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What do fish learn in schools?
Life cycle diversity within populations, mechanisms and consequences

Mechanisms and consequences of life cycle diversity of beaked redfish, *Sebastes mentella*

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ABSTRACT

Recent genetic research, supported by life history information, indicates that there are three biological stocks of *S. mentella* in the Irminger Sea and adjacent waters: a 'Deep Pelagic' stock (>500m), a 'Shallow Pelagic' stock (<500m), and an 'Icelandic Slope' stock. Throughout their range, *Sebastes* species are adapted to a diversity of ecological niches, with overlapping spatial distributions of different species that have little or no morphological differences. Divergence of behavioral groups into depth-defined adult habitats has led to reproductive isolation, adaptive radiation and speciation of several *Sebastes* species. Congruent differences in fatty acid composition and parasites suggests that the three genetically distinct populations of *S. mentella* are adapted to disparate trophic habitats in pelagic waters (shallower and deeper than the deep-scattering layer), and in demersal habitats on the continental slope. Patterns of morphology are also consistent with adaptation to different habitats, because pelagic forms are more streamlined. Although genetic differences and evidence for reproductive isolation are clear, these populations appear to share common nursery habitats on the Greenlandic Shelf. Spatial overlap at early life stages and depth-defined adult populations present challenges for stock identification and fishery management. Effective resource monitoring, conservation and fishery management requires that the spatial definition of management units reflects biological stock structure. We describe a proposal for a re-definition of practical management units that are based on geographic proxies for biological stocks which minimizes mixed-stock catches according to spatial patterns of the recent fishery.

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INTRODUCTION

Stock structure of beaked redfish, *Sebastes mentella*, and appropriate spatial units for fisheries management have been debated for decades (e.g., Magnússon and Magnússon 1995, SGRS 1998, SGSIMUR 2005). Analysis of new genetic markers indicates reproductive isolation among groups of adults in different, but overlapping habitats (Johansen et al. 2000, Johansen 2003, Danielsdottir et al. 2008, Pampoulie & Danielsdottir 2008, Stefánsson et al. 2009a). In 2009, ICES organized a workshop to reconcile the new genetic results with all previous information on stock structure to identify the most likely definition of biological stocks and recommend practical management units in the Irminger Sea and adjacent waters (WKREDS 2009). This manuscript summarizes the scientific aspects of the workshop and discusses how *Sebastes mentella* offers an instructive case study in behavioral mechanisms of reproductive isolation and their practical consequences for resource management.

The genus *Sebastes* has unique life history characteristics that influence population structure. Throughout their wide geographic range in the North Pacific, North Atlantic and southern hemisphere, *Sebastes* species are adapted to a diversity of ecological niches, with overlapping spatial distributions of different species that have little or no morphological differences (Johns & Avise 1998, Alesandrini & Bernardi 1999). For some species of *Sebastes*, divergence of behavioral groups into depth-defined habitats has led to reproductive isolation (e.g., Hyde et al. 2008). Sympatric diversity of the genus *Sebastes* is a commonly used example of adaptive radiation, a relatively rapid evolutionary diversification characterized by an increase in the morphological and ecological diversity of a single, rapidly diversifying lineage (Schluter 2000).

The reproductive biology, early-life history and longevity of *Sebastes* species is unique in that they are viviparous with wide dispersal and long lifespans. Vivipary involves internal fertilization and development of ova that also hatch internally. Mate recognition, courtship behavior and mate choice are prerequisites of fertilization, providing an additional mechanism of reproductive isolation (Johns & Avise 1998). However, unlike most live-bearers, *Sebastes* species produce many, small larvae that are extruded soon after they hatch from eggs. The small larvae have a longer planktonic period than most viviparous species, and they can disperse far from the location of extrusion. The relatively strict reproductive constraints and extensive larval dispersal allow adaptive radiation into a diversity of ecological niches (Rocha-Olivares 2004). The typically long life span of *Sebastes* species also tends to promote adaptation to diverse habitats (Mangel et al. 2007). *S. mentella* exhibits all of these traits that tend to facilitate divergence within populations.

Research on *S. mentella* population structure reflects the historical development of fisheries. The fishery traditionally targeted mixed redfish species on the continental slopes of Iceland, Greenland, and the Faroe Islands, and a pelagic fishery developed in the Irminger Sea in the early 1980s (Sigurdsson et al. 2006a). Icelandic researchers considered that the pelagic fishery targeted a separate stock than the traditional demersal fishery, and the pelagic stock (referred to as 'oceanic' redfish) could be discriminated

from the 'deep-sea' stock on the basis of darker, patchy skin color, heavy parasite infestations and associated muscle spots, as well as smaller size at maturity (Magnússon & Magnússon 1995). In the mid-1990s, the fishery expanded geographically and vertically to depths greater than 500m (Sigurdsson et al. 2006a) and the relationships between the traditional demersal resource, the shallow pelagic resource and the newly developed pelagic, deep-sea fishery were unknown.

Stock identification became a critical issue in the science and management of *S. mentella*. In 1998, the ICES Study Group on Redfish Stocks met to coordinate future research on redfish stocks, including the acoustic survey in the Irminger Sea and adjacent areas, but recognized that stock identification was a critical issue for surveying *S. mentella* resources and managing the redfish fisheries (SGRS 1998). Information on morphology, parasites and early genetic analyses were reviewed, but the Study Group concluded that the evidence for one or two pelagic stocks was not conclusive.

In response to the SGRS recommendation for research on stock identification of *S. mentella*, the EU Redfish project was established to study population structure, reproductive strategies and demography of redfish in the Irminger Sea and adjacent waters (ICES V, XII and XIV; NAFO 1; Anon. 2004; Figure 1). The project involved collaborative sampling efforts and analyses of genetics, morphometrics, reproduction and maturation, otolith shape, otolith chemistry and growth. A related initiative was funded by the Faroe Islands, which included analysis of genetics, morphometrics, otolith shape, and fatty acids (Joensen 2002). Morphometric and otolith analyses did not indicate stock structure in the Irminger Sea and adjacent areas, but genetics revealed weak, significant differences between demersal, 'oceanic' (<500m) and 'deep-sea pelagic' components (Anon. 2004). However, there was disagreement on the cause of genetic differences, either from reproductive isolation among three distinct subpopulations in the Irminger Sea or as an artifact of age-related effects, misrepresentative sampling, or selection.

A one-stock hypothesis was proposed by Saborido-Rey et al. (2004), who reviewed the ecology of *S. mentella* in the vicinity of the Irminger Sea. Their conclusion was based on deductive inference supported by information that suggests a continuous distribution of larvae in the Irminger Sea, a common nursery area on the Greenland Shelf, and ontogenetic movement of fish from nursery areas, to shallow areas, then to deep pelagic habitats. As the EU Redfish Project was in the final stages of documenting final results, the ICES Study Group on Stock Identity and Management Units of Redfishes met to review all stock identification material, identify most likely biological stocks and suggest practical management units (SGSIMUR 2005). The Study Group concluded that there is population structure of *S. mentella*, but the nature of the structure (i.e., reproductively isolated groups or demographic groups) is not clear. Research recommendations were that microsatellite analyses were the most reliable approach to stock identification, sampling should be based on locations rather than 'phenotypes,' and temporal stability of all geographic differences should be evaluated (SGSIMUR 2005).

The ICES Stock Identification Methods Working Group (SIMWG) in collaboration with the North-Western Working Group on the stock identification issues related to redfish

(SIMWG 2007) concluded that recent genetic information was compelling, and that the new results should be reviewed and considered for a re-evaluation of ICES management units. A group of experts on redfish biology and stock identification methods were invited to the Workshop on Redfish Stock Structure to consider new information on genetic stock structure in the context of existing biological information (WKREDS 2009).

STOCK STRUCTURE INFORMATION

Geographic Distribution

Spatial patterns of abundance offer a basic indication of stock structure, contribute to our understanding of isolating mechanisms or connectivity in a population, and should be the first point of reference for identifying stock structure (Begg 2005). The geographic range of *S. mentella* extends across the North Atlantic, from the Grand Bank to the Barents Sea (Figure 2). The species' distribution is essentially continuous throughout its range on continental shelves or in pelagic waters near continental shelves to 1000m deep (Garabana 2005, Bakay and Melnikov 2008).

Spatial analysis of spawning fish (i.e., with developing gonads) in fishery catches suggests three different, but overlapping distributions of spawning fish: 1) on the Icelandic Slope, 2) in the deep layer of the northeast Irminger Sea and 3) the shallow layer of the southwest Irminger Sea (Anon. 2004). Although spawning areas can indicate separate or continuous spawning groups, the viviparous reproductive strategy of *S. mentella* complicates any inference of reproductive mixing. Spawning areas are where larvae are extruded, but the seasonality of gonad development indicates that copulation occurs approximately six months earlier (Anon. 2004), and males and females have different distributions during larval extrusion (Magnússon and Magnússon 1995), suggesting that the copulation takes place in a different area than extrusion.

Distribution of early life history stages can reflect separate spawning groups, larval dispersal and connectivity among spawning groups (Hare 2005). *S. mentella* release their larvae from April to May (Saborido-Rey et al. 2004, Anon. 2004). Distribution of *S. mentella* larvae in the Irminger Sea varies among years, with a relatively continuous distribution in some years, and discontinuous northeast, southwest concentrations in other years (WKREDS 2009).

Fishing patterns reflect geographic and depth distribution of the resource. Sigurdusson et al. (2006a) provide an overview of the development of the pelagic *S. mentella* fishery, including locations, depth, season and size composition of catches. In 1981, after exploratory surveys, a commercial fishery began on pre-spawning and spawning schools west of the Reykjanes Ridge from early April to mid-May at depths of 80-150m at night and 150-250m during day. In 1994, the fishery expanded to the southwest in the NEAFC area (Figure 3), to depths of 600m within a longer fishing season (March to December). Since 1996, the fishery extended even further southwest in relatively shallow water (150-350m), eventually expanding into the NAFO area (Figure 4). Spatial analysis of survey data show that the shift in the fishery to the southwest since 1996 (Sigurdusson et al.

2006a) reflects a similar change in the distribution of the resource and is coincident with environmental changes (SGSIMUR 2005).

A synthesis of geographic distributions of *S. mentella* in the Irminger Sea and adjacent waters for successive ontogenetic stages is provided by Saborido-Rey et al. (2004) and Melnikov et al. (2007). Shelf, deep-sea and shallow pelagic fisheries catch *S. mentella* with developing gonads in separate, but overlapping areas of the Icelandic Shelf and Irminger Sea. Larvae are distributed in the Irminger Sea, in more or less continuous concentrations. Juveniles and adults are caught on the Greenlandic Shelf. Adults are distributed across continental shelves and in the Irminger Sea, where size distributions are larger in deep habitats (>500m) than in shallow habitats. When the fishery expanded to deep waters of the Irminger Sea (i.e., >500m), the average size of fish in deep water was 7cm larger (Sigurdusson et al. 2006a). Size distributions of fish caught in the deep, northeast fishery are still generally larger than those in the shallow, southwest fishery. Size distributions in the deep Irminger Sea are also bimodal is some years, suggesting recruitment from other areas. There are no reliable age data for *S. mentella* to track year-classes from nursery grounds to adult habitats. Reviews by Saborido-Rey et al. (2004) and Melnikov et al. (2007) concluded that there is one stock of *S. mentella* in the Irminger Sea and adjacent areas based on spatial distribution of larvae, juveniles, and adults. However, several alternative inferences of movement and connectivity between ontogenetic stages can be deduced from spatial distributions. For example, Rikhter (1996) examined the same distributional data of larvae, juveniles and adults to conclude that there is strong evidence of two *S. mentella* populations in the Irminger Sea. Although, distributional data offers valuable exploratory information for developing stock structure hypotheses, it cannot be used to rigorously test alternative hypotheses.

Geographic Variation

Genetic characters

Among the suite of approaches for stock identification, genetic analyses are the most rigorous to test for reproductive isolation among population components (Begg & Waldman 1999). The history of applying genetic methods to stock identification involved early development of allozyme markers, then mitochondrial DNA (mtDNA) sequences, and most recently a series of nuclear DNA markers (nDNA, including microsatellite loci and single nucleotide polymorphisms), each with increasing sensitivity to detect genetic differences that reflect reproductive isolation. Although technological development of new genetic markers improves the ability to detect genetic differences and identify discrete stocks, reconciling new results with information from traditional approaches, including previous genetic research, life history patterns, phenotypic variation and connectivity can be challenging. Earlier research on genetic variation of *S. mentella* provided weak or equivocal evidence for genetic structure or weak differences among locations. However, a common scenario in the investigation of stock structure of marine resources is that early studies reveal little variation among areas, but as more sensitive molecular markers are developed and applied to the resource, new and stronger differences are found among groups that were previously perceived to be genetically similar (Wirgin & Waldman 2005).

Over the last decade, several molecular genetic markers have been used in studies of *S. mentella* and other redfish species. These markers vary remarkably in terms of function, response to natural selection, mutational features, mode of inheritance and statistical properties. Therefore, the unique perspective of each type of genetic marker should be considered in the synthesis of information from different studies. Furthermore, the sampling design and the type of statistical analyses conducted also play a significant role in determining results.

Allozymes – Protein expressions of a genetic locus (or gene), were the first genetic markers used to study population structure (Koljonen & Wilmot 2005). Before the discovery of the deep-sea resource, no geographic variation was detected in allozymes of *S. mentella* sampled in shallow waters (<500m). Dushchenko (1986) found polymorphism in the malic enzyme (MEP), but allozyme frequencies were not different among six shallow locations in the Irminger Sea. Similarly, in their study of genetic differences among *Sebastes* species, Nedreaas and Nævedal (1991) and Nedreaas et al. (1994) found genetic uniformity among shallow samples from off West Greenland, East Greenland, the Irminger Sea, the Faroe Islands and off Norway and Svalbard. However, soon after the deep-sea fishery began, preliminary information indicated a difference in allozyme frequencies between the 'oceanic' and 'deep-sea' phenotypes, with some alleles that were unique to deep-sea specimens, and large-scale regional differences between samples from Canadian waters, the Irminger Sea and off Norway (SGRS 1998).

Johansen et al. (2000) and Johansen (2003) found significantly different allozyme frequencies among *S. mentella* sampled in the Irminger Sea, on the Flemish Cap and off southern Canada. Johansen and Sevigny (2003) determined that the source of regional variation was hybridization of *S. mentella* and *S. fasciatus* where their distributions overlap (i.e., on the Flemish Cap and in Canadian waters). Johansen et al. (2000) and Johansen (2003) also found significant differences between 'oceanic' and 'deep-sea' phenotypes in the Irminger Sea, with only minor differences between the 'deep-sea' type and those from the Icelandic Slope. However, these studies compared each locus separately which provided limited power for detecting differences. Allozyme differences were identified at the polymorphic MEP and IDHP (isocitrate dehydrogenase) loci and were supported by haemoglobin analyses. They concluded that the *S. mentella* in the Irminger Sea is composed of two different stock units. However, these comparisons were not based on depth-structured samples, and many of the 'deep-sea' specimens were sampled above the deep-scattering layer (270-500m).

Subsequent investigations by Novikov et al. (2006) and Melnikov et al. (2007) also found differences in frequency of the MEP allozyme between 'oceanic' and 'deep-sea' phenotypes. The Faroese Redfish project found differences in allozyme frequencies between shallow samples (the southwest Irminger Sea, the western Icelandic shelf, north and east of the Faroes, and off Norway) and deep samples (the northeast Irminger Sea, the eastern Icelandic slope, and southwest of the Faroe Islands; Joensen 2002, SGSIMUR 2005).

The most recent study of *S. mentella* allozymes was by Danielsdottir et al. (2008), who sampled nearly 2000 specimens, tested a large number of allozymic loci (33, 13 of which were polymorphic), and analyzed all loci simultaneously to test for differences between 'oceanic' and 'deep-sea' phenotypes. Although nearly all of the 'deep-sea' samples (95%) were collected from deeper than 500m, and nearly all 'oceanic' samples (93%) were collected from shallow water (<500m), comparisons were not depth-based, and some sample locations included a mix of both phenotypes. Allozyme differences were persistent over the three-year sampling period, suggesting the existence of two pelagic stocks on the southwest Icelandic slope and the central Irminger Sea. This conclusion is supported by significant heterozygote deficiency at all loci in pooled samples, significant differences in allele frequency between samples classified as belonging to the deep-sea and oceanic phenotypes, and clustering of the samples from different phenotypes.

Given that substantial differences in allelic frequencies are only observed in a minority of loci (mainly MEP), an alternative interpretation for the pattern observed between 'oceanic' and 'deep-sea' phenotypes is that the allozyme frequencies are influenced by different selective pressures above and below the deep-scattering layer. Such a scenario would not rule out exchange of genes between the shallow and the deep pelagic populations, but it would indicate the existence of some degree of local adaptation. Adaptive differences between shallow and deep populations could affect fitness and demographic dynamics of these populations, which should be considered in the fishery management process. Saborido-Rey et al. (2004) and Melnikov et al. (2007) contend that the pattern of divergence at the MEP enzyme locus reflects a shift of allelic frequencies resulting from selective forces that act after larger, older fish move into the deeper zone. Unfortunately, age determination is unreliable, particularly from deep samples (Stransky et al. 2005b, 2005c), and the ontogenetic movement hypothesis is not rigorously tested. Assuming that most spawning would be achieved by the larger, older fish in the deep layer, there is no reasonable explanation for the maintenance of high frequencies in the juveniles of the alleles that are selected against after the movement to the deeper layer. Thus, variation at the MEP locus between 'oceanic' and 'deep-sea' phenotypes is more parsimoniously explained as the result of adaptation to different environments by two diverging populations.

Mitochondrial DNA – In contrast to allozymes, that are the protein expressions of DNA, DNA structure and polymorphisms can also be analyzed directly. Mitochondria contain a small amount of DNA (mtDNA), which is maternally inherited and simpler in form than nuclear DNA. Alternative sequences of mtDNA (i.e., haplotypes) are easier to analyze than nuclear DNA (Magoulas 2005). One corollary of the simplicity of mtDNA is that its mutation rates are relatively constant, and mtDNA divergence can be used as a 'molecular clock' to indicate the duration of reproductive isolation between two populations.

Sundt & Johansen (1998) found a low level of mtDNA variation among *Sebastes* species in the North Atlantic, suggesting a recent evolutionary divergence. As a component of the EU Redfish Project, Schmidt (2005) also found a low level of genetic differentiation in mtDNA among North Atlantic *Sebastes* species. A phylogenetic analysis revealed a

pattern and levels of divergence similar to those normally observed within the same species, which suggests that speciation rate in this group is rapid. Analysis of molecular variance indicated that most of the genetic variation occurred between species, but there was also significant variation among samples within species. Haplotype frequencies differed between samples of the 'deep-sea' phenotype and other samples of *S. mentella*, because one haplotype was frequent in 'deep-sea' samples and only occurred in two other *S. mentella* samples. Ingimarsdóttir (2008) also found differences in mtDNA haplotype frequencies among 'oceanic,' 'deep-sea,' and demersal samples of *S. mentella*, and estimated that the subgroups in the Irminger sea diverged approximately 4 000 years ago.

Nuclear DNA - Several aspects of nuclear DNA (nDNA) are commonly used to study population structure, and each has different sensitivities and interpretations. When little is known about the genome of a species (i.e., DNA sequences have not been indentified), Random Amplified Polymorphic DNA (RAPD) can be used to explore patterns of variability, because RAPD primers recognize simple nucleotide sequences that should arise frequently in any DNA (Smith 2005). Johansen et al. (1997) and Johansen and Dahle (2004) found significant differences in allele frequencies of four RAPD primers among all samples of *S. mentella* from the Gulf of St. Lawrence, Norway and the Irminger Sea ('oceanic' and 'deep-sea'). However, RAPDs produce results that may not be repeatable, and are no longer considered to be a reliable approach for testing population structure hypotheses.

Amplified Fragment Length Polymorphism (AFLP) is another type of nDNA character that can be used for stock identification. Similar to RAPD, AFLP can be applied to species without prior information about its genome, but it uses fragment lengths between arbitrary restriction sites to measure genetic variation (Liu 2005). Schmidt (2005) found genetic patterns among *S. mentella* sampled from the Irminger Sea, Greenland and Iceland, but the significant differences between all samples indicated that AFLP markers may be too variable to detect biologically meaningful patterns of genetic structure among subpopulations of *S. mentella*. Similar to RAPD, AFLP results are not always repeatable among laboratories, and AFLP characters are inherited as dominant markers (Liu 2005). Therefore, both RAPD and AFLP are considered to be more exploratory than confirmatory for stock identification studies.

Microsatellites are segments of nDNA consisting of tandem nucleotide repeats. Microsatellites are generally non-coding, so they are not subjected to selection and have a rapid mutation rate, because all microsatellite mutations are non-lethal. Both of these characteristics make them the most effective character for studying population structure (Wirgin and Waldman 2005). A series of increasingly rigorous analyses of microsatellite characters indicate a general pattern of population structure of *S. mentella* that involves three distinct genetic groups located in 1) the deep Irminger Sea, 2) shallow pelagic habitats and 3) demersal habitats.

The Faroese Redfish project found differences in microsatellite frequencies between three geographically overlapping, but genetically distinct groups: 1) shallow (<500m) samples from the southwest Irminger Sea, the northern and eastern Faroese Shelf and the

Norwegian coast, 2) deep (>500m) samples from the northeast Irminger Sea, the eastern Icelandic Slope and the southwest Faroese Slope, and 3) the western Icelandic Shelf and southwest Faroese Shelf (Figure 5; Joensen 2002, SGSIMUR 2005).

Roques et al. (2002) used microsatellite characters to demonstrate the presence of hybridisation between *S. mentella* and *S. fasciatus* in the Gulf of Saint Lawrence, which appears to represent a unique evolutionarily significant unit. They concluded that there are three distinct populations of *S. mentella*: 1) in the area of hybridization with *S. fasciatus* off southern Canada, 2) in a 'panoceanic' area from Labrador to the Faroe Islands, and 3) in the Barents Sea. However, all 'panoceanic' samples in the Irminger Sea and adjacent areas were from shallow habitats (<500m).

Using eight highly variable microsatellite loci, Schmidt (2005) found weak but significant genetic structure in *S. mentella*. Significant genetic differences were found between three groups of samples: 1) on the Flemish Cap, 2) in the deep (>500m), central Irminger Sea, and 3) in shallow (<500m) samples off Greenland, off Iceland, and in southern Irminger Sea (Figure 6).

Pampoulie & Danielsdottir (2008) used nine microsatellite loci to distinguish all the Atlantic species of *Sebastes*, but analyses also indicate that the 'oceanic' and 'deep-sea' phenotypes of *S. mentella* are genetically distinct, with considerable misclassification of genotype using 'phenotyping.' Although the comparisons tested by Pampoulie & Danielsdottir (2008) were primarily based on phenotypic identification, the data were re-grouped by depth by Stefánsson et al. (2009a). The revised and expanded analysis of nearly two thousand specimens shows that populations below and above the 550 m depth boundary are well differentiated based on microsatellite variation (Figure 7). The analyses also suggest that the shallow and deep pelagic subpopulations may represent incipient species that were allopatric (i.e., geographically separate) during the Pleistocene glaciation but secondarily came in contact to form their current sympatric (i.e., overlapping) distribution (Stefánsson et al. 2009b).

A spatially expanded analysis rigorously tests for genetic differences between shallow (<550m) and deep (>550m) *S. mentella* in the Irminger Sea. The analyses show temporally stable differences between deep and shallow pelagic samples, providing evidence that fish inhabiting waters deeper than 550m are genetically distinct from the shallower ones. Analyses of shallow samples are similar to that reported by Roques et al. (2002), with the addition of genetically distinct deep samples and samples on the Icelandic slope. Geographic distributions of the three genetically distinct clusters are shown in Figure 8 and the proportion of each group by depth is shown in Figure 9.

Synthesis of all genetic information suggests that *S. mentella* from Newfoundland and the Gulf of Saint Lawrence are genetically distinct from *S. mentella* in the rest of the North Atlantic because of strong evidence of adaptive local hybridization with *S. fasciatus*. A 'panoceanic' shallow (<500m) subpopulation of *S. mentella* extends from Labrador to at least the coast of Norway, perhaps to the Barents Sea (Roques et al. 2002 found one Norwegian sample was significantly differentiated from the panoceanic group, but

Stefansson et al. 2009b did not). *S. mentella* in the deep Irminger Sea (> 500 m) and *S. mentella* on the Icelandic slope are also distinct subpopulations.

This new perception of genetic structure in the Irminger Sea and adjacent waters contrasts with the previously posed single-stock hypothesis (Saborido-Rey et al. 2004, Melnikov et al. 2007). The revised view of stock structure is a result of more extensive genetic testing, the use of neutral and powerful markers, refinement of analyses by depth (rather than by phenotype), and robust statistical approaches. The hypothesis that fish move to deeper habitats as they age is refuted by the substantial differences between deep and shallow pelagic samples in microsatellite allelic frequencies (which are not vulnerable to selection, and have been tested for temporal stability). Saborido-Rey et al. (2004) suggest that genetic differences may result from genetic drift or a 'sweepstakes' effect (i.e., each year class is genetically distinct because it is produced from a small, randomly selected portion of the adult population), both of which imply genetic population structure and reproductive isolation, therefore refuting the assumption of panmixia. The revised perception of genetic structure explains some of the previously observed patterns in genetic analyses. For example, the lack of correlation between genetic distance and geographic distance (e.g., Roques et al. 2002) probably results from depth-based differences among locations that are geographically close.

Based primarily on microsatellite information, but also supported by results from analyses of allozyme, AFLP and RAPD characters, we conclude that there are four genetic stocks of *S. mentella* (three in the Irminger Sea and adjacent waters):

1. The 'western' stock extends south and west of the Flemish Cap
2. The 'shallow pelagic' stock extends from Greenland and the Irminger Sea to the coast of Norway, perhaps to the Barents Sea (ICES I-II). The stock primarily consists of *S. mentella* in pelagic habitats (though demersal habitats east of the Faroe Islands appear to be part of this stock).
3. The 'deep pelagic' stock also primarily consists of *S. mentella* in pelagic habitats, but includes demersal habitats west of the Faroe Islands. Note that this genetic stock does not necessarily equate to the 'deep-sea' phenotype.
4. The 'Icelandic slope' stock inhabits demersal habitats of the continental slope, and the northwest Faroese Slope may be part of this stock.

Note that juveniles on the Greenland Shelf may be from the 'shallow pelagic,' 'deep pelagic,' and 'Icelandic Slope' stocks (Johansen and Sevigny 2003, Schmidt 2005).

Phenotypic variation

Geographic variation in phenotypic characters (measurable traits that are influenced by both genetics and environmental factors) is valuable for stock identification, because maintenance of phenotypic differences among groups indicates limited mixing, and adaptive differences may have a genetic basis. Investigation of phenotypic variation can be used to define putative genetic stocks (for confirmation using genetic techniques). If phenotypic differences are indicative of distinct biological stocks and they are temporally stable, they can offer a practical measure for stock discrimination or stock composition analysis.

The study of phenotypic variation has played a large role in the investigation of *S. mentella* population structure. Soon after the discovery of the deep-sea resource, phenotypic differences between 'oceanic' and 'deep-sea' forms were recognized (Magnússon & Magnússon 1995). Several phenotypic characters have been used to study stock structure of *S. mentella*, including life history traits (e.g., size distributions, size at maturity), morphology (e.g., body form, meristics, otolith shape) and fatty acid composition.

Phenotypic variation can be particularly valuable for stock identification when it is associated with life history characteristics and vital rates (e.g., growth, reproduction, mortality) that are also critically important for population dynamics, stock assessment and fishery management (Begg 2005). There are some indications of different growth rates among the genetic stocks of *S. mentella* identified above. Size distributions are relatively smaller in the shallow, southwest Irminger Sea than in the deep, northeast area, and this relative difference has persisted over time. However, age determination is not reliable for *S. mentella* (Stransky et al. 2005b, 2005c), so the cause of different size distributions (i.e., growth differences, mortality differences, movement patterns) is difficult to interpret. Pelagic phenotypes have been partially identified based on size-at-maturity, with the 'deep-sea' types having larger size at maturity than the 'oceanic' type (Magnússon & Magnússon 1995, SGRS 1998). Melnikov et al. (2007) used length distributions, maturity stages and distribution of various life stages to infer that fast growing and early maturing individuals of each year-class recruit to the pelagic areas of the Irminger Sea, whereas slow growing and late maturing individuals recruit to the deepwater habitat along the slopes of East-Greenland, along the Iceland-Greenland Ridge to the slopes west and south of Iceland (the deep-sea *S. mentella* stock).

Geographic differences in morphology can also indicate subpopulations that have limited mixing and morphological patterns can reflect life history differences and possibly adaptations to different environments (Cadrin 2000). Several studies have investigated patterns of morphology for *S. mentella*. Nagel et al. (1991) found that *S. mentella* on the Reykjanes Ridge had more vertebrae than those collected in other areas (off east and west Greenland, the Irminger Sea, off Norway and in the Barents Sea). Rikther (1996) also found significantly greater number of vertebrae, anal fin rays and pectoral fin rays in *S. mentella* sampled from the Icelandic Slope than from those from the Irminger Sea. Significant differences in meristic features usually indicate environmental differences experienced during early life stages (Waldman 2005). Reinert and Lastein (1992) found morphometric differences between samples from the Irminger Sea, the Faroes and off Norway, with some morphometric heterogeneity within Faroe samples, but not among Irminger Sea samples (which were all collected from shallow depths).

After the discovery of the deep Irminger Sea resources of *S. mentella*, pelagic phenotypes were defined primarily on the basis of color ('deep-sea' types are redder, and 'oceanic' types are more grayish red), body shape ('deep-sea' are more stout), as well as size at maturity and parasites (Magnússon & Magnússon 1995, SGRS 1998). Pelagic phenotypes were secondarily identified on the basis of general appearance ('deep-sea' are brighter, and 'oceanic' are less 'clean'), color pattern ('oceanic' have black and red

spots), filets ('oceanic' filets have dark spots), and morphometry ('oceanic' have narrower head; Figure 10; SGRS 1998).

Garabana (2005) found morphometric differences between 'deep-sea' and 'oceanic' phenotypes, but morphometric variation could not accurately classify individuals to 'type.' Specimens from the Irminger Sea were more fusiform than those from other areas, and the orientation of third and fifth preopercular spines was more forward-pointing in 'deep-sea' types. Morphology was compared among samples from the Flemish Cap, Faroe Islands, Greenland Shelf, Icelandic Slope, Irminger Sea, and Norwegian Sea, but all were morphometrically too similar to support accurate classification of specimens to locations.

Stransky (2005) measured outline shape of otoliths collected from *S. mentella* throughout the North Atlantic. Otolith shape could not accurately classify specimens to specific areas (Flemish Cap, Davis Strait, West Greenland Shelf, East Greenland Shelf, Irminger Sea, Icelandic Slope, Faroe Islands, and Barents Sea), but could accurately classify specimens to three broad regions: 1) Flemish Cap and Davis Strait, 2) Greenland Shelf, Irminger Sea, Icelandic Slope, and Faroe Islands, and 3) Barents Sea. Stransky (2002) compared otolith shape among samples in the Irminger Sea by depth, but no clear differences between depth groups were found.

Daníelsdóttir et al. (2008) found significant differences in allelic frequency of allozyme loci between specimens classified to 'oceanic' or 'deep-sea' phenotypes based on external morphology. However, there was considerable misclassification between phenotypes and genotypes. Stefánsson et al. (2009a) found significant differences in meristics and morphometry between specimens of 'oceanic' or 'deep-sea' genotypic groups within the Irminger Sea, but statistical analyses suggest that these differences could not be used alone for stock identification. Phenotyping has had limited utility for stock identification, because the two types have overlapping geographic and depth distributions (Kristinsson & Sigurdsson 2007).

A relatively new approach to stock identification is the investigation of fatty acid composition. Fatty acids are phenotypic characters in that they reflect both genetic and environmental factors, with some specific fatty acids concentrations more heritable than others (Grahl-Nielsen 2005). Joensen and Grahl-Nielsen (2004) measured fatty acid profiles in heart tissue of *S. mentella* from eleven areas in the North Atlantic from Norway to the Irminger Sea. Significant differences were found among four stocks: 1) the shallow Irminger Sea, 2) the deep Irminger Sea, southeast Icelandic Slope and southwest Faroese Slope, 3) the western Icelandic Shelf, and 4) north and northeast Faroe Islands and Norway (Figure 11). Stocks identified through fatty acid profiles are similar to those identified from microsatellite DNA analysis, supporting the conclusions drawn from genetic analysis. Fatty acid profiles, however, must be viewed cautiously in the context of stock identification, because they may be influenced by environmental factors such as diet or temperature (Joensen 2002).

In summary, geographic variation in life history is apparent from size distributions and size-at-maturity, but precise evaluation of growth or maturity is difficult without reliable age determination. Subtle morphological differences exist between 'oceanic' and 'deep-sea' forms, and geographic patterns of fatty acid profiles are similar to those from genetic analysis. Although interpretation of phenotypic traits is somewhat subjective (i.e., can be validly interpreted in several ways), all information on phenotypic variability is consistent with our perception of genetic stocks.

Connectivity

The degree of isolation or mixing of subpopulations is an important aspect of defining stock structure. Connectivity can be evaluated by modeling dispersal of early life stages, mark-recapture analysis of artificial tags or examination of natural tags (e.g., otolith chemistry, parasite infestation). Mixing of groups can involve two distinct patterns that have different influence on population structure and reproductive dynamics: 1) 'overlap' is a pattern in which individuals from reproductively isolated subpopulations share the same habitats in some seasons, but have isolating mechanisms (e.g., separate areas or seasons for reproduction), and 2) 'diffusion' or reproductive mixing, which allows gene flow and correspondence in reproductive dynamics among groups (Cadrin and Secor 2009).

Connectivity among geographic groups of *S. mentella* has been studied using several approaches. Rikhter (1996) inferred larval drift of *S. mentella* from distribution of larvae, surface currents and distribution of age-0 demersal stages. He concluded that there are two different stocks in the area of the Irminger Sea: 1) a coastal stock, inhabiting the Iceland and eastern Greenland shelf slopes and 2) a pelagic stock, which occurs in the open sea. The significant differences in number of vertebrae and fin rays found by Rikhter (1996) may also indicate different larval environments, because those features are typically determined during early life stages (Waldman 2005). Saborido-Rey et al. (2004) reviewed previous investigations of *S. mentella* larval drift in the Irminger Sea and adjacent areas and concluded that larvae drift from the central and eastern Irminger Sea towards the Greenlandic Shelf (Figure 12).

A traditional approach to stock identification and connectivity is the use of parasites as biological tags, and the approach has been revived through advancements in methodology (MacKenzie and Abaunza 2005). Patterns of parasite infestation have played a large role in the study of *S. mentella* stock structure. Pelagic phenotypes are partially defined by the prevalence of the parasitic copepod *Sphyrion lumpi*. Unfortunately, there are conflicting patterns of *S. lumpi* infestation (SGRS 1998). Some researchers found increasing infection rates with depth (Magnússon et al. 1995, Magnússon & Magnússon 1995), but others found decreasing infection with depth (Del Rio et al. 1996, Sarralde et al. 1997).

Parasites and pigmented patches have been used as indicators of population structure of *S. mentella* in the Irminger Sea and adjacent waters by a long series of Russian investigations (1983-2008). Infestation rate of *S. lumpi* and the entire parasite fauna was similar in all the areas of the pelagic Irminger Sea and adjacent waters (Bakay 1988,

2000, 2001). Parasite fauna above (0-500 m) and below (501-1000 m) the deep-scattering layer were also similar (Bakay & Melnikov 2002, 2008). No geographical variability and considerable annual differences were found in the occurrence of pigment patches on the skin (Bogovski and Bakay 1989). Bakay & Melnikov (2008) interpreted the predominance of pigment patches in individuals at depths greater than 500m and the decrease in occurrence of pigment patches on the skin and muscular melanosis of individuals longer than 40cm and to be a consequence of age-dependent changes and ontogenetic movement to deeper pelagic habitats. Bakay & Melnikov (2008) concluded that the *S. mentella* resource in all depths of the Irminger Sea and adjacent Labrador waters is single stock. However, this interpretation of movement from shallow to deep pelagic environments is refuted by recent genetic evidence of reproductively isolated groups.

By contrast, parasite fauna are distinctly different for pelagic and demersal *S. mentella* in the Reykjanes Ridge area (Melnikov et al. 2005, Melnikov & Bakay 2006). Pelagic *S. mentella* are frequently infected by *S. lumpi*, but those on the Icelandic Slope are not. Conversely, pelagic *S. mentella* do not have some parasites that are found on the slope, such as *Microcotyle sebastis* (Monogenea), and some rarer parasites: *Spinitectus oviflagellis* (Nematoda), *Echinorhynchus gadi*, *Corynosoma strumosum*, *Acanthocephalus* sp. (Acanthocephala). The infestation rate of the nematod *Anisakis simplex* is also significantly different between pelagic and demersal *S. mentella*. Similarity in parasite faunas of *S. mentella* from different areas of the southeastern slope of Greenland and the pelagic Irminger Sea suggests that redfish concentrations in these regions are closely related. A shift in composition of parasite fauna suggests that maturating specimens of redfish migrate from shallow habitats on the slope to the Irminger Sea and to deep waters of the Greenland slope. An ontogenetic change in parasite fauna of fish in the Irminger Sea occurs as a result of fish moving from the continental shelf, which is the indigenous area of myxosporidians, to a pelagic environment where they feed on copepods, meso- and bathypelagic fish and young squids. The decrease in the composition of trematodes, nematodes and acanthocephalans is accounted for by a shift in diet away from near-bottom crustaceans. The presence of the copepod *S. lumpi* indirectly suggests a movement of maturing specimens of *S. mentella* from the slope to pelagic waters during summer (Melnikov et al. 2005).

A more recently developed natural tag for stock identification is otolith chemistry. As otoliths grow, they incorporate the chemical signature of the fish's environment, so that each growth zone is an archive of the fish's environmental history (Campana 2005). Stransky et al. (2005a) used otolith microchemistry to investigate connectivity between redfish habitats on the East Greenland Shelf and in the Irminger Sea. The study confirmed that elemental signatures in cores of otoliths collected from East Greenland were temporally stable. Similar elemental concentrations (Li, Sr, Mg, Ba, and Cu) were found between redfish otoliths collected in the Irminger Sea and East Greenland. The lack of clear spatial differences in otolith chemistry could indicate either common natal origin of adults or a lack of variation in elemental chemistry across large expanses of the ocean in this region.

Tagging has a long history in fishery research and the study of movement patterns (Thorsteinsson 2002). A particular challenge in tagging redfish is the barotraumas associated with bringing fish to the surface. Sigurdsson et al. (2006) solved this dilemma using an innovative in situ tagging device. Although the objective of the tagging project was to demonstrate effectiveness of in situ tagging technology, there were some tag releases and a few long-term recaptures that offer valuable insights into movement patterns. Sample sizes were low and not designed to represent a management unit or biological stock, but the 49 recaptured tags include several movements from deep, pelagic environments to demersal habitats on the Icelandic Slope (Figure 13). These movements document distributional overlap between the two groups and perhaps connectivity.

Information from larval drift, parasites, otolith chemistry and tagging suggest that subpopulations of *S. mentella* mix during early life stages, as larvae and juveniles, then adults recruit to different habitat groups that have overlapping distributions. Synthesis of information on connectivity and genetic composition indicates that over-lapping adult distributions do not involve reproductive mixing.

INTERDISCIPLINARY ANALYSIS

A synthesis of all available information was used to test each of the a priori stock structure hypotheses. The single-population hypothesis was rejected on the basis of significant differences in microsatellite allelic frequencies among deep Irminger Sea, shallow Irminger Sea and Icelandic Slope samples, as well as significant differences in allozymes and fatty acid profiles among the same three groups, and distinct parasitological differences between Icelandic Slope and pelagic specimens.

Several two-stock hypotheses were also considered. The current management unit hypothesis (one pelagic stock and one demersal stock; ICES 2008) was rejected on the basis of significant differences in microsatellite allelic frequencies between deep and shallow Irminger Sea samples, as well as significant differences in allozymes and fatty acid profiles. The two depth-defined stocks (one stock <500m and one stock >500m) was rejected on the basis of significant differences in microsatellite allelic frequencies between continental slope and pelagic samples, as well as significant differences in allozymes, fatty acid profiles and parasite fauna. The two phenotype hypothesis (‘oceanic’ and ‘deep-sea’) was similarly rejected on the basis of significant differences in microsatellite allelic frequencies between continental slope and pelagic samples, as well as significant differences in allozymes, fatty acid profiles and parasite fauna.

An a priori three-stock hypothesis (slope, shallow and deep pelagic stocks) was not entirely consistent with all data, because heterogeneity within continental slope samples from Iceland and the Faroe Islands was indicated by microsatellites and fatty acids. However, this heterogeneity was recognized in the a priori evaluation as a possible alternative hypothesis.

The alternative three-stock hypothesis was consistent with all information on stock structure. Based primarily on microsatellite information, supported by analyses of allozymes, fatty acids, as well as some parasite patterns, we conclude that there are four biological stocks in the entire geographic range of *S. mentella*, and three stocks in the area of concern, the Irminger Sea and adjacent waters:

1. 'Western' (NAFO 3+)
2. 'Deep Pelagic' (NAFO 1-2, ICES Vb XII XIV >500m). The adults of this stock are primarily in pelagic habitats, but are also in some demersal habitats west of the Faroe Islands. Note that this stock is not equivalent to the 'deep-sea' phenotype.
3. 'Shallow Pelagic' (NAFO 1-2, ICES Vb XII XIV <500m). The adults of this stock are primarily in pelagic habitats, but are also in some demersal habitats east of the Faroe Islands. This stock also appears to extend further north and east (i.e., ICES I-II).
4. Icelandic Slope (ICES Va XIV)

Juveniles on the Greenland Shelf may be from the 'shallow pelagic,' 'deep pelagic,' and 'Icelandic Slope' stocks. This perception of biological stock structure is based primarily on genetic patterns among adult samples. Other stock identification information (e.g., overlapping distributions of life stages, growth and maturity patterns, generally similar morphometry and parasite patterns) cannot be used to rigorously reject any hypothesis, because several alternative interpretations of those data are equally valid. This view of biological stock structure cannot be rejected by any information available. On the contrary, many of the phenotypic patterns can be interpreted as a reflection of this biological stock structure (e.g., subtle morphological differences among areas, different size distributions by depth, different size-at-maturity, and 'phenotypes').

Although biological stocks of *S. mentella* are partially defined by depth, we recognize that definition of management units by depth and the associated fishery monitoring by depth would be impractical. Depth-based differences in genetic stocks can be viewed as geographically separated units. Based on this view of biological stock structure, ICES revised its advice for management of *S. mentella* fisheries as three management units that are based on geographic proxies for biological stocks that minimize mixed-stock catches (ICES 2009). Spatial and seasonal patterns in the pelagic fishery have been relatively stable since 1996 (Sigurdusson et al. 2006, NWWG 2008). Spatial analysis of pelagic fishery catch and effort by depth, inside and outside the recommended 'deep pelagic' management unit boundaries indicate that the boundaries effectively delineate the deep, pelagic fishery from the shallow, pelagic fishery, with a small portion of mixed-stock catches (Figure 14). Given the overlapping distributions of the associated biological stocks, mixed-stock catches in Irminger Sea should be monitored for stock composition.

DISCUSSION

Synthesis of recent genetic results with information from previous stock identification research demonstrates the interdisciplinary analysis required for a holistic perception of population structure. Spatial complexities, sampling difficulties, unstandardized methods and technological subtleties present challenges for determining stock structure, but all sources of information should be considered to form a conclusion that is comprehensive and consistent. Although results from various studies of *S. mentella* population structure appeared to be contradictory, many apparent contradictions resulted from differences in sampling designs (particularly with respect to depth). Precise interpretations of what aspect of stock structure each methodological approach represented (e.g., the different perspectives gained from genetic vs. phenotypic approaches; or the different sensitivities of genetic markers, as developed by Cadrin et al. 2005) helped to resolve incongruent results. This synthesis required collaboration of many scientists with complementary expertise.

The unique life history of *Sebastes* species offers an illustrative example of the mechanisms of population structure. Reproductive isolation of oviparous fish species is usually associated with discrete spawning areas or seasons, forming spatial or temporal barriers to gene flow among groups. The viviparous nature of *Sebastes* species and the associated mate recognition, courtship behavior and mate choice act as additional mechanisms of reproductive isolation (Johns & Avise 1998). These isolating mechanisms, together with high fecundity and wide larval dispersal allow relatively rapid adaptive radiation (Rocha-Olivares 2004).

Species of *Sebastes* in the North Pacific are considered to be ancient species flocks, because adaptive radiation was relatively rapid, but present species are completely isolated (Johns & Avise 1998, Alesandrini & Bernardi 1999). By contrast, Atlantic *Sebastes* species are relatively young, formed from North Pacific ancestors that moved to the North Atlantic during the 'great transarctic biotic interchange', when the Bering land bridge opened and Arctic waters warmed, allowing movement of sub-Boreal species through the Arctic Ocean (Love et al. 2002). Patterns of variation in genetics and otolith shape between Pacific and Atlantic *Sebastes* species are consistent with the movement of a common ancestor species (Stransky & MacLellan 2005).

Recent and rapid evolutionary divergence of Atlantic *Sebastes* species is indicated by a low level of mtDNA variation among *Sebastes* species in the North Atlantic (Schmidt 2005). Ingimarsdóttir (2008) estimated that the subgroups in the Irminger sea diverged approximately 4 000 years ago. Hybridization between *S. mentella* and *S. fasciatus* and the high frequency of back-crossed genotypes indicates that reproductive isolation between species is not complete. Therefore Atlantic *Sebastes* represent a more recent species flock, and the formation of distinct genotypes within *S. mentella* representing even more recent divergence.

Population structure of *S. mentella* illustrates how divergent behavioral groups (i.e., adults from the same nursery grounds exploiting different habitats) can lead to demographic independence, reproductive isolation, and adaptive differences. Phylogeny of *Sebastes* species shows how intraspecific variation (i.e., the 'stock concept') and interspecific variation (i.e., 'the species concept') are a continuum of divergence over ecological and evolutionary time.

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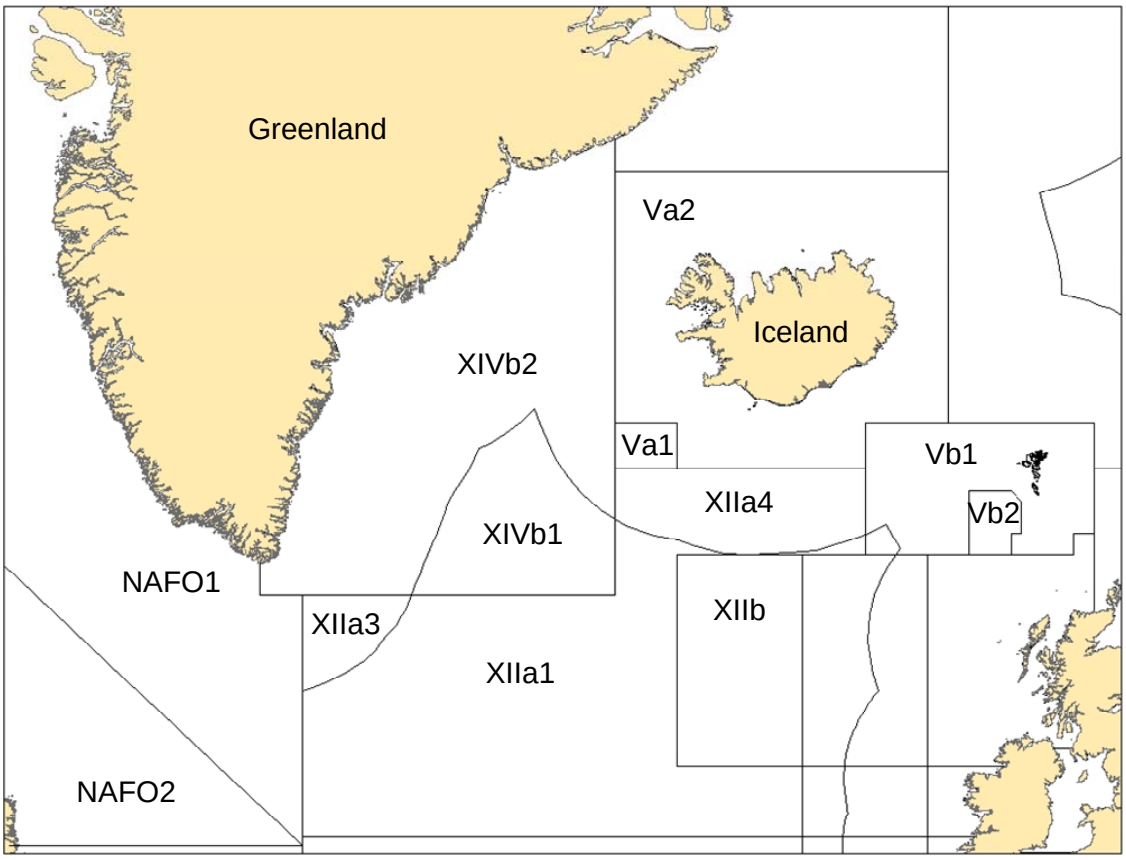

Figure 1. ICES and NAFO areas comprising *S. mentella* resources in the vicinity of the Irminger Sea.

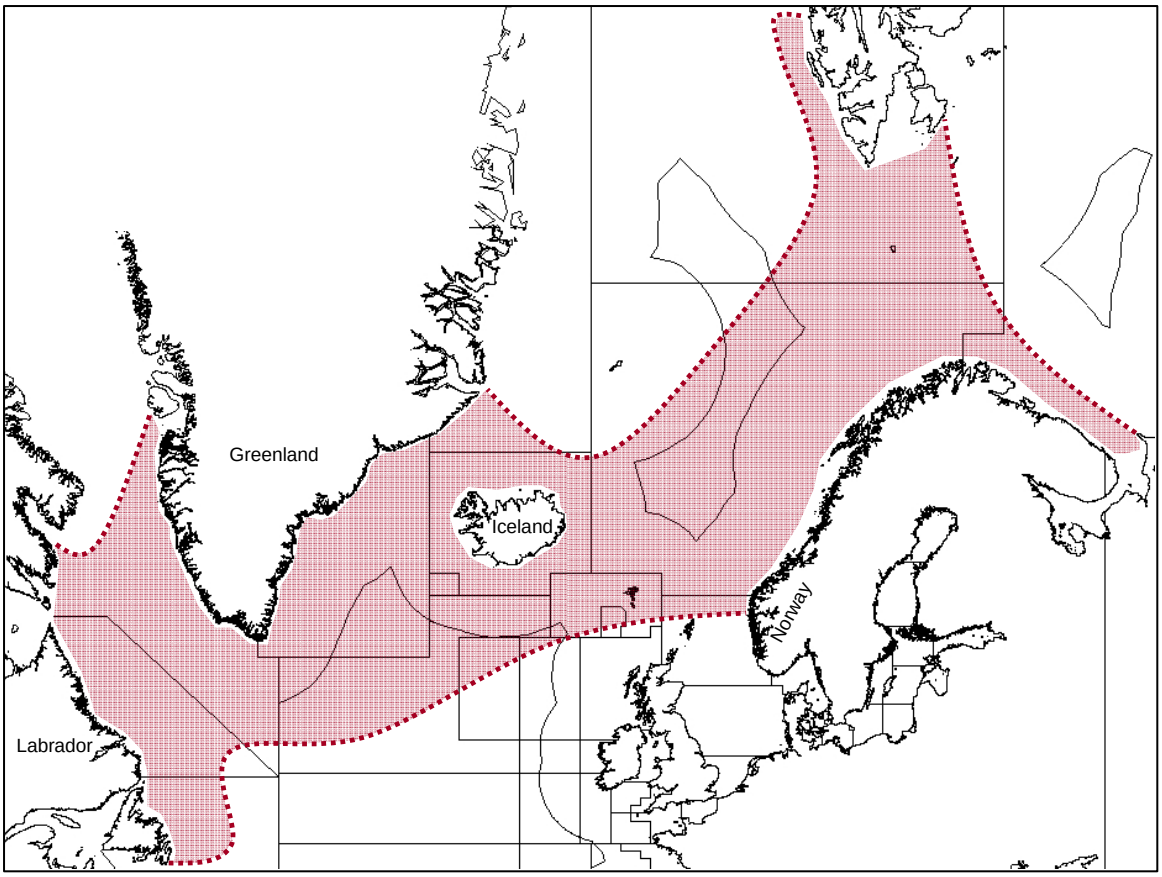

Figure 2. Geographic range of *Sebastes mentella*.

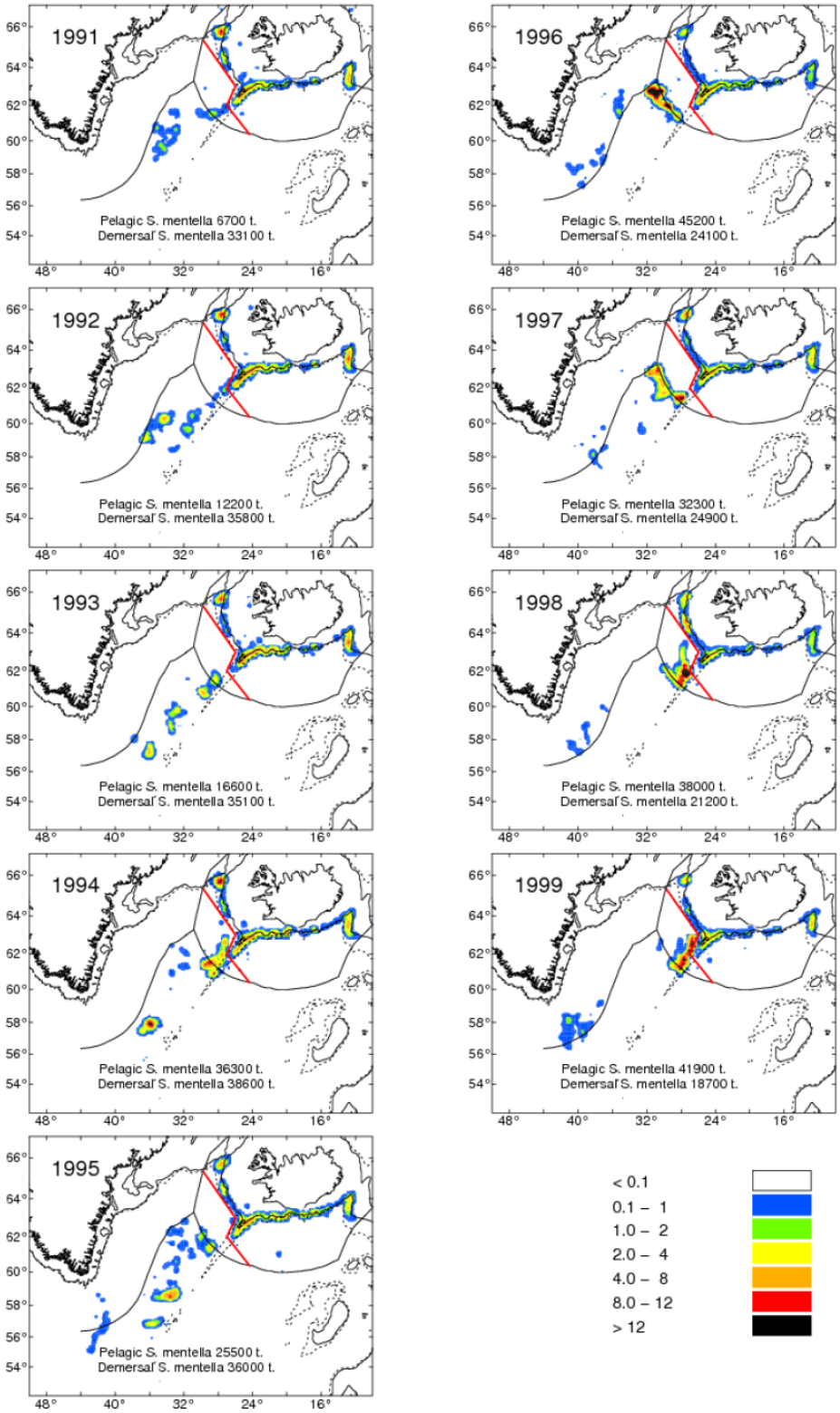

Figure 3a. Geographical distribution of the Icelandic catches of *S. mentella* 1991-1999. The col-our scale indicates catches (tonnes per nat. mi.^{2})..

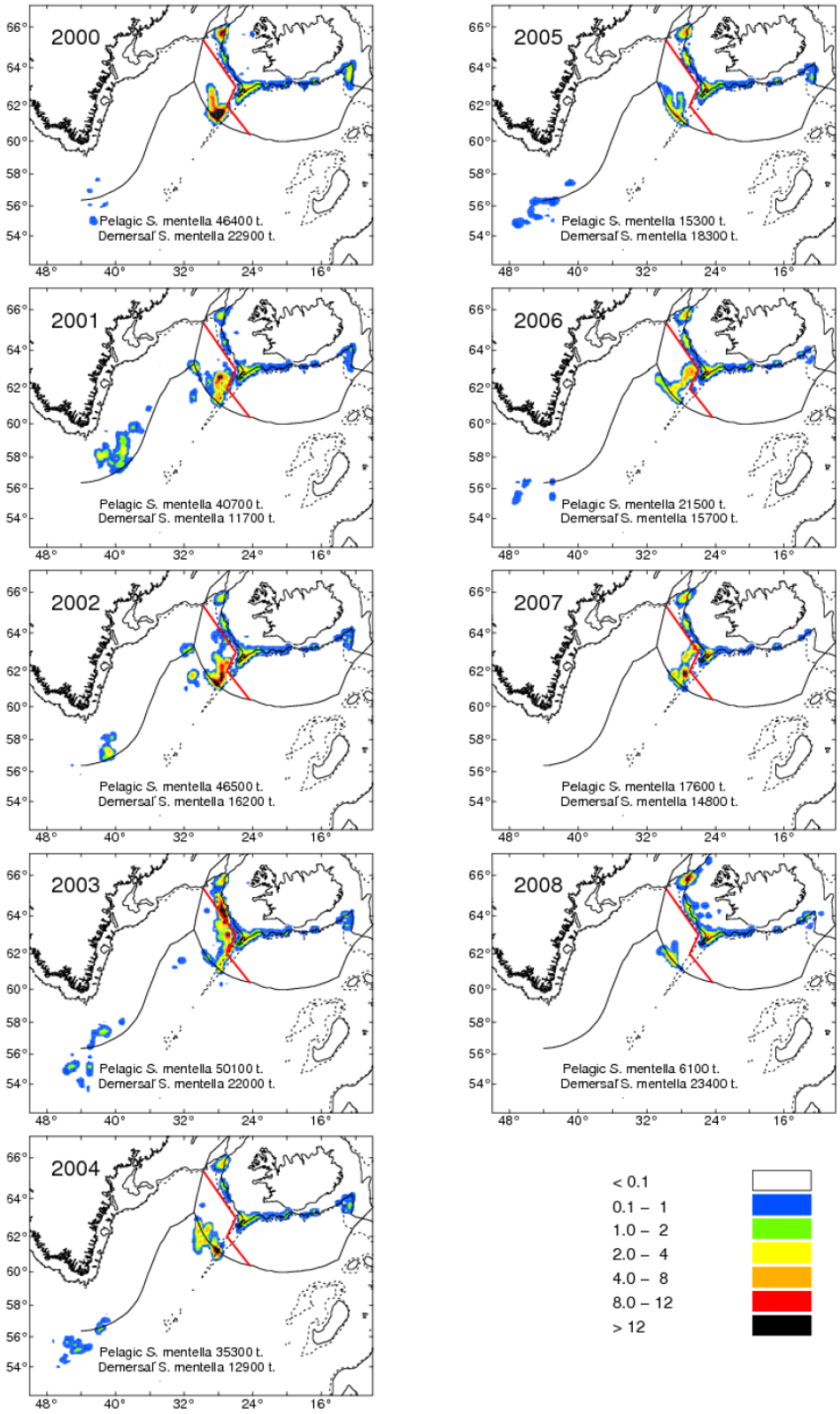

Figure 3b. Geographical distribution of the Icelandic catches of *S. mentella* 2000-2008. The colour scale indicates catches (tonnes per naut.mi.^{2})..

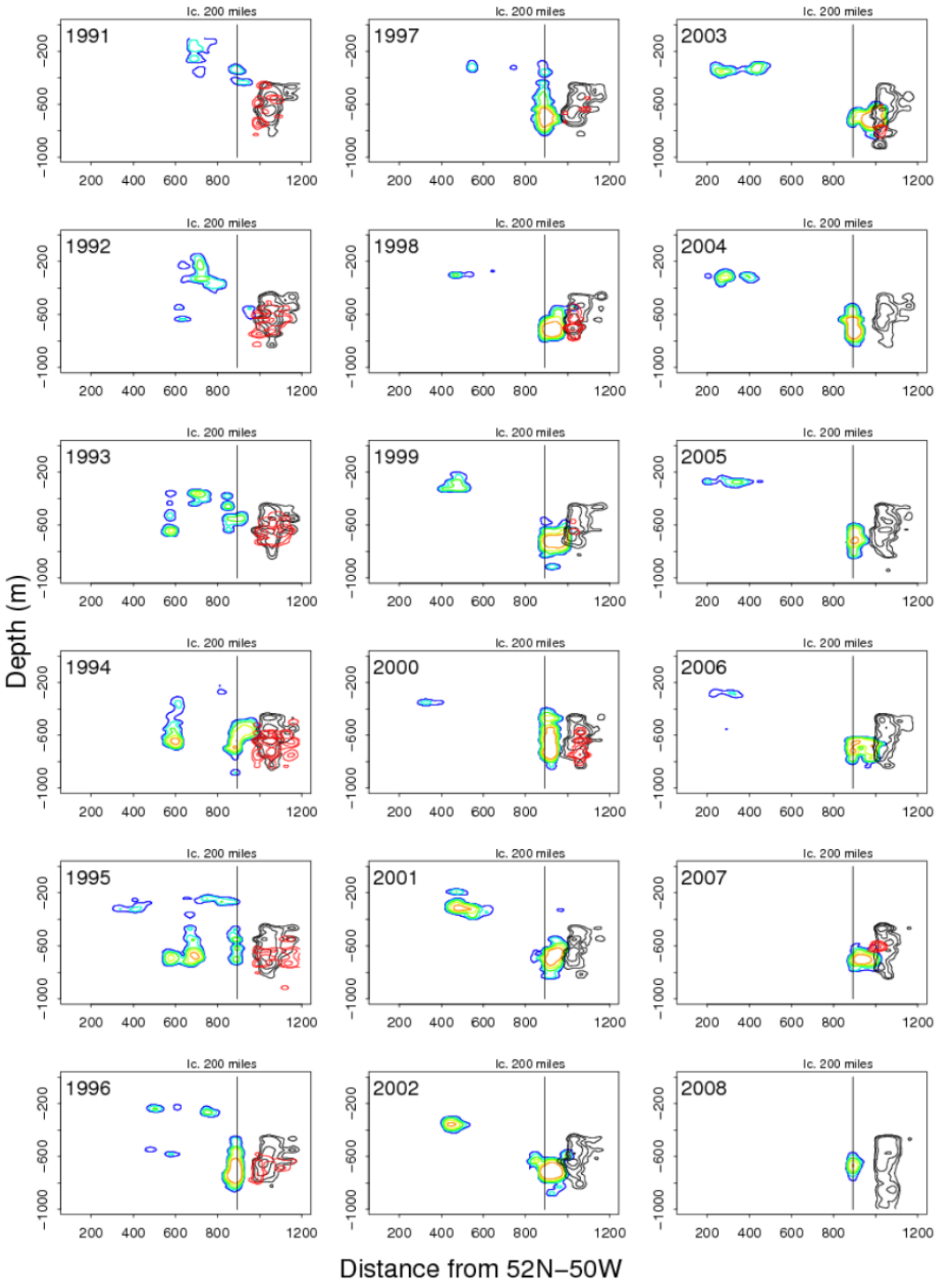

Figure 4. Distance-depth plot for Icelandic *S. mentella* catches, where distance (in naut.mi.) from a fixed position (52°N 50°W) is given. The coloured contours represent the fishery catches of pelagic *S. mentella*, the black contours indicate bottom trawl catches of demersal *S. mentella*, and the red contours represent catches of demersal *S. mentella* taken with pelagic trawls.

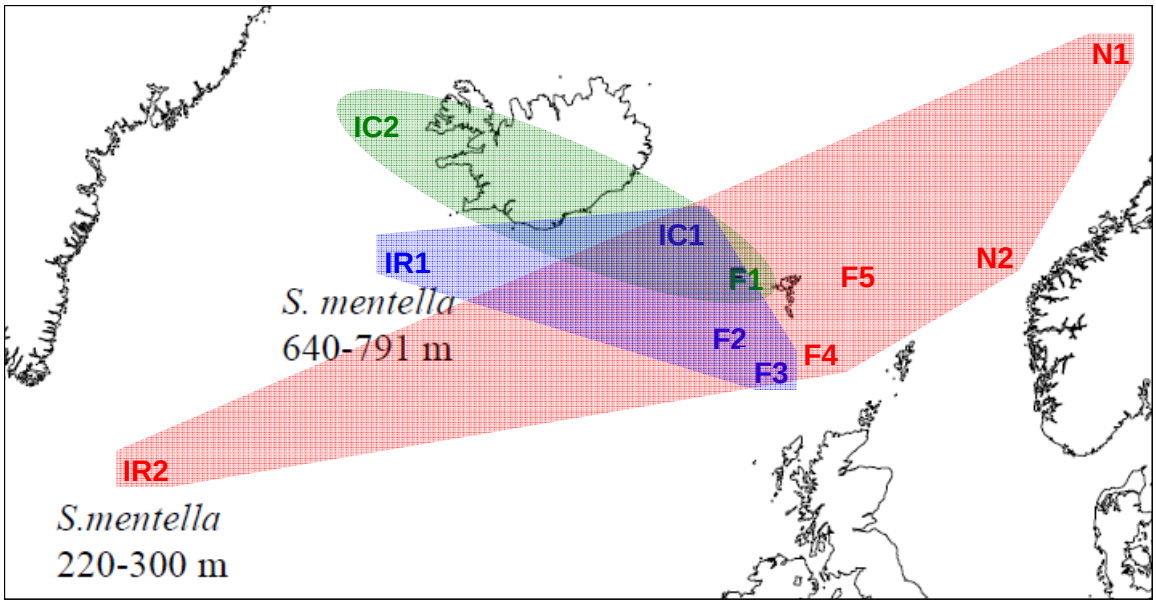

Figure 5. Eleven locations where *S. mentella* were sampled for the Faroese Redfish Project. Colors indicate three genetically distinct clusters detected by analysis of microsatellites. Samples were collected in shallow (IR2, F4, F5, N1 and N2, depth < 540m) and deep (depth > 580m) waters, as well as on continental shelf of Iceland and Faroe island (depth > 500m).

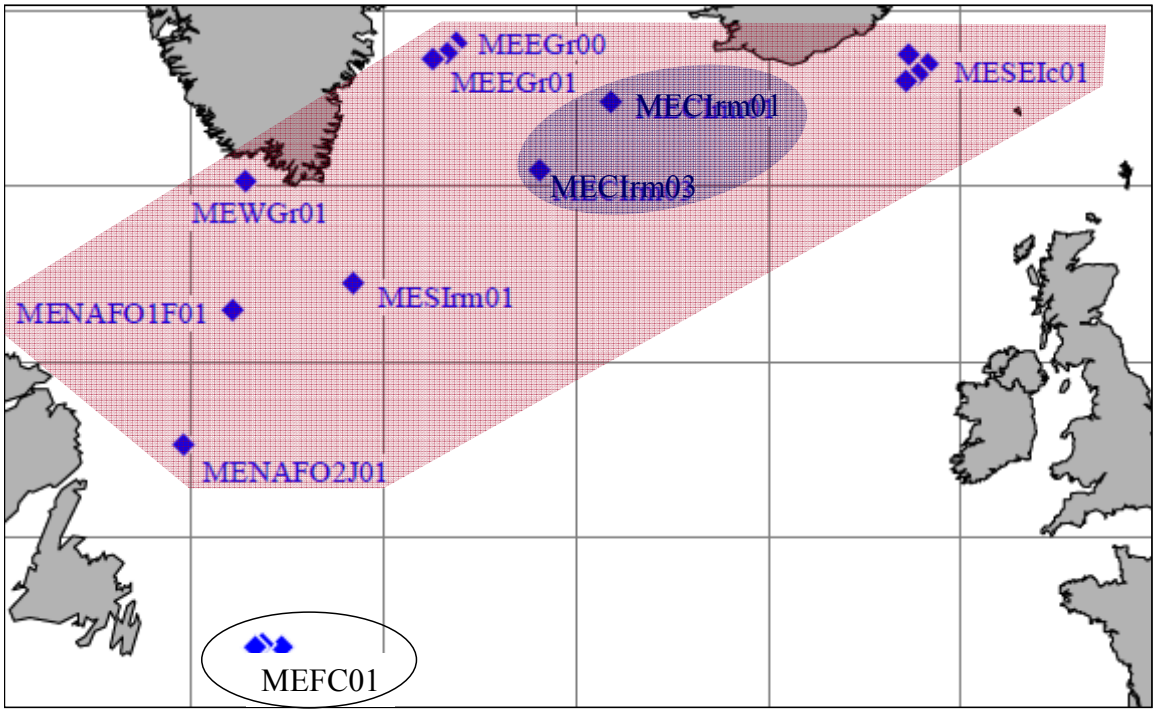

Figure 6 Sampling locations for the microsatellite analysis of *S. mentella*. Colors, ellipses and the polygon indicate three genetically similar clusters (modified from Schmidt 2005).

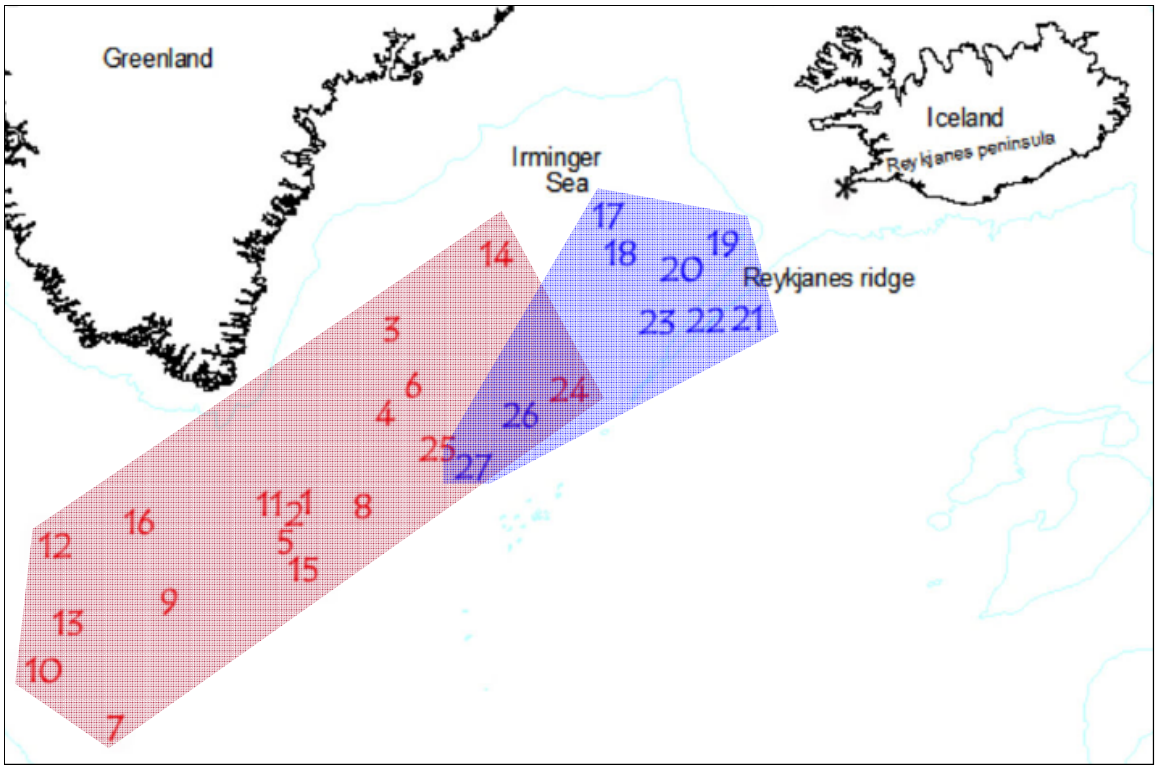

Figure 7. Sample locations of *S. mentella* from the shallow (red, depth < 500m) and deep (blue, depth > 500m) mesopelagic-zones of the Irminger Sea collected for microsatellite loci analyses. Microsatellite analyses revealed the presence of two genetically distinct clusters represented by shaded areas: red = shallow mesopelagic-zone and blue = deep mesopelagic-zone. The asterisk shows the location of the centre of circle (south-west tip of the Reykjanes peninsula, Iceland; 63°82N, 811 22°77W), which was used for calculations of distance (modified from Stefánsson et al. 2009a).

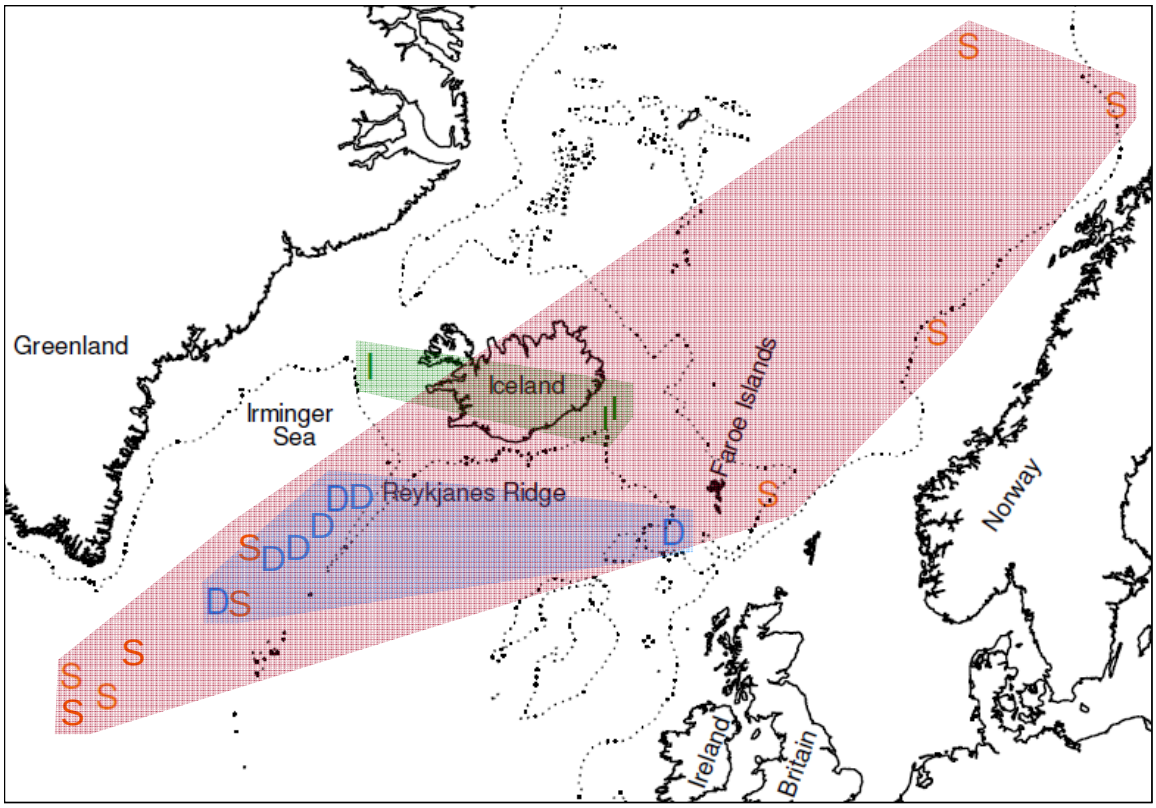

Figure 8. Samples location of *S. mentella* and clustering of groups according to microsatellites loci as interpreted from Bayesian based cluster analysis. Different clusters are represented in different shaded areas and by letters: D: 'deep pelagic' (blue, depth > 500m), I: 'Icelandic Slope' (green, depth < 500m) and S: 'shallow pelagic' (red, depth < 500m).

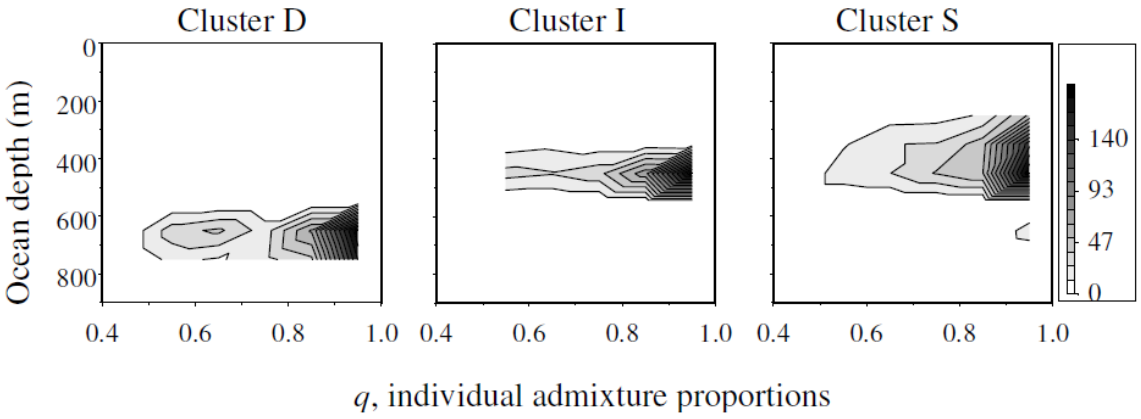

Figure 9. Contour plots representing the proportional distribution of samples (q) by depth (m) and cluster (D: 'deep pealgic'; I: 'Icelandic Slope'; S: 'shallow pelagic'). Only values that were ≥ 0.5 were plotted for each cluster. Scale bar represents number of individuals.

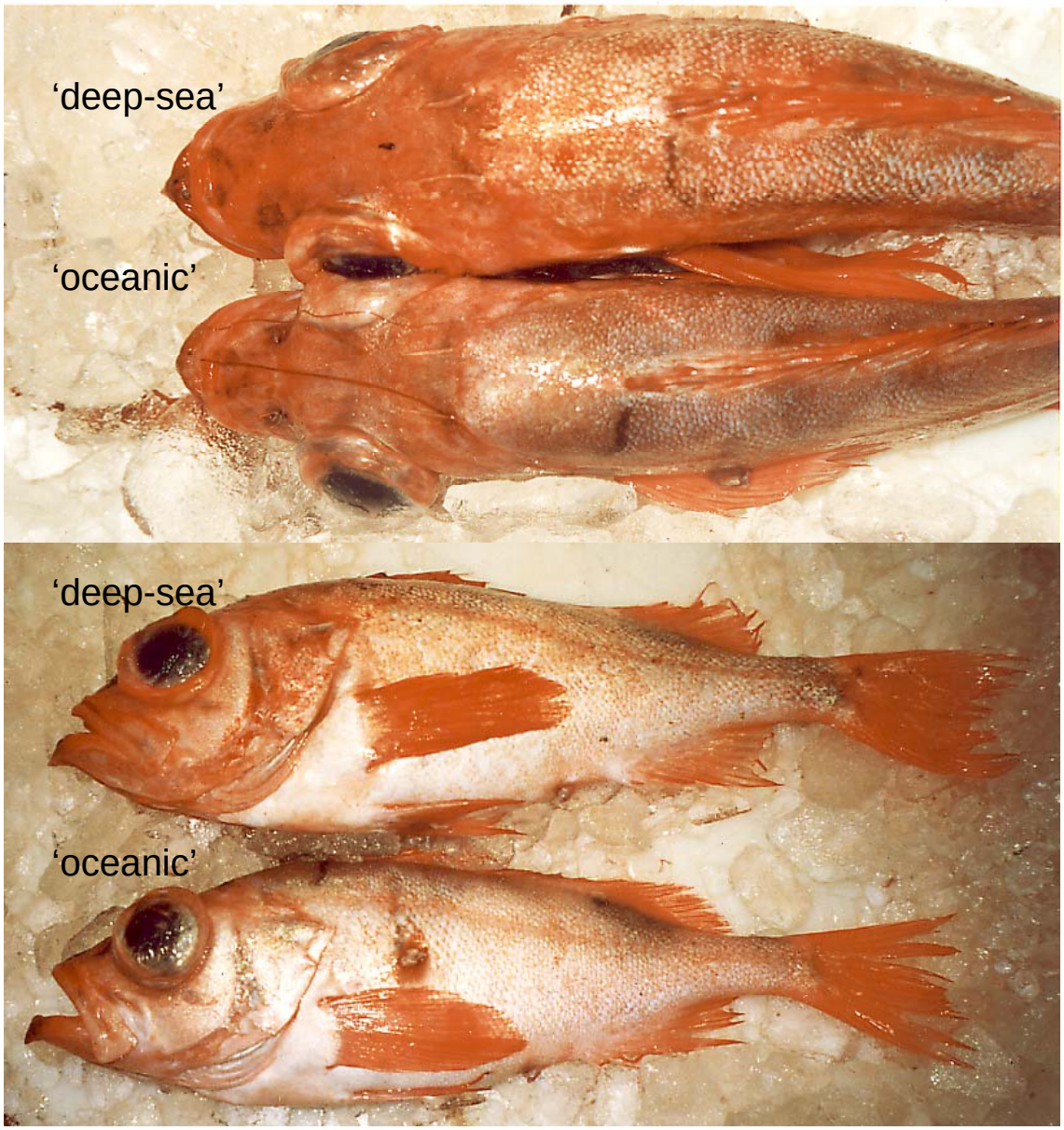

Figure 10. General morphology of ‘deep-sea’ and ‘oceanic’ phenotypes in the Irminger Sea.

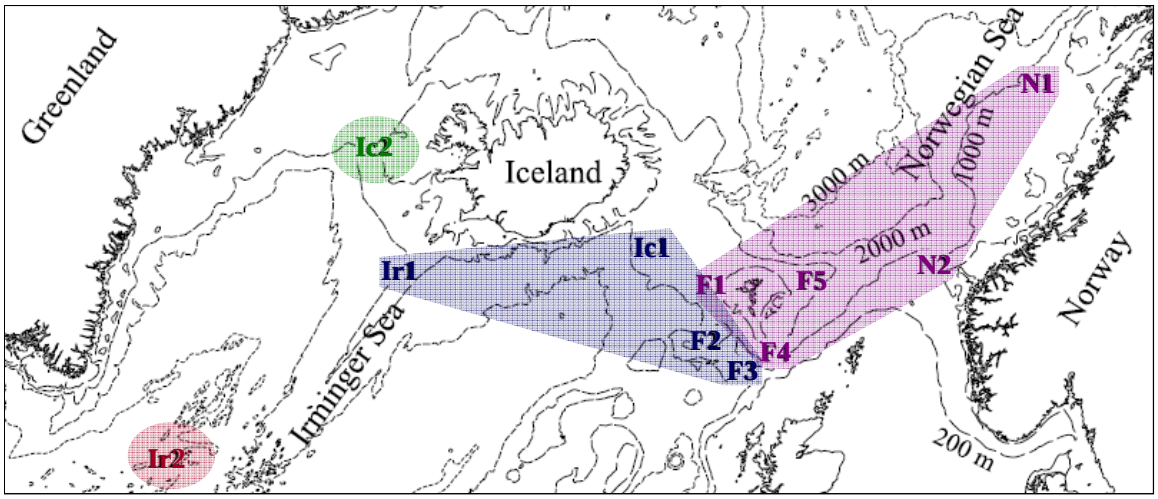

Figure 11. Locations where *S. mentella* were sampled for fatty acid analysis. Colors indicate statistical cluster (modified from Joensen and Grahl-Nielsen 2004). Samples were collected in shallow (IR2, F4, F5, N1 and N2, depth < 540m) and deep (depth > 580m) waters, as well as on continental shelf of Iceland and Faroe Islands (depth > 500m).

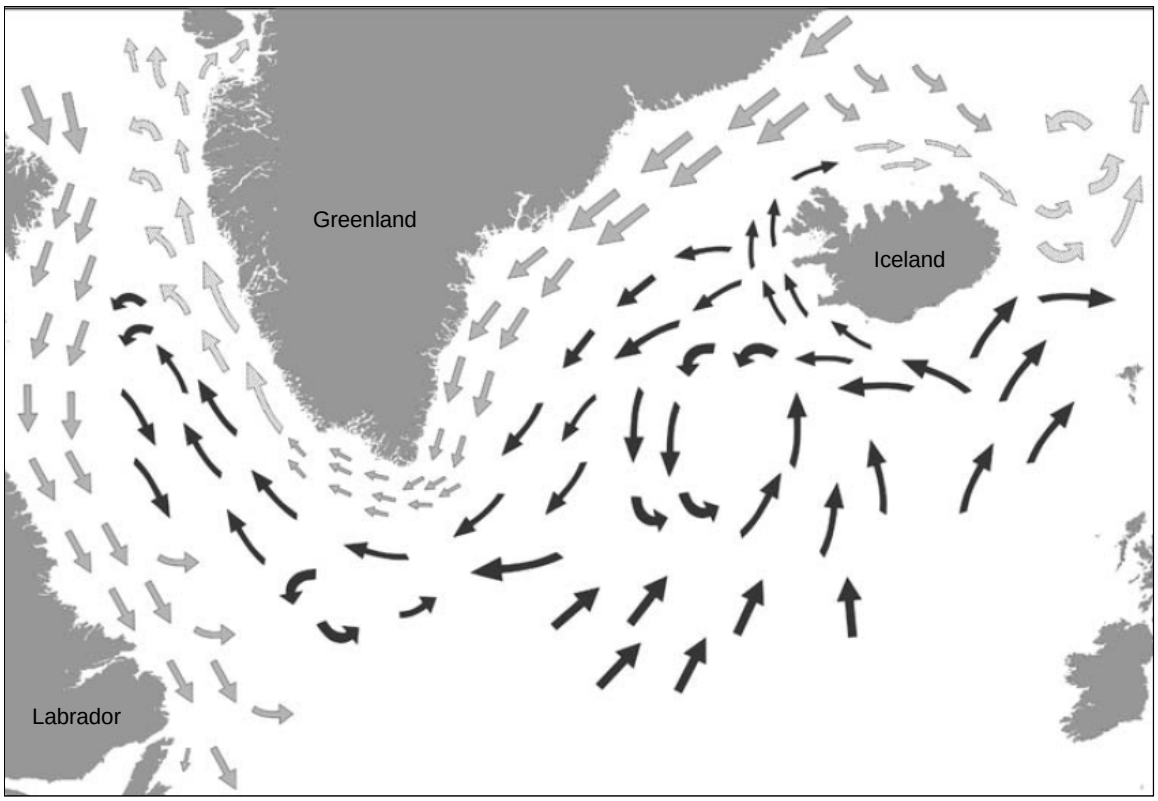

Figure 12. General trends of ocean currents in the Northwest Atlantic. Grey arrows represents cold, Labrador and Irminger currents. Dark arrows are the North Atlantic current and their branches.

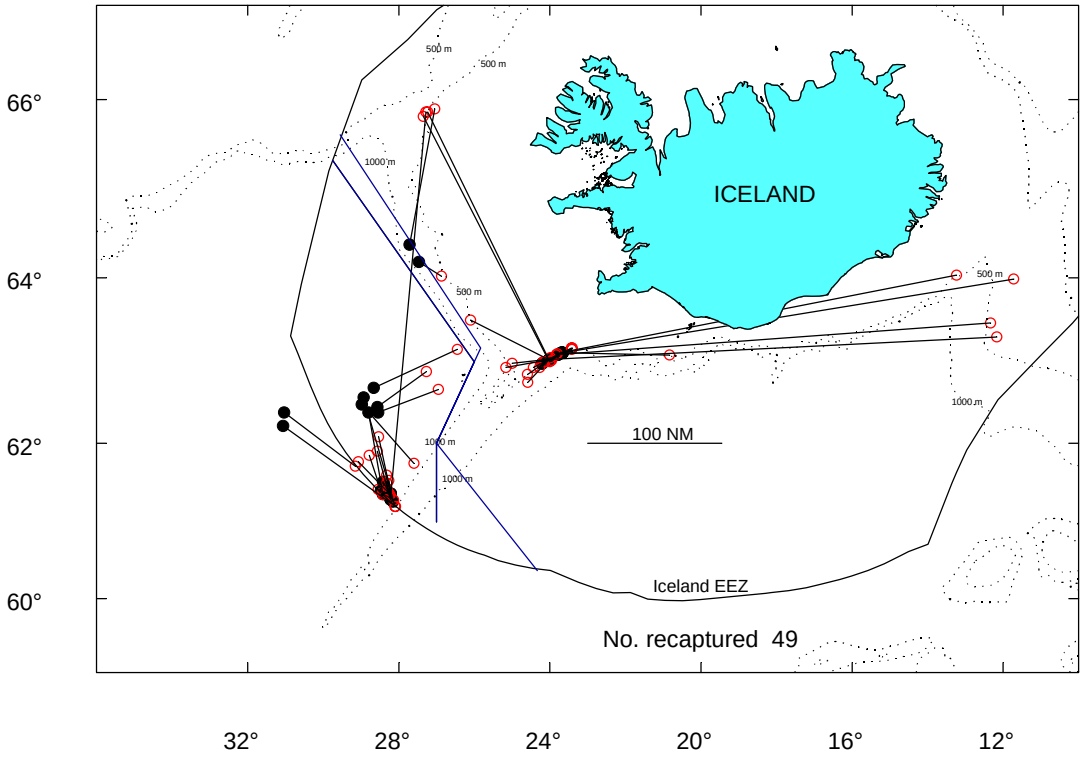

Figure 13. Results of tagging experiments, updated from Sigurðusson et al (2006b). Black dots indicate the tagging site and red, open cirles indicates the recapture site. The line for different management units are shown as blue lines.

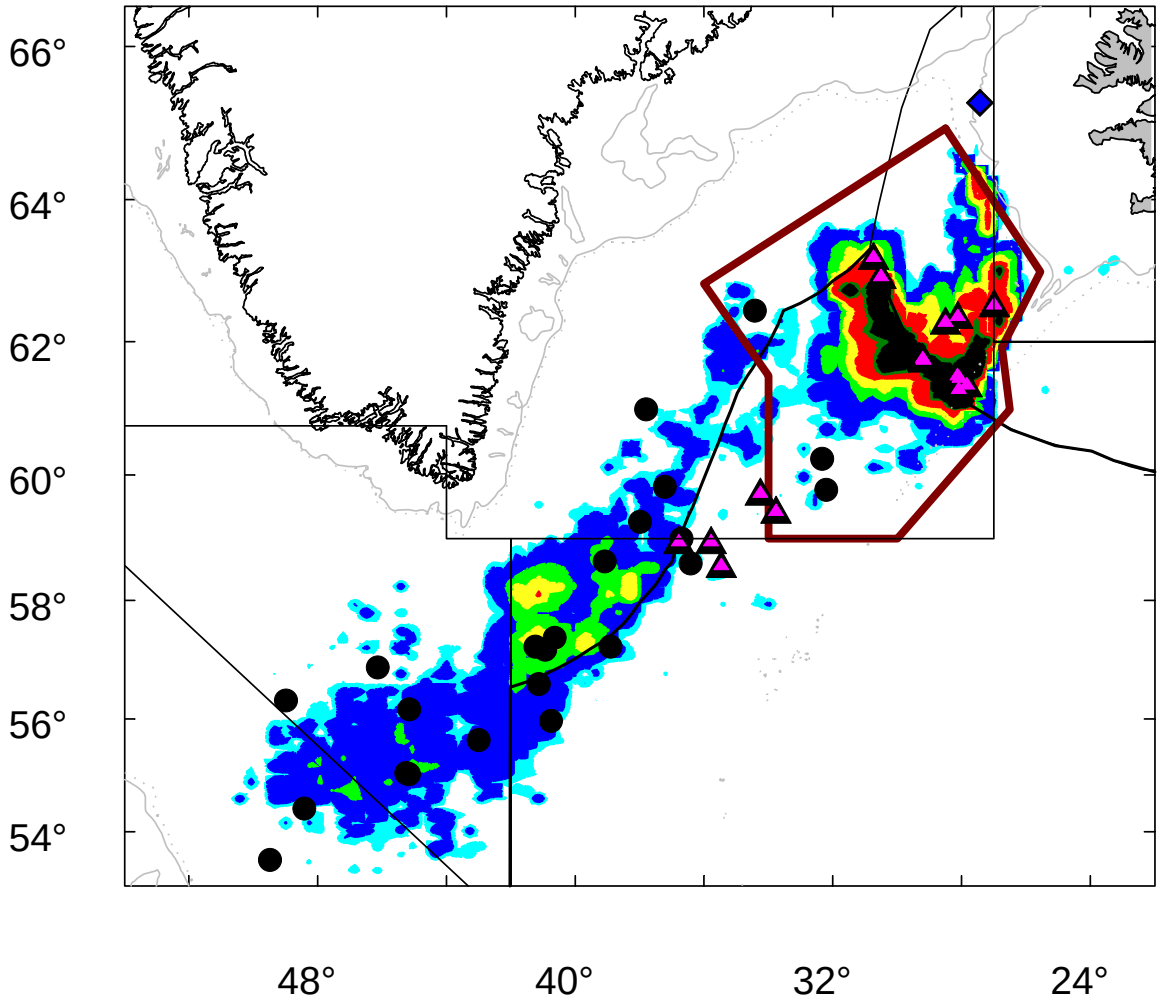

Figure 14. Revised management unit boundaries (red polygon), with fishing distribution and genetic sample locations. Fishery data are from Iceland, Russia, Germany, Norway, Faroe Island and Greenland (1996-2007). Black circles: 'shallow pelagic' genotype; pink triangles: 'Deep Pelagic' genotype; blue dimonds = 'Icelandic Slope' genotype.