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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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General introduction Decline in oxygen in the oceans due to global change is altering the composition and productivity of marine biota, but the scarcity of long time series, deficient understanding of the processes involved and complex interactions make it difficult to identify the causes of change with confidence. For oxygen, the effects are most evident in enclosed coastal seas, such as the Baltic Sea, where oxygen decline has been observed for several decades due to eutrophication, irregular re-supply of oxygen-rich water from the North Sea and increasing temperature. The Baltic Sea can in some respects be regarded as a global “canary in the coalmine” for the progressive effects of oxygen decline on fish species and their fisheries. The salinity and oxygen environment is extreme for marine species, such as cod, therefore small changes will quickly have effects and these changes will be detected quickly, because the hydrographic and biological environment is and has been closely monitored for many years. During the past century there have been major fisheries for cod, sprat and herring, but the fishery for cod was closed in 2019 due to the low abundance and poor condition of the fish. In addition to decline in oxygen and salinity and increasing temperature, possible causes for the decline in cod include fishing pressure, parasites, predators and lack of prey as well as combinations or interactions between them. Some of the causes (or pressures) can actually or potentially be altered by management action, but management will only be effective if the processes are correctly identified. This is the frame within which the current paper is important; any lessons learned will be valuable in both the immediate Baltic Sea management context but also as a guide to studying similar cases on a global scale. One of the main lessons however is that even in a low biodiversity system, such as the Baltic Sea, there are many interactions; processes that drive changes during one period of years or decades may be relatively unimportant in another. Subject of the paper - novelty, adequacy and value This paper (I will refer to it by the first letters of the authors names CHOL) relates the observed decline in body condition of cod since the mid-1990s to the observed deepening of their distribution, which is concurrent with observed shallowing of the well-oxygenated upper layer of the water column. Over time the fish are increasingly exposed to oxygen levels that we know from experimental studies to inhibit their growth and condition. A review is required to consider whether the evidence and explanations are novel and whether the analysis and interpretation stand up to peer scrutiny. Much has been published on the causes of the decline in growth and condition of Baltic Sea cod, including a number of prominent recent papers by these authors, so the question of novelty has to be addressed in that context. The decline in condition of cod has been known and commented on for some time, indeed it is one of the reasons that the cod fishery has become uneconomic, as

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fillet size and quality decreased. The shallowing of the well-oxygenated upper layer is also well known. The second sentence of the Abstract in CHOL states that "the processes relating hypoxia to condition remain elusive", but the third sentence states that low oxygen levels are "known to be detrimental for cod performance". In fact the underlying physiological processes relating condition and growth to oxygen levels are well known and CHOL base much of their analysis on published experimental work that shows how low oxygen affects cod growth and condition ((Chabot & Dutil, 1999)âĄă, henceforth C&D). The novelty of CHOL comes from the way in which they present the relationship between the observed changes in condition and change in vertical distribution of cod related to oxygen levels, which they support with previously published evidence from otolith microchemistry (Limburg & Casini, 2019)âĄă. I will go into detail about some of the analysis and interpretation later, since CHOL raise a number of issues that are important in furthering our understanding of what is happening to Baltic Sea cod, however first I will explain why I do not think that the relationship they seek to establish between oxygen and fish body condition adds much to our understanding of the causal relationships and processes involved. It is well know that inferring causal relationships from correlations is slippery for at least two reasons (i) the "chicken and egg" problem, of which an example in the context of Baltic cod is that fish with high parasite loads are in poor condition, but how do we determine whether parasite load causes poor condition or poor condition makes fish more vulnerable to parasites? (ii) the "lurking variable" problem of which a classic example is the correlation between number of daily shark attacks at a beach and number of ice creams sold – both depend on the number of people on the beach. Nevertheless, causal inference is possible and in the case of Baltic Sea cod I suggest that the "lurking" cause of their poor condition has already been identified as reduced food and energy intake over the period since the mid 1990s ((Neuenfeldt et al., 2019)âĄă. If there is a "chicken and egg" case for ascribing low feeding to poor condition rather than the reverse, then CHOL should put it forward in their paper. If reduced food and energy intake is indeed a sufficient causal explanation for poor condition then we are of course still left with the question of what causes reduced feeding, which is an active subject of debate. The principal causes currently put forward include hypoxia (Brander, 2020)âĄă and/or lack of prey for cod (Neuenfeldt 2019), but others include parasites, predators (seals and cormorants) and dietary deficiencies (thiamine), combined in various ways with each other and with density dependence. I would argue that in terms of causal inference, hypoxia has prior status because it is based on known, general processes of metabolism that always apply. Since we know that the condition of cod is affected by their oxygen environment and we have observed an ongoing decline in oxygen in the Baltic Sea, it would be surprising if cod condition did not decline. 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. If declining oxygen is not a sufficient explanation then other factors, such as availability of suitable food also need to be evaluated. Unfortunately our knowledge of changes in prey, particularly benthos, is poor, compared with our knowledge of changes in oxygen. Evaluating causality and the case made by CHOL CHOL base their argument that declining condition of cod is due to increasing exposure to low oxygen conditions on three sets of evidence: (i) experimental evidence (C&D) that the condition of cod is lower at low oxygen (ii) time series showing concurrent declines in cod condition and their ambient oxygen (which is dependent on changes in depth distributions of both variables) (iii) evidence from otolith microchemistry that cod have been increasingly experiencing low levels of oxygen. As I argued earlier, the experimental evidence is consistent with axiomatic physiological processes. Before evaluating the other two let us consider the use of the term "hypoxia" since it affects the form of analysis and the perception of how oxygen affects cod. "Hypoxic" can apply to a process or to a metric (e.g metabolism, growth, condition) being impaired due to lack of oxygen. In aquatic systems it can also refer to a state of low oxygen (typically <2-3ml/l) that results in mortality of fish and benthos, resulting in "dead" areas or zones. Either continuous impairment or discrete zones, which divide the continuous oxygen spectrum in a water column into two or more discrete layers, may be used when analysing the effect of low oxygen on fish feeding and condition. CHOL divide the water column into three layers, with a boundary at 4ml of oxygen per l separating the well-oxygenated “normoxic” surface layer from the layer they call “sublethal” or “hostile” and a boundary at 1ml/l dividing this from the “hypoxic” bottom layer, which they state that cod avoid. (In their Discussion they also call everything below the normoxic layer “hypoxic”). This allows them to estimate the change in depth and area of the “hostile” layer and then the change in overlap between this and the layer in which cod occur. I am not convinced that this is the best way to proceed and suggest treating oxygen as a continuous variable with progressive effects on cod, as shown by the experimental results by C&D that they use for defining boundaries. Treating oxygen as three discrete layers may make some forms of analysis easier, but it also raises a number of issues. Firstly, in studying the effects of oxygen, the sensitivity of the receptor or process matters; for example even within the experimental results of C&D the effects of oxygen on length, mass and condition of cod gave differing boundaries between normoxic and sub-lethal layers. Secondly, if the “normoxic” or well oxygenated layer is defined as the layer within which differences in oxygen have no detectable adverse effect then the boundary depends not only on what effects are being studied but also on how sensitive the tests for adverse effects are. This is analogous to the controversy over “thresholds” for effects of radioactivity or pollutants on human health. I do not question the utility of using such defined layers for general descriptive purposes, but I do question whether they are the best way of carrying out the analysis in this study. CHOL use the study of oxygen effects on growth and condition of cod by C&D in defining the boundary between the normoxic and sub-lethal layers. The assumption that Baltic Sea cod, which live in a very different temperature and salinity environment from the Gulf of St Lawrence, respond in the same way to low oxygen is acceptable, however it is not obvious how they calculated the boundary value (4ml/l) that they take from C&D. The relationship between oxygen and condition factor in Figure 1c of C&D shows the “critical level of dissolved oxygen” i.e. the lower boundary of normoxia at 73% saturation. At the temperature and salinity of the experiments (10°C

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and 28) this corresponds to 4.822ml/l of oxygen, not 4ml/l. An earlier paper (Casini et al., 2016) cited the same experimental source but said it “showed a significant decrease in condition already at 3 ml/l”. To put these differences in context, the level of oxygen in the Bornholm Basin drops by 1ml/l every 10m depth increase; a 1ml/l drop in oxygen caused a roughly 10% drop in food intake in the experiments by C&D. Moving the boundary between the normoxic and sub-lethal layer up to 4.8ml/l will affect the correlations between oxygen and condition shown in CHOL, quite likely strengthening them. The task of defining boundaries between layers disappears if oxygen is treated as a continuous variable with progressive effects. The Abstract and the final paragraph of the Introduction of CHOL give the impression that the otolith microchemistry work was carried out as part of this paper; they should make it clear that all the results were published previously. Figure 6 in CHOL presents the same information as Figure 2 of Limburg and Casini 2019. Unresolved questions and other possible causes of declining condition of cod Why are cod moving into deeper water and thereby subjecting themselves to lower oxygen conditions? The likeliest explanation is that there is a life-history gain sufficient to offset the harmful effect of low oxygen on growth and condition. If prey availability is greater in deeper water, then even if it is not sufficient to prevent the observed decline in condition, it may still be better than their condition would have been if they had maintained their previous shallower depth distribution. An explanation put forward by CHOL (and others) is that cod avoid predation by seals and cormorants by moving into deeper water. Predators would thereby be having an indirect effect – not eating the cod, but causing their growth and condition to decline. This explanation may be valid, but is hard to test. CHOL and others (e.g. Neunfeldt 2019, 2020) have proposed that observed decline in stomach fullness, energy intake and the resultant effects on growth and condition of small cod may be due to decline in benthic prey, but they cite no direct evidence of decline in benthos, therefore this remains an untested hypothesis. Neunfeldt 2020 argue that the decline of benthic prey in cod stomachs is evidence that the availability of benthos has declined, but this seems like circular reasoning. Direct evidence of declining populations of benthos would be more convincing, especially since our basic physiological knowledge and experimental results tell us that during current low oxygen conditions cod will eat less. Neunfeldt 2020 also argue that cod are able to avoid the negative effects of declining oxygen by making frequent (diel or shorter) vertical migrations into well-oxygenated water. If this were the case then it should undermine the distributional and otolith microchemical relationships between decline in oxygen and cod condition shown by CHOL. A full exploration of the evidence for vertical migration needs to take into account the changing diet and depth distribution of different life stages of cod (pelagic and settling juveniles, small benthic feeding cod, larger pelagic feeding cod) and also the estuarine hydrographic strucuture of the Baltic Sea, with a warmer, saline bottom layer separated from a cooler, fresher upper layer by a permanent halocline and seasonal stratification of the upper layer. Neunfeldt 2020 cite a study of otolith opacity (Hüssy, 2010)âĄă as showing that small cod migrate across thermal gradients, but the resolution of the otolith rings is insufficient to show that this is a regular, short term pattern of behaviour and vertical migration by benthic-feeding small cod that live on the seabed below the halocline would take them into colder water. It is only when they grow to over 25cm and begin to switch their diet to pelagic prey that small cod are caught well above the seabed, as shown by pelagic trawling (Figure 3c (Andersen, Lundgren, Neuenfeldt, & Beyer, 2017)âĄă) This by no means exhausts the list of unresolved questions and possible explanations of declining condition in cod, but probably takes us as far as is justified in the context of a review of CHOL. Minor editorial comments line 23 and 62 -The expansion of hypoxic areas has been quite rapid, but not exponential line 76 – make it clear that this explanation is inference and not based on evidence line 178 “these” presumably refers to “large fish” - better to say so.

Brander, K. (2020). Reduced growth in Baltic Sea cod may be due to mild hypoxia. ICES Journal of Marine Science, (December 2019), 2019–2021. https://doi.org/10.1093/icesjms/fsaa041 Casini, M., Käll, F., Hansson, M., Plikshs, M., Baranova, T., Karlsson, O., . . . Hjelm, J. (2016). Hypoxic areas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish predator. Royal Society Open Science, 3(10). https://doi.org/10.1098/rsos.160416 Chabot, D., & Dutil, J. D. (1999). Reduced growth of Atlantic cod in non-lethal hypoxic conditions. Journal of Fish Biology, 55, 472–491. Hüssy, K. (2010). Why is age determination of Baltic cod (Gadus morhua) so difficult? ICES Journal of Marine Science, 67(6), 1198–1205. https://doi.org/10.1093/icesjms/fsq023 Limburg, K. E., & Casini, M. (2019). Otolith chemistry indicates recent worsened Baltic cod condition is linked to hypoxia exposure. Biology Letters, 15(12), 20190352. https://doi.org/10.1098/rsbl.2019.0352 Neuenfeldt, S., Bartolino, V., Orio, A., Andersen, K. H., Andersen, N. G., Niiranen, S., . . . Casini, M. (2019). Feeding and growth of Atlantic cod (Gadus morhua L.) in the Eastern Baltic Sea under environmental change. https://doi.org/10.1093/icesjms/fsz224 Neuenfeldt, S. et al (2020) Response to Brander (2020) in press ICES Journal of Marine Science

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