deep-water bathymetric gradient, Nordic Seas, deep-sea

1. Introduction

The Nordic Seas (Greenland-Iceland-Norwegian Seas) represent the most northern part of the Atlantic Ocean and constitute the connection to the Arctic. Whereas the coastal and continental shelf areas have been extensively studied, especially along the European coasts, the continental slope and deep-water areas (approximately 500 to 4,000 m) have received far less attention. The deep-water fauna was first described in reports from the Norwegian North Atlantic Expedition 1876-78 and Danish expeditions in the early twentieth century. In recent years, several new and comprehensive studies have been initiated, but present knowledge is still incomplete and fragmentary. In several cases, the most relevant information actually dates back to the pioneering expeditions. With regard to open-sea offshore systems, the best studied ecosystem components are the pelagic systems, including fish, seabirds and sea mammals (Skjoldal, 2004).

Studies of the benthic fauna hitherto conducted have generally indicated that the fauna in the deep areas is sparse and of low diversity. This appeared to be the case in studies of crustaceans (Dahl et al., 1976; Svavarsson et al., 1990; Svavarsson, 1997), gastropods (Stuart and Rex, 2009; Høisæter, 2010), polychaetes (Dauvin et al., 1994) and demersal fish (Bergstad et al., 1999; Bjelland and Holst, 2004). On a depth gradient, there appears to be a faunal diversity maximum at the outer shelf and upper slope in 400-800 m depth (Weslawski et al., 2003; Narayanaswamy et al., 2005, 2010; Høisæter, 2010), with major changes in the faunal composition occurring from about 400 to below 700 m. The Nordic Seas are characterised by a particularly strong difference between the water masses in shelf and coastal areas that are part of the North Atlantic circulation system and the water masses in deeper areas that are connected to the Polar Sea and are of Arctic origin. Species changes have been related to temperature conditions (e.g. Narayanaswamy et al., 2005; Høisæter, 2010), although habitat heterogeneity also remains a factor (Narayanaswamy et al., 2010).

Based on studies of molluscs and crustaceans, species diversity in the Nordic Seas deep-sea areas appears low compared with other deep sea areas (Stuart and Rex, 2009; Rex and Etter, 2010). Dauvin

et al. (1994) indicated a similar pattern for the polychaetes, but commented that taxonomic problems prevented testing diversity patterns and their relationships to environmental conditions. Bluhm et al. (2011) noted that the number of currently known polychaete taxa may be lower in the Arctic deep sea (presumably including the deep Nordic Seas) than in other deep-sea basins, but pointed out that comparisons are hampered by poor sampling coverage and methodological differences. Rex and Etter (2010) noted that the limited knowledge of polychaetes precluded general assessments of deep-sea faunal patterns based on all major faunal groups. The polychaetes constitute one of the most important groups in the deep Nordic Seas (Weslawski et al., 2003; Włodarska-Kowalczyk et al., 2004; Narayanaswamy et al., 2005; Bluhm et al., 2011). Recent taxonomic studies have indeed confirmed that the polychaete fauna is imperfectly known. This appears from a number of newly described species (Koh et al., 2003; Parapar, 2006; Parapar et al., 2011a; Kongsrud et al., 2011; Bakken et al., 2014; Alvestad et al., 2014). Further, several species that had not been reported since their original description in the pioneering investigations have been found to be common and abundantly occurring (Kongsrud et al., 2011; Parapar et al., 2011a). The recent results imply that in-depth taxonomic studies are essential for assessing diversity patterns in the Nordic Seas and for carrying out comparisons with other deep-sea areas.

The present paper presents results on species distributions and diversity patterns in the Nordic Seas for selected polychaete groups (families) that have been subjected to critical taxonomic studies. The study particularly aims at illustrating the diversity of the deep sea polychaete fauna in comparison with shelf and slope areas and identifying depth zones where major shifts in species composition take place. In addition, we provide some general data on polychaete distribution at the family level. The material has been collected in a number of sampling cruises carried out over three decades. The most important material was collected using epibenthic sledges in a series of cruises organised and carried out by the University of Bergen during 1981-87. Taxonomic accounts covering parts of the material were presented by Kongsrud et al. (2011), Bakken et al. (2014) and Alvestad et al. (2014). Crustaceans and gastropods from the epibenthic sledge samples have previously been reported by Svavarsson et al. (1990), Svavarsson (1997) and Høisæter (2010).

2. Material and methods

2.1 Study area

The Nordic Seas are composed of the Norwegian Sea, Iceland Sea and Greenland Sea (Fig. 1). The eastern part (the Norwegian Sea) is characterised by a relatively warm surface and shelf water masses of Atlantic origin ($t > 5-7^{\circ}\text{C}$), whereas the deep water masses below 750 m are of Arctic origin, with temperatures constantly below 0°C (Blindheim and Østerhus, 2005) (Fig. 2). In the western part (Iceland Sea, Greenland Sea), surface and shelf waters are of Arctic origin and generally cold. The deep water of the Nordic Seas is separated from deep waters of the North Atlantic by a ridge running from Shetland across Iceland to Greenland, with a threshold depth at 650 m. In a boundary zone about 500 to 750 m at the upper continental slope, the temperature (bottom water) may fluctuate by $4-5^{\circ}\text{C}$ in short periods, presumably due to internal waves (Narayanaswamy et al., 2005, 2010; Høisæter, 2010) and seasonal variations (Blindheim, 2004). The largest depth ($> 4,200$ m) is found between Iceland and northern Norway. The shelf areas in the eastern part (the Norwegian Sea) span from boreal waters in the North Sea to Arctic waters at Svalbard.

Høisæter (2010) used a system for defining and naming depth zones in the Norwegian Sea that is mainly based on the temperature distribution and topographic features, but which may diverge somewhat from common usage elsewhere. His system is followed here. Thus, the shelf is considered to extend to 490 m, the upper slope to 750 m, the middle slope to 1,000 m, the lower slope to 2,000 m and the abyssal basin from 2,000 m to the maximum depth (about 4,000 m).

2.2 Sampling and sample workup

The material included in this study was collected from the continental slope (> 500 m) and deep basins of the Norwegian Sea, the Iceland Sea and the southern part of the Greenland Sea (Fig. 3). The main part of the material was collected in the period 1981-87, using a Rothlisberg-Pearcy epibenthic sledge (RP-sledge) (Brattegard and Fosså, 1991). Sampling was particularly concentrated on a depth transect between 62 and 64°N west of the continental shelf of Norway. Generally, the sledge was towed a

distance of 600-1,500 m on the bottom at a speed of 1-1.5 knot. It was fitted with a 0.5 mm mesh net. A few samples were taken with a D-sledge, which is a predecessor of the "Sneli-sledge" (Sneli, 1998). Other material was collected during environmental monitoring studies (Vøring oil field 1998, Ormen Lange oil field 2004, 2009), hydrothermal vent studies at the Jan Mayen deep ridge (CGB 2006-2011) and the Mareano seabed mapping program (2008-2009). In these studies, samples were collected using a box-corer (Vøring, Ormen Lange, CGB), 0.2 m² van Veen grab (Mareano), beam trawl (Mareano), RP-sledge (CGB, Mareano) and ROV (CGB). Table 1 shows the distribution of samples included in the present study according to gear and depth zones. The samples were arranged into depth strata of 500 m depth intervals, except for the upper and middle slope and the abyssal basin below 3,000 m.

The samples from the RP-sledge material (1981-87) were sieved through a series of graduated screens (4, 2, 1, 0.5 mm) after having been elutriated in a large container. Samples from the grab and boxcorer were sieved through 1 mm screens. All specimens were fixed in 4-6% formaldehyde solution, except samples from the CGB studies and some from Mareano that were fixed in 96% ethanol. The total material comprised 205 samples. Specified data for samples taken up to 2008 are presented in Schander et al. (2010) and Kongsrud et al. (2011). Data for later samples are available upon request from the University Museum, Bergen.

The samples from 1981-87 (RP-sledge) were partly sorted into major taxonomic groups (phyla/classes) shortly after collection, but most samples were stored mainly as bulk fixed sample fractions. Starting in 2006, the polychaete material was further sorted to the family level. Some few sample fractions had dried up, but most samples were well preserved. Upon sorting, the material for eight families (Onuphidae, Lumbrineridae, Acrocirridae, Opheliidae, Flabelligeridae, Scalibregmatidae, Maldanidae, Ampharetidae) was further processed and subjected to taxonomic studies at the species level. Specimens were identified under stereo- and light microscopes. Staining with methyl blue was used to aid in identification. SEM was used for critical examination of diagnostic characters. The material from the more recent environmental studies (1998-2011) was mostly already processed, but specimens from the selected families were re-identified for the present

study. Complete taxonomic accounts of the families Opheliidae and Scalibregmatidae with descriptions of new species based on the present material are given by Kongsrud et al. (2011) and Bakken et al. (2014), where also further details on methods may be found.

The material is deposited in the collections of the University Museum of Bergen, University of Bergen (ZMBN), and the Norwegian University of Science and Technology, NTNU University Museum, Trondheim (NTNU-VM).

2.3 Depth distribution

Based on the initial sorting to family level, a depth distribution of all recorded polychaete families was assembled. The samples range from the upper slope (550 m) to the deep basin (3,900 m). Depth distribution of species is reported for the examined families, providing upper and lower limits of the included species. The depth distributions were further supplemented with lists of species previously known from shelf and inshore waters on the west coast of Norway to illustrate species changes across the shelf break. Data for coastal and shelf species were assembled from published taxonomic studies added with information from own ongoing projects in coastal waters.

2.4 Species richness and diversity

Patterns in species diversity (alpha, beta, gamma) were assessed using the data from the RP-sledge in 1981-87 (109 samples) for the examined families. Data from one gear only was used to ensure maximum compatibility in the data set. Brattegard and Fosså (1991) demonstrated that the RP-sledge had high replicability among hauls. The analyses are based on presence/absence data, because it proved impossible to obtain complete and quality-controlled quantitative data for all samples. Species richness was calculated for samples (alpha diversity sensu Gray, 2000) and for large areas (gamma diversity sensu Gray, 2000) within depth zones of 500 m vertical extent (as in Table 1). Alpha diversity ($\bar{\alpha}$) is here set equal to the average number of species in a haul in a depth zone, whereas gamma diversity (γ) is equal to the total number of species in each depth zone. Patterns in species richness across depth zones (beta- or turnover diversity) were assessed using Whittaker's beta index,

Cody's beta index and Sorensen's similarity index (Magurran, 1988). Whittaker's index is calculated according to the formula $\beta_w = (\gamma/\bar{\alpha}) - 1$ (as cited by Magurran, 1988) and measures to which degree an area is richer in species than each sample from the area (Gray, 2000). Cody's index is calculated according to $\beta_c = (gh + lh)/2$, where gh is the number of species gained and lh is the number of species lost when moving along a transect. Sorensen's index is calculated by $S = 2\gamma_{\text{shared}}/(\gamma_a + \gamma_b)$, where γ_{shared} is the number of shared species in two areas (depth levels) and γ_a and γ_b are the numbers of species in each area. We used Cody's and Sorensen's indices to assess the changes from one depth zone to the next, moving from the upper slope into the deep basin. Both indices take species identities into account and thus reflect the changes in species composition along the depth gradient.

3. Results

3.1 Depth distribution of polychaete families

In total, 35 families were represented in the material. All families were found at the shelf break and the uppermost part of the continental slope, but some, e.g. Orbiniidae and Cossuridae, did not penetrate into the cold water masses below 800 m depth. The number of families gradually decreased with depth and was reduced to 25 at 2,000 m depth and 15 below 3,000 m depth (Figure 4). There appeared to be a particularly strong decline between 2,500 and 3,000 m. In the deepest samples (3,500-3,800 m), we found 11 families.

The best represented families with regard to total abundance and vertical distribution (wide distribution) were Acrocirridae, Ampharetidae, Amphinomidae, Cirratulidae, Nephtyidae, Opheliidae, Oweniidae, Sabellidae and Spionidae. The oweniids were extremely abundant and by volume amounted to several litres in some samples. At the continental slope (<2,000 m), Onuphidae, Flabelligeridae and Scalibregmatidae were also abundant. Below 3,000 m the dominant families in abundance of specimens were Ampharetidae, Opheliidae and Oweniidae.

3.2 *Species composition*

In total, we identified 50 species from the eight families that were selected for taxonomic studies and assessment of species distribution (Table 2). The most species-rich families were Ampharetidae and Lumbrineridae, whereas Acrocirridae was represented by one species only. Rather many species did not comply with presently known species descriptions and are here referred to with provisional names (species A, B, etc.). There are also some species that, with doubt, were assigned to named species (indicated with cf.).

3.3 *Depth distribution of species*

Most species were found from the shelf break and down to the middle and lower slope (Figs. 5, 6). We found no species of Onuphidae, Flabelligeridae and Scalibregmatidae below 1,600-1,800 m depth, and no species of Acrocirridae and Maldanidae below 2,400-2,600 m depth. For the other families, one or two species extended down into the deepest part of the abyssal basin. Ampharetidae was the best represented family in the deep basin, with six species present at depths greater than 2,500 m. Generally, the number of species decreased rapidly below 1,500-2,000 m, and not more than six species were found at 3,000 m depth. Roughly, the fauna may be divided into a fairly large category of slope species that is found no deeper than about 2,000 m and a considerably smaller category of abyssal species that occur from the middle and lower slope and down into the deep basin.

The eight families in the present study include about hundred species on the continental shelf and in coastal waters of western Norway (Figs 5, 6). Not more than about 20 of the species here recorded were from the continental slope and deep-water, and most were found in the upper and middle slope. None of the species were found in the deep basin below 3,000 m depth. This indicates that there is a major faunal shift at the shelf break and upper slope at about the border between the warm Atlantic water and the cold Norwegian Sea water with sub-zero temperatures (see Fig. 2). The difference between shelf and slope fauna was distinct in all families, but appeared particularly prominent for the maldanids and ampharetids, which are well represented in Norwegian shelf and coastal waters (Fig. 6).

It may also be noted that several species that are reported both from the shelf and slope may represent species complexes (see below).

The most frequently occurring species (> 50 occurrences) were the acrocirrid *Macrochaeta polyonyx*, the opheliids *Ophelina abranchiata*, *O. cylindricaudata* and *O. opistobranchiata*, the scalibregmatids *Pseudoscalibregma parvum* and the ampharetids *Ampharete undecima*, *Amphicteis wesenbergae* and *Glyphanostomum pallescens*. Generally, the most frequent species had rather wide depth distributions, and several were found both on the slope and in the deep basin. It also seems that some of the frequently occurring species were among the most common or dominant species in the species assemblages (although abundance data are incomplete). This seems for instance to be the case for *P. parvum* (Bakken et al., 2014), *A. undecima* (Alvestad et al., 2014) and, in particular, *O. opistobranchiata*, for which the material consisted of more than 18,000 specimens (Kongsrud et al., 2011).

3.4 Species taxonomy

Ten species in the present study (20%) appear to be undescribed. These include the lumbrinerids *Abyssoninoe* sp. A, *Augeneria* sp. A and *Augeneria* sp. B (Oug, own obs.), the flabelligerid *Flabelligera* sp. A (Kongsrud, own obs.), the scalibregmatids *Asclerocheilus* sp. A and *Scalibregma* sp. A (near *inflatum*) (= *S. inflatum* in Bakken et al., 2014) (Eibye-Jacobsen pers. comm.; Bakken and Kongsrud, own obs.), the maldanids *Eupraxillella* sp. A (= *Macroclymene* sp. A in Schander et al., 2010 and Bakken et al., 2010) and *Praxillella* sp. A (Kongsrud, own obs.), and the ampharetids *Ampharete* sp. A and *Anobothrus* sp. A (Alvestad and Kongsrud, own obs.). In addition, three species have recently been described based on the material in the present study, i.e. *Ophelina brattegardi*, *Scalibregma hansenii* and *Ampharete undecima* (Kongsrud et al., 2011; Bakken et al., 2014; Alvestad et al., 2014). Presently, several of the undescribed species are under further study. As far as possible, ethanol-fixed new material will be collected in ongoing sampling programmes from as many of the species as possible in order to support the taxonomic studies with molecular genetic analyses. Recent

results from DNA barcoding of material from slope areas suggest that more species are present than identified from the morphology-based studies (Kongsrud et al., unpublished).

Some species that are reported from both coastal waters and the continental slope may turn out to be species complexes. This may be the case for several lumbrinerids that have been tentatively assigned to species originally described from rather distant parts of the world (e.g. *Augeneria cf. tentaculata*). The opheliid *Ophelina cylindricaudata*, which was described from the Norwegian Sea (900 m depth), appears to involve two separate species in shelf and coastal waters (Kongsrud, own obs.). The scalibregmatids appear to entail several taxonomic problems. Shelf data has scarcely been studied for this group, restricted to the work by Støp-Bowitz (1945) and Mackie (1991). Data from ongoing projects demonstrate a higher diversity in *Scalibregma* in shelf areas and on the shelf break based on morphological characteristics, but also by evidence from DNA barcoding (Kongsrud et al., unpublished). Forthcoming data will further elucidate bathymetric distribution of species in this group.

3.5 Diversity

The number of families and number of species from the eight selected families collected in individual samples are shown for the RP-sledge samples 1981-87 (109 samples) in Fig. 7. Both families and species decreased with depth. At the upper and middle slope, most samples contained 15-25 families and 10-15 species. The numbers decreased to 10-20 families and 5-10 species at the lower slope, whereas not more than 11 families and 6 species were recorded in samples from the deepest areas below 3,000m. At all depth levels, both numbers of families and species varied rather significantly among samples, but the number of samples with few specimens (families and species) was low, indicating a generally good sampling performance of the sledge (see also Brattegard and Fosså, 1991).

Changes in species richness with depth, based on the data from the RP-sledge samples 1981-87, are illustrated in Fig. 8. Sample species richness (alpha) was about stable in slope areas (550-1,500 m), but gradually decreased below 1,500 m. Large area species richness (gamma) showed a largely similar pattern, but decreased more strongly at depths greater than 1,500 m. In the deep basin (> 2,500 m),

sample species richness was low (average < five species), and the total number of species (gamma) was less than ten.

Turnover or beta diversity along the depth gradient is illustrated in Fig. 9. Whittaker's beta index, measuring the degree to which an area is richer in species than samples taken within the area, indicates that the depth levels from 1,000 to 2,500 m are more heterogeneous than the depth levels above and below this depth. This pattern results from the relationship between alpha and gamma diversity, showing the greatest contrast between alpha and gamma diversity at 1,500-2,000 m depth (Fig. 8). The contrast was least for the deepest levels. Cody's beta index and Sorensen's similarity index, showing species changes from one depth level to the next, illustrate that the greatest change occurs at about 2,000 m. In the middle and lower slope, the average number of gaining and losing species (Cody's beta) was 5-8, whereas the number increased to about 10 passing into the deep basin at 2,000 m. This high value is due to a clear overweight of losing species. Below 2,000 m, the average species changes are small, with less than four species. The Sorensen's index illustrates that the species composition is rather homogeneous in the slope areas above 2,000 m, then undergoes a marked shift at about 2,000 m, and is thereafter rather homogeneous in the deep basin. The Sorensen's index roughly mirror-images Cody's index, except for in the deep basin, where it reached high values due to the presence of few, but persistently occurring, species.

4. Discussion

The present study shows that the polychaete fauna on the continental slope and in the deep basin of the Nordic Seas can be roughly divided into a fairly diverse group of slope species and a rather species-poor group of deep-basin species. The species richness gradually decreases on a depth gradient from the middle slope (approx. 1,000 m) to the deepest areas (> 3,000 m), with a distinct break at about 2,000 m. In the deepest areas, we found only six species (12% of slope and deep-basin species) from the eight examined families. With regard to families, the number gradually decreased from 35 in the upper slope to 11 in the deepest areas. It is reasonable to assume that the species richness in the families that have not been examined so far will vary more or less similar to the patterns described

here for the examined families. It may therefore be generally assumed that the abyssal polychaete fauna of the Nordic Seas is of low diversity.

The deepest areas (> 2,500 m) were sampled with lower intensity than the slope and upper abyssal areas. The species richness (large area or gamma diversity) could therefore possibly be underestimated for the deepest areas in this study. However, the low species changes and homogeneous fauna below 2,000 m, illustrated by the turnover diversity indices, suggest that not many new species would have been found in additional samples. The low values of Whittaker's beta index, in particular, indicate that an appreciable number of the present species was caught in each sample. It is therefore assumed that the present data reflect well the depth gradient in species richness.

The study also shows that the slope and deep-water polychaete fauna in the Nordic Seas differs substantially from the shelf and coastal fauna of Norwegian waters. In all families studied here, there appeared to be a strong shift in species composition at about the continental margin ("Egga") and the upper slope (500-750 m). Of the 50 species from slope and deep-water areas in the present study, not more than 16 (32%) have been recorded in shelf and coastal waters, and several may refer to species complexes. With regard to polychaete families, 64 families are present in Norwegian waters (data from the Norwegian Biodiversity Information Centre), but only about half of them were found on the slope and deeper. Common and abundant families that were not found include for instance Sigalionidae, Goniadidae, Eunicidae and Pectinaridae. The strong faunal change coincides with the upper border for water masses with temperatures below 0°C. Shelf and coastal waters on the Norwegian western coast, being influenced by Atlantic water (5-7°C), support a benthic fauna that is generally similar to the North-East Atlantic fauna. These results corroborate the findings from other faunal groups, such as isopods (Svavarsson et al., 1990) and gastropods (Høisæter, 2010), that are partly based on the same material as the present study, and demersal fish (Bergstad et al., 1999).

Svavarsson (1997), Narayanaswamy et al. (2003, 2005) and Høisæter (2010) all demonstrated a diversity maximum at about the continental margin and upper slope (400-700 m) on a depth gradient

from shelf to deep-sea. The diversity maximum has been related to the particular hydrographic conditions with fluctuating temperatures and possibly bottom currents due to internal waves in the boundary zone between the relatively warm Atlantic water masses and the cold deep-water (Narayanaswamy et al., 2003; Høisæter, 2010). In the present study, the highest polychaete richness was found on the upper and middle slope (550-1,000 m), essentially in accordance with their results, but the maximum area diversity (large-area or gamma diversity) was observed somewhat deeper at 1,000-2,000 m. No direct comparison to the shelf diversity could be made, however, because of lack of relevant data, i.e. samples from the shelf taken with the same gear and taxonomically treated in the same way for the current species groups. Høisæter (2010), in particular, identified an 'ecotone group' of species specifically confined to the upper slope in 500-750 m that contributed to the diversity maximum. In the present study, some few species were restricted to the upper slope (500-750 m), e.g. *Lumbrineris cf. coccinea* and *Asclerocheilus* sp. These species may fit into the 'ecotone' group as defined by Høisæter (2010), but the number of records was low and not sufficient to ascertain their depth distribution. The present data thus do not support the presence of an 'ecotone' group of polychaetes that would be corresponding to the gastropods, but further studies of the species complexes in the shelf and upper slope area may provide new data to elucidate the matter.

The gradually decreasing species richness from upper slope to abyssal depth and the low abyssal diversity generally comply with results for other faunal groups, such as crustaceans (Svavarsson et al., 1990; Svavarsson, 1997), gastropods (Stuart and Rex, 2009; Høisæter, 2010) and demersal fish (Bergstad et al., 1999). They further corroborate results from gastropods in describing the abyssal fauna as poor in species, but with high abundances for the species represented (Bouchet and Warén, 1979; Høisæter, 2010). The results are also in general accordance with depth gradient studies of benthic fauna in the northern Nordic Seas (Piepenburg et al., 2001; Weslawski et al., 2003; Włodarska-Kowalczyk et al., 2004) and inventories compiling data from various sources (Bluhm et al., 2011), although these studies mostly were of lower taxonomic resolution. There was no indication of a mid-depth diversity maximum (1,500-3,000 m) that has been reported from deep-sea studies in the North Atlantic south of the Shetland-Iceland-Greenland ridge and deep-sea studies elsewhere

(Paterson and Lamshead, 1995; Rex and Etter, 2010), as also was noted by Piepenburg et al. (2001) and Bluhm et al. (2011).

The assessments of diversity patterns and comparisons among different geographic areas rely heavily on the status and precision of the species taxonomy. Bluhm et al. (2011) pointed out that lack of consistent taxonomic resolution could mask diversity patterns in comparisons of pan-Arctic deep-sea fauna. The same holds true for environmental surveillance and time-trend monitoring, for instance with relevance to climatic change. In current monitoring, the general biodiversity is a decisive contributor to characterise and evaluate anthropogenic-driven environmental changes. The polychaetes play a major role due to their abundance and high species diversity. Obviously, cases of inaccurate identifications and confusion of morphologically similar species will reduce the ability to detect changes, which might be critical, although little is known on the methodological consequences of improper taxonomy. The taxonomy of the currently studied families, however, suggests that consequences might be severe. Of the 50 presently recorded and examined species in continental slope and deep-water areas, ten appear as undescribed (Table 2), five have been recently described (since 2010) (*Ophelina basicirra*, *O. brattegardii*, *Scalibregma hansenii*, *Ampharete undecima*, *Amphicteis wesenbergae*: Parapar et al., 2011a; Kongsrud et al., 2011; Bakken et al., 2014; Alvestad et al., 2014), and four are of unclear taxonomic status and may represent species complexes. It may also be noted that some of the commonly occurring species had not been reported since their original description about hundred years ago (Kongsrud et al., 2011; Parapar et al., 2011a). Essentially then, about 40% of the species have been recorded and characterised during the recent taxonomic studies, illustrating that the taxonomic knowledge just a few years ago was quite inadequate.

Inadequate taxonomy has previously been demonstrated for other polychaete groups from the Nordic Seas, e.g. oweniids (Koh et al., 2003; Parapar, 2006) and terebellomorphs (Parapar et al., 2011b, 2011c). In addition, recent evidence from DNA-barcoding suggests that several slope and shelf species may represent groups of morphologically similar species (Kongsrud et al., unpublished). The importance of genetic studies in critical taxonomy has recently been documented for hesionid and

phyllodocid polychaetes (Nygren et al., 2005, 2010). Cryptic species among polychaetes are common (Nygren, 2014), which advocates the use of critical taxonomic studies to unveil masked biological diversity, and not only in polychaetes, as similar results have been demonstrated in other groups. Studies of different morphospecies of the polychaete group *Glycera* from the Antarctic and gastropods in the western North Atlantic have demonstrated different bathymetric gradients (Schüller, 2011; Glazier and Etter, 2014).

Of great importance for the present study was the availability of a quantity of specimens from a high number of samples, most of them collected with one gear in a standardised way. It may also be noted that all material is deposited in museum collections and hence ready for examination, and not being dispersed around in separate institutions. Bluhm et al. (2011), in their compilation of Arctic deep-sea benthos data, commented that uneven distribution of samples, lack of consistency in sampling gear and varying taxonomic resolution posed several problems when comparing data from different data sets, sources and geographic regions. The taxonomic resolution is particularly critical for the assessment of bathymetric gradients and latitudinal trends, since improper species discrimination will tend to 'stretch out' distribution gradients and conceal real differences. Being aware of the pitfalls from varying data quality, Bluhm et al. (2011) concluded that there was a large overlap between Arctic deep-sea fauna (presumably including the Nordic Seas) and Arctic shelf species and a strong Atlantic influence in the occurrences of the polychaetes. The results from the present study suggest that the bathymetric gradients are far more distinct and the species composition between Atlantic and Arctic deep-sea fauna considerably more different than indicated in their study. Essentially, few species names in the currently studied polychaete families are shared between slope and basin species in the Nordic Seas and the North Atlantic south of the Shetland-Iceland-Greenland ridge. Svavarsson (1997) indicated a similar result for isopod crustaceans. Compilations, such as Bluhm et al. (2011), provide important overviews of available data giving broad insight into diversity relationships, but are hampered by methodological differences and taxonomic inaccuracies when assessing bathymetric and latitudinal gradients. In order to assess the generality of the patterns found in the present study, more studies on broader taxonomic groups based on material collected in standardised ways and treated with

high taxonomic consistency are needed. Based on the results from the present study, we hypothesise that the cold Nordic Sea deep-water fauna differs significantly from the North Atlantic deep fauna, both with regard to species richness and species composition, and rather is more similar to the fauna of deep Arctic waters. It may also be worth to examine more closely the faunal change between deep-water and coastal and shelf species in Arctic waters. High taxonomic resolution is especially important when it comes to relating and understanding species diversity patterns in response to natural environmental factors and anthropogenic influence. Better knowledge on species-environment relationships and biodiversity patterns is much needed for the Nordic Seas and Arctic waters, considering the recent climate change and increased human pressure in these areas.

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TABLE LEGENDS

Table 1

Number of samples studied arranged according to depth zones and sampling gear. Naming of depth zones is according to Høisæter (2010).

Table 2

List of species in the eight families examined in the present study.

FIGURE LEGENDS

Fig. 1. The Nordic Seas: Norwegian Sea, Iceland Sea and Greenland Sea. The red line indicates position of hydrographic transect shown in Fig. 2.

Fig. 2. Temperature distribution in a cross section of the Norwegian Sea from the west coast of Norway into the Iceland Sea (see Fig. 1). Modified from Blindheim (2004).

Fig. 3. Location of samples included in the present study. Different symbols indicate type of gear used for sampling. Green dots show location of RP-sledge samples used for assessing patterns in species diversity.

Fig. 4. Depth distribution of polychaete families on the continental slope (> 500 m) and in the deep basin of the Nordic Seas. Line illustrates number of families in relation to depth, line dots and family names indicate deepest occurrence of each family. Families listed in the bottom box are found at all depths along the depth transect.

Fig. 5. Depth distribution of species in the families Onuphidae, Lumbrineridae, Acrocirridae, Flabelligeridae, Opheliidae and Scalibregmatidae in the Nordic Seas. Vertical bars show depth range of species identified in the present study. Number of records (occurrences) is indicated below the column for each species. X = species found in shelf and coastal waters (< 500 m depth) at the west coast of Norway. Records of shelf and coastal species from Støp-Bowitz (1945, 1948a, 1948b), Fauchald (1972), Winsnes (1980, 1981), Salazar-Vallejo (2012) and own observations.

Fig. 6. Depth distribution of species in the families Maldanidae and Ampharetidae in the Nordic Seas. Vertical bars show depth range of species identified in the present study. Number of records (occurrences) is indicated below the column for each species. X = species found in shelf and coastal waters (< 500 m depth) at the west coast of Norway. Records of shelf and coastal species from Arwidsson (1906), Holthe (1986) and own observations.

Fig. 7. Number of polychaete families and species in RP-sledge samples 1981-87 in relation to depth of samples. Number of species comprises the examined families (Onuphidae, Lumbrineridae, Acrocirridae, Opheliidae, Flabelligeridae, Scalibregmatidae, Maldanidae, Ampharetidae). Added trendlines were fitted using the logarithmic function, $R^2 = 0.32$ (families) and 0.40 (species).

Fig. 8. Alpha (sample) and gamma (large area) diversity in depth zones from RP-sledge samples in the Nordic Seas. Data for the families Onuphidae, Lumbrineridae, Acrocirridae, Opheliidae, Flabelligeridae, Scalibregmatidae, Maldanidae and Ampharetidae. Standard deviation for alpha diversity is indicated by bars.

Fig. 9. Beta- or turnover diversity: Whittaker's beta index was calculated for depth zones, whereas Cody's beta index and Sorensen's similarity index were calculated between succeeding depth zones.

Table 1

Number of samples studied arranged according to depth zones and sampling gear. Naming of depth zones is according to Høisæter (2010).

Depth zone	Depth (m)	RP-sledge 1981-87	RP-sledge 1990, 2008-2009	Box-corer / van Veen grab 1998, 2004-2009	Beam trawl / ROV 2006-2011
Upper slope	500-750	16	3	11	6
Middle slope	750-1000	16	6	38	1
Lower slope	1000-1500	24	2	17	1
	1500-2000	19	1	7	
Abyssal basin	2000-2500	17	1		
	2500-3000	9	1		1
	> 3000	8			

Table 2

List of species in the eight families examined in the present study.

Onuphidae

Nothria conchylega (M. Sars, 1835)

Paradiopatra quadricuspis (M. Sars in G.O. Sars, 1872)

Lumbrineridae

Abyssoninoe cf. *abyssorum* (McIntosh, 1885)

Abyssoninoe scopa (Fauchald, 1974)

Abyssoninoe sp. A

Augeneria algida (Wirén, 1901)

Augeneria cf. *tentaculata* Monro, 1930

Augeneria sp. A

Augeneria sp. B

Lumbrineris aniara Fauchald, 1974

Lumbrineris cf. *coccinea* (Renier, 1804)

Lumbrineris futilis Kinberg, 1865

Lumbrineris latreilli Audouin & Milne-Edwards, 1833

Acrocirridae

Macrochaeta polyonyx Eliason, 1962

Flabelligeridae

Brada tzetlini Jirkov & Filippova in Jirkov, 2001

Diplocirrus hirsutus (Hansen, 1878)

Diplocirrus longisetosus (Marenzeller, 1890)

Flabelligera sp. A

Opheliidae

Ophelina abranchiata Støp-Bowitz, 1948

Ophelina basicirra Parapar, Moreira & Helgason, 2011

Ophelina brattegardii Kongsrud, Bakken & Oug, 2011

Ophelina cylindricaudata (Hansen, 1879)

Ophelina helgolandiae Augener, 1912

Ophelina opisthobranchiata Wirén, 1901

Scalibregmatidae

Asclerocheilus sp. A

Polyphysia cf. *baffinensis* (Blake, 1972)

Pseudoscalibregma parvum (Hansen, 1879)

Scalibregma hansenii Bakken, Oug & Kongsrud, 2014

Scalibregma sp. A (near *inflatum*)

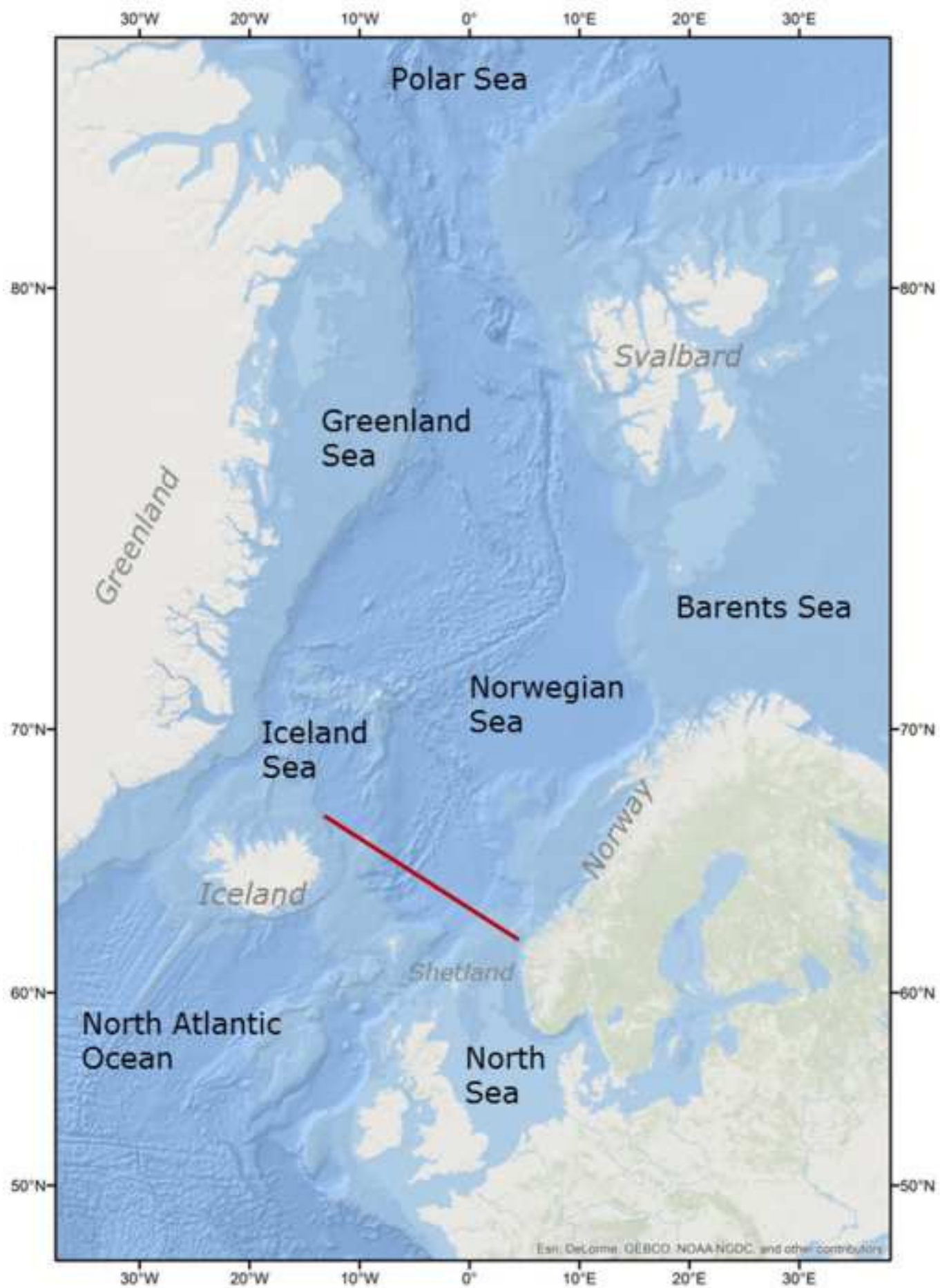
Maldanidae

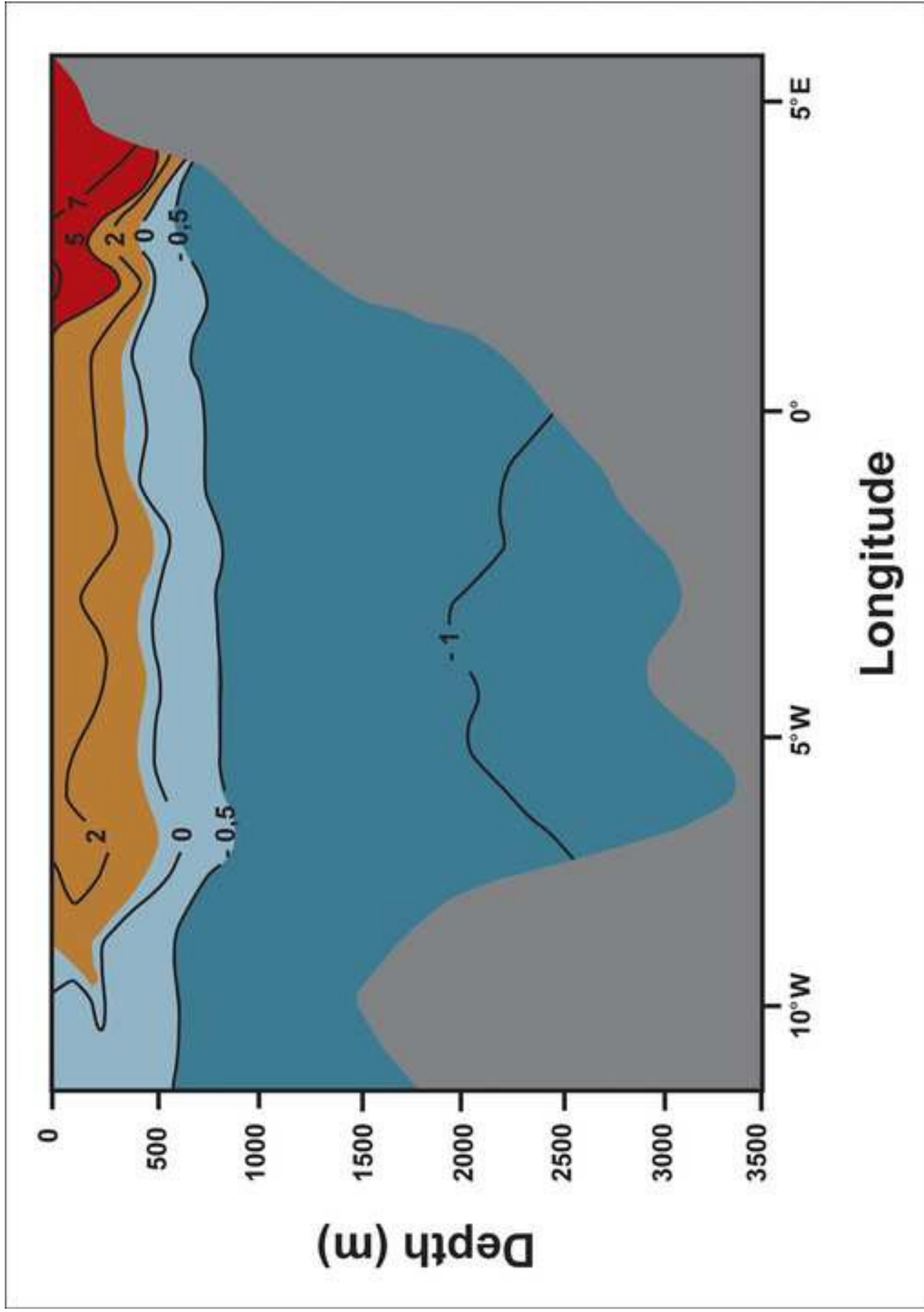
Eupraxillella sp. A*Maldane koreni* (Hansen, 1878)*Nicomache quadrispinata* Arwidsson, 1906*Notoproctus oculatus arcticus* Arwidsson, 1906*Petaloproctus tenuis* (Théel, 1879)*Praxillella* sp. A*Praxillura longissima* Arwidsson, 1906

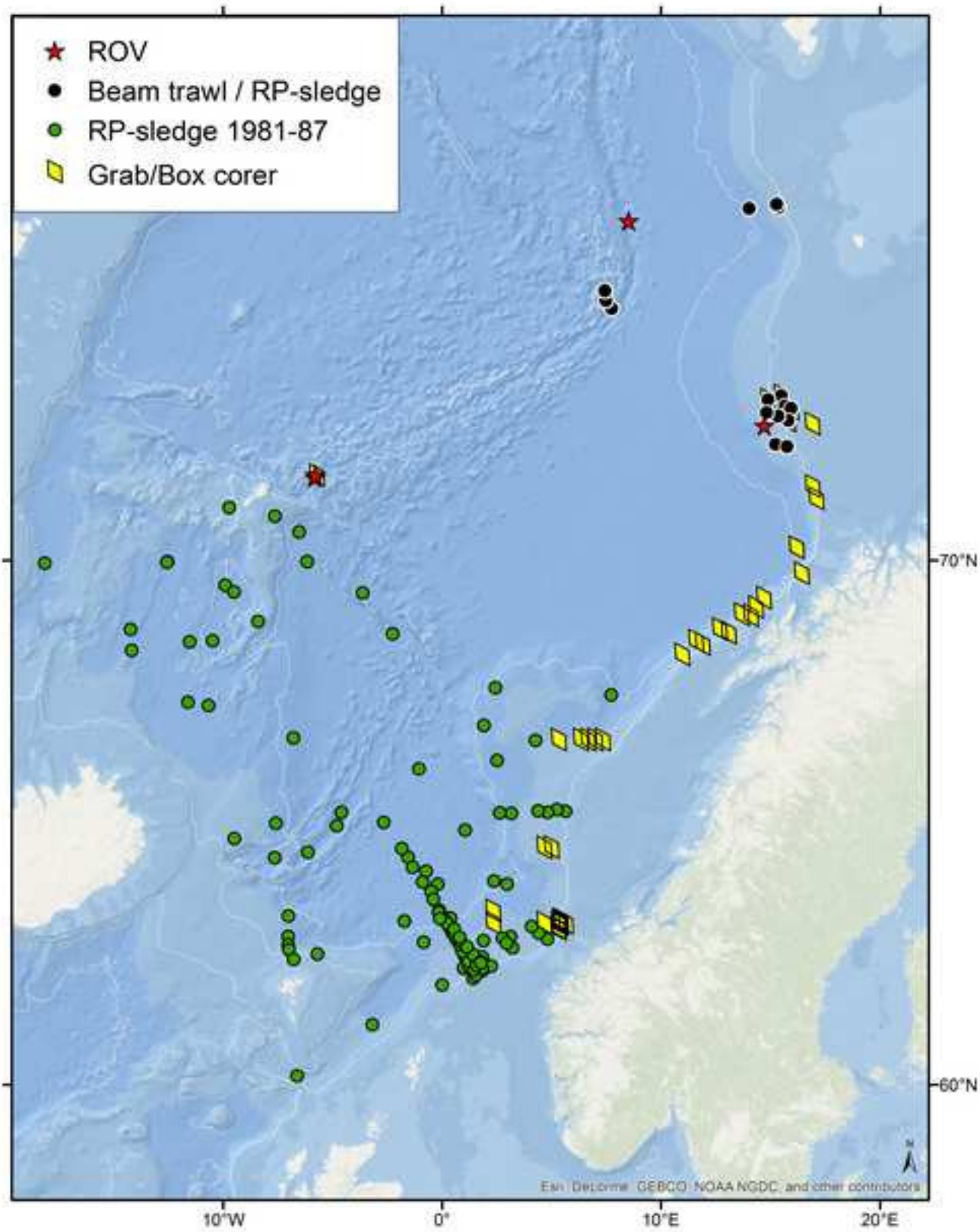
Ampharetidae

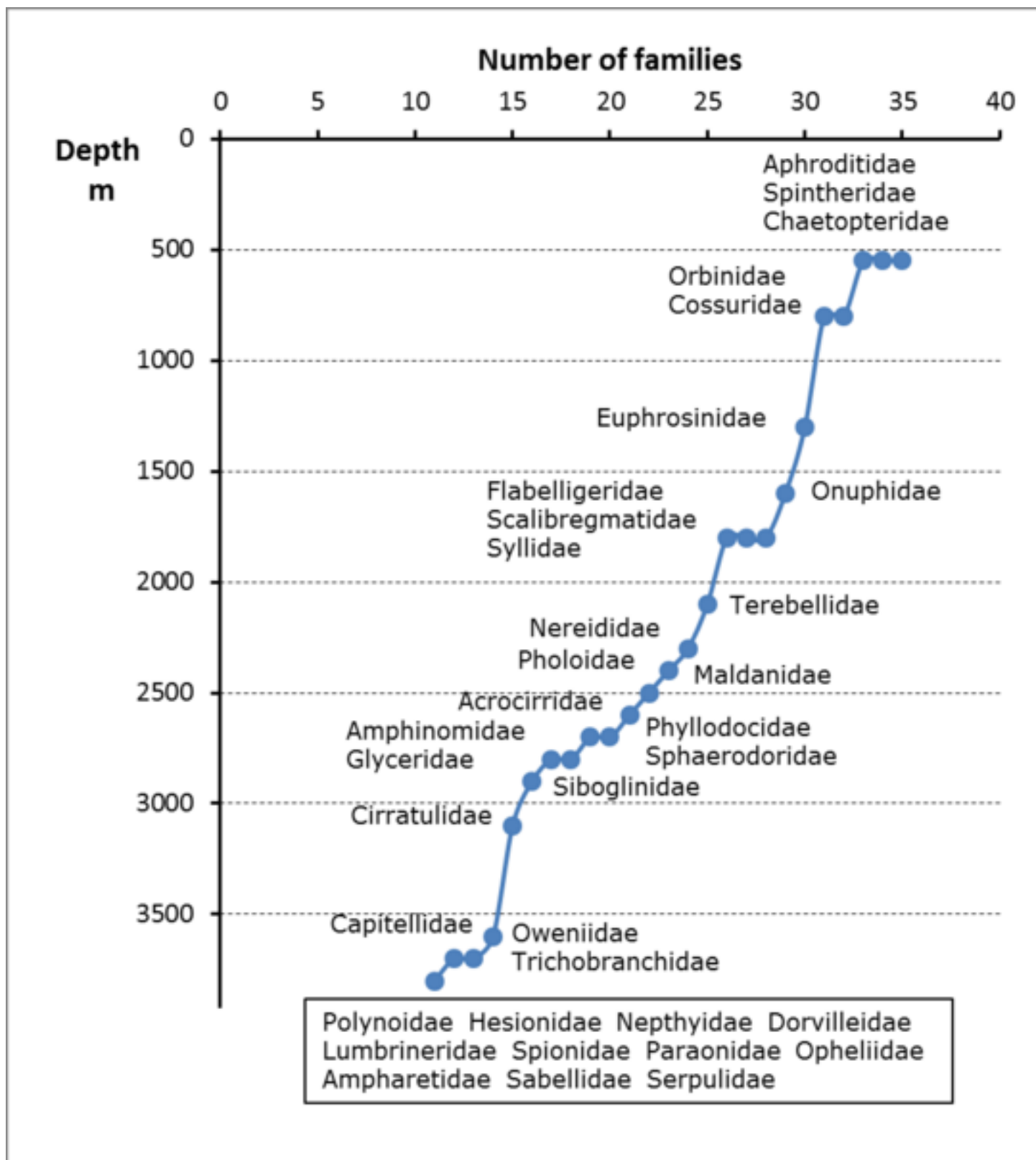
Amage auricula Malmgren, 1866*Ampharete finmarchica* (M. Sars, 1865)*Ampharete undecima* Alvestad, Kongsrud & Kongshavn, 2014*Ampharete* sp. A*Amphicteis ninonae* Jirkov, 1985*Amphicteis wesenbergae* Parapar, Helgason, Jirkov & Moreira, 2011*Anobothrus laubieri* (Desbruyères, 1978)*Anobothrus* sp. A*Glyphanostomum pallescens* (Théel, 1879)*Grubianella klugei* (Pergament & Khlebovich, 1964)*Samythella neglecta* Wollebaek, 1912*Sosane bathyalis* (Holthe, 1986)*Sosane wireni* (Hessle, 1917)*Ymerana pteropoda* Holthe, 1986

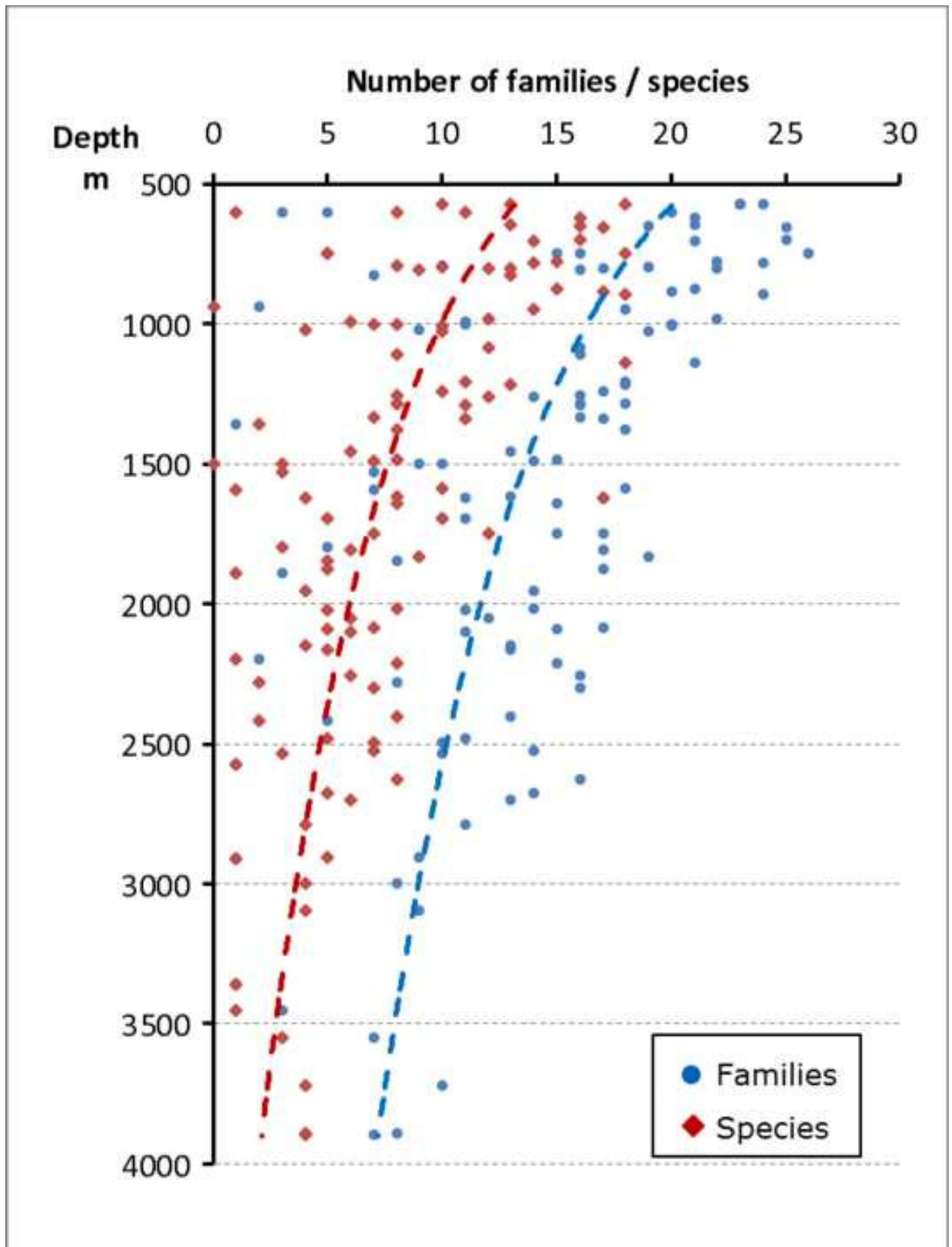
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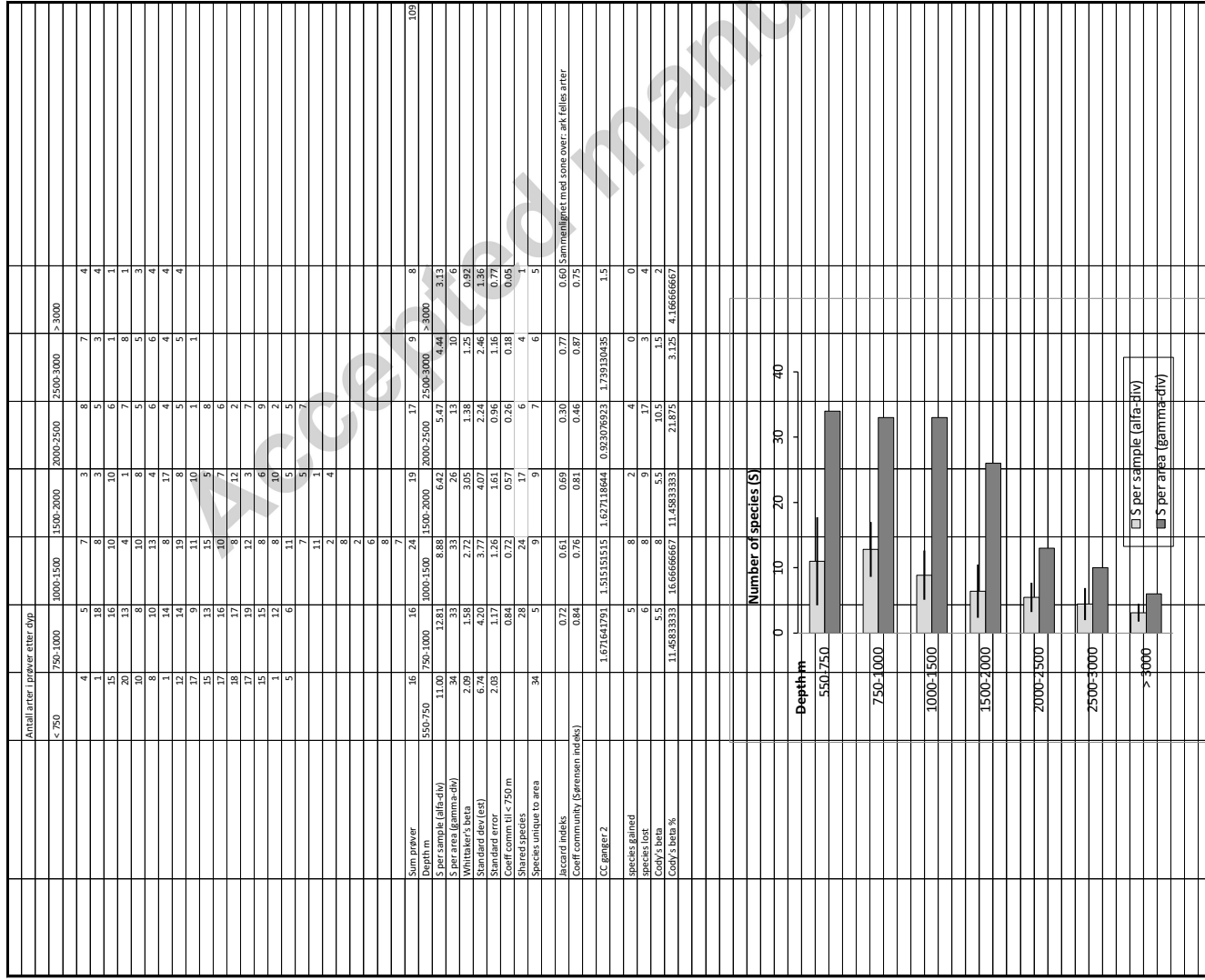












Figure

