



Effect of sea cage aquaculture on the length, weight, and condition of wild Atlantic cod *Gadus morhua*

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ABSTRACT: Wild fish have been shown to associate with sea cage aquaculture and consume waste feed; however, little is known about the effects of waste feed consumption on wild fish. We used Atlantic cod *Gadus morhua* collected in the direct vicinity of sea cages and reference North-west Atlantic Fisheries Organization divisions, either outside the direct vicinity ('local division') or completely removed from aquaculture ('outside divisions'), to compare length, weight, and condition for cod ages 2 to 4. Concentrations of vegetable oil-based fatty acids (linoleic acid and α -linolenic acid) were then used as biomarkers for waste feed consumption to determine their role in explaining differences in length, weight, and Fulton's condition index among cage-associated cod. Age 2 cage-associated cod were in lower condition than age 2 cod from the local division and lighter than age 2 cod from all outside divisions. Age 3 cage-associated cod were comparable to age 3 cod from the local division but in lower condition than age 3 cod from all outside divisions. However, age 4 cage-associated cod were longer and heavier than age 4 cod from the local division, but in lower condition than age 4 cod from 2 of 3 outside divisions. Additionally, there were positive relationships between fatty acid concentrations and length and weight for age 2 cage-associated cod, but no significant relationships for age 3 or 4 cage-associated cod. Results suggest the effects of waste feed consumption are contradictory but not consistent enough to disrupt established growth and condition patterns among divisions.

KEY WORDS: Sea cage aquaculture · Waste feed · Artificial structure · Biological effects · Growth · Condition · Fatty acid biomarkers · *Gadus morhua*

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1. INTRODUCTION

Open net sea cages, such as those used to farm Atlantic salmon *Salmo salar* along sheltered coastlines (Hvas et al. 2021), can attract and aggregate wild fish species across large spatial scales (Gianoulaki et al. 2005, Goodbrand et al. 2013) and increase abundances of local wild fishes (Machias et al. 2004, 2005). The physical structure of the cage and moorings may provide a common 'meeting

point' for wild fishes (Dagorn & Fréon 1999, Fréon & Dagorn 2000) and facilitate schooling, hunting, and shelter-seeking behaviours (Beveridge 1984, Soria et al. 2009, Izquierdo-Gómez et al. 2015). Additionally, unconsumed waste aquafeed, and potentially farm fish faeces (reviewed by Uglem et al. 2014), can be consumed directly and indirectly, through consumption of cage-associated prey fish, benthic invertebrates, and zooplankton (Sanchez-Jerez et al. 2008, Fernandez-Jover et al. 2009) that routinely

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consume farm fish faeces and waste feed themselves (Sæther et al. 2012, Callier et al. 2013, Fernandez-Jover et al. 2016). Therefore, regardless of consumption route, waste feed should provide a predictable energetic subsidy that minimizes consumer foraging time and energetic expenditures (Scales et al. 2016). According to classical foraging theorems (see Stephens & Krebs 1987), even small quantities of waste feed should be highly profitable to cage-associated fishes (MacArthur & Pianka 1966, Charnov 1976) and result in increased growth and condition (Skog et al. 2003, Fernandez-Jover et al. 2007). However, additional factors such as life stage, competition, and predation rates also require consideration (Fretwell & Lucas 1969, Dahlgren & Eggleston 2000, Craig & Crowder 2002, Bartolino et al. 2011) and could affect sea cage habitat quality and associated benefits to wild fishes.

Increased proportions of vegetable oil-based fatty acid signatures associated with waste feed composition, in particular linoleic acid (LA, 18:2n6) and α -linolenic acid (ALA, 18:3n3), are essential fatty acids (EFAs) that assimilate into cage-associated pelagic and benthic communities (Fernandez-Jover et al. 2009, Woodcock et al. 2018, 2019) but cannot be synthesized de novo in marine fish species (Tocher 2003, Wu & Chen 2012). Given their rapid assimilation, elongated retention times (Torstensen et al. 2004, Olsen et al. 2015), and natural rarity in marine ecosystems (Dalsgaard et al. 2003), LA and ALA have been shown to be suitable biomarkers for tracing waste feed consumption in cage-associated wild fishes (Abaad et al. 2016; reviewed by White et al. 2017, McAllister et al. 2021).

We used wild Atlantic cod *Gadus morhua* collected in the direct vicinity of sea cages and reference Northwest Atlantic Fisheries Organization (NAFO) divisions, either outside the direct vicinity of sea cages or completely removed from aquaculture, to (1) compare length, weight, and condition of cod ages 2–4 yr and (2) identify the role, if any, of waste feed consumption in explaining differences in length, weight, and condition among cage-associated cod. Assuming that waste feed represents a significant energetic subsidy not available to non-cage-associated cod populations, we hypothesized that (1) cod collected from sea cages would be longer, heavier, and in better condition than cod collected from reference sites and (2) increased LA and ALA concentrations (i.e. biomarkers of waste feed consumption) would result in positive correlations with length, weight, and condition in younger cage-associated cod (2–3 yr old), but correlations would be reduced

or non-existent in older cod (4 yr old) due to an ontogeny-linked reduction in waste feed consumption and dependency (McAllister et al. 2021). Together, this study provides empirical evidence of the influence of sea cage aquaculture, and particularly waste feed consumption, on the length, weight, and condition of cage-associated cod.

2. MATERIALS AND METHODS

2.1. Wild fish sample collection

Wild Atlantic cod were separated into 'cage-associated' and 'reference' groups based on collection location. Cage-associated *Gadus morhua* were collected between 5 and 8 August 2019 from the immediate vicinity (10–300 m) of sea cages in Pools Cove, Newfoundland and Labrador, Canada (n = 72; Table 1, Fig. 1) with permission, using a combination of hook and line fishing with a rod and benthic longline. Reference cod were collected from multiple sampling trips that were completed between 31 March and 18 December 2019, from sites either outside the immediate vicinity of sea cages (>10 km), hereafter referred to as 'local division' (NAFO subdivision 3Ps: n = 329, 31 March to 18 December; Table 1, Fig. 1) or completely removed from Atlantic salmon aquaculture, hereafter referred to as 'outside divisions' (NAFO divisions 3L: n = 546, 28 May to 26 November; 3N: n = 245, 16 May to 15 October; and 3O: n = 162, 4 May to 27 September; Table 1, Fig. 1). Sampling trips included Fisheries and Oceans Canada (DFO) survey trawls and beach seines. Once captured, cod were euthanized by concussion (CCAC 2010, MUN ACP no. 20200342) and either placed on ice or frozen, prior to measurements of fork length and round weight, and the removal of liver tissue (≥ 250 mg) and sagittal otoliths for fatty acid analysis and aging, respectively.

2.2. Correction for a common sampling date

Given the extensive spatial coverage of sampling, it was impossible to collect all reference cod on the same date as the cage-associated cod. Therefore, length, weight, and condition indices for reference cod, from both the local division and outside divisions, were adjusted to the sampling month in which the cage-associated cod were collected (August), to ensure that any effects were not simply due to sampling period (Mello & Rose 2005).

Table 1. Sample groups, sample sizes (n), and length (cm), weight (g), and Fulton's condition index (condition) corrected to a common sampling month \pm standard error (SE) for wild Atlantic cod *Gadus morhua* ages 2–4 yr old collected from the direct vicinity of sea cages in Pools Cove (study site) and reference sites removed from aquaculture operations within the local NAFO division (3Ps) and outside divisions (3L, 3N, 3O) in Newfoundland, Canada. See Table A2 for length, weight, and condition values prior to correction for a common sampling month

Groups	n	Length	Weight	Condition
Study site	72			
Age 2	42	23.90 \pm 0.42	117.39 \pm 7.33	0.83 \pm 0.02
Age 3	16	35.88 \pm 0.77	368.78 \pm 23.67	0.78 \pm 0.01
Age 4	14	44.57 \pm 0.84	745.75 \pm 46.05	0.83 \pm 0.02
3Ps	329			
Age 2	43	23.79 \pm 0.38	145.01 \pm 9.23	1.03 \pm 0.02
Age 3	142	34.98 \pm 0.40	350.41 \pm 14.98	0.79 \pm 0.01
Age 4	144	40.80 \pm 0.44	561.19 \pm 29.09	0.81 \pm 0.02
3L	546			
Age 2	190	25.00 \pm 0.25	142.09 \pm 4.90	0.85 \pm 0.01
Age 3	182	31.54 \pm 0.33	285.68 \pm 8.60	0.86 \pm 0.01
Age 4	174	40.84 \pm 0.33	617.59 \pm 15.01	0.88 \pm 0.01
3N	245			
Age 2	107	28.46 \pm 0.39	214.83 \pm 8.63	0.88 \pm 0.01
Age 3	64	34.84 \pm 0.55	397.17 \pm 20.31	0.89 \pm 0.01
Age 4	74	44.55 \pm 0.57	851.39 \pm 36.45	0.92 \pm 0.01
3O	162			
Age 2	75	25.90 \pm 0.36	158.32 \pm 7.34	0.87 \pm 0.01
Age 3	62	33.21 \pm 0.63	356.23 \pm 19.19	0.91 \pm 0.01
Age 4	25	42.04 \pm 1.07	736.30 \pm 69.85	0.93 \pm 0.02

This adjustment was made for the length and weight of each age class of both the local division and outside divisions (ages 2–4 yr old; for slope and intercept values, see Table A1 in the Appendix), using a linear regression between measurements that were collected during the spring and summer and at least one additional month during the fall and winter seasons (Lambert & Dutil 1997). Percent changes in monthly averages were applied to each sample from the local division and outside divisions (Parrish & Malli-coate 1995). Corrected length and weight values were then used to calculate Fulton's condition index (FCI) as a general measurement of fish condition (reviewed by Nash et al. 2006):

$$K = \frac{W}{L^3 \times 100} \quad (1)$$

where W = seasonally corrected fish weight (g), and L = seasonally corrected fish length (cm)³. FCI values >1 indicate above-average condition, whereas FCI values <1 indicate below-average condition.

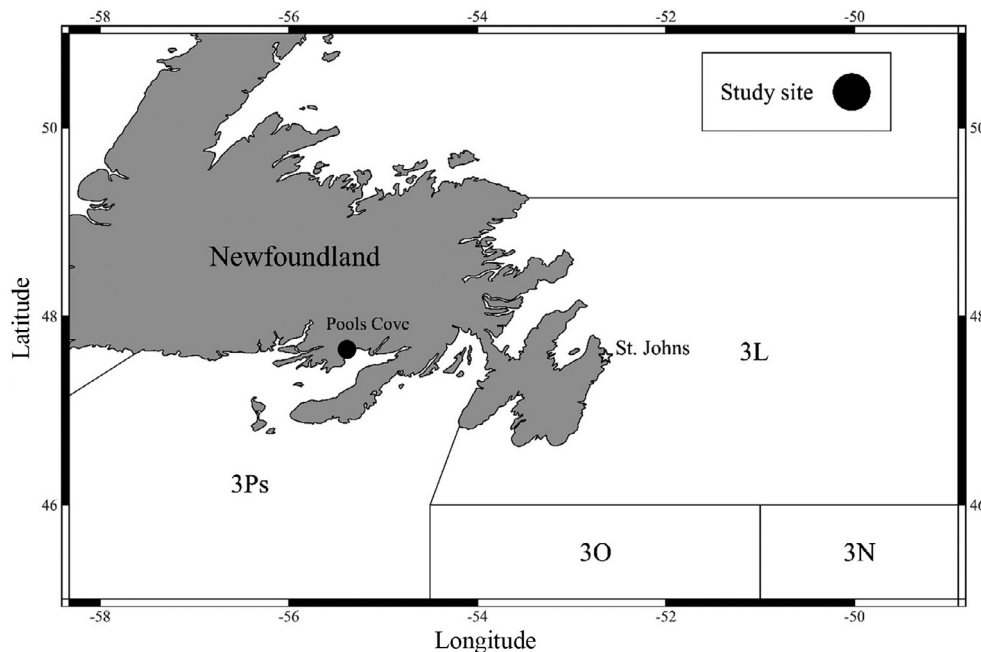


Fig. 1. Overview of commercial fishing divisions in Newfoundland, Canada, used to represent collection sites for the study. Wild cage-associated Atlantic cod *Gadus morhua* were collected in the direct vicinity of sea cages in Pools Cove (study site) with permission from local aquaculture companies, and reference wild *G. morhua* were collected from sites removed from aquaculture operations within the local NAFO division (3Ps) and outside divisions (3L, 3N, 3O)

2.3. Thin section preparation and sample aging

2.3.1. Thin section preparation

Sagittal otoliths provide accurate age measurements for teleost fish (reviewed by Campana 2001), and are most commonly used for microstructure analysis (Campana & Neilson 1985). Sample otoliths were removed from cod brain cavities and rinsed, and the right otolith from each fish was embedded (Stuers, 25:3 epoxy: hardener), cured overnight, and sectioned (Buehler, Isomet low-speed saw) to identify the core. Four blades (0.5 mm), separated by spacers (0.65 mm), were used to obtain the otolith core (S. Campana pers. comm.). Thin sections were polished in 10 s intervals (Gator, 800-grit sanding cloth) to improve microstructure and growth ring clarity (DFO 2019), prior to being photographed (Nikon, SMZ1500).

2.3.2. Aging (visual and laser ablation inductively coupled plasma mass spectrometry)

Aging was conducted using 2 methods, visually and laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS). For visual aging, sectioned annuli rings (i.e. thin sections) were identified under a microscope, using offsetting summer (opaque) and winter (hyaline) zones and a standard northern hemisphere birth date of 1 January. A double-blind review was completed with a trained secondary reader. LA-ICP-MS was conducted using the ablation process and equipment detailed in D'Avignon & Rose (2013). Briefly, cod thin sections were fixed horizontally and pre-ablated (10 Hz repetition rate). An ultraviolet light excimer laser ablation system (Coherent, GeoLasHD) with a wavelength of 193 nm was used to ablate transects (core–edge) using an energy density of 4 J cm^{-2} , a scanning speed of $20 \text{ } \mu\text{m s}^{-1}$, and a spot size of $50 \text{ } \mu\text{m}$. The laser ablation system was coupled to an ICP-MS (Thermo Fisher, Element XR), which measured elemental concentrations (ppm) of magnesium (^{25}Mg), manganese (^{55}Mn), and strontium (^{88}Sr), using ^{43}Ca as an internal standard (40%) and National Institute of Standards and Technology 610 as an external standard, and United States Geological Survey MACS-1 for quality control. Seasonal changes in abiotic conditions (i.e. salinity, temperature, oxygen availability) and metabolic activity result in consistent shifts in otolith magnesium, manganese, and strontium elemental concentration ratios ($^{88}\text{Sr}:^{25}\text{Mg}$, $^{25}\text{Mg}:^{43}\text{Ca}$, and $^{55}\text{Mn}:^{43}\text{Ca}$) that are considered applicable for aging (reviewed by Heimbrand et al. 2020).

Therefore, seasonal variation pattern peaks in $^{88}\text{Sr}:^{25}\text{Mg}$, $^{25}\text{Mg}:^{43}\text{Ca}$, and $^{55}\text{Mn}:^{43}\text{Ca}$ were identified, counted, and used to determine cod age (Hüssy et al. 2016).

All cod collected during DFO survey trawls and beach seines were aged visually under a microscope ($n = 1282$), whereas all cage-associated cod were aged using a combination of microscopy ($n = 72$) and LA-ICP-MS ($n = 30$). Of the 30 thin sections aged with both techniques, no discrepancy in aging was found. Elemental concentrations were determined in the Micro Analysis Facility of the Core Research Equipment and Instrument Training network at Memorial University of Newfoundland.

2.4. Lipid biomarker extraction

Waste feed consumption can be detected through lipid-based LA (18:2n6) and ALA (18:3n3) concentrations, which were extracted following Parrish (1999) and detailed by McAllister et al. (2021). Briefly, liver samples (~250 mg) were removed from each cage-associated cod and placed in 15 ml glass vials that had been previously weighed and muffled to degrade any potential contaminants (muffle furnace, 8 h, 450°C). Samples were covered in 2 ml of chloroform (CHCl_3 , $\geq 99.9\%$), and the tube headspace was filled with nitrogen (N_2 , $\geq 99.9\%$), before being sealed with lipid-cleaned caps (methanol: [CH_3OH , $\geq 99.9\%$] and CHCl_3 wash repeated 3 times) and stored at -20°C until lipid extraction. For extraction, samples were homogenized (Omni International, Tissue Master 125) using a 7 mm probe in a chilled chloroform:methanol (2:1) mixture. Chloroform-extracted water was added to produce a chloroform:methanol:water (8:4:3) mixture. Samples were sonicated for 4 min (Fisher Scientific, FS30H) using an ice bath, centrifuged for 2 min at $1800 \times g$ (Fisher Scientific, 74634H), and the organic layer was then removed by a double-pipetting technique. A chloroform rinse was completed using an extraction vial, with each organic layer pooled in lipid-cleaned vials (2 ml, 1.5 ml full), and repeated 3 times. Organic layers were concentrated with nitrogen, capped, and sealed, and stored at -20°C until gas chromatography analysis (GCA).

For GCA, samples were transesterified for 1 h at 100°C using sulfuric acid (H_2SO_4 , $\geq 99.9\%$) and CH_3OH to produce fatty acid methyl esters (FAMES), that were analyzed using a gas chromatograph (HP, 6890) with a 7683 autosampler. The gas chromatography column (Phenomenex USA, ZB wax+) with a

30 m length and 0.32 mm internal diameter was heated to 65°C for 30 s and 195°C (40°C min⁻¹) for 15 min and 220°C (2°C min⁻¹) for 45 s. Samples were injected (~1.5 ml by volume) with hydrogen gas (H₂) at 2 ml min⁻¹ using an injector temperature of 150°C that was heated to 250°C (120°C min⁻¹) and a detector temperature of 260°C. Sample peaks were identified using retention times for standards (Sigma Chemical, Supelco 37): component FAME mix (47885-U), bacterial acid methyl ester (BAME) mix (47080-U), polyunsaturated fatty acid (PUFA) 1 (47033), and PUFA 3 (47085-U), and chromatograph flame ionization detector (FID) accuracy was tested with a quantitative standard (Nu-Chek prep, GLC490) after approximately 300 samples. Chromatographs of lipid profiles were then developed (Agilent OpenLAB Data Analysis, Build 2.203.0.573).

2.5. Statistical analyses

We tested for the effects of group (cage-associated, local division, outside divisions), age (2, 3, 4 yr old), and the interaction between group × age on sample values for length, weight, and condition using linear models and a significance level of 0.05. Given a significant interaction between group and age, separate models were developed for length, weight, and condition for each age class with group as a fixed effect.

Further, we used separate models for each age class to test for the effect of LA and ALA concentrations on length, weight, and condition values of cage-associated cod. Model assumptions of homogeneity of variances and normality were checked prior to analyses using a Bartlett's test and a Shapiro-Wilk test, respectively. Statistical analyses were completed using R statistical software (R Core Team 2021, v. 4.1.1) with the package 'emmeans' (Lenth 2021, v. 1.6.2-1) used to visualize interactions and compare levels within a factor.

2.6. Ethics statement

All research activities were completed under the guidelines of the Canadian Council on Animal Care – Euthanasia of Animals used in Science (Memorial University Animal Care Committee permit 19-01-MA).

3. RESULTS

3.1. Length, weight, and condition comparisons

There was no significant difference in length and weight between age 2 and 3 Atlantic cod *Gadus morhua* from the cage-associated group and age 2

Table 2. General linear modelling results for length (cm), weight (g), and Fulton's condition index (condition) for *G. morhua* ages 2–4 yr old collected from the direct vicinity of sea cages in Pools Cove (study site) and reference sites removed from aquaculture operations within the local NAFO division (3Ps) and outside divisions (3L, 3N, 3O) in Newfoundland, Canada. Initial models contained group (G), age (A), and their interaction (G × A). Given a significant interaction between group and age, separate models were developed for length, weight, and condition for each age class with group as a fixed effect (shown below)

Study site vs.	Length			Weight			Condition		
	df	<i>t</i>	<i>p</i>	df	<i>t</i>	<i>p</i>	df	<i>t</i>	<i>p</i>
3Ps									
Age 2	4, 452	-0.16	0.87	4, 449	1.80	0.07	4, 449	9.92	<0.001
Age 3	4, 461	-0.74	0.46	4, 426	-0.50	0.62	4, 426	0.09	0.93
Age 4	4, 426	-2.79	<0.01	4, 358	-2.55	<0.05	4, 358	-0.77	0.44
3L									
Age 2	4, 452	1.89	0.06	4, 449	2.06	<0.05	4, 449	1.61	0.11
Age 3	4, 461	-3.63	<0.001	4, 426	-2.30	<0.05	4, 426	3.35	<0.001
Age 4	4, 426	-2.78	<0.01	4, 358	-1.85	0.06	4, 358	1.67	0.09
3N									
Age 2	4, 452	7.37	<0.001	4, 449	7.60	<0.001	4, 449	3.03	<0.01
Age 3	4, 461	-0.81	0.42	4, 426	0.73	0.46	4, 426	4.30	<0.001
Age 4	4, 426	-0.02	0.99	4, 358	1.46	0.15	4, 358	3.14	<0.01
3O									
Age 2	4, 452	3.05	<0.01	4, 449	3.02	<0.01	4, 449	2.28	<0.05
Age 3	4, 461	-2.08	<0.05	4, 426	-0.32	0.75	4, 426	5.27	<0.001
Age 4	4, 426	-1.57	0.12	4, 358	-0.11	0.91	4, 358	2.87	<0.01

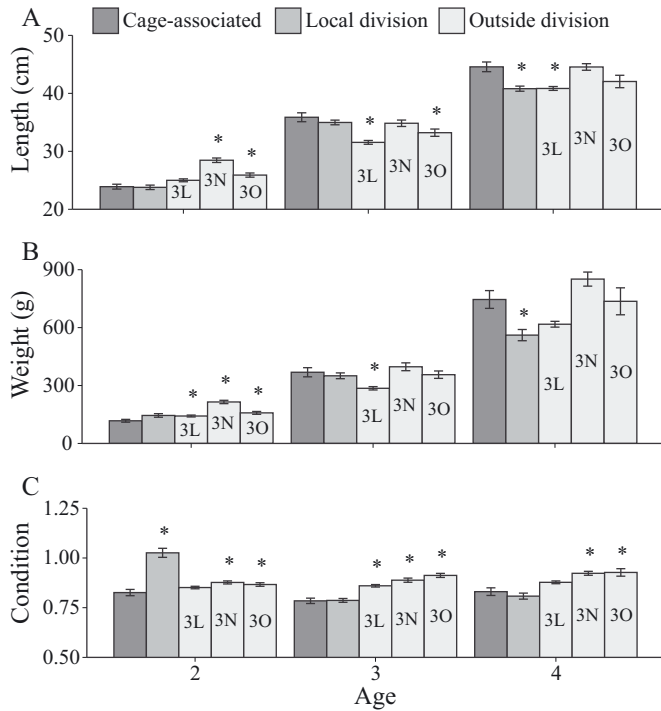


Fig. 2. Mean (A) length (cm), (B) weight (g), and (C) Fulton's condition index (condition) values \pm standard error (SE), corrected for a common sampling month, for *G. morhua* ages 2–4 yr old collected in the direct vicinity of sea cages in Pools Cove, Newfoundland, Canada (cage-associated; darkest grey) and reference sites removed from aquaculture operations within the local NAFO division (3Ps; lighter grey) and outside divisions (3L, 3N, 3O; lightest grey). Asterisks denote significant differences ($p < 0.05$) from the cage-associated group

and 3 cod from the local division group (Table 2, Fig. 2A,B), though age 2 cage-associated cod were, on average, ~27.6 g (i.e. 21%) lighter than age 2 cod from the local division ($p = 0.07$; Table 1). However, age 2 cage-associated cod were of significantly lower condition than age 2 cod from the local division (Table 2, Fig. 2C), whereas age 3 cage-associated cod were of similar condition (Table 2, Fig. 2C). Age 4 cage-associated cod were both significantly longer (~3.8 cm, 9%), and heavier (~184.6 g, 28%) than age 4 cod from the local division (Table 2, Fig. 2A,B), but of similar condition (Table 2, Fig. 2C).

To determine whether length, weight, and condition patterns were large enough to transcend those of surrounding populations, cage-associated cod were also compared to cod from 3 outside divisions. Results of this analysis were highly variable among traits and age classes, with age 2 cage-associated cod being significantly lighter than age 2 cod from all 3 outside divisions (i.e. mean = 19, 59, and 30% lighter than 3L, 3N, and 3O, respectively; Table 2, Fig. 2B). Additionally, age 3 cage-associated cod were of significantly lower condition

than age 3 cod from all outside divisions (i.e. mean = 9, 12, and 15% lower than 3L, 3N, and 3O, respectively; Table 2, Fig. 2C).

3.2. LA and ALA concentrations vs. length, weight, and condition relationships

There was a significant positive relationship between LA and ALA and length and weight for age 2 cage-associated cod (Table 3, Fig. 3A,B) but no significant relationships between LA or ALA and length and weight for age 3 and 4 cage-associated cod (Table 3, Fig. 3A,B). Similarly, there was no significant relationship between LA or ALA and condition across all ages of cage-associated cod (Table 3, Fig. 3C).

Table 3. General linear modelling results for length (cm), weight (g), and Fulton's condition index (condition) and linoleic acid (18:2n6) and α -linolenic acid (18:3n3) concentrations (i.e. biomarkers of waste feed consumption) for *G. morhua* ages 2–4 yr old collected from the direct vicinity of sea cages ('cage-associated') in Pools Cove, Newfoundland, Canada

Age (yr)	Measurement	Fixed effects	df	n	t	p
2	Length	Linoleic acid	1, 24	26	3.05	<0.01
		α -Linolenic acid	1, 24	26	3.24	<0.01
	Weight	Linoleic acid	1, 24	26	3.66	<0.01
		α -Linolenic acid	1, 24	26	3.95	<0.001
	Condition	Linoleic acid	1, 24	26	1.63	0.12
		α -Linolenic acid	1, 24	26	1.66	0.11
3	Length	Linoleic acid	1, 13	15	0.41	0.69
		α -Linolenic acid	1, 13	15	0.52	0.61
	Weight	Linoleic acid	1, 13	15	0.23	0.82
		α -Linolenic acid	1, 13	15	0.35	0.74
	Condition	Linoleic acid	1, 13	15	-0.93	0.37
		α -Linolenic acid	1, 13	15	-0.87	0.40
4	Length	Linoleic acid	1, 6	8	-0.26	0.80
		α -Linolenic acid	1, 6	8	-0.45	0.67
	Weight	Linoleic acid	1, 6	8	-0.54	0.61
		α -Linolenic acid	1, 6	8	-0.40	0.70
	Condition	Linoleic acid	1, 6	8	-0.66	0.54
		α -Linolenic acid	1, 6	8	0.15	0.89

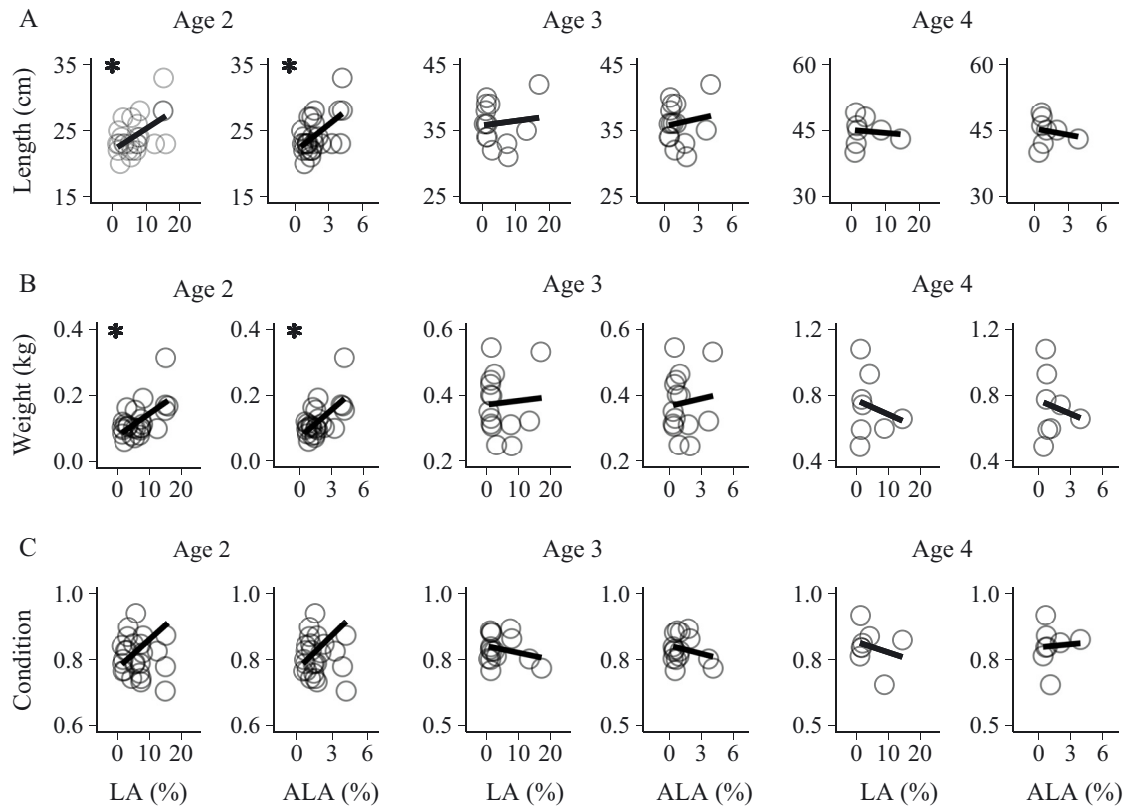


Fig. 3. Relationships between (A) length (cm), (B) weight (kg), and (C) Fulton's condition index (condition) and linoleic acid (LA, 18:2n6) and α -linolenic acid (ALA, 18:3n3) concentrations (i.e. biomarkers of waste feed consumption) for *G. morhua* ages 2–4 yr old collected in the direct vicinity of sea cages in Pools Cove, Newfoundland, Canada. Asterisks denote significant relationships ($p < 0.05$) between length, weight, and condition and LA or ALA concentrations

4. DISCUSSION

When length, weight, and condition of cage-associated Atlantic cod *Gadus morhua* were compared to those from outside divisions, weight of age 2 cage-associated cod and condition of age 3 cage-associated cod were the only traits significantly different across all outside divisions. Thus, one may conclude that the effects of Atlantic salmon aquaculture were large enough to suppress weight and condition of wild cod; however, this is unlikely to be the case here. The lower values for age 2 and age 3 cage-associated cod are consistent with an average lower weight and condition of cod throughout the local division, even in the absence of aquaculture operations, and thus more likely attributable to consistent reduced weight and condition trends of cod from the local division (Rideout et al. 2017). Structural ecosystem changes, particularly warming water temperatures and consequent novel competition from relatively warmer-water fishes, such as silver hake *Merluccius bilinearis* (Koen-Alonso & Cuff 2018), has resulted in highly variable prey availability for cod from the local

division when compared to cod from outside divisions (DFO 2022). However, even though comparisons of length, weight, and condition between cage-associated cod and the local division were mostly non-significant ($p \geq 0.05$), some exceptions were found. For example, age 2 cage-associated cod were of lower condition than age 2 cod from the local division, whereas age 4 cage-associated cod were both longer and heavier than age 4 cod from the local division.

Local division cod migration patterns are complex (DFO 2021, 2022), and their stock structure can consist of inshore and offshore components that mix amongst divisions (Varkey et al. 2022). However, results of a recent tagging study suggested that less than 3% of local division cod from Placentia Bay were recaptured in adjacent division 3L (Rideout et al. 2016). Additionally, interdivisional cod migration from both the local division or outside divisions 3L and 3N are not of substantial management concern (Rideout et al. 2015, Ings et al. 2019, DFO 2022b), though limited seasonal mixing of the local division and outside division 3O may occur (Rideout et al. 2015). Lastly, recently tagged cod from our study

area, Fortune Bay, were recaptured throughout the local division (Varkey et al. 2022). Therefore, our cage-associated and reference cod groups are likely representative of their respective divisions, as well as sufficiently homogeneous on a divisional scale, and limited in comparison to large-scale stock mixing and migration characteristics of cod populations elsewhere (see Nordeide et al. 2011, Cao et al. 2014).

LA and ALA, used here, and previously (McAllister et al. 2021), as biomarkers for waste feed consumption, revealed some contradictory relationships. For example, given the significant positive relationships between both LA and ALA and length and weight among age 2 cage-associated cod, one would have expected that increased waste feed consumption would have resulted in longer and heavier age 2 cod when compared to those from the local division. However, this was not the case, as the age 2 cage-associated cod were of a comparable length and weight to age 2 cod from the local division, and of lower condition. Further, despite the absence of any significant relationships between LA or ALA and length, weight, and condition, age 4 cage-associated cod were both longer and heavier than age 4 cod from the local division. Waste feed can provide a predictable energetic subsidy that minimizes foraging time and energy expenditures (Stephens & Krebs 1987, Scales et al. 2016), and consequently has been observed to increase length, weight, and condition of wild cage-associated fishes (Skog et al. 2003, Fernandez-Jover et al. 2007, Dempster et al. 2011). However, the nutritional benefits of waste feed consumption may only result in increased growth and condition when the cage-associated fish are of a comparable life stage and species as the farmed fish (Masagounder et al. 2016, Hua et al. 2019). Whenever this is not the case, such as in our study (i.e. juvenile cod consuming adult *Salmo salar* feed), it is possible that the benefits of farm waste consumption may be reduced or non-existent (Fernandez-Jover & Sanchez-Jerez 2015). Rosenlund et al. (2004) determined that optimal juvenile cod nutrition and growth requires increased levels of crude protein (500–600 g kg⁻¹) and decreased levels of dietary lipid (130–200 g kg⁻¹) when compared to optimal salmonid nutrition, due to an inability of cod to metabolize ALA to eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) (Turchini et al. 2009). However, while cod can tolerate similar vegetable oil-based feed formulations to those used for salmonid aquaculture, without reductions in growth or condition (Olsen et al. 2015), it requires additional supplementation of long-chain marine fatty acids, such as EPA and DHA (Hansen & Hemre 2013).

Modern aquaculture feed is formulated to maximize the developmental efficiency of the farmed species (Encarnaç o 2016); however, nutritional requirements vary by species (Molina-Poveda 2016) and change with development (Carter 2015). Therefore, aquafeed may not satisfy nutrition and EFA concentration requirements considered critical for proper marine fish development (Sargent et al. 1999, Glen-cross 2009) in some species. For example, increased *S. salar* farming and aquafeed availability has been linked to marginally reduced egg and larvae size in cod (Barrett et al. 2018), and the lack of long-chain marine fatty acids in salmonid aquafeed, particularly EPA and DHA (Nichols et al. 2014, reviewed by Hua et al. 2019), has resulted in reduced fertilization rates, egg symmetry, and survival to hatching rates of cod during laboratory trials (Salze et al. 2005). Although previous research has shown *S. salar* farming has not influenced spatiotemporal spawning dynamics of local *G. morhua* in Norway (Skj eraasen et al. 2021), waste feed consumption could negatively affect reproductive success (Skj eraasen et al. 2022) and fitness and survivorship of offspring later in life (Barrett et al. 2018). Furthermore, a lack of nutritious food options for young cage-associated cod can result in periods of reduced growth, typically attributable to poor food quality and restrictive feeding regimens, as well as size-dependent mortality (reviewed by Ali et al. 2003), which has been followed by a period of accelerated 'compensatory' growth in cod once conditions improve (B elanger et al. 2002).

Compensatory growth has been shown to increase risk tolerance and consequently predation risk of wild fishes ( lvarez 2011), which may contribute to reduced size and fecundity consistent with an accelerated life-history strategy (Petrik 2019), in young cage-associated cod that accept a readily accessible food source trade-off for an elevation in predation risk and mortality rates (Gilliam & Fraser 1987, Abrahams & Dill 1989). Sea cage aquaculture environments appear to fulfill food availability, predator protection, and complex shelter prerequisites of high-quality nursery habitat (Heck et al. 2003), but environmental cues produced by sea cages can be misleading and may result in ecological traps for young wild fishes (Robertson et al. 2013). Furthermore, Fernandez-Jover et al. (2008) suggested that increased anthropogenic activity and pressure around Mediterranean cages may explain the reduced growth and size of juveniles associated with sea cages (Fernandez-Jover & Sanchez-Jerez 2015) and similar artificial structures (Hallier & Gaertner 2008, Zhou et al. 2018). Although it is

unclear whether sea cages act as ecological traps (Swearer et al. 2021), the reduction in risk-aversion during foraging behaviour (Álvarez 2011) could increase accessibility of juvenile cod to aggregated predatory fishes (Serra-Llinares et al. 2013) and local fishers (Akyol & Ertosluk 2010). Furthermore, the increased mortality of cod associated with poor nursery habitat (Lilley & Unsworth 2014) and reduced life span of an accelerated life history strategy in marine fishes (Petrik 2019), could further limit young cage-associated cod maturation and stock recruitment success, and particularly in the susceptible local division (DFO 2021, 2022) where cod populations are of concern.

Alternatively, young cage-associated cod could provide recruitment to older cod, despite increased presence of tertiary predators (Sanchez-Jerez et al. 2008, Arechavala-Lopez et al. 2013, 2015), predation risk (Dempster et al. 2002), and conspecific competition (Fernandez-Jover et al. 2009). For the young cage-associated cod that survive these stressors, our results suggest that these individuals may benefit from compensatory growth, which has been shown to increase feed utilization and growth efficiency (Russell & Wootton 1992, reviewed by Abdel-Tawwab et al. 2006, Yengkokpam et al. 2014), assuming age 4 cod were also associated with sea cages as juveniles and experienced a similar life history (i.e. waste feed consumption, growth, and condition patterns) as age 2 and age 3 cod from our study. Fernandez-Jover et al. (2007) found increased condition of cage-associated horse mackerel *Trachurus mediterraneus* in the Mediterranean and cage-associated saithe *Pollachius virens* and *G. morhua* in Norway (Fernandez-Jover et al. 2011), through predominately adult aggregations (Dempster et al. 2002) which experience reduced predation risk (Baird et al. 2020), as well as an energetic benefit through the consumption of aggregated prey fishes (Sanchez-Jerez et al. 2008, Arechavala-Lopez et al. 2015). Additionally, cannibalism comprises a significant dietary input for cod (Ciannelli et al. 2007, Puvanendran et al. 2008) and the consumption of escaped farmed juvenile cod by wild adult cod has been observed in the vicinity of sea cages in Norway (Serra-Llinares et al. 2013). Therefore, cannibalism may be associated with an increased mortality risk and result in a lower condition of young cage-associated cod but an additional energetic benefit to older cod. This ontogenetic shift is consistent with Bagdonas et al. (2012), who observed that younger cage-associated cod in Norway fed directly on waste feed, while older cod fed on aggregated prey fishes, predominately *P. virens*.

Waste feed consumption has been shown to assimilate into cod fatty acid profiles within weeks to months (Olsen et al. 2015). Therefore, the lack of LA and ALA concentrations overall of age 3 and age 4 cage-associated cod is somewhat surprising, and suggests either insufficient waste feed consumption or poor LA and ALA retention and transfer to higher trophic levels (reviewed by Dalsgaard et al. 2003, White et al. 2017), with indirect consumption and limited cage-association capable of obscuring cage-associated fatty acid signatures (Barrett et al. 2018). Therefore, an alternative explanation could be that age 4 cod demonstrate limited fidelity to sea cages but instead to nearby spawning areas (Skjæraasen et al. 2011, 2021), with the majority of wild cod tagged around Norwegian cages still present 2–3 mo later (Uglem et al. 2008). Alternatively, older cod demonstrate larger habitat connectivity patterns in coastal areas (reviewed by Petitgas et al. 2013), and may associate with sea cages opportunistically (reviewed by Uglem et al. 2014), with previous research demonstrating that most cod associate with sea cages for less than 1 wk (Skjæraasen et al. 2022). Furthermore, low rates of waste feed consumption, previously recorded in only ~20% of cod (Skjæraasen et al. 2022), can lead to time frames and/or consumption rates insufficient for LA and ALA assimilation in the liver. Additionally, sea cages can alter the distribution of wild fish at spatial scales upwards of 82 km² (Giannoulaki et al. 2005), and their structural and energetic benefits (reviewed by Callier et al. 2018) may attract a disproportionate number of longer and heavier transient cod from outside divisions to sea cages.

Although the association of wild fish assemblages with sea cages is clear, the results of this study were somewhat contradictory, and suggest evaluations for costs and benefits of cage association are complex (Bacher et al. 2015). Due to an observed variation in cod growth and condition patterns in cage-associated cod, future research areas should address this variation in relation to life stage and wild fish species associating with sea cages. Identifying older cage-associated cod natal grounds could improve our understanding of younger cage-associated cod mortality, recruitment rates, and associated life history strategies, and eventually our understanding of species–ecosystem interactions within these novel environments. Additionally, otolith microchemistry has been used previously to identify wild fish natal grounds (reviewed by Campana 1999, 2005) including cod natal grounds within the local division (Stanley et al. 2016), artificial habitat use (Andronis et al. 2017), and pollu-

tant assimilation (Søndergaard et al. 2015). Therefore, otolith microchemistry may be a logical next step to determine the residency of wild cage-associated fish, relative to life stage and species, and consequently to determine whether age 4 cage-associated cod in this study were associated with sea cages at younger ages (2–3 yr old). Moreover, rapid environmental change from cage development can increase stress-linked glucocorticoid concentrations in fishes (reviewed by Sadoul & Geffroy 2019) and suppress growth and condition (Pickering et al. 1991, Sadoul & Vijayan 2016). Therefore, an analysis of environmental stress to younger cage-associated fish could investigate the role, if any, of environmental change, and particularly predation risk, on the growth and condition of cage-associated wild fishes that include *G. morhua*. Our control/impact sampling design was improved through the use of multiple control locations, large sample sizes (72–546 individuals per control location), and sampling variation across months and locations (Underwood 1992); however, sampling more impact sites (sea cage farms), ideally before and after beginning aquaculture operations or during a fallow period, may have proven useful in identifying external environmental effects on cage-associated cod. Therefore, the use of a single impact site in this study should be treated as a limitation.

In conclusion, the significant positive relationships between waste feed consumption (i.e. LA and ALA concentrations) and length and weight in age 2 cage-associated cod supported our hypothesis of waste feed consumption in younger cage-associated cod; however, the effects of waste feed consumption were contradictory, as the consumption of waste feed resulted in poorer condition in age 2 cod. Furthermore, accelerated growth was demonstrated by age 4 cage-associated cod, despite no evidence to support direct or indirect waste feed consumption by age 4 cod. Nevertheless, effects of waste feed consumption were not consistent enough or of sufficient quantities to disrupt growth- and condition-related patterns across large spatial areas.

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Appendix. Additional data

Table A1. Slope (m) and intercept (b) values used to correct length (cm) and weight (g) to a common sampling date, and R-squared (R^2) model fit values, for wild Atlantic cod *Gadus morhua* ages 2–4 yr old collected from reference sites within the local NAFO division (3Ps) and outside divisions (3L, 3N, 3O)

Reference divisions	Length			Weight		
	m	b	R^2	m	b	R^2
3Ps						
Age 2	0.30	21.36	0.57	12.57	44.47	0.82
Age 3	1.90	19.69	0.92	50.28	-51.82	0.73
Age 4	0.70	35.16	0.59	25.59	356.45	0.43
3L						
Age 2	0.88	17.94	0.99	18.40	-7.77	0.99
Age 3	1.04	23.22	0.80	36.92	-10.73	0.89
Age 4	0.78	34.57	0.82	46.54	241.88	0.96
3N						
Age 2	1.02	20.31	1	30.33	-27.84	1
Age 3	1.33	24.20	1	55.06	-43.27	1
Age 4	1.06	36.08	1	97.51	71.30	1
3O						
Age 2	0.91	18.64	1	18.49	10.42	1
Age 3	1.41	21.92	1	49.40	-38.93	1
Age 4	1.04	33.72	1	66.20	206.68	1

Table A2. Sample groups, collection season (spring, summer, fall), sample size (n), and mean length (cm), weight (g), and Fulton's condition index (condition) values \pm standard error (SE) for wild Atlantic cod *Gadus morhua* ages 2–4 yr old collected from reference sites removed from aquaculture operations within the local NAFO division (3Ps) and outside divisions (3L, 3N, 3O). SE values for condition index were all <0.01

Group	Season	n	Length	Weight	Condition
3Ps		329			
Age 2	Spring	41	22.90 \pm 0.38	94.88 \pm 6.5	0.8
	Fall	2	25.0 \pm 3.00	190 \pm 0.0	0.9
Age 3	Spring	102	28.3 \pm 0.43	183.43 \pm 8.3	0.8
	Summer	4	39.3 \pm 0.95	–	–
Age 4	Fall	36	39.3 \pm 0.81	438.00 \pm 89.8	0.8
	Spring	67	39.3 \pm 0.69	496.25 \pm 30.3	0.8
	Summer	17	40.1 \pm 0.97	–	–
	Fall	60	43.5 \pm 0.72	667.86 \pm 59.5	0.9
3L		546			
Age 2	Spring	50	22.8 \pm 0.3	93.6 \pm 4.3	0.8
	Fall	140	27.4 \pm 0.4	193.8 \pm 8.5	0.9
Age 3	Spring	78	29.3 \pm 0.5	207.1 \pm 10.5	0.8
	Summer	1	39.0 \pm 0.0	470.0 \pm 0.0	0.8
Age 4	Fall	103	35.2 \pm 0.5	407.9 \pm 16.0	0.9
	Spring	60	38.8 \pm 0.6	493.2 \pm 23.8	0.8
	Summer	12	39.8 \pm 0.8	570.8 \pm 33.0	0.9
	Fall	102	43.3 \pm 0.5	769.7 \pm 23.2	0.9
3N		245			
Age 2	Spring	47	25.4 \pm 0.5	123.8 \pm 7.5	0.7
	Fall	60	30.5 \pm 0.6	275.5 \pm 14.9	0.9
Age 3	Spring	20	30.9 \pm 1.1	232.0 \pm 27.5	0.7
	Fall	44	37.5 \pm 0.6	507.3 \pm 26.6	0.9
Age 4	Spring	35	41.8 \pm 0.8	558.9 \pm 39.1	0.8
	Fall	39	46.7 \pm 0.8	1046.4 \pm 54.9	1.0
3O		162			
Age 2	Spring	28	23.2 \pm 0.5	102.9 \pm 8.3	0.8
	Summer	1	27.0 \pm 0.0	150.0 \pm 0.0	0.8
	Fall	46	26.8 \pm 0.5	177.4 \pm 10.3	0.9
Age 3	Spring	46	29.0 \pm 0.7	208.0 \pm 13.4	0.8
	Summer	3	36.3 \pm 3.3	503.3 \pm 114.7	1.0
Age 4	Fall	13	34.2 \pm 1.2	383.1 \pm 42.8	0.9
	Spring	13	38.9 \pm 1.7	537.7 \pm 90.0	0.8
	Summer	5	44.8 \pm 1.4	906.0 \pm 115.0	1.0
	Fall	7	41.9 \pm 1.4	728.6 \pm 85.5	1.0

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