# **Introduction**

Global warming and nutrient enrichment have contributed to a reduction in dissolved oxygen levels and the expansion of dead zones in coastal marine ecosystems worldwide (Diaz, 2001; Breitburg, 2002; Diaz and Rosenberg, 2008; Carstensen *et al.*, 2014). Extreme hypoxia (low dissolved oxygen) leads to a direct loss of fauna from increased mortality (Diaz and Rosenberg, 1995; Sampaio *et al.*, 2021), and causes habitat compression, which forces organisms to occupy sub-optimal habitats and suffer effects of density dependence (Diaz and Rosenberg, 2008; Orio *et al.*, 2019; Gogina *et al.*, 2020). Even milder hypoxia can alter individual physiology by imposing metabolic constraints on organisms (Kramer, 1987; Chabot and Dutil, 1999; Claireaux *et al.*, 2000; Hrycik *et al.*, 2017; Sampaio *et al.*, 2021). Hence, it is critical to understand the impacts of global deoxygenation on the fitness of aquatic organisms.

Experimental studies show that fishes lower their food intake rates during hypoxic conditions. This is likely to avoid overshooting the oxygen budget when processing food, which can lead to declines in growth rates (Chabot and Dutil, 1999; Thetmeyer *et al.*, 1999; Pichavant *et al.*, 2001) and body condition. The body condition describes the “plumpness” of an individual and reflects accumulated energy reserves (Beverton and Holt, 1957; Ricker, 1975; Nash *et al.*, 2006). Hence, condition is often positively associated with fitness (Morgan *et al.*, 2010; Thorson, 2015), and individuals with high condition have greater reproductive success (Hislop *et al.*, 1978; Marshall and Frank, 1999). Poor condition increases the likelihood of skipped spawning (Jørgensen *et al.*, 2006; Mion *et al.*, 2018) and can lower chances of survival (Dutil and Lambert, 2000; Casini *et al.*, 2016b). Therefore, it is important to study the effects of the ongoing de-oxygenation of marine coastal areas on body condition of fishes.

Despite the concurrent de-oxygenation of coastal ecosystems and the known effects from experimental studies, support for effects of dissolved oxygen on fish condition in field conditions is limited (Chabot and Dutil, 1999). For instance, (Cavraro *et al.*, 2019) found no significant effect of dissolved oxygen on the body condition in the sand smelt *Atherina boyeri* in the Mediterranean, while expansion of hypoxic zones has been linked to the decline in the body condition of Atlantic cod (*Gadus morhua*) in the Baltic Sea (Casini *et al.*, 2016a, 2021; Limburg and Casini, 2019). The Baltic Sea constitutes an interesting case study for studying the impacts of hypoxia, because it is a semi-enclosed brackish arm of the Atlantic Ocean that contains the largest anthropogenically induced hypoxic area in the world (Carstensen *et al.*, 2014). Factors that make the Baltic Sea exposed to hypoxia is the irregular inflows of saline and oxygenated water from the North Sea together with a long residence time (25-30 years) (Carstensen *et al.*, 2014).

While variables related to the extent of hypoxic areas correlate with a decline in body condition, the story in the Baltic Sea is more complicated than that. In fact, several interlinked density-dependent hypotheses have been put forward to explain the negative trend in body condition and growth starting after the collapse of the Eastern Baltic cod stock in the early 1990’s and the following regime shift (Casini *et al.*, 2009; Möllmann *et al.*, 2009; Gårdmark *et al.*, 2015). These include increased intra- and intraspecific competition for benthic prey, such as the isopod *Saduria entomon*, and lack of pelagic prey caused by changes in the spatial distribution of sprat (*Sprattus sprattus*). The former has been linked to fishery-induced size truncation of the cod stock increasing intraspecific competition (Svedäng and Hornborg, 2014), and a hypoxia-driven spatial range contraction causing an increased spatial overlap with the potential competitor European flounder (*Platichtys flesus*) (Casini *et al.*, 2016a; Orio *et al.*, 2019; Neuenfeldt *et al.*, 2020). Hypoxia has also been suggested to lower the condition of cod directly via physiological stress, including increased ventilation costs and lower food intake rates (Limburg and Casini, 2019; Brander, 2020).

The association between these covariates and body condition has previously been analysed using average values over large spatial scales (basin level), despite that these hypothesised density-dependent processes operate on a finer scale. Modelling body condition on a fine scale however leads to spatially residual patterns, as the processes governing condition (local environmental conditions and food availability) are spatially and temporally correlated. Only relatively recently have spatiotemporal models been applied to study variation in condition (Thorson, 2015; Grüss *et al.*, 2020). In these studies, spatially correlated residual variation was accounted for with spatial random effects through Gaussian random fields in a GLMM framework. This approach to model spatiotemporal data is an increasingly popular method for explicitly accounting for spatial and spatiotemporal variation – likely due to its ability to improve predictions on range shifts (Thorson *et al.*, 2015a) as well as estimates of density (Thorson *et al.*, 2015b), and its availability in standard open source software such as the R-packages INLA, VAST (Thorson, 2019) or sdmTMB (Anderson and Ward, 2019; Anderson *et al.*, 2021; Barnett *et al.*, 2021). In the first such application to body condition, (Thorson, 2015) found that spatial processes (spatial variation in condition that is constant in time) and spatiotemporal processes (spatial variation that varies among years, respectively) explained more variation than density and temperature covariates in the California current ecosystem. Studies like these reveal the importance of accounting for spatial and spatiotemporal variation in condition for clarifying the sources of variation in body condition in relation to unmeasured variation and independent variables.

In this study, we apply spatiotemporal predictive-process GLMMs to characterize spatiotemporal variation in body condition of Eastern Baltic cod. We use data from the Baltic International Trawl Survey between 1991-2020, which corresponds to a period of initially high but deteriorating condition (Casini *et al.*, 2016a). We then seek to (1) identify which set of covariates (density of flounder, cod, availability of pelagic prey or oxygen concentration) provide a parsimonious fit to weight-length and (2) estimate the variation explained by these covariates and contrast that to variation explained by spatial and spatiotemporal variation. + End with a fitting concluding sentence