

Interactive comment on “Changes in population depth distribution and oxygen stratification explain the current low condition of the Eastern Baltic Sea cod (*Gadus morhua*)” by Michele Casini et al.

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We thank the reviewer for his thorough comments.

In literature, there have been only two studies investigating the relation between Baltic deoxygenation and cod condition, i.e. Casini et al. (2016) and Limburg & Casini (2019). In the former paper, a strong correlation was found between the extent of hypoxic areas (defined in that paper as km² with oxygen < 2 ml/l) and condition, but the mechanisms potentially explaining the statistical relationships were not investigated but just

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proposed, i.e. decline in benthic food, changes in cod behavior/distribution, direct physiological stress, or of course a combination of these. In the second paper (Limburg & Casini 2019) it was shown that fish in low condition at capture were exposed during their lives to lower oxygen levels than those in good condition (at least from the mid-1990s), without saying anything about the distribution of the population, and therefore whether or not a large part of the population indeed experienced stressful circumstances. Therefore, the original triggers and the mechanisms relating hypoxia to the average Baltic cod condition in the population were indeed elusive (and we think they still need attention), as we state in the abstract of the new paper (referred to as CHOL, from the initial of the authors names, following the terminology of the Reviewer; we refer here to the Reviewer as KB).

The CHOL paper takes a further step, showing that the cod population went progressively deeper in autumn and this, concomitant with a shallowing of the low-oxygen layers, increased the spatial overlap between cod distribution and low-oxygen waters, and thus generating stressful circumstances for the cod population (exposure to waters with oxygen < 4 ml/l, detrimental for cod condition as found in experiments by Chabot & Dutil, 1999) (see below about the choice of the oxygen sub-lethal threshold in the CHOL paper). We finally showed that this increased overlap relates statistically to the decline in the mean population condition and to the proportion of fish with very low condition, both for juveniles and large fish. Therefore, the CHOL paper shows the original processes (deepening of the cod population concurrent with the shallowing of low-oxygen layers) creating the stressful circumstances relating to a decline in condition, for both small and large cod. In our opinion, this is a very important step forward in the understanding of the link between low-oxygen and cod condition, and in general for understanding the causes of the declined cod condition. Additionally, it is not so obvious that condition has to be directly linked to a general deoxygenation phenomenon, since mobile fish can change their distribution in response to that, as done by other fish species in other areas. This did not happen for the Baltic cod (conversely it went deeper, in autumn), and we think that finding the answer to why this has happened is

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one of the next challenges for the scientists. Cod prey should also suffer from deoxygenation, although some are more tolerant to low oxygen; therefore, the question of why cod went deeper is not so trivial in our opinion and should be investigated as we suggested for future studies.

We are therefore totally in line with KB about the fact that “the issues to resolve are firstly whether cod redistribute themselves to remain in areas and depths with sufficient oxygen and if not then secondly whether the magnitude of ambient oxygen decline that cod experience is sufficient to explain all or only part of the observed change in their condition.” This is exactly what we have done in the paper for both small and large cod in autumn. In addition, we have also investigated the original reasons creating these circumstances (i.e. both deepening of the population and shallowing of the low-oxygen layers), as well as estimated the overlap with the low-oxygen layers, known to affect cod condition, and estimated the relation between this overlap, the mean population condition and the percentage of fish with very low condition, for both small and large cod. This does not mean that direct exposure to low-oxygen is the sole driver of condition (even if oxygen decline is sufficient to explain a large part of the decline in condition), because there can be other contributing drivers and/or drivers that have co-varied with deoxygenation (food availability, parasites, inter- and intra-specific competition, etc. . .) that could also explain the reduced feeding level (see below). That is why further work is needed here too.

In the CHOL paper, we used 4 ml/l as sub-lethal oxygen threshold impairing cod condition. As KB correctly stated, 73% oxygen saturation (sub-lethal threshold in Chabot & Dutil (1999)) corresponds to 4.8 ml/l at the experimental conditions, but 65% oxygen saturation is the level from which the decline in condition was significant in Chabot & Dutil (1999) experiment, corresponding to 4.3 ml/l. We can therefore use either 4.3 or 4.8 ml/l in the revised version of the paper, to improve our analyses.

We agree with KB that the real oxygen levels experienced by cod would be informative, so in the revised paper we will be showing also the oxygen levels corresponding to the

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annual depth distribution of cod in autumn, both for small and large cod. However, we think that the information about the shallowing of the 1 ml/l and 4 ml/l (the latter will be 4.3 or 4.8 ml/l in the revised paper) depths enriches the story, and together with the deepening of the cod distribution depth, it visually delivers a very clear message. Therefore, we would prefer to retain this.

The otolith analysis was already published in Limburg and Casini (2019), but the analysis was re-arranged as a new figure in CHOL. We thought that this was a nice conclusion of the story, but if the Reviewer and/or Editor prefer, we could either specify better that the idea was already presented previously, or delete the last figure and explain in the text the link between our results and those of Limburg and Casini (2019).

Exploring mechanistic relationships would need experimental setups. Using time-series, the statistical relationships have to be interpreted in light of what is known about the biology and ecology of the fish. In our case, we used the experimental results from Chabot & Dutil (1999) to relate the distribution of the cod population with the oxygen levels resulted to affect cod in experimental setups, and in the revised paper we will use more information coming from stomach content analysis (see below).

We agree with KB that Neuenfeldt et al. (2020) is an extremely important paper, showing that the lower energy intake observed in cod (using stomach content time-series) would predict a decrease growth in length that could explain the shift in size distribution of cod population towards lower sizes. The lower amount of benthos and pelagic fish in the diet of cod could be due to a decline in their availability (as suggested in Neuenfeldt et al. 2020) but also to a decline in cod appetite due to low-oxygen exposure (Chabot & Dutil 1999, Brander 2020) or other low oxygen-related physiological stress. Food intake can surely be the main driver of growth, but other factors can cause fish to allocate more energy to basic metabolism, reproduction etc. . . in some circumstances. For example, currently Baltic cod reproduce at a smaller size (around 20 cm) than before (30-35 cm) and this could mean a lower allocation of energy to growth and therefore also explain the growth decline. We agree with KB that such reasoning produces the

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egg-chicken problem, but it brings us outside the scope of the CHOL paper.

In our analyses we investigate fish condition, not growth in length, and since the two traits are different (fish can grow fast in length, utilizing the stored energy reserves, but this at the detriment of condition, that is a ratio between weight and length) we do not want to mix them, and moreover the link between condition and growth has not been well established to our knowledge. However, in the revised paper, we will add more discussion about the decline in feeding level found in Neuenfeldt et al. (2020) that could link the increased exposure to low-oxygen levels to declined condition. However, there are some aspects that make this link not as straight forward as it seems. Neuenfeldt et al. (2020) show that feeding level has not declined for large cod, but the observed decline in condition has been more severe for large cod (Casini et al. 2016 and the new CHOL paper), suggesting perhaps that feeding level is not the sole driver of large cod condition and that therefore low oxygen has impacted cod condition also through different mechanisms, other than food intake. For example, large cod could experience shortage of benthic prey and therefore, proportionally, could be forced to eat more pelagic fish that require higher energy to catch. Moreover, cod was not in low-oxygen conditions before the early 1990s (see our CHOL paper), but the feeding level was already low (Neuenfeldt et al. 2020; see also ICES 2016), and so was condition (Casini et al. 2016, new CHOL paper), indicating that direct exposure to hypoxia is not always the driver of feeding level and condition (matching therefore with the results from otolith analyses in Limburg & Casini (2019)). In the revised paper, we will however discuss more our results in relation to Neuenfeldt et al. (2020)'s findings about feeding levels, to link the increased overlap with low-oxygen waters to feeding level and condition after the early 1990s. We will moreover discuss more the CHOL paper results in view of Brander (2020) paper recently published.

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