ESTIMATING THE IMPACT OF NATURALLY OCCURRING HYPOXIA ON GROWTH PRODUCTION OF ATLANTIC COD (*GADUS MORHUA*) FROM THE NORTHERN GULF OF ST. LAWRENCE (CANADA)

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Introduction

In the laboratory, Atlantic cod (*Gadus morhua*) are fairly sensitive to hypoxia. Within 96 hours of exposure, 5% of the subjects died when dissolved oxygen was 28.1% (95% CI: 25.8-30.5) of saturation, and 50% of the subjects died when dissolved oxygen was 21% (95% CI: 19.9-22.1) (Plante et al. 1998). Temperature (2 and 6° C) and cod size (45.2 cm ± 4.2 [mean ± SD] and 57.5 cm ± 3.8) did not affect hypoxia tolerance, within the range tested. Furthermore, chronic sub-lethal hypoxia (45-65% saturation) reduced both food ingestion and growth of cod (Chabot & Dutil 1999).

The Gulf of St. Lawrence is an enclosed sea located in Eastern Canada (Figure 1). It is characterised by a permanent cold layer (temperature < 0° C and average salinity = 32.4) extending from circa 50 to 100 m depth in summer, and from the surface to circa 100 m in winter. This cold layer keeps warmer (2-6° C) and saltier (34-35) deep waters from mixing with oxygenated surface waters (Lauzier & Trites 1958; Bugden 1991; Koutitonsky & Bugden 1991; Gilbert & Pettigrew 1997). Near the entrance of the Gulf (Cabot Strait), deep waters are circa 50-70% saturated in oxygen. Oxygen levels become progressively more depleted as these waters flow north or west (Bugden 1991; Gilbert & Pettigrew 1997), and levels of 20-30% are common in the western Gulf and the estuary (Figure 1). Oxygen levels in the deep layer are subject to long-term changes, but hypoxia is a permanent feature of the northern part of the Gulf of St. Lawrence and of the estuary. Because it is shallower, the southern part of the Gulf of St. Lawrence has generally normoxic waters, except for its northern fringe, along the edge of the Laurentian Channel.

The northern part of the Gulf of St. Lawrence (Northwest Atlantic Fisheries Organisation, NAFO, divisions 3Pn4RS) is home to a cod stock. In winter, cod from this stock are found in the deeper channels inside the Gulf and, in particular since 1991, outside the Gulf, south of Newfoundland (Castonguay et al. 1999). In spring, cod disperse into the northern Gulf and the estuary to spawn and for the post-spawning feeding period. In late autumn cod older than 2 years old return to deep waters in the Esquiman and Laurentian Channels (Chouinard & Fréchet 1994; Castonguay et al. 1999).

The northern Gulf of St Lawrence cod stock inhabits cold waters (Brander 1995; Campana et al. 1995), exhibits poor productivity (Dutil et al. 1999) and slow growth (Chouinard & Fréchet 1994). Our objective was to construct a simple model to estimate the impact of hypoxia on growth production for this stock.

Methods

Dissolved oxygen

Bottom levels of dissolved oxygen for the Gulf of St. Lawrence were obtained by Winkler titration. During a first survey, 104 random samples from the northern Gulf of St. Lawrence were taken between 11 Aug 1995 and 04 Sep 1995, and 32 samples from the southern Gulf of St. Lawrence were taken between 08 Sep 1995 and 15 Sep 1995 (Figure 1). Two samples from the northern Gulf were rejected because they were obvious outliers on a plot of dissolved oxygen as a function of depth. Because this survey did not provide an adequate coverage of the Esquiman Channel, where cod are common, we added 39 determinations of dissolved oxygen near the bottom taken during two other surveys conducted from 15 Oct 1995 to 04 Nov 1995 and on 17 Nov 1995, respectively (Figure 1). Combining data from these surveys was justified because oxygen levels do not change much within the year below the cold layer. Indeed, stations from the summer and fall surveys that were located within a distance of 25 km and a depth of 25 m had very similar levels of dissolved oxygen (usually within 2-3% saturation). The regression of the fall values of dissolved oxygen on the summer values ($n = 10$) was:

$y = 0.989x + 1.905$, $r^2 = 0.95$

Cod abundance and distribution

Cod distribution and cod abundance in relation to oxygen levels were estimated from three random stratified bottom-trawl surveys. First, a Sentinel Fishery survey (no. 3) did 311 sets between 25 Jul 1995 and 15 Aug 1995 using 9 different trawlers, all equipped with a Rock Hopper 300 bottom trawl. Second, the Fisheries and Oceans shrimp and demersal fish survey no. 6 did 194 sets between 11 Aug 1995 and 04 Sep 1995, all from the CCGS Alfred Needler, but with a URI 81-114 shrimp trawl. Finally, a second Sentinel Fishery survey (no. 4) did 322 sets between 06 Oct 1995 and 04 Nov 1995, using the same 9 vessels as in July-August.

The study area was restricted to NAFO areas 4R, 4S and 3Pn, and the northern part of 4T (slope of the Laurentian Channel). The estuary and the southern Gulf of St. Lawrence were excluded. In addition, depths < 50 m and some coastal zones at depths > 50 m along the northern shore of the Gulf of St. Lawrence or the northwest tip of Anticosti Island were excluded because they were not fished (strata 825, 826, 839 and 841). Historical assessments of cod distribution at this time of the year suggest this stock is distributed almost entirely within the remaining 50 strata, which cover 104 230 km^2.

Distribution of cod in relation to dissolved oxygen

We used the following classes of dissolved oxygen: <30% saturation, where survival is compromised (Plante et al. 1998), 30-39.9, 40-49.9, 50-59.9, and 60-69.9% saturation, where growth is limited by oxygen availability, and ≥70% saturation where growth is independent of oxygen availability (Chabot & Dutil 1999) in the laboratory.

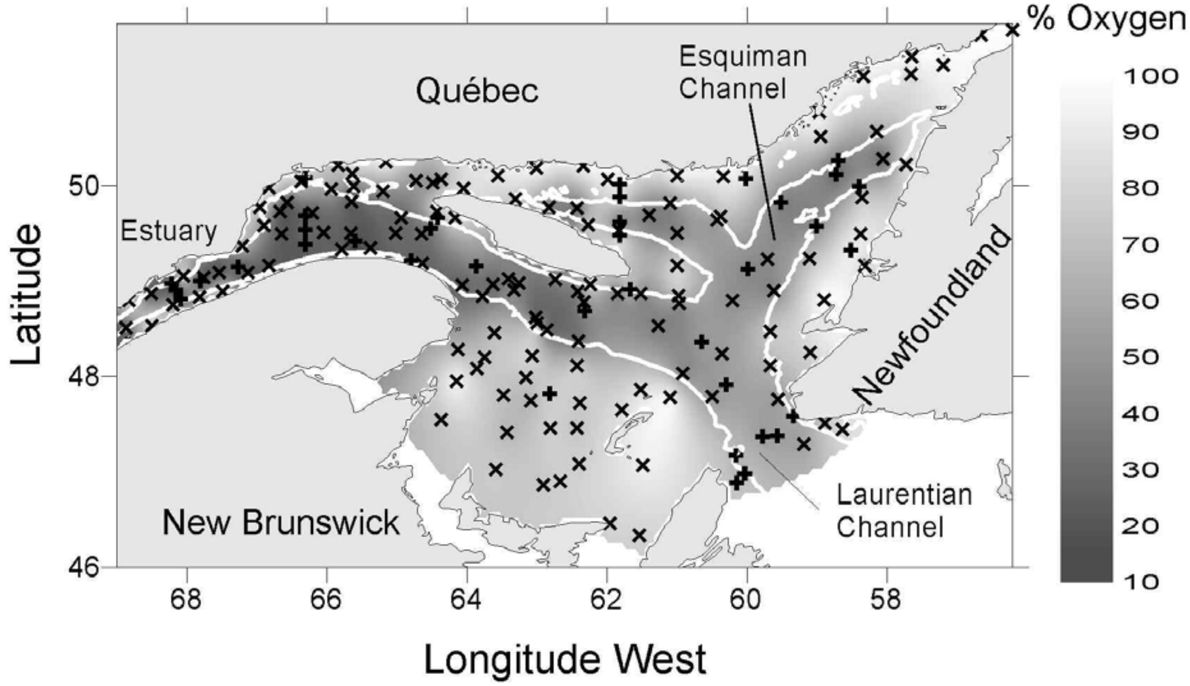

Figure 1. Level of dissolved oxygen (% saturation) on the bottom of the Gulf of St. Lawrence. × : Winkler stations sampled between 11 Aug 1995 and 15 Sep 1995; + : stations sampled between 15 Oct 1995 and 17 Nov 1995. The 200 m isobath is shown as a white line.

The coordinates of the oxygen stations and of the cod survey stratum boundaries were available as decimal degrees and with longitudes expressed as negative numbers. These were transformed into km (relative to 62 °W and 49 °N, near the center of the study area) using the following equations (Rivoirard et al. 2000, p. 12):

$$y = 1.852 \cdot (\text{longitude} + 62) \cdot 60 \cdot \cos(\text{latitude})$$

$$x = 1.852 \cdot (\text{latitude} - 49) \cdot 60$$

Kriging (1 km between nodes) with the Surfer software (Golden Software Inc. 1999) was used to produce a map of bottom levels of dissolved oxygen for the study area (Figure 1 and 2). Using Surfer to determine areas, the area associated with each oxygen class was calculated for each stratum. The number of cod estimated for each stratum was then distributed among the six oxygen classes in proportion to their respective area. Results were summed across all strata to obtain the proportion of the total number of cod that inhabited each oxygen class.

Impact of hypoxia on growth production

Because there are no data on the interaction between oxygen, temperature, cod size and cod growth, we estimated the growth of a typical cod from our laboratory experiment at 10° C (Chabot & Dutil 1999, 44 cm, 700 g, Fulton K = 0.8). Thus the rate of food ingestion, in $g \cdot d^{-1}$, was determined from Chabot and Dutil (1999, Figure 4a):

$$\text{Ingestion} = -74.22 + 54.51 \cdot \log(\text{dissolved oxygen,\% sat.})$$

Furthermore, for a given ingestion rate, growth (biomass increment in $g \cdot d^{-1}$) was Chabot and Dutil (1999, Figure 5)::

$$\text{Growth} = -0.283 + 0.285 \cdot \text{Ingestion}$$

For each oxygen class, growth was expressed as a proportion of growth in normoxia. The impact of hypoxia on production growth for the stock was estimated by calculating the average growth rate across all oxygen classes, weighting growth in each class by the number of fish estimated in the class.

Results

Figure 2 shows the distribution of the six classes of dissolved oxygen in relation to the strata used to estimate fish numbers in the study area. Table 1 shows the extent, in km^2, of the six classes of dissolved oxygen, and the expected rate of food ingestion and growth of a cod with length, mass and condition similar to that of cod used in Chabot and Dutil (1999).

Cod avoided areas characterized by hypoxia levels that were lethal for cod in the

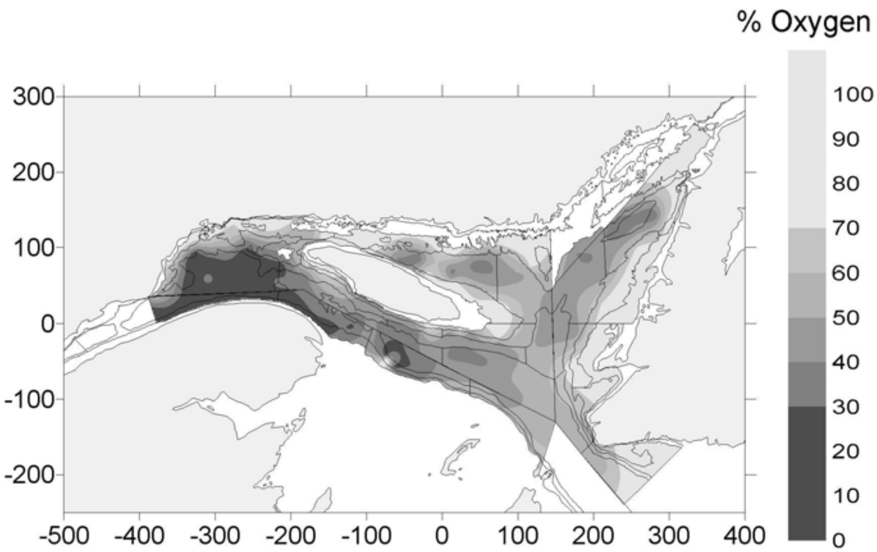

Figure 2. Distribution of the six classes of dissolved oxygen (% saturation) in relation to the strata used to estimate cod biomass and cod numbers. Strata outside the study area are left blank. Latitudes and longitudes are in km relative to 49° N and 62° W.

laboratory (< 30% saturation). This can be seen in Figure 3, which shows the number of cod caught during each set of the Sentinel Fishery survey no. 3, in relation to the bottom level of dissolved oxygen. Results were very similar for the other two surveys. This is better seen by comparing cod density in each of the six classes of dissolved oxygen, for each survey (Figure 4)

Cod avoided areas characterized by hypoxia levels that were lethal for cod in the laboratory (< 30% saturation). This can be seen in Figure 3, which shows the number of cod caught during each set of the Sentinel Fishery survey no. 3, in relation to the bottom level of dissolved oxygen. Results were very similar for the other two surveys. This is better seen by comparing cod density in each of the six classes of dissolved oxygen, for each survey (Figure 4)

Furthermore, there were few sets with large numbers of cod in areas of sub-lethal hypoxia (30-70% saturation) (Figure 3). Thus in areas of below 30%

oxygen saturation, cod density was almost nil, and increased with oxygen levelthereafter (Figure 4). This relationship was closely approximated by an exponential function.

However a large proportion of the stock was found in sub-lethal hypoxic waters during each of the three surveys (Figures 3 and 4). In late July and early August, 44.3% of the biomass and 45.3% of the total number of cod were estimated to inhabit waters with 70% or less dissolved oxygen (Table 2). We estimated that during this period, growth production was decreased by 18.5% as a result of hypoxia. In the second half of August and early September, 47.1% of the biomass and 46.2% of the total number of cod were found in hypoxic waters, which resulted in a decrease in production of 16.9% (Table 3). Finally, in October and early November, 35.3% of the cod biomass, and 24.9% of the total number of cod experienced hypoxia, and growth production was estimated to be 8.7% lower than if the stock had been in normoxic waters (Table 4).

Table 1. Main characteristics of the six oxygen classes used in this study: surface area in the northern Gulf of St. Lawrence, rate of food ingestion and of growth expected for a 44 cm, 700 g (Fulton K = 0.8) cod feeding in each oxygen class (Chabot & Dutil 1999). For the "< 30" and "≥ 70" classes, oxygen values of 25 and 85% were used, respectively, to calculate the rate of food ingestion.

Dissolved Oxygen (% sat)	**Area (km^2)**	**Area (% of total)**	**Food ingestion ($g \cdot d^{-1}$)**	**Growth ($g \cdot d^{-1}$)**	**Growth (% relative to normoxia)**
< 30	9 647	9	2.0	0.3	3.3
30-40	11 542	11	9.9	2.6	29.9
40-50	22 825	22	15.9	4.2	49.7
50-60	21 540	21	20.6	5.6	65.6
60-70	11 895	11	24.6	6.7	78.8
≥70	26 781	26	31.0	8.5	100.0
Total	104 230	100			

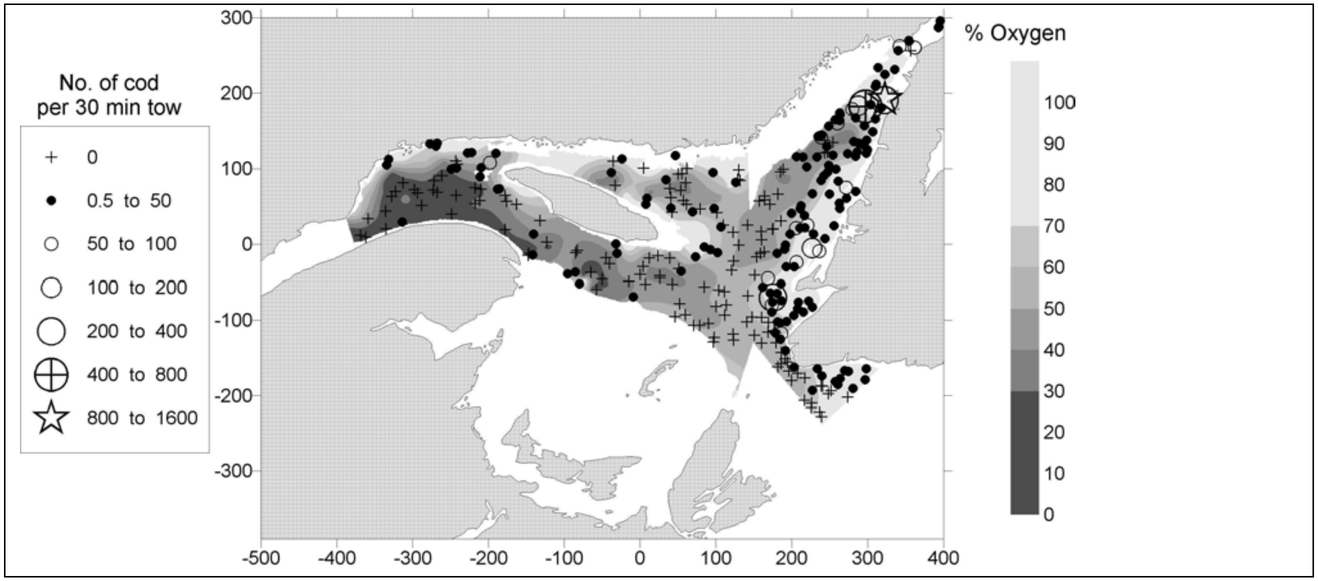

Figure 3.	Number of cod caught in each 30 min tow during the Sentinel Fishery survey no. 3 carried out between 25 Jul 1995 and 15 Aug 1995, in relation to bottom level of dissolved oxygen. Coordinates are in km relative to 49° N and 69° W.

Discussion

D'Amours (1993) has shown that cod in the northern Gulf of St. Lawrence avoid areas with less than 30% oxygen saturation, which is close to the incipient lethal threshold (28%) determined in the laboratory (Plante et al. 1998). This study confirms his findings for three different surveys in 1995. D'Amours results also suggest that cod avoid non-lethal hypoxic waters. This is quantified in the present study, in which the relationship between cod density and the level of dissolved oxygen was exponential. This is similar to the situation in the Kattegat (Denmark), where catches of demersal fish, mostly gadoids and pleuronectids, in standard trawl sets were directly related to oxygen concentration (Pihl 1989).

Even though cod tended to avoid hypoxic waters during the feeding season, a large proportion of the stock, up to almost 50% in number, was found in waters hypoxic enough to reduce growth in laboratory fish. This happens to be when the impact of hypoxia on cod survival and growth is expected to be highest. Because it imposes a limit on maximum metabolism (Claireaux et al. 2000), hypoxia can limit swimming capacity, making cod more vulnerable to predation or fishing, and less able to hunt for food. But more importantly, this reduction in metabolic scope also reduces the ability of fish to digest their food, as was shown in Chabot and Dutil (1999): the hypoxia- induced reduction in growth was almost entirely explained by a reduction in food consumption. This reduction in food consumption appears, in turn, to be due to a slower digestion (Claireaux et al. 2000; Chabot et al. 2001).

Table 2. Estimation of the biomass and number of cod present in each class of dissolved oxygen between 25 Jul 1995 and 15 Aug 1995 (Sentinel fishery mobile gear survey no. 3), and of the average production growth relative to growth in normoxia.

Dissolved oxygen (%)	**Cod biomass (kg)**	**Cod biomass (% of total)**	**Cod number**	**Cod number (% of total)**	**Production growth (% relative to normoxia)**	**Growth x cod number**
<30	346731	1.1	344008	0.8	3.3	1135295
30-40	2389431	7.2	3164556	7.0	29.9	94580430
40-50	3590185	10.8	5375367	11.9	49.7	267401340
50-60	3569794	10.8	4960555	11.0	65.6	325423369
60-70	4801864	14.5	6581443	14.6	78.8	518633656
>70	18444115	55.7	24692663	54.7	100.0	2469266269
Total	**33142120**	**100.0**	**45118592**	**100.0**		3676440359
					Average growth relative to normoxia	**81.5**
					Decrease in growth due to hypoxia	**18.5**

Table 3. Estimation of the biomass and number of cod present in each class of dissolved oxygen between 11 Aug 1995 and 04 Sep 1995 (CCGS Alfred Needler survey no. 6), and of the average production growth relative to growth in normoxia.

Dissolved oxygen (%)	**Cod biomass (kg)**	**Cod biomass (% of total)**	**Cod number**	**Cod number (% of total)**	**Production growth (% relative to normoxia)**	**Growth x cod number**
<30	30927	0.3	29063	0.2	3.3	95914
30-40	710049	5.9	783729	5.6	29.9	23423631
40-50	1212497	10.2	1350228	9.7	49.7	67168030
50-60	1276650	10.7	1497134	10.7	65.6	98215309
60-70	2400859	20.1	2794650	20.0	78.8	220225207
>70	6316553	52.9	7523001	53.8	100.0	752300070
Total	**11947535**	**100.0**	**13977805**	**100.0**		1161428160
					Average growth relative to normoxia	**83.1**
					Decrease in growth due to hypoxia	**16.9**

Table 4. Estimation of the biomass and number of cod present in each class of dissolved oxygen between 06 Oct 1995 and 04 Nov 1995 (Sentinel fishery mobile gear survey no. 4), and of the average production growth relative to growth in normoxia.

Dissolved oxygen (%)	**Cod biomass (kg)**	**Cod biomass (% of total)**	**Cod number**	**Cod number (% of total)**	**Production growth (% relative to normoxia)**	**Growth x cod number**
<30	139384	0.5	171586	0.4	3.3	566266
30-40	625152	2.2	775852	1.6	29.9	23188220
40-50	2069680	7.2	2612753	5.3	49.7	129973207
50-60	2695704	9.3	3124703	6.3	65.6	204987421
60-70	4693170	16.2	5654529	11.4	78.8	445590593
>70	18702456	64.7	37248043	75.1	100.0	3724804263
Total	**28925546**	**100.0**	**49587465**	**100.0**		4529109970
					Average growth relative to normoxia	**91.3**
					Decrease in growth due to hypoxia	**8.7**

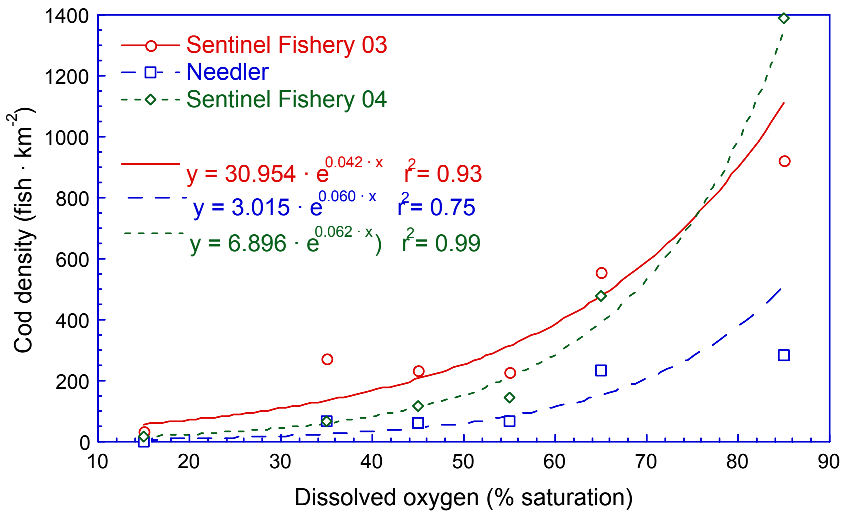

Figure 4. Relationship between cod density within the area associated with a class of dissolved oxygen, and the level of dissolved oxygen (in% saturation).

It is believed that the peak of the feeding period for this stock is July to September, even though there is no seasonal sampling of cod stomachs to clearly define the feeding season. Spawning generally occurs from May to early July (Lambert & Dutil 1997), and in the laboratory, mature cod do not eat during spawning (Fordham & Trippel 1999). Condition is at a minimum during the spring, and increases rapidly in July and August (Lambert & Dutil 1997). Condition declined in early fall 1993, but it is not clear if this was due to poor feeding conditions that year, or if it is a normal feature of the feeding cycle in this stock (Lambert & Dutil 1997). A large sample collected in the northern Gulf in January 1994 suggests that cod eat little in winter, as over 80% of the stomachs were empty, and average stomach fullness was very low (D. Chabot, unpublished data). In the neighboring southern Gulf cod stock the feeding cycle is better documented and agrees very well with this proposed cycle (Schwalme & Chouinard 1999). Therefore the three surveys used in this study encompass most of the post-spawning feeding season.

Our model estimates that, for the stock as a whole, hypoxia curtails production growth by 17-19% in summer, during the peak of the feeding season, and 9% in fall. Hypoxia appears to exert a significant constraint on production growth for this stock, especially considering its low productivity due to the cold temperatures of the Gulf of St. Lawrence (Dutil et al. 1999).

This first model is simplistic and makes assumptions that clearly are not correct. The single most important omission is the effect of temperature. Cod are found at temperatures varying from –1 to 6° C and at a salinity of 30 to 35 in the northern Gulf of St. Lawrence. The model does not allow for temperature effects on the solubility of oxygen or on metabolic and digestion rates.

The hypoxic waters that cod encounter are typically between 3 and 6° C, with a salinity of 34-35. Oxygen solubility is 10-11 mg $\cdot$ L^{-1}, at these temperatures and salinity, whereas it was only 9.4 mg $\cdot$ L^{-1} in our laboratory experiments (10° C and a salinity of 28) (Benson & Krause 1984). Thus at similar oxygen saturation, the concentration of oxygen is almost 10% greater for wild cod than during our experiments. This would lower the lethal threshold and the incipient threshold for growth relative to what we observed in the laboratory (28 and 73%, respectively, Chabot & Dutil 1999), as shown by Claireaux et al. (2000).

But wild fish need to spend more energy swimming to capture prey, avoid predators, and migrate, than cod in our laboratory experiments, which could result in even less oxygen being available to process food in wild fish than in laboratory fish. These opposing trends may minimize the impact of leaving the effect of temperature out of the model. But clearly, data on the interaction between temperature, oxygen, and growth are needed, and experiments in our laboratory are planned to fill this gap. In addition to improving this model, these data would allow calculation of the relationship between metabolic scope and growth, making it possible to use the model of Claireaux et al. (2000) to assess the impact of hypoxia and temperature on growth production.

This model also assumes that the impact of hypoxia on cod growth is the same for cod of all sizes and condition. There are no data on the interaction between cod size, oxygen and growth, and experiments are needed to include the effect of cod size in the model. However, available data suggest that there is a negative relationship between condition and food ingestion, regardless of oxygen level (Chabot et al. 2001). The effect of cod condition, which varies with the month of the year, should thus be included to make the model more realistic.

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