The effect of the North Atlantic Subpolar Front as a boundary in pelagic biogeography decreases with increasing depth and organism size.

Michael Vecchione[a]*, Tone Falkenhaug[b], Tracey Sutton[c], April Cook[c], Astthor Gislason[d], Hege Øverbø Hansen[b], Mikko Heino[e,f], Peter I. Miller[g], Uwe Piatkowski[h], Filipe Porteiro[i], Henrik Søiland[e], Odd Aksel Bergstad[b].

ADDRESSES

[a]NOAA/NMFS National Systematics Laboratory, National Museum of Natural History, Washington, DC 20013 USA.

[b]Institute of Marine Research, Flødevigen, N-4817 His, Norway.

[c]Oceanographic Center, Nova Southeastern University, 8000 North Ocean Drive, Dania Beach FL 33004

[d]Marine Research Institute, Box 1390, IS-121, Reykjavik, Iceland.

[e]Institute of Marine Research and Hjort Centre for Marine Ecosystem Dynamics, PO Box 1870 Nordnes N-5817 Bergen, Norway.

[f]Department of Biology and Hjort Centre for Marine Ecosystem Dynamics, University of Bergen, N-5020 Bergen, Norway.

[g]Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL1 3DH UK.

[h]Leibniz-Institut fuer Meereswissenschaften an der Universitaet Kiel, Forschungsbereich Marine Oekologie, Duesternbrooker Weg 20, 24105 Kiel, Germany.

[i]DOP, University of the Azores, Horta, Faial, Azores, Portugal.

*Corresponding author: Tel. +1-202-633-1751, Fax +1-202-633-8848.
E-mail addresses: vecchiom@si.edu (M. Vecchione); Tone.Falkenhaug@imr.no (T. Falkenhaug); tsutton1@nova.edu (T. Sutton); acook1@nova.edu (A. Cook); astthor@hafro.is (A. Gislason); hege.oeverboe.hansen@imr.no (H. Ø. Hansen); mikko.heino@uib.no (M. Heino); pim@pml.ac.uk (P. I. Miller); upiatkowski@ifm-geomar.de (U. Piatkowski); filipe@uac.pt (F. Portiero); henrik.soiland@imr.no (H. Søiland); oddaksel@IMR.no (O. A. Bergstad).

Abstract: Broad-scale patterns in the distribution of deep-sea pelagic species and communities are poorly known. An important question is whether biogeographic boundaries identified from surface features are important in the deep mesopelagic and bathypelagic. We present community analyses of discrete-depth samples of mesozooplankton and micronekton to full-ocean depth collected in the area where the Mid-Atlantic Ridge is crossed by the Subpolar Front. The results show that the distributional discontinuity associated with the front, which is strong near the surface, decreases with increasing depth. Both the frontal separation near the surface and the community convergence at increasing depths were clearer for mesozooplankton than for micronekton.

Keywords. Deep-sea, bathypelagic, mesopelagic, zoogeography, oceanic, nekton, zooplankton.

Abbreviations: AZ - Azorean Zone, CGFZ - Charlie-Gibbs Fracture Zone, FSZ - Faraday Seamount Zone, LSW - Labrador Sea Water, MAR - Mid-Atlantic Ridge, MDS - Multi-Dimensional Scaling, MNAW - Modified North Atlantic Water, MW - Mediterranean Water, NAC - North-Atlantic Current, NACW - North Atlantic Central Water, NADW - North Atlantic Deep Water, RR - Reykjanes Ridge, SAIW - Sub-Arctic Intermediate Water. SPF - SubPolar Front.

1. Introduction.

Recent progress in understanding oceanic biogeography has been substantial. For example, a review of the topic under the auspices of the Intergovernmental Oceanographic Commission of UNESCO resulted in the most comprehensive global biogeographic classification system to date for the open ocean and deep seabed (UNESCO, 2009). Watling et al. (2013) further refined the biogeographic classification of deep-sea benthic communities. However, as noted in the pelagic review by UNESCO (2009),

> "Little information was available ... that could be used to explore the power of the proposed system to reflect biogeographic patterns of the deeper pelagic biota. The expert view of the scientists was that patterns will diverge from

surface water patterns with increasing depth. The current work is focused on observations in the photic zone, down to 200m. Of course the influence of this zone into deeper waters will be considerable, but available information on taxonomic patterns or even of the abiotic drivers of such patterns remains so poor that it is unlikely that any distinct and global scale classification of deep-pelagic biogeography is possible at the present time. Further follow-up by experts is warranted."

A more recent review focusing on global pelagic biogeography (Spalding et al. 2012) found that only surface provinces could be delineated confidently. Furthermore, they said that "More complex patterns would emerge if we were to include deeper waters, however the paucity of knowledge of distribution patterns among deeper-dwelling organisms precludes any such study at the present time. We cannot assume that surface patterns are maintained in deeper waters…"

The pelagic provinces proposed in UNESCO (2009) and Spalding et al. (2012), after thorough review of the literature, included the North Atlantic Current province and the Sub-Arctic Atlantic province, separated by the Subpolar Front (SPF). These provinces and the boundary between them are defined primarily by surface features and biota living near the surface. However, most of the ocean is much deeper than the epipelagic (or the euphotic) zone. Because many animals of the mesopelagic conduct daily vertical migrations into the near-surface epipelagic, strong linkage of mesopelagic distributions with surface features can be expected (Robinson et al., 2010). The truly deep, bathypelagic realm is the largest ecosystem on the planet and may be very isolated from surface phenomena. However, the deep pelagic has been very poorly sampled (Webb et al., 2010). It therefore remains an important research challenge to understand how structure in surface biogeography, such as the biogeographic boundary at the SPF, translates into large-scale distribution of organisms in the deep ocean.

A project of the Census of Marine Life, entitled "Patterns and Processes of the Ecosystems of the northern Mid-Atlantic" (MAR-ECO), included pelagic sampling to full ocean depths along and on the flanks of the Mid-Atlantic Ridge (MAR) between Iceland and the Azores (Bergstad et al., 2008; Vecchione et al. 2010a). The MAR-ECO study

area included the North Atlantic Current province and the Sub-Arctic Atlantic province, with the SPF crossing the middle of the study area.

Several taxon-specific studies of MAR-ECO material from the R.V. *G.O. Sars* 2004 expedition (e.g., Gaard et al., 2008; Sutton et al., 2008; Hosia et al., 2008; Vecchione et al., 2010b; Letessier et al., 2011) and the ECOMAR project (Priede et al., 2013) indicated that the surface hydrography and particularly the SPF affects the distribution of species assemblages mainly in the epipelagic and upper mesopelagic. Below this depth, the species assemblages were more consistent throughout the area studied. Also, the horizontal distribution of several taxa across the SPF seems to be asymmetric: "southern species" have limited dispersal north of the SPF, while cold-water species are not so restricted by the SPF (Sutton et al, 2013). Are the patterns that were found in a few taxonomic groups general for the pelagic community? We address this question using community analytical methods applied to a large range of taxa, and including information on both horizontal and vertical distributions. Our specific hypothesis is that the SPF influences the community distribution inferred from many taxa, but the effect declines with depth. Our overarching goal is to understand whether frontal zones defining biogeographic boundaries are valid for meso- and bathypelagic communities, as they are for those of the epipelagic. We emphasize that the current publication is not intended to be a global review of deep-sea or pelagic biogeography, but rather a community-scale test of specific hypotheses about the influence of an important surface feature, amenable to satellite based remote sensing, on deep-pelagic biogeography.

2. Methods

2.1 Sampling

We include here data from two cruises. Leg 1 of the R/V *G.O. Sars* expedition sampled from near Iceland at 60°N, 28°W to just north of the Azores Islands at 41°N, 28°W in June 2004. In addition, we used data from NOAA FSV *Henry B. Bigelow* cruise

HB 09-02 which conducted follow-up studies in the Charlie-Gibbs Fracture Zone (CGFZ, around 53° N, 035° W) in June-July 2009 (Cook et al., 2013).

G.O. Sars Leg 1 focused on pelagic sampling with a variety of gear (Wenneck et al., 2008). Station locations for this cruise were selected *a priori* to characterize geographic ridge sections (Fig. 1a), based on known bathymetry. For this analysis we used data from the two samplers that provided the best depth resolution. Micronekton catch data came from the krill trawl (also called a "macrozooplankton trawl" in Wenneck et al., 2008), a double-warp trawl with standard, pelagic-trawl doors, 6×6-m mouth opening, 3×3-mm mesh (6 mm, stretched) from the mouth to the cod end, length of 45 m, and five cod ends opening and closing by a pre-programmed timer, each with a 7-l collection bucket. It was towed on the *G.O. Sars* cruise in a stepped oblique pattern at 18 stations from a maximum depth of about 2500-3000 m, or close to the bottom in shallower depths, to the surface while closing and opening successive cod ends to sample quasi-discrete depths. We have included for this analysis the catches, standardized to number per 10^6 m^3 water filtered, of fishes, euphausiids, decapod crustaceans, lophogastrids, cephalopods, and the dominant net-caught cnidarians *Periphylla periphylla* and *Atolla* spp. Additionally, five to nine depth-stratified mesozooplankton samples from 2500 m (bottom depth permitting) to the surface were collected at each of 11 stations using a Multinet (Hydro-Bios Multi Plankton Sampler) with a 50×50-cm mouth, 180-μm mesh and five cod ends. The analysis uses abundances (per m^3) of copepod and cnidarian species. See Wenneck et al. (2008) for additional sampling details. Concurrent physical oceanographic observations have been analyzed and presented in detail elsewhere (Søiland et al., 2008) together with a summary of the literature on the physical oceanography of the study area.

In order to assess the effects of temporal and small-scale variability on the *G.O. Sars* data, the *Bigelow* cruise intensively sampled in the area of CGFZ, within the SPF. We analyzed a subset of these collections to determine the possible magnitude of short-term and small-scale variability for interpretation of the primary results from the *G.O. Sars* sampling. The same krill trawl with five cod ends as the one used on the *G.O. Sars* cruise was used to target depths from near the bottom to the surface at 11 stations in two transects, one northwest and one southeast of CGFZ. This allowed closely-spaced diel

comparisons. Bottom depths in CGFZ range from <1000 m to >4500 m. Target depths were therefore selected based on bottom depth and topography while attempting to standardize the depth layers sampled to match those on the *G.O. Sars* cruise (Table 1). Midwater sampling was conducted at all stations but focused on bottom depths >1000 m with maximum sampled depth approaching 3000 m. After preliminary attempts to do stepped-oblique tows indicated that precise coordination of the steps with the timer on the multiple cod ends was not feasible, a continuous-oblique strategy was adopted, with the cod ends fishing discrete layers within the oblique. At deep stations, this resulted in five discrete-depth oblique samples. At shallow stations, the first cod end was fished obliquely from the surface to the target depth, the second was a horizontal tow at target depth, and the third through fifth were timed to match the depths of cod ends 3-5 at the deeper stations. The data analyzed here include only the discrete-depth samples. A net-mounted, recording temperature/pressure sensor was used on each tow. See Cook et al. (2013) for additional sampling details.

2.2 Analyses

2.2.1. Assignment of samples to water masses

Based on physical characteristics (Tables 2-3), we assigned each sample to the following water masses, or combinations in cases where the sampling net passed through more than one water mass: Labrador Sea Water (LSW), Modified North Atlantic Water (MNAW), Mediterranean Water (MW), North Atlantic Central Water (NACW), North Atlantic Deep Water (NADW), and Sub-Arctic Intermediate Water (SAIW).

2.2.2. Temporal and small-scale geographic variability

In order to assess the generality of the *G.O. Sars* data, seven *Bigelow* stations were chosen for diel comparisons, with primary criterion being that all 4 or 5 nets sampled wholly within daytime or nighttime (calculated using the NOAA ESRL Sunrise/Sunset Calculator http://www.srrb.noaa.gov/highlights/sunrise/sunrise.html). This resulted in four “daytime” stations and three “nighttime” stations. The remaining four pelagic stations were not included in this analysis because they included individual discrete-depth

samples taken during twilight (± 1 h before/after sunrise and sunset). Diel comparisons were based on pelagic fish data, as this taxon strongly dominated net samples numerically.

Four parameters were investigated to discern diel and small-scale geographic differences in water column-integrated catch composition. These were Margalef's species richness index (D), the Shannon–Wiener diversity index (H'), Pielou's evenness index (J), and abundance (individuals per 10^6 m^3). Individual net data were pooled per station for each species, resulting in a species-by-station matrix for the seven stations encompassing water-column depths from 578 m (station 16, night station over seamount) to 2903 m. Analyses were conducted on all seven stations and a 4-station subset, chosen by location (all north of the transverse fracture), time (2 day, 2 night) and depth (2 ridge crest, 2 ridge valley/flank). Single-factor ANOVA was used to determine significance ($p<0.05$) of differences between day and night stations. Additionally, richness, diversity and evenness were compared for the samples north and south of the CGFZ.

2.2.3. Community analyses

Community-structure analyses were conducted separately for krill trawl and Multinet samples using the ecological software package PRIMER v6 (Plymouth Routines in Multivariate Ecological Research; Clarke and Gorley, 2006). Agglomerative hierarchical cluster analysis was used to group samples according to their micronekton or mesozooplankton composition. Species abundances at stations, standardized for volume filtered (individuals 10^{-3} m^{-3} for micronekton and individuals m^{-3} for mesozooplankton), were arranged in M × N matrices for each gear type where M is species or higher-level taxon, and N is the sample. Prior to analysis, standardized abundances of micronekton taxa were fourth-root transformed, which reduced the weighting of dominant species (e.g., *Cyclothone microdon*) and increased the importance of rare ones (Field et al. 1982). For mesozooplankton analyses the abundance data were square-root transformed to down-weight the importance of numerically dominant species (e.g. *Oithona* spp.); the stronger fourth-root transformation was not used because this produced higher stress values in the Multi-Dimensional Scaling (MDS) analyses. The similarity between stations was calculated using the Bray–Curtis measure (Bray and Curtis, 1957; Field et al., 1982).

Samples were classified by cluster analysis based on both group-average and complete-linkage methods; only complete-linkage results are presented here. Ordination of the data was accomplished using non-metric, multi-dimensional scaling (MDS; Kruskal, 1964; Kruskal and Wish, 1978).

Based on bathymetry, the MAR was separated *a priori* into sections, with sections in the north (Reykjanes Ridge - RR) and south (Azorean Zone - AZ and Faraday Seamount Zone - FSZ) divided by the position of the CGFZ (Fig. 1). The mesozooplankton and micronekton samples in these sections were compared using various subroutines of PRIMER. One-way analysis of similarity without replication (ANOSIM, Clarke and Gorley, 2006, 999 iterations, $p<0.05$) was run to test the null hypotheses that there were no differences among groups of samples as a function of five *a priori* defined factors. These factors were: ridge section (Fig. 1a), location relative to ridge axis (east, west or centered over the ridge axis); solar cycle (day/night/twilight), water mass (Tables 2-3), and depth stratum.

In order to assess the appropriate similarity level for assemblage discrimination, similarity profile permutation tests (SIMPROF; 1000 iterations, $p<0.05$) were run. The similarity level at which the departure statistics exceeded the 5% probability criterion was used to define assemblage groups via cluster analysis.

2.2.4. Taxon-specific contributions to community structure

In order to examine the ordering of both micronekton and mesozooplankton species, the data matrices used in the initial MDS exercise were reduced to include only species that were relatively abundant (important because species that occur only in a few samples may confound the species ordering; Clarke and Warwick, 2001). The aim of the "species cluster analysis" was to investigate if the different taxa (e.g., cnidaria versus copepods) grouped together to form taxon-specific clusters; i.e., if abundance values of taxa fluctuated in a similar manner across samples. For mesozooplankton, we first graphically explored the frequency distribution of species; we subsequently decided to include only species that occurred in 10 samples or more in this analysis. Similar analyses were performed for micronekton under several criteria, both in terms of frequency of

occurrence and total abundance, but no taxon-pair groupings were found in any analysis and detailed results are therefore not presented here.

3. Results

3.1. Physical structure

Søiland et al. (2008) summarized the physical-oceanographic conditions during the *G.O. Sars* cruise. The position of the Subpolar Front (SPF) south of the Charlie-Gibbs Fracture Zone (CGFZ) is indicated in Fig. 1b. Most of the variability in water masses was in the upper 500 m of the water column. Northern stations on the RR (CTD stations 391-394, cf. Søiland et al., 2008) formed one group with Modified North Atlantic Water (MNAW) in the top 500 m. Stations immediately north of the CGFZ (395-398 and 400-401) had Sub-Arctic Intermediate Water (SAIW) in the top 500 m. South of CGFZ, stations 399 and 403 were in a transition zone and 402 in an eddy. At the remaining stations there was a thick surface layer (~800 m) with warm and saline water. In the Azorean Zone (AZ) the surface salinity was above 36 PSU. There were thus four main regions (Table 3): a northern domain dominated in the upper layers by Modified North Atlantic Central Water (NACW) (region 1); a CGFZ domain, including stations at the south end of the Reykjanes Ridge (RR), dominated by SAIW (region 2); a transition zone south of the CGFZ (region 3); and a southern domain with NACW (region 4).

3.2. Vertical and temporal variability

Average abundances of fishes calculated for night *Bigelow* stations were higher by a factor of two relative to daytime stations when all seven stations were considered (Table 5a), although the difference was only marginally significant ($p=0.066$), reflecting the influence of a high daytime catch at station 20 (Table 4) and low statistical power. Diversity estimates were not significantly different with respect to sampling time of day ($p=0.50$). When only the four stations north of CGFZ were considered, the differences in average abundance estimates for day and night stations were more dramatic,

approximately threefold, but due to even lower sample size, the difference was not statistically significant (Table 5b). Diversity estimates were not significantly different with respect to diel period of sampling (p=0.285).

3.3. Assemblage structure

3.3.1. Geographic/depth patterns

Mesozooplankton. Fifteen assemblages, plus four individual samples, were discriminated by the SIMPROF method (Fig. 2). The MDS analysis for samples (Fig. 3) yielded an ordination having two major axes with a stress value of 0.11 (Kruskal and Wish, 1978). Results demonstrated a principal pattern of variance reflecting a gradient by depth, from samples collected near the surface (to the right in Fig. 3) to those taken in deep waters (to the left). The MDS plot shows that the samples grouped into at least four assemblages. In addition, a weaker gradient was observed reflecting latitudinal variation, which was more evident in surface waters (2-3 groups) than at depth (1-2 groups). The ANOSIM test revealed that of the five factors investigated, depth was the most important ($R=0.555$, $p<0.001$), followed by water mass ($R=0.518$, $p<0.001$) and ridge section ($R=0.161$, $p<0.001$). The null hypothesis (no differences among groups) could not be rejected for position relative to ridge axis ($R=0.031$, $p>0.202$) or diel solar cycle ($R=0.01$, $p>0.407$).

Geographically, the AZ differed significantly from the RR and the CGFZ with respect to mesozooplankton assemblage structure. The other ridge sections, including the Faraday Seamount Zone (FSZ), did not differ significantly from each other.

Among depth zones, the strongest difference in mesozooplankton assemblage structure was found between the upper epipelagic layer 1 (0-100 m) and layers below 200 m. Depth layer 2 (100-200 m) was significantly different from layer 6 (1000-1500 m). There were no significant differences among depth layers below 200 m (layers 3-9).

Micronekton. Eighteen clusters plus four individual samples were discriminated by the SIMPROF method (Fig. 4). The epi- and mesopelagic samples from the AZ formed a group of three clusters completely dissimilar from all others. The epi- and mesopelagic samples from other ridge sections (i.e. RR, CGFZ and FSZ) also showed a

clear tendency to group together and to split from samples taken in deeper layers. Within the group of northern epi- and mesopelagic samples, those from RR and those from the CGFZ and FSZ tended to group into two distinct clusters, but this clustering was not significant according to SIMPROF.

The assemblage structure pattern of deeper samples was less clear: a cluster grouping mainly the AZ and the RR upper bathypelagic layers (750-1500 m, but also including deeper samples from the AZ) grouped with the upper-layer samples, but at a low similarity level. AZ deepwater samples (> 1500 m) and near-bottom RR samples clustered apart from deepwater samples from the FSZ and CGFZ, which associated more by depth than by ridge section (i.e. mixed CGFZ and FSZ samples).

The MDS plot of micronekton assemblages (Fig 5a) revealed a pattern similar to that of the cluster analysis, though with less two-dimensional structure (stress = 0.16) than the MDS plot for mesozooplankton (stress = 0.11). AZ epi- and mesopelagic samples, and the bottom RR samples, formed the most distinct groupings. Within the remaining samples there were three main groups: bathypelagic AZ samples (3 clusters), epi- and mesopelagic “northern” stations (RR, CGFZ, and FSZ; one cluster); and bathypelagic northern stations (3 clusters). Of the three clusters in the latter group, RR samples made up two clusters containing near-bottom samples (taken within 200 m of the seafloor), while FSZ and CGFZ deep samples clustered together.

ANOSIM comparisons of depth zones indicated that the differences between the upper (epipelagic and mesopelagic) depth zones (0-200 and 200-750 m) and most of the groups of samples from deeper layers (>750 m) were statistically significant ($p<0.05$). Differences between samples from (a) 200-750 m and 750-1500 m, (b) 750-1500 m and 1500-2300 m, and (c) 750-1500 m and >2300 m were also significant. No differences were detected between samples from 0-200 m and 200-750 m and between samples from 1500-2300 m and >2300 m. Comparisons between near-bottom 750-1500 m samples and all other pelagic levels sampled showed no significant differences. Some differences among ridge sections (RR vs CGFZ, AZ vs RR, and AZ vs CGFZ) were significant. No significant differences were found between FSZ and any of the other sections (i.e. AZ, RR and CGFZ). Unexpectedly, comparisons of RR and CGFZ groups showed that the

samples were different whereas the RR vs FSZ (which are more separated geographically) samples were not significantly different.

3.3.2. Water masses

Mesozooplankton. The samples were more separated (less similar) in the upper layers than in deeper layers. When water masses were used as factors in the MDS plot rather than geography (Fig 3b), the picture was not so clear. Samples from NACW epi- and upper mesopelagic each formed discrete assemblages. Labrador Sea Water (LSW) samples grouped within a single assemblage (Fig 3b). ANOSIM pairwise comparisons between sample groups revealed that samples classified by LSW were significantly different from NACW, MNAW and SAIW ($p<0.01$). Significant differences were also found between the samples from NADW vs SAIW, NADW vs NACW and NACW vs SAIW. No significant differences were found between MNAW and any of the other water masses. No significant difference was found between NADW and either SAIW or LSW samples. Groups of samples that passed through more than one water mass were not statistically different.

Micronekton. The pattern depicted by MDS using samples assigned to water mass instead of geography also showed a somewhat less clear picture (Fig. 5b). The NACW AZ epi- and mesopelagic samples split from the others. Note the exception of the two epi-/mesopelagic samples taken in a pocket of NACW in the FSZ; that group was closer to the other samples taken in the northern stations. The plot did not show any clear difference between the epi- and mesopelagic samples taken from SAIW, SAIW-LSW, MNAW and MNAW-LSW. The bathypelagic samples from the AZ and FSZ were taken in NADW, but those from the FSZ were more similar to those taken at northern stations in the LSW and LSW-NADW. However, there was a progression from the LSW to the NADW. Upper bathypelagic samples from AZ that sampled more than one water mass (i.e. NACW/MW/NADW) were intermediate between the AZ epi- and mesopelagic samples and those from deeper strata.

The differences detected by the pairwise comparisons between sample groups classified by pure water masses were significant (i.e. SAIW vs NACW; MNAW vs LSW; MNAW vs NADW; MNAW vs NACW; LSW vs NADW; LSW vs SAIW; LSW vs

NACW; NADW vs NACW; NADW vs SAIW). The only exception was between the northern upper-layer water masses MNAW vs SAIW, which showed no differences. The remaining 33 comparisons showed that groups of samples taken from tows that fished through more than one water mass were not statistically different, except for the comparisons between the NACW/MW/NADW and LSW and SAIW, which showed significant differences.

3.3.3. Taxon-specific patterns

The taxon-specific cluster analysis showed no obvious pattern or grouping (MDS plot not shown), consistent with the high stress value of 0.20 indicating a poor fit between species and the 2-dimensional ordination space. Thus, cnidarians and copepods did not form taxon-specific clusters. Similarly, no obvious patterns were observed for micronekton taxa.

4. Discussion

4.1. Deep-pelagic biogeography

The pelagic realm is a three-dimensional environment, most of which has little or no direct interaction with the interfaces at the ocean's bottom and surface. The deep-sea pelagic is the largest ecosystem on Earth, encompassing $>10^9$ km^3 (Ramirez-Llodra et al., 2010). The major structuring variable in all of that volume is depth and its covariance with temperature, density, and the penetration of sunlight, resulting in the layering of the ecosystems of the open-ocean pelagic. The transitions between the various vertical layers are gradients, not fixed surfaces, so ecological distinctions among the zones are somewhat "fuzzy" across the transitions (Sutton, 2013). The abundance and biomass of organisms generally varies among these layers from a maximum near the surface, decreasing through the mesopelagic, to very low levels in the bathypelagic, increasing somewhat in the benthopelagic (Angel, 2003).

The bathypelagic comprises almost 75% of the volume of the ocean and is generally remote from the influence of the bottom and its ecological communities

(Robison, 2009). It is worth noting that although the abundance (i.e., number per m^{-3} of seawater) of animals in the bathypelagic is very low, because such a huge volume of the ocean is bathypelagic, even species that are rarely encountered may have very large total population numbers. A species with only one animal in 1000 m^3 of water but a depth range of 1-2 km and a broad geographic distribution can have a population of many millions (Herring, 2002). Therefore, the currently unknown biogeographic patterns of this huge volume of the biosphere can profoundly affect our understanding of the ecological structure of life on Earth.

Another characteristic of pelagic ecosystems is great temporal dynamics. These temporal changes result from both physical and biological processes (Robison et al., 2010). Water movements transport entrained swimming and drifting organisms. Because of the huge volume of water moving in the deep, even slow currents can transport very large numbers of organisms, and on annual time scales the distances can be large. Temporal biological dynamics include the active vertical movements of the animals over various time scales. The life cycles of deep-pelagic animals often involve shifts in vertical distribution among developmental stages. Additionally, many deep-benthic species spend part of their life cycles, typically the early stages but for some the reproductive stage, at some level in the pelagic realm. Such ontogenic vertical migrations expand the dependence of species on the physical and biological dynamics of the various layers, often including the surface layer. Even more spectacular are the diel vertical migrations by very many species of the mesopelagic and upper bathypelagic, generally (but not universally) upward at night to feed in the higher biomass closer to the surface and back down during the day. When the temporal component is superimposed on the massive volume of the deep ocean, the deep pelagic can be considered to be effectively four-dimensional.

The *G.O. Sars* cruise was designed around broad geographical coverage, from Iceland to the Azores. Pelagic sampling on the *Bigelow* cruise provided more intensive coverage of smaller spatial scales as well as closer temporal comparisons. Although the *Bigelow* results indicated higher total numbers of fishes, the numerically dominant micronekton taxon, at night, other community measures such as diversity and evenness did not vary significantly over the diel period. We interpret this, together with the lack of

significance of diel comparisons in the *G.O. Sars* data, as an indication that the broad-scale biogeographic patterns in the *G.O. Sars* results are not excessively compromised by diel variability resulting from time of sampling. Analysis of trawl catch rates supports this (Heino et al., 2011). Furthermore, higher numbers caught at night were down-weighted in the analyses by the data transformation prior to analysis.

Horizontal patterns exist in the distribution of deep-pelagic organisms. However, these patterns seem less distinct than in either surface waters or on the bottom. For example, Mironov et al. (2006) provide evidence of a clear distributional discontinuity in benthic fauna on the MAR at the CGFZ. The drivers of these patterns are not well known for either the bottom communities or those in the deep water column. Primary productivity at the surface is certainly an important factor. Whether by passive sinking or active biological transport, surface productivity feeds life in the deeper waters. Surface patterns are therefore reflected in the deep pelagic (Fock, 2009; Robinson et al., 2010; Robison et al., 2010). In addition to variation in the total abundance and biomass that can be supported, some deep species are known typically to live beneath oligotrophic waters whereas others are typically below higher productivity areas (Herring, 2002).

The biogeographic importance of deep features undetectable at surface (e.g., interactions between deep currents and topography) is generally unknown. Additionally, major oceanic frontal boundaries such as the Polar and Subpolar Fronts extend down into deep waters and appear to form biogeographic boundaries. The results of this study suggest that the distinctness of those boundaries decreases with increasing depth, across a multitude of the taxa comprising the pelagic community.

4.2. Subpolar Front as biogeographic boundary

4.2.1. Physical structure

During the *G.O. Sars* cruise, the geographic structure of water-mass distribution decreased at depths below 500-800 m relative to that seen in near-surface layers. Overall water-mass structure in the study area comprised three main regions with a broad mixing zone located south of the CGFZ. These regions corresponded approximately with the ridge sections defined by bathymetry.

At the MAR the SPF is not a single oceanic front but rather a mixing zone between the warmer Atlantic and cooler sub-Arctic water masses. The mixing zone extends meridionally for hundreds of kilometers, shaped by the topography. To the north, the RR is too shallow to allow the North-Atlantic Current to pass over, and the deep CGFZ acts to channel the main flow across the MAR. A persistent front delineating the northern extent of the SPF zone forms above the CGFZ (Fig. 1b), and has been considered to be the most important biogeographic boundary in this region, affecting a majority of the pelagic realm, at least down to the lower mesopelagic. Farther south the SPF comprises a zone of eastward-flowing eddies and meanders, which may cause temporary barriers interspersed with periods of intense mixing. This results in patchy surface productivity on the scale of 10s of kms. There are believed to be several persistent strands of the North-Atlantic Current between the CGFZ and Azores, coinciding with smaller fracture zones (Schott et al., 1999; Bower et al., 2002; Read et al., 2010); these strands are also reflected in surface thermal fronts detected by satellite remote sensing (Miller et al., 2013).

Within the SPF zone the bottom topography exerts little direct influence at the surface. Only the RR farther north is shallow enough to generate internal waves that can cause mixing at the surface, which can enhance the surface and pelagic productivity. Therefore the CGFZ would be expected to delineate the most distinct biogeographic differences; as elsewhere within the SPF, there is considerable spatial and temporal variability in the mixing processes.

4.2.2. Assemblage structure

The influence of the SPF as a faunal boundary for the mesozooplankton can be observed in the MDS analysis as a separation between northern and southern clusters, especially in the epipelagic layer (Figs. 2 and 3a). In the MDS plot, clusters in the epipelagic-upper mesopelagic were more separated than clusters from meso- and bathypelagic depths. A cluster of epipelagic samples from the RR and CGFZ is clearly separated from those of the AZ. However, the cluster with the AZ surface samples also includes two samples from one of northernmost stations (superstation 2, cf. Wenneck et al., 2008), which is located on the eastern side of the RR. This station was probably

affected by the north-westward trajectory of the North Atlantic Current, which may have transported species of southern warm-temperate association (Gaard et al., 2008). The biological history of a body of water may be more important for assemblage structure than the present physical and chemical properties of the water masses. In fact, the plankton may be more conservative than the hydrographical properties of the water mass, since the plankton assemblage indicates the origin of the water even after the water has been mixed with other waters and its hydrography transformed beyond recognition (Vinogradov, 1968).

The separation between northern and southern mesozooplankton assemblages is less obvious at meso- and bathypelagic depths, where assemblages are clustered more closely together. Therefore, in this study, the SPF can be observed as a faunal boundary for the mesozooplankton assemblages at all depths, but below 500 m the influence of the front is very weak.

The distribution of zooplankton species assemblages may also be related to current patterns and the distribution of water masses. Several investigations of plankton distribution patterns have shown a pelagic biogeographic boundary at ~ 45°- 46°N (Vinogradov, 1968; Fasham and Foxton, 1979; Van Soest, 1979; van der Spoel and Heyman, 1983) which correlates with the position of the North Atlantic Current and the SPF. However, the nature of the faunal boundaries, which might limit plankton dispersal, is not clear. Latitudinal differences in the distribution of species assemblages may also be associated with the trend from seasonal pulsing of high production at high latitudes to more continuous low production at lower latitudes (Angel, 1993; Ward and Shreeve, 2001).

Water mass was found to be one of the significant factors (ANOSIM test) explaining the differences among clusters of mesozooplankton. The dominant water masses in the upper layers (MNAW, SAIW, NACW) are inter-correlated with ridge section, and thus the MDS plot with water masses as a factor (Fig. 3b) shows a similar geographical (latitudinal) pattern as in Fig 3a. However, samples classified by LSW tended to group together in the MDS. Indeed, one cluster is purely from LSW, and characterized by the presence of arctic-boreal species like *Calanus finmarchicus, C. hyperboreus* and *Heterorhabdus norvegicus*.

The micronekton distribution was similar to that of the mesozooplankton although the patterns were not as clear. Separation between the AZ and the other ridge sections was strong, especially in the upper layers. The MDS plot of sample groups identified by clustering showed a gradient with depth, both in the AZ and in the other sections. Although the other ridge sections tend to separate geographically in the MDS plot, the strongest pattern outside of the AZ is related to depth, with significant depth-related clustering indicated by SIMPRO. ANOSIM also indicated strong separation of the epi- and mesopelagic samples from those of deeper strata. Interpretation of water masses on the micronekton MDS plot was even less clear than the geographic pattern. Inclusion of more than one water mass in a sample was more of a problem in the micronekton data than for the mesozooplankton. However, the MDS plot indicated a gradient from LSW through NADW to NACW, with MNAW and SAIW forming a distinct shallow cluster. Thus, the major patterns for the micronekton data are (1) separation of the AZ section from the rest of the study area, (2) similar depth gradients within the AZ and the rest of the area, and (3) increasing similarity between AZ and the rest of the area with increasing depth.

4.3. Conclusions

The SPF is a conspicuous feature of North Atlantic surface hydrography that can be observed using remote-sensing methods. At the surface, it is most distinct along its northern edge, generally coinciding with the CGFZ, whereas to the south it forms a more diffuse mixing zone. Water-mass distribution based on *G.O. Sars* CTD stations indicates that north-south hydrographic structure is strongest down to depths of 500-800 m. As predicted by UNESCO (2009), the biogeographic signature of the SPF for both micronekton and mesozooplankton is strong near the surface but decreases with increasing depth to very weak separation of assemblages in the bathypelagic. This strong surface feature is therefore not a good predictor of deep-pelagic biogeography. It remains to be seen whether important barriers to the distribution of deep-pelagic fauna result from deep-physical phenomena that are not amenable to remote sensing.

5. Acknowledgments. This study was an element of the Census of Marine Life field project MAR-ECO 2001-2010, partly funded by the Sloan Foundation. The Institute of Marine Research and the University of Bergen, Norway, and NOAA National Marine Fisheries Service contributed ship-time. P. Miller was supported by the NERC consortium grant ECOMAR. T. Sutton was supported by a grant from the NSF Ocean Sciences Division – Biological Oceanography Program (OCE 0623551).

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Figure captions.

Fig. 1. (a) Bathymetry of the study area. Ridge sections RR: Reykjanes Ridge; CGFZ: Charlie-Gibbs Fracture Zone; FSZ: Faraday Seamount Zone; AZ: Azorean Zone. (b) Sea-surface temperature during the *G.O. Sars* cruise (06 Jun.-02 Jul. 2004), with axes of the MAR and CGFZ indicated (yellow line) as well as locations of *G.O. Sars* CTD stations. Boxes and numbers correspond with hydrographic regions described in Table 3.

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List of Tables.

Table 1. Target depths for sampling macroplankton (multinet sampler) and micronekton (krill trawl with multiple cod-ends).

Macroplankton Depth zone	Depth (m)	Micronekton Depth zone	Depth (m)
1	0-100	1	0-200
2	100-200		
3	200-500	2	200-750
4	500-800		
5	800-1000	3	750-1500
6	1000-1500		
7	1500-1900	4	1500-2300
8	1900-2300		
9	2300-2500	5	>2300

Table 2. Characteristics used to classify water masses (modified from Søiland et al., 2008).

Water Mass	Temperature	Salinity/Sigma- θ
North Atlantic Central Water (NACW)	$\theta > 7°$ C	S >35.00[a]
Modified North Atlantic Water (MNAW)	$6.6° < \theta < 9°$ C	sigma-θ ~27.4
Sub-Arctic Intermediate Water (SAIW)	$5° < \theta < 9°$ C	S < 35.00[a]
Mediterranean Water (MW)		S maximum at sigma-θ = 27.5-27.6
Labrador Sea Water (LSW)	$3.3° < \theta < 3.4°$ C	34.84 < S < 34.89[b]
North Atlantic Deep Water (NADW)	$\theta < 5°$ C	Deep salinity minimum at ~1500 m

[a] Sy et al., 1992
[b] Talley and McCartney, 1982

Table 3. Hydrographic regions and occurrence of water masses during the 2004 *G.O. Sars* cruise. For locations of CTD stations, see Søiland et al. (2008). RR: Reykjanes Ridge; CGFZ: Charlie-Gibbs Fracture Zone; SPF: Sub-Polar Front; FSZ: Faraday Seamount Zone; AZ: Azorean Zone.

A. Region 1 (RR):

CTD stations 391 to 394 (north of 57°N).
0-600 m: MNAW
1000-1800 m: LSW
1800 and down: NADW
Note: The MNAW found at these stations was colder and less saline than found farther south (stations 406 and southward), but still within the definition below.

B. Region 2 (including Southern RR and Northern CGFZ):

CTD stations 395 to 398 and 400 and 401 (53°N-56°30'N).
0-500 m: SAIW – formed in the Irminger Sea.
800-1800 m: LSW
2500-3500 m: NADW
4000 m and down: AABW (only observed at station 397)

C. Region 3 (Transitional, including Southern CGFZ and FSZ):

CTD stations 399 and 403 (50°N-53°N).
These stations were in a frontal zone with complex hydrography, with both SAIW and NACW found in the upper 500 m.
800-1800 m: LSW
2500 m and down NADW

D. CTD station 402

Probably in an eddy with similar properties as station 404.

E. Region 4 (AZ):

CTD stations 404-414 (south of 50°N).
0-800 m NACW
~1000 m at many stations an intrusion of Mediterranean Water
NADW below 1100 m
Note: the NACW at the southern stations was much warmer and more saline than at stations 391-394

Table 4. Abundance (ind. 10^{-6} m^{-3}), species richness (S), evenness (J') and Shannon-Wiener diversity (H') of deep-pelagic fishes at stations from the 2009 *Bigelow* cruise

station	Position N Lat/W Long	Treatment	ind. 10^{-6} m^{-3}	S	J'	H'
9	53°17'/36°46'	Night	8099	44	0.6	2.4
11	53°16'/35°31'	Night	14328	42	0.6	2.3
12	52°58'/34°52'	Day	1607	16	0.3	0.9
15	53°01'/33°36'	Day	4385	44	0.6	2.1
16	52°16'/31°00'	Night	14591	34	0.4	1.5
17	51°32'/30°58'	Day	5977	47	0.5	2.1
20	51°45'/29°33'	Day	10622	50	0.5	2.0

Table 5. Analysis of variance results for diel comparisons of abundance of deep-pelagic fishes from the 2009 *Bigelow* cruise stations in Table 3.

Table 5a. Results of 7-station analysis of abundance (individuals per 10^6 m^3) versus solar cycle

Groups	*Count*	*Average*	*P-value*
day	4	5647	0.066
night	3	12339	

Table 5b. Results of 4-station (all north of CGFZ) analysis of abundance (individuals per 10^6 m^3) versus solar cycle

Groups	*Count*	*Average*	*P-value*
day	2	2995	0.138
night	2	11213	

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Clustering at 42.5% (dotted line) and 35% (solid line) similarity indicated.

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Figure
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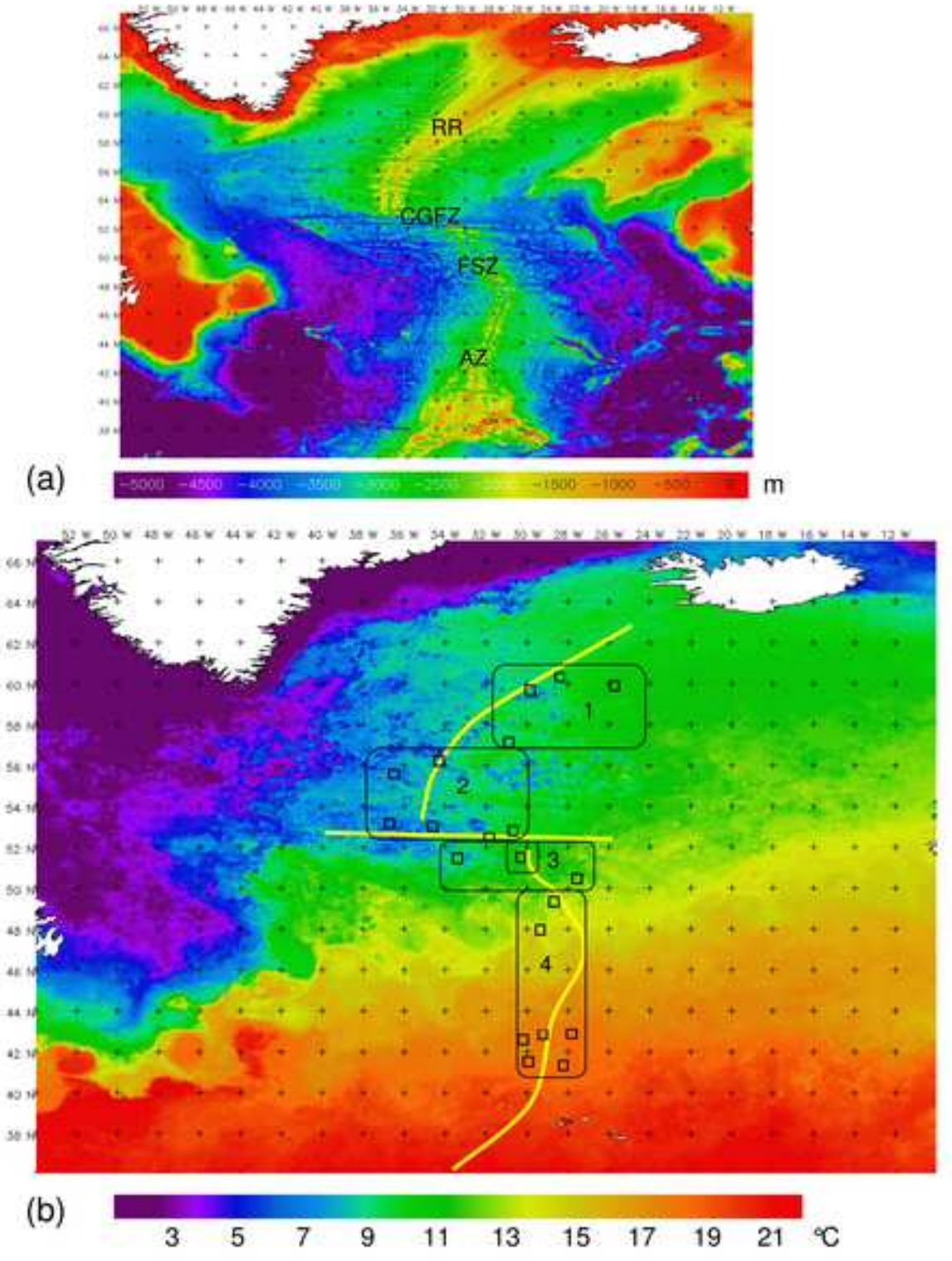

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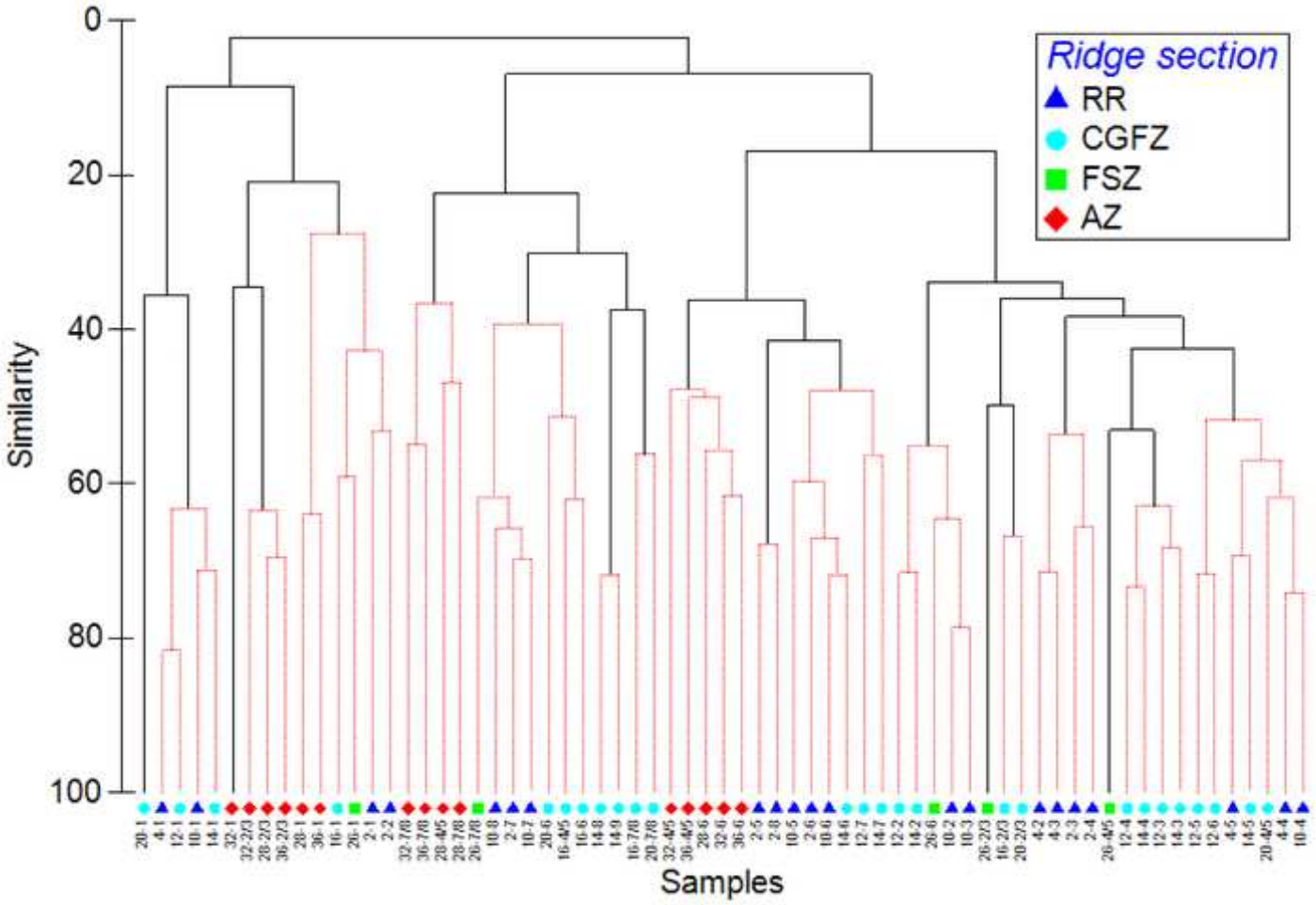

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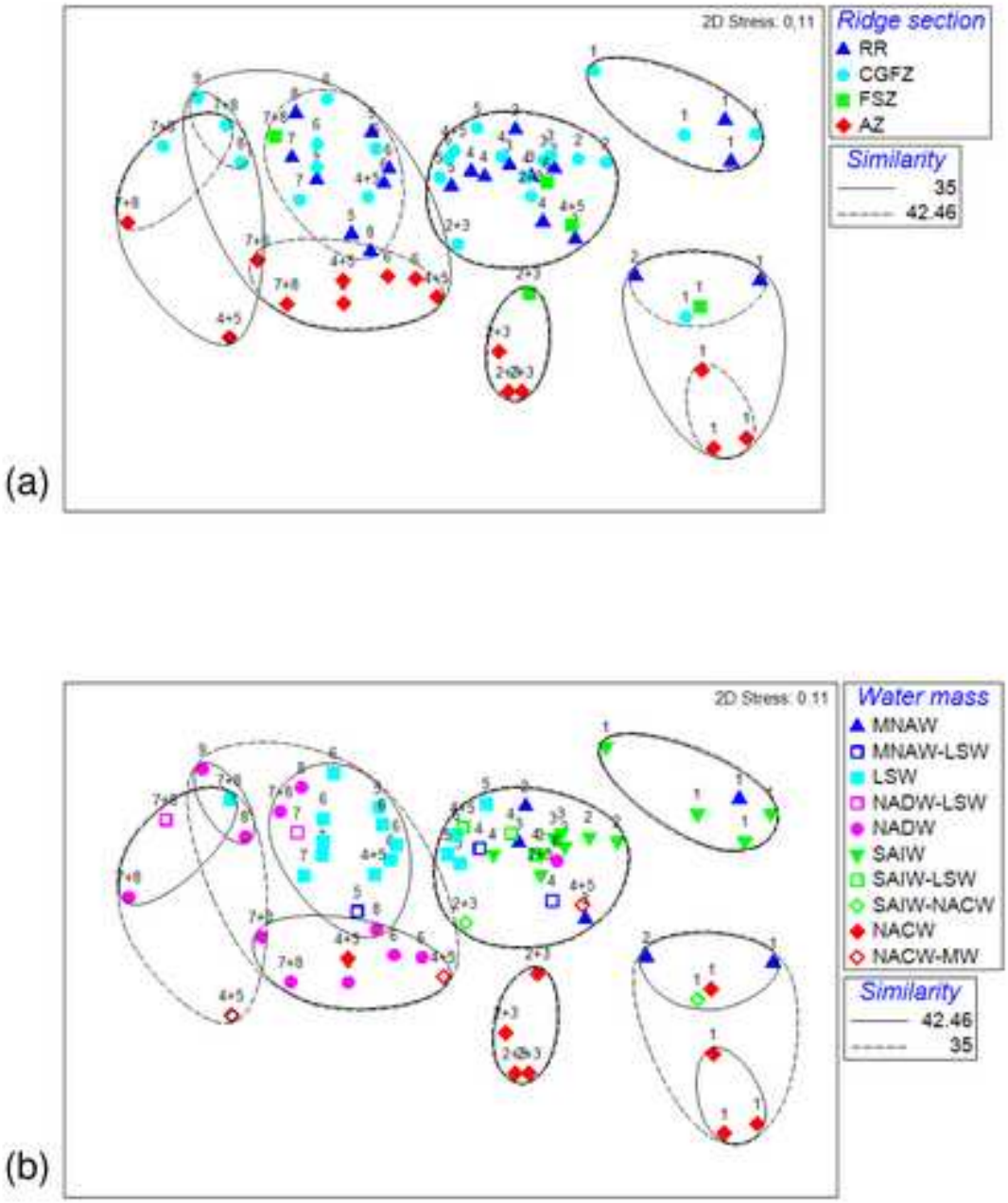

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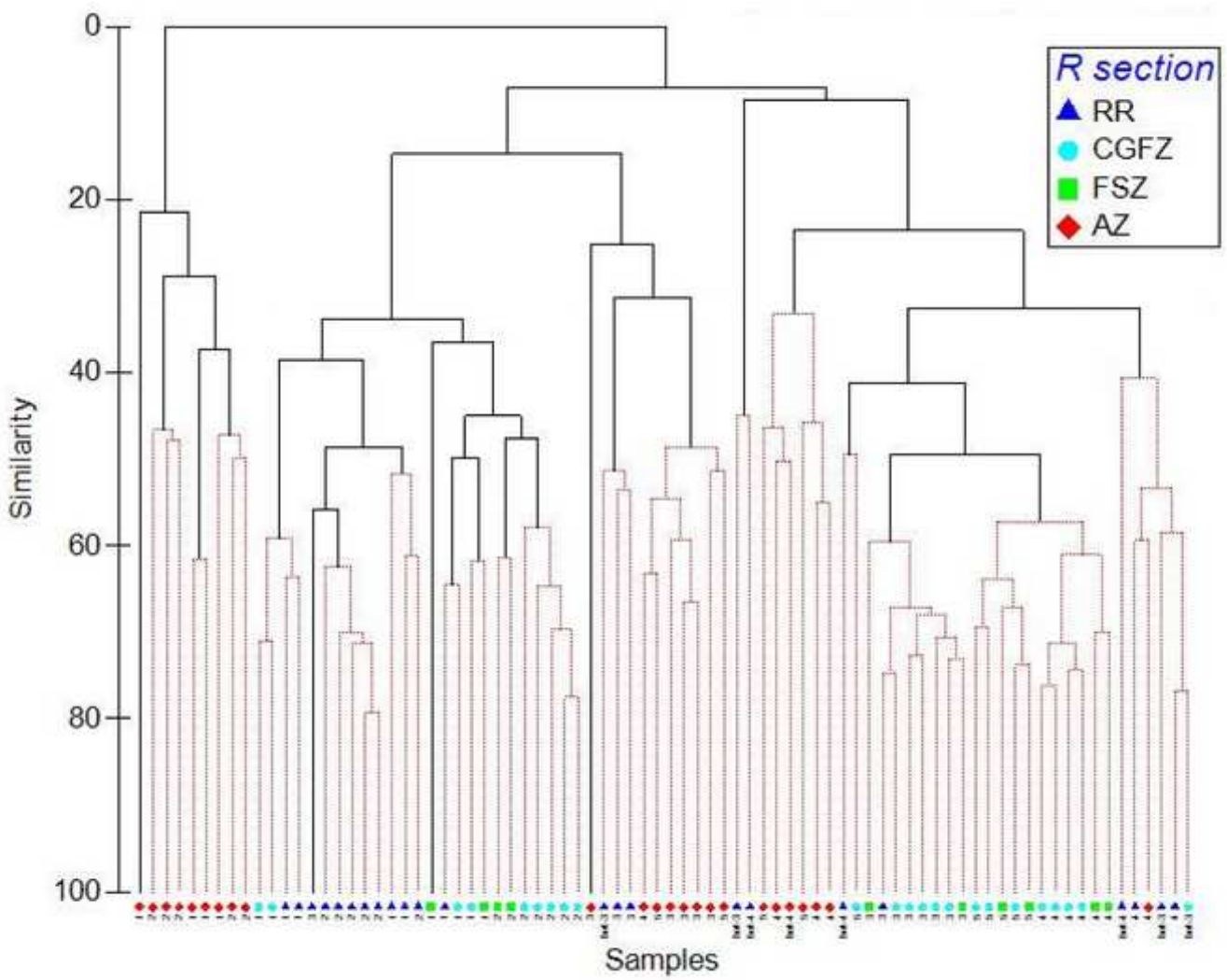

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