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Behavioural responses to pressure changes in cultured Atlantic cod (*Gadus morhua*): Defining practical limits for submerging and lifting sea-cages

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ABSTRACT

Farmed Atlantic cod (*Gadus morhua*) are occasionally exposed to buoyancy changes in sea-cages, through lifting or lowering of cage nets. Physiological processes regulate the level of gas in the closed swim bladders of cod and thus the ability of cod to control their buoyancy. Rapid net lifting may cause positive buoyancy, leading to barotrauma, while net lowering may lead to negative buoyancy and alter cod behaviours. We tested how groups of farmed cod responded immediately after lifting events from 5 different start depths equivalent to 40% pressure reductions, and how long they took to return to pre-lifting pressure levels. In addition, we tested immediate responses and recovery times to cage lowering events equivalent to 100–300% pressure increases. Trials were conducted with 100 cod of 1.1–1.7 kg in a 63 m^3 sea-cage at the lower (5 °C) and upper (16 °C) water temperature limits experienced during culture. Swimming behaviours were measured at fixed intervals before and after cage lifting or lowering, and a feeding test was used to assess appetite. In general, lifting events increased swimming speeds 1.5–4 times and tail beats 2–3 times and fish swam with an average −14° head-down angle, indicating positive buoyancy. The depth before lifting affected the immediate response as the fish became more active after lifting events from shallow compared to deeper depths. Appetite levels decreased for about 2 h after cage lifting, independent of temperature or start depth. The overall recovery time of 8 h after lifting did not depend upon start depth or temperature. Lowering events appeared to cause negative buoyancy. Swimming speeds (1.3–2.3 times) and tail beat frequencies (1.4–2.3 times) increased immediately after cage lowering, and cod swam with an average 30° head-up swimming angle. Neither pressure level nor temperature affected this immediate response. Time to recover to neutral buoyancy for 300% pressure increases took 42–90 h, but only 18–34 h for 100% pressure increases. We conclude that a 40% pressure reduction is an upper limit for lifts of healthy farmed cod. Secondary lifts should not be done until at least 10 h after the first lift. Cage lowering should be done slowly to avoid potentially stressful crowding of negatively buoyant fish on the cage bottom, especially at low temperatures.

1. Introduction

Many modern fish farms use up to 50 m deep cages to allow fish to choose swimming depths based on the ambient environment. In addition, the limited availability of sheltered areas may stimulate increased use of partially or fully submersible cages that can be localized in wave exposed areas (Chambers and Howell, 2006). These farming technologies entail specific challenges for fish with different types of swim bladders. Recent studies have investigated the effects of submergence on the behaviour and growth of Atlantic salmon in industry-scale sea-cages (Dempster et al., 2008, 2009; Korsøen et al., 2009). Atlantic salmon have open swim bladders (physostome) that must be filled by swallowing air at the surface, thus submergence results in fish becoming negatively buoyant and causes fish to compensate through behavioural changes such as faster swimming and tighter schooling. Fish with closed swim bladders (physoclist) will face very different challenges in sea-cages as they have slow swim bladder inflation- and deflation-rates. Therefore, the rate at which sea-cages are lowered and lifted will be critical.

Rapid lifting of deep nets or submerged cages has resulted in barotrauma for fish. When swim bladders inflate beyond levels that fish can cope with through the resorption of gas from the swim bladder (Fänge, 1953; Steen, 1963) or behavioural adaptations, they float with the belly up, causing stress, internal injuries, and in some

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cases mortality (Gitschlag and Renaud, 1994; Nicol and Chilton, 2006). In contrast, rapid lowering of a submersible cage might cause negative buoyancy in fish as their swim bladder becomes compressed. Data from tagged wild cod in natural habitats indicates that cod rarely ascend rapidly to depths corresponding to more than a 50% pressure reduction relative to neutral buoyancy depth (Godø and Michalsen, 2000; Stensholt et al., 2002), and pressure reduction >60% can cause swim bladder rupture (Blaxter and Tytler, 1978; Harden Jones and Scholes, 1985). Harden Jones and Scholes (1981) followed individual cod in the sea, and suggested a "free vertical range" corresponding to a 25% reduction and a 50% increase in pressure as limits for cod to maintain buoyancy control. Kristiansen et al. (2006) found that free swimming farmed cod tagged with depth loggers, voluntarily ascended to depths equivalent to a maximum of 40% pressure reduction. From pressure tank experiments, the resorption of gas by the swim bladder is known to occur more rapidly than secretion, with gas resorption rates positively correlated with pressure, but not with temperature (Blaxter and Tytler, 1978; Harden Jones and Scholes, 1985). In a farming situation, crowded fish might be stressed during rapid lifting events, which may reduce their resorption capacity, as stress leads to an ionic/osmotic disturbance (McDonald and Milligan, 1997). A 40% pressure reduction, as suggested by Kristiansen et al. (2006), might thus leave little 'safety buffer'; thus, explicit testing of the 40% pressure reduction recommendation in sea-cages is required. Moreover, the recovery time, which is an important parameter to enable safe lifting to the surface if several steps are required, was not measured in Kristiansen et al. (2006) and cannot be defined from data from wild cod in the sea.

For cage submergence, the rate of secretion of gas into the swim bladder will determine how long physoclists take to compensate for possible negative buoyancy. Gas secretion rates into the swim bladder depend on temperature and pressure. The refilling rate for cod was studied by Harden Jones and Scholes (1985) where cod in a pressure tank attained neutral buoyancy at a rate of 0.5 m h^{-1} at low temperature (0–6 °C) and low pressure (1–3 ATA, absolute atmosphere), and 1.5 m h^{-1}, at higher temperature (13–17 °C) and higher pressure (4–6 ATA). However, wild cod in the sea on average dive slightly slower (average 0.4 m h^{-1}), and dive rates are independent of temperature (Kooij et al., 2007). Rapid cage lowering in a farming situation will induce negative buoyancy and may lead to stress.

Fish can adapt behaviourally to changes in buoyancy in five ways; (1) gliding with extended pectoral fins to generate lift, (2) tilted swimming (optimal around 7° head-up; Strand et al., 2005), (3) body shape creating hydrodynamic lift through swimming movements (Ona, 1990), (4) "hovering" in a steady position, which involves only movement of the pectoral fins (Horn, 1975), and (5) engaging in "sawtooth" swimming, involving repeated bouts of swimming upwards and sinking downwards to maintain a position in the water column (Huse and Ona, 1996). Measuring swim bladder volumes of individual fish in experimental setups is difficult. However, an alternative is to use behavioural proxies to indicate the onset of buoyancy changes.

In this study, we investigated the behavioural responses of cultured cod inside a sea-cage exposed to different pressure changes to assist in defining the tolerance limits for sudden pressure changes and sufficient acclimation time at each depth. We tested the behavioural responses and recovery time to neutral buoyancy of cod after individual lifts which corresponded to 40% pressure reductions (Kristiansen et al., 2006), from five different start depths and in temperature conditions representing the upper (~16 °C) and lower (~5 °C) levels for cod held in sea-cages. Similarly, we investigated the behavioural responses and recovery time to neutral buoyancy of cod subjected to a range of submergences equivalent to pressure increases of 100–300%. In contrast to previous studies of gas secretion and resorption rates of physoclist species in pressure chambers with limited space, the sea-cage experimental set-up enabled farmed cod to swim freely and potentially adapt behaviourally to compensate for changes in buoyancy in addition to the physiological mechanisms of gas regulation in the swim bladder. Finally, we compared the results from these trials with theoretical values from the model of buoyancy regulation for cod developed by Strand et al. (2005).

2. Materials and methods

2.1. Study location, experimental fish and water temperature

Four experiments were conducted at the Institute of Marine Research, Austevoll Research Station in western Norway (60 °N). Experiments 1 and 2 were done at ~16 °C in September 2008. Experiments 3 and 4 were conducted at ~5 °C in March/April 2009.

Approximately 2000 Atlantic cod of a Norwegian coastal strain were hatched in spring 2007, farmed at the Institute of Marine Research's Parrisvatnet (saltwater lake) from larvae to ~20 g, and transferred to 125 m^3 sea-cages at Austevoll for on-growing. Fish size, condition, liver index and gonado-somatic index were measured in a sub-set of individuals used in the experiments (Table 1). At the start of the experiment in September 2008, the fish weighed ~1.1 kg, while in March 2009 they weighed ~1.7 kg. At the beginning of each experiment, 100 different cod were randomly selected from the pool of ~2000 fish and were acclimated in the experimental pen at the surface for three days prior to the first lowering event.

The experimental pen was constructed as a 5×5×2.5 m "box" with black netting (mesh size 20 mm) kept spread with aluminium frames at the top and bottom with a flat roof and bottom.

Feed used during experiments was of the same type as the fish was normally given (Amber Neptun 7 mm, Skretting, Norway), and was provided with water through a 30 m long pipe (4.5 cm diameter) with an opening fitted immediately below the roof in the centre of the cage.

At a reference point close to the experimental unit, a vertically profiling CTD (SD204, SAIV AS, Bergen, Norway, http://www.saivas.no) measured the temperature from the surface to 30 m depth weekly during the experimental period.

2.2. Experimental design

We conducted a series of cage lowering and lifting steps in experiments 1–4 to test the behavioural effects of changes in pressure on Atlantic cod (Fig. 1). The rate of lifting and lowering was standardised; an electrical winch was used to adjust cage depth at a rate of 3.5 m min^{-1} in steps of 0.5 m with 10 s intervals. Lowering steps corresponded to pressure increases of 100% (0 to 10 m submergence),

Table 1
Characteristics of Atlantic cod (*Gadus morhua*) used in Experiments 1 and 2 in August (16 °C) and in Experiments 3 and 4 in March/April (5 °C). K = Fulton's condition factor, HSI = hepato-somatic index, and GSI = gonado-somatic index. F = female and M = male (all data; mean ± SE).

Experiments	n	Fork length (cm)	Body weight (g)	K	HSI	GSI	
						F	M
1 and 2	40	46 ± 0.50	1118 ± 38	1.17 ± 0.01	14 ± 3.0	<1	<1
3 and 4	54	53 ± 0.36	1758 ± 45	1.20 ± 0.02	11 ± 0.3	16 ± 1.0	3 ± 0.2