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RECENT TRENDS IN TEMPORAL AND GEOGRAPHICAL VARIATION IN BLUBBER THICKNESS OF COMMON MINKE WHALES (*BALAENOPTERA ACUTOROSTRATA ACUTOROSTRATA*) IN THE NORTHEAST ATLANTIC

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ABSTRACT

The common minke whale (*Balaenoptera acutorostrata acutorostrata*) is a migratory species, and the summer period is generally characterized by intensive feeding and consequently seasonal fattening at high latitudes. The fat deposited is stored as energy reserves for overwintering at lower latitudes where feeding is supposed to be greatly reduced. It is therefore expected that their body condition on the summer feeding grounds will reflect foraging success during their most intensive feeding period and thus indicate how well the high latitude ecosystems can support the populations. During the commercial catch operations on feeding grounds in Norwegian waters, body condition data (blubber thickness and girth) have been collected from 13 937 common minke whales caught during the period 1993-2020. To investigate associations between body condition and area usage in minke whales, we applied three statistical approaches: regressions, canonical correlations, and spatiotemporal effect estimations. The analyses revealed a significant negative trend in blubber thickness from 1993 until 2015. After 2015, the trend was reversed, and blubber thickness values increased significantly. It has previously been suggested that there may be a link between the decreased minke whale blubber thickness and the abundance of the Northeast Arctic cod (*Gadus morhua*) stock which increased to a record high level between 2006 and 2013. Recruitment to the cod stock in more recent years has been low with a subsequent and continuous decrease in the total stock after 2013 to a current level which is presumably approximately 60% of the 2013 level. Interestingly, the observed common minke whale body condition was at its lowest in 2015, after which it has increased. This may support a connection between cod abundance and common minke whale body condition.

Keywords: Northeast Atlantic, common minke whales, blubber deposition, Northeast Arctic cod

INTRODUCTION

The North Atlantic common minke whale (*Balaenoptera acutorostrata acutorostrata*) is a migratory species, and the summer period is generally characterized by intensive feeding and consequently seasonal fattening at high latitudes (Haug, Lindstrøm & Nilssen, 2002; Næss, Haug & Nilssen, 1998; Solvang, Yangihara, Øien & Haug, 2017). The fat deposited is stored as energy reserves for overwintering at lower latitudes where feeding is suggested to be greatly reduced (Folkow, Haug, Nilssen & Nordøy, 2000). As a consequence, it is assumed that their body condition on the summer grounds will reflect food availability during their most intensive feeding period and thus indicate how well the high latitude ecosystems can support the populations (Solvang et al., 2017).

Common minke whales are generalist foragers and are normally able to switch among species without compromising their body condition (Haug et al., 2002). As a result, their diet varies much in time (year and season) and space due to spatio-temporal variation in prey availability (Haug et al., 2002; Windsland, Nilssen, Lindstrøm & Haug, 2007). The whales exploit a variety of species and sizes of fish and crustaceans with an apparent preference for capelin (*Mallotus villosus*), herring (*Clupea harengus*) and occasionally krill (*Thysanoessa spp*) (Lindstrøm & Haug, 2001). Relationship have been observed between minke whale body condition and ecological changes in their feeding areas: In the Barents Sea, Haug et al. (2002) observed that common minke whales were in poor condition in years with low habitat quality, primarily caused by insufficient availability of herring and capelin.

Sampling during scientific whaling operations under special permit in 1993-1994 (see Haug, Lindstrøm, Nilssen, Røttingen & Skaug, 1996) and commercial whaling operations in 1993-2020 have provided a time series of minke whale body condition data including blubber thickness and girth. Previous analyses of the body condition data collected in 1993-2013 were performed using different statistical approaches: an ordinary linear regre-

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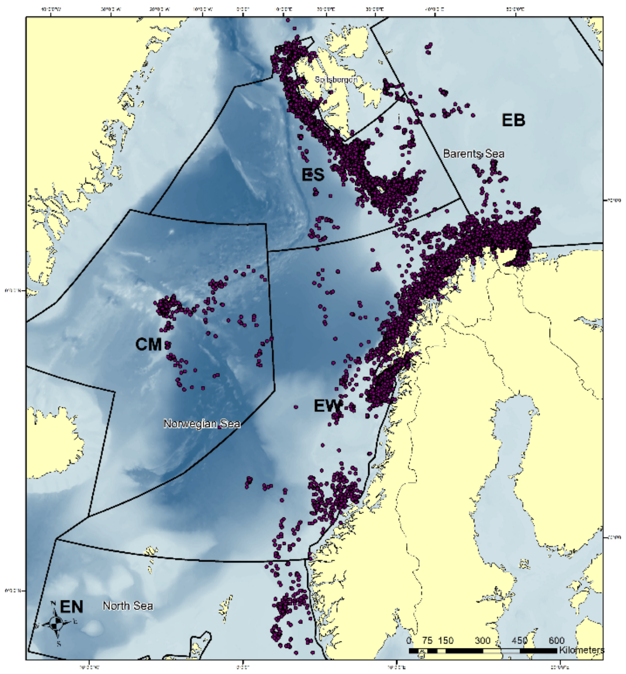

Figure 1. Map of the study area, showing the location of common minke whale catches between 1993 and 2020.

-ssion model, a random effect model, and a varying coefficients model (VCM) (Solvang et al. 2017). The proposed VCM was represented by combinations of simple polynomial expressions for complicated variations of the random effects from year and area. Furthermore, two expanded approaches for the VCM proposed in Solvang et al. (2017) have been applied. One was the integrating canonical correlation procedure in varying coefficient estimation for geographical and temporal responses (Yamamura, Yanagihara, Solvang, Øien & Haug, 2016). The other one was spatiotemporal effects estimation by the so-called fused lasso (Fukui et al., 2018; Yamamura et al. 2018). The method worked for high-dimensional data with sparse structure such as the data in this study. These previous studies clearly indicated that the blubber thickness in common minke whales captured in Norwegian waters varied over the years, and Solvang et al. (2017) concluded that the total trend over the two decades of data then available (1993 to 2013) suggested a decrease in body condition. Their analyses showed a significant negative trend in blubber thickness over the entire period with particularly low values in 2011-2013. The trend was clearer in mid-summer (June-July) than in autumn (August-September) and spring (April-May).

The Northeast Arctic cod (*Gadus morhua*) stock in the Barents Sea was at record high levels around 2013, and the distribution of the stock had expanded north and north-eastwards during the preceding decade (Bogstad, Gjøsæter, Haug & Lindstrøm, 2015; ICES, 2020). Solvang et al. (2017) suggested that the declining body condition in common minke whales might have a link to this record high cod stock through competition over common food resources. Similar observations have been made in Barents Sea harp seals (*Pagophilus groenlandicus*) where there was a negative trend in body condition after 2000 (Øigård, Lindstrøm, Haug, Nilssen & Smout, 2013). In their review of the competition for food among common minke whales, harp seals and cod in the Barents Sea, Bogstad et al. (2015) suggested that the decreased body condition in the two mammal stocks might be an indication that they had simply been outperformed by the record high cod stock.

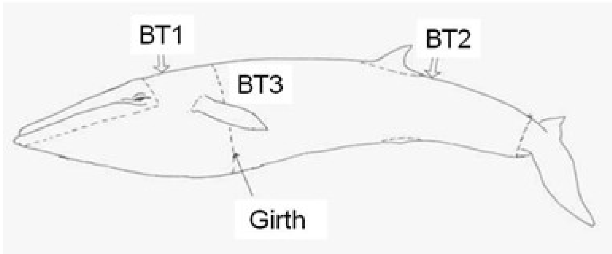

Figure 2. Measurement positions BT1 (dorsally behind the blowhole), BT2 (behind the dorsal fin) and BT3 (laterally just above the center of the flipper) of blubber thickness and half girth measurements on the common minke whales. Blubber measurements were made perpendicular from the skin surface to the muscle-connective tissue interface. Total length and girth measurements were made to the nearest centimeter, while blubber measurements were to the nearest millimeter.

After 2013, the biomass of the Northeast Arctic cod stock has declined more or less continuously and is now considerably lower than the peak in 2013 (ICES, 2020). To explore possible effects of this cod decline on the body condition of common minke whales, analyses similar to those used in previous studies (for more detailed descriptions of the applied statistics, see Fukui et al., 2018; Solvang et al., 2017; Yamamura et al., 2016; Yamamura et al. 2018) have been applied to the extended time series, now spanning the entire period from 1993 to 2020 to investigate the most recent tendency in temporal and geographical variation in common minke whale body condition. In addition, we applied a Spearman linear regression model to assess a possible relationship between the common minke whale body condition and the abundance of the Northeast Arctic cod stock over the same period.

MATERIALS AND METHODS

<u>The data</u>

Over the period 1993-2020, body condition data were obtained from a total of 14,147 common minke whales taken in Norwegian scientific (1993-1994) and commercial (1993-2020) whaling operations in the Northeast Atlantic during the months April to September (Figure 1). Immediately after death, the whales were taken onboard and hauled across the foredeck of the whaling vessel. Total body length was measured in a straight line from the tip of the upper jaw to the apex of the tail fluke notch; total girth was measured directly behind the flipper; and blubber thickness (BT) was measured at three sites (Figure 2): Dorsally behind the blowhole (BT1) and behind the dorsal fin (BT2), and laterally just above the centre of the flipper (BT3). Blubber measurements were made perpendicular from the skin surface to the muscle–connective tissue interface. Length and girth measurements were made to the nearest centimeter, while blubber measurements were to the nearest millimeter. Some of the measurements were taken by dedicated samplers onboard whaling vessels, but most of them were collected by the whalers.

For all whales, the year, month, day, latitude and longitude were recorded. In Solvang et al. (2017), it was recognized that BT2 and girth were difficult to measure consistently and therefore potentially included more measurement errors. For

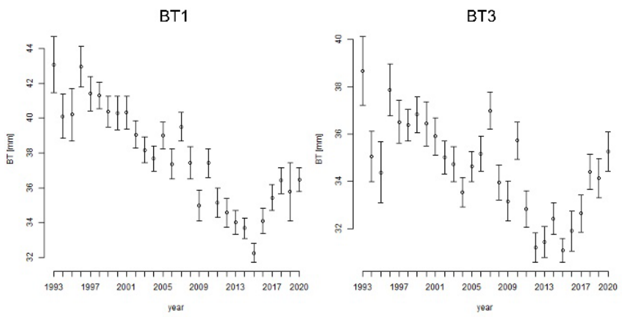

Figure 3. Common minke whale body condition data (blubber thickness BT1 and BT3) with 95% confidence intervals versus year in the period 1993-2020. X-axis indicates year and y-axis indicates measured blubber thickness (mm).

BT2 the particular challenge was large local variations in blubber thickness between the actual spot and close neighbouring areas on the whale body. There are considerable variations in both blubber thickness, seasonal changes in blubber thickness, and in blubber lipid concentration over the body of common minke whales (Christiansen, Vikingsson, Rasmussen & Lusseau, 2013; Næss et al., 1998). Nevertheless, the results previously presented by Solvang et al. (2017) clearly indicate that some standard blubber measurements, easily obtained from the hunt, could serve well as indicators for the body condition of common minke whales. Therefore, we focused the analysis on the data obtained for the measurements BT1 and BT3 in this paper. After removing missing data, the final number of individuals included in the analyses were 13,937.

In Solvang et al. (2017), the effect of total body length on the girth measurements as well as blubber thickness measurements were tested, yielding as results that there was some effect on the girth but no significant effect on blubber thickness. Here we re-confirmed the non-significant effect of body length on the blubber thickness BT1 and BT3 also of the latest data using a linear regression model. The estimated intercept and coefficient of body length were 0.95 and 0.0037 for BT1, and 1.2 and 0.0030 for BT3. The p-values obtained for these estimations were less than 2.2×10^{-16}, probably caused by large sample sizes. Cohen's effect size (Cohen 1988) to the estimated coefficients were 0.14 for BT1 and 0.11 for BT3 respectively, which are interpreted as small effect. of total body length on BT1 and BT3. Therefore, we decided not to correct for the effect of body length in the analyses of BT1 and BT3, as was also the case in previous analyses done by Solvang et al. (2017). Here we considered blubber thickness as a proxy of body condition and used both terms interchangeably through the text.

Analyses by three different regression models

These models were used in previous analyses of common minke whale body condition data by Solvang et al. (2017). An ordinary multiple regression model (OLM), a random effect model (REM) and a varying coefficient model (VCM) have been applied to the blubber thickness measurements BT1 and BT3 which we consider as the single response variables. The covariates of the three models include sex, longitude, latitude and year. To select the best fit for various model candidates, we used a Bayesian information criterion (BIC). For the selected models, we also considered whether the seasonal effect should be included. Furthermore, we applied ordinal t-tests to assess whether the estimated coefficients of OLM were significant and the

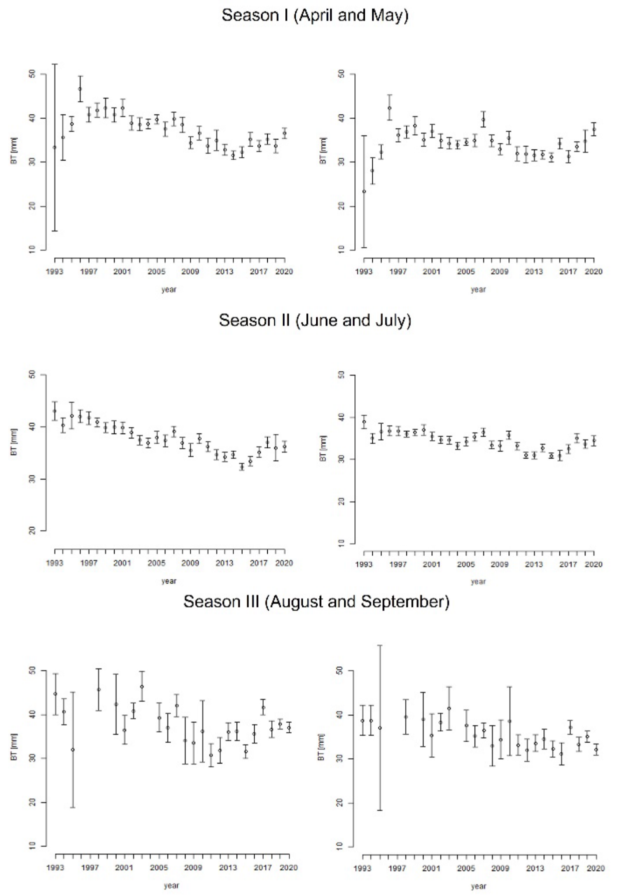

Figure 4. BT1 (left side) and BT3 (right) versus year for season I, II and III, in the period 1993-2020. X-axis indicates year and y-axis indicates measured blubber thickness (mm) with 95% confidence intervals.

statistical testing proposed in Solvang et al. (2017) to assess whether the estimated VCMs were significant.

As an alternative model, similar to the VCM, a generalized additive model (Hastie and Tibshirani 1990) or generalized linear mixed models (Breslow and Clayton 1993) were also considered. Such models would require numerical optimization for maximum likelihood estimation, which is time consuming, depending on the number of parameters involved. In contrast, the VCM simply use a least squares method to estimate all parameters, and computation is faster even if the number of parameters increase.

Canonical correlation analysis by innovating VCM

This approach (see Yamamura et al., 2016) considers the case where we include multiple response variables. Here we create a synthesis variable from the multiple response variables and apply a regression model which corresponds to canonical correlation analysis (CCA). In CCA, we are interested in investigating relationships between two sets of response variable and explanatory variables. The goal of CCA, as developed by Hotteling (1936), is to construct two new sets of canonical variates for the response and explanatory variables, and the parameters of the model are estimated by maximizing the correlation between two variates. In our model, the multiple response variables include BT1 and BT3, and the explanatory variables include sex, longitude, latitude, year and calendar day. The approach investigates association with geographical and chronological variation to the integrated variation of BT1 and BT3.

Table 1. Number of minke whales sampled by sex and catch season in each sampling year: Season I, April and May; Season II, June and July; Season III, August and September.

Year	Season I		Season II		Season III		Total
	Male	Female	Male	Female	Male	Female	
1993	0	3	70	100	13	7	193
1994	2	13	110	111	19	12	267
1995	13	100	19	81	2	1	216
1996	2	72	51	255	0	0	380
1997	19	162	94	220	0	0	495
1998	27	146	92	331	9	8	613
1999	24	91	137	301	0	0	553
2000	29	116	129	150	10	2	436
2001	9	120	170	221	15	3	538
2002	26	107	169	254	31	24	611
2003	50	165	149	245	14	8	631
2004	37	190	118	186	0	0	531
2005	33	304	96	158	24	13	628
2006	47	105	147	188	24	20	531
2007	29	56	103	320	26	25	559
2008	47	148	117	199	4	9	524
2009	57	147	60	203	8	9	484
2010	8	118	89	240	3	4	462
2011	23	125	113	218	25	8	512
2012	11	56	108	236	22	6	439
2013	48	119	100	243	37	19	566
2014	80	179	131	310	25	6	731
2015	27	156	104	315	27	29	658
2016	31	139	99	269	12	36	586
2017	18	85	31	248	4	35	421
2018	46	103	46	210	10	34	449
2019	24	66	70	199	25	38	422
2020	38	147	83	166	20	47	501
Total	805	3338	2805	6177	409	403	13937

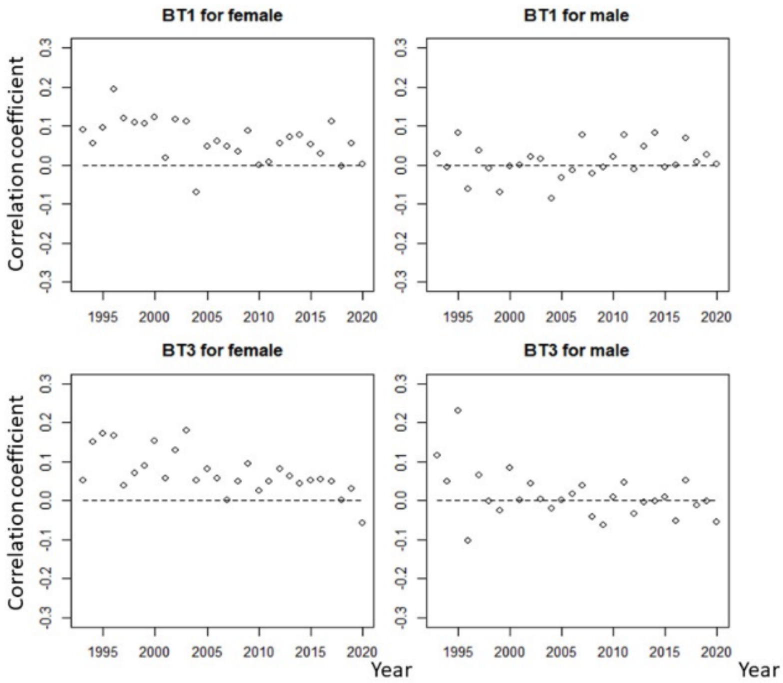

Figure 5. The estimated coefficients (y-axis) obtained by applying a linear trend to the scatters of days vs. blubber thickness within one year. X-axis indicates the observed year. Positive coefficient means inrease of blubber thickness from spring to autumn in a year and negative coefficient means decreases of blubber thickness through the summer.

Table 2. Estimated parameters for time and areas in the best fit regression models OLM (regression coefficients) and REM (variance for the random effect), and test statistics for varying coefficients in the best fitting VCM. The applied data for year, latitude and longitude were standardized. The final best fitting model of all was VCM. The values in parentheses for OLM indicate p-value to assess whether the estimated coefficients are significant. The p-value less than 0.05 means significant. The values in parentheses for VCM are the threshold τ_{α} that is defined to assess the VCMs in the Appendix in Solvang et al. (2017) and assess whether the estimated VCs are larger than the threshold, which means significant.

Model	Term	BT1	BT3
OLM	year	-2.58 (p < .05)	-1.37 (p < .05)
	latitude	0.51 (p < .05)	0.12 (p > .05)
	longitude	-0.67 (p < .05)	-0.82 (p < .05)
REM	1|year	8.85	4.32
	1|latitude	2.05	1.09
	1|longitude	1.20	1.35
VCM	year	22.19 (> 2.65)	16.59 (> 2.64)
	area	7.75 (> 2.76)	5.28 (> 2.76)

<u>Spatiotemporal effect estimation by the Adapted Fused Lasso</u>

Fused lasso is a least absolute shrinkage and selection operator ("lasso") with respect to temporal or spatial structure. Lasso is known as a method of the regularized or penalized regression to estimate the coefficients of regression models (Tibshirani, Saunders, Rosset, Zhu & Knight, 2005). The estimation of regularized regression is conducted by an additional constraint whose objective is to shrink unimportant regression coefficients towards zero. Lasso penalizes a least squares regression by the sum of the absolute coefficients called the L1-norm. Fused lasso penalizes the L1-norm of both the sparsity of coefficients and sparsity of their differences (Tibshirani et al., 2005). The method works for high-dimensional data with sparse structure such as the data in this study.

As seen in Figure 1, catches have been taken both in high density and low-density areas. It may be difficult to correctly estimate the spatiotemporal effects in the low-density areas for the two analytical approaches outlined above. To address this challenge, Fukui et al. (2018) and Yamamura et al. (2018) proposed an estimation method to integrate spatial effect based on the subdivision by Fused Lasso. The response variable is BT1 or BT3 and the explanatory variables include sex, year and calendar day in the regression model. This approach investigates the effect from each subdivided area in the established IWC management area to the blubber thickness in addition to the association with other explanatory variables.

<u>Linear regression analysis of minke whale body condition vs cod abundance</u>

The cod abundance data from 1993-2020 (ICES 2020) were compared with the blubber thickness (BT1 and BT3) to investigate the relationship. First, we visually inspected the shape of the distributions of BT1 and BT3 using histograms for the 28 years and determined medians as the representative values in each year for BT1 and BT3. Then, we applied a linear regression model, where the response variables were the median of BT1/BT3 and the explanatory variable was the cod abundance. We used the *lm* functions of the stats library in R version 4.1.2 (R Core Team, 2021).

RESULTS

<u>General temporal patterns of the data</u>

The general patterns of the body condition data, BT1 and BT3, pooled by catch season, with confidence intervals for each year are shown in Figure 3. The means for the two measurements over all data are BT1 = 37.5 mm (standard deviation (SD) = 10.3) and BT3 = 34.4 mm (SD=9.1). Furthermore, Figure 4 presents the plots of BT1 and BT3 by season I (April-May), II (June-July) and III (August-September), respectively. Number of observations for season I of 1993 and season III of 1995 are few compared with number of other observations. This is reflected in the large confidence intervals of these mean values. Both BT1 and BT3 showed negative tendencies in development during the period 1993-2013, but eventually positive tendencies from 2014 to 2020. Table 1 summarizes the number of observations by sex in each season.

We also described the scatter plots of BT1 and BT3 vs calendar day from April to September within single years and applied a linear regression model to the scatter plots (Supplementary file 1, Figure S1a-d). The estimated coefficients of the linear regression model are plotted for females and males in Figure 5. Positive coefficients are indicating increasing body condition throughout the feeding season in a year, while negative coefficients suggest a decreasing body condition over the same period. In general, the BT1 measurements were more responsive throughout the season than the BT3 measurements. In females, BT1 and BT3 coefficients are positive, except for BT1 in 2004 and BT3 in 2020, thus indicating a general increase in the body condition over the season. After 2013 the BT3 coefficients in females showed more moderate increase effects when compared to the situation before 2013. For males the BT1 and BT3 coefficients did not show any consistent positive/negative effect to the body condition over the sampling period. However, after around 2005, BT1 for males showed an increased or stable pattern during the season.

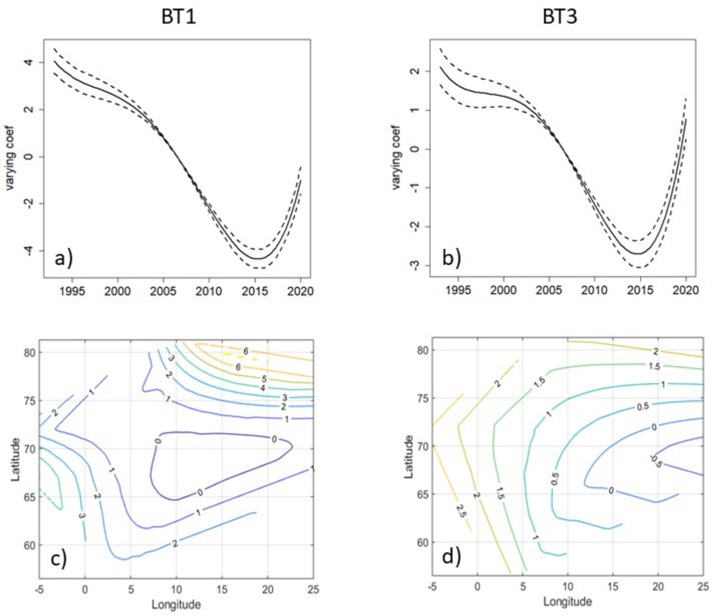

Figure 6. Upper panels: estimated varying coefficients (VCs) by year (solid line is the estimated VC, dotted lines are the confidence intervals). Lower panels: estimated VC contour plots by area (x-axis: latitude, y-axis: longitude) for BT1 (left-hand side) and BT3 (right-hand side). The change in colour of VC contour plots from blue to yellow corresponds to a change from poor to good effect to the blubber thickness.

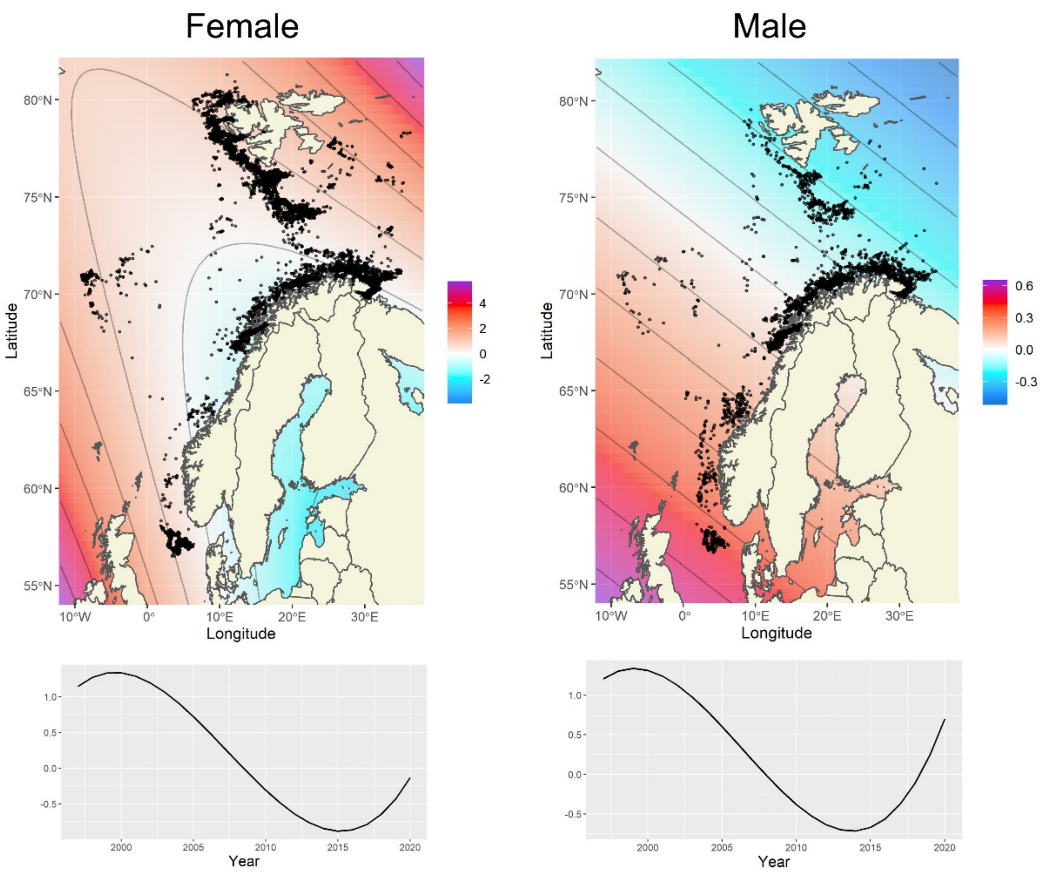

Figure 7. Results from canonical correlation analyses: the two upper panels indicate contour plots of the estimates for the geographical effect on the blubber thickness, females to the left, males to the right. Black markers in upper panels are actual catching positions. The contour plots shown by colourd area indicate increased (from blue to red) effect to the blubber thickness. Lower panels indicate the estimated coefficients for year changes.

Year and area effect on BT1 and BT3 by the regression models

The three regression models OLM, REM and VCM for all possible combinations of covariates were applied to BT1 and BT3. The calculated log-likelihoods and BICs are summarized in the Supplementary file 2, Table S1. For the minimum BIC model, we also applied the models with seasonal effect. Table 2 summarizes the estimated terms for year, latitude and longitude in the model selected by minimum BIC. The estimated coefficients for OLM are significant. Variance for the random effect of these terms indicates that the random effect of year is larger than the random effect of locations. The estimated VCs for year and locations were statistically significant as seen in Table 2. The estimated VC curves regarding year and area are illustrated in Figure 6. The curves for year, with confidence intervals, exhibited an initial negative effect followed by a more recent (after 2015) positive effect with respect to body condition. The VC contour plots calculated by the VC area terms were illustrated for longitudes (x-axis) and latitudes (y-axis). BT1 and BT3 data clearly indicated a gradient with higher blubber thicknesses in the north (and west for BT3) than further to the south.

Geographical and temporal associations with integrated blubber thickness data

As seen from Figure 7, there was almost no variation by area in the case of the males, which means that the integrated measurements for BT1 and BT3 are not much different between the geographical areas. In females, higher contours along the Norwegian coast and up towards Svalbard was observed. The estimated effect for year change shows a decrease before 2015 and an increase after that year.

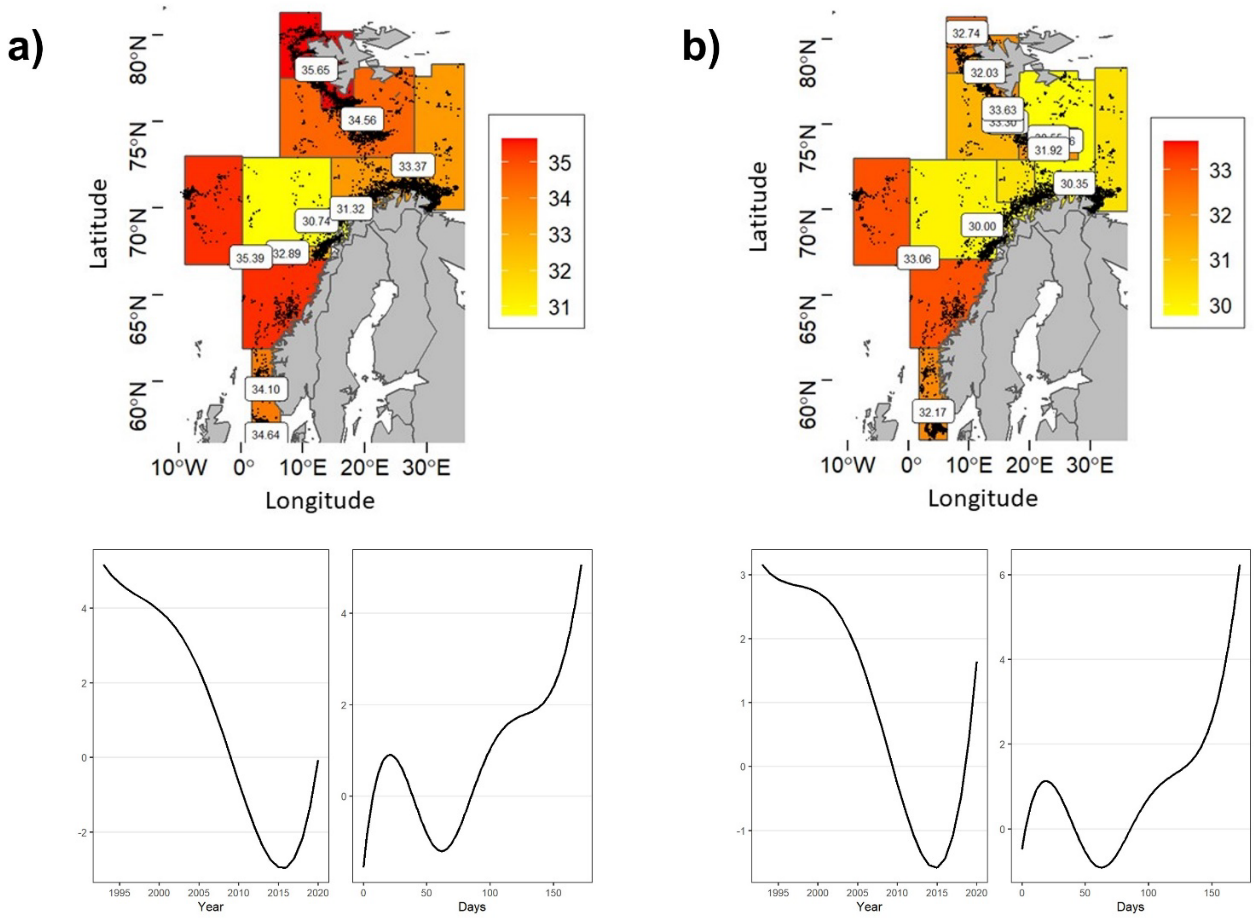

Figure 8. Estimated spatial (upper panel) and temporal (lower panel) effects to blubber thickness using fused lasso estimation on BT1 (a) and BT3 (b). Black markers in the upper panels are actual catch positions and the warmer coloured areas indicate higher associations with blubber thickness. The lower panel plots the estimated coefficients with the change of years and days.

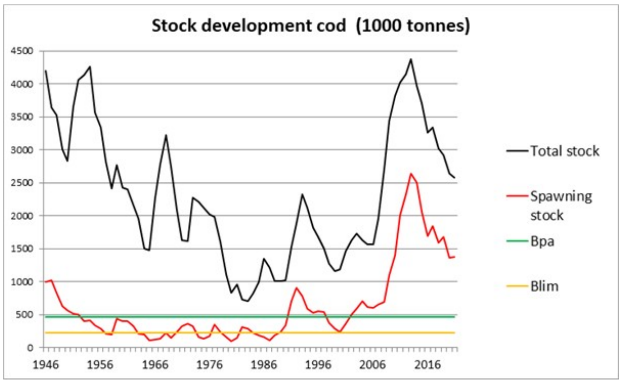

Figure 9. Yearly variation in abundance of the spawning stock and total stock of northeast Arctic cod in 1946-2020. From ICES (2020).

Spatiotemporal effects by the Adapted Fused Lasso

Using the Adapted Fused Lasso method, Figure 8 reveals that higher effects by area are shown in north and west for BT1 and west for BT3. In addition, the year effects on BT1 and BT3 show decreasing trends prior to 2015 and increasing thereafter. The overall effect from calendar day on both BT1 and BT3 is an increase throughout the season. However, both measurements show a downward dip around May/June before increasing monotonically for the rest of the feeding season.

Northeast Arctic cod abundance vs common minke whale condition

There was a general downward trend in the development in the Northeast Arctic cod stock from 1946 to ca 1980 (Figure 9). After a peak in the early 1990s, both the total stock and the spawning stock decreased up to 2000, whereafter the stock size increased to an all-time high peak in 2013. After 2013, however, a continuous stock decrease has prevailed although the level observed in 2020 is still somewhat above the long-term mean (ICES, 2020).

To do the linear regression of the minke whale body condition vs the cod abundance data, we checked the distributional shape of BT1 and BT3 from 1993-2020 using histograms. Some histograms appeared normally distributed while others appeared more skewed. Therefore, we used the median as the representative value when summarizing the condition data in a year.

The outputs from the linear regressions were:

For BT1: The estimated coefficient of cod biomass was - 0.89 ($p = 6.4 \times 10^{-2}$). The *R*-squared value was 0.62, *F*-statistic was 42.6 with 26 degrees of freedom. For BT3: The estimated coefficient of cod biomass was – 0.85 ($p = 5.3 \times 10^{-6}$). The *R*-squared value was 0.54 and the *F*-statistic was 32.6 with 26 degrees of freedom. These outputs indicated that the association between cod abundance and minke whale body condition were negative and significant.

DISCUSSION AND CONCLUSIONS

In accordance with Haug et al. (2002) and Solvang et al. (2017), this study shows that blubber thickness in common minke whales captured in Norwegian waters varies over the years. A time series of consistent blubber measurements, sampled during commercial whaling in the period 1993-2020, showed a significant negative trend from the start until 2015. After 2015, the trend has reversed and body condition values increased significantly. The trends were more evident for the midsummer season (June-July) than for the autumn (August-September) and the spring (April-May). Apparently, the BT1 measurements were more responsive throughout the season than the BT3 measurements. This finding makes sense as it has been demonstrated by Christiansen et al. (2013) that BT1 has a closer correlation with the overall blubber volume of common minke whales than BT3.

While, at least for the northern areas, there was no strong spatial variation in the body condition of males, there was a somewhat clearer spatial pattern for females with an increased trend from the south via coastal areas of mid Norway, to the northern areas Bear Island and Svalbard. These areas are all known as important feeding grounds where the common minke whales are nourished and deposit fat reserves not only in the blubber, but also in muscles and visceral fat during summer (Gunnlaugsson et al., 2020; Haug et al., 2002; Næss et al., 1998; Windsland et al., 2007). According to the estimated spatial effect from location, a positive random effect was observed for all whales in the Norwegian Sea around 65ºN and in the Jan Mayen area. Solvang et al. (2017) suggested that feeding on summering herring might have contributed to this. Even though a tremendous increase in mackerel (*Scomber scombrus*) has occurred in the Norwegian Sea during the past decade, there is no clear evidence that this species is an important prey species for common minke whales in the area (Solvang et al., 2017).

Apparently, females had a general increase in the body condition over the season while the males showed both decreases and increases. It is well known that Northeast Atlantic common minke whales have a strong segregation pattern where females, and especially mature ones, arrive earlier on the feeding grounds than males, and are found in surplus numbers in the Svalbard area as well as in the eastern and southern Barents Sea (Horwood, 1990; Jonsgård, 1951). These areas also seem to provide the best feeding conditions both spatially and temporally, thus giving reproductive females the best possible feeding conditions.

It is well known that common minke whales are generalist foragers and are normally able to switch among many prey species without compromising the body condition (Haug et al., 2002; Solvang et al., 2017; Windsland et al., 2007). Consequently, their diets vary much in time (year and season) and space due to spatio-temporal variation in prey availability (see also Bogstad et al., 2015). In the Barents Sea, the whales exploit a variety of species and sizes of fish and crustaceans, but they appear to have a particular preference for capelin, herring and occasionally krill during early summer (Lindstrøm & Haug 2001). Solvang et al. (2017) emphasized that even though capelin and herring are generally considered fat fishes with high caloric content compared to krill, they are all subject to seasonal variations. An implication of the dynamics of lipid transfer in high latitude marine ecosystems is that krill contains more lipids (and thereby energy) than the pelagic fishes during spring, whereas capelin and herring need to feed over the summer to acquire similar energetic potentials (e.g., Falk-Petersen, Hopkins & Sargent, 1990; Grahl-Nielsen, Haug, Lindstrøm & Nilssen, 2011; Meier et al., 2016). Certainly, an energy-rich diet has greater potential for allowing a surplus that can be stored

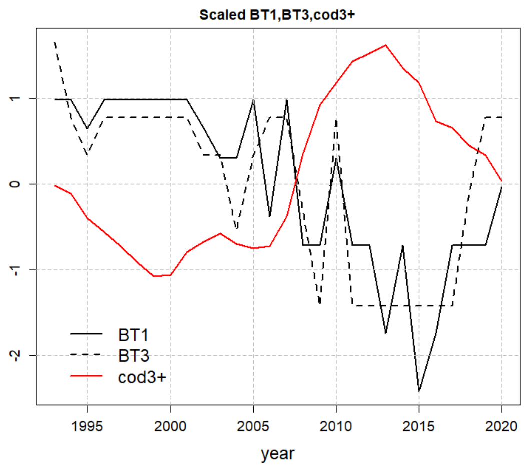

Figure 10. Plots of standardized abundance of Northeast Arctic cod (cod3+) and standardized values of common minke whale blubber thickness (BT1 and BT3) during the period 1993 to 2020.

as fat in top predators such as minke whales (Solvang et al., 2017).

In extreme events, such as in the Barents Sea in 1995-1996, when the abundances of capelin and herring were low simultaneously, the common minke whales were forced to switch to krill and gadoid fish and as a result their body condition declined (Haug et al., 2002). As also observed by Solvang et al. (2017), changes in body fattening, which could be related to food availability, have been observed in other baleen whale species such as fin whales (*Balaenoptera physalus*) in Icelandic waters (Lockyer, 1986), Antarctic minke whales (*Balaenoptera bonarensis*) (Cunen, Walløe, Konishi & Hjort, 2021; Ichii, Shinohara, Fujise, Nishiwaki & Matsuoka, 1998; Konishi et al., 2008;), and bowhead whales (*Balaena mysticetus*) in arctic waters of North America (George, Druckenmiller, Laidre, Suydam & Person, 2015).

Between 2006 and 2013, the Barents Sea stock of Northeast Arctic cod increased to a record high level (Figure 9), and the distribution of the stock expanded substantially north and north-eastwards (Bogstad et al., 2015; Haug et al., 2017; Solvang et al., 2017). The distribution of cod, particularly medium and large individuals, and minke whales overlap to various degrees during the year. Given our dietary knowledge of these predators they may well compete for krill as well as capelin in these periods (Haug et al., 2002; Johannesen et al., 2012). A recent study focussed on the intra- and interspecific competition among top predators (cod, common minke whale and sea birds), and concluded that common minke whales and cod competed for food and that their diets depended on the abundance of herring and capelin, respectively (Durant et al., 2014). Figure 10, showing the annual variation in whale body condition and cod abundance in 1993-2020 support this conclusion.

Apparently, it may look as if the common minke whale responded to a big cod stock by showing a declining body condition over the entire period from1993 to 2013 (Solvang et al., 2017). Similar observations have been made in Barents Sea harp seals where there is a negative trend in body condition between 2000 and 2011(Øigård et al., 2013). In their review of the competition for food among common minke whales, harp seals and cod in the Barents Sea, Bogstad et al. (2015) suggested that the decreased body condition in the two mammal stocks might be an indication that they had simply been outperformed by the record high cod stock. Competition also from other baleen whales, i.e. humpback (*Megaptera novaeangliae*) and fin whales for which the abundances have increased, and the distribution has shifted more towards the northeast in the Northeast Atlantic in recent decades (Moore, Haug, Vikingsson & Stenson, 2019; Skern-Mauritzen et al., 2022), cannot be ruled out.

After very good recruitment to the cod stock in 2006-2008, recruitment in recent years has been from medium to low with a subsequent and continuous decrease in the total stock biomass and distribution after 2013 to a current level which is presumably less than 60% of the 2013 level (Figure 9; ICES, 2020). Interestingly, the observed common minke whale body condition was at its lowest in 2015, showing an increasing trend thereafter. This may suggest a connection between cod abundance and feeding conditions for other top predators such as common minke whales, that is, a possible competing feeding situation. For minke whales, this suggestion was confirmed in our current regression analysis which revealed a significant negative correlation between cod abundance and common minke body condition, indicating that more cod in the ecosystem is associated with reduced body condition for the common minke whales. Recent sightings surveys have demonstrated that the summer abundance of minke whales in the Northeast Atlantic is stable or increasing, however, large shifts in the distribution have been observed where at present a large portion of the population is feeding in the Barents Sea proper.

ADHERENCE TO ANIMAL WELFARE PROTOCOLS

The research presented in this article has been done in accordance with the institutional and national laws and protocols for animal welfare that are applicable in the jurisdictions where the work was conducted.

AUTHOR CONTRIBUTION STATEMENT

Solvang, H.K.: Contribution for conceiving and designing the study, Contribution for all statistical analyses in subsequent analyses and interpreting data, Contribution for relevant discussion, Contribution for preparing manuscript; **Haug, T:** Contribution for conceiving and designing the study, Contribution for responsible for the whale measurements, Contribution for relevant discussion, Contribution for preparing manuscript; **Øien, N:** Contribution for responsible for the whale measurements, Contribution for relevant discussion, Contribution for preparing manuscript

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