



Short communication

The effect of oxygen saturation on the growth and feed conversion of juvenile Atlantic cod (*Gadus morhua* L.)

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ABSTRACT

In land-based fish farms, water quality can be controlled to support maximum growth and good feed conversion. Oxygen is an important water quality parameter in aquaculture and the objective of this study was to detect the range of oxygen saturations that maximizes growth of juvenile Atlantic cod. The fish (initial body mass 21.9 g) were reared at five different levels of oxygen saturation: 65%, 81%, 103%, 121% and 150% of air saturation, for 98 days. At oxygen saturation under 100%, the growth of the fish decreased linearly with progressively lower oxygen saturation with the final body mass of fish reared at 65% saturation being 24% lower than that of fish reared at 103% saturation. The final body mass of fish reared at 150% saturation was significantly higher (7%) than that of fish reared at 103% saturation. Feed intake was also affected by oxygen saturation and was proportional to growth while the feed conversion ratio was not significantly affected by oxygen levels. The results suggest that oxygen saturation of at least 100% is required to obtain maximum growth of juvenile Atlantic cod.

1. Introduction

Oxygen saturation in water is one of the most important environmental factor that can limit the growth rate of aquaculture fish. This has been confirmed in many of studies on different species of fish including rainbow trout, *Oncorhynchus mykiss*, (Dabrowski et al., 2004; Glencross, 2009), Atlantic salmon, *Salmo salar*, (Bergheim et al., 2006; Thorarensen and Farrell, 2011; Remen et al., 2012) sea bass, *Dicentrarchus labrax*, (Thetmeyer et al., 1999; Pichavant et al., 2001), spotted wolffish, *Anarhichas minor*, (Foss et al., 2002), turbot, *Scophthalmus maximus*, (Pichavant et al., 2000; Pichavant et al., 2001; Person-Le Ruyet et al., 2003), and Atlantic halibut, *Hippoglossus hippoglossus*, (Thorarensen et al., 2010).

Reduced oxygen saturation affects the survival (Plante et al., 1998), behaviour (Schurmann and Steffensen, 1997; Herbert and Steffensen, 2005) and growth (Chabot and Dutil, 1999; Olsvik et al., 2006; Remen et al., 2008) of Atlantic cod, *Gadus morhua*. At oxygen saturation near or below 20–30% of air saturation, mortality rates of Atlantic cod increase and no fish survived below 10% saturation in a 96-h challenge

test (Plante et al., 1998). The growth of Atlantic cod at different levels of oxygen saturation has been compared in at least three studies. Chabot and Dutil (1999) compared growth at saturation levels between 45% and 93% of air saturation and concluded that the growth of Atlantic cod (mean body-mass: 715 g) is reduced as oxygen saturation is decreased below 65–73%, while increasing oxygen saturation to higher levels did not appear to improve growth rate. Olsvik et al. (2006) found no difference in growth performance of juvenile Atlantic cod (mean body-mass: 20 g) reared at either 76% or 145% of air saturation but both groups grew significantly better than fish reared at 42% saturation. Interestingly, Olsvik et al. (2006) found no growth at 42% of air saturation while Chabot and Dutil (1999) found positive growth at 45% saturation, possibly reflecting the larger size of the fish in the latter study. Remen et al. (2008) found that the growth rate of Atlantic cod (mean body-mass: 20 g) was significantly higher at 101% than at 57% of air saturation while the growth rate at 81% was intermediate and not significantly different from either the higher or lower saturation level. Combined, these results may suggest that the minimal oxygen saturation required for maintaining maximum growth of Atlantic cod may be

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between 60% and 100% of air saturation. However, the only study that has investigated this threshold in Atlantic cod, found it to be 73% of air saturation (Chabot and Dutil, 1999), but fragmented results from later studies suggest that it may be higher, up to 100% of air saturation (Remen et al., 2008) or higher (Olsvik et al., 2006). It is, therefore, not known what level of oxygen saturation is required to maximize the growth of Atlantic cod.

There is some evidence that moderate hyperoxia may improve the growth of fish (Foss et al., 2003; Dabrowski et al., 2004; Hosfeld et al., 2008) while other studies have failed to find any improvement of growth when oxygen saturation is increased above 100% of air saturation (Caldwell and Hinshaw, 1994; Person-Le Ruyet et al., 2002). While moderate hyperoxia may in some cases improve the growth rate of fish, too high levels of oxygen may be detrimental (Lygren et al., 2000; Espmark and Baeverfjord, 2009). Currently there is no information available on the effect of hyperoxia on the growth of Atlantic cod.

The objective of this study was to find the oxygen saturation where production efficiency (growth and feed conversion ratio) is maximized, without negative effects of either hypoxia or hyperoxia.

2. Materials and methods

2.1. Experimental fish

Atlantic cod (20.9 ± 0.3 g mean body mass \pm SE) were obtained from the Marine Research Institute (MRI) in Grindavík, Iceland and brought to Verið research station in Sauðárkrúkur where the experiments were performed. At MRI, the cod larvae were fed rotifers, *Brachionus plicatilis*, from 2 to 35 days post hatch (dph), *Artemia* nauplii, *Artemia franciscana*, from 15 to 25 dph and *Artemia* metanauplii from 22 dph until weaning to artificial feed at 53–56 dph. The rearing water had stable 32–33 ppt salinity and the temperature was raised gradually from 7 °C during the egg stage to 10 °C at 14 dph and 12 °C at 30 dph onwards until transport. Upon arrival at Verið research station, the fish were distributed at random among 20 fibreglass tanks (800 L, square tanks with rounded corners), 50 fish in each tank. Before the experiment started, the fish were given 15 days to acclimate to the tanks and conditions during the experiment; water temperature of 10 °C, salinity of 29 ppt and 24 h light photoperiod regime.

2.2. Control of oxygen saturation

During the experiment, the fish were subjected to five different levels of oxygen saturation. The target levels were: Hypoxia: 60%; mild hypoxia: 80%; normoxia: 100%, mild hyperoxia: 120% and hyperoxia: 150% of air saturation. However, mean values for oxygen saturation in the five treatments were (mean \pm standard deviation): hypoxia $65 \pm 11\%$; mild hypoxia: $81 \pm 6\%$; normoxia: $103 \pm 8\%$, mild hyperoxia: $121 \pm 10\%$ and hyperoxia: $150 \pm 12\%$. Each treatment was tested in a separate system with four tanks in each system. Each rearing system had a separate aerator and a low head oxygenator (LHO) (Timmons et al., 2002). The oxygen saturation was adjusted by injecting pure nitrogen (low oxygen treatments) or oxygen (high oxygen treatments) gas into the LHO of each system. Oxygen saturation was measured daily with a hand-held oxygen meter (YSI 550A) in the tank outlet each morning before the fish were fed and adjusted, if required, by adjusting the inflow of oxygen and nitrogen into the LHO. The total water flow into each tank was $17 \text{ L} \cdot \text{min}^{-1}$ consisting of a mixture of reused water ($12 \text{ L} \cdot \text{min}^{-1}$) and of new water ($5 \text{ L} \cdot \text{min}^{-1}$). These high rates of water turnover in the tanks and the low biomass limited daily fluctuations in oxygen saturation due to a variation in metabolic rate to less than $\pm 4\%$ oxygen saturation.

2.3. Measurements of feeding and growth

The fish were handfed with dry pellets (LAXÁ, Akureyri, Iceland, size: 3–4 mm, containing 52% crude protein, 19% crude fat, 9.0% crude ash) two times each day except Sundays when the fish were not fed. The first feeding was around 9 am and the second feeding around 2 pm. To ensure satiation, fish were fed until uneaten feed pellets were observed in the tank bottom and in feed traps located in the effluent of each rearing tank. The amount of feed presented each day was recorded. The feed conversion ratio (FCR) for fish in each tank was calculated as:

$$\text{FCR} = \text{weight of feed presented} / \text{increase in biomass}$$

The fish were individually weighed to the nearest 0.1 g at the beginning of the experiment and then at approximately one month intervals until the experiment was terminated after 98 days. Before the fish were measured, they were anaesthetised with 2-phenoxy ethanol (0.3:1000 PE:water). The specific growth rate (SGR) was calculated as ($\% \cdot \text{day}^{-1}$) based on the mean body mass in different tanks:

$$\text{SGR} = 100 \times (\ln(w_2) - \ln(w_1)) / (t_2 - t_1)$$

where w_1 is the initial mean body mass at time t_1 and w_2 is the mean body mass at the end of the growth period (at t_2).

2.4. Statistical analysis

The mean weight of the fish was compared at each sampling date with a nested two-way ANOVA (tanks nested as random factors within treatment) and Tukey's test used for post hoc comparison of different treatments. The growth trajectories of different groups were also compared with a two-way (treatment \times time) nested ANOVA (Ling, 2007). Given average variation in aquaculture growth studies, the combination of quadruplicate design and 50 fish in each tank are expected to allow differences of 16% (effect size) of the grand mean to be detected with 80% statistical power (Thorarensen et al., 2015). The FCR for different treatments was compared with a one-way ANOVA. Mortality rates were compared with a χ^2 test. All statistical analyses were performed using SYSTAT® 11 (Systat Inc., Point Richmond, CA).

3. Results

Oxygen saturation significantly affected the growth of the juvenile cod. At the end of the experiment there was a significant ($P < 0.001$) difference in body mass (Fig. 1a) and length (Fig. 1b) among the groups. The average body mass of the groups subjected to 65% and 81% of air saturation were 24% and 9% less, respectively, than that of the group subjected to 103% saturation and significantly different from all other groups (Fig. 1a). Furthermore, there was significant difference in the final body mass of the groups subjected to 103% and 150% of air saturation with the latter group having a 7% larger average body mass. The oxygen saturation also significantly affected the final length of the fish (Fig. 1b): The final length of fish subjected to 65% and 81% of air saturation was significantly different from that of all other groups. Similar trend as was observed for body mass was seen for final length (Fig. 1b) among the experimental groups. These differences in final length and weight were reflected in the SGR (Fig. 2a). The SGR of the fish subjected to 65% of air saturation was lowest; the growth rate of the fish subjected to 81% saturation was intermediate and significantly different from all other groups. However, there was not a significant difference in the SGR of fish subjected to 103% and 150% oxygen saturation.

There was a significant ($P < 0.01$) difference in the initial condition factors of the fish (Fig. 1c), but as the experiment progressed, the condition factor increased significantly in all groups ($P < 0.001$) from day 0 to day 71 and then remained stable or decreased slightly from day 71 to day 98. There was a significant interaction between time and oxygen saturation (three way ANOVA, $P < 0.002$) indicating that the

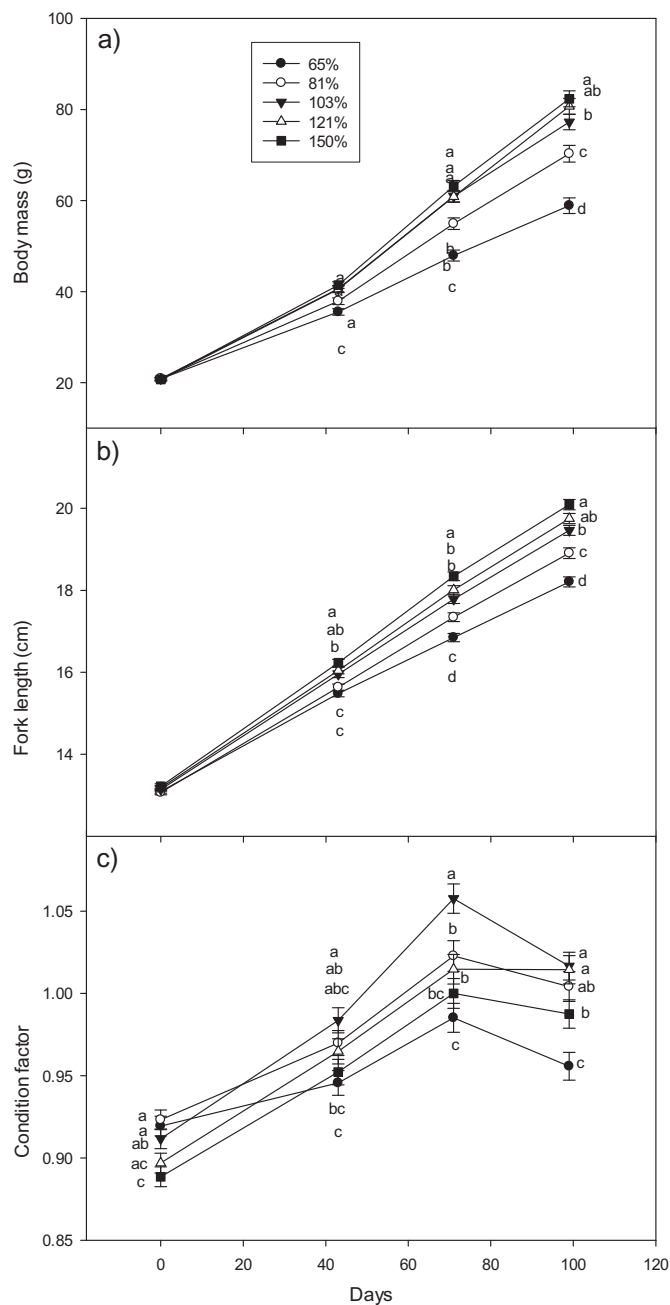


Fig. 1. Growth of juvenile Atlantic cod subjected to different levels of oxygen saturation in water: a) Mean body mass, b) mean length and c) mean condition factor. The error bars indicate the standard error of the mean. Values indicated with different letters are significantly different.

increase in condition factor over time was not uniform among all groups. The condition factor of the groups subjected to 103%, 121% and 150% of air saturation increased by 11–13% during the experiment. The condition factor of the group subjected to 81% of air saturation increased by 9% while the condition factor of the group subjected to 65% saturation increased by only 3%.

Feed intake was significantly ($P < 0.001$) affected by oxygen saturation (Fig. 2b) and appeared to follow a similar pattern as did the SGR. In contrast, FCR was not significantly affected by the oxygen saturation.

The mean mortality rate in all treatments during the experiment was 9% (Table 1) and did not vary among the experimental groups (χ^2 : 0.79; $P < 0.94$).

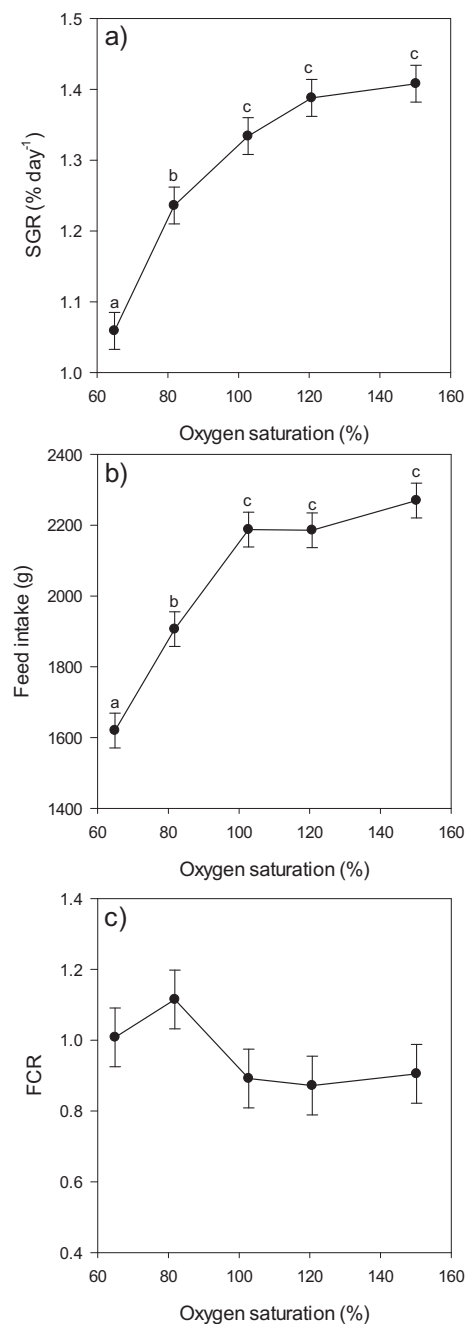


Fig. 2. Specific growth rate (a), feed intake (b) and FCR (c) of juvenile Atlantic cod reared at different levels of oxygen saturation. The error bars indicate the standard error of the mean. Values indicated with different letters are significantly different.

4. Discussion

The results of the present study show, that oxygen saturation affects the growth of juvenile Atlantic cod and indicate that the critical limits in oxygen saturation, under which the growth of Atlantic cod is compromised, are higher than suggested by earlier studies (Chabot and Dutil, 1999; Olsvik et al., 2006; Remen et al., 2008). Our results suggest, these critical limits lie between 100% and 150% of air saturation, although the effects of reduced oxygen levels are most apparent below 100% saturation. Other studies have also reported reduced growth of Atlantic cod under hypoxia. Chabot and Dutil (1999) estimated the minimal oxygen saturation for maximum growth as 65% and 73% of air saturation for growth in length and weight respectively. Furthermore, Olsvik et al. (2006) found significantly lower growth rate

Table 1
Survival of juvenile cod subjected to different levels of oxygen saturation in water.

O ₂ sat.	Day 0		SD	Day 43		SD	Day 71		SD	Day 99		SD
65%	100%	±	0%	98%	±	3%	96%	±	4%	92%	±	11%
81%	100%	±	0%	97%	±	2%	92%	±	10%	91%	±	16%
103%	100%	±	0%	96%	±	2%	93%	±	5%	91%	±	6%
121%	100%	±	0%	95%	±	3%	91%	±	3%	92%	±	4%
150%	100%	±	0%	93%	±	8%	91%	±	9%	90%	±	10%
Average	100%	±	0	96%	±	4%	93%	±	7%	91%	±	10%

at 45% than at 76% of air saturation, while the growth rate at 145% was higher (albeit not significantly) than at 76%. The reason for this apparent discrepancy between the results of the present and previous studies could be due to different experimental design and statistical analysis. In the study of Chabot and Dutil (1999), the critical oxygen saturation for maximum growth was determined by regression analysis where the critical level is defined as the intersection of two lines: the regression line fitted to the data for the three lowest levels of dissolved oxygen (45, 56, 65%), and a line representing the mean in the two highest levels of dissolved oxygen (84 and 93%). Thus, the fidelity of their estimate of critical oxygen saturation is limited both by the few points through which the line was fitted and no replication of treatments. Furthermore, that study did not include oxygen saturation above 93% thus possibly missing critical oxygen saturation. The primary objective of the study of Olsvik et al. (2006) was not to measure antioxidant and stress enzyme activity rather than growth. By investigating such a wide range of oxygen saturations and with a robust experimental set-up, i.e. treatments tested in quadruplicates with 50 fish in each tank, the statistical power of the present study is higher (Thorarensen et al., 2015) and allows detection of smaller differences between means than the previous studies. Based on this we argue that the present findings suggest that Chabot and Dutil (1999) underestimated the minimum oxygen saturation required for maximal growth.

The results of the present study are in accordance with results from studies on species such as Atlantic halibut (Thorarensen et al., 2010), Atlantic salmon (Berghheim et al., 2006) and spotted wolffish (*Anarhichas minor*) (Foss et al., 2003), which suggest that the minimal oxygen saturation for growth is close to 100% of air saturation or even higher. Hyperoxia appears to stimulate growth of juvenile cod beyond normoxic values which is consistent with results from some studies on rainbow trout (Dabrowski et al., 2004), Atlantic salmon (Hosfeld et al., 2008), spotted wolffish (Foss et al., 2003) and sea bass (Cecchini and Caputo, 2003). However, other studies have not found any benefit of hyperoxia for growth (Caldwell and Hinshaw, 1994; Lygren et al., 2000; Espmark and Baevefjord, 2009). The reasons for this discrepancy are not clear although in some cases they might be caused by differences in total gas pressure rather than hyperoxia (Hosfeld et al., 2008).

The feed intake at different oxygen levels closely matched the growth of the fish in the present study. These results are in accordance with the results of Chabot and Dutil (1999) who found a near linear relationship between feed intake in cod and oxygen saturation. A similar relationship between growth and feed intake at reduced oxygen levels has been observed for other species (Thetmeyer et al., 1999; Pichavant et al., 2000, 2001; Foss et al., 2002; Glencross, 2009). In fact, it has been suggested that the reduced growth during hypoxia is caused by the reduced feed intake (Chabot and Dutil, 1999; Pichavant et al., 2001; Glencross, 2009), possibly mediated through the effects of hypoxia on leptin levels (Bernier et al., 2012).

Fry (1971) proposed a model to explain the effects of environmental factors, such as oxygen, on the survival and performance of fish through their effects on metabolic rate (usually measured as oxygen consumption as a proxy for aerobic metabolism). A key concept of this model is the metabolic scope (MS: The difference between standard and maximum metabolic rates) which defines how much energy can be

allocated to functions other than those required for basic maintenance metabolism. Fry (1971) suggested, that environmental oxygen was a limiting factor to metabolism, which could curtail the MS and, thus, leaving less energy available for metabolic activities such as growth. The specific dynamic action (SDA) is the metabolic cost of feed intake, digestion, absorption and assimilation (Secor, 2009) and, in essence, the metabolic cost of growth. If hypoxia limits the MS, the maximum oxygen consumption during the SDA could be reduced and the duration of the SDA prolonged (Eliason and Farrell, 2014) resulting in reduced growth due to extended digestion time. Similar arguments, based on Fry's paradigm, have been employed to explain the effects of hypoxia on the growth of Atlantic cod (Claireaux et al., 2000; Chabot and Claireaux, 2008). Although this has not been directly tested in experiments, there is circumstantial evidence in favour of this suggestion such as the significant correlation between the growth rate of Atlantic cod and MS (Claireaux et al., 2000). Furthermore, in more severe hypoxia than tested in the present study (30% saturation) the peak oxygen consumption of the SDA and the MS were both reduced (Jordan and Steffensen, 2007). In juvenile cod (< 8 g), the peak oxygen consumption during SDA occupies nearly the entire MS (Hunt von Herbing and White, 2002), which suggests that even small changes in MS could affect the growth of small cod. However, in larger cod (137–184 g) the peak oxygen consumption during SDA occupied only about 50% of the MS (Jordan and Steffensen, 2007), which may suggest that near normoxia, oxygen saturation is unlikely to affect maximum oxygen uptake during SDA in fish of this size. Furthermore, there appear to be only very modest changes in the MS (5–20%) of Atlantic cod when oxygen saturation is reduced from 100% to 81% (Claireaux et al., 2000; Dutil et al., 2007; Jordan and Steffensen, 2007) suggesting, that the reduced growth at 81% saturation, found in present study, may not have been due to respiratory limitations to the SDA.

5. Conclusions

Present findings suggest that oxygen saturation of at least 100% is required to obtain maximum growth of juvenile Atlantic cod.

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