



Individual variation in aerobic scope affects modeled vertical foraging migration in Atlantic cod *Gadus morhua*, but only in moderate hypoxia

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ABSTRACT: Vertical migration is the most widespread migration in the aquatic world, yet the mechanisms limiting the extent of this behavior are largely unknown. In the Baltic Sea, some Atlantic cod *Gadus morhua* perform vertical foraging migrations into severely hypoxic demersal zones where aerobic metabolism is insufficient to cover energy requirements. After foraging, the fish return to better oxygenated waters for physiological recovery and digestion. To test the influence of phenotypic variation in aerobic scope (AS; the difference between the maximum and the minimum metabolic rate) on the capacity to migrate into severely hypoxic zones, we incorporated AS into a state-dependent individual-based model simulating vertical foraging migrations of *G. morhua*. We found little effect of individual variation in AS on the capacity for vertical migration when the zone used for physiological recovery was normoxic. In contrast, when there was moderate hypoxia (30% air saturation, O_{2sat}) in the zone used for physiological recovery, the high AS phenotype had a clear advantage because it could forage 3–4 times longer in the severely hypoxic (16% O_{2sat} , i.e. below the threshold for aerobic metabolism of the species) demersal zone compared to the low AS phenotype. Thus, phenotypic variation in AS is only important when there is moderate hypoxia in the zone used for physiological recovery, suggesting that the influence of AS variation on the capacity for vertical migration is context dependent. We propose that elevated AS may be evolutionarily favorable when hypoxia prevails in the water column.

KEY WORDS: Physiology · Behavior · Baltic Sea · Bioenergetics · Aerobic scope · Hypoxia · *Gadus morhua* · Individual-based model

INTRODUCTION

Vertical migration is the most widespread migration in the aquatic world, occurring throughout the oceans and lakes and common to both vertebrates and invertebrates (Hinch et al. 2006), yet the mechanisms limiting the extent of this behavior remain uncertain. In the Baltic Sea, Atlantic cod *Gadus morhua* inhabit areas with combined halo-, thermo- and oxyclines (Matthäus & Franck 1992). Interestingly, data from data-storage tags (DSTs) employed on individ-

ual *G. morhua* have revealed that some fish perform vertical migrations into severely hypoxic demersal zones, presumably to forage (Neuenfeldt et al. 2009). In this environment, ambient oxygen levels are below the critical level for the species, and as the aerobic metabolism is insufficient to cover energy requirements, the fish will build up an oxygen debt (Schurmann & Steffensen 1997, Plambech et al. 2013). Following the vertical foraging migration, physiological recovery and digestion occur higher in the water column, where there is normoxia or moderate

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hypoxia. Here, *G. morhua* face a trade-off between favorable temperature and oxygen for digestion, while low salinity constrains the fish closer to the water surface (Schaber et al. 2009, Andersen et al. 2017). Indeed, these observations suggest that the physiological capacity of the individual may influence the temporal extent of vertical foraging migrations.

Emerging evidence indicates that individual aerobic scope (AS; the difference between minimal and maximal rate of aerobic metabolism) correlates with a suite of fitness-related traits in fish (Killen et al. 2012, Auer et al. 2015), highlighting the importance of AS in relation to individual performance. Considering that all aerobically fueled processes above minimal metabolic requirements compete for the available AS, we hypothesized that phenotypic variation in AS influences the temporal extent of foraging migrations into severely hypoxic demersal zones. The hypothesis was motivated by recent modeling studies using fish AS to predict (1) optimal life histories and behaviors at different temperatures (Holt & Jørgensen 2015) and (2) species distributions and responses to changes in climate (Marras et al. 2015, McKenzie et al. 2016) and similar abiotic variables (Behrens et al. 2017). Furthermore, Del Rave & Weng (2015) developed an aerobic scope-based habitat suitability model to forecast the response of marine fishes to simultaneous ocean acidification, warming and deoxygenation, including interactions between all 3 stressors.

To test the hypothesis that phenotypic variation in AS may influence the temporal extent of foraging migrations into severely hypoxic demersal zones, we integrated AS variation into an individual-based model (IBM) parameterized with literature-derived equations describing the physiology of *G. morhua*. The model assumes that vertical migration behavior is state-dependent (i.e. based on stomach fullness). By running the model for a typical range of AS phenotypes, we used the model to address 3 questions: (1) Is phenotypic variation in AS affecting foraging time in severely hypoxic demersal zones? (2) Is oxygen availability in the upper zone, where physiological recovery and digestion occur, influencing foraging time in the severely hypoxic demersal zone? (3) Are high and low AS phenotypes affected equally by the oxygen availability in the upper zone?

MATERIALS AND METHODS

To address the hypothesis that phenotypic variation in AS influences the temporal extent of foraging migrations into severely hypoxic demersal zones, we

developed an IBM for adult *Gadus morhua* foraging in a vertically stratified water column. Model configuration and parameterization were based on published experiments and standards for bioenergetics models (all equations and parameter values are explicitly explained in Table 1, including references; see Hanson et al. 1997 regarding bioenergetic models in general). The vertical foraging migrations simulated in the model covered transitions between an upper normoxic or moderately hypoxic (30, 40, 50 or 100% air saturation, O_{2sat}) recovery zone with no food and a severely hypoxic demersal foraging zone with 16% O_{2sat} , which is below the oxygen threshold (S_{crit}) for aerobic metabolism of *G. morhua* under most temperature conditions (Eq. 3c in Table 1) (Schurmann & Steffensen 1997). The model was designed to produce the average daily foraging time ($h\ d^{-1}$) integrated over a period of 20 d (i.e. number of hours spent foraging in the severely hypoxic demersal zone divided by 20). Foraging activity in fishes is often influenced by stomach fullness. This has been shown both in behavior optimization models (Kirby et al. 2000), in laboratory experiments (Salvanes & Hart 1998) and in field studies on gadoids (Rindorf 2002). Therefore, the decision to make a transition between the normoxic or moderately hypoxic recovery zone and the severely hypoxic demersal zone was based on the individual stomach fullness in each time step (t), using predefined stomach fullness trigger levels. Stomach fullness (g) was derived from Eq. (4c) (Table 1) based on information about the amount of food entering and exiting the stomach (Eq. 4b,c). Stomach evacuation in a given time step was derived from the energetic cost of digesting a meal (the rate of specific dynamic action, R_{SDA} [$J\ t^{-1}$]) (Eq. 2c) and free AS (F_t [$J\ t^{-1}$], Eq. 1a). AS is defined as the maximum metabolic rate (R_{max} [$J\ t^{-1}$], Eq. 1b) minus the standard metabolic rate (R_S [$J\ t^{-1}$], Eq. 2a), where R_{max} is a function of both temperature and ambient oxygen conditions (Claireaux et al. 2000, Tirsgaard et al. 2015). As a result, F_t was modeled as AS minus the cost of swimming (R_A [$J\ t^{-1}$], Eq. 2b) and the cost of eliminating any oxygen debt (D [J]) (R_{ED} , Eq. 3b), where oxygen debt is also known as excess post-hypoxic oxygen consumption (Svendsen et al. 2012, Genz et al. 2013, Plambech et al. 2013). Note that R_{SDA} was not explicitly used in Eq. (1a) to calculate F_t . This is because whenever F_t was insufficient to accommodate R_{SDA} associated with the maximum rate of digestion (i.e. calculated in Eq. 2c), a feedback loop in the model downscaled R_{SDA} to exactly match F_t , which in turn led to a reduced stomach evacuation in Eq. (4a,b). Oxygen debt (D) accumulated when-

Table 1. Summary of the individual-based bioenergetics model (IBM) of an adult Atlantic cod *Gadus morhua*. All rate equations in the table apply to standardized 1 h time steps, as this is how data from experiments are commonly reported. However, in the present application of the model, time steps (t) of 0.2 h were used to match the resolution of data recovered from the data-storage tag (DST; see 'Materials and methods' for further details). Hence, all rate values (i.e. $J t^{-1}$) were effectively divided by 5. The rate of food acquisition (ϵ) in the severely hypoxic demersal zone was fixed at $10 g h^{-1}$, and initiation of foraging was triggered when gut fullness reached 5% of maximum gut capacity (δ). Return to the normoxic or moderately hypoxic upper zone for physiological recovery and digestion was triggered at 50% of δ

Eq. no.	Explanation	Equation	Description of parameters
1a,b	<p>F_t = free aerobic scope ($J t^{-1}$) available in a given time step for energy consuming activities such as digesting food</p> <p>R_{max} = maximum metabolic rate ($J t^{-1}$)</p>	$F_t = R_{max} - R_S - R_A - R_{ED}$ $R_{max} = (17.29 \times T_t^{-0.015 \times T_t + 1.06} + 30) \times (1 - e^{-0.035 \times O_{2sat} + 0.34})$ <p>(Claireaux et al. 2000)</p>	<p>R_S is the standard metabolic rate (modeled in Eq. 2a). R_A is the metabolic cost of swimming (modeled in Eq. 2b). R_{ED} is the cost of repaying any oxygen debt per time unit ($J t^{-1}$) (modeled in Eq. 3a).</p> <p>O_{2sat} is the air saturation (%) in time step t in the ambient environment.</p>
2a,b,c	<p>R_S = standard metabolic rate ($J t^{-1}$) (i.e. metabolic rate of a resting fish)</p> <p>R_A = metabolic cost of swimming ($J t^{-1}$)</p> <p>R_{SDA} = metabolic cost of digesting consumed food ($J t^{-1}$) (i.e. related to specific dynamic action)</p>	$R_S = (0.0687 \times e^{0.06 \times T_t}) \times (W^{-0.00089 \times T_t^2 + 0.02 \times T_t + 0.79}) \times 14$ <p>(Tirsgaard et al. 2015)</p> $R_A = \left(\frac{W}{1000}\right) \times (24.4 \times v + 4.1) \times 14$ <p>(Melzner et al. 2009)</p> $R_{SDA} = \rho \times M_t \times \alpha$	<p>W = fish weight (g). The value 14 is the caloric conversion factor that takes the experimental respiratory metric, mg O_2, and converts it to joules.</p> <p>v = swimming speed (0.2 body lengths [bl] s^{-1}; Schurmann & Steffensen 1994). ρ = proportion of ingested energy that is used to support processes related to digestion ($\rho = 0.15$) (Kerr 1982). M_t = amount of food evacuated in a given time step (g) (see Eq. 4a). T_t = ambient temperature in time step t (based on data from DSTs used by Neuenfeldt et al. 2009; $T = 5^\circ C$ in the hypoxic zone and $6^\circ C$ in the recovery zone). α = energy density of food ($J g^{-1}$). We used $\alpha = 4000 J g^{-1}$, which is applicable to both fish and energy-rich invertebrates.</p>
3a,b,c	<p>R_{ED} = cost of eliminating oxygen debt ($J t^{-1}$)</p> <p>D_t = oxygen debt in a given time step (J)</p> <p>S_{crit} = critical O_{2sat} level (% air saturation). Below S_{crit} metabolic processes run partly anaerobically and oxygen debt (D) builds up</p>	$R_{ED} = \begin{cases} \text{if } (O_{2sat} > S_{crit}) \rightarrow \\ \gamma_1 \times D_t \\ \text{if } (O_{2sat} \leq S_{crit}) \rightarrow \\ 0 \end{cases}$ $D_t = \begin{cases} \text{if } [O_{2sat} > (S_{crit})] \rightarrow \\ D_{t-1} - R_{ED} \\ \text{if } [O_{2sat} \leq (S_{crit})] \rightarrow \\ D_{t-1} + [\gamma_2 \times (R_S + R_A)] \end{cases}$ $S_{crit} = 1.38 \times T_t + 9.53$ <p>(Schurmann & Steffensen 1997)</p>	<p>γ_1 is a parameter that defines the fraction of the oxygen debt that is eliminated at each time step (if an oxygen debt exists), whenever environmental oxygen levels are above S_{crit}. Here we used $\gamma_1 = 0.25$ (adapted from Plambech et al. 2013). γ_2 = rate at which oxygen debt builds up when $O_{2sat} < S_{crit}$ given as a proportion of R_S. Here we used $\gamma_2 = 0.5$ (adapted from Plambech et al. 2013). Lastly, we assumed that swimming speed was $1 bl s^{-1}$ during the vertical foraging migrations.</p>
4a,b,c	<p>M_t = amount of food evacuated (g) in time step t after accounting for limitation induced by F_t</p> <p>M_t^* = potential amount evacuated (g) from stomach at time step t</p> <p>m_t = stomach fullness (g) at the beginning of time step t</p>	$M_t = \begin{cases} \text{if } (R_{SDA} < F_t) \rightarrow \\ M_t^* \\ \text{if } (R_{SDA} \geq F_t) \rightarrow \\ M_t^* \times \left(\frac{F_t}{R_{SDA}}\right) \end{cases}$ $M_t^* = -(\sigma \times L^{1.3}) \times (e^{0.083 \times T_t}) \times \left(\frac{\alpha}{10^3}\right)^{-0.85} \times \sqrt{m_t}$ <p>(Andersen 2012)</p> $m_t = \begin{cases} \text{if } (m_{t-1} - M_{t-1} + \epsilon_{t-1} > \delta) \rightarrow \\ \beta \\ \text{if } (m_{t-1} - M_{t-1} + \epsilon_{t-1} \leq \delta) \rightarrow \\ m_{t-1} - M_{t-1} + \epsilon_{t-1} \end{cases}$	<p>δ = maximum gut capacity (g) = 5.5% of fish weight^a. ϵ = food acquisition rate ($g h^{-1}$). α = energy density of food ($J g^{-1}$). σ = basal stomach evacuation rate coefficient. We used $\sigma = 0.002$, which represents a value between invertebrates and fish (Andersen 2012). L = fish length (m).</p> <p>^a5.5% of fish weight is derived from our own compilation and analysis of stomach data from 108 000 <i>G. morhua</i></p>

ever oxygen levels dropped below S_{crit} (i.e. when the fish was in the severely hypoxic demersal foraging zone). The accumulation rate was equal to R_S plus R_A (Schurmann & Steffensen 1997, Plambech et al. 2013) and was gradually eliminated upon return to the recovery zone at a specific rate (R_{ED} [$J\ h^{-1}$], Eq. 3a) derived directly from experiments by Plambech et al. (2013).

To observe the different physiological dynamics that the model kept track of during the simulations, we forced the model with temperatures and oxygen levels recovered from a DST tag revealing a typical vertical migration pattern (derived from data in Neuenfeldt et al. 2009) (Fig. 1).

The final model was thereafter applied to different oxygen levels in the upper recovery zone, from moderate hypoxia to normoxia (30, 40, 50 or 100% O_{2sat}),

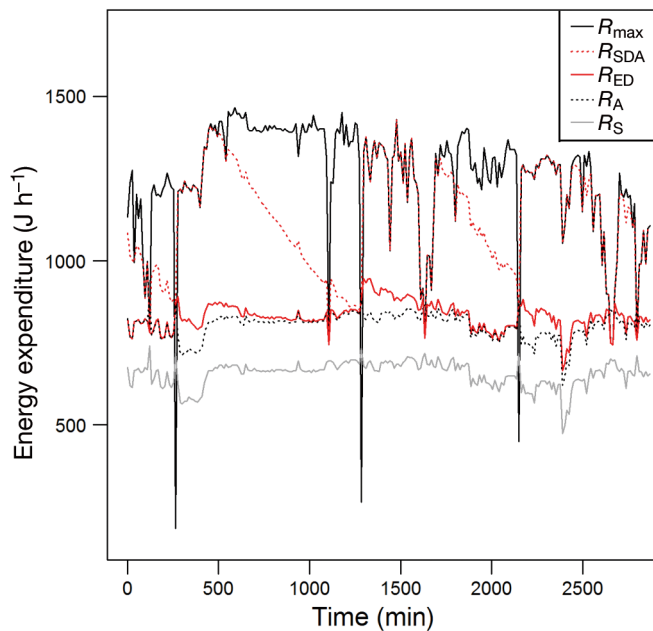


Fig. 1. Energy expenditures ($J\ h^{-1}$) in an Atlantic cod *Gadus morhua* performing vertical migrations in the Baltic Sea. Shown are stacked data tracks of maximum metabolic rate (R_{max} ; black), cost of eliminating specific dynamic action (R_{SDA} ; red dotted), cost of eliminating oxygen debt (R_{ED} ; red), metabolic cost of swimming (R_A ; black dotted) and standard metabolic rate (R_S ; grey). Integrating over time, free aerobic scope is defined as the difference between R_{max} and R_{SDA} . Environmental forcing (i.e. temperature and oxygen level) follows recordings by a typical data storage tag recovered from a *G. morhua* in the Baltic Sea (Neuenfeldt et al. 2009). The fish migrated into the severely hypoxia demersal zone 3 times within a 40 h period (i.e. when the R_{max} graph drops below $500\ J\ h^{-1}$). In the model, the fish was foraging during each vertical migration into the severely hypoxic demersal zone, causing R_{SDA} and R_{ED} responses. Details of the model are provided in Table 1

and a continuum of different AS phenotypes, ranging from 80 to 120% of the species average (Tirsgaard et al. 2015), reflecting the typical range of phenotypic variation in AS (Norin et al. 2016). Both types of adjustments influenced mainly Eq. (1b) and involved varying the O_{2sat} value (30, 40, 50 or 100%) and employing different multiplication factors on R_{max} , ranging from 0.8 to 1.2. The temperature was kept the same in all final simulations ($6^\circ C$ in the upper normoxic/moderately hypoxic recovery zone and $5^\circ C$ in the severely hypoxic demersal zone). The chosen temperatures were derived from the DST tag retrieved from a *G. morhua* in the Bornholm Basin (Neuenfeldt et al. 2009). Fish length and weight were kept constant at 0.5 m and 1.2 kg, where 1.2 kg corresponds to the average weight of a 0.50 m long *G. morhua*, which was the size of fish used in the DST study from which we derived information for the model (Neuenfeldt et al. 2009). The rate of food acquisition (ϵ) and lower and upper stomach fullness trigger levels, determining when the fish would transition between the upper normoxic/moderately hypoxic recovery zone and the severely hypoxic demersal foraging zone, were adjusted to match consumption rates observed in the Bornholm Basin (Neuenfeldt et al. 2009) (feeding rate was $10\ g\ h^{-1}$, and the lower and upper trigger values were 5% and 50% of the maximum gut capacity [δ], respectively). To examine the sensitivity of our conclusions to the choice of food acquisition rate (ϵ) and trigger levels, model simulations were repeated with ϵ adjusted to 8 and $12\ g\ h^{-1}$, respectively (i.e. $\pm 20\%$ of the observed feeding rate). Note that increasing ϵ produces the same effect on the model output as decreasing the upper trigger level. Hence, we only varied feeding rate in the sensitivity analysis presented here.

RESULTS

When R_{SDA} and R_{ED} occurred in normoxia (i.e. 100% O_{2sat}), the mean daily foraging time in severe hypoxia was largely unaffected by phenotypic variation in AS and varying between 1.19 and 1.28 h (Fig. 2; green line). In contrast, for the high AS phenotype, the foraging time was reduced by 16% (i.e. to 1.07 h) when R_{SDA} and R_{ED} occurred in 30% O_{2sat} instead of normoxia, whereas the foraging time of the low AS phenotype was reduced by $\sim 79\%$ (i.e. to 0.25 h) (Fig. 2; green line versus red line) in 30% O_{2sat} . Thus, compared to the low AS phenotype, the high AS phenotype had the physiological capacity to forage 3–4 times longer when physiological recovery

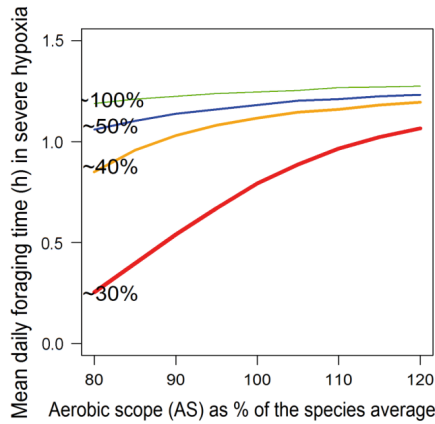


Fig. 2. Mean daily foraging time in severe hypoxia as a function of aerobic scope (AS; the difference between the maximum and the standard metabolic rate, R_{\max} and R_s , respectively) and oxygen levels in the upper zone of the water column where physiological recovery and digestion occur. Model details are provided in Table 1. Phenotypic variation in AS ranged between 80 and 120% of the species average (Tirsgaard et al. 2015). Oxygen levels in the upper zone of the water column ranged from 30% $O_{2\text{sat}}$ (red line) to 100% $O_{2\text{sat}}$ (green line). Oxygen levels between 30 and 50% $O_{2\text{sat}}$ are considered moderate hypoxia and 100% is normoxia

occurred in moderate hypoxia (30% $O_{2\text{sat}}$). The average AS phenotype was intermediate in the capacity to forage in the severely hypoxic demersal zone, with the foraging time reduced by ~40% when R_{SDA} and R_{ED} occurred in 30% $O_{2\text{sat}}$ instead of normoxia (Fig. 2; green line versus red line). At intermediate levels of moderate hypoxia (40–50% $O_{2\text{sat}}$) in the upper zone, the foraging times also decreased with declining AS, but the effects were much less pronounced (Fig. 2; green line versus orange or blue lines, respectively). Importantly, the results were largely insensitive to

the choice of feeding, i.e. the relative difference in performance between the high and the low AS fish remained when feeding rate varied between 8 and 12 g h^{-1} (Fig. 3), corresponding to $\pm 20\%$ of the observed feeding rate used in the model.

DISCUSSION

Our data suggest that phenotypic variation in AS plays a minor role in relation to vertical migration and foraging time in severe hypoxia when *Gadus morhua* return to recover and digest in normoxia. In contrast, when the fish return to moderate hypoxia upon foraging in severe hypoxia, high AS phenotypes have a clear advantage because they have the physiological capacity to forage 3–4 times longer in severely hypoxic demersal zones compared to low AS phenotypes. Consumption rate did not affect these relationships. These findings suggest that individual variation in AS may influence vertical migrations across oxygen gradients; however, the observation that high AS is only advantageous under sub-optimal conditions (i.e. moderate hypoxia in the recovery zone) is not immediately intuitive, highlighting the importance of modeling studies to reveal context dependency in fitness advantages of superior physiology. Notably, when the fish was allowed to return to normoxia to recover and digest, its physiological capacity for foraging in severe hypoxia (between 1.19 and 1.28 h, depending on AS phenotype) corresponds well with actual field observations derived from individually DST-tagged *G. morhua* (Neuenfeldt et al. 2009), indicating a degree of realism in our model.

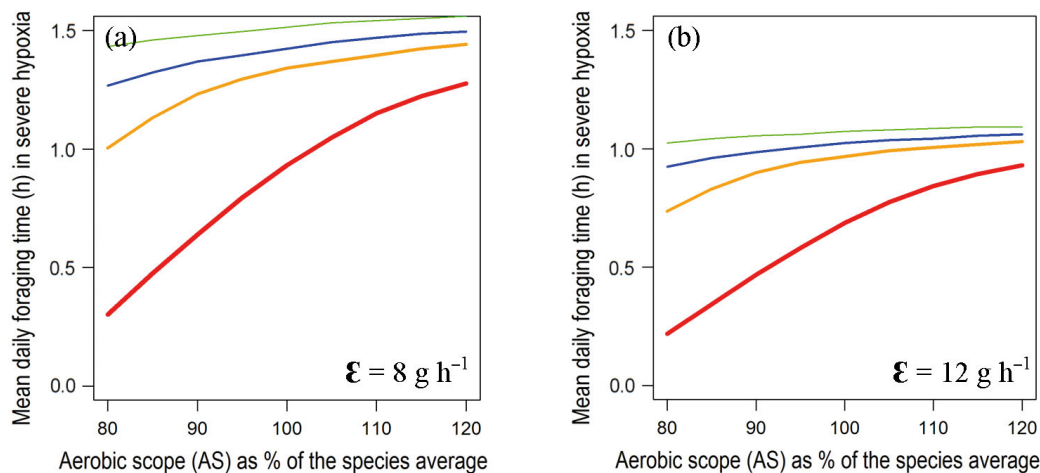


Fig. 3. Sensitivity of the model to the choice of feeding rate. Model configurations corresponded to the configurations used in Fig. 2, except for the food rate acquisition rate (ϵ), which enters the model in Eq. (4c) in Table 1. (a) $\epsilon = 8 \text{ g h}^{-1}$, (b) $\epsilon = 12 \text{ g h}^{-1}$

The phenotypic variation in individual AS may reflect both gill and cardiac performances (Wilson et al. 1994, Claireaux et al. 2005, Eliason et al. 2011, Casselman et al. 2012, Rosewarne et al. 2014, Hess et al. 2017). Moreover, high AS may also relate to higher hematocrit levels (with more erythrocytes enhancing the blood oxygen-carrying capacity) as observed in *G. morhua* with hemoglobin genotype HbI-2/2 (reviewed by Ross et al. 2013). Interestingly, only some Baltic *G. morhua* undertake brief foraging migrations into the severely hypoxic bottom waters (Neuenfeldt et al. 2009). Whether it is the fish possessing HbI-2/2 should be investigated in the future, not least considering that this genotype presumably exhibits superior oxygen transport capabilities under hypoxic conditions (Ross et al. 2013). Nevertheless, the mechanisms allowing for a higher AS may entail an additional cost for the high AS fish, included in the R_S . In a recent study, elevated R_{max} and AS were associated with elevated R_S across a broad interspecific comparison (Killen et al. 2016). This would suggest an additional energetic cost associated with elevated AS (the cost of a higher R_S). However, whether an elevated R_S is a prerequisite for elevated AS in intraspecific comparisons remains less clear. For example, Auer et al. (2015) did not identify a relationship between R_S and AS in brown trout *Salmo trutta*, indicating no or limited additional energetic costs of having a higher AS. Whether R_S and AS are correlated positively in *G. morhua* remains unclear, warranting further studies.

This study not only provides novel findings on *G. morhua*, but also presents a mechanistic modeling framework for future studies. The model can be adapted to many other aquatic organisms facing the challenges of stratified environments, provided that sufficient energetic and behavioral information exists to ensure solid model parameterization. Using the model framework, effects of intraspecific variation in traits besides AS (e.g. digestive capacity and S_{crit}) on other performance measures could be tested.

In the present study, we used fish of 1.2 kg, corresponding to the average weight of a 50 cm *G. morhua*, which was the body size of the fish used in the DST study from which we derived information for the model. Preliminary model runs with fish sizes between 600 g and 2.5 kg (i.e. various sizes of adult *G. morhua*) did not alter the results from the model. It is uncertain if juvenile conspecifics undertake comparable vertical migrations, and we did not test the model with sizes of fish corresponding to juvenile life stages. However, even though the magnitude of AS may differ between life stages in *G. morhua* and

other fish species (Killen et al. 2007, Tirsgaard et al. 2015), we have no reason to believe that intraspecific variance in AS would be found only in certain size groups of fish.

Consistent with our findings, laboratory studies on snapper (silver seabream *Pagrus auratus*) have shown that low AS phenotypes exhibit reduced hypoxia tolerance and are more likely to avoid severe hypoxia (Cook et al. 2011), highlighting the role of AS in terms of behavioral decision making. Moreover, Herbert et al. (2011) also supported our findings by demonstrating that *G. morhua* are more prone to spend time in severe hypoxia when provided access to a normoxic refuge.

Our data are consistent with the conjecture that fitness-related advantages of various metabolic phenotypes may be context dependent (Norin et al. 2016). For example, the optimal combination of R_S and AS for somatic growth may depend on food availability (Auer et al. 2015). Adding environmental variation to the context dependency, we found that high AS phenotypes may have a foraging advantage when moderate hypoxia prevails in the upper zone where physiological recovery and digestion occur. Importantly, the advantage is eliminated when the upper zone is normoxic. The cause-effect explanation for enhanced foraging performance of high AS fish is found in the recovery phase. More specifically, even though the AS of all fish is reduced in moderate hypoxia (Claireaux et al. 2000, Svendsen et al. 2012), the AS of high AS fish is still proportionally larger, allowing high AS fish to recover faster from the oxygen debt and complete R_{SDA} quicker as compared to low AS fish. Thus, the enhanced foraging performance of high AS fish is explained by faster recovery and completion of R_{SDA} that allow the high AS fish to engage in another foraging excursion into severe hypoxia after a shorter time span than the low AS fish.

In the Baltic Sea, *G. morhua* occur in highly stratified areas where even small vertical movements often result in changes in oxygen contents (Neuenfeldt et al. 2009). Dissolved oxygen concentration not only sets the lower distribution limits for *G. morhua*, but the fish also face a trade-off between favorable temperature and oxygen for digestion, causing an accumulation of fish at depths between 55 and 65 m within the oxy- and thermocline (Andersen et al. 2017). Here, *G. morhua* experience oxygen contents ranging between 25 and 80% O_{2sat} (increasing toward the surface). The upper distribution is further constrained by low salinities, forcing the fish to parts of the water column where oxygen content is re-

duced (Schaber et al. 2009). Over the past 2 decades, the spatial extent of hypoxic zones in the Baltic Sea has increased 5-fold (Carstensen et al. 2014), and on a global scale, oceanic oxygen content is also decreasing (Schmidtko et al. 2017). While these changes are likely to have severe ecosystem effects, predicting the direct deoxygenation-induced changes on ecosystems requires data that are derived from individual organisms, which can then be scaled to communities, food webs and fish populations (Breitburg et al. 2018). We propose that the high AS phenotypes will have an advantage in a future, more hypoxic water column, because this phenotype exhibits faster recovery from the oxygen debt and quicker completion of the R_{SDA} than low AS fish. The high AS phenotype allows increased frequency of foraging excursions into severely hypoxic bottom waters and thus provides better access to needed food resources.

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