

Counter-comment on: [Cadrin *et al.* \(2010\)](#) “Population structure of beaked redfish, *Sebastes mentella*: evidence of divergence associated with different habitats. ICES Journal of Marine Science, 67: 1617–1630.”

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A one-stock hypothesis for *S. mentella* in the Irminger Sea was rejected in favour of one involving depth-segregated stock structure based on the best scientific information available, including recent genetic results. The depth-based hypothesis is maintained and supported, despite the criticisms by [Makhrov *et al.* \(2011\)](#), which can all be explained and refuted.

Keywords: adaptation, depth, fisheries management, molecular genetics, multidisciplinary approach, North Atlantic, stock structure.

Background

Fisheries science and management proceed based on hypotheses about spatial population structure, but the rejection of previously applied hypotheses is difficult and often controversial, particularly when there are considerable economic implications. Spatial management units of beaked redfish (*Sebastes mentella*) in the Irminger Sea were revised to reflect new information on stock structure. [Saborido-Rey *et al.* \(2004\)](#) posed a one-stock hypothesis for *S. mentella* that was generally consistent with information available at the time. However, in a more recent examination of *S. mentella* stock structure ([Cadrin *et al.*, 2010](#)), new genetic information compelled us to reject the earlier hypothesis in favour of one supporting a depth-segregated stock structure that is based on the best scientific information available now.

We respect the expert opinions of our Russian colleagues, and we encourage alternative interpretations and considerations of uncertainty in stock identity. However, the comments of [Makhrov *et al.* \(2011\)](#) can be explained and refuted using scientific arguments previously raised ([ICES, 2010](#)), summarized below. The intention of the ICES Stock Identification Working Group (SIMWG) was to determine best practice for stock

identification to avoid subjective interpretation or political gerrymandering of stock delineation ([Cadrin *et al.*, 2005](#)). The approach used by the ICES Workshop on Redfish Stock Structure (WKREDS; [ICES, 2009](#)) was to consider all the information available on population structure, to test alternative hypotheses rigorously, and to form objective recommendations. Despite uncertainties and equivocal interpretations of some information, the conclusions of WKREDS provide the most parsimonious, realistic, and probable scenario for *S. mentella* stock structure based on the available evidence to date ([Cadrin *et al.*, 2010](#)). Contrary to the assertion by [Makhrov *et al.* \(2011\)](#), the participants in WKREDS agreed with the consensus conclusions during the meeting, but a minority opinion was submitted after the workshop adjourned.

As summarized below, we conclude that the comments by [Makhrov *et al.* \(2011\)](#) are either incorrect or easily accounted for in our interpretations. The SIMWG reviewed an earlier draft of the comments provided now by [Makhrov *et al.* \(2011\)](#), and the substantive 2010 report provides detail on the technical problems ([ICES, 2010](#)).

Analytical design

Although many of the genetic analyses considered by WKREDS were based on testing differences between phenotypes, data from nearly 2000 fish, collected over several years and belonging to many age classes, were grouped by depth, showing that populations below and above the 500–550-m depth boundary were consistently and clearly differentiated based on microsatellite variation (Stefánsson et al., 2009a, b).

Wahlund effect

This effect involves an increase in the F_{IS} index as a result of pooling data from several demes, reflecting the loss of heterozygosity through population substructure (Wahlund, 1928). The phenomenon is useful for detecting departures from Hardy–Weinberg expectations and to rule out the hypothesis of panmixia. The theory underlies some of the most common analytical tools for studying population structure (Pritchard et al., 2000; Corander et al., 2003), which were used to help identify separate genetic clusters of *S. mentella* (Pampoulie and Daniélsdóttir, 2008; Stefánsson et al., 2009a, b). Makhrov et al. (2011) do not possess the allozyme data from Daniélsdóttir et al. (2008) needed to calculate pooled F_{IS} values. Moreover, the allozyme data exhibit a systematic deficit of heterozygotes, so high and significant F_{IS} values, across all loci and populations, likely for reasons other than the Wahlund effect, and most likely mask its signal. It would be more appropriate to test the Wahlund effect using microsatellite data, which were the primary basis of the population structure conclusions for *S. mentella*.

Temporal stability

Collectively, the available stock identification information summarized by Cadrin et al. (2010) supports the inference of two distinct groups, approximately separated by depth habitats. This conclusion is supported by data sampled over a period of 15 years, including samples from many annual cohorts. Given the magnitude and consistency of F_{ST} values observed between *S. mentella* populations, it is inappropriate to support the alternative hypothesis of panmixia based on the species' longevity. One of the problems hindering the application of genetics in fisheries management is assuming a single-stock unit only based on a "lack of detectable genetic differences", which could simply result from type I error (failure to reject the null hypothesis), and may dangerously ignore the ecological dimension of demographic independence (Waples, 1998; Waples et al., 2008).

Divergent selection

The potential effect of disruptive selection between shallow oceanic and deep sea *S. mentella* only strengthens the inference of different stocks. The usefulness of genetic markers subject to selection for stock identification has been confirmed, because they might reflect local adaptation processes and genetic differentiation among locally adapted populations that should be considered as evolutionarily significant units and consequently as different management units (Hemmer-Hansen et al., 2007; Zane, 2007; Hauser and Carvalho, 2008; Nielsen et al., 2009; Bradbury et al., 2010). Disruptive selection may occur at some allozyme loci in *S. mentella*, such as MEP, which shows divergent frequencies above and below the 500-m isobath. On the other hand, the significant differentiation observed at several microsatellite loci, none of which has been shown to be under selection, provides

evidence of restricted gene flow between shallow oceanic and deep-sea *S. mentella*. Therefore, collective evidence from allozymes and microsatellites cannot justify an interpretation of panmixia, or single stock in *S. mentella* in the Irminger Sea.

Interspecific hybridization

There is evidence for a low incidence of hybridization, mainly between *S. mentella* and *S. marinus*, as well as between *S. fasciatus* and *S. viviparus* (Pampoulie and Daniélsdóttir, 2008). However, *S. viviparus* has never been observed in the Irminger Sea (Hureau and Litvinenko, 1986). Contrary to the belief of Makhrov et al. (2011), neither Johansen (2003) nor Pampoulie and Daniélsdóttir (2008) mention *S. viviparus* as present in the Irminger Sea. The potential noise introduced by the *IDHP-1*60* allele, which is more frequent in *S. marinus*, is negligible, because it refers to only a single allozyme locus. Clustering of microsatellite data yields robust results, including the detection of possible hybrids (Pampoulie and Daniélsdóttir, 2008).

Vertical migration

Makhrov et al. (2011) pose a hypothesis based on vertical migration of fish with different genotypes. They cite the example of Atlantic cod (*Gadus morhua*), which exhibits different migration patterns depending on the *Pan I* genotypes they carry (Pampoulie and Daniélsdóttir, 2008), and for Atlantic salmon (*Salmo salar*), the well-known relation of the *MEP-2** locus and time at feeding grounds (see references in Artamonova, 2007). However, Makhrov et al. (2011) may have misunderstood the fact that the relationship between the *Pan I* genotypes and cod migration patterns is found within a single population and is related to habitat choice during feeding migrations. Some cod tend to stay in shallow waters, whereas others migrate to deeper, colder waters, where most forage at temperature fronts. These behaviour types are likely to reflect local adaptation related to food resources of the different genotypes. These genotypes are part of the cod life-history portfolio (Greene et al., 2010), and they need to be considered as different management units (Schindler et al., 2010), because the *Pan I*^{BB} genotypes are likely to be more vulnerable to harvest than sedentary fish (Biro and Post, 2008) because they migrate such long distances, a fact recently corroborated by Jakobsdóttir et al. (2011).

Conclusion

In our opinion, it is most likely that there are at least two distinct genetic stocks of *S. mentella* in the Irminger Sea, approximately delineated by depth. The historical development of scientific perceptions of *S. mentella* stock structure, through application of advanced technologies, sampling designs, statistical analyses, and interdisciplinary evaluation serves as an example of how hypotheses about spatial management units need to be tested continually with new data and approaches. When the evidence for rejecting hypotheses becomes overwhelming, we are compelled to recognize that certain management units do not reflect population structure. We believe that new genetic information improves the view outlined in Saborido-Rey et al. (2004) and is strong evidence for rejecting the hypothesis of panmixia. Despite the economic implications of changing management units, a mismatch between management units and population structure can be damaging to the resource, and costly to the fishery (ICES, 2011).

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