



## Comment

### Comments 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.*

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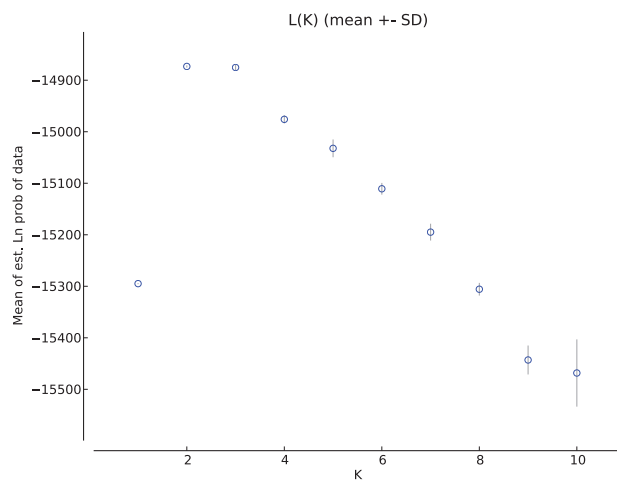
Svedäng *et al.* (2018) concluded that “the occurrence of locally spawned cod eggs suggests that spawning on the Swedish Skagerrak coast takes place, which belong to either a coastal subpopulation that is a remnant stock of a once much larger cod population, or a newly formed subpopulation that is now successfully inhabiting the coastal ecosystems along the Swedish Skagerrak coast”. However, after carefully reviewing the results and the data presented by the authors, we were no longer convinced that the information presented provided enough evidence for a local, distinct, coastal cod population in the Swedish Skagerrak. Thus, we requested the original genotype data, which the authors kindly provided to us. This allowed us to explore the substructure of these samples further using STRUCTURE 2.3.2. Re-analysis of the data consistently rejects the existence of an independent coastal Swedish stock in contrast with Svedäng *et al.* (2018) conclusions. We acknowledge the observation of cod spawning in the area but, based on re-analysis of the original genetic data of Svedäng *et al.* (2018), we currently lack the scientific basis to assume the existence of established local stocks, and even less the demographic expansion of an older, relict population in the area.

**Keywords:** cod, local populations, Skagerrak

Svedäng *et al.* (2018) analysed the genetic variation of Atlantic cod (*Gadus morhua*) in the Swedish west coast and inside fjords using newly collected data from egg trawling surveys in the Skagerrak, aimed to study the present cod local spawning activity along the Swedish west coast [see Figure 1 in Svedäng *et al.* (2018)]. The egg surveys were carried out during two consecutive years, in 2013 and 2014 (203 hauls in total), in combination with population genetic analyses (425 individual eggs genotyped at 25 SNPs). The authors combined the newly collected genetic data of the eggs with available genotypes of adult reference samples from adjacent populations in the North Sea, Kattegat, and Öresund, which were analysed by Barth *et al.* (2017). In the Svedäng *et al.* (2018) paper, the authors presented a Principal component analysis [PCA; Figure 3 in Svedäng *et al.* (2018)] of the various

genetic samples, combined with a table of genetic differentiation (using pairwise  $F_{ST}$ ) among cod eggs collected in Skagerrak, and putative source populations of adult cod as presented in Barth *et al.* (2017). Based on the PCA and the  $F_{ST}$  table [Table 5 in Svedäng *et al.* (2018)], the authors concluded that “the occurrence of locally spawned cod eggs suggests that spawning on the Swedish Skagerrak coast, in fact, takes place” and that “these eggs could belong either to a coastal subpopulation that is a remnant stock of a once much larger cod population, or to a newly formed subpopulation that is now successfully inhabiting the coastal ecosystems along the Swedish Skagerrak coast. In either case, the discovery of locally spawned cod eggs in an area where Atlantic cod were believed to be extirpated due to the overfishing is encouraging news.”

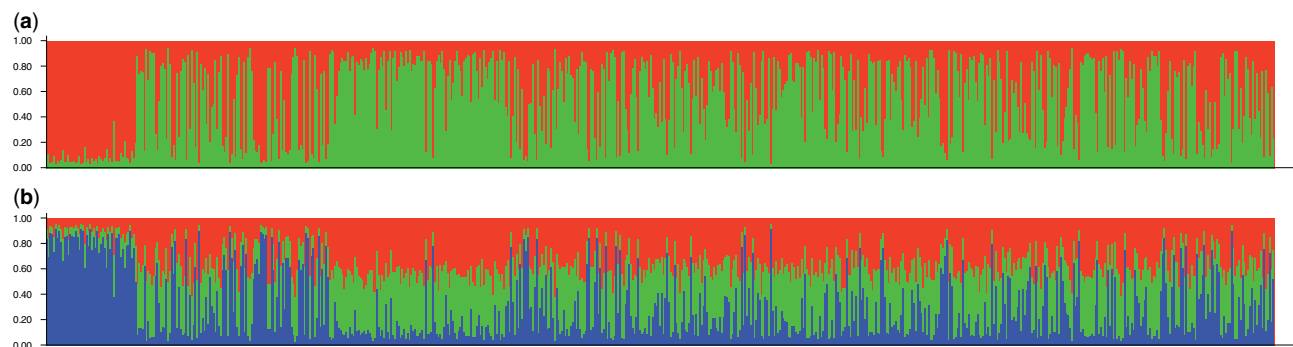
When we read the paper, we also acknowledged these results as good news and extremely important, and especially for future fisheries management in Sweden. However, when we carefully reviewed the results and the data presented, we were no longer convinced that the information presented provided enough evidence for a local, distinct, coastal cod population in the Swedish Skagerrak. Rather, we felt that both the PCA presented in Figure 1 in Svedäng *et al.* (2018) and the  $F_{ST}$  table [Table 5 in Svedäng *et al.* (2018)], might suggest an alternative interpretation. What we noticed as a bit peculiar was that the authors stated that: “Inspecting the separate pairwise  $F_{ST}$  comparisons in more detail (Table 5), we find, however, that the egg samples were not differentiated from the two adult Skagerrak samples collected



**Figure 1.** Mean and variance of posterior probabilities for a range of presumed scenarios estimated using 350 000 MCMC iterations (50 000 burn-in) and default settings. Highest values of the likelihood (expressed in the natural logarithm) are achieved for the scenario with two populations ( $K = 2$ ) and with three populations ( $K = 3$ ) although  $K = 2$  is better than  $K = 3$  due to its narrower variance, and because inspection of individual-based barplots (Figure 2) does not show any further meaningful substructuring. The error bars are based on five replicates MCMC runs for each of the scenarios.

furthest inside the fjord system (adult Gullmarfjord 2005 and Havstensfjord), and to a varying degree to the two Gullmarfjord samples collected closer to the fjord mouth, and even more strongly differentiated to Kattegat and Öresund adult samples (Table 5).” In contrast, when we inspected Figure 3 and Table 5, we interpreted the results differently, leading to a rather different picture. What we observed and what we concluded to be the main result was that eggs, Kattegat adults and Öresund adults are clearly separated from the Central North Sea, while a mix of separation and similarity is observed between coastal Skagerrak cod and the Southeastern North Sea, which is clearly a much more distant sampling location than the Central North Sea [Figure 1 in Svedäng *et al.* (2018)]. Furthermore, Kattegat adults appear significantly separated from all other adult samples, but not from all other egg samples in the different fjords in Skagerrak. Unambiguously, Svedäng *et al.* (2018) show a clear genetic separation of the egg samples collected along the Swedish west coast and inside fjords from those collected in the Central North Sea, but a rather complex mixture in all other samples, irrespective of their origin. Furthermore, and rather strikingly, the Gullmarfjord egg samples in 2013 and 2014 are not separated from the Southwest North Sea [Table 5 in Svedäng *et al.* (2018)]. In other words, the data seem to show that there is a separation between cod in the North Sea and the Kattegat/Öresund, but that fish along the coastal areas and in the fjords of the Swedish west coast is a mixture of individuals of North Sea and Kattegat origin. The entire Skagerrak is therefore representing an area of mixing between North Sea and Kattegat/Öresund cod populations. The data also showed that coastal cod (egg samples) is instead more linked to Öresund than to Kattegat, which suggests that coastal cod and Kattegat/Öresund may form a complex mosaic of spawning aggregations and not separate genetic units. This conclusion is also in line with the conclusions made by Barth *et al.* (2017). Thus, paraphrasing Svedäng *et al.* (2018), notwithstanding the occurrence of locally spawned cod eggs, these fresh data do not support the hypothesis of the existence of a separate unique genetic unit along the Swedish west coast and inside fjords, but point instead to a mixture of cod of different origins.

To further support our alternative observations based on Svedäng *et al.* (2018), we requested the original genotype data,



**Figure 2.** (a) Posterior probabilities of assignment of each individual to any of the two putative populations: colours of each bar represent the relative likelihood of an individual to belong to each cluster. Samples: 1 is NOR02, 2 is NOR14, 3–5 are GUL05, GUL13, GUL14, 6 is HAV09, 7 is KAT04, 8 is ORE03, 9 is 2013A, 10 is 2013B, 11 is 2013C, 12 is 2013D, 13 is 2014B, 14 is 2014C, 15–17 are 2014D, 18 is 2014E, and 19–22 are 2014F. HAV/GUL location shows much influx of “red” North Sea type genotypes, which is the samples 1 and 2. (b) Posterior probabilities of assignment of each individual to any of the three putative populations: colours of each bar represent the relative likelihood of an individual to belong to each cluster. Samples: 1 is NOR02, 2 is NOR14, 3–5 are GUL05, GUL13, GUL14, 6 is HAV09, 7 is KAT04, 8 is ORE03, 9 is 2013A, 10 is 2013B, 11 is 2013C, 12 is 2013D, 13 is 2014B, 14 is 2014C, 15–17 are 2014D, 18 is 2014E, and 19–22 are 2014F.

which the authors kindly provided to us. That allowed us to explore the substructure of these samples further, using STRUCTURE 2.3.2 (Hubisz *et al.*, 2009). This method allowed us to infer the most likely number of genetic clusters in the data set, and then, on that basis, investigate the likely ancestry of eggs and fish from the Skagerrak Swedish coast. We find strong support for the existence of only two main genetic clusters (see Figure 1). One of essentially North Sea Origin and another from the Western Baltic (Kattegat/Öresund), with the genotypes in the Skagerrak area appearing to arise from a primarily physical mixture of genotypes transported from both the North Sea, on one end, and the Western Baltic on the other: samples 3, 4, 5, 6 (adults) and samples 11, 14, 18, and 20 (eggs) in Figure 2a are from coastal or fjord locations and demonstrate a significant influx of North Sea genotypes (red bars). Even when three clusters are assumed, no clear separation is obtained for the Gullmarfjord and Havstensfjord samples (Figure 2b) compared to North Sea or the Western Baltic (Kattegat/Öresund). Collective evidence, including, ordination techniques, fixation indices, and Bayesian clustering, consistently rejects the existence of an independent coastal Swedish stock in Gullmarfjord and Havstensfjord and

along the Swedish coast of Skagerrak, in contrast with Svedäng *et al.* (2018) conclusions. We acknowledge the observation of cod spawning in the area but, based on re-analysis of the original genetic data of Svedäng *et al.* (2018) presented here, we currently lack the scientific basis to assume the existence of established local stocks, and even less the demographic expansion of an older, relict population in the area.

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