

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”

Alexander A. Makhrov^{1*}, Valentina S. Artamonova¹, Viktor I. Popov², Aleksei Yu. Rolskiy², and Yuri I. Bakay²

¹Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky Prospekt 33, Moscow 119071, Russia

²Knipovich Polar Research Institute of Marine Fisheries and Oceanography, 6 Knipovich Street, Murmansk 183038, Russia

*Corresponding Author: tel: +7 903 666 7215; fax: +7 495 954 5534; e-mail: makhrov12@mail.ru

Makhrov, A. A., Artamonova, V. S., Popov, V. I., Rolskiy, A. Yu., and Bakay, Y. I. Comment on: Cadrin *et al.* 2011. “Population structure of beaked redfish, *Sebastes mentella*: evidence of divergence associated with different habitats. ICES Journal of Marine Science, 67: 1617–1630” – ICES Journal of Marine Science, 68: 2013–2015.

Received 10 February 2011; accepted 6 May 2011; advance access publication 2 September 2011.

An analysis of the genetic data used in the paper by Cadrin *et al.* (2010) indicates that they do not disprove the hypothesis of the existence of a single population of *S. mentella* in the Irminger Sea.

Keywords: depth, fisheries management, selection, stock structure criteria.

Narrative

Saborido-Rey *et al.* (2004) provides a convincing scientific argument based on combined biological, parasitological, and genetic data of the hypothesis of a single population of *Sebastes mentella* inhabiting the Irminger Sea. However, at the Workshop on Redfish Stock Structure (WKREDS) arranged by ICES in January 2009, participants disagreed on the population structure of *S. mentella* in pelagic waters of the Irminger Sea (ICES, 2009). Some argued that the species in the Irminger Sea comprised two stocks separated by depth, whereas others argued that there was only a single stock.

The arguments supporting the two-stock hypothesis were summarized by Cadrin *et al.* (2010); the central argument was based on recently published surveys of genetic variation among redfish populations. However, despite the valuable information summarized in that paper, it should not be used to draw conclusions about stock structure, because the collection of samples and analyses of the data did not satisfy five criteria generally established to define stocks, enumerated below.

Criterion 1. If the aim is to substantiate the existence of two stocks of *S. mentella* in pelagic waters of the Irminger Sea (those living above and below a depth of 500 m), studied (compared) samples need to be collected adequately above and below 500 m (ICES, 2009). However, in many of the studies cited in the overview of redfish, individual fish were selected by the morphological criterion rather than by depth for the statistical comparisons (Johansen *et al.*, 2000; Daniélsdóttir *et al.*, 2008; Pampoulié and Daniélsdóttir, 2008). The collection method is therefore methodologically unacceptable because it may have biased the conclusions of a stock boundary assessment or be inadequate for defining a

stock. For example, five of ten “deep-sea” type samples were collected at <500 m (Johansen *et al.*, 2000).

Criterion 2. Fish samples are determined to belong to different populations only if statistically significant differences in their traits are found between two groups of samples (Weir, 1990). Balloux and Lugon-Moulin (2002, p. 157) describe a test to determine whether the boundary between groups of populations was drawn correctly: “As long as samples from the same deme are pooled together, no significant change in F_{IS} is expected. However, when a sample from a different breeding unit is incorporated in the pooling strategy, a significant increase in F_{IS} should occur”. This test was not used by the authors of genetic work on Irminger Sea redfish, but the genotypic data of Daniélsdóttir *et al.* (2008) can be used to conduct such a test. The mean inbreeding coefficient, F_{IS} , was 0.182 for the “deep-sea” *S. mentella* phenotype and 0.178 for the “oceanic” phenotype. The F_{IS} value for the pooled sample was 0.163 after the two groups were pooled. This absence of an increase in the value for the pooled sample indicates at least that the border between “deep-sea” and “oceanic” groups of *S. mentella* was drawn incorrectly.

Criterion 3. In population studies, special attention needs to be paid to the temporal stability of allele frequencies at the diagnostic loci used to differentiate supposed populations (Waples, 1998). However, the studies arguing for a difference between “deep-sea” and “oceanic” groupings used microsatellite and allozyme markers as diagnostic loci, and for both these markers, year-on-year differences in allele frequencies between samples collected at the same depth have been demonstrated (Schmidt, 2005; Melnikov *et al.*, 2007).

Neither Daniëlsdóttir *et al.* (2008) nor Stefansson *et al.* (2009) found significant differences in the allelic frequencies of microsatellite and allozyme genes between the samples they collected over 3–7 consecutive years. However, such a period is too short for analysing data on such a long-lived species as *S. mentella*, whose lifespan can exceed 30 years (Stransky *et al.*, 2005). The temporal stability of allele frequencies was not tested in other studies (Johansen *et al.*, 2000; Johansen and Dahle, 2004; Pampoulie and Daniëlsdóttir, 2008).

Criterion 4. If diagnostic loci are to be used to identify independent demographic units, they should not be influenced by natural selection (Beaumont and Nichols, 1996), at least during the span of a single generation. The gradient in depth-related variation in allele frequency at the *MEP** locus (Melnikov *et al.*, 2007) mitigates against the hypothesis of two stocks. A frequency cline is strong evidence that selection operates on *S. mentella* cohorts over a single generation, because maturing fish migrate deeper in the Irminger Sea. This variation in frequency at the *MEP** locus appears to be related to selection for resistance to infestation by the copepod *Sphyrion lumpi* (Makhrov *et al.*, 2010). Moreover, the study by Pampoulie and Daniëlsdóttir (2008) presents evidence that selection affects four of nine microsatellite loci in redfish (genus *Sebastes*).

Cadrin *et al.* (2010, p. 1621) argued against the selection hypothesis: “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. Therefore, 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”. However, age-specific selection, in which the direction of selection changes with age, is well known (Mitton, 1997, and references therein) and may also occur in *S. mentella*. Moreover, genetic differences between samples of *S. mentella* collected at different depths can be explained not only by selection, but also by differences in vertical migration among individual fish with different genotypes. In particular, individual Atlantic cod (*Gadus morhua*) carrying an allele of a protein-coding locus have show different vertical migration behaviour than individual cod carrying another allele (Pampoulie *et al.*, 2008). Also, Atlantic salmon (*Salmo salar*) carrying different genotypes of the *MEP-2** locus have different durations of feeding at sea (see references in Artamonova, 2007). However, possible behavioural differences in vertical migration in *S. mentella* with different genotypes were not taken into consideration by Cadrin *et al.* (2010).

Criterion 5. The possibility of interspecific hybridization influencing allele frequencies at diagnostic loci must be ruled out. This criterion is important, because it has been demonstrated that *S. mentella* and *S. fasciatus* hybridize at a large scale in other areas of the North Atlantic (Roques *et al.*, 2001). Additional observations indicate that *S. mentella* hybridizes with *S. marinus* (Pampoulie and Daniëlsdóttir, 2008) and with *S. viviparus* or *S. fasciatus* (Makhrov *et al.*, 2010) in the Irminger Sea. *Sebastes viviparus* has been found in the Irminger Sea (Hureau and Litvinenko, 1984; Johansen, 2003; Pampoulie and Daniëlsdóttir, 2008), although just 18 *S. fasciatus* were found in the area by Hureau and Litvinenko (1984).

Interspecific hybridization can affect the frequency of the *IDHP-1*60* allele, which is more often found in *S. marinus* than

in *S. mentella* (Johansen, 2003). Along with the haplotype common to the “deep-sea” and “oceanic” samples, work has revealed the presence of a specific haplotype in “deep-sea” samples that is absent from “oceanic” redfish, but this haplotype is typical of *S. marinus* (Johansen and Nævdal, 2004) and its carriers are, most probably, hybrids of *S. mentella* and *S. marinus*.

Conclusion

In our opinion, close examination of these five criteria for defining a stock indicates that none of the papers cited as describing the genetic structure of *S. mentella* in the Irminger Sea provides sufficient evidence to conclude with high probability that the hypothesis of two pelagic populations (stocks) of redfish (<500 and >500 m) in the Irminger Sea is correct. Analysis based on the holistic approach to population studies and available long-term data from ecological and population investigations of *S. mentella* (Saborido-Rey *et al.*, 2004) demonstrate the presence of only a single population/stock of the species in the Irminger Sea and adjacent waters. Genetic differences between several samples of *S. mentella* collected at different depths are likely to be linked to the presence of interspecific hybrids in some cases and to selection at certain loci. Therefore, those differences cannot disprove the concept of a single stock of *S. mentella* in the area.

References

- Artamonova, V. S. 2007. Genetic markers in population studies of Atlantic salmon *Salmo salar* L.: karyotype characters and allozymes. Russian Journal of Genetics, 43: 221–233.
- Balloux, F., and Lugon-Moulin, N. 2002. The estimation of population differentiation with microsatellite markers. Molecular Ecology, 11: 155–165.
- Beaumont, M., and Nichols, R. 1996. Evaluating loci for use in the genetic analysis of population structure. Proceedings of the Royal Society of London, Series B: Biological Sciences, 263: 1619–1626.
- Cadrin, S. X., Bernreuther, M., Daniëlsdóttir, A., Hjörleifsson, E., Johansen, T., Kerr, L., Kristinsson, K., *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.
- Daniëlsdóttir, A. K., Gíslason, D., Kristinsson, K., Stefansson, M. Ö, Johansen, T., and Pampoulie, C. 2008. Population structure of deep-sea and oceanic phenotypes of deepwater redfish in the Irminger Sea and Icelandic continental slope: are they cryptic species? Transactions of the American Fisheries Society, 137: 1723–1740.
- Hureau, J.-C., and Litvinenko, N. 1984. Scorpaenidae. In Fishes of the North-eastern Atlantic and the Mediterranean, 3, pp. 1211–1229. UNESCO, Paris
- ICES, 2009. Report of the Workshop on Redfish Stock Structure (WKREDS). ICES Document CM 2009/ACOM: 37.
- Johansen, T. 2003. Genetic study of genus *Sebastes* (redfish) in the North Atlantic with emphasis on the stock complex in the Irminger Sea. Thesis for the partial fulfilment of the Doctor Scientiarum degree, University of Bergen, Norway.
- Johansen, T., and Dahle, G. 2004. Discrimination among species of the genus *Sebastes* in the North Atlantic by random amplified polymorphic DNA. Sarsia, 89: 478–483.
- Johansen, T., Daniëlsdóttir, A., Meland, K., and Nævdal, G. 2000. Studies of the genetic relationship between deep-sea and oceanic *Sebastes mentella* in the Irminger Sea. Fisheries Research, 49: 179–192.
- Johansen, T., and Nævdal, G. 2004. Population genetic studies of *S. mentella* in the North Atlantic with emphasis on the stock

- complex in the Irminger Sea. Working Document Prepared for the ICES SGSIMUR Meeting, 31 August–3 September 2009. 25 pp.
- Makhrov, A. A., Artamonova, V. S., Popov, V. I., Rolskiy, A. Yu., and Bakay, Yu. I. 2010. Single population of beaked redfish (*Sebastes mentella*) in the Irminger Sea: biological characteristics and dynamics of gene pool. NEAFC Document, 2010/30. 31 pp.
- Melnikov, S., Shibanov, V., Stroganov, A., and Novikov, G. 2007. On the issue of biological and genetic studies of *Sebastes mentella* in the open areas of the North East Atlantic. ICES Document CM 2007/L: 02. 25 pp.
- Mitton, J. 1997. Selection in Natural Populations. Oxford University Press, Oxford, UK. 240 pp.
- Pampoulie, C., and Daniélsdóttir, A. 2008. Resolving species identification problems in the genus *Sebastes* using nuclear genetic markers. Fisheries Research, 93: 54–63.
- Pampoulie, C., Jakobsdóttir, K., Marteinsdóttir, G., and Thorsteinnsson, V. 2008. Are vertical behaviour patterns related to the pantophysin locus in the Atlantic cod (*Gadus morhua* L.)? Behavioural Genetics, 38: 76–81.
- Roques, S., Sevigny, J-M., and Bernatchez, L. 2001. Evidence for broadscale introgressive hybridization between two redfish (genus *Sebastes*) in the Northwest Atlantic: a rare marine example. Molecular Ecology, 10: 149–165.
- Saborido-Rey, F., Garabana, D., Stransky, C., Melnikov, S., and Shibanov, V. 2004. Review of the population structure and ecology of *S. mentella* in the Irminger Sea and adjacent waters. Reviews in Fish Biology and Fisheries, 14: 455–479.
- Schmidt, C. 2005. Molecular genetic studies on species and population structure of North Atlantic redfish (genus *Sebastes*; Cuvier 1829). PhD thesis, University of Hamburg. 303 pp.
- Stefánsson, M. Ö., Reinert, J., Sigurðsson, P., Kristinsson, K., Nedreaas, K., and Pampoulie, C. 2009. Depth as a potential driver of genetic structure of *Sebastes mentella* across the North Atlantic Ocean. ICES Journal of Marine Science, 66: 680–690.
- Stransky, C., Gudmundsdóttir, S., Sigurdsson, T., Lemvig, S., Nedreaas, K., and Saborido-Rey, F. 2005. Age determination and growth of Atlantic redfish (*Sebastes marinus* and *S. mentella*): bias and precision of age readers and otolith preparation methods. ICES Journal of Marine Science, 62: 655–670.
- Waples, R. S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. Journal of Heredity, 89: 438–449.
- Weir, B. S. 1990. Genetic Data Analysis. Methods for Discrete Population Genetic Data. Sinauer Associates, Sunderland MA. 400 pp.