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Recent development in temporal and geographical variation in body condition of common minke whales (*Balaenoptera acutorostrata acutorostrata*) in the Northeast Atlantic

Hiroko Solvang¹, Tore Haug² and Nils Øien¹

¹Institute of Marine Research, PO Box 1870 Nordnes, N-5817 Bergen, Norway ²Institute of Marine Research, Fram Centre, PO Box 6606 Langnes, N-9296 Tromsø, Norway

Abstract

The common minke whale (Balaenoptera acutorostrata acutorostrata) is a boreo-arctic 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 greatly reduced. It is therefore expected 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. During the commercial catch operations on feeding grounds in Norwegian waters, body condition data (blubber thickness and girth) have been collected from 13,216 common minke whales caught in 1993-2018. Using this time series to investigate associations between body condition and time/area in minke whales, we applied several statistical approaches. The analyses revealed a significant negative trend from the start until 2015. After 2015, the trend was reversed and body condition values increased significantly. It has previously been suggested that there may be a link between the decreased minke whale body condition and the abundance of the Barents Sea cod stock which increased to a record high level between 2006 and 2015. Recruitment to the cod stock in more recent years has been low with a subsequent and continuous decrease in the total stock after 2015 to a current level which is presumably approximately 60% of the 2015 level. Interestingly, the observed common minke whale body condition was at its lowest in 2015, whereafter it has increased. This may support a connection between cod abundance and feeding conditions for other top predators such as common minke whales.

Introduction

The common minke whale (*Balaenoptera acutorostrata acutorostrata*) is a boreo-arctic species, and the summer period is generally characterized by intensive feeding and consequently seasonal fattening at high latitudes (Næss et al. 1998; Haug et al. 2002; Solvang et al. 2017). The fat deposited is stored as energy reserves for overwintering at lower latitudes where feeding is suggested to be greatly reduced. It is therefore expected 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.

Common minke whales have a flexible foraging behaviour and are normally able to switch among species without compromising the body condition. 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 et al. 2007). The whales exploit a variety of species and sizes of fish and crustaceans, however they appear to selectively forage on capelin (*Mallotus villosus*), herring (*Clupea harengus*) and occasionally krill (Lindstrøm and Haug 2001). Nevertheless, relationships 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 et al. 1996) and commercial whaling operations in 1993-2018 have provided a time series of minke whale body condition data.. We have previously analyzed the body condition data collected in 1993-2016 using different statistical approaches: an ordinary linear regression model, a random effect model, and a varying coefficients model (Solvang et al. 2017). Furthermore, canonical correlation analysis for geographical and chronological responses (Yamamura et al. 2016), and spatiotemporal effects estimation by the fused lasso (Fukui et al. 2018) have been applied to the data.

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 condition. The analyses showed a significant negative trend over the entire period with particular low values in 2011-2013. The trend was clearer in mid-summer (June-July) than in autumn (August-September) and spring (April-May). The Barents Sea cod (*Gadus morhua*) stock was at record high levels around 2013, and the distribution of the stock had expanded north and northeastwards during the preceding decade (Bogstad et al. 2015; ICES 2018). Solvang et al. (2017) suggested that the declining body condition in common minke whales might have a link to this record high cod stock. Similar observations had been made in Barents Sea harp seals (*Pagophilus groenlandicus*) where there was a negative trend in body condition in the most recent decade (Øigård et al. 2013). In their review of the battle 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.

In this article, analyses similar to those used in previous articles (for more detailed descriptions of the applied statistics, see Yamamura et al. 2016; Solvang et al. 2017; Fukui et al. 2018) have been applied to

the extended time series, now spanning the entire period from 1993 to 2018 to investigate the most recent tendency in temporal and geographical variation in common minke whale body condition.

Data

Over the period 1993-2018, body condition data were obtained from a total of 13,216 common minke whales taken in Norwegian scientific (1993-1994) and commercial (1993-2018) whaling operations in the Northeast Atlantic during the months April to September (Fig.1). Immediately after death, the whales were taken onboard and hauled across the fore-deck of the boat. Total body length was measured in a straight line from the tip of the upper jaw to the apex of the tail fluke notch; girth was measured right behind the flipper; and blubber thickness was measured at three sites (Fig. 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 and therefore potentially included more measurement errors. Therefore, we focus on the analysis on the data obtained for the measurements BT1 and BT3, in addition to total length, in this paper. After removing missing data, the final number of individuals included in the analyses were 13,015.

Methods

Analyses by three different regression models (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 body condition which we consider as the single response variable. 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). The estimated coefficients of OLM and VCM were assessed by t-tests where the p-values turned out to be small due to large sample size. For the selected models, we also consider whether the seasonal effect should be included.

Canonical correlation analysis by innovating VCM (Yamamura et al. 2016)

This approach 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 variable. The goal of CCA, as developed by Hotelling (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, BT3 and total length, 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 for BT1, BT3 and length.

Spatiotemporal effect estimation by the Adapted Fused Lasso (Fukui et al. 2018)

As seen in Fig.1, catches have been taken both in high 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 adress this challenge, Fukui et al. (2018) proposed an estimation method to integrate spatiotemporal effects based on the subdivision by *Fused Lasso*, which is a regression model with regularization. The approach applies a regression model to subdivided areas in each established area. The response variable is BT1 or BT3 and the explanatory variables include sex, year, calendar day, and length. This approach investigates the effect from each separate area to the body condition in addition to the association with other explanatory variables.

Results

General temporal patterns of the data

The general patterns of the body condition data, BT1 and BT3, pooled by catch season, with confidence intervals for each year are shown in Fig.3. The means for the two measurements over all data are BT1 = 37.6 mm (standard deviation (SD) = 10.1) and BT3 = 34.4 mm (SD=9.1). Furthermore, Fig.4 presents the plots of BT1 and BT3 by season I (April-May), II (June-July) and III (August-September), respectively. BT1 and BT3 showed negative tendency until 2013, but eventually positive tendency from 2014 to 2018. Table 1 summarizes number of observations by sex in each season.

Year and area effect on BT1 and BT3 by the regression models in Solvang et al. (2017)

The OLM, REM and VCM for all possible combinations of covariates were applied to BT1 and BT3.To the minimum BIC models, we also applied the models with seasonal effect. Table 2 summarizes the estimated terms for year, latitude and longitude. The final best-fit models were VCM with seasonal effects on both BT1 and BT3. The estimated VC were statistically significant as seen in Table 2. The estimated VC curves regarding year and area are illustrated in Fig.5. 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). The change in color from blue to yellow corresponds to a change from poor to good body condition. BT1 and BT3 data clearly indicated a gradient with better body condition in the north (and west for BT3) than further to the south.

Geographical and chronological associations with integrated body condition data by Yamamura et al. (2016)

Fig.6 summarizes contour plots (upper panel) for geographical and line plots (lower panel) for chronological association with body condition, estimated by canonical correlation analysis. White markers in upper panels are actual catching positions and estimates are showed by contour plots where better body condition is associated with warmer coloured areas. Uniform green colour of contour plots indicates almost no variation by area in case of the males, which means that the integrated body condition for BT1, BT3 and length are not much different between the geographical areas. In females, the low contour in dark blue at

the bottom left in the map and higher contour along the Norwegian coast and up towards Svalbard may signify habits of whales that they migrate from low-food areas in the south, and move northward to take advantage of the high-food areas up north. Some areas presenting high contour do not include observations and must presumably be artefacts. In the lower panels, body condition decreases linearly in males and quadratically in females by year. The calendar day has positive effects on both male and female body conditions. This result supports that the common minke whales are nourished and deposit fat reserves in the blubber on their northern feeding grounds during summer.

Spatiotemporal effects by the Adapted Fused Lasso (Fukui et al. 2018)

Fig.7 summarizes the geographical effects for the separated areas to body condition in the upper panels, and the effects from year, days and total length to body condition in the lower panels. Black markers in the upper panels are actual catching positions and the warmer colored areas, such as the northern and western areas, indicate higher associations with body condition BT1(left side) and BT3 (right side). The area between Svalbard and the northern coast of Norway indicate comparatively lower associations. For BT1, negative year effect, positive day effect and positive association with body length are seen quite clearly in the lower panels, while no such trends were observed for BT3.

Discussion

As also concluded by Solvang et al. (2017), this study indicates that the blubber thickness in common minke whales captured in Norwegian waters, varied over the years. A time series of consistent blubber measurements, sampled during commercial whaling in the period 1993-2018, showed a significant negative trend from the start until 2015. After 2015 the trend was reversed in that body condition values increased significantly (Figs 3 and 5). The trends were clearer in midsummer (June-July) than in autumn (August-September) and spring (April-May) (Fig. 4).

The estimated random effect by area shown in Fig. 6 seemed to affect the males quite little. In females, however, there was somewhat clearer pattern with low associations in the south and stronger associations in coastal areas of mid Norway, to some extent also further north towards the Bear Island. These are all known as important feeding grounds for the common minke whales (Haug et al. 2002; Windsland et al. 2007).

Between 2006 and 2013, the Barents Sea cod stock increased to a record high level (Fig. 8), and the distribution of the stock expanded substantially north and northeastwards (Bogstad et al. 2015; Haug et al. 2017). The distribution of cod, particularly medium and large individuals, and minke whales overlap to various degree 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. 2013). 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). Apparently, it may look as if the common minke whale was paying a price for having a big cod stock by declining body condition over the entire period 1993-2013 (Solvang et al. 2017). Similar observations have been made in Barents Sea harp seals where there is a negative trend in body condition in recent years (Øigård et al. 2013). In their review of the battle 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.

After very good recruitment to the cod stock in 2006-2008, recruitment in more recent years has been from medium to low with a subsequent and continuous decrease in the total stock after 2015 to a current level which is presumably less than 60% of the 2015 level (Fig. 8; ICES 2018). Interestingly, the observed common minke whale body condition was at its lowest in 2015, whereafter it has increased. This may support a connection between cod abundance and feeding conditions for other top predators such as common minke whales.

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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
Total	743	3125	2652	5812	364	318	13014

Table1. Number of individuals by sex and catch season in each sampling year: Season I, April and May; Season II, June and July; Season III, August and September.

Model	Term	BT1	BT3	
OLM	year	-0.40 (p < .05)	-1.66 (p<.05)	
	latitude	0.12 (p < .05)	0.05 (p<.05)	
	longitude	-0.09 (p < .05)	-0.11 (p<-05)	
REM	1 year	9.52	4.73	
	1 latitude	2.66	1.53	
	1 longitude	1.56	1.43	
VCM	year	20.6 > 2.66	14.4 > 2.65	
	area	11.7 > 1.98	5.80 > 1.98	

Table 2. Estimated parameters for time and areas in the best fit regression models OLM, REM and VCM.



Fig. 1. Over the period 1993-2018, body condition data were obtained from a total of 13,216 common minke whales taken in Norwegian scientific and commercial whaling operations in the Northeast Atlantic during the months April to September.



Fig. 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.



Fig.3 Common minke whale body condition data (blubber thickness BT1 and BT3) with confidence intervals versus year in the period 1993-2018. X-axis indicates year and y-axis indicates measured blubber thickness (mm).



Season III (August and September)

Fig.4 BT1 (left side) and BT3 (right side) versus year for season I (April-May), II (June-July) and III (August-September) in the period 1993-2018. X-axis indicates year and y-axis indicates measured blubber thickness (mm).



Fig. 5 Upper panels: Estimated vary coefficients (VCs) by year (solid line is estimated VC, dotted lines arethe confidence intervals). Lower panels: Estimated VC contour plots by area for common minke whale condition measurement BT1 and BT3. The change in color of VC contour plots from blue to yellow corresponds to a change from poor to good body condition.



Fig.6 Upper two panels indicate contour plots of the estimates for the geographical effect on the body condition. White markers in upper panels are actual catching positions and estimates are showed by contour plots that become higher in warmer coloured areas (dark blue is lowest, yellow is highest). Lower two panels indicate the effect on the estimates for catching year and calendar day to the body condition.



Spatial effect to BT1 (left) and BT3(right)



Effect from year, days and length to BT1 (upper) and BT3(lower)

Fig. 7 Estimated spatial (upper panel) and temporal (lower panel) effect to body condition data using *fused lasso* estimation. Black markers in the upper panels are actual catching positions and the warmer colored areas indicate higher associations with body condition.



Fig. 8. Development in abundance of the spawning stock and total stock of northeast Arctic cod in 1946-2019. Form ICES (2018).