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Quantifying regional feed utilization, production and nutrient waste emission of Norwegian salmon cage aquaculture

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ABSTRACT: We analyzed growth performance and waste emissions of cage aquaculture responding to biophysical conditions that vary along the coastline of Norway. The analysis is based on a published mass balance model predicting waste emissions and open quality-assured data from the Norwegian Directorate of Fisheries between 2016 and 2020. Results showed significant regional variation in feed conversion rate, with a steady increase from the Northern to Southern region ($p < 0.001$) and a co-occurring reduction in waste emission. The retention rate of feed carbon (C), nitrogen (N) and phosphorus (P) in tissues of farmed Atlantic salmon *Salmo salar* Linnaeus, 1758 varied from 39 to 43% of consumed nutrients across regions. The estimated defecation rate of C, N and P was 18% of consumption, whereas excretion or respiration varied from 39 to 43% across regions. This variability, along with farming methods and location characteristics, could potentially impact regional differences in benthic ecosystems. The regional differences in feed and environmental cost could potentially attract salmon farming to shift towards the Northern region, and this trend might become strengthened as water temperatures rise due to climate change. Additionally, salmon growth and feed intake rate interacted significantly with temperature ($p < 0.001$) and showed regular seasonal variation. The regulation of maximum allowed biomass restricts salmon farmers from increasing biomass beyond their maximum allowed level at any time. Nevertheless, the same biomass may cause higher waste in the summer. Therefore, we suggest an awareness of the seasonal increase in waste emissions and consideration of implementing environmental assessment for surface waters, which might be beneficial for decreasing the risk of reduced water quality.

KEY WORDS: Aquaculture · Atlantic salmon · Feed conversion ratio · Mass balance · Waste emission

1. INTRODUCTION

Aquaculture has been the world's fastest-growing food-producing sector during the past 5 decades and can contribute to food security for the growing human population in the decades to come (FAO 2021). Despite this optimistic future, aquaculture is also under increasing pressure to become more sustainable (Lindland et al. 2019, Bailey & Eggereide 2020, Bottema et al. 2021). One of the historically most critical environmental concerns has been the utilization of wild fish resources as aquafeed ingredients (Naylor et al. 2000, Olsen 2011). Another concern is the metabolic release of dissolved and solid organic wastes (Cromey et al. 2002, Carroll et al. 2003, Bannister et al. 2014). If the organic waste emission exceeds the environmental carrying capacity, this may cause degradation of the structure and function of pelagic and benthic ecosystems (Ross et al. 2013). Unpolluted waters are paramount for the

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quality of seafood production, and cage aquaculture is sensitive because it is exposed to open waters. Aquaculture itself will generally be the first industry to suffer from a polluted environment (Olsen & Olsen 2008).

The Food and Agriculture Organization of the United Nations (FAO) has introduced the concept of the ecosystem approach to aquaculture (EAA), implying that aquaculture in the sea should be managed as a component of the marine ecosystem to ensure ecological resilience (FAO 2010). This concept of ecosystem-based management is implemented in EU environmental legislation, for example in the Water Framework Directive. To put this ecosystem concept into practice, further research is required to assess and quantify the overall influence of aquaculture on the ecosystem.

The concept of EAA implies that the sustainability of aquaculture development should consider the overall environmental pressure instead of the influence of a single variable. We should also consider that variables such as feed utilization efficiency and rates of nutrient emission are related and should be analyzed together. Commonly used indicators for feed utilization efficiency include feed conversion rate (FCR) and protein retention efficiency (PRE). These indicators are partly independent and reflect both growth capabilities and the emission rates of inorganic nutrients and organic wastes.

The local impact of biogenic wastes can be assessed using simple mass balance methods, which are robust and allow estimation of nutrient release rates (Olsen & Olsen 2008, Wang et al. 2012, Ytrestøyl et al. 2015). Wang et al. (2013) established coefficients for a simple mass balance model to quantify the nutrient release rate in cage aquaculture of Atlantic salmon farming. In a preliminary test of single cages by Wang et al. (2013), the method has revealed that about 62 % of feed carbon (C), 57 % of feed nitrogen (N) and 76 % of feed phosphorus (P) were not incorporated in salmon tissues but became released into the environment as organic particulate and inorganic wastes of N, P and C (ammonia, phosphate and CO_2, respectively). The method can readily be applied to estimate aquaculture waste generation for single salmon cages, single farms, regions or for national scales over short-time, seasonal or longer time scales. Life cycle assessment can provide information on the remote environmental influence of the aquaculture production system (Schau & Fet 2008, Pelletier et al. 2009).

To analyze the influence of national commercial aquaculture activity on marine ecosystems on different geographical and temporal scales using the mass balance method, reliable, quality-assured spatial time-series data on the use of feed and fish production are needed. Such data are available to the public on the website of the Norwegian Government (Thyholdt 2014, Directorate of Fisheries 2021), a precondition for our analysis. The Norwegian Government has also established and implemented an obligatory and regular sea floor assessment protocol to monitor aquaculture influence on seabed ecosystems according to the standard NS 9410, previously referred to as Monitoring-On-growing fish farm-Modeling (MOM) (Ervik et al. 1997). The assessments are now named b- and c-assessments (Standards Norway 2016), dependent on actual environmental influence. All fish farms must regularly carry out such assessments and make the data public.

Studies have shown that environmental variables such as temperature, day length and salinity can affect salmon growth, meaning that the feed utilization and nutrient emission may vary as well (Austreng et al. 1987, Oppedal et al. 1997, 2011, Boeuf & Le Bail 1999, Thyholdt 2014). Norway has a long coastline of 2650 km (straight line), ranging from 74° to 81° N latitude, and salmon cage farms located along this coastline are exposed to a pronounced variation in biophysical conditions (Thyholdt 2014). Environmental variability will affect salmon feeding rate, FCR, growth rate and the release rates of inorganic nutrients and organic wastes in large-scale farming activities. Faced with variable natural conditions, the Norwegian aquaculture industry will benefit from adjusting its farming techniques and strategies to achieve an optimal outcome. Hence, despite the extensive research conducted on salmon feed utilization and nutrient emissions, a comprehensive analysis of the interaction between aquaculture activity and the variable regional environment of marine waters on a national level for the industry will be meaningful for maintaining sustainable environmental aquaculture development (Wild-Allen et al. 2010, Thyholdt 2014, Taranger et al. 2015, Hadley et al. 2018).

The objective of this study was to quantify and analyze how the varying biophysical environmental conditions affect the feed utilization, energy retention and the release of organic and inorganic nutrient wastes from commercial salmon farming along the Norwegian coastline. We achieved this based on the mentioned mass balance model (Wang et al. 2013) and the use of input data on feed use, fish produced and other essential information available from government institutions.

2. MATERIALS AND METHODS

2.1. Data

Quality-assured data on benthic ecosystem assessment (b-assessment), monthly feed use, standing biomass and harvested production at the county level were obtained from the Norwegian Directorate of Fisheries, collecting data reported for each farm (https://www.fiskeridir.no/Akvakultur/Tall-og-analyse/Akvakulturstatistikk-tidsserier). Data on water temperature at 3 m depth reported from salmon farms were obtained from the BarentsWatch portal (https://www.barentswatch.no/fiskehelse).

We grouped county-level data for farming locations into 3 regions: the Northern region included Troms og Finnmark and Nordland, the Central region included Trøndelag and Møre og Romsdal, and the Southern region included Vestland and Rogaland og Agder (Fig. 1).

2.2. Calculations

2.2.1. Growth rate and feed intake rate

Daily growth rate (DGR) expresses the increased salmon body fresh weight (% d^{-1}), and daily feed intake (DFI) expresses the dry feed intake per salmon body fresh weight (% d^{-1})(Helland et al. 1996), estimated as:

$$\mathrm{DGR}\ (\%) = e^{\frac{\ln W_2 - \ln W_1}{d}} - 1 \tag{1}$$

$$\mathrm{DFI}\ (\%) = \frac{\Delta F}{d \times (W_2 - W_1)} \times 100 \tag{2}$$

where W_1 and W_2 are initial and final fresh weight of salmon, respectively; d is the number of days; and ΔF is feed intake (dry weight) during the period.

2.2.2. Feed conversion rate

FCR is a variable expressing the efficiency of feed utilization. In our study, we adapted the economic FCR, which also includes feed losses, fish losses and mortality. FCR was calculated as:

$$\mathrm{FCR} = \frac{\text{Dry feed given}}{\text{Salmon fresh weight gained}} = \frac{\Delta F}{\Delta B + \Delta H + \Delta L} \tag{3}$$

where ΔF is feed intake (dry weight) during the period; ΔB is increased biomass (fresh weight) during the period; ΔH is harvested production (fresh weight) during the period; and ΔL represents losses, mainly including mortality and escape.

2.2.3. Nutrient retention efficiency

The retention efficiency expresses nutrient transfer from feed to farmed fish, which are further classified as protein efficiency ratio (PER), lipid efficiency ratio (LER) and energy efficiency ratio (EER). They were calculated as:

$$\mathrm{PER} = \frac{\text{Weight of salmon produced}}{\text{Weight of protein fed}} = \mathrm{FCR}^{-1} \times F_{pt}^{-1} \tag{4}$$

$$\mathrm{LER} = \frac{\text{Weight of salmon produced}}{\text{Weight of lipid fed}} = \mathrm{FCR}^{-1} \times F_{lp}^{-1} \tag{5}$$

$$\mathrm{EER} = \frac{\text{Weight of salmon produced}}{\text{MJ of energy fed}} = \mathrm{FCR}^{-1} \times F_{eg}^{-1} \tag{6}$$

where F_{pt}, F_{lp} and F_{eg} are fractions of crude protein, crude lipid and energy in feed, respectively, and were assumed to be 35.6, 33.5 and 23.7%, respectively, in this study (Wang et al. 2013, Aas et al. 2019).

The retention (%) of nutrients and energy from feed to salmon was calculated using:

$$\text{Nutrient or energy retention (\%)} = \frac{\text{Nutrient or energy incorporated in salmon}}{\text{Nutrient or energy fed}} \times 100 = \mathrm{FCR}^{-1} \times F_x^{-1} \times G_x^{-1} \tag{7}$$

where F_x is a fraction of crude protein, crude lipid, or energy in feed, respectively, and G_x is a concentration of crude protein, crude lipid or energy in salmon, assumed to be 16.9, 21.5 and 12.7%, respectively, in this study (Wang et al. 2013, Aas et al. 2019).

2.2.4. Nutrient flow and release rates of nutrients and organic wastes

We estimated the flow of nutrients and release rates of inorganic nutrients and organic wastes of salmon by adapting the simple mass balance equation (Wang et al. 2012, 2013):

Fig. 1. Salmon aquaculture regions and site distribution in Norway in 2020. Circles indicate locations with salmon farm licenses. The Northern region in this study includes Troms og Finnmark and Nordland, the Central region includes Trøndelag and Møre og Romsdal, and the Southern region includes Vestland and Rogaland og Agder

$$I = A + D = G + E + D \quad (8)$$

where I is feed intake, A is assimilated food, D is defecation, G is growth or retention in biomass, and E is excretion. Assimilation efficiency (AE) is defined as the proportion of assimilated food to feed intake:

$$AE = A / I \quad (9)$$

Growth efficiency (GE) is defined as the proportion of growth or retention in biomass to feed intake:

$$GE = G / I \quad (10)$$

We further quantified the components of carbon (C), nitrogen (N) and phosphorus (P) in various types of emission, including dissolved inorganic matter (DIM), particulate organic matter (POM) and dissolved organic matter (DOM) (Sterner & George 2000, Olsen & Olsen 2008, Reid et al. 2009, Wang et al. 2012). Fig. 2 and Table 1 show the steps in the calculations of nutrient flows and the equations used for calculating the release rate of individual waste components. The coefficients adopted in this study are listed in Table 2. The C, N, P and water contents in feed and salmon were obtained from previously published literature (Wang et al. 2013, Aas et al. 2019, 2020). The AEs for C, N and P were determined using their respective digestibility values, as reported in the aforementioned literature. The method was conceptually established by Wang et al. (2012) and further adapted for salmon by Wang et al. (2013).

2.3. Statistical analysis

Statistical analyses of data were performed using MATLAB (release 2021). Data on FCR were assumed to be normally distributed. Differences in FCR between regions were compared by 1-way ANOVA followed by Tukey's tests for multiple comparisons at a significance level of 0.05. Data on FCR are given as means ± SE. The correlation between water temperature and DGR, between water temperature and DFI and between water temperature and FCR were examined by regression. The regression curves were determined by choosing the best R^2 value. The significance limits were set at 0.05.

3. RESULTS

3.1. Trend of production growth and environmental condition change

The annual national salmon production has grown by 78% in the Northern region in the past decade (2011–2020) and has increased much faster than in the Southern and Central regions, which both grew by 19% (Directorate of Fisheries 2021) (Fig. 3A). In

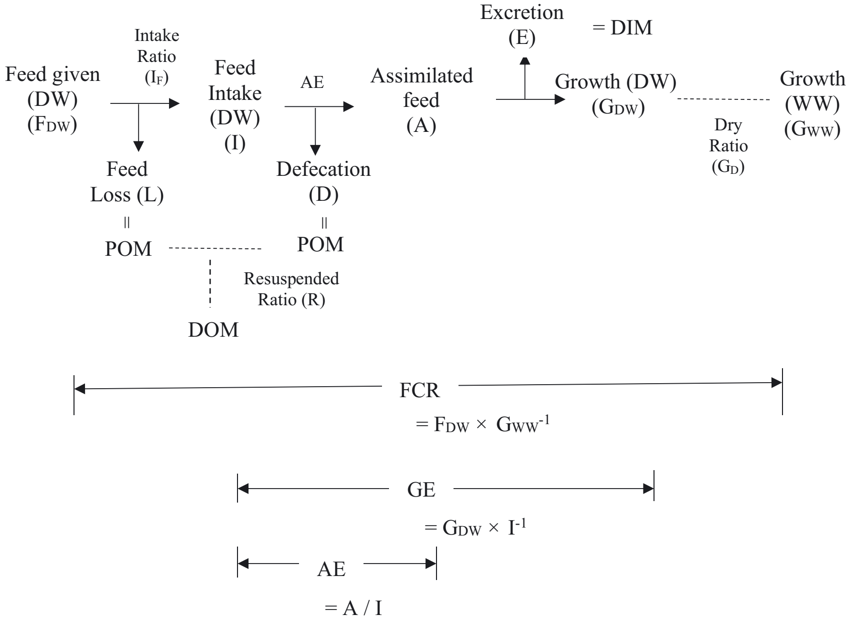

Fig. 2. Stepwise schematic nutrient flow, from feed given through fish growth and nutrient and organic wastes. DIM: dissolved inorganic matter; POM: particulate organic matter; DOM: dissolved organic matter; DW: dry weight; WW: wet weight; GE: growth efficiency; AE: assimilation efficiency

addition, data revealed a pronounced interannual variation in production in the Central region. Annual production showed an alternating annual variation, while the Northern and the Southern regions showed a more steadily growing trend.

The data obtained for the benthic ecosystem assessment (b-assessment) revealed that the Central region showed the lowest negative influence of the benthic ecosystem (i.e. lowest percentage of 'bad' and 'very bad' environmental state), whereas the Southern region showed the highest. In 2020, only 5% of the salmon farms in the Central region obtained bad or very bad b-assessments, while this percentage was 9 and 16% in the Northern and the Southern regions, respectively. In addition, assessments of the benthic ecosystem in the Southern region showed an increasing trend of bad and very bad results year by year after 2012, while such trends were not found in other regions (Fig. 3B).

Table 1. Equations used for calculation of nutrient emissions. DIM: dissolved inorganic matter; DIC: dissolved inorganic carbon; DIN: dissolved inorganic nitrogen; DIP: dissolved inorganic phosphorus; DOC: dissolved organic carbon; DON: dissolved organic nitrogen; DOP: dissolved organic phosphorus; POC: particulate organic carbon; PON: particulate organic nitrogen; POP: particulate organic phosphorus (POP); E: excretion; A: assimilated food; AE: assimilation efficiency; AE_C: AE of C; AE_N: AE of N; AE_P: AE of P; C: carbon; DW: dry weight; F_C: C content in feed (DW); FCR: feed conversion rate; F_D: feed dry matter ratio; F_{DW}: feed given (DW); F_N: N content in feed (DW); F_P: P content in feed (DW); F_{WW}: feed given (wet weight, WW); G_C: C content in salmon (DW); G_D: salmon growth dry ratio; G_N: N content in salmon (DW); G_P: P content in salmon (DW); G_{WW}: salmon growth (WW); D: defecation; I: feed intake; I_F: feed intake ratio; L: feed loss; L_F: feed loss ratio; N: nitrogen; P: phosphorus; R: resuspended rate

Parameter	Equation
DIM	$\mathrm{DIM} = \mathrm{E} = \mathrm{A} - G_{DW}$
	$= (\mathrm{AE} \times \mathrm{I}) - (F_{DW} \times \mathrm{FCR}^{-1} \times G_D)$
DIC	$\mathrm{CO_2} = (AE_C \times F_{WW} \times I_F \times F_D \times F_C) - (F_{DW} \times \mathrm{FCR}^{-1} \times G_D \times G_C)$
DIN	$\mathrm{DIN} = (AE_N \times F_{WW} \times I_F \times F_D \times F_N) - (F_{DW} \times \mathrm{FCR}^{-1} \times G_D \times G_N)$
DIP	$\mathrm{DIP} = (AE_P \times F_{WW} \times I_F \times F_D \times F_P) - (F_{DW} \times \mathrm{FCR}^{-1} \times G_D \times G_P)$
DOM	$\mathrm{DOM} = (\mathrm{L} + \mathrm{D}) \times \mathrm{R}$
	$= \{(F_{DW} \times L_F) + [F_{DW} \times I_F \times (1 - \mathrm{AE})]\} \times \mathrm{R}$
DOC	$\mathrm{DOC} = \{(F_{DW} \times L_F \times F_C) + [F_{DW} \times I_F \times F_C \times (1 - AE_C)]\} \times \mathrm{R}$
DON	$\mathrm{DON} = \{(F_{DW} \times L_F \times F_N) + [F_{DW} \times I_F \times F_N \times (1 - AE_N)]\} \times \mathrm{R}$
DOP	$\mathrm{DOP} = \{(F_{DW} \times L_F \times F_P) + [F_{DW} \times I_F \times F_P \times (1 - AE_P)]\} \times \mathrm{R}$
POM	$\mathrm{POM} = (\mathrm{L} + \mathrm{D}) \times (1 - \mathrm{R})$
	$= \{(F_{DW} \times L_F) + [F_{DW} \times I_F \times (1 - \mathrm{AE})]\} \times (1 - \mathrm{R})$
POC	$\mathrm{POC} = \{(F_{DW} \times L_F \times F_C) + [F_{DW} \times I_F \times F_C \times (1 - AE_C)]\} \times (1 - \mathrm{R})$
PON	$\mathrm{PON} = \{(F_{DW} \times L_F \times F_N) + [F_{DW} \times I_F \times F_N \times (1 - AE_N)]\} \times (1 - \mathrm{R})$
POP	$\mathrm{POP} = \{(F_{DW} \times L_F \times F_P) + [F_{DW} \times I_F \times F_P \times (1 - AE_P)]\} \times (1 - \mathrm{R})$

Table 2. Coefficients used in the mass balance model derived from a comprehensive salmon study (Wang et al. 2013) and other literature. AE: assimilation efficiency; FCR: feed conversion rate; DW: dry weight; WW: wet weight; C: carbon; N: nitrogen; P: phosphorus

Parameter	Symbol	Unit	Value	Reference
Feed given (WW)	F_{WW}	WW	Variable	
Feed dry matter ratio	F_D	Dry matter × WW^{-1}	0.934	Aas et al. (2019)
Feed given (DW)	F_{DW}	$F_{WW} \times F_D^{-1}$	Variable	
Salmon growth (WW)	G_{WW}	WW	Variable	
FCR	FCR	$F_{DW} \times G_{WW}^{-1}$	Variable	
Salmon growth dry ratio	G_D	Dry matter × WW^{-1}	0.409	Aas et al. (2019), Wang et al. (2013)
Feed intake ratio	I_F	Fraction of feed given	0.97	Wang et al. (2013)
Feed loss ratio	L_F	Fraction of feed given	0.03	Wang et al. (2013)
Resuspended rate	R	Fraction of total organic matter	0.15	Sugiura et al. (2006), Wang et al. (2013)
AE of C	AE_C	Fraction of digestion	0.85	Wang et al. (2013)
C content in feed (DW)	F_C	g C × g DW^{-1}	0.54	Wang et al. (2013)
C content in salmon (DW)	G_C	g C × g DW^{-1}	0.61	Wang et al. (2013)
AE of N	AE_N	Fraction of digestion	0.9	Aas et al. (2020), Wang et al. (2013)
N content in feed (DW)	F_N	g N × g DW^{-1}	0.061	Aas et al. (2019)
N content in salmon (DW)	G_N	g N × g DW^{-1}	0.066	Aas et al. (2019)
AE of P	AE_P	Fraction of digestion	0.3	Wang et al. (2013)
			0.407~0.475	Aas et al. (2020)
P content in feed (DW)	F_P	g P × g DW^{-1}	0.0139	Aas et al. (2019)
P content in salmon (DW)	G_P	g P × g DW^{-1}	0.0076	Aas et al. (2019)

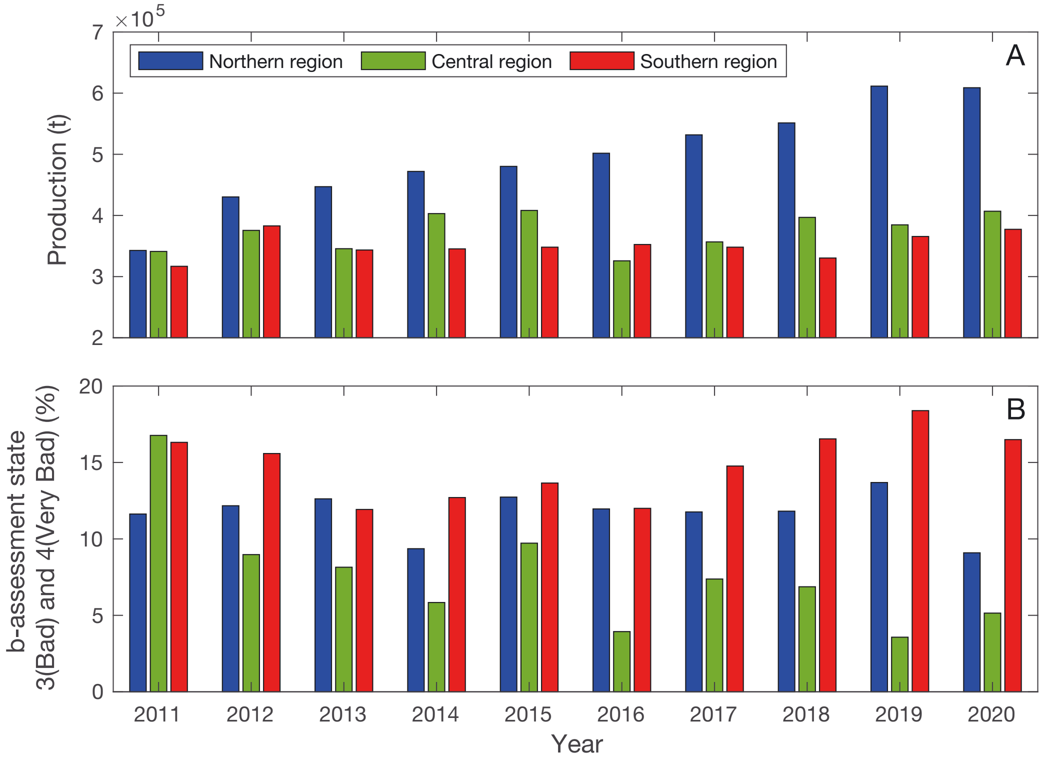

Fig. 3. Summary data on Norwegian salmon cage aquaculture in the Southern, Central and Northern regions from 2011 to 2020. (A) Annual production and (B) b-assessment for environment condition (Directorate of Fisheries 2021)

3.2. Growth rate and feed intake rate

The average water temperature increased from the Northern to the Southern region and showed a similar pattern of variation within all regions. The annual minimum temperature usually occurred in March, and the temperature began to increase from April, reaching the highest value in August, whereafter it decreased gradually from September (Fig. 4A).

The salmon growth rate, expressed in terms of DGR (Eq. 1), reflects the increase in body fresh weight (BW) in % per day. The DGR value exhibited a pronounced seasonal variation in all regions, highly correlated with the variation in average monthly temperature ($p < 0.001$; Fig. 4B,D). DGR increased with increasing temperature and responded fastest in the Northern region (Fig. 4D). The average DGR varied between 0.24 and 0.73% in the Northern region, 0.34 and 0.64% in the Central region, and 0.24 and 0.63% in the Southern region.

The feeding rate is expressed in terms of daily dry feed intake relative to fish body fresh weight (DFI, Eq. 2), showing the consumed dry weight (DW) of feed per day and fresh BW (%). DFI showed the same pattern of variation with temperature as DGR ($p < 0.001$; Fig. 4C,E). The average DFI value varied between 0.35 and 0.78% in the Northern region, 0.43 and 0.81% in the Central region, and 0.40 and 0.74% in the Southern region.

Our results accordingly revealed that DGR and DFI in all regions showed a similar pattern of seasonal variation. However, the response to changes in water temperature revealed by the DFI versus temperature slope varied slightly among regions (Fig. 4D,E). Fish in the Northern region were more sensitive to rising temperatures, showing a greater response than those in other regions.

3.3. Feed conversion rate

The efficiency of feed-to-fish conversion was expressed in terms of economic feed conversion rate (FCR, Eq. 3), the ratio of DW feed intake to fish wet weight gained. Unlike DGR and DFI, the FCR value did not show a clear seasonal variation (Fig. 5), but FCR values were significantly different among regions (ANOVA, $p < 0.001$). The FCRs in the Northern, Central and Southern regions were 1.06 ± 0.05, 1.11 ± 0.05 and 1.17 ± 0.07 kg dry feed per kg fish wet weight produced, respectively, suggesting

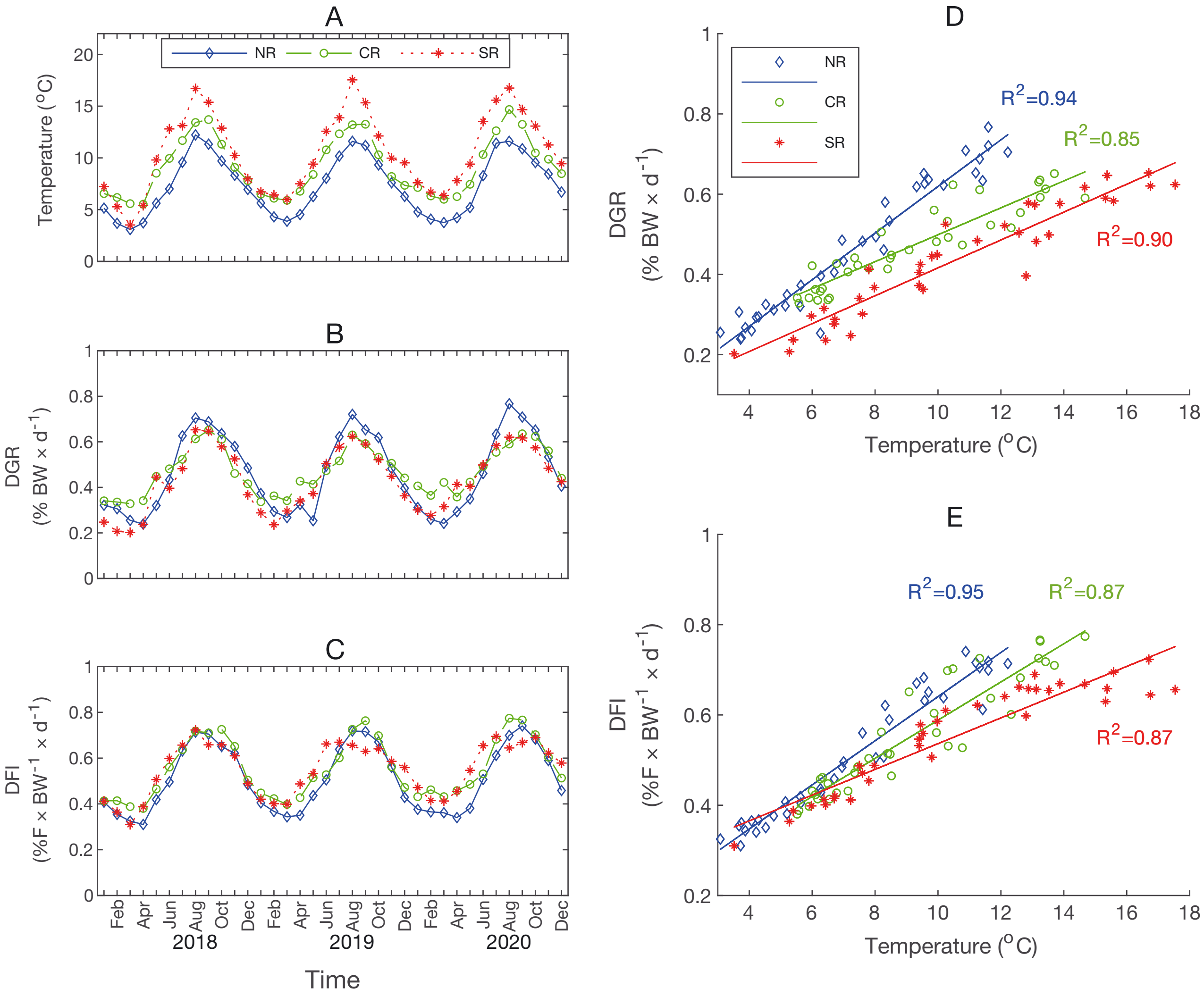

Fig. 4. Seasonal variation in temperature, salmon growth rate and feed intake for regions from 2018 to 2020. (A) Water temperature (°C); (B) daily growth rate (DGR); (C) daily feed intake relative to body weight (DFI) with time; (D) relationship between water temperature and DGR; (E) relationship between water temperature and DFI. NR: Northern region; CR: Central region; SR: Southern region; BW: body weight; d: number of days; F: feed dry weight

that farmed salmon in the Northern region utilized feed more efficiently than fish in the other regions.

3.4. Nutrient retention efficiency

The retention of protein, lipid and energy in the salmon was expressed in terms of 2 different variables. The first was the efficiency ratio, including PER (Eq. 4), LER (Eq. 5) and EER (Eq. 6). These ratios represent the weight of salmon gained relative to nutrients or energy consumed. The second variable was nutrient or energy retention in percentage (%, Eq. 7) showing the amount of feed protein, lipid or energy that became retained in salmon.

Values of PER, LER and EER varied in the range of 2.25–2.48, 2.39–2.64 and 3.38–3.73, respectively. Values for retention (%) of protein, lipid and energy were in the range of 38–42, 51–57 and 43–47%, respectively. Similar to the FCR, the values of both variables declined gradually from the Northern to the Southern region along the Norwegian coastline (Fig. 6). This implied that, given the same amount of feed, farmed salmon in the Northern region retained more nutrients in the body than fish in other regions.

3.5. Release rates of inorganic and organic wastes

For 1 t of feed consumed by salmon from 2016 to 2020, 223–247 kg of DIM and 88 kg of POM were

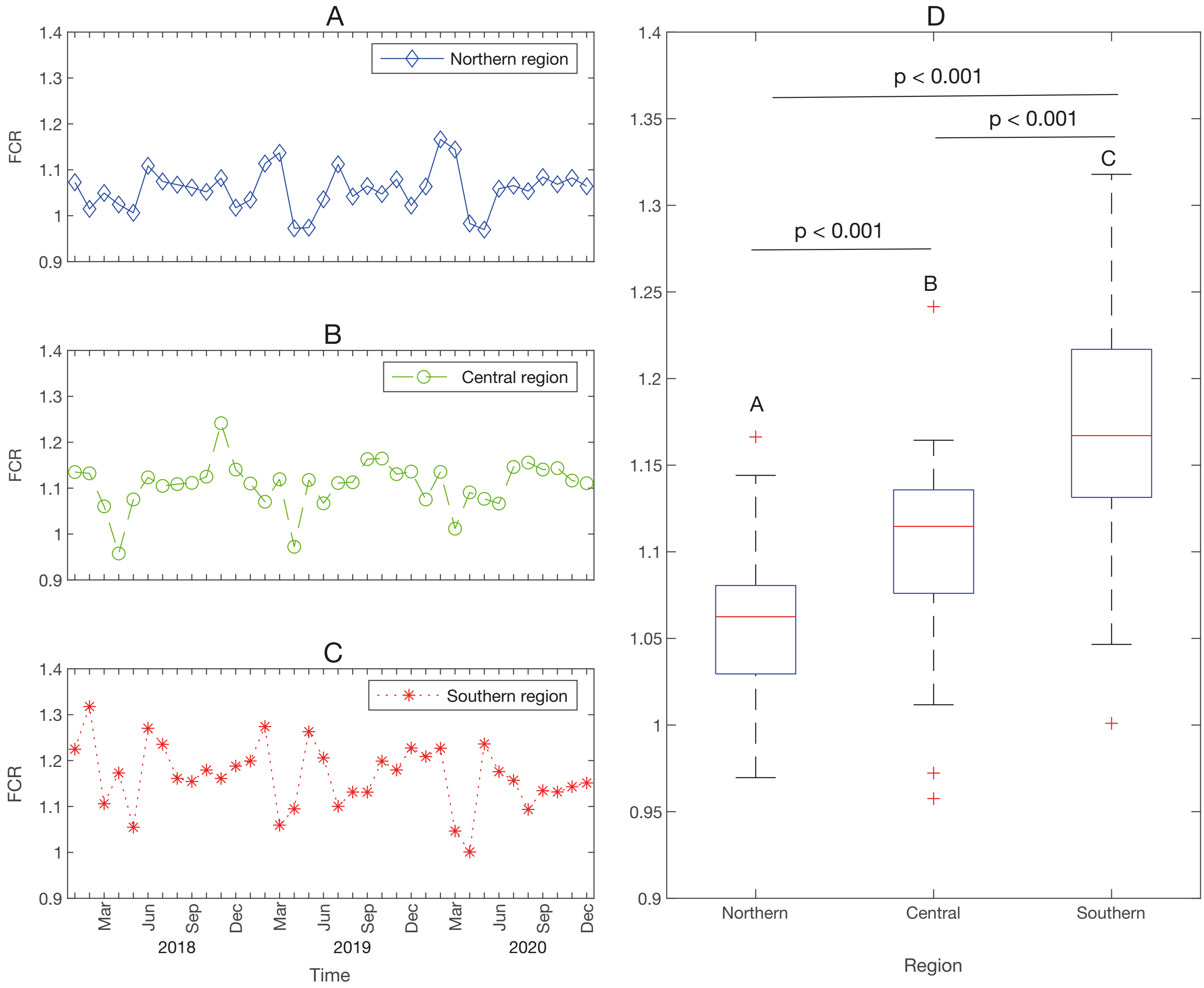

Fig. 5. Monthly average feed conversion rate (FCR) of Norwegian salmon cage aquaculture from 2018 to 2020: (A) Northern region, (B) Central region, (C) Southern region. (D) Monthly FCR distribution among regions. The lines in the middle, lower, and upper ends of the boxes represent the median, 25%, 50% and 75% quantiles, respectively; the lower and upper whiskers represent the minimal and maximal values; and '+' symbols beyond the whiskers represent outliers

released into the environment (Fig. 7). A fraction of POM will resuspend in water, forming DOM. Like Wang et al. (2013), we used a value of 15% of POM (Table 2). The loss rate of DIM increased from the Northern to the Southern regions along the Norwegian coastline (Fig. 7A–C). The phosphorus (P) released as POM was higher than the fraction released as DIM, i.e. phosphate. This pattern of variation was opposite to that found for carbon (C) and nitrogen (N) and resulted from a lower AE, or digestibility, of P from the feed components than that of C and N. These differences in AE caused different chemical C:N:P composition of feed, fish and wastes.

In natural pristine seawater, the molecular ratio of N to P in NE Atlantic deep and winter water is ~16, in accordance with the Redfield ratio (Redfield 1934). In the present study, the molecular N:P ratio of released DIM was 23.6–24.1 (by weight), whereas the ratio for POM was 2.04, again showing that inorganic N release (NH_4) is more abundant than inorganic P release (PO_4). P was accordingly most abundant in POM waste accumulating on the sea floor beneath salmon farms (Fig. 7D).

These results were a consequence of assuming an AE of P (digestibility) of 0.407 (AE_P, Table 2), while the AE of N was set to 0.9 (AE_N, Table 2). Previous studies have shown that the AE_P could vary from 0.3 to 0.475 depending on feed ingredients and physical pellet quality (Wang et al. 2013, Aas et al. 2020). The AE used for C and N were more robust, in part because the AE of protein was declared by the feed manufacturing company (Table 2).

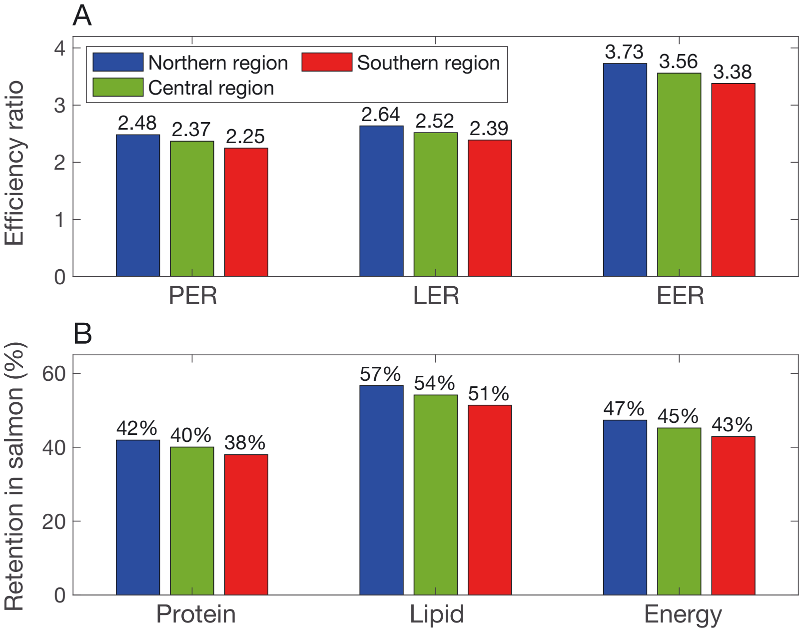

Fig. 6. Nutrient retention for Norwegian salmon cage aquaculture. (A) Nutrition efficiency ratio; (B) nutrition retention. PER: protein efficiency ratio; LER: lipid efficiency ratio; EER: energy efficiency ratio

3.6. Salmon waste generation

We estimated the monthly amount of wastes released (Fig. 8) based on the release rate of POM, DOM and DIM (kg t^{-1} of feed; Fig. 7A–C). The annual inorganic nutrient and organic wastes discharged by Norwegian salmon cage aquaculture in 2020 were estimated to be 629 826 t (DW), including 164 547 t of POM, 29 038 t of DOM and 436 241 t of DIM. The waste emission was not distributed equally throughout the year. The release of wastes was highest in the late summer season. We found that the annual emissions were higher from August to October compared to other months, whereas the biomass did not reveal such a pronounced pattern.

Fig. 8 shows monthly POM discharged from Norwegian salmon cage aquaculture during 2010–2020

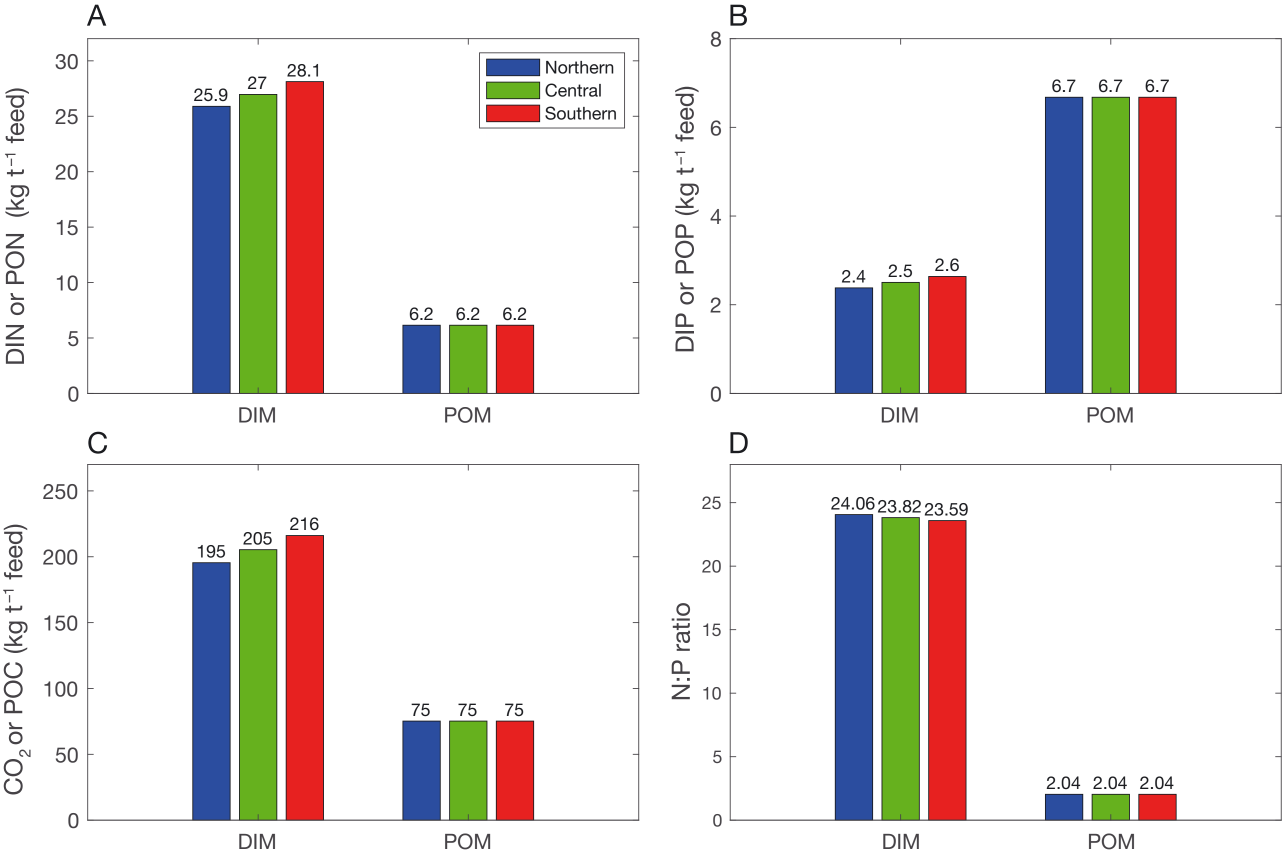

Fig. 7. Organic waste and nutrient release rates for Norwegian salmon cage aquaculture by region. (A) Nitrogen; (B) phosphorus; (C) carbon; (D) N:P ratio of dissolved inorganic matter (DIM) and particulate organic matter (POM) (assumed assimilation efficiency of phosphorus is 0.407)

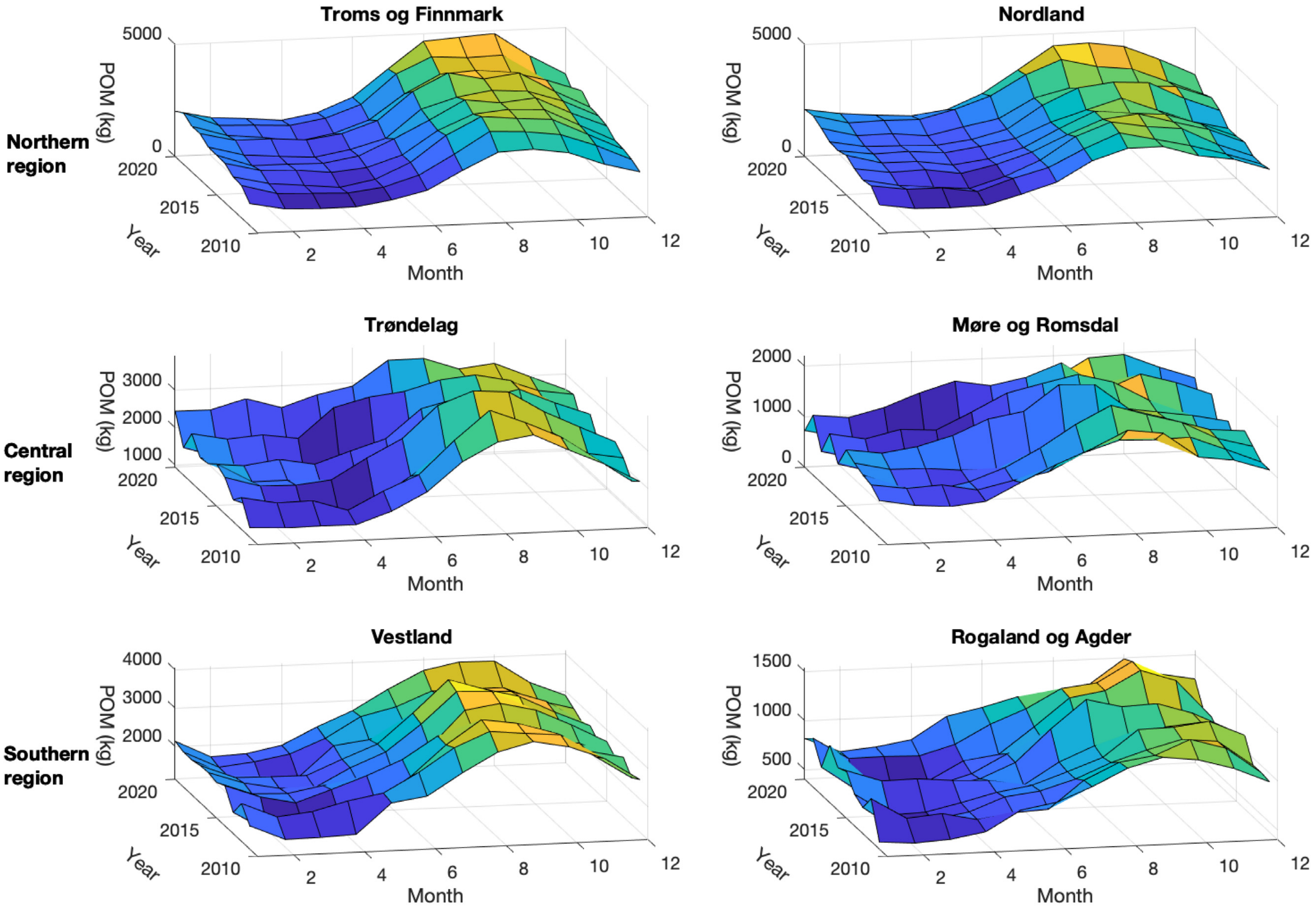

Fig. 8. Monthly particulate organic matter (POM) discharged from Norwegian salmon cage aquaculture during 2010–2020 by region and county. The colors of surface plots vary according to the level of POM

by county. The release of POM peaked throughout the summer season and was related to production. Values increased most in the Northern region over the season (Fig. 8). Additionally, we observed that counties in the Central region did not follow this trend of increase, showing a notable inter-annual variation.

3.7. Flows of nutrients

The estimated flows of inorganic and organic C, N and P components through the process of feeding, waste generation and retention in salmon are summarized in Fig. 9. The results revealed that of the total input of feed C, N and P, about 39–43%, was retained in salmon meat, 18% was discharged as organic wastes and 39–43% was discharged as inorganic nutrient wastes.

The fraction retained in the salmon (39–43%) decreased gradually from the Northern to the Southern regions along the Norwegian coastline, while the fraction of nutrient wastes (39–43%) increased. This may suggest that farmed salmon in the Southern region, which is exposed to higher temperatures, spend more energy for metabolism. In addition, the input values of feed P (~2% of DW of feed) were higher than the content of salmon P (~1% of DW of fish). Feed C and feed N showed similar values as salmon C and salmon N, suggesting that the utilization of feed P was less efficient than that of feed C and feed N (Fig. 9).

Fig. 10 reveals pronounced differences in the elemental composition of C, N and P for salmon, nutrients and organic wastes, resulting in slight variations among regions. The majority of consumed P was released as organic wastes, while C and N were mainly released as inorganic wastes of CO_2 and ammonia, respectively. This means that P wastes will affect mainly the sea floor ecosystem, whereas N wastes will potentially mainly affect the planktonic ecosystem of surface waters.

4. DISCUSSION

The main finding of our study was that the FCR, nutrient utilization efficiency and biogenic waste emissions were mostly significantly different among the Southern, Central and Northern regions ($p < 0.001$). These differences might involve a considerable difference in feed costs, utilization efficiency of

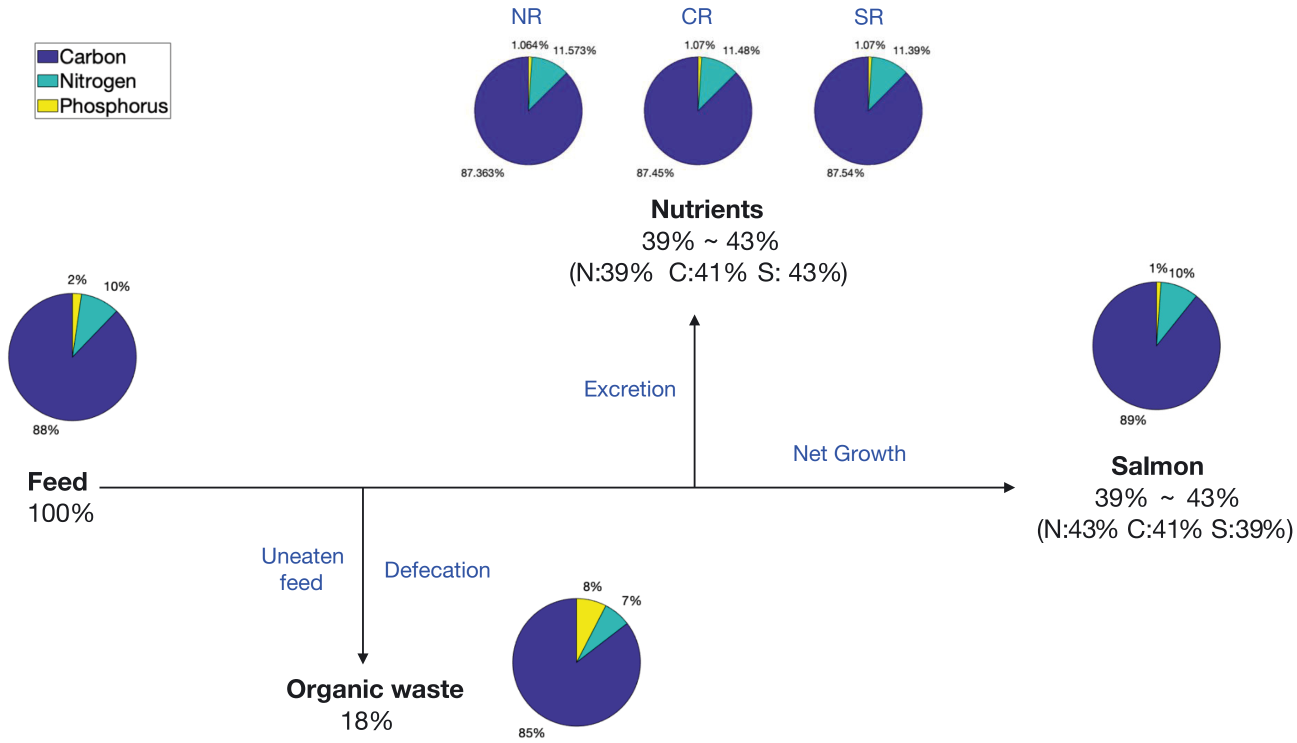

Fig. 9. Nutrient flows estimated for Norwegian salmon cage aquaculture. NR: Northern region; CR: Central region; SR: Southern region

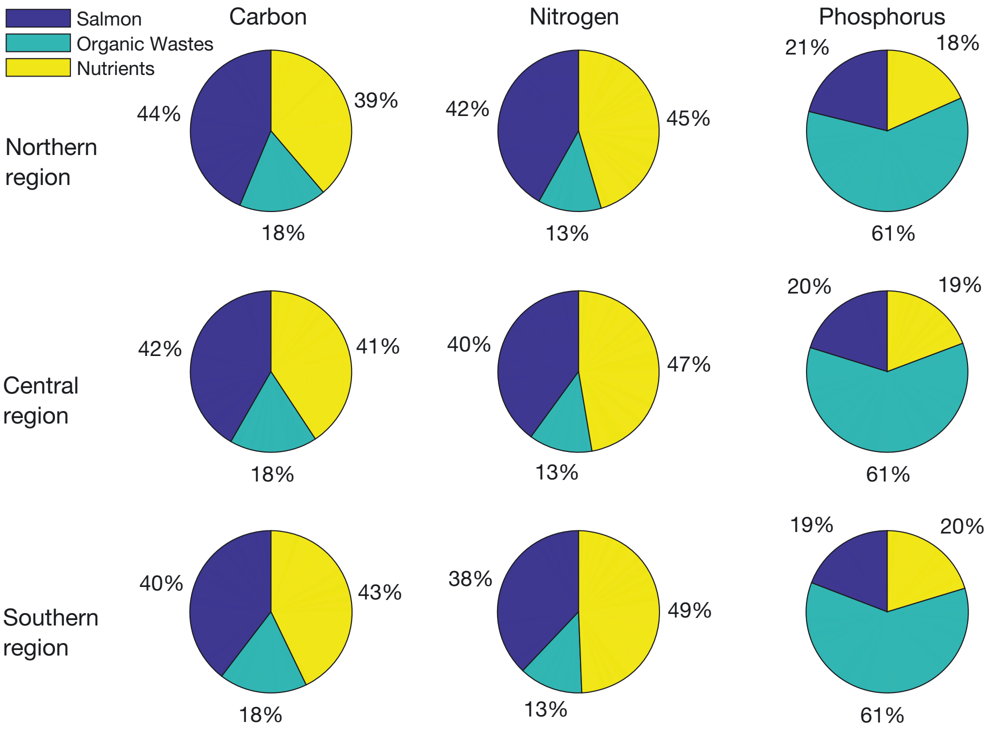

Fig. 10. Nutrient flows of carbon, nitrogen and phosphorus for Norwegian salmon cage aquaculture in the 3 different regions

wild fish feed ingredients and the potential environmental influence of biogenic wastes released. Additionally, the DGR and DFI showed significant seasonal variation. The salmon grew faster and consumed more feed during summer to early autumn, also reflecting variation in production and waste generation. Such seasonal variations were also slightly different among regions.

4.1. Regional differences in production costs

The FCR showed significant differences ($p < 0.001$) among regions and revealed a gradual decrease from the Southern to the Northern region. This implies that producing 1 kg of salmon in the Northern regions requires 10.4% less feed than in the Southern region, accounting for a considerable reduction in costs, unless other unknown losses must be considered. Taking the production in 2020 as an example, the annual overall consumption of feed in the Northern regions was ~798 000 t. The same salmon production in the Southern region would require an additional ~83 000 t of feed, equivalent to increasing the cost by around 1.38 billion Norwegian kroner (NOK) (153 million USD) if the feed cost was 16.6 NOK (1.84 USD) kg^{-1} (BarentsWatch 2022). Therefore, lower production costs might represent one important incentive for the Norwegian salmon industry to further develop salmon farming in the Northern region.

This trend might be strengthened, as climate change could potentially raise seawater temperature (Høyer & Karagali 2016), given that water temperature is known to have significant impacts on fish metabolism. Higher temperature can increase the metabolic rates of salmon, leading to a higher demand for oxygen. The solubility of oxygen is inversely related to temperature, and increasing temperatures may result in a decreased availability of oxygen to the fish (Austreng et al. 1987, Pörtner & Knust 2007, Elliott & Elliott 2010, Stehfest et al. 2017). Previous studies have reported that the optimal and suboptimal water temperature for Atlantic salmon is between 7 and 16°C, and warmer temperature may result in reduced feed intake, slower growth rates, increased stress and mortality and outbreaks of fish disease and salmon lice infections (Handeland et al. 2000, Kullgren et al. 2013, Hvas et al. 2017, Falconer et al. 2020, 2022, Sandvik et al. 2021). The water temperature can occasionally exceed the optimum level in the Southern region during summer (Hermansen & Heen 2012), whereas it is securely within the optimum range in the Northern region during summer but may fall below the optimum level during winter. Thus, increasing temperature in winter may benefit Norwegian salmon farming in the Northern region, while increasing temperature in summer may cause adverse impacts for the Southern region.

4.2. Seafloor impact and environmental costs

The higher feed utilization efficiency was necessarily related to reduced release rates of biogenic wastes because more feed became retained in biomass. Defecation (POM) was constant, as there is no information on variable digestibility of the feed with varying latitudes. The biogenic waste emissions accordingly showed an inverse regional variation as compared to feed utilization efficiency. We estimated that 39–43% of the given feed, increasing from the Southern to the Northern regions, became retained in salmon biomass, whereas 57–61%, decreasing from the Southern to the Northern regions, were released as biogenic wastes discharged to the surrounding environment.

The organic enrichment of the sea floor is influenced by biophysical conditions and farming operations, including water depth, water current velocity and fish production (Carroll et al. 2003, Bannister et al. 2014). Thus, the release rate of biogenic waste is considered a critical factor affecting regional differences in the assessment of the sea floor ecosystem (see Fig. 3B). Despite this regional difference, the result of the b-assessment in all regions showed no harmful degradation during the past decade, suggesting that the current overall production is still well within the environmental carrying capacity for salmon farming.

According to Norwegian regulation NS 9410, fish farmers are obligated to conduct a benthic ecosystem assessment (b-assessment) at least once per production cycle during the period of maximum salmon biomass. One or 2 additional assessments will be required if the result of the b-assessment is below condition 2 (good). Salmon farmers accordingly incur environmental costs that vary by site, but are generally higher in the Southern region than in the Northern. Reduced environmental costs might be another incentive attracting the industry to increase production in the Northern region.

Additionally, the Central region apparently showed the best result following the sea floor ecosystem assessment. We suggest it might be related to the interannual variation in production and biogenic wastes (see Figs. 3A & 8). Extended periods with low production or longer rest intervals between production cycles may cause reduced organic enrichment of the sea floor, which may result in an enhanced benefit of ecosystem services of environmental decomposition or self-purification.

4.3. Growth characteristics correlated to water temperature

Both DGR and DFI were significantly positively correlated to water temperature (all $p < 0.001$), again supporting the fact farmed salmon grew faster and consumed more feed during the summer–early autumn period than during other periods (Nordgarden et al. 2003). This relationship was found within all regions, but the response of DGR and DFI variables to an increasing temperature was strongest in the Northern region and lowest in the Southern (Fig. 4D,E). Statistical assessment showed a positive response of DGR and DFI to temperature in all regions (Table 3).

The FCR was not, or only very weakly, related to temperature and showed no seasonal variation (Fig. 5). In fact, FCR in the Northern and Southern regions showed values independent of temperature (Table 3, $p > 0.05$), whereas FCR values in the Central region still showed a slight correlation (Table 3, $p < 0.05$). The independence of temperature likely reflected that the amount of feed given was closely related to the needs of the salmon through the seasons, as feeding was reduced or stopped when salmon stopped consuming feed. This reduction might be attributed to modern advanced feeding technology, applying visual observation combined with multiple sensors to observe salmon feeding behavior and prevent overfeeding (Moe Føre et al. 2022).

4.4. Effect of seasonal variation

The seasonal variation in DFI could cause considerable difference in release rate of biogenic waste for the same biomass of salmon. The biogenic waste emission showed an annual peak during summer–early autumn and was relatively low during winter–spring. The result is also in agreement with previous studies that the release of biogenic wastes was highest during summer–autumn periods, and seasonal variation was suggested to be considered for evaluating environmental impact of salmon farming (Wang et al. 2012, 2013). The trends in seasonal variations were found to be similar among all regions (Fig. 9). Comparing regions during winter (December–January), the waste emission in the Southern region was ~20% higher than in the Northern region. During summer (August–September),

Table 3. Statistical coefficients for linear regressions of metabolic variables vs. temperature for the 3 regions. Data from Fig. 4. DGR: daily growth rate; DFI: daily feed intake; FCR: feed conversion ratio. Significant at *p < 0.05, ***p < 0.001

Variable	Slope ± SE	Intercept ± SE	R^2	p
DFI vs. temperature				
Northern region	0.0489 ± 0.002	0.1517 ± 0.016	0.945	<0.001***
Central region	0.0424 ± 0.003	0.1638 ± 0.027	0.867	<0.001***
Southern region	0.0286 ± 0.002	0.2511 ± 0.021	0.873	<0.001***
DGR vs. temperature				
Northern region	0.0580 ± 0.003	0.0390 ± 0.020	0.937	<0.001***
Central region	0.0334 ± 0.002	0.1646 ± 0.023	0.849	<0.001***
Southern region	0.0345 ± 0.002	0.0720 ± 0.023	0.896	<0.001***
FCR vs. temperature				
Northern region	0.0016 ± 0.003	1.0446 ± 0.022	0.009	0.572
Central region	0.0075 ± 0.003	1.0389 ± 0.028	0.162	<0.05*
Southern region	−0.0020 ± 0.003	1.1873 ± 0.036	0.011	0.538

however, the biogenic waste emission in the Southern region became ~10% lower than in the Northern region. Thus, we suggest increasing awareness of high biogenic waste emissions during the summer season, which might be beneficial for reducing the risk of reduced oxygen and environmental degradation in sensitive locations (Olsen & Olsen 2008).

The Norwegian regulation of maximum allowed biomass (MAB) associated with the b-assessment is a functional means to help control the risk of overloading biogenic wastes during summer. The MAB regulates the salmon biomass that cannot be exceeded at any time. This regulation can prevent fish farmers from largely increasing biomass during summer, which could indirectly affect control of the release of biogenic wastes. Moreover, the b-assessment can reveal the environmental conditions of a sea floor ecosystem at the maximum biomass period and provide an early warning for fish farmers to implement counteractive measures. As a result of the national MAB regulation, comprehensive databases for ecological and chemical conditions of the seafloor ecosystems in different sites and regions have been established (Standards Norway 2016). Because the data are open to the public, data on ecosystems of the sea floor may be further analyzed to study how the ecosystems are regionally affected and how conditions vary during the season and during salmon production.

4.5. Impact and reuse of nutrient wastes

The release of inorganic and organic nutrient wastes is considered an environmental challenge of fish farming, causing potentially harmful effects to surface waters and seafloor ecosystems (Olsen & Olsen 2008). Many have suggested that wastes from fish farming can become a valuable source for establishing integrated multitrophic aquaculture (IMTA), e.g. salmon aquaculture integrated with macroalgae and animals cultured based on the reuse of wastes, e.g. shellfish or other invertebrates (Wang et al. 2012, 2013, Broch et al. 2013, Bergvik et al. 2019). It is essential to estimate the amount of available released nutrient wastes, and their nutritional quality, likely expressed in terms of the proportion of C, N and P or their contents of essential nutrients (Wang et al. 2012, 2013).

The majority of nitrogenous wastes of farmed salmon is, as mentioned previously, inorganic N (ammonia, NH_4), constituting as much as 45–49% of the consumed feed N, whereas ~61% of the consumed feed P is released in the form of particulate organic P (Wang et al. 2013; Fig. 10, Table 2). This causes a large difference in the N:P ratio between surface-water ecosystems, receiving inorganic nutrients, and sea-floor ecosystems surrounding cages, which receive particulate nutrients (Fig. 7D). These differences for N and P wastes may become important for a holistic environmental assessment of the marine ecosystem.

4.6. Implications for variables in related studies

The estimated FCR in the present study ranged from 1.06 to 1.17; a similar value (~1.08–1.11) was measured and reported by Wang et al. (2013) in a study in the Central region, suggesting that feed utilization efficiency has not been further improved since 2009. This is in agreement with the fact that no major changes in feed ingredients in salmon feed are reported for the period (Ytrestøyl et al. 2015, Aas et al. 2019, 2020). Although the FCR has remained relatively stable compared to 2012, there has been a moderate further reduction in the use of wild fish as a feed ingredient, which has been replaced by plant sources or by reutilizing by-products from other sources, as reported by Aas et al. (2020). This improvement in feed ingredients contributes to sustainability in the aquaculture industry.

The estimation of FCR in the present study was based on cumulative data collected from all salmon farms in different regions along the Norwegian coastline. Our estimates of growth rate, feed intake rate and FCR are accordingly representative for mixed populations with all different sizes of salmon. The present growth variables are affected by the fish size and ages (Brett 1979, Refstie et al. 1998, Nordgarden et al. 2003), and we emphasize that our values are representative of mixed populations.

Some variables of the mass balance model (Table 2) were taken from fish farmers or the literature. For example, feed loss is difficult to measure regularly. Based on information from salmon farmers, the fraction of feed losses were assumed to be 3% in the present study, as also suggested by Cromey et al. (2002), Reid et al. (2009) and Wang et al. (2013). The fraction of DOM resuspending from POM was set to 15%, based on one main reference (Sugiura et al. 2006; also used by Wang et al. 2012). These values are not important for our overall conclusions.

This study was based on cumulative data from all commercial salmon farms (~1000 sites) in Norway from 2018 to 2020, and the results are in agreement with other relevant studies. This further confirms that the mass balance method is robust (Olsen & Olsen 2008, Wang et al. 2012, Ytrestøyl et al. 2015). Despite our focus on Atlantic salmon, the method can be applied to other farmed species if their representative coefficients (Table 2) are established and data on feed and production are available.

There is a lack of clear evidence linking the occurrence of harmful algal blooms (HABs) with inorganic nutrients from salmon cage sites, and the correlation between HABs and the N:P ratio is not yet fully understood (Davidson et al. 2012). Studies have indicated that the occurrence of HABs is site-specific and can be influenced by multifactorial conditions, including water temperature, dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), salinity, wind stress, cloud cover, rainfall, hydrodynamic conditions and potential effects of climate change (Davidson et al. 2014, Wells et al. 2015, Karlson et al. 2021, John et al. 2022). Our research findings suggest that the N:P ratio in the affected waters may be remarkably lower than the Redfield ratio. The main limiting nutrient for phytoplankton growth based on only farmed salmon wastes will then be DIP. However, it is important that other sources can be more important in supplying DIP and DIN for phytoplankton growth. The main source of DIN and DIP in Norwegian temperate coastal water is deep water (Olsen et al. 2014), while other contributing sources are land runoff of fertilizers, sewage and other animal wastes (Anderson et al. 2002, Davidson et al. 2014).

The Norwegian government has implemented an environmental assessment to monitor the impact of organic wastes from aquaculture on the sea floor ecosystem (Standards Norway 2016), receiving ~18% of the total given feed (Fig. 9). However, there is still no governmental requirement of environmental assessment on surface waters affected by aquaculture, even though 39–43% of given feed are released as inorganic N (ammonia, NH_4) and inorganic P in the form of phosphate. Water quality of surface waters may become a critical factor for reduced oxygen and the occurrence of HABs in sensitive locations as production continues to increase. As a means for mitigation, inorganic nutrients like ammonia can also be reused in aquaculture of macroalgae (Olsen & Olsen 2008, Broch et al. 2013, Wang et al. 2013, 2014, Bergvik et al. 2019).

5. CONCLUSION

We found a significant regional variation in FCR, with a steady increase from the Northern to the Southern region ($p < 0.001$) and a co-occurring reduction in nutrient waste emission. The result revealed that producing 1 kg of salmon in the Northern regions could save 10.4% of feed costs needed in the Southern region. Moreover, we estimated that of given C, N and P in feed, about 57–61% were released as biogenic wastes discharged to the surrounding environment, decreasing from the Southern to the Northern regions. The variation in the release rate of biogenic waste may be one of the critical factors affecting the regional differences in the assessment of the sea floor ecosystem. Thus, the regional differences might involve a considerable difference in feed and environmental costs that might be essential factors attracting Norwegian farming to expand to the Northern regions, and this trend might be strengthened as climate change could potentially raise surface seawater temperature.

The seasonal variation in feed intake rate caused an increase in biogenic wastes during the summer. Although the regulation of MAB restricts salmon farmers from increasing biomass beyond the maximum level at any time, the same biomass may still cause higher biogenic wastes in summer. Therefore, we suggest some awareness of the seasonal increase in biogenic wastes and suggest further consideration for implementing environmental assessment also for surface water. This might be beneficial for reducing the risk of reduced oxygen and HABs in sensitive locations.

Data availability. The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

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