Received: 4 December 2020 | Revised: 3 February 2021 | Accepted: 3 March 2021

DOI: 10.1111/anu.13260

ORIGINAL ARTICLE

Aquaculture Nutrition WILEY

The effect of alternate-day feeding on growth and feed conversion in Atlantic cod *Gadus morhua*

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Funding information
Norges Forskningsråd, Grant/Award Number: 87291/120

Abstract

This study aimed to investigate the effect of alternating feeding (Alt) compared with control being fed every day (Con) in the on-growth face of Atlantic cod. Individually marked fish (198 and 98 in the Con and Alt groups, respectively) was sampled for weight and length on 6 occasions over a 15-month period, where mean weight increased from 628 and 758 g to 2635 and 3041 g, for the Con and Alt groups, respectively. Feeding alternate day resulted in 13 percentage more weight gain in the alternating feeding group (2283 vs. 2007 g) and improved feed conversion ratio (FCR, 1.07) compared with control (FCR 1.45). The Alt group consumed significantly less feed (27%) compared with control. The results demonstrate that feeding costs can be drastically reduced without compromising biomass growth by using feeding on alternate days during the on-growing period of Atlantic cod.

KEYWORDS

alternate days, Atlantic cod, feeding regime, growth, on-growth face, SGR

1 | INTRODUCTION

Atlantic cod (*Gadus morhua*) has been a promising candidate for marine aquaculture in Norway, with a rise around 1990–2000. The commercial aquaculture production of cod increased rapidly for several years, but biological (low growth rates, early maturation in captivity, poor disease control) and economical (high production costs, increased wild catches putting pressure on prices) factors resulted in the downfall of the industry. The number of farmers was reduced from 2005 and onwards, and most of the industry was closed down. Despite this, there has ever since been an ongoing work aiming at improving the quality of the fish through the 'National breeding program for cod' at Nofima, Tromsø, Norway. The cod available for farming today is the fifth generation since the start-up of the programme, and through the breeding programme, the growth has increased by 9%–10% per generation, early maturation of males is reduced from 95% to 5%, and larval survival has increased significantly (Walker, 2019). Due to this, there is a growing optimism again for cod farming in Norway, and a few companies have put juvenile cod into the sea for farming during 2019 and 2020.

Growth in fish is regulated by factors such as access to food, water temperature and photoperiod (Moyle & Cech, 1982). The feed normally makes up 50%–70% of the expenses in fish farming (Rana et al., 2009). In general, farmed fish is fed every day, but several studies have investigated how different feeding regimes may affect growth and feed conversion ratio. Cyclic starvation/re-feeding regimes have been applied to induce compensatory growth in several species, such as Atlantic cod (Bjørnevik et al., 2017; Hanssen et al., 2012; Jobling et al., 1994), gilthead sea bream (*Sparus aurata)* (Bavčević et al., 2010), Atlantic halibut (*Hippoglossus hippoglossus)* (Foss et al., 2009; Heide et al., 2006), turbot *(Scophthalmus maximus)* (Sæther & Jobling, 1999) and Atlantic salmon (*Salmo salar)* (Stefansson et al., 2009; Young et al.,

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2005). Such restricted feeding and cyclic starvation/re-feeding regimes have documented an improved feed conversion ratio (FCR) in fish following a starvation period (Foss et al., 2009; Heide et al., 2006; Skalski et al., 2005). Less is known about how growth in large cod will be affected by alternate-day feeding compared with daily feeding. There is also a lack of long-term feeding regime studies on larger fish.

The aim of this study was to investigate the effect of alternate-day feeding compared with daily feeding on growth and feed utilization in on-growing cod over a 15-month period.

2 | MATERIALS AND METHODS

2.1 | Experimental fish and conditions

The juvenile Atlantic cod (*Gadus morhua)* used in the present study (n = 400) originated from a commercial hatchery (Sagafjord AS) and hatched in December. From 320 to 530 days posthatch, the fish were reared at the research facility of the University of Nordland (Mørkvedbukta) and thereafter moved by truck to the production site of Fjord Marine Cod in Brønnøysund (65°280 N) where the feeding trial took place from 24 September 2009 to 12 December 2010, 451 days. The fish (mean weight ± SD; 704 ± 277 g) were distributed in 2 sea cages (5 × 5 × 5 m) where 296 out of the total of 400 fish were tagged intraperitoneally using Biomark MK25 implant gun and Biomark GPT 12 12.5-mm needle tags (Biomark Inc.). Two feeding regimes were established. One cage was fed daily 100% ration (control, Con) according to a commercial growth table (Biomar AS), and one cage was fed every second day (alternating, Alt), both under natural light (Brønnøysund, 65°28′30 N). The experiment lasted for 444 days.

The fish were hand-fed either daily or once every second day with a commercially formulated feed (Classic Marine, containing 15-20 g kg-1 fat, 48-54 g kg-1 protein) from Biomar (Myre). The pellet size was gradually increased from 5 to 12 mm according to producer recommendations. The fish were reared at ambient temperatures (annual mean temperature, 7.7°C, max 13.9°C in September, min 3.8°C in March).

The experiment as described here did not include procedures that exposed the fish to pain. The fish were also not exposed to stress beyond what can normally occur in a farming situation. The experiment therefore did not require permission from an experimental animal committee at the time.

2.2 | Growth and feed consumption

All tagged fish (198 fish in Con and 98 in Alt) were anaesthetized with benzocaine and sampled for individual weight and length measurements on 24 September 2009 and then on 13 January, 5 May, 1 August, 23 September and 8 December 2010. The fish were starved for 24 h prior to weighing. Condition factor (CF) was calculated as (weight × length^{-3}) × 100. Mean weight gain was calculated as mean final weight − mean initial weight per group.

Specific growth rate (SGR) of the individually tagged fish was calculated according to the formula of Houde and Schekter (1981):

$$\mathbf{Y}(n \times p) = \mathbf{X}(n \times q)\mathbf{B}(q \times p) + \mathbf{E}(n \times p)$$

where $g = (\ln W_2 - \ln W_1)\,(t_2 - t_1)^{-1}$ and W_2 and W_1 are weights (g) at days t_2 and t_1, respectively.

Biological feed conversion ratio (*b*FCR) per group was calculated based on feed presented/(biomass gain + mortality biomass) for each group. The sea pens were checked for mortalities every day. Any mortalities present were removed, and their weight, length and pit-tag number were registered.

2.3 | Statistics

Statistical analyses were performed using the PASW Statistics version 25.0 (SPSS Statistical Software, IBM Corp.) and STATISTICA^{TM} 13.0, TIBCO Software Inc.). Data are presented as mean ± standard deviation of mean (SD) in tables and as mean ± standard error of mean (SE) in figures. To assess the normality of distributions, a Kolmogorov–Smirnov test (Zar, 1996) was used and the homogeneity of variances was tested using Levene's F test (Brown & Forsythe, 1974). Possible differences in mortality between dietary groups were tested with a chi-square tests (Zar, 1996).

Weight, length, condition factor and SGR data are based on individually tagged fish. The two-way analysis of covariance (ANCOVA, Zar, 1996) with initial weight was used to investigate for possible differences between the experimental groups in weight, length, condition factor and SGR. Significant differences revealed in ANCOVA were followed by the Student–Newman–Keuls (SNK) post hoc test to determine the differences among experimental groups.

Mean individual growth trajectories were analysed using a longitudinal growth curve analysis (GCM) multivariate analysis of covariance (MANCOVA) model (Chambers & Miller, 1995; Timm, 1980) with initial weight as covariate. This method does not demand independency (Diggle et al., 1994) between observations (here fish in the same sea cage).The model equation of the GCM had the form:

$$\mathbf{Y}(n \times p) = \mathbf{X}(n \times q)\mathbf{B}(q \times p) + \mathbf{E}(n \times p) \tag{1}$$

where $\mathbf{Y}$ ($n \times p$) is the growth-at-age vectors.

$$\mathbf{y} = (y_1, y_2, \ldots, y_p) \tag{2}$$

for each p (age) measurements on n individual fish; $\mathbf{X}$ ($n \times q$) is the design matrix or the set of extraneous variables measured for each individual, that is q = age$_p$ + feeding regime$_i$ (i = control, alternate days); $\mathbf{B}$ ($q \times p$) is the matrix of parameters estimated by the model; and $\mathbf{E}$ ($n \times q$) is the matrix of deviations for each individual from the expected value of $\mathbf{Y} = \mathbf{XB}$.

A significance level of .05 was used if not stated otherwise.

3 | RESULTS

3.1 | Growth and feed conversion ratio

Fish density in the cages was low and under 4 kg m^{-3} during the whole experimental period. The total mortality throughout the experiment was significantly higher (chi-square test, $p < .05$) in the Con group (20.3%) compared with the Alt group (4.3%). The Alt group was significantly heavier throughout the trial period (SNK test, $p < .05$) and grew from (mean ± SE) 758 ± 27 to 3041 ± 68 g compared with 628 ± 20 to 2635 ± 85 g for the Con group (Figure 1). No differences were found in the length of the fish in the two groups (two-way ANCOVA, $p > .10$, Table 1). The condition factor (CF) varied between the two feeding groups as the fish in the Alt group had higher CF (SNK post hoc test, $p < .05$, Table 1) throughout the trial period.

Specific growth rate (SGR) varied between the groups and was higher for the Alt group during January to August and during September to December (SNK post hoc test, $p < .05$, Table 2), but higher for the Con group in August–September (SNK post hoc test, $p < .05$, Table 2). Overall, the weight gain was 13% higher in the Alt group (2283 g) compared with the Con group (2007 g). Individual growth trajectories of the two experimental groups differed (MANCOVA ($_{\text{TREATMENT}}$), Wilk's $\Lambda_{5,134} = 0.86$, $p < .01$). Significant differences were also found in growth-at-age trajectories between the experimental groups (MANOVA$_{\text{TREATMENT} \times \text{AGE}}$, Wilk's $\Lambda_{4,134} = 0.91$, $p < .05$).

During the experiment, the Con group was fed for 400 days and the Alt group for 206 days (93% vs. 45% of experimental days). Overall, the Con group was fed 574 kg and the Alt group 422 kg of feed. The Alt group had a significantly lower biological FCR (1.07) compared with control (1.45) (SNK post hoc test, $p < .01$).

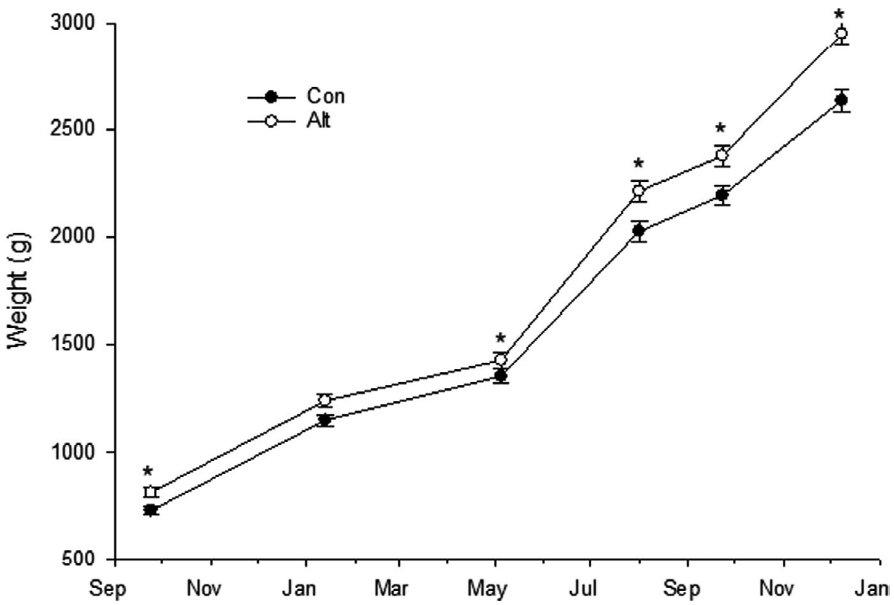

FIGURE 1 Mean body weight (g) of Atlantic cod reared under either daily (Con) or alternative days (Alt) feeding from September 2009 until December 2010. Values represent means ±SE. * indicates significant differences (SNK test, $p < .05$) between the two experimental groups

TABLE 1 Mean (±SD) length (cm) and condition factor in Atlantic cod being fed every day (Con) or fed alternative days (Alt) from September 2009 until December 2010

		September	January	May	August	September	December
Length	Con	37.5 ± 4.0	42.3 ± 4.7	44.4 ± 3.8	52.1 ± 4.0	54.5 ± 4.1	57.5 ± 4.3
	Alt	39.5 ± 3.9	44.2 ± 4.6	46.2 ± 4.0	52.9 ± 4.2	55.6 ± 4.3	58.1 ± 4.5
Condition factor	Con	1.09 ± 0.23^b	1.28 ± 0.22^b	1.07 ± 0.17^b	1.22 ± 0.20^b	1.23 ± 0.17^b	1.35 ± 0.18^b
	Alt	1.21 ± 0.19^a	1.39 ± 0.22^a	1.23 ± 0.20^a	1.40 ± 0.20^a	1.32 ± 0.18^a	1.52 ± 0.20^a

Note: Mean values not sharing a letter were found to be significantly different by the two-way ANCOVA and by the Student–Newman–Keuls multiple range post hoc test.

TABLE 2 Mean (±SD) specific growth rate (SGR) in Atlantic cod being fed every day (Con) or alternative days (Alt) from September 2009 until December 2010

		September–January	January–May	May–August	August–September	September–December
SGR	Con	0.45 ± 0.24	−0.02 ± 0.33^b	0.35 ± 0.16^b	0.42 ± 0.30^a	0.35 ± 0.18
	Alt	0.45 ± 0.19	0.02 ± 0.24^a	0.41 ± 0.10^a	0.26 ± 0.40^b	0.40 ± 0.18

Note: Mean values not sharing a letter were found to be significantly different by the two-way ANCOVA and by the Student–Newman–Keuls multiple range post hoc test.

4 | DISCUSSION

In general, 0–2 fish died per month in each cage. But on random occasions, the mortality was higher in the control group. With the relatively low number of fish per cage, even small increases in mortality will have a large effect on the mortality rate. There were no specific health issues, which could explain the increased mortality in the control group. As the mortality was irregular, it is unlikely to be caused by the feeding regime itself.

After distributing fish into the experimental cages, it discovered a difference in weight and condition factor. To cope with this matter, the initial weight was taken into account in the statistical analysis of the fish growth. The observed increase in weight and length, as well as the variation in SGR of the fish, ranging from negative values and up to 0.5% per day during a year, is similar to that seen in earlier growth studies on Atlantic cod within the size range investigated in the present study (Solberg et al., 2006). Similar to the findings of Solberg et al., (2006) and Imsland et al., (2013), the growth of the cod was found to be depressed during the wintertime and resulted in a growth around or slightly lower than 0% day^{-1}. Björnsson et al., (2001) and Imsland et al., (2006) have shown that the optimal temperature for cod decreases with the size of the cod. In the food-unlimited growth rate model by Björnsson and Steinarsson (2002), a 2000 g cod is expected to have a SGR of 0.29 at 4°C. In the present trial and the trials of Solberg et al., (2006) and Imsland et al., (2013), the SGR was negligible from December/January to May. Solberg et al., (2006) suggested that the discrepancy from the expected growth rate according to the food-unlimited growth rate model by Björnsson and Steinarsson (2002) and the near 0% day^{-1} growth found during this winter period was due to the concomitant strong development of gonads. In the trial of Imsland et al., (2013) and Bjørnevik et al., (2017), neglectable or negative growth was found from January to May concurrent with onset of first maturation in fish reared at simulated natural photoperiod (LDN), whereas fish reared at continuous light during this period displayed growth near or above the modelled value of Björnsson and Steinarsson (2002). It is, therefore, likely that the combined effect of gonad development and the long dark period from November to March could explain the neglectable or negative growth seen in both the Con and Alt groups in this study.

Overall, the current findings indicate that Atlantic cod can deal well with short fasting periods (here Alt) during the whole on-growing period. The mean individual growth trajectories differed between the two groups, and the Alt group gained 13% more mean weight compared with the Con group but was fed 27% lower amount of feed. The present findings indicate that Atlantic cod fed alternate days have similar or higher growth rate as fish fed every day in agreement with other studies on gadoids (Hanssen et al., 2012; Rosenlund et al., 2004; Treasurer et al., 2006). Also, in Nile tilapia *Oreochromis niloticus* better or similar growth was found when fed every other day (Bolivar et al., 2006; El-Araby et al., 2020), or 1-day low feeding ration followed by one-day high feeding ration (Hezron et al., 2019). Economically, intermittent feeding decreased the feed costs over regular feeding, but the feed cost kg^{-1} gain was not effected (Bolivar et al., 2006) Recent studies on other teleost species have shown that alternate feeding results in similar growth as fish fed continuously. Arguello-Guevara et al. (2018) investigated the effect of two days of fasting—one-day feeding repeated for 89 days and compared to continuously fed juvenile longfin yellowtail, *Serioia ravoliana*, and found that specific growth rate, feed intake, feed efficiency and morphological indices were not statistically different between 2 days of fasted fish and continuously fed fish. However, all these studies were performed on smaller fish over shorter time periods than in the present experiment. But also in other experiments with large cod growing from 0.5 to 2.5 kg, no effect on growth was found when being fed 2–3 days a week or 5 days a week (Solberg et al., 2006).

In the study by Bolivar et al. (2006), it was suggested that the improved performance attained by alternate-day feeding is a result of reduced feed waste, either through more complete consumption or through improved nutrient absorption from available feeds. In the present study, the fish fed alternate days only had half the days of feeding compared with control but utilized the feed better as the FCR was lower in the Alt group compared with the Con group. Lower FCR for Atlantic cod fed alternating days was also found in the study of Solberg et al. (2006). In their study, Atlantic cod were fed with dry feed, in sea net pens for 18 months. The fish was either fed five times or two to three times a week for the whole period. No differences in growth were found, but the fish fed five times a week had a higher FCR of 1.47 compared with fish fed three to twice a week for the entire period with FCR of 1.35. Reduced FCR with alternate feeding is also supported by Bolivar et al. (2006), who reported FCR of 1.0 in the alternate group compared with 2.4 in the group fed every day. Also, in this study the amount of feed and thereby the feed costs were cut in half when fed alternate days compared with every day in a period of 120 days, without reducing growth. From an economic perspective, a lower FCR is of vital importance as the feed normally makes up 50%–70% of the expenses in fish farming (Rana et al., 2009).

Previous studies have shown that growth in Atlantic cod (>400 g) was not influenced by the intervals between the feeding (ad libitum), when fed five times a week or two times a week (Solberg et al., 2006). A previous trial by our research group (Hanssen et al., 2012) investigated the effect of different feeding regimes (fasting/re-feeding and reduced feeding) for Atlantic cod juveniles between 132 and 400 g. It was found that short fasting, that is 50% feeding for 2 weeks and 100% for 4 weeks (S50), and 100% every second day and 0% the following day (i.e. Alt), gave similar body mass increment compared with control (fed 100% according to a commercial growth table every day), but consumed significantly less feed (42.9 and 37.5% less feed, respectively) compared with control. However, longer fasting periods, that is, starving 1 week and fed 100% 2 weeks and starved 2 weeks and fed 100% 4 weeks, lead to lower growth compared with control. These findings on juvenile Atlantic cod are in line with the findings here, and both studies demonstrate that feeding costs can be drastically reduced without compromising biomass growth by using feeding on alternate days.

It has been demonstrated that Atlantic cod freely skips feeding on a daily basis. In a study by Rillahan (2008), where cod were fed once per day, 23% of the individuals frequently skipped meals. Though it is unclear the long-term dynamic of individual feeding behaviour, the data presented by Rillahan (2008) suggest that on any given feeding event 23% of individual do not feed. Information of this nature will prove important in fine-tuning daily feeding regime and indicate that a combination of large- and small-scale studies is required to adequately assess feeding behaviour. The selection of alternative feeding strategies may also reduce potential competition (Juell & Westerberg, 1993) between conspecifics in the sea pen. Earlier studies have shown that Atlantic cod have displayed hierarchical aggressive feeding behaviour in the laboratory directed towards smaller conspecifics (Björnsson, 1993).

5 | CONCLUSION

Feeding alternating days over a 15-month period resulted in higher weight gain, improved growth and lower feed conversion ratio. It is concluded that feeding costs can be drastically reduced without compromising biomass growth by using feeding on alternate days during the on-growing period of Atlantic cod.

ACKNOWLEDGEMENTS

This study was financed by the Norwegian Research Council (NORTHERNCOD 87291/120). We would like to extend our thanks to the technical staff at Fjord Marine Cod Brønnøysund for their assistance in maintaining the fish and sampling. The authors declare that there is no conflict of interests in relation to this study.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article due to commercial restrictions.

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How to cite this article: Bjørnevik M, Imsland AK, Hanssen H, Roth B, Vikingstad E, Foss A. The effect of alternate-day feeding on growth and feed conversion in Atlantic cod *Gadus morhua*. *Aquacult Nutr*. 2021;27:1206–1211. https://doi.org/10.1111/anu.13260