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Review

Long-term carbon dioxide experiments with salmonids

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ABSTRACT

Oxygen is generally the first limiting factor for the water flow requirement in a land based aquaculture system, while carbon dioxide and pH are secondary limiting factors. This means that if oxygen is added to the inlet water or directly to the water in a fish tank carbon dioxide becomes the limiting factor. pH is easy to regulate by addition of bicarbonate, while carbon dioxide always will be elevated in both single pass oxygenated systems and in recirculation systems. Carbon dioxide has both direct physiological effects on the fish, as well as indirect effects by changing the pH and thereby the chemistry of metals in the water.

During the last 20 years several long-term carbon dioxide experiments have been performed at Bergen University College. In the present paper general methods and findings from the research at Bergen University College are described. These findings are compared with studies performed elsewhere. Increased plasma PCO_2 increases the plasma bicarbonate concentration and reduces the plasma chloride concentration. In a long-term carbon dioxide experiment on Atlantic salmon postsmolts about 94% of the total variation in plasma carbon dioxide partial pressure was explained by the partial pressure in the water in a simple linear regression model, and 72% of the total variation in plasma chloride was explained by the plasma bicarbonate concentration. There was a reduction in about 1 mM Cl^- for every 1 mM increase in plasma bicarbonate.

For carbon dioxide the safe criterion used for the Norwegian production of Atlantic salmon smolts is 15 mg L^{-1}. In low alkalinity fresh water carbon dioxide has adverse effects on fish in combination with labile Al/pH at concentrations around 8–10 mg L^{-1} CO_2, and the smolts are not acclimated to such conditions. When toxic Al is not present in the water 8–10 mg L^{-1} carbon dioxide may have slight but significant effects on condition factor during the first month, but the smolts seem to be acclimated to these conditions after 2 months. However, when the concentration of carbon dioxide is 17–19 mg L^{-1} (5–6 mm Hg) in low alkalinity water, condition factor or specific growth rate is reduced after 2 months exposure.

In high alkalinity fresh water, carbon dioxide had only minor effects on growth up to 24 mg L^{-1}, however, further research may be needed to validate this and to study how the safe threshold level for carbon dioxide is influenced by temperature and salinity.

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1. Introduction

1.1. Carbon dioxide and fish physiology

Oxygen is generally the first limiting factor for the water flow requirement in a land based aquaculture system. Once oxygen is added in pure form, carbon dioxide may become the limiting factor. Water quality includes parameters such as oxygen, carbon dioxide, pH, alkalinity and hardness. The present paper will concentrate on carbon dioxide, pH and alkalinity since these factors are closely related as part of the carbonate system. The carbonate system is the most important buffer system in both fresh water and sea water and in blood plasma for fish and humans. There is much information available concerning the effects of carbon dioxide on fish, especially from short term experiments on freshwater fish. In general plasma PCO_2 increases with increasing ambient PCO_2 levels. The venous plasma PCO_2 in fish is mostly in the range 2.5–4.5 mm Hg in normoxic and normocarbic water (Ultsch, 1996). The fish acid-base response to an elevation in plasma PCO_2 is first a reduction in plasma pH, which significantly reduces oxygen transport, however after a few hours considerable compensation has occurred as a result of increased bicarbonate concentration (Eddy et al., 1977). Plasma pH is restored close to control values within 2–7 days as a result of this (Heisler, 1984, 1986). Other physiological effects on fish exposed to hypercapnia include increased adrenaline levels (Perry et al., 1986b), hyperventilation (Janson and Randall, 1975; Smith and Jones, 1982; Fivelstad et al., 1999; Hosfeld et al., 2008), reduced branchial chloride influx rates (Perry et al., 1986a; Goss et al., 1994) and reduced plasma chloride (Lloyd and White, 1967; Eddy et al., 1977; Fivelstad et al., 1999, 2003a,b). During acute carbon dioxide exposure elevated plasma cortisol levels have been observed (Petochi et al., 2011). Reduced growth, reduced feed conversion efficiency and nephrocalcinosis are commonly observed effects of long-term freshwater exposures to carbon dioxide in rainbow trout and Atlantic salmon (Smart et al., 1979; Smart, 1981; Fivelstad et al., 1999, 2003a,b, 2007; Hosfeld et al., 2008).

1.2. Carbon dioxide, alkalinity and pH/Al

Carbonic acid is formed when carbon dioxide is dissolved in water:

$$CO_{2(aq)} + H_2O \leftrightarrow H_2CO_3 \quad (1)$$

Only a minor part of the $CO_{2(aq)}$ is converted to H_2CO_3. Because it is difficult to distinguish between $CO_{2(aq)}$ and H_2CO_3 analytically, a hypothetical compound $H_2CO_3{}^*$ has been introduced (Gebauer et al., 1992). $H_2CO_3{}^*$ is the sum of $CO_{2(aq)}$ and H_2CO_3. The equilibrium equations are stated as:

$$H_2CO_3{}^* \leftrightarrow H^+ + HCO_3{}^- \quad (2)$$

$$HCO_3{}^- \leftrightarrow H^+ + CO_3{}^{2-} \quad (3)$$

The sum of $H_2CO_3{}^*$, $HCO_3{}^-$ and $CO_3{}^{2-}$ is defined as total carbonate:

$$C_T = [H_2CO_3{}^*] + [HCO_3{}^-] + [CO_3{}^{2-}] \quad (4)$$

Alkalinity is the capacity of the water to neutralize acid (Millero, 1996; Stumm and Morgan, 1996). For freshwater aquaculture single pass systems it can be written as:

$$\text{Alkalinity} = [HCO_3{}^-] + 2[CO_3{}^{2-}] + [OH^-] - [H^+] \quad (5)$$

For sea water systems and for recirculation systems the terms to be included are (Blancheton et al., 2007):

$$\text{Alkalinity}_{\text{extra}} = [B(OH)_4{}^-] + [NH_3] + [SiO(OH)_3{}^-] + [HPO_4{}^{2-}] + 2[PO_4{}^{3-}] - [H_3PO_4] \quad (6)$$

When carbon dioxide is accumulated in a fish tank the magnitude of the pH-drop is dependent on the alkalinity. Most of the Norwegian Fish farms have low alkalinity in their freshwater supply (Kristensen et al., 2009). The water also contains aluminium, because aluminium is leached from the soil as a cause of acid precipitation (Jenssen and Leivestad, 1989). The toxicity is pH dependent with the highest toxicity below pH 6.0 and above pH 7.0. Because of the pH-drop in the water in the fish tanks the toxic forms of aluminium may become remobilized. Therefore Al has to be considered in all our experiments.

1.3. The scope of the present paper

In the present paper the long-term carbon dioxide experiments performed at Bergen University College from 1994 until today are summarized. General trends and findings are described. The results will be related to alkalinity, pH, labile Al, temperature and life stage of the fish. The presentation is based on published and unpublished data. In most of the fresh water experiments there have been an experimental group exposed to 15–20 mg L^{-1} CO_2 in addition to a control group. The widely held safe criterion for carbon dioxide for fresh water fish was 20 mg L^{-1} (Smart, 1981), and one of the groups was therefore exposed to a slightly lower concentration than this. This concentration range also became a reference point for most of the experiments. In our low alkalinity experiments, the range 0.06–0.09 mM was also a reference point. The reason for this was the low alkalinity in the Norwegian fresh water.