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Reply

Reply to "Reduced growth in Baltic Sea cod may be due to mild hypoxia"—a comment to Neuenfeldt *et al.* (2020)

Neuenfeldt, S., Bartolino, V., Orio, A., Andersen, K. H., Andersen, N. G., Niiranen, S., Bergström, U., Ustups, D., Kulatska, N., and Casini, M.
Reply to "Reduced growth in Baltic Sea cod may be due to mild hypoxia"—a comment to Neuenfeldt *et al.* (2020). – ICES Journal of Marine Science, 77: 2006–2008;

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We thank Keith Brander (KB) for his interest in, and comments (Brander, 2020) on, our paper (Neuenfeldt et al.*, 2020). We agree with him that increased hypoxia has played a major role in the reduced growth of Eastern Baltic cod,* Gadus morhua, *especially during the last two decades, and we acknowledge this in our paper. We also agree with KB that the actual mechanisms remain to be fully disclosed (Brander, 2020).*

As KB correctly mentions (Brander, 2020), we (Neuenfeldt *et al.*, 2020) propose that the principal mechanism linking hypoxia and juvenile cod growth in the Eastern Baltic Sea is that increased extent of hypoxia has reduced the abundance of benthic prey suitable for post-settlement cod. We further propose that the growth reduction has resulted in a change in cod size distribution by an accumulation of smaller cod, which intensifies the competition for food in the benthivorous life stage and leads to a feedback loop that further reduces the growth. KB, on the other hand, argues that the observed changes in the oxygen environment alone may be sufficient to explain the decline in food uptake observed in our paper, because cod feed less when oxygen saturation is low (Chabot and Dutil, 1999). An implicit conclusion of KB's arguments is then that benthic prey does not necessarily have to be scarce, as assumed in our paper, because hypoxia itself may be limiting the food intake.

In this reply, we argue that the part of the benthic fauna preyed upon by cod has decreased, because this is important for our argument that small cod are food limited and hence increased density of smaller sizes due to decreased growth leads to the aforementioned feedback loop. Furthermore, we deal with the main assumption that KB bases his argument upon, namely that small cod may dwell in hypoxic waters to an extent that significantly reduces their ability to process the food. We argue that small cod probably are not subjected to a critical lack of oxygen that would decrease their physiological potential for consuming and processing food.

We argue that cod feeding level has declined because of a hypoxia-related decline in benthic prey species, assuming that *Saduria entomon* abundance has decreased in the hypoxic parts of the seabed of the Baltic Sea and that, especially for small cod, there is no other benthic species possibly substituting *S. entomon* in their diet. Evidence on abundance, biomass, or distribution trends for *S. entomon* is sparse. Karlson *et al.* (2019) found for the Baltic proper that *S. entomon* populations in the seabed of the open sea have declined. HELCOM's fact sheet on *S. entomon* states that "The loss of oxygen in the Baltic Sea bottoms has caused some declines in the population" (https://helcom.fi/media/red%20list%20species%20information%20sheet/HELCOM-Red-List-Saduria-entomon.pdf). The mass of *S. entomon* in the stomachs of both small cod and larger cod has decreased (Figure 1). The larger cod would have had the opportunity to reach *S. entomon* in hypoxic water, if it was there (Neuenfeldt *et al.*, 2009). The mass of "other prey" (i.e. not cod, clupeids, *Mysis mixta* and *S. entomon*) has increased only in the stomachs of cod >45 cm (Fig. 2 in Neuenfeldt *et al.*, 2020). It would be interesting to see if the increase in "other prey" at least partially was due to alternative benthos organisms, and if so, whether these potentially would be inedible for cod <45 cm. Nevertheless, we interpret the low biomass of *S. entomon* in the stomachs of cod of all sizes as a clear indication that this benthic isopod indeed has decreased in abundance in the distributional area of cod simultaneously with the increase in hypoxia after the mid-1990s (Fig. 7 in Neuenfeldt *et al.*, 2020) as explained in our discussion section. Moreover, the other prey type that declined in the cod stomachs was sprat, *Sprattus sprattus* (Figure 1), corresponding to a decline in sprat abundance in the area of cod distribution (Casini *et al.* 2016), and therefore it would be logical and coherent to suppose that also *S. entomon* declined in cod stomachs for a decrease in this resource.

Finally, the average amounts of herring (*Clupea harengus*) in the stomachs of cod <30 cm did not decrease, but variability between years increased (Figure 1). The amount of nekto-benthic *M. mixta* in the stomachs is much lower since 2008 (Figure 1). These observations would be difficult to explain, if mere exposure to hypoxia should have limited the food uptake of cod.

While hypoxia generally addresses oxygen saturation below 100%, oxygen saturation well below 100% is not critical for cod (Plante *et al.*, 1998; Chabot and Dutil, 1999) and Eastern Baltic cod >45 cm even dive down into oxygen saturations below 20% for a few hours at a time, probably in search of food

(Neuenfeldt *et al.*, 2009). Behrens *et al.* (2012) have shown experimentally that after such dives, there were no indications of an oxygen debt, implying that there were no indications of a negative effect on digestive capacity (Behrens *et al.*, 2012). Hence, on a short time scale (hours), cod >45 cm can cope with very low oxygen saturation and return to waters with sufficient oxygen to evacuate their stomachs, by swimming a few metres upwards in the stratified water column, without any effects on their feeding capability.

There is some indication that also smaller cod between 20 and 30 cm show this behaviour, although we agree with KB that there is no conclusive evidence. Acoustics measurements in the Bornholm Basin from March 2002 have shown that larger cod apart from the vertical feeding raids stay some metres above the bottom (Andersen *et al.*, 2017, Fig. 6b). This applies to small cod as well, according to cod target strength groups that are not shown in Andersen *et al.* (2017). Measurements from otoliths further support the hypothesis that 20–30 cm cod perform vertical migrations similar to >45 cm cod (Hüssy, 2010, Fig. 3). Here, the daily fluctuating levels of opacity during the growth season imply vertical migration in a thermal gradient. Since in the Baltic Sea the thermal gradient is often overlaying with the oxygen gradient, the observed opacity pattern implies varying oxygen environment, too.

Hence, both acoustics and otolith data indicate that also small cod perform vertical migration.

The vertical distance small cod would have to move to get from oxygen saturation below 28% (lethal as to Plante *et al.*, 1998) to oxygen saturation above 65% (not affecting growth according to Chabot and Dutil, 1999) is variable, but usually only few metres. For example, in observations described in Andersen *et al.* (2017), oxygen saturation at the bottom was 25%, while 3.5 m above bottom oxygen saturation was ≥65% and hence uncritical for food conversion and growth as experimentally deduced in Chabot and Dutil (1999).

Even if the small cod would not migrate vertically, the extrapolation of results from the experiment by Chabot and Dutil (1999) is a problematic point in the arguments of KB. Except for high temperatures well above the optimum, ∼15–16°C for cod (Andersen, 2012), the limitation of maximum sustained feeding rate at high oxygen levels is due to the intrinsic physiological performance of the fish rather than the actual content of oxygen at high saturation levels (e.g. Buentello *et al.*, 2000; Remen *et al.*, 2016). In the Baltic Sea, cod experience temperatures within the range of 6.23 ± 2.21°C (Righton *et al.*, 2010). Hence, the maximum sustained food consumption rate would not be higher in the Baltic Sea because oxygen content at saturation in the colder and less saline water is higher as compared to the conditions of 10°C and salinity of 28 in the experiments of Chabot and Dutil (1999).

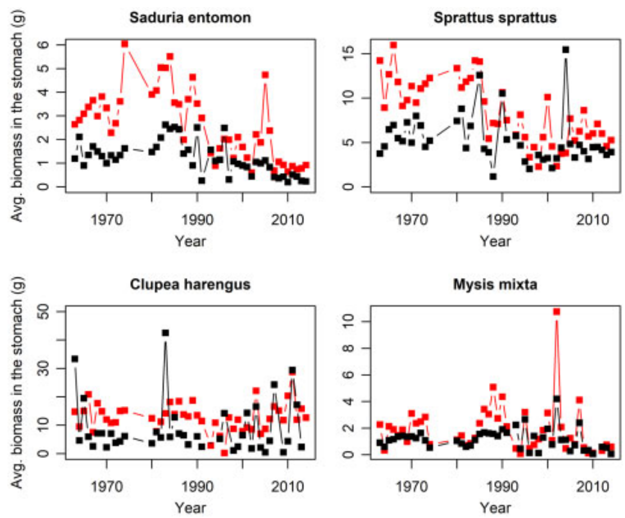

Figure 1. Stomach contents over time in *Gadus morhua* by average mass, given that the specific prey is found in the stomach. Note that the listed prey groups do not comprise the complete cod diet. The time series are displayed separately for 21–30 cm cod (dark closed dots) and 31–45 cm cod (light closed dots).

Therefore, the relationship between oxygen saturation and maximum feeding rate estimated by Chabot and Dutil (1999) cannot be extrapolated to 100% oxygen saturation in the Baltic Sea for the provision of 40 g/d maximum feeding rate in the Baltic Sea as compared to 32.6 g/d by Chabot and Dutil (for cod with an initial size of 44.1 ± 3.1 cm total length; 1999). On the contrary, the lower temperatures in the Baltic Sea imply lower physiological rates including metabolic expenses and maximum feeding rates. The decrease in feeding level to 68% of the maximum sustained feeding rate due to low O_2 concentrations of 4.73 ml/l as suggested by KB is therefore not realistic and probably heavily overestimated. We would also like to clarify that, in Limburg and Casini (2019), the analyses of the effects of low-oxygen exposure (indexed by Mn/Mg in otoliths) on cod condition were all in relative terms and not related to a specific threshold of 2 ml/l.

We agree with KB that, given the problems the small cod apparently are facing currently, their behaviour and feeding biology should be a topic of high priority. Further dietary analyses based on the abundantly available cod stomach data, as well as time series of the benthos that is consumed by small cod, would be desirable. We also agree that it would be valuable to have better information on the behaviour of small cod. Further empirical knowledge on the direct effects of hypoxia on feeding is needed from experimental work, as hypoxia may be a factor contributing to lowering the ingestion rates, which in the future can be expected to be more severe as a consequence of increasing temperatures. We furthermore think that targeted field observations using hydroacoustics and data storage tags are needed to answer the questions on individual behaviour, which form the basis to disentangling the effects of hypoxia and benthic food availability on the poor condition and slow growth of Eastern Baltic cod.

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