

Reply

Response to comments by Cardinale *et al.* on “Local cod (*Gadus morhua*) revealed by egg surveys and population genetic analysis after longstanding depletion on the Swedish Skagerrak coast” by Svedäng *et al.* (2019)

André, C., Barth, J. M. I., Jonsson, P., Jentoft, S., Knutsen, H., and Svedäng, H. Response to comments by Cardinale *et al.* on “Local cod (*Gadus morhua*) revealed by egg surveys and population genetic analysis after longstanding depletion on the Swedish Skagerrak coast” by Svedäng *et al.* (2019). – ICES Journal of Marine Science, 76: 1212–1213; advance access publication 4 July 2019.

Introduction

Cod stocks have declined in many places, so also in the eastern part of Skagerrak (Svedäng and Bardon, 2003; Cardinale *et al.*, 2017). Recently we reported findings of early stage cod eggs on the Swedish coast (Svedäng *et al.*, 2019). The eggs were only a few days old, too young to have been transported from distant spawning areas, thus strongly indicating that they were locally spawned and fertilized. This is of course encouraging news, and also the main result of our study. Using population genetic analysis, we further investigated the possible origin of the cod eggs and found that the cod eggs were genetically differentiated from adult North Sea cod and to a lesser degree also from Kattegat and Öresund cod, together indicating a possible recovery of a local cod stock on the eastern Skagerrak coast.

Cardinale *et al.* (2019) question our results, and by reanalysing our genetic data using Bayesian cluster analysis, suggest that the coastal cod eggs represent a mixture of individuals of different origins (i.e. North Sea and Kattegat/Öresund cod stocks) rather than a separate coastal population.

We agree with Cardinale *et al.*'s view in that the existence of physically mixed eggs spawned inside the fjord by adults genetically resembling Kattegat/Öresund or North Sea cod cannot be excluded; however, Cardinale *et al.* have largely overinterpreted our genetic data and results. Their reanalysis of our genotype data is invalid since the statistical method they use is not suitable for detecting a “third local” population with the data at hand. Below we clarify our findings.

Genetic analysis of cod egg origin

Our initial and main goal with the genetic analysis was to distinguish between eggs of North Sea vs. Kattegat/Öresund origin, based on earlier findings regarding genetic similarities of

cod in this area (Knutsen *et al.*, 2004; André *et al.*, 2016; Barth *et al.*, 2017, 2019). Using two marker panels of up to 8809 SNPs used to investigate cod population structure in the North Sea, Kattegat, and Öresund area (Heath *et al.*, 2014; Berg *et al.*, 2015), we identified a small, high-graded marker panel with 25 loci that were used to genotype the eggs. These 25 loci were selected to maximize the power to distinguish individuals from the two spawning populations (North Sea vs. Kattegat/Öresund), and are thus expected to have limited power to detect individuals belonging to any third, genetically differentiated, population. This is detailed in both Material and methods and Discussion in Svedäng *et al.* (2019). Our individual-based analysis, using non-model-based Principle Component Analysis, showed a scattered clustering of the cod eggs, which is also expected with a small number of loci. Importantly, however, is that the individual egg clusters centre in between North Sea and Kattegat adults, and closer to Kattegat (Figure 3 in Svedäng *et al.*, 2019).

Using our original genetic data, Cardinale *et al.* (2019) applied the Bayesian clustering algorithm implemented in the software STRUCTURE (Hubisz *et al.*, 2009) to calculate K , the most likely number of genetic clusters in the data set. STRUCTURE attempts to find the combination of ancestral frequencies and admixture proportions that best fit the genetic data. Choosing few SNP markers with high F_{ST} and possibly under selection increases the power for detecting small-scale structure, but also come with the cost that these markers have limited power in detecting individuals from genetically differentiated populations not present in the baseline, or not used to select the marker panel (Ogden and Linacre, 2015; Jorde *et al.*, 2018). Thus, applying STRUCTURE to our data in the hope to detect a third “fjord” population (i.e. $K = 3$ clusters) is meaningless.

The eggs we found in fjords on the Swedish west coast were only few days old so it is also highly unlikely that they have been transported with oceanographic currents directly from spawning grounds in the Öresund, southern Kattegat, or the North Sea (Jonsson *et al.*, 2016; Jorde *et al.*, 2018). Other possible scenarios include local origin of the eggs, or a scenario where individuals genetically resembling North Sea/Kattegat adults spawned inside the fjord.

While with the present genetic data it is difficult to determine whether locally spawned cod eggs represent the recovery of a local coastal population or a metapopulation with subpopulations connected to Kattegat/Öresund and/or North Sea populations, the exciting and important finding of locally spawned eggs inside the fjords on the Swedish west coast should encourage the initiation of new studies using careful sampling of all life stages and the use of appropriate genetic tools. Indeed, subpopulation diversity is essential for preserving biodiversity, ecosystem structure, and productivity (Hughes *et al.*, 2008; Schindler *et al.*, 2010) as well as adaptive potential (Baltazar-Soares *et al.*, 2018).

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