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Modeling the impact of hypoxia on the energy budget of Atlantic cod in two populations of the Gulf of Saint-Lawrence, Canada

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ABSTRACT

Like many marine species around the globe, several stocks of Atlantic cod (*Gadus morhua*) live in increasingly hypoxic waters. In the Gulf of Saint Lawrence (GSL) in Canada, the deep channels traversing the semi-enclosed sea exhibit year-round hypoxia, identified as one of the limiting factors for the recovery of GSL cod in its northern part. While many individuals in the northern GSL are known to venture in deeper, warmer, and more hypoxic waters of the Gulf channels, those in the southern GSL live in a shallower, colder, and more oxygenated environment. In this study, we use the modeling framework of the Dynamic Energy Budget (DEB) theory to disentangle the effects of hypoxia, temperature and food on the life-history traits of these two populations of cod in the GSL. Following recent advances by Thomas et al. (2018, this issue) on the mechanisms for the effects of hypoxia within the context of DEB theory, we implemented a correction of ingestion depending on dissolved oxygen (DO) saturation. We successfully developed and validated a set of parameters for a GSL Atlantic cod DEB model. Using simulations of historical growth trajectories from 1990 until 2004 estimated from data collected through fisheries research surveys, we found that temperature explained about half (48%) of the difference in length and 59% of the difference in mass between the two populations. The remaining proportion was attributed to exposure to hypoxia and food input. We also used our model to explore scenarios of duration, frequency, and intensity of hypoxia on cod's life-history traits, which showed that decreasing DO linearly reduces growth and reproduction while young cod seem to avoid impairing conditions resulting in limiting effects on developmental stages.

1. Introduction

Hypoxia in coastal marine ecosystems is a growing concern around the world, affecting a wide range of species (Zhang et al., 2010; Breitburg et al., 2018). It refers to low dissolved oxygen (DO) saturation levels. Hypoxic waters occur naturally in oxygen minimum zones, deep basins, upwelling areas of eastern boundary currents, and fjords (Helly and Levin, 2004). However, during the last century, the extent and severity of hypoxia has accelerated as a result of human activities (e.g. nutrient loading), and the number of areas suffering from human-caused coastal hypoxia has grown from 195 in the 1990s to over 500 in the 2000s (Diaz and Rosenberg, 2008; Breitburg et al., 2018). Hypoxic conditions in different systems vary across a wide range of temporal and spatial scales. Five broad categories of hypoxia can be defined, depending on their duration: permanent, persistent seasonal, both

stratified and vertically mixed, episodic, and diel (Kemp et al., 2009).

Consequences of hypoxia on marine organisms can be observed directly at the individual level. Reduction of DO levels modifies behavior and physiological processes such as feeding, ventilation or endocrine functions, leading to reduced growth, reproductive success, resistance to diseases, and increased mortality (see e.g. Wu, 2002; Rabalais et al., 2010; Claireaux and Chabot, 2016). At the population and community levels, such changes can result in the reduction of suitable habitat, altered migration, losses of biomass and species richness, or even massive mortality (Rabalais et al., 2002; Vaquer-Sunyer and Duarte, 2008; Ekau et al., 2010).

Mechanistic modeling appears as a suitable tool to quantify the response of marine organisms to various stressors (Hartman and Brandt, 1995; Claireaux et al., 2000; Miller Neilan and Rose, 2014; Deutsch et al., 2015). Within the variety of possible modeling approaches, our

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work is based on Dynamic Energy Budget (DEB) theory, which has been particularly successful for integrating multi-stressor effects on species life-history traits (e.g. Freitas et al., 2010; Galic et al., 2017; Kooijman, 2017; Lavaud et al., 2017). DEB theory quantifies, at the individual level, energy uptake and use through metabolic fluxes, which modulate the dynamics of life-history traits: growth rate, development, reproduction and mortality (Kooijman, 2010). The DEB model takes into account the complete life cycle, from the embryo to juvenile and adult stages and considers that mechanisms responsible for metabolic organization are not specific and thus apply to all organisms (micro-organism, plants, and animals). This offers a sufficiently general framework to explore geographical intraspecific differences or interspecific variability through the comparison of model parameters (Kooijman, 2017) given relatively simple environmental forcing.

A recent study by Thomas et al. (2018, this issue) reviewed the effects of hypoxia on several metabolic functions in marine organisms and explored potential mechanisms for these effects within the context of DEB theory. These authors studied Atlantic cod in particular, based on controlled experiments performed by Chabot and Dutil (1999), which showed that the main effect of hypoxia in controlled conditions could be applied to ingestion.

Atlantic cod (*Gadus morhua*) is an iconic species for North Atlantic fisheries, facing important challenges from its changing environment, the pressure of human activities and, in some populations, intense predation (Shelton et al., 2006; Swain and Benoît, 2015). The recovery of the stocks to a healthy state is a priority, which requires a better understanding of the environmental and ecological factors impacting cod populations. As in other regions, the two cod stocks found in the Gulf of Saint Lawrence (GSL) suffered from intense fishing activities until a first moratorium was declared in 1993. Recovery has been slowed in the northern GSL (nGSL) population, in part as a result of renewed fishing since the late 1990s. Meanwhile, the population in the southern GSL (sGSL) continues to decline despite a very low fishing mortality, as a result of an elevated rate of natural mortality among adults (Swain and Benoît, 2015). Cod from the GSL are well recognized for being among the slowest growing of Atlantic cod stocks (Brander, 1995; Campana et al., 1995), which contributes to their lower productivity. Among the hypotheses to explain this growth pattern, cold temperatures appear to be the predominant contributor (Neuheimer and Taggart, 2007), but cod from these stocks are also exposed to hypoxia (D'Amours, 1993; Chabot and Dutil, 1999).

The GSL is a large (230,000 km²) semi-enclosed sea with an average depth of 152 m traversed by three deep troughs: the Laurentian, Esquiman and Anticosti channels (300–540 m, Fig. 1). Communication between the GSL and the Atlantic is through Belle Isle Strait in the northeast and the large Cabot Strait to the southeast. A mix of Labrador Current water (cold, rich in oxygen) and North Atlantic central water associated with the Gulf Stream (warmer, poor in oxygen) enters into the GSL through the mouth of the Laurentian Channel, south of Newfoundland, and moves toward the head of the channels (Bugden, 1991; Gilbert and Pettigrew, 1997). Surface water is characterized by a large seasonal variation in temperature and low salinity caused by a high annual river runoff. Waters deeper than ~150 m are relatively warm (3–6 °C) and salty (> 33) and remain isolated from surface waters by a permanent halocline. In summer, vertical stratification is enhanced by the formation of a thermocline, the cold intermediate layer, from around 50 to 120 m (above the halocline). Above the halocline DO is high, close to full saturation, while waters at depth > ~150 m remain hypoxic in the channels, with minimum DO at about 250 m (Koutitonsky and Bugden, 1991; Gilbert et al., 2005). DO is generally between 30 and 60% saturation relative to air (% sat. hereafter) at depths > 200 m in the GSL, but decreases to 20–30% sat. at the head of the three main channels, reaching even 18–20% in parts of the Estuary, the most severely hypoxic area in the GSL (Fig. 2). The reduced proportion of oxygen-rich Labrador Current Water in the water mass entering the GSL in recent years is thought to aggravate oxygen depletion

that occurred over the last 70 years and led to the current situation (Gilbert et al., 2005).

Adults and large juveniles from both stocks are exposed to mild hypoxia (55–65% sat.) in winter when they aggregate in deep water (~6 °C) near Cabot Strait, mostly just outside the GSL in the Northwest Atlantic Fisheries Organization (NAFO) division 3Ps (Fig. 1). From spring to autumn, a large proportion of the nGSL cod population are found in the deep channels (NAFO divisions 3Pn, 4R, and 4S) and are exposed to more severe hypoxia (30–40% sat.) (Gilbert et al., 2007; Le Bris et al., 2013). Chabot (2004) calculated that up to 45% of the population in numbers and biomass were found at DO levels < 70% in July and August of 1995. Similarly, Fig. 3 shows that 50% of the fish were caught at DO levels < 70% in August of 2004–2009. Cod in the sGSL do not face hypoxia at this time of the year, as the area (NAFO division 4T) is characterized by shallower banks that typically have DO levels > 70% sat.

Considering that chronic (sub-lethal) hypoxia in the laboratory was found to reduce food consumption, and in turn growth rate (Chabot and Dutil, 1999), hypoxia exposure during the feeding season could be a major determinant of growth rate for a large proportion of nGSL cod. Unlike the situation in the laboratory, however, fish movements from the shelves to the deep channels in the GSL do not only involve a change of DO, but also a change in temperature, as deep waters typically are a few degrees warmer than the shelf waters. Temperature also exerts a strong influence on the growth rate of cod (Björnsson et al., 2007) and the model of Claireaux et al. (2000) suggests that growth rate at 50% sat. and 6 °C may be better than at 100% sat. and 2 °C, assuming food is not limiting. Modeling is required to tease apart the effects of temperature and DO on individual life-history traits (i.e. growth, maturation, reproduction) in the two populations of the GSL, in order to accurately estimate the consequences on the growth and production of the stocks.

In this study, our objective was to further study the assumption that hypoxia mainly affects ingestion (Thomas et al., 2018, this issue) by using DEB theory to simulate the response of Atlantic cod in the GSL to contrasted DO conditions. We first developed and validated a set of parameters for a GSL Atlantic cod DEB model. Then, we quantified the effect of DO saturation on the two populations from the GSL, based on historical growth trajectories. Finally, we used our model to explore scenarios of duration, frequency, and intensity of hypoxia on cod's life-history traits.

2. Material and methods

2.1. DEB model calibration and validation

DEB theory describes the rate at which an organism assimilates and utilizes energy and mass throughout its life cycle as a function of its state and its environment (i.e. food density and temperature) for maintenance, growth, maturation, and reproduction (Kooijman, 2010). In a standard DEB model, the energy budget of an individual is described by the dynamics of four state variables: the structural volume V (i.e. compounds requiring maintenance, in cm³), the reserve energy E (J), the cumulated energy allocated to maturity E_H (J), and the reproduction buffer E_R (J). Energy from ingested food is assimilated into reserve through the assimilation rate \dot{p}_A (Table S3, eq. 4). Reserve energy is utilized according to the mobilization rate \dot{p}_C (eq. 5). A fixed fraction (κ) of mobilized energy is allocated to the maintenance of structure (\dot{p}_M ; eq. 6) and its growth (\dot{p}_G ; eq. 7) while the remaining fraction (1- κ) is allocated to the maintenance of the maturity level (\dot{p}_j ; eq. 8) and development in juveniles (\dot{p}_H ; eq. 9) or reproduction in adults (\dot{p}_R ; eq. 10). Maintenance processes have priority over growth and development or reproduction. Stage transitions from embryo to juvenile (birth) and juvenile to adult (puberty) occur at fixed maturity levels: at E_H^b , the individual starts feeding; at E_H^p , allocation to maturity is redirected to reproduction. Temperature affects all rates in the same

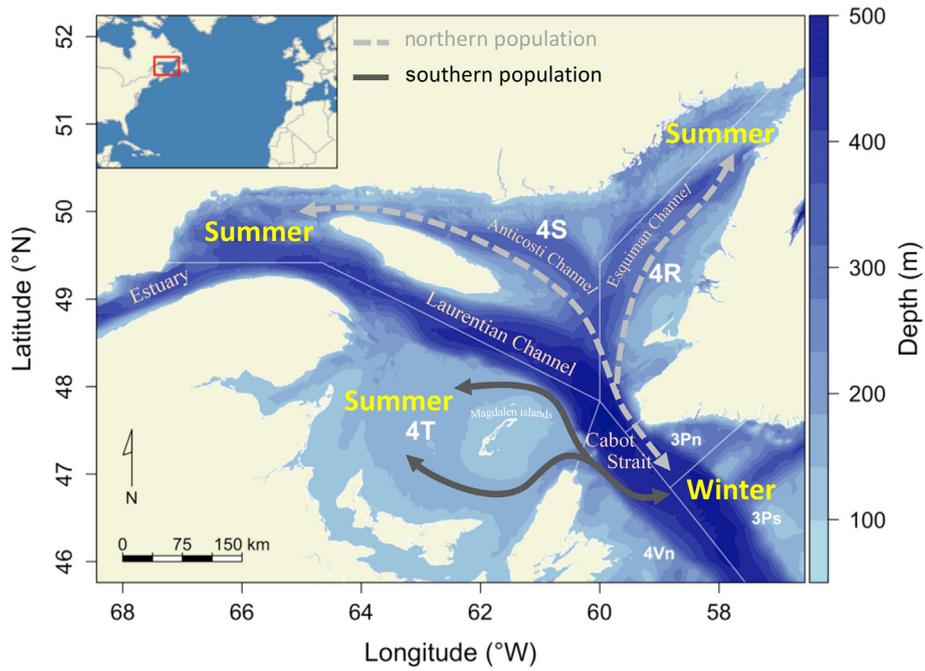


Fig. 1. Location of the northern and southern populations of Atlantic cod in the Gulf of Saint-Lawrence. The arrows indicate the schematic seasonal migration of each population. Also shown are the Northwest Atlantic Fisheries Organization fishing subareas.

way according to the Arrhenius relationship (Table S3, eq. 2; Kooijman, 2010).

In this study, we added four additional assumptions to the standard DEB model: (1) as for other fish DEB models (Kooijman et al., 2011; Kooijman, 2014), we considered metabolic acceleration from birth to metamorphosis, accounting for the observed exponential growth during this period (Campana and Hurley, 1989; Otterlei et al., 1999; McCollum et al., 2006) and resulting in a permanent increase of assimilation and reserve mobilization rates (Kooijman, 2014), (2) a fifth state variable, the energy allocated to egg production $E_{Go}(J)$, was included to control the gametogenesis and spawning (as formulated in Bernard et al., 2011), (3) the energy stored in the reproduction buffer, eggs, and, as a

last resort, structure can be used during extreme starvation to pay maintenance costs (Pecquerie et al., 2009; Table S3, eq. 15–19), and (4) food ingestion was impacted by the level of DO saturation as explained further in Section 2.2. All equations and model parameters are presented in Supplementary material Supp. 1.

Parameters of the GSL cod DEB model were estimated through the AmP procedure (DEBtool package retrieved on 17/04/2017 from http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/, see details in Supp.1 and in Marques et al., 2018). Although an entry for Atlantic cod exists in the AmP collection, preliminary trials showed that its application to GSL cod populations failed to accurately reproduce observed life-history traits in this area. Therefore, additional local data (from the

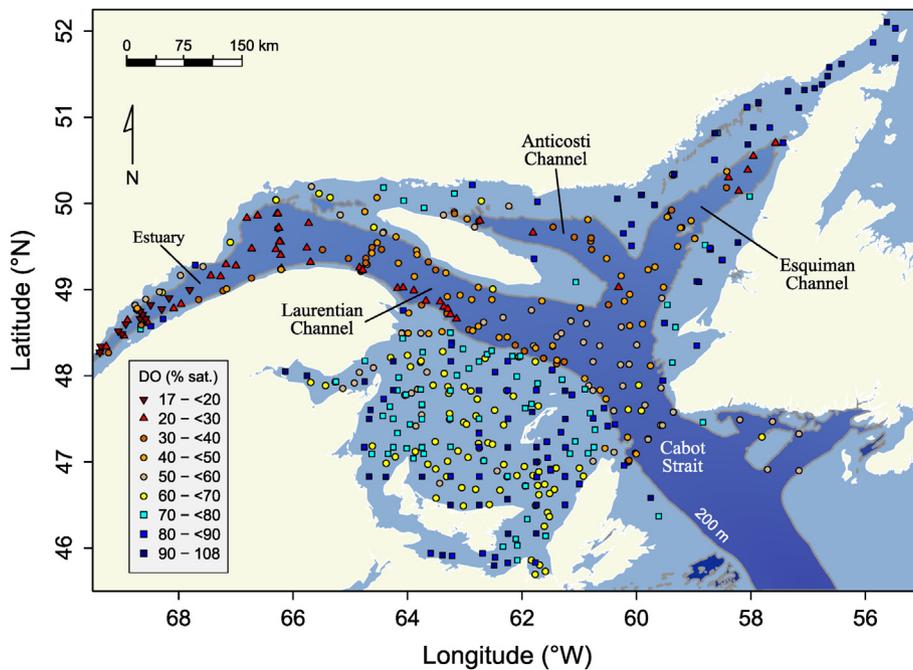


Fig. 2. Near-bottom DO saturation data in the GSL in 2012. Data from D. Chabot (unpublished data).

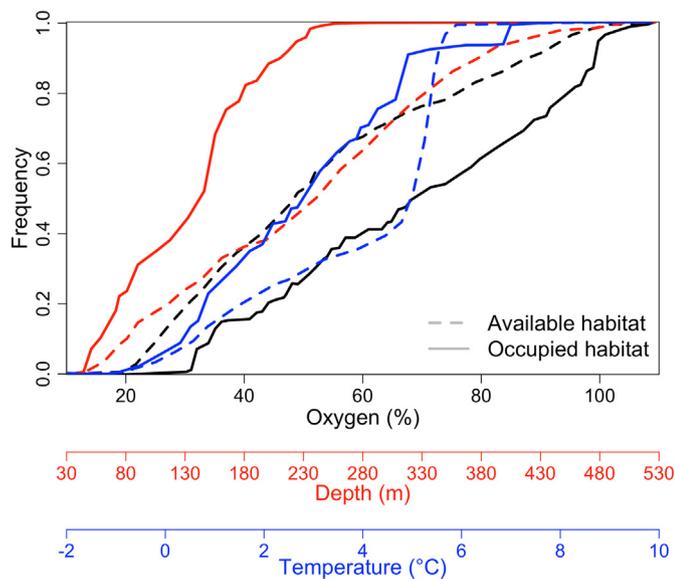


Fig. 3. Cumulative frequency distribution of Atlantic cod (strait lines), calculated using the method of Perry and Smith (1994) as a function of DO (black), temperature (blue) and depth (red), and cumulative frequency distribution of available habitat (dashed lines) as a function of DO, temperature and depth, using data from August depth-stratified random trawl surveys conducted in the nGSL from 2004 to 2009 (RV surveys). For instance, half of the cod population occupies waters colder than 2.8 °C, deeper than 142 m, and which DO level is below 68.5% sat. Courtesy of D. Gilbert (unpublished data). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

GSL and Newfoundland area) were included to estimate a new set of parameters (Fahay et al., 1999; Lambert and Dutil, 2000; Ouellet et al., 2001; Brown et al., 2003; Brander, 2005). Values of Root Mean Squared Error (RMSE) between data and predicted values were calculated to evaluate this set of parameter.

Two studies provided the validation datasets for the newly obtained set of parameters: a time series of length-at-age during 1970–1980 and 1980–1990 (Hanson and Chouinard, 1992) and a time series of total wet mass and gonadal wet mass for two size classes during 1992–1993 (Schwalme and Chouinard, 1999). Both datasets relate to sGSL cod. We used the environmental forcing (temperature, food, and DO) described in Section 2.3.2 for the sGSL population. Schwalme and Chouinard (1999) provided time series of seasonal stomach content mass, which were used as a proxy for food availability (see Section 2.3.2 for details).

2.2. Modeling metabolic response to hypoxia

According to Thomas et al. (2018, this issue), the decrease in energy uptake related to hypoxia appears to be one of the most sensitive processes driving growth and reproduction. The effect of DO variations on Atlantic cod energetics was thus included into the DEB model as a correction factor (c_{DO}) applied to the ingestion rate, which is consistent with the results of Chabot and Dutil (1999). The c_{DO} was defined as a function of ambient DO saturation experienced by the organism and was expressed as a Michaelis-Menten saturation function, modified to include a low critical DO threshold DO_{crit} as follows:

$$c_{DO}(t) = \begin{cases} \alpha \frac{DO(t) - DO_{crit}}{DO(t) - DO_{crit} + \beta}, & \text{if } DO(t) > DO_{crit} \\ 0, & \text{if } DO(t) \leq DO_{crit} \end{cases} \quad (1)$$

with $DO(t)$ the ambient DO saturation at time t , α (–) and β (% sat.) two constants for which $c_{DO} = 1$ at 100% sat., and DO_{crit} (% sat.) the DO saturation below which the correction factor is null (i.e. no ingestion). Thomas et al. (2018, this issue) estimated these parameters by fitting

the correction function on an experimental dataset of ingestion rates measured at various levels of dissolved oxygen (Supplementary material Supp. 2; Chabot and Dutil, 1999). Using the nonlinear (weighted) least-squares estimates function (nls) in the R software, they estimated the following parameter values: $\alpha = 1.43$, $\beta = 29.7\%$ sat., and $DO_{crit} = 31.7\%$ sat. We draw attention to the fact the ingestion rate is also impacted by temperature through the Arrhenius correction factor, which identically affects every rate in the model according to DEB theory (Table S3, eq. 2; Kooijman, 2010).

2.3. Application to the cod populations in the Gulf of St-Lawrence

2.3.1. Cod data

The cod stocks in the GSL are monitored through annual Research Vessel (RV) surveys in August (nGSL) and September (sGSL). These surveys provide length and total wet mass at age data since 1990 in the nGSL and since 1971 in the sGSL. Stomach contents of a subsample of fish are available for 1993–2009 and 2015–2016 for nGSL cod ($N = 21,908$). For sGSL cod, stomach content data for this study were collected over several years since 1990 (1990–1995; 2000–2010; 2013; $N = 16,871$). Additional data for sGSL cod, notably with respect to stomach fullness, came from a physiological condition monitoring conducted annually since 1992 (typically monthly in April and June–October) and January surveys of cod overwintering grounds in 1994 and 1995 ($N = 32,182$). Cod were sampled at additional times of the year through “sentinel fisheries” in the nGSL: fishing vessels collecting data for DFO using protocols provided by DFO scientists. These data include length, wet mass, as well as stomach content for a subsample of the fish (1995–2009).

2.3.2. Environmental data

Monthly averaged environmental conditions were estimated from the same data sources as cod data for each of the two cod populations in the GSL and linearly interpolated to a daily time step (Fig. 4).

2.3.2.1. Temperature. Abundance-weighted mean monthly water temperatures were calculated for small (< 43 cm) and large individuals (> 43 cm) from data collected during the RV surveys, the physiological condition monitoring and the January surveys. Because a particularly cold period occurred from 1987 to 1991 (Swain, 1999), we calculated mean monthly temperatures during the spring–fall months of this period. For the nGSL we used the seasonal measurements provided by Le Bris et al. (2013). The average temperature difference between small and large individuals and between the whole study period and the cold period observed in the sGSL (c.a. 1 °C in both cases) was applied to temperature time series in the North. Benoît and Rail (2016) provided the inter-annual variability in late summer temperatures.

2.3.2.2. Food. DEB theory uses a hyperbolic functional response (f) to describe the feeding of an organism as a function of food availability. As no direct measurement of food availability were available, we relied on monthly length-specific mass of stomach contents from the RV surveys (sGSL population: Benoît and Rail, 2016, adjusted to account for empty stomachs; nGSL population: D. Chabot, unpublished data, see details in Supplementary material Supp. 3) and the physiological condition monitoring to represent seasonal feeding intensity. Mass of stomach contents were standardized between [0, 1] within each size classes ([0, 10] cm, [11, 20] cm, [21, 30] cm, etc.) each month of the year. These data were used to estimate the scaled functional response of the DEB model according to: $f = SC_{std}^{1/4}$, where f is the scaled functional response, and SC_{std} refers to the standardized mass of stomach content (the exponent $1/4$ being a calibration constant). Because stomach content data were obtained on a monthly basis and for certain years only, feeding frequency and inter-annual variability is not well estimated. The application of the calibration exponent allows

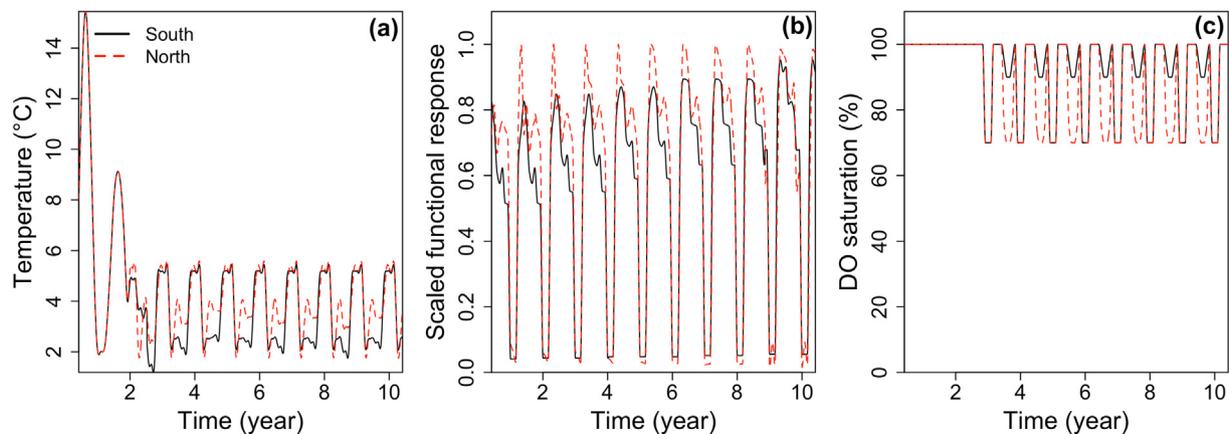


Fig. 4. Examples of time series of the environmental variables used in the DEB model. (a) Temperature, (b) scaled functional response, and (c) DO saturation taking into account the ontogenic effect and seasonal migratory history of the cod, as described in the methods section. Time starts at spawning in July.

buffering ingestion variability as a function of feeding frequency (Chabot et al., 2001) in particular during the months prior and after winter (when ingestion is limited; Benoit and Rail, 2016).

2.3.2.3. Oxygen. Annual profiles of DO saturation were built from measurements obtained during RV surveys and a set of near-bottom DO saturation data in the GSL (Fig. 2). In summer and early fall, a large proportion of nGSL cod are known to venture deep in the hypoxic channels that characterize the nGSL ecosystem (where DO saturation typically reaches 30%; Figs. 1 and 3). Because we model an average individual, mean DO saturation was set at 70% sat. from July to October; half of the individuals occupying waters with lower a DO saturation and the other half occupying waters with a higher DO saturation (Fig. 3). In contrast, sGSL cod do not face hypoxia in summer as they stay in the shallower waters of the Magdalen shallows. Both nGSL and sGSL cod face mild hypoxia in winter (~70% sat.).

During the first year of their development, young cod stay in shallow waters which warm up during summer (Tremblay and Sinclair, 1985; Swain and Kramer, 1995). Consequently, temperatures used in the model for larval to age-0 cod followed the general pattern of shallow waters in the GSL, described by Galbraith et al. (2012): 10 °C in June, 15 °C in August, and 5 °C in November. As these coastal waters remain normoxic, no reduction of the DO saturation was applied during the first two years of life. Environmental conditions experienced by age-1 cod were defined as an intermediate pattern between early and later life stages to ensure a smooth transition to deeper environment.

2.3.3. Simulation scenarios

To better understand the specific impact of temperature and DO level on energy fluxes, we ran three different scenarios:

- S1 scenario was a reference simulation for each population, i.e. with the specific environmental conditions available for each population (temperature and food). No DO effect was applied to the ingestion function as we assumed that stomach contents (that were used to construct the scaled functional response) already reflected the impact of DO conditions experienced by the individuals.
- In scenario S2, we tested the assumption that warmer temperatures (in nGSL) could outweigh the disadvantages of hypoxia, potentially resulting in a net increase in their energy uptake. The nGSL population was exposed to the temperature conditions experienced by sGSL cod (i.e. we compared S1 South with S2 North), while keeping food conditions and all other parameters identical to scenario S1.
- In scenario S3, we aimed to quantify the costs of hypoxia in each population. Because DO saturation affects feeding rate, observed stomach content data can underestimate actual food availability (although giving an accurate estimate of energy uptake). Therefore,

we removed the effect of DO on energy uptake by multiplying the scaled functional response f by $1/c_{DO}$ (Eq. (1)) and measured the resulting gain in growth in both populations. Temperature conditions were the same as in scenario S1.

Each year from 1990 to 2004, simulations started with an embryo (0.42 cm) and lasted until age 10 years. Growth in length and total wet mass were simulated for nGSL and sGSL individuals. The accuracy of predictions was evaluated through the comparison of model results and observations from the yearly surveys using the RMSE as a measure of model goodness-of-fit (scenario S1). Differences in length and mass between nGSL and sGSL populations due to temperature were quantified by calculating the mean differences between predictions for each population between scenarios S1 and S2. The quantification of hypoxia effects was calculated through the mean differences between predictions for each population between scenarios S1 and S3.

2.4. Exploring the effects of hypoxia on cod life-history traits

The actual foraging behavior of cod living in hypoxic waters and how it may vary in a changing environment remain uncertain. Therefore, we explored the sensitivity of several life-history traits to the duration, frequency, and intensity of exposure to hypoxia through additional scenarios. The reference scenario for the nGSL population (see previous section) was compared to three different durations of summer hypoxia, averaging 50, 100, and 200 days, combined with four intensities of DO saturation, reaching a minimum of 30, 50, 70, and 100% sat. For these comparisons, winter DO was maintained at the reference level, i.e. DO in the Laurentian Channel east of Cabot Strait (70% sat.). Diel vertical migrations of > 100 s of meters have been evidenced through data-storage tags (Le Bris et al., 2013). In order to reproduce these high-frequency variations in the environmental conditions, a last scenario simulating daily oscillations in DO saturation was added, with a single minimum level of 70% sat. (corresponding to the reference scenario).

For these simulations, we used a climatology of the monthly observations of temperature and f , described in Section 2.3, i.e. the conditions each year were the same but we kept a seasonal variability. Simulations started with an embryo (0.42 cm) and lasted 15 years. The consequences of the different DO scenarios were evaluated by comparing (1) the asymptotic length reached after 15 years of simulation, (2) the age at 40 cm, corresponding to the length at which young cod recruit to the fishery, (3) the reproductive investment expressed as a cumulated number of eggs produced over 15 years of simulation, and (4) the age at maturity (i.e. time to reach E_H^P). The energy investment into reproduction (E_{G_o} , J) was converted to a number of eggs produced using an average energy content of an egg of 1.9 J (Ouellet et al., 2001).

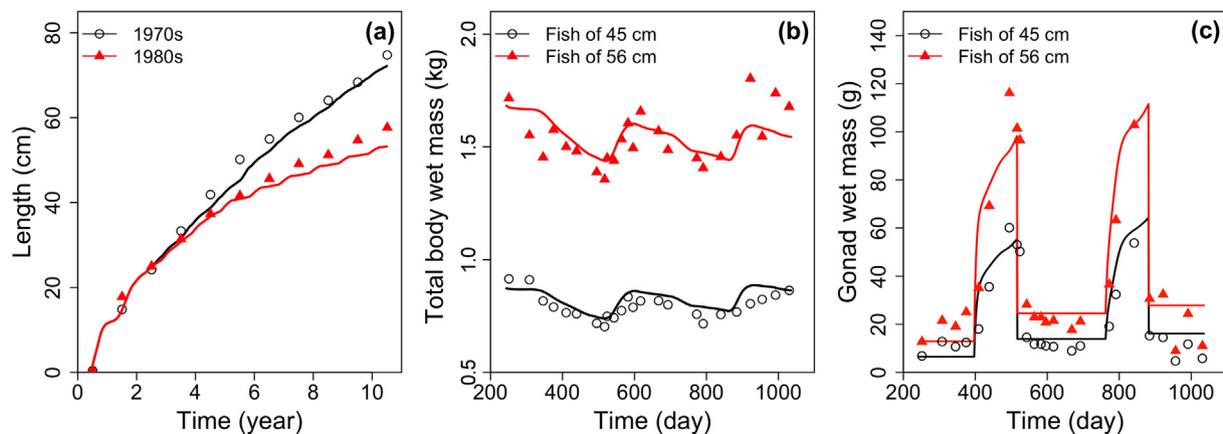


Fig. 5. Validation of the DEB model for sGSL cod. Time series of observed (points) and simulated (lines) growth in (a) length, (b) total wet mass, and (c) gonad wet mass. Data from (a) Hanson and Chouinard (1992) and (b and c) Schwalme and Chouinard (1999).

3. Results

3.1. Validation of the DEB model

The set of parameters estimated for GSL cod was successfully applied to the two validation datasets as predictions closely matched observations (Fig. 5). Length simulations over 10 years in sGSL cod reproduced very well the slower growth pattern observed during the 1980s compared to the 1970s (Fig. 5a). The total wet mass and gonad wet mass of two size classes of sGSL cod was also reasonably well reproduced over a 2-year period (Figs. 5b and c), although the model tended to under-estimate observed variability and the predicted seasonal pattern of gonad wet mass over-estimated observations in autumn (Fig. 5c).

3.2. Impact of temperature and hypoxia on the two GSL cod populations

The average difference observed between the two populations each year amounted to 5.5% in length (Fig. 6a) and 12.7% in total wet mass (Fig. 6b). Under reference scenario (S1), the model accurately predicted 10 years of length at age and total wet mass at age of average individuals born between 1990 and 2004. The RMSE of the model simulations of length and mass for nGSL individuals was 2.62 cm and 0.24 kg, respectively, and 3.39 cm and 0.21 kg for sGSL individuals (Fig. 7). A slight under-estimation of total wet mass was noted for small sGSL cod.

Scenario S2 aimed at determining if the faster growth rate observed in nGSL cod could be attributed to the warmer temperature of the area. Simulated length and total wet mass were reduced when applying sGSL temperatures but remained higher than the predictions and observations for sGSL cod. Growth in length in the nGSL under scenario S2 was reduced by 7% on average compared to scenario S1 (Fig. 6a). Growth in total wet mass was reduced by 23.5% on average (Fig. 6b). By comparing model predictions under scenario S1 and scenario S2, the difference of temperature between nGSL and sGSL explained 48% of the difference in length and 58.5% of the difference in mass between the two populations.

Under scenario S3, testing for the effect of hypoxia on growth, there was little change to the predicted length (0.9%, Fig. 6c) and total wet mass (< 5%, Fig. 6d) for sGSL cod (RMSE of 3.15 cm and 0.19 kg, respectively) compared to the reference scenario. Conversely, drastic increases of both length and mass were observed in the simulation for nGSL cod (RMSE of 5.49 cm and 0.89 kg, respectively). When feeding rates were adjusted to remove the effect of hypoxia, growth in length increased 4% on average and growth in total wet mass increased by 18.5% on average for nGSL cod. The effect of hypoxia was two times lower for sGSL cod with an increase of 2% in length and 9% in mass on

average.

3.3. Impact of hypoxic conditions on cod life-history traits

Different scenarios of summer hypoxia exposure were simulated, and for each scenario the mean DO level for the year was calculated (Fig. 8). The reference scenario (blue star) corresponds to the realistic scenario, using the forcing variables for nGSL cod, with a mean yearly DO level of 83.2% sat. The scenario with daily fluctuations in DO corresponding to vertical migrations resulted in almost the same yearly DO level (81.6% sat.) and the same performance on all four response variables as in the reference scenario. The asymptotic length predicted in the different scenarios ranged from 89.5 cm, in the more extreme hypoxia scenario of 200 d of exposure to DO reaching 30 at its minimum, to 127.6 cm in the no-effect scenario (i.e. DO of 100% sat. all year long; Fig. 8a). The theoretical maximum length of actual cod in the nGSL was predicted at 116.2 cm. A similar pattern was observed when looking at the cumulated investment in reproduction (measured as a cumulated number of eggs; simulations running over 15 years), with $1.66 \cdot 10^6$ eggs predicted in the extreme hypoxia scenario, $4.30 \cdot 10^6$ eggs in the no-effect scenario and $3.45 \cdot 10^6$ eggs in the realistic scenario (Fig. 8c). The age at which a cod would reach 40 cm in the extreme hypoxia scenario was 7.4 years while it was estimated at 5.8 years in the no-effect scenario and 6 years in the realistic scenario (Fig. 8b). Finally, the age at maturity (i.e. puberty or the onset of allocation to gamete production in DEB theory) was reached after 4.6 years in the extreme hypoxia scenario and 4.1 years in the no-effect scenario and 4.2 years in the realistic scenario (Fig. 8d).

4. Discussion

In this study, we aimed to quantify the effects of reduced DO levels on the life-history traits of two Atlantic cod populations living in the GSL by developing a dedicated DEB model. We validated our set of parameters using empirical observations for sGSL and nGSL cod and successfully applied the model to the two populations. Our results confirmed that decreased DO levels can severely impact growth and reproductive processes depending on its intensity and duration. But despite being exposed to lower DO during the feeding season, nGSL cod showed higher growth performance than sGSL cod. Our simulations revealed that these patterns might be explained by a combination of higher temperature and food consumption.

4.1. A full life cycle energetic model for *G. morhua*

Using data from the wild, as opposed to controlled laboratory conditions, remains a challenge, as it requires a good knowledge of both

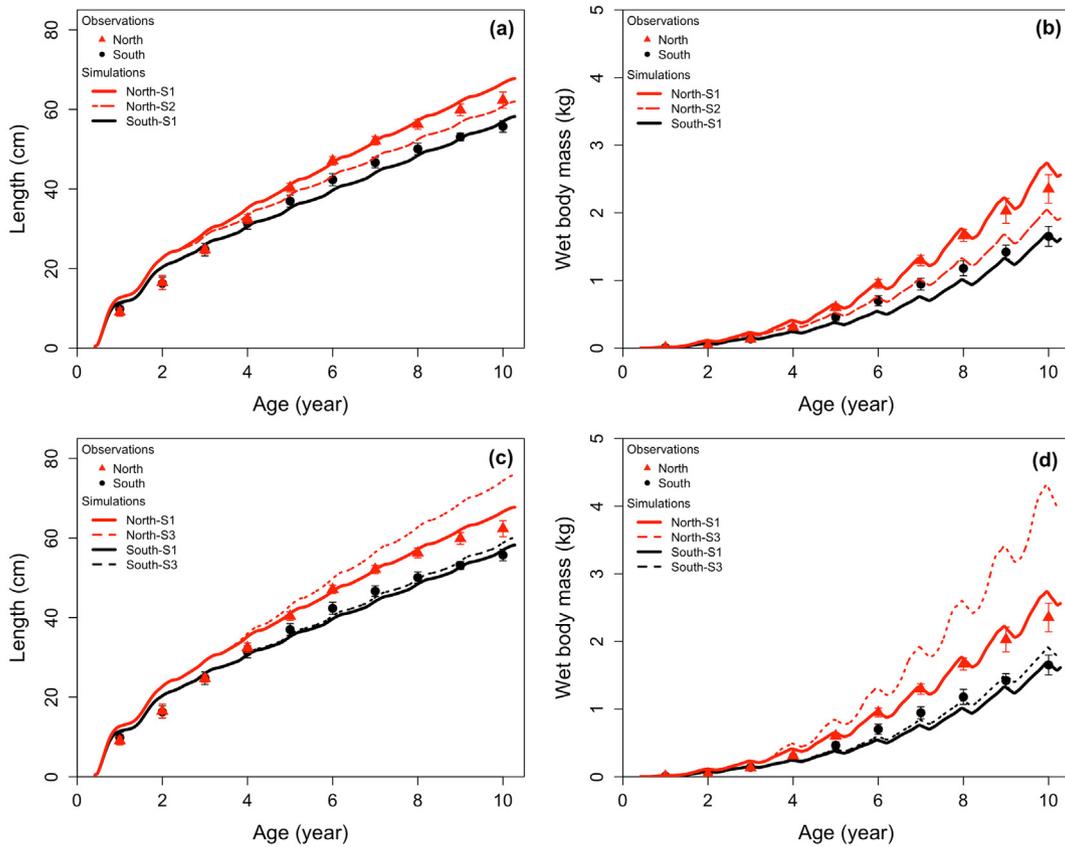


Fig. 6. Observed and simulated (a and c) length at age and (b and d) total wet mass at age. Dots and Triangles (\pm SD) correspond to observations for nGSL and sGSL cod, respectively and lines to the different scenarios: S1 corresponds to actual conditions, S2 to the scenario using the sGSL temperature profile for both populations (upper panels), and S3 to the scenario with removed effect of hypoxia on feeding rates (lower panels).

the biology and the physiology of the organism as well as the environment they live in. Although the Atlantic cod is a species of interest for its historic importance and its economic value, understanding the causes of the differences in life-history traits between stocks or populations is still limited (Brander, 2005), due to the complexity of the environments it occupies seasonally (physico-chemical properties of the water column, characterization and dynamics of food availability, etc.) and the inter-individual variability in behavior (migratory history, vertical movements, etc.) (Le Bris et al., 2013). The use of a DEB model to investigate and understand physical and physiological responses to environmental conditions in the two cod populations was of particular interest for the following reasons. In the past, most modeling studies focused exclusively on either juvenile or adult performances (Campana et al., 1995; Björnsson and Steinarsson, 2002; Björnsson et al., 2007; Holt and Jørgensen, 2014) or on larval growth (Hinrichsen et al., 2002;

Folkvord, 2005). Within the DEB framework, all life stages are accounted for, which leads to an integration of environmental effects on life-history traits through time. A developing juvenile experiencing low temperature or food conditions would take longer to reach maturity. Our exploratory results showed that current DO conditions do not impact development duration. However, more extreme scenarios produced important delays in reaching age at maturity, which could have important implications for population dynamics (e.g. Hutchings, 2005). Being able to model the entire life cycle gives a broader set of life-history traits for which predictions can be made and compared to empirical observations allowing for more fulsome model validation. This also offers opportunities to scale such predictions up to the population level (Pethybridge et al., 2013; Saraiva et al., 2014; Le Goff et al., 2017). While in the present study the DEB model was used to simulate an average individual in each population of the GSL, effort should be

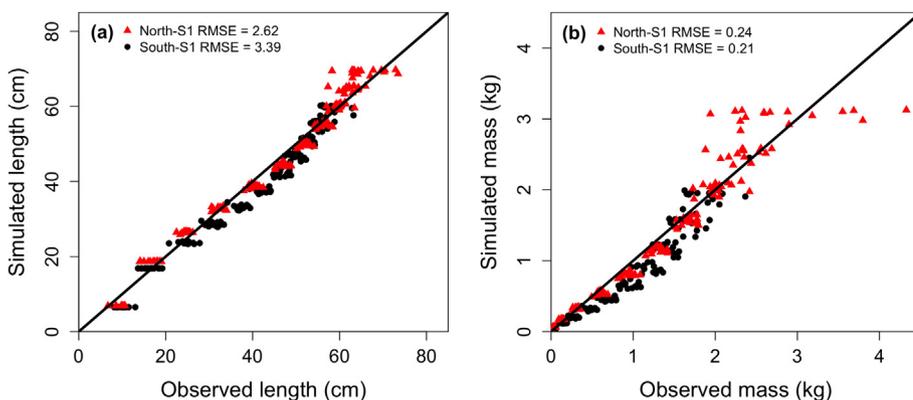


Fig. 7. Observed vs. simulated (a) length at age and (b) total wet mass at age. Each point corresponds to a year in the life of individuals born each year between 1990 and 2004 in the nGSL (red) and the sGSL (black) and modelled until age 10 years under scenario S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

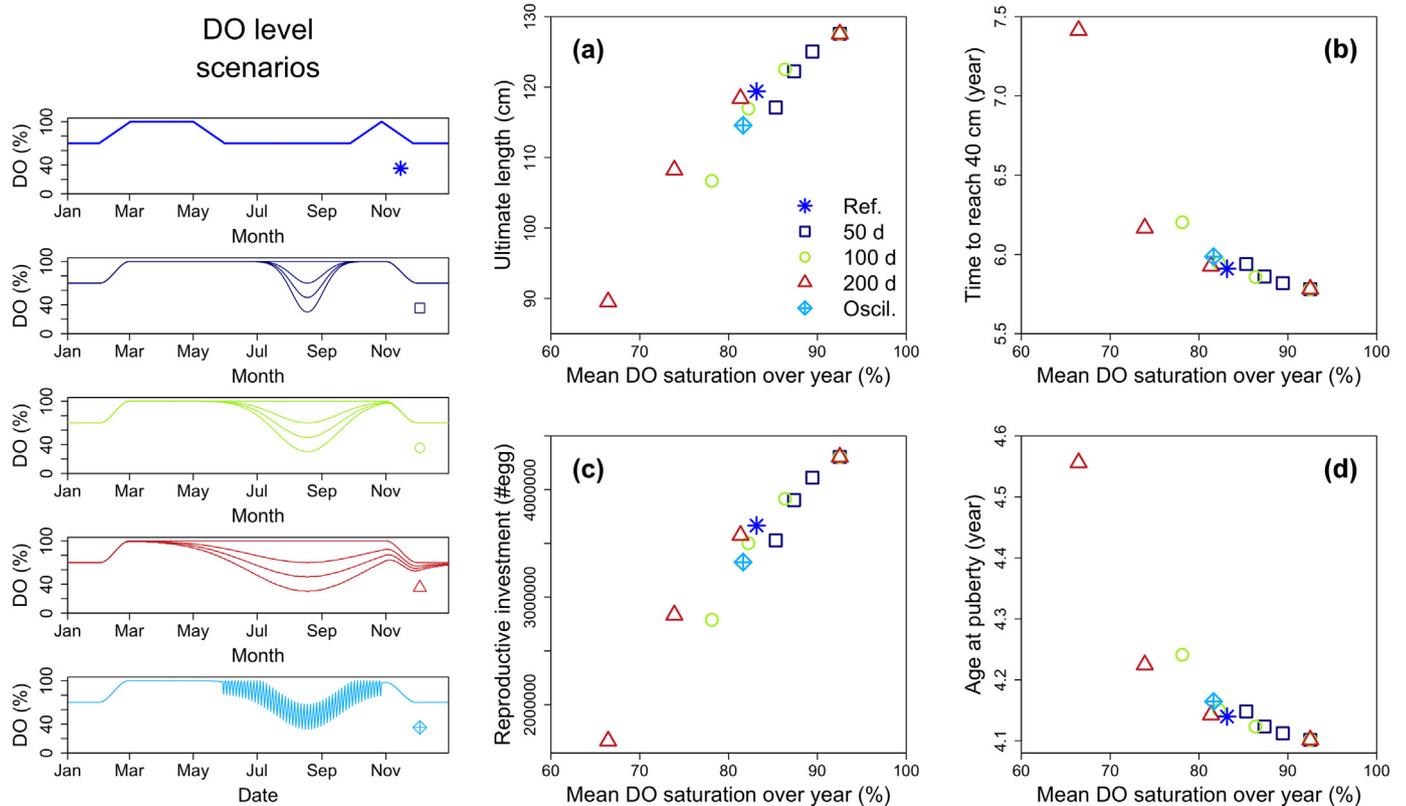


Fig. 8. Life-history traits for theoretical DO trajectories. Left panels give the DO trajectories of the different scenarios, with a combination of intensity (100, 70, 50, 30% sat.), duration (50, 100, and 200 d), and frequency (continuous or oscillating). Panels on the right illustrate the simulated effect of these scenarios on (a) asymptotic length after 15 years, (b) age at 40 cm, (c) cumulated number of eggs produced, and (d) age at maturity.

put toward modeling growth trajectories of a variety of individuals that occupy areas with different temperature and DO (Fig. 3; Le Bris et al., 2013).

The main result of this study is the successful modeling of length and total wet mass at age, in simulations starting each year from 1990 to 2004 with an embryo until age 10 years, for the two cod populations in the GSL (Fig. 7). The growth time series for the sGSL population goes further back to 1970 but only years from 1990 were included in this study in order to make comparable predictions for identical years in both populations (i.e. between 1990 and 2004); simulations for years 1970–1989 can be found in the Supplementary material (Supp. 4). Most of the discrepancies between model predictions and observations occurred at young (< 3 years) and older ages (> 8 years), in both populations. Two hypotheses might explain this pattern: 1) an over-estimation of the stomach content mass used to reconstruct the functional response and 2) a size-specific mortality. Available data used to estimate stomach content mass were mostly for cod measuring between 20 and 80 cm (Benoît and Rail, 2016; D. Chabot, unpublished data, see Supplementary material Supp. 3). The misrepresentation of small and large individuals in the samples might generate bias in the estimated stomach fullness and be responsible for the curved shape of the distribution of simulated vs. observed points in Fig. 7. Moreover, the availability of data for stomach content mass is uneven throughout the year, with higher numbers of sampled stomachs in summer months than in winter. Further improvement of predictions would require better biological sampling of inter-annual seasonal feeding activity, which would be a logistically challenging and expensive endeavor.

4.2. Multiple stressors explain growth patterns of cod in the GSL

Variations in size-at-age can reflect both growth variability and size-selective mortality. Based on the back-calculated sizes-at-age and a

modified von Bertalanffy growth model, Sinclair et al. (2002) estimated that inter-annual changes in observed size-at-age from the 1970s to the mid-1990s were most strongly affected by variation in size-selective mortality, followed by a negative effect of population density and a weak positive effect of occupied temperature. Persistent small size-at-age in sGSL despite good conditions for growth and little fishing after 1993 has been attributed to an evolutionary response to the size-selective fishing that occurred prior to the 1993 moratorium (Swain et al., 2007). The difference in conclusions of this study and that of Sinclair et al. (2002) concerning the causes of size-at-age variation in sGSL is one that should be investigated further. The current DEB model does not account for possible evolutionary change in growth, though the outcomes of the evolutionary process could be accommodated by the model by varying key parameters such as the energy conductance \dot{v} and the specific somatic maintenance rate [\dot{p}_M]. Furthermore, scaling the current DEB model up to the population level could allow evaluating the contributions of size-selective mortality and environmentally-driven growth variability to variation in size-at-age.

The cod population in nGSL has been reported to be more productive than the population in the sGSL (Dutil and Brander, 2003). The growth data from RV surveys presented in our study reflect this pattern with nGSL cod growing on average 5.5% more in length and 12.7% more in total wet mass than sGSL cod (between 1990 and 2004). From this observation, it would seem that hypoxia may not have an effect on growth performance of cod, or that other factors overcome the negative impact of hypoxia on their energy budget (i.e. temperature and food). Despite the amount of data on this species in the GSL, it is still difficult to know precisely how much time cod spend in the different layers of the water column. Data from the RV surveys show that close to 50% of the nGSL population (in numbers) is captured at DO levels below 70% sat. in July and in August (Fig. 3), but only 20% is similarly exposed in October, when cod had likely started their winter migration out of the

GSL (Chabot, 2004). Therefore close to half of the population may face DO levels that reduce food consumption and growth during the peak of feeding season (June–September). If warmer temperature conditions are more favorable in the nGSL, the reduced ingestion in individuals facing hypoxia in this region (leading to slower growth) could be balanced by the better performance of the remaining part of the population. As evidenced in the vertically stratified Bornholm Basin of the Baltic Sea, *G. morhua* may frequently dive into deep hypoxic waters in order to forage on deep-burrowing prey species easy to access (Neuenfeldt et al., 2009). A recent study by Le Bris et al. (2013) brought insights into the vertical and horizontal swimming behavior of cod in the nGSL population by equipping a small number of fishes with individual data loggers. Some individuals seem to be sedentary while others take on seasonal migrations; some exhibit daily vertical migrations which bring them in hypoxic waters and others seem to stay in normoxic areas. The model reaches here a limit, in its actual form, by simulating an average individual and further developments using individual based modeling approaches could bring valuable information on these differential behaviors. The use of individual growth trajectories obtained from otolith measurements could be appropriate to take this step forward (Fablet et al., 2011; Pecquerie et al., 2012). A number of individuals could be modelled in order to take into account the diversity of conditions experienced by cod in the GSL (Figs. 3 and 4).

Temperature plays a major role in the physiological performance of organisms (Pörtner et al., 2017) and is a crucial variable in DEB theory as it modulates all energy fluxes. Differences in temperature regime across the distribution area of Atlantic cod (e.g. between-stock differences) are often considered to be responsible for the variability observed in life-history traits (Brander, 2005; Neuheimer and Taggart, 2007; Pörtner et al., 2017), though these studies have generally failed to account for seasonal variations in occupied temperature that result from seasonal temperature change and cod migrations. While some populations have been reported to experience frequent high temperatures (Murawski and Finn, 1988; Righton et al., 2010), the vast majority of cod from the GSL (> 95%) are found at temperatures between -0.5 and 8.5 °C (Fig. 4; Rose and Leggett, 1988). Other factors such as the local phenotypical adaptations to water hydrography (MacKenzie et al., 1996; Dutil et al., 1999) and fishery pressure (Olsen et al., 2007) likely contribute to this variability as well. At the scale of the GSL, temperature differences between the two populations are in the order of 1 °C during the summer (Galbraith et al., 2012; Benoît and Rail, 2016). According to the simulations run in scenario S2, this temperature difference was responsible for 48% of the difference in length and of 58.5% of the difference in total wet mass between the populations. The remaining gap of growth between the two populations is therefore imputable to prey quality and/or abundance despite hypoxia. Indeed, stomach content mass data being the only indicator of energy input available, it was impossible to disentangle the impact of hypoxia on food consumption. We would need to have an estimate of the concentration of prey in the environment to overcome this issue. Nevertheless, based on the knowledge of the effect of hypoxia on ingestion rates (Chabot and Dutil, 1999) we could give an estimate of the amount of energy not assimilated due to hypoxia by reversing the correction of Thomas et al. (2018, this issue). The obtained predictions under scenario S3 show an important growth increase in the nGSL population if it did not face hypoxia in summer.

4.3. Effects of hypoxia on cod life-history traits

In the exploratory part of this study we investigated the effect of hypoxia on various life-history traits of cod in a range of scenarios in order to identify possible exposure thresholds. This approach is justified as limited information is available on the degree of exposure to hypoxia of cod in the GSL. It seems that both the duration and the intensity of exposure to reduced DO levels have a linear negative effect on the maximum length and the cumulated investment in reproduction based

on a 15 years simulation horizon. As the effect of hypoxia is imposed on ingestion, the DEB model predicts that energy allocated to both somatic and reproductive processes would be impacted in a similar way. A different pattern emerged when looking at events occurring earlier in life, such as the age at puberty (i.e. maturity) or the age at which young cod recruit to the fishery (i.e. 40 cm). In most of the scenarios (including the realistic simulations), the model predicted that cod reached 40 cm at about 6 years old and puberty at about 4.1–4.2 years and did not deviate much from the predictions under the no-effect scenario (5.8 years at 40 cm, puberty reached at 4.1 years). As young cod (< 3 years) do not experience hypoxia in the shallower water depth they occupy (Swain and Kramer, 1995), the impact of hypoxia on juvenile development seems to be limited. This is not to say that hypoxia does not have an effect on younger stages, but only that given the biology of this species and the fact that larvae and juveniles tend to live in shallower and more oxygenated waters, they might not be as exposed to reduced DO levels as older juveniles and adults can be.

Chabot and Dutil (1999) brought evidence that almost all (97%) of the variability in growth observed between experimental treatments at different levels of hypoxia was explained by an effect of DO saturation on ingestion rate; we therefore modelled this process accordingly. The value of DO threshold, $DO_{crit} = 31.7\%$ sat., calculated by Thomas et al. (2018, this issue) in the DO correction factor equation agrees well with the fact that the risk of mortality becomes significant at 28% sat. (Plante et al., 1998), although the lethal threshold (median lethal level after a 96 h exposure) has been estimated at 21% sat. (Plante et al., 1998). In nature, cod avoid levels < 30% sat. (D'Amours, 1993) probably because they risk death below this DO level, but also because the potential energy gain is very limited. A recent study suggested that hypoxia might also reduce gastric evacuation time (Chabot et al., 2015). Their results indicate that at equal stomach content, the duration of assimilation of nutrient through their passage in the gut is increased under hypoxia. As ingestion depends on the state of fullness of stomach, increased transit time results in a reduced quantity of food processed over time. In the context of DEB theory, this could be implemented through the application of a DO correction factor to the digestion process, which can be described as a simple Michaelis-Menten kinetics (Kooijman, 2010), or a correction of the conversion efficiency of food to assimilated energy κ_X . All these effects are obviously inter-related and factors that influence the amount of food eaten are likely to affect the assimilation efficiency and any factor that influences the rate of the digestive processes and assimilation is likely to have an influence upon the amount of food ingested (Wang et al., 2009). While laboratory experiments have already demonstrated a reduction of growth in cod exposed to hypoxia (Chabot and Dutil, 1999), no study on cod has yet demonstrated a negative effect of hypoxia on reproductive output, although this has been demonstrated for other species (e.g. Wu et al., 2003; Landry et al., 2007; Thomas et al., 2007). More data from both field monitoring and controlled experiments is warranted to answer this question.

4.4. Conclusions

This work constitutes a first step in the development and application of a full life cycle DEB model for Atlantic cod. The integration of the effect of hypoxia as a third environmental variable is an important feature of the model for a species living under natural and human-induced pressures in a rapidly changing environment. More global approaches investigating such effects on population dynamics and biogeographical distribution should be pursued (Kearney et al., 2010). The application of our model to other cod stocks facing hypoxia, such as in the Baltic Sea (Brander, 1995; Neuenfeldt et al., 2009), would be interesting to compare the response of different populations to multiple stressors. The vast knowledge gathered through decades by fishery biologists, physiologists and managers on the biology and ecology of *G. morhua* should help adapting and applying this model to other stocks

throughout the distribution area of this species. Finally, exploring individual growth trajectories should allow a better appreciation of the tradeoff faced by fishes venturing in hypoxic, yet warm and potentially prey-rich waters on life-history traits, especially in populations exhibiting inter-individual behavior variability (Le Bris et al., 2013).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2018.07.001>.

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