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Sexual segregation of common minke whales (*Balaenoptera acutorostrata*) in Greenland, and the influence of sea temperature on the sex ratio of catches

Kristin L. Laidre, Patrick J. Heagerty, Mads Peter Heide-Jørgensen, Lars Witting, and Malene Simon

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The harvest of common minke whales (*Balaenoptera acutorostrata*) in West Greenland has historically been skewed towards female whales, yet a complete analysis of spatial and temporal patterns of catch sex ratio has never been conducted. We examined trends in the sex ratio of catches over time, season, space, and relative to sea temperature using 2400 records from inshore Greenland subsistence whaling operations (1960–2006) and 2072 records from offshore Norwegian commercial operations (1968–1985). Logistic regression models were developed to examine the trend in sex ratio in three regions (Northwest, NW; Central West, CW; Southwest, SW) and by latitude. The highly skewed proportion of females in all catches was strongly positively correlated ($r^2 = 0.8$) with latitude in the offshore catches (>100 km). Generalized linear models of inshore catches indicated slightly increasing though non-significant trends in the proportion of females taken off CW and NW Greenland and a significant declining trend off SW Greenland. Sensitivity analyses show that the declining inshore SW trend was entirely accounted for by the past 5 years (2002–2006) of data. Models containing both year and temperature interactions suggested that either parameter provided an equivalent explanation of the variation in trends across regions.

Keywords: Greenland, minke whale, oceanography, sea temperature, sex ratio, whaling.

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K. L. Laidre: Polar Science Center, APL, University of Washington, Seattle, WA 98105, USA. P. J. Heagerty: Department of Biostatistics, University of Washington, Seattle, WA 98105, USA. K. L. Laidre, M. P. Heide-Jørgensen, L. Witting, and M. Simon: Greenland Institute of Natural Resources, Box 570, 3900 Nuuk, Greenland. Correspondence to K. L. Laidre: tel: +1 206 616 9030; fax: +1 206 616 3142; e-mail: klaidre@apl.washington.edu.

Introduction

Population segregation is found in a wide variety of species and ecosystems and can have a basic importance for conservation and management (Ruckstuhl and Neuhaus, 2005). In cetaceans, sex or age segregation is broadly observed (Laws, 1961; Horwood, 1990; Lyrholm *et al.*, 1999; Whitehead, 2003; Loseto *et al.*, 2006; Heide-Jørgensen *et al.*, 2007a), with the adaptive advantage attributed to many explanations ranging through social structure, environmental constraints, or habitat needs timed with life-history events.

Greenland is one of several traditional summer feeding grounds utilized by North Atlantic minke whales (*Balaenoptera acutorostrata*), which move north from winter breeding grounds to feed during summer (Horwood, 1990). The species is found in a continuum in summer from the west coast around the southernmost point of Greenland (Cape Farewell) and along the east coast. Currently, minke whales are recognized in two separate management areas on either side of Greenland (Donovan, 1991). Catch data from harvest operations indicate sexual segregation between coasts. Females dominate catches in the west, averaging ~75% of the catch annually (Christensen, 1976; Kapel, 1980; Larsen and Øien, 1988), and males dominate catches in the east (Christensen, 1976; Larsen and Øien, 1988), with an almost reciprocal relationship comprising >66% of the annual catch (Christensen, 1976). North Atlantic minke whales are annually harvested for subsistence in West Greenland beginning in spring (when they arrive in the area) and continuing through late autumn. During the winter breeding season before minke whales migrate to West Greenland, they are widely distributed in the central Atlantic along with minke whales from other summer feeding areas (Horwood, 1990; Andersen *et al.*, 2003). The phenomenon of the harvest being skewed towards females in West Greenland has not been fully explored or analysed using all available catch data, nearly half a century of records. Given the importance of understanding spatial and seasonal patterns in the harvest and how the sex ratio of catches has changed, we present a rigorous investigation of the spatial and temporal patterns in sexual segregation and the sex ratio of minke whale catches using all available subsistence and commercial data from the 1960s through 2006. Moreover, our analysis contrasts inshore and offshore harvests across season and geography and examines potential environmental factors that might explain the patterns observed. Specifically, the potential influence of surface temperature (0–40 m) on the sex ratio of catches was examined in light of the dramatic temperature changes observed in West Greenland since 2000 (Myers *et al.*, 2007). Temperature has a large impact on the distribution and abundance of primary prey species for minke whales. Buch *et al.* (1994) found that the abundance of prey such as young Atlantic cod (*Gadus morhua*) increases with the strength of the warm Irminger Current from East Greenland, and Rose (2005) found a northward shift in the distribution of capelin (*Mallotus villosus*), another important prey item, with increasing water temperature. We also examine whether sea temperature has a measurable relationship with observed trends in the sex ratios of the minke catch.

Methods

Catch data

Records from individual catches were obtained from the International Whaling Commission (IWC) and the Greenland home rule for each of three time-series: (i) early inshore subsistence catches by Greenland spanning the years 1960–1981, (ii) offshore commercial catches by Norway spanning the period 1968–1985, and (iii) late inshore subsistence catches by Greenland spanning the years 1987–2006. Error checks were performed on each dataset, and all records without date (year or month) or sex were removed from the analysis (<2% of the records). Harvesting of minke whales in West Greenland begins in March and ends by December each year. Data on individual catches are available from the IWC (www.iwcoffice.org).

The exact latitude and longitude of catch sites were missing for some records, most often for the inshore Greenland datasets. Latitude–longitude values of catch locations were removed from the database if they were clearly erroneous (i.e. on land). However, the region along the coast where each catch was made was available for most records. This coarse spatial scale was designated as NW, CW, and SW (Northwest, Central West, and Southwest) in all three datasets, after Kapel (1980). NW was defined as 75.0–67.5°N, CW as 67.5–63.0°N, and SW as 63.0–60.0°N (Figure 1). Annual sea temperatures between 0 and 40 m taken on an oceanographic cruise at a standard station each June off the coast of West Greenland were obtained from the Danish Meteorological Institute (DMI, unpublished data) for the years 1968–2006. The average temperature (°C) across those depths was used as a time-series in the analysis. The station was located at 63°58.1′N 52°44.3′W, south of Nuuk. June temperatures were representative of the period that minke whales were present and being harvested off West Greenland.

Data analysis

Predictor variables included MONTH (treated as a factor variable), YEAR (treated as a continuous variable expressed in years since 2000), LATITUDE of catch (degrees and minutes), LONGITUDE of catch (degrees and minutes), category (early inshore, late inshore, or Norwegian offshore), and REGION (NW, CW, or SW treated as factors). The response variable was sex and 0 = male. The NW and CW regions were combined in basic regression models for Greenland data.

Trends in the sex ratio of minke whale catches were investigated by fitting standard logistic regression models using the glm() function in the open-source statistical package R (R Development Core Team, 2004). To account for potential autocorrelation not captured by linear or quadratic time models, we used generalized estimating equations (GEEs) clustering on year within region (Heagerty and Lumley, 2000). For comparison, regression estimates were also obtained for both time-series using the NLMIXED procedure in SAS to explore the potential for overdispersion using a 20-point adaptive Gaussian quadrature to obtain maximum likelihood estimates.

A key question was whether the trend over years was similar across regions, or whether there were region-specific temporal trends. Region-by-year interactions in the logistic regression models were tested. Annual trends in the proportion female were examined by estimating a linear temporal trend at a finer spatial resolution (degrees latitude). A linear trend over time was estimated for each latitude using locally weighted regression analyses, allowing the estimation of regression parameters specific to each latitude using only those observations in a "neighbourhood" around the specific latitude, and weighting the contribution from each observation as a decreasing function of the distance to the point of interest (Hastie and Tibshirani, 1993). Specifically, a span of 30% of the data was centred on each latitude, and a kernel weight equivalent to the Epanechnikov kernel was used (Epanechnikov, 1969). Results were evaluated with respect to a range of spans (between 10 and 30%), and similar conclusions were obtained. The local estimates can be considered "varying coefficient model" estimates using the logistic regression model

$$\log\left[\frac{P(\text{female})}{P(\text{male})}\right] = b_0(L) + b_1(L) \times (\text{YEAR} - 2000) + b_2(L) \times (\text{MONTH} - 6) + b_3(L) \times (\text{MONTH} - 6)^2,$$

where L denotes latitude. In this representation, the parameter $b_0(L)$ determines the prevalence of females in YEAR 2000 and MONTH 6:

$$P(\text{female}|\text{YEAR} = 2000, \text{MONTH} = 6, \text{Latitude} = L) = \frac{\exp[b_0(L)]}{1 + \exp[b_0(L)]},$$

and the parameter $b_1(L)$ determines the annual rate of change in the log odds of a female catch.

All local regression models controlled for month of catch using a quadratic polynomial function that captured the apparent pattern in the data and allowed for a more parsimonious model when using local regression estimation. For local regressions, the estimated percentage female for a given year (2000 for Greenland catches, 1975 for Norwegian catches) was plotted as a function of latitude, and the estimated linear change in the logistic transformed percentage female as a function of spatial location (latitude).

We tested the assumption of a linear temporal trend by fitting a model that allowed quadratic terms for YEAR and evaluated whether it was a significantly better fit to the offshore and inshore time-series. Temporal trends and significance were also evaluated using the early and late Greenland datasets combined.

The potential role of the environment was examined by correlating the fraction of females with the annual sea temperature (°C). In regression models, we considered the overall fit for each of three models which included YEAR and TEMP in addition to certain interactions with REGION. The three models included different interaction terms as follows: Model 1 included YEAR × REGION; Model 2 included TEMP × REGION; and Model 3 included both YEAR × REGION and TEMP × REGION interactions. A comparison of Models 1 and 2 using the Akaike's information criterion (AIC) allowed for evaluation of whether differences across regions could be relatively more or less

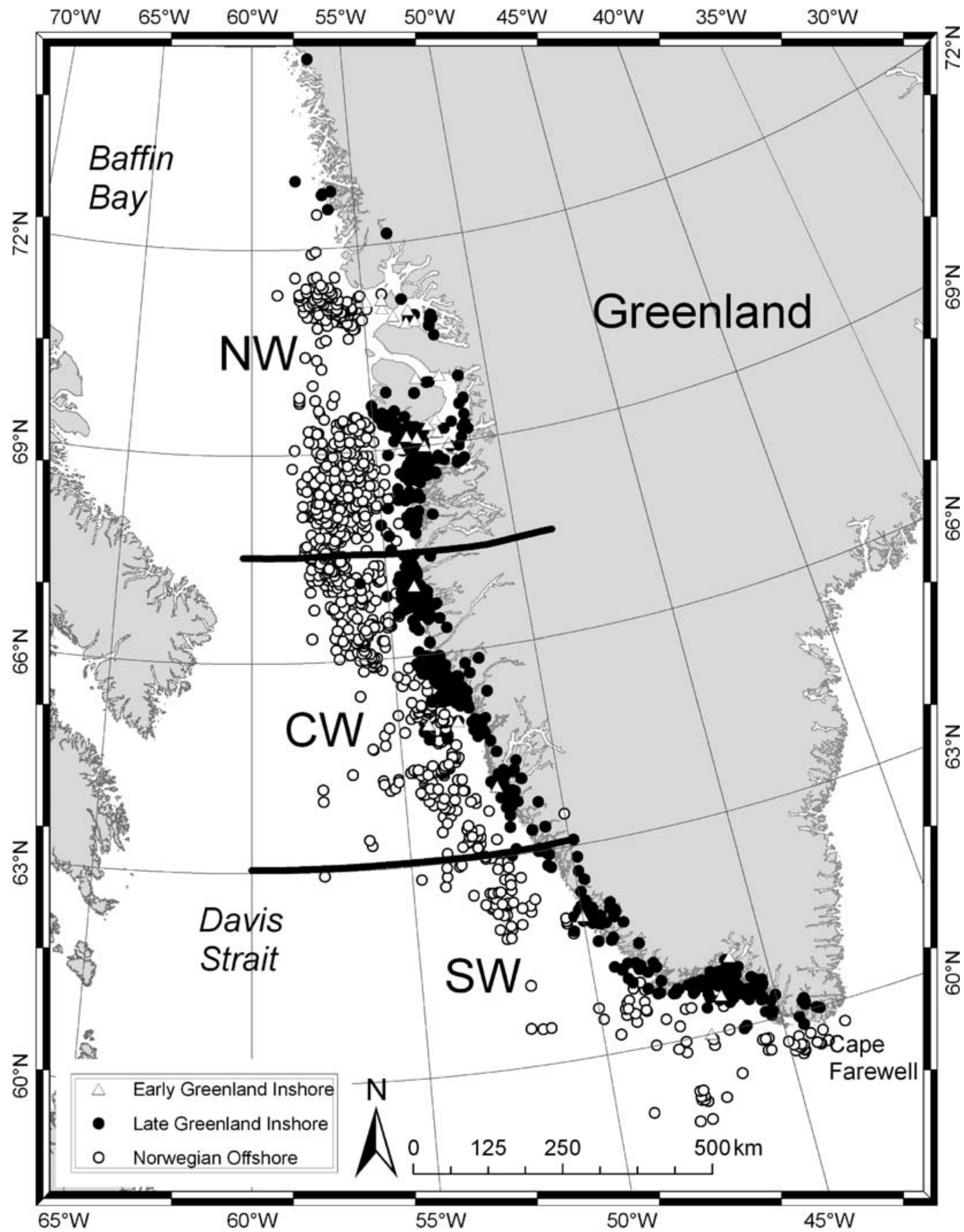

Figure 1. Map of minke whale catches used in the analysis (early inshore Greenland, late inshore Greenland, and Norwegian offshore) together with regions (NW, CW, and SW) and localities mentioned in the text.

attributed to TIME or to TEMP, whereas Model 3 evaluated whether there were significant independent interactions with both TIME and TEMP. For these model comparisons, we interpolated the missing value of temperature in 1991 (a year with no oceanographic cruise) using the values for 1990 and 1992.

Sensitivity analysis

We examined the robustness of our conclusions in the inshore Greenland time-series by performing a sensitivity analysis on the predictor variables MONTH and YEAR. Monthly sensitivity was examined to ensure that our conclusions drawn about trends in sex ratio were not impacted by the quota distribution system. A fixed harvest quota is given to each municipality by the Greenland Home Rule government for the communal hunt in spring, yet whales are more abundant in southern municipalities in August and September (when municipalities to the north have taken most of the quota already). Therefore, there is an occasional redistribution of the quota by the Home Rule government after August with preference given to southern municipalities. Sensitivity analyses on MONTH were conducted removing all months after September and after October, and re-running the models.

We also performed a sensitivity analysis on YEAR to examine the impact the most recent period has had on the trends in sex ratio, the rationale being that sea surface temperature (SST) warmed in recent years off West Greenland and that this warm period may have had an effect on catches. We incrementally dropped 1 year at a time from the model and examined the parameter estimate and *p*-value for the interaction between region (specifically SW) and year.

Results

Greenland (inshore) catches

Data were available from 2400 catch records in the late inshore Greenland time-series (Figure 1). An additional 158 records were available from the early inshore time-series before 1985, but several of these records were missing information and usually general latitude/longitude positions had been assigned to catches. In the late time-series, a few observations recorded in March ($n = 5$) were grouped with those of April.

Most catches were taken close to the coast, and the highest densities were clumped near populated areas or towns (Figure 1). Catches were disproportionately weighted towards females (Table 1), with $>3\times$ as many females taken in inshore waters as males. This fraction was relatively constant across each of the three regions, ranging from 71 to 79%. Seasonal patterns suggested a larger proportion of females taken early in spring ($>$80%; April–June), with a decline over summer (July–September), and an increase in autumn (October–December; Table 1). Catches peaked in July and August in the NW and CW, yet were delayed until September in the SW (Figure 2a, Table 2). The monthly catches were also stratified by 5-year periods, but few differences between different year groupings were detected.

Catches were broken down to finer spatial scales by examining trends at each degree of latitude. The analysis (restricted to catches $\geq$58°N) reduced the sample size by 50% ($n = 1052$) because of missing geographic positions. Catches were relatively well distributed across latitude, with high-density peaks falling in each of the three regions (Figure 3a). This pattern was fairly consistent when data were split into pre- and post-2000 year groups, and the density of catches was highest in the SW during both periods (Figure 3a). Visually these graphs demonstrated no overall shift of effort towards the north or the south. Moreover, a logistic regression examining SW female sex ratio in catches as a function of year resulted in a non-significant year coefficient when controlling for month (year $= -0.012$, $p = 0.164$).

The general patterns in the proportion of females in the catch across latitude were weak and relatively flat for the entire west coast (Figure 4a). Results of the linear regression analysis indicated insignificant yet slightly increasing trends in the proportion of females in the NW + CW region, where females constituted between 65 and 80% of the catch (Figure 5a, Table 3). In contrast, there was a significantly declining trend of females in the SW (estimate -0.06, $p = 0.01$), where the proportion of females in the catch declined from ~85 to ~72% in ~15 years. The mixed-effects models and standard logistic regression results were similar, and the magnitude of overdispersion was 11% based on residual deviance of 2603.1 on 2352 degrees of freedom (d.f.), also reflected in the estimated standard deviation (s.d.) for random effects (0.185, s.e. = 0.202).

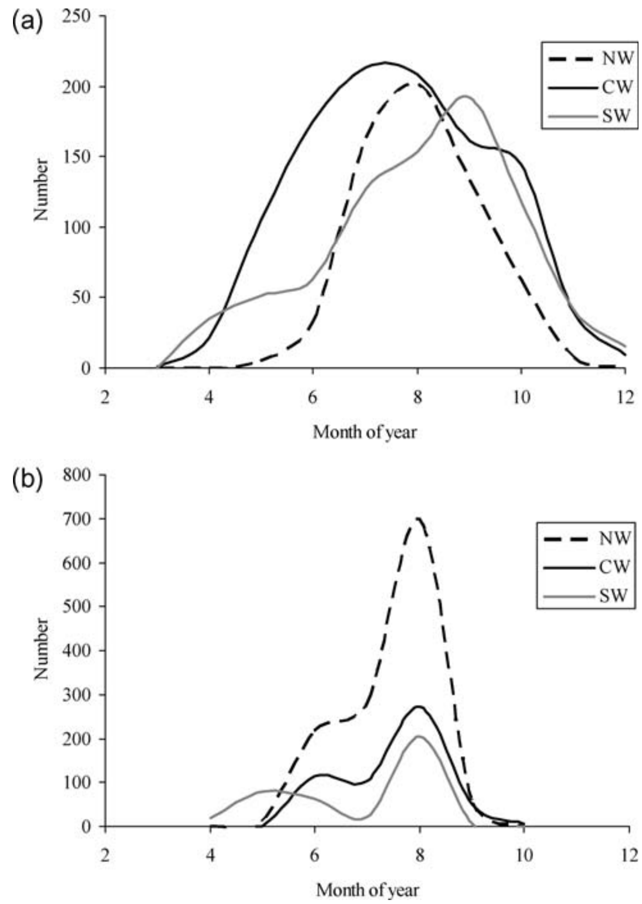

Figure 2. Distribution of catches from (a) the inshore Greenland time-series, 1960–2006, and (b) the offshore Norwegian time-series, 1968–1985.

Table 1. Female minke whale proportions and total catch numbers in the late inshore Greenland dataset by region and year [database available from the IWC (www.iwcoffice.org)].

Year	NW	CW	SW
1987	0.70/10	0.40/5	0.75/4
1988	0.80/19	1.0/12	0.89/9
1989	0.60/17	0.38/8	0.84/25
1990	0.73/30	0.67/15	0.96/28
1991	0.77/22	0.81/26	0.74/34
1992	0.80/21	0.84/32	0.77/39
1993	0.68/25	0.66/41	0.90/29
1994	0.82/22	0.76/42	0.82/33
1995	0.49/41	0.76/63	0.79/47
1996	0.68/37	0.73/70	0.87/55
1997	0.64/45	0.71/58	0.78/40
1998	0.78/36	0.68/78	0.82/51
1999	0.72/32	0.79/80	0.80/56
2000	0.82/33	0.73/41	0.75/32
2001	0.70/29	0.69/52	0.86/35
2002	0.70/29	0.77/52	0.77/47
2003	0.73/30	0.59/63	0.72/79
2004	0.70/33	0.80/81	0.68/57
2005	0.85/33	0.81/80	0.75/56
2006	0.72/29	0.77/111	0.66/29

Table 2. Catch (total numbers) and proportion of females in the inshore Greenland and offshore Norwegian datasets by month.

	Greenland inshore			Norwegian offshore		
Month	**Number of males**	**Number of females**	**Proportion female**	**Number of males**	**Number of females**	**Proportion female**
April	7	45	0.87	–	–	–
May	12	131	0.92	4	14	0.78
June	50	206	0.80	77	296	0.79
July	129	371	0.74	84	309	0.79
August	163	396	0.71	445	730	0.62
September	139	332	0.70	51	62	0.55
October	74	236	0.76	–	–	–
November	20	64	0.76	–	–	–
December	6	17	0.74	–	–	–

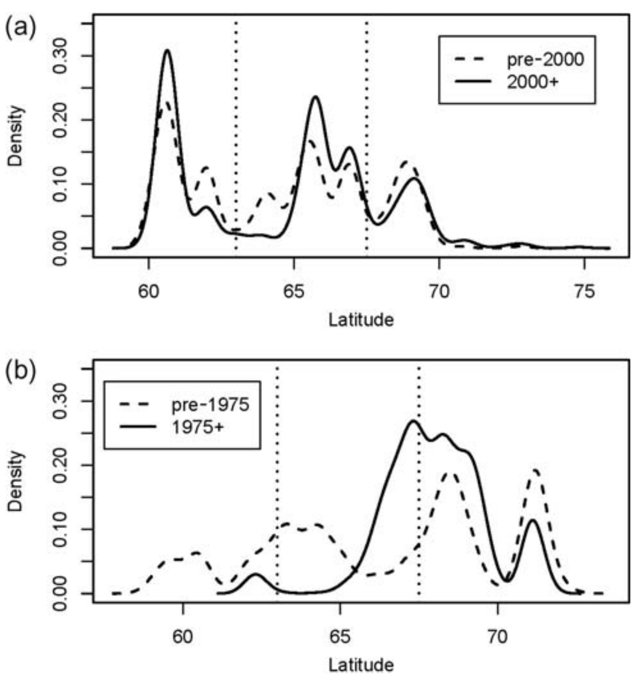

Figure 3. Catch densities of (a) late inshore Greenland and (b) offshore Norwegian with respect to latitude along the West Greenland coast. The dotted vertical lines denote the delineations between the SW, CW, and NW regions.

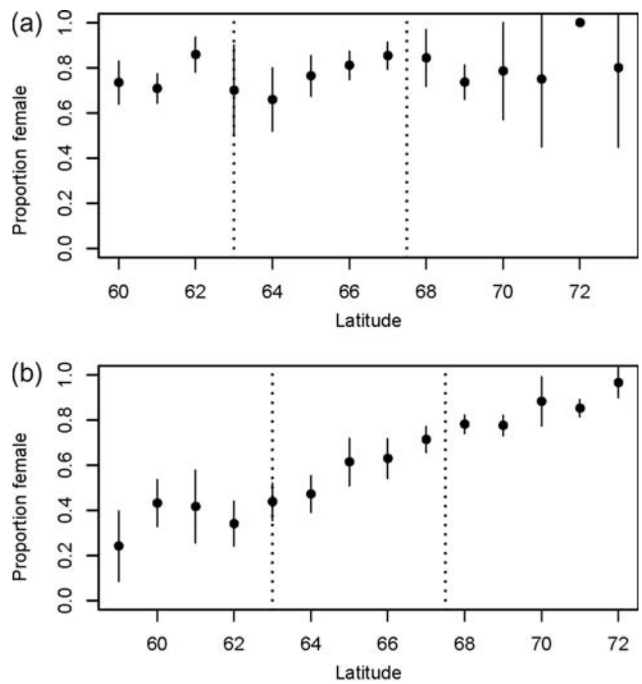

Figure 4. Plot of the proportion of females in (a) the late inshore Greenland catches and (b) offshore Norwegian catches with respect to latitude, showing 95% confidence intervals (except at 72°N for late inshore Greenland where $n = 1$). Vertical dotted lines denote the SW, CW, and NW regions.

The local linear regression plot for the interaction between space and time at the scale of latitude demonstrated a relatively constant trend in the proportion female over latitude (Figure 6a), similar to the raw data trends in Figure 4. The model examining the linear change in percentage females as a function of space revealed that the decline occurred at every latitude in the SW (below line = 0; Figure 6b) and most extreme between 61 and 63°N. This decline, however, stopped at 64°N, and the trend became positive north to 69°N.

The assumption of linearity over time was tested, but there was no significantly improved fit using quadratic terms in time (likelihood ratio test = 3.67, d.f. = 3, $p = 0.3$). Linear models were also run with the early and late inshore time-series combined, adding an additional 158 records to the analysis. The addition of those records did not produce any significant changes to the results using the late time-series alone, with the SW temporal decline in proportion female still present (parameter estimate -0.042, $p = 0.008$). Therefore, the analysis presented here focuses on the late time-series.

Norwegian (offshore) catches

Patterns and trends in the Norwegian offshore catches differed somewhat from those in the inshore Greenland data. In all, 2202 records were available from the Norwegian dataset, and 2072 were used in subsequent analyses (the balance had some data missing). Geographic distribution of catches demonstrated a clear spatial division between the Greenland catches (Figure 1), with most Norwegian catches taken >100 km from the coast. Females made up a similarly disproportionate fraction of the total catch (twice that of males; Table 4).

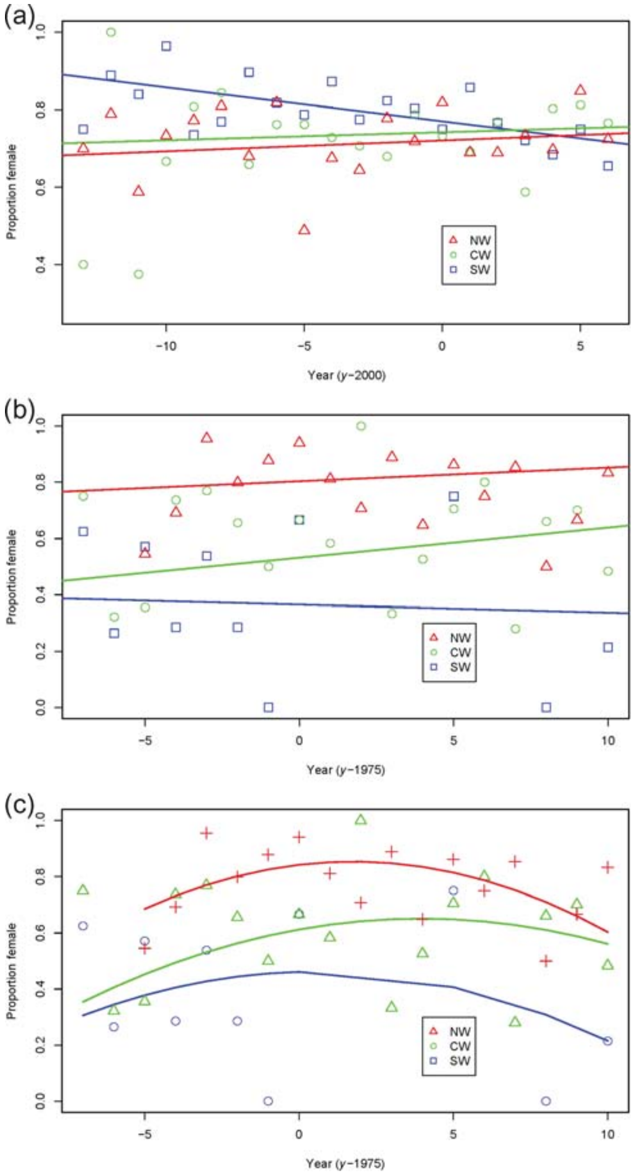

Figure 5. Linear model fits to the proportion of females in (a) the late Greenland catch and (b) the offshore Norwegian catch, and (c) quadratic model fits of the proportion of females in the Norwegian offshore catch in each of the three regions. The proportion of females was weighted by sample size for each region and year to characterize graphically the trends in the data.

The Norwegian catches were taken over a shorter period of the year than the Greenland catches (April–September), with a peak (in all three regions) in August (Table 2, Figure 2a and b). The largest proportions of females in the catch were between May and July (∼78%), declining to 55% in August and September.

About three times the total number of whales was taken in the NW compared with the CW or SW for the entire period (Figure 2b, Table 4). There was greater variability in the annual number of catches in each region in the offshore data. The division of data into NW, CW, and SW regions was not well founded in the Norwegian data given the pre- and post-1975 density distribution of catches over latitude (Figure 3b). There was a shift away from the NW towards the CW in later years, and a reduction in catches in the SW (Figure 3b).

Table 3. Generalized linear model results for the late Greenland inshore time-series with NW and CW combined (the reference value for month is 4).

Parameter	Estimate	s.e.	*z*-value	Pr(>|z|)
Intercept	1.57	0.37	4.21	<0.0001
Month = 5	0.71	0.44	1.60	0.11
Month = 6	−0.17	0.39	−0.43	0.67
Month = 7	−0.60	0.37	−1.64	0.10
Month = 8	−0.76	0.35	−2.22	0.03
Month = 9	−0.80	0.38	−2.13	0.03
Month = 10	−0.50	0.41	−1.24	0.22
Month = 11	−0.55	0.44	−1.25	0.21
Month = 12	−0.75	0.58	−1.29	0.20
Year	0.01	0.01	0.93	0.35
SW region	0.23	0.09	2.49	0.01
Year × SW region	−0.06	0.02	−2.65	0.008

The total number of catches increased with latitude with a peak in the NW (>68°N), a pattern opposite to that of the inshore Greenland time-series (Table 4, Figure 3b). Unlike the flat latitudinal trend in the inshore catch, the proportion of females in the offshore data was strongly and significantly correlated with latitude ($r^2 = 0.8$; Figure 4b). Between 60 and 63°N, catches were <40% females, but the proportion increased rapidly between 64 and 72°N, peaking at >90% females north of 70°N (Table 1, Figure 4b).

Trends in the sex ratio of offshore catches using linear models were similar to the trends detected in the inshore catches (Figure 5b). In both the NW and CW regions, there were non-significant and slightly increasing trends, and the SW region had a non-significant decrease. In contrast to the inshore time-series, however, there was a significant improvement in the fit using models with quadratic time terms, driven by the significant non-linearity for the NW region ($p = 0.02$; Table 5, Figure 5c). The mixed-effects models and GEE regression results were similar, and the magnitude of overdispersion was 10%, based on the residual deviance of 2267.9 on 2059 d.f., also reflected in the estimated s.d. for random effects (0.61, s.e. = 0.10).

Although negative for all regions, significantly different curvatures were detected between the NW and CW regions, indicating different patterns of change over time across regions. The significant quadratic fit was significantly better even when the last 3 years of data from the NW were removed from the model (years where sample sizes were very small). The NW was the region with the greatest degree of non-linearity (Figure 5c), and the SW and CW had less departure from a linear rate of change.

Local quadratic fits were used to estimate the prevalence and the linear rate of change in the proportion female for each latitude, and estimates were plotted for 1975 (the approximate median year for the offshore series). There was an increase in the proportion of females with increasing latitude beginning at ∼64°N (Figure 7a). The slope plot suggested that there was a general increase in the proportion of females across latitude, except latitude 66°N, where in 1975 the trend decreased (Figure 7b). The trend in quadratic terms across latitude shows a significant departure from linearity in the NW (Table 5, Figure 7c), but this was not the case in the SW or CW. Overall, this result suggests that change over time differed across regions and across the finer spatial scales of latitude.

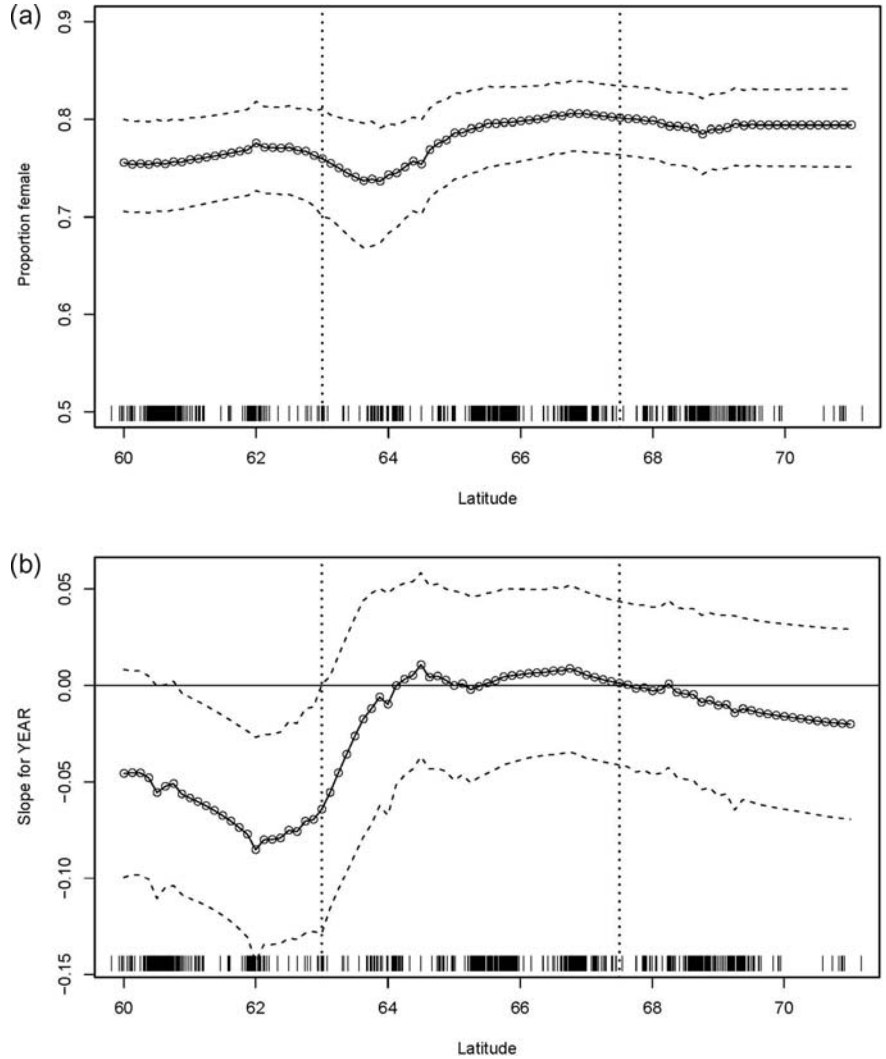

Figure 6. Proportion of females in the inshore Greenland catches of minke whales. (a) Local linear regression plot for the interaction between space and time, and (b) the slope or rate of change. The scale on the bottom shows the density of data at each latitude. Vertical dotted lines denote the SW, CW, and NW regions.

Although the specific comparisons do not parallel the temporal patterns found in the inshore Greenland data, the ultimate conclusion is that with either series, a single common prevalence or change was not found across spatial locations.

Sensitivity analysis

A sequential sensitivity analysis was conducted on MONTH and YEAR for the late Greenland time-series to examine the effects of season or a specific subset of years. When the final model was re-run excluding all months after October, there were no changes in observed trends or significance. When the final model was re-run excluding all months after September, a similar estimate for the declining fraction of females was produced for the SW, but the diminished sample size significantly reduced the power to detect the effect.

The final 5 years of the catch series (2002–2006) had a notable effect on the trend observed in the SW. Removing 2006 from the analysis removed the significance of the trend in the SW ($p = 0.06$). The removal of the final 3 years (2004–2006) halved the parameter estimate for the interaction between SW REGION and YEAR (-0.0078) and resulted in a non-significant p-value ($p = 0.807$). Removing the final 5 years of data reduced the trend in the SW to zero (parameter estimate = 0.0002), and it became non-significant ($p = 0.9968$). These results suggest that recent changes in the sex ratio are driving the observed declining trend in the inshore SW time-series. The difference in the final 5 years of the catch series is also shown by computing the averages in 5-year periods, the average fraction of females being 84% from 1987 to 1991, 83% from 1992 to 1996, 80% from 1997 to 2001, and 72% from 2002 to 2006.

Sex ratio and sea temperatures

The mean SST (0–40 m) on the banks of West Greenland over the entire whaling period (since 1968) was 1.68°C (s.d. 0.85). During the late inshore catch period, the mean temperature rose to 2.04°C (s.d. 0.86), and between 2002 and 2006 it rose to 2.8°C (s.d. 0.74). The temperatures between 2002 and 2006 were significantly

Table 4. Female minke whale proportions and total catch numbers in the offshore Norwegian dataset by region and year [database available from the IWC (www.iwcoffice.org)].

Year	NW	CW	SW
1968	–	0.75/4	0.62/16
1969	–	0.32/59	0.26/102
1970	0.55/22	0.36/90	0.57/14
1971	0.69/208	0.74/38	0.29/14
1972	0.96/45	0.77/26	0.54/52
1973	0.80/154	0.66/32	0.29/35
1974	0.88/221	0.50/30	0.00/1
1975	0.94/84	0.67/9	0.67/9
1976	0.81/175	0.58/12	0
1977	0.71/72	1.00/3	0
1978	0.89/72	0.33/3	0
1979	0.65/37	0.53/38	0
1980	0.86/58	0.71/17	0.75/4
1981	0.75/56	0.80/5	0
1982	0.85/41	0.28/25	0
1983	0.50/6	0.66/59	0.00/3
1984	0.67/3	0.70/67	0
1985	0.83/6	0.48/31	0.21/14

Table 5. Generalized linear model results for Norwegian catches with a quadratic term for time (the reference value for month is 5, and for region is CW).

Parameter	Estimate	s.e.	z-value	Pr(>|z|)
Intercept	0.78	0.46	1.67	0.09
Month = 6	0.004	0.44	0.01	0.99
Month = 7	−0.31	0.40	−0.76	0.45
Month = 8	−0.91	0.38	−2.38	0.02
Month = 9	−1.12	0.42	−2.65	0.01
Year	0.04	0.03	1.30	0.19
NW region	1.56	0.31	5.03	<0.0001
SW region	−0.45	0.72	−0.63	0.53
Year^2	−0.0004	0.006	−0.06	0.95
Year × NW region	0.009	0.05	0.20	0.84
Year × SW region	−0.05	0.07	−0.78	0.43
NW region × year^2	−0.02	0.009	−2.30	0.02
SW region × year^2	−0.005	0.01	−0.32	0.75

warmer than the mean in all other years during the whaling period ($F = 8.11$, $p < 0.001$; Figure 8).

The annual proportion of females in the late Greenland catch series in the SW was significantly negatively correlated with annual SST on the banks ($F = 6.09$, $p = 0.02$; Figure 8). Opposite but insignificant relationships with temperatures were found in the CW ($F = 0.52$, $p = 0.48$) and in the NW ($F = 4.63$, $p = 0.05$) for the late Greenland catch series (Figure 9).

A sequence of logistic regression models was fitted to the inshore catch series to separate empirically the effects attributable to year and temperature. Each regression model included region, month, year, and temperature. The AIC for Model 1 (YEAR × REGION) was 2599.7, and that for Model 2 (TEMP × REGION) was 2600.2. Therefore, the YEAR × REGION and TEMP × REGION models yielded nearly identical AIC values, suggesting that either of the models provided an equivalent explanation of the variation in trends across regions. The AIC for Model 3 (YEAR × REGION and TEMP × REGION) was 2597.3, suggesting that the inclusion of both sets of interactions was not a significant improvement in fit compared with either model with one set of interactions.

The Norwegian catch series was derived from a cold regime around West Greenland and catches therefore span only half the temperature range (0–2°C) of the late Greenland catch series (0.8–4°C). In the NW and CW regions, the Norwegian catch series had similar (yet insignificant) relationships with increasing female proportion and increasing temperature to the late Greenland catch series (Figure 9). Trends in the SW region were different, but that region was both data-sparse (8 of 19 years were without catches) and had a large interannual variation in the proportion of females in the catch, likely caused by some catches being in the catch taken nearly 300 km offshore.

Discussion

Off Greenland, there is a clear segregation by sex between minke whales on the west and the east coasts. Females inherently constitute a larger proportion of the catch off West Greenland and males dominate the catch off East Greenland. This phenomenon is already well described, having been reported in the literature decades ago based on observations from commercial whaling operations (Christensen, 1976). The observed skewed sex ratio off Greenland is clearly a result of adult segregation, rather than demography, because the foetal sex ratio between male and female minke whales is even (Horwood, 1990).

In this study, all recorded catches from the west coast of Greenland since 1960 were examined in detail. A nearly constant proportion of females was found inshore, ranging between 71 and 78% of the catch, regardless of latitude. Offshore in the Norwegian catches, however, the proportion female was positively correlated with latitude. In the SW offshore region, the catch was ~30% females offshore, increasing to a maximum of 90% in the NW. The real reasons for the latitudinal segregation of the sexes are unknown. Similar patterns are apparent in other areas such as the Northeast Atlantic and the Antarctic, where female minke whales prefer higher latitudes during summer (Laws, 1961; Jonsgard, 1962; Øien, 1988; Horwood, 1990). A female preference for higher latitudes has also been found in other species of baleen whale off West Greenland (Heide-Jørgensen *et al.*, 2007a, 2008). Mechanisms behind sexual segregation are likely to reflect social preferences and/or underlying ecological niche selection.

The latitudinal sex-ratio pattern off West Greenland may also be due to the association of feeding minke whales with the banks (<200 m) and offshore edge of the banks, an area with significant upwelling (Ribergaard *et al.*, 2006). This important feeding habitat supports high densities of sandeel (*Ammodytes* spp.), capelin, and cod. The banks are narrow off South Greenland, double or triple in area around 64°N, and extend >200 km from the coast north of 69°N. This offers a greater quantity of foraging habitat and likely supports a greater offshore abundance of whales. The area where the banks begin to broaden (north of 64°N) is also the area where the proportion of female minke whales in the catches increases (Figure 7b).

General trends in sex ratio over time

Temporal trends in the proportion of female minke whales in inshore Greenland catches have been relatively constant in the NW and CW since 1987, if not slightly increasing. The most dynamic area is the SW, where the proportion of females has dropped by ~15% since 1987. This decline reduced the proportion of females in the SW to similar values to those found in

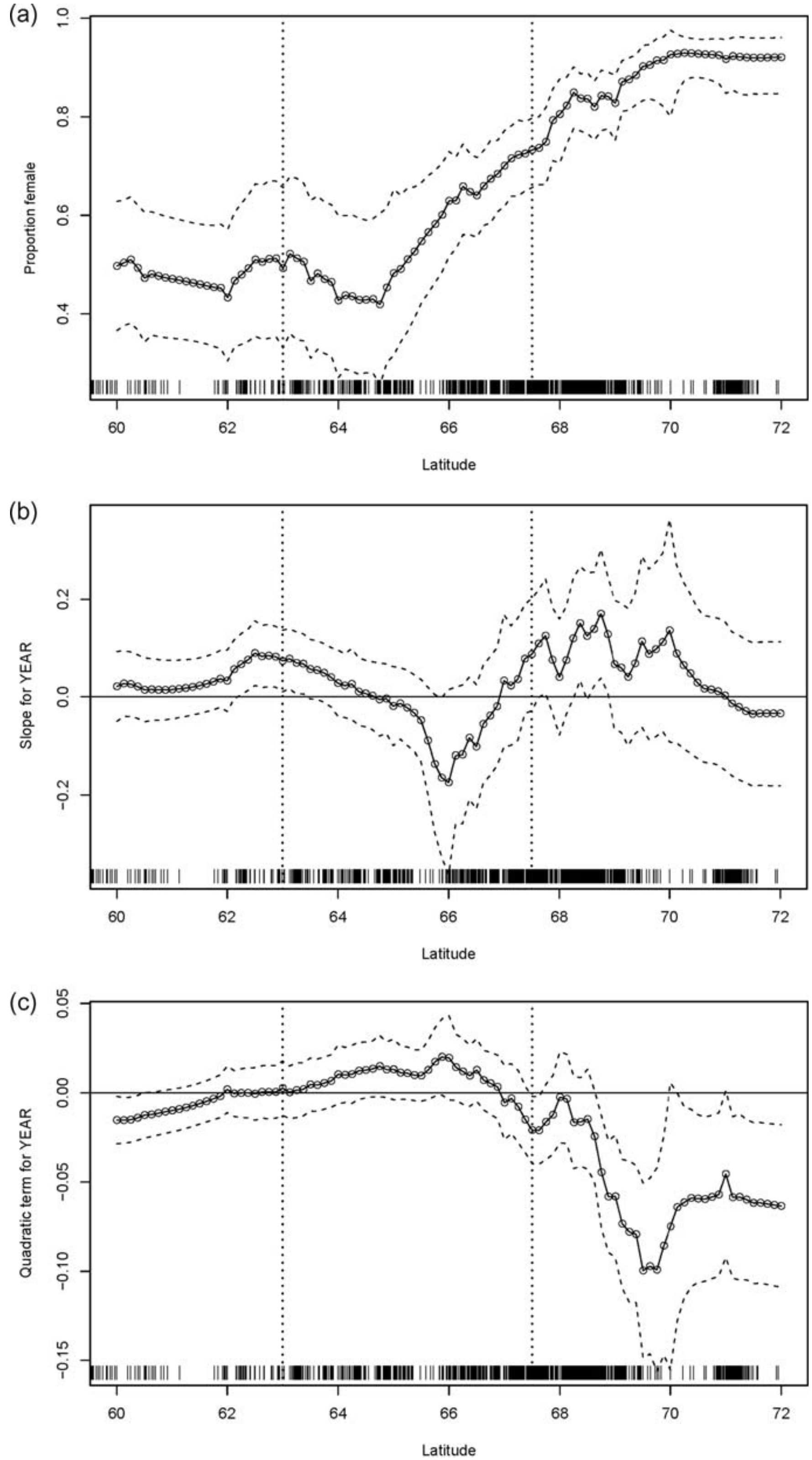

Figure 7. Proportion of females in the offshore Norwegian catches of minke whales. (a) Local linear regression plot for the interaction between space and time, (b) the slope or rate of change, and (c) the quadratic term as a function of latitude. The scale on the bottom shows the density of data at each latitude. Vertical dotted lines denote the SW, CW, and NW regions.

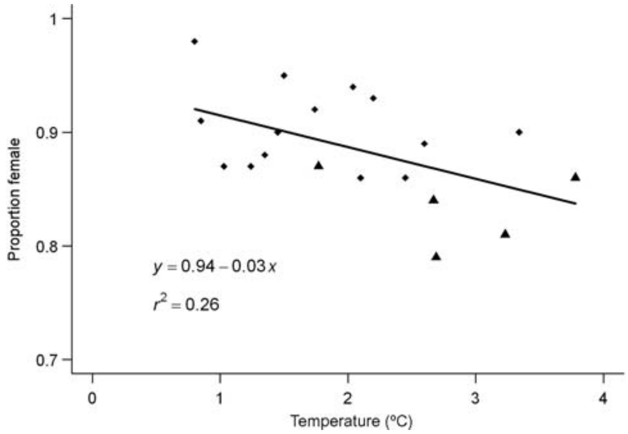

Figure 8. Relationship between the proportion of female minke whales in the Greenland catch off SW Greenland and the temperature between 0 and 40 m on the banks. Data are displayed for the late time-series (1987–2006). The final 5 years of the catch series (2002–2006), or datapoints that drive the declining trend in the fraction of females in the SW, are shown by triangles. The diamonds represent the years 1987–2001.

the NW and CW regions (or 72% females in the catch from 2002 to 2006).

Temporal trends in the proportion of female minke whales in offshore Norwegian catches were first fitted with a linear model. When testing for non-linearity, it was found that a quadratic model fitted best and was more parsimonious for at least the NW. Estimates from the quadratic model suggested that changes over time differed across regions and across the finer spatial scales of latitude. The highest percentage of females was found in the NW, as was the greatest degree of non-linearity. The CW region was relatively flat and least quadratic, though had the largest sample size of the three regions. The SW region had the lowest proportion of females and departed from a linear rate of change, but had few catches. These results are limited and exploratory, and it is unclear if the quadratic model is optimal given that ecological theory should underpin the specification of models and model selection (Burnham and Anderson, 2002). The overall basic distribution of sex ratio and the associated latitude trends in the offshore Norwegian catches did not parallel the temporal patterns found in the inshore Greenland data. This suggests that variability in the sex ratios of minke whales off West Greenland may occur over smaller spatial or temporal scales than the distance or period between the inshore and offshore catches.

Influence of SST

Sea surface temperature and year were equally good predictor variables for the explanation of the variation in sex ratio across regions. Note that temperature is a relatively noisy signal, yet was as important as a discrete measure such as year. The significance of our relatively crude temperature index (a single month in a single location in each year) suggests that the inclusion of finer-scaled temperature measurements from other locations and seasons might reveal higher order interactions between SST and sex-ratio variations.

Other predictor variables such as the North Atlantic Oscillation (NAO) and sea-ice coverage may also influence the sex ratio, but of these, SST is likely the variable that most directly affects the whales' environment owing to its influence on production and prey advection. Ocean temperature affects the reproductive dynamics of other large baleen whales, influencing calving rates in North Atlantic right whales (*Eubalaena glacialis*; Greene *et al.*, 2003) and calving success in southern right whales (*E. australis*; Leaper *et al.*, 2006). In the late Greenland inshore catch series, the SW region revealed a reduction in the proportion of females significantly correlated with temperature. Sensitivity analyses demonstrated that the SW decline was clearly driven by the last 3–5 years of the time-series, when the most significant warming occurred off West Greenland. Simultaneously, there was an increase in the proportion of females with SST in both the inshore and offshore NW and CW regions (Figure 9). The Norwegian catch series only covered a period with cold temperatures <2°C, and there was no warming.

The temperatures of the surface water on the banks of West Greenland have, since 2001, been the highest recorded since the beginning of the whaling period analysed here. The SST off SW Greenland is an indicator of the strength of the warm, saline Irminger Current. This current originates off East Greenland, travels south along the east coast around Cape Farewell, then north along the west coast (Figures 10 and 11; Myers *et al.*, 2007). Mixing is intense before the water travels north and, when the current is strong, warm water is carried north along the west coast. This warm water plays a crucial role in the West Greenland ecosystem, stimulating production, bringing fish larvae (e.g. Atlantic cod and capelin) from spawning areas off East Greenland to the banks off West Greenland (Storr-Paulsen *et al.*, 2004; Pedersen *et al.*, 2005), attracting top predators, and driving trophic cascade impacts on the ecosystem.

A potential hypothesis for explaining the observed patterns is that female minke whales move farther north in warmer years. This hypothesis would explain several of the observed phenomena: (i) the decline in the proportion of females in the catches in the SW, (ii) the sensitivity to the final 5 years of data, during which time the sea temperature off West Greenland increased most markedly, (iii) the increases in the proportion of females in the catches in the CW and NW regions, and (iv) the equivalent weight of year and temperature in the models. Furthermore, warmer temperatures are associated with the advection of warm, productive waters (and associated prey) in the Irminger Current from East Greenland. Minke whales caught off East Greenland have been primarily males (70% of the catch; Christensen, 1976; Larsen and Øien, 1988), and any movement of whales from east to west around Cape Farewell in response to the ecological conditions would likely increase the proportion of males in the SW and explain the reduction in the female proportion there. A connection between West and East Greenland is manifested through both oceanography (Myers *et al.*, 2007) and biology because several commercially important fish species, including Atlantic cod and Greenland halibut (*Reinhardtius hippoglossoides*), recruit off East Greenland and are transported to West Greenland with ocean currents (Buch *et al.*, 1994; Jørgensen, 1997; Laidre *et al.*, 2004). Therefore, the well-documented ecological connection between the two areas may extend to other species, including minke whales, especially in light of their continuous distribution around the southern tip of Greenland.

Potential mechanisms driving sex-ratio changes

Sea temperature is unlikely to drive the observed changes in sex ratio directly, but may be a proxy for temperature-driven

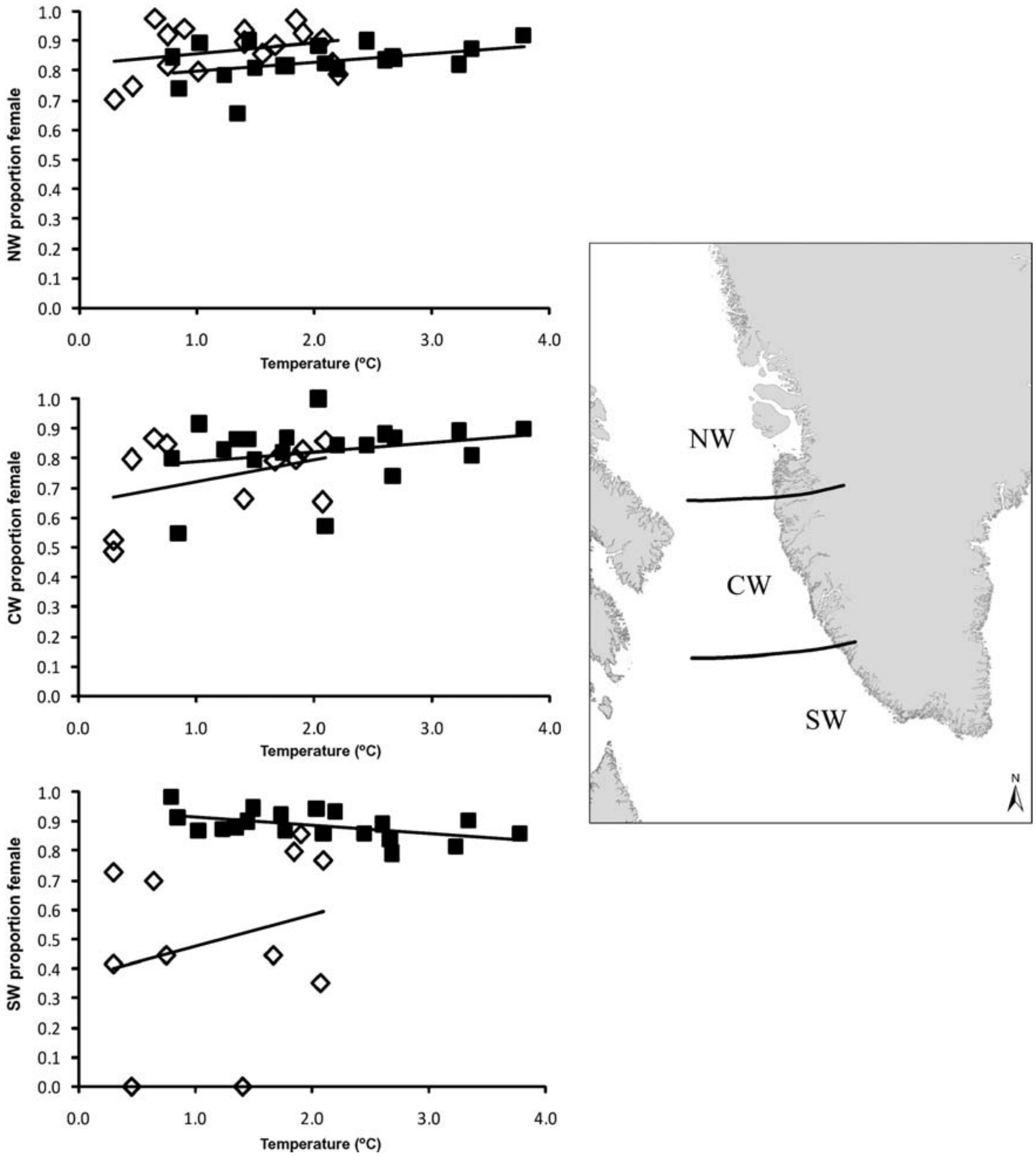

Figure 9. Correlation between the proportion of females in the catch and temperature (°C) at 0–40 m off West Greenland for each of three regions (NW, CW, and SW) for the late Greenland catch series (black squares) and the Norwegian offshore catch series (open diamonds).

large-scale ecological conditions that stimulate prey abundance and/or prey species composition off West Greenland. The relative spatial and temporal distribution of feeding male and female minke whales should reflect those patterns. The abundance of the important prey of minke whales, such as young Atlantic cod, varies with the strength of the Irminger Current (Buch *et al.*, 1994). Moreover, a rise in SST favours another important prey item, capelin. Rose (2005) found that capelin reacted positively to rises in temperature >2°C and shift their distribution very quickly; this temperature fits well with the observed changes in sex ratio here (Figure 9).

In the Antarctic, female minke whales move farther into the pack ice (to higher latitudes), and in the Subarctic, move north into seasonal ice in the Barents Sea (Horwood, 1990). Sea ice off West Greenland has retracted with increases in SST (Heide-Jørgensen *et al.*, 2007b). Perhaps female minke whales move farther north earlier in the season following the retraction of the sea ice and its associated fauna, which stimulates aggregations of polar cod. Ultimately, pregnant minke whales (51% of the females caught, not only the mature females, had a foetus) may separate socially to avoid niche overlap or to avoid males. If pregnant females move north, this would result in an increasing proportion of males in the SW.

Harvest itself has the potential to influence sex ratios of animal populations under certain conditions, specifically when there is sexual selection in the catch, low immigration, and low

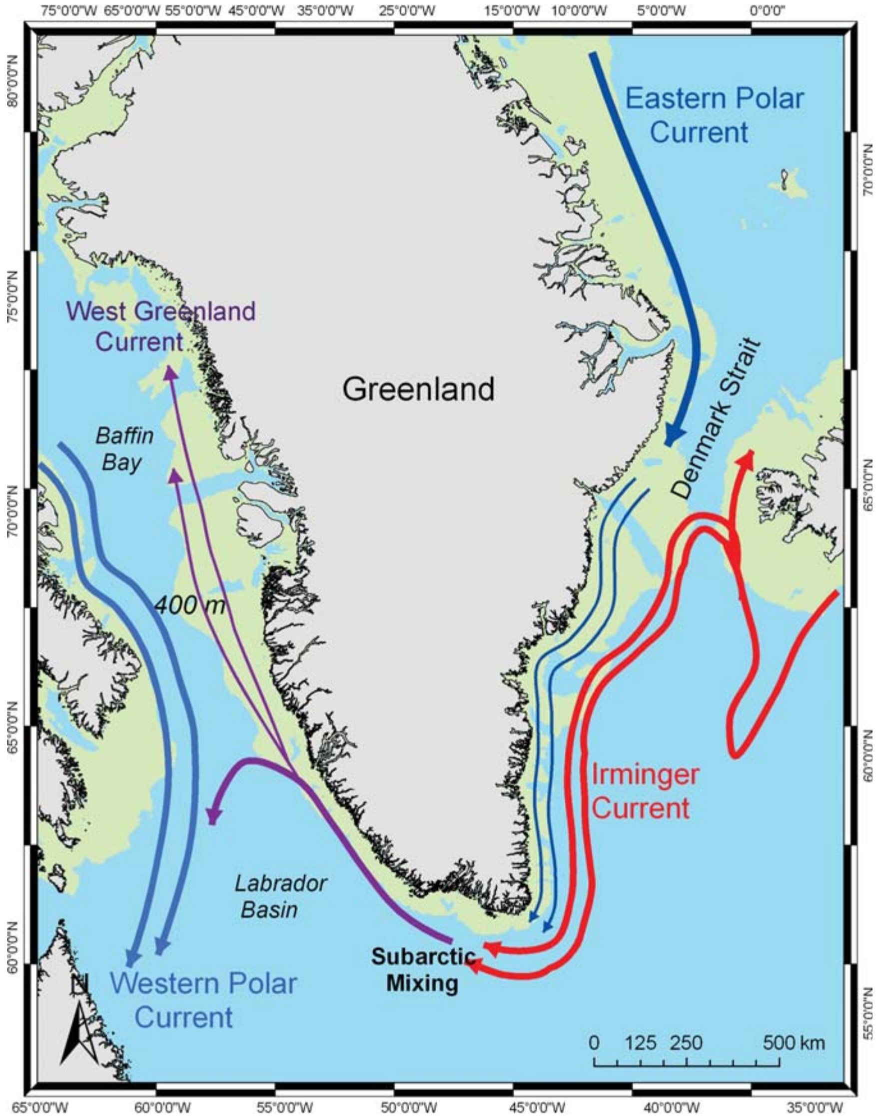

Figure 10. Currents in the North Atlantic and around Greenland. Note the warm water in the Irminger Current off East Greenland moving south around the southern tip of Greenland and north along the west coast.

reproductive potential (McLoughlin *et al*., 2005). It is reasonable to consider whether the harvest of minke whales off West Greenland could be an explanation for the decline in the fraction of females in the catch in the SW. A continued and skewed harvest towards female whales would deplete the population of females, causing the proportion female to decline. Such a decline, however, should be observed over the entire range of the population. This was not the case in our study. Instead, the decline in the proportion of females was only detected in the SW. In the CW (where the harvest is 2–3 times that in the SW) as well as in the NW, non-significant increases in the female proportion were found in the catch. These differences could be explained by harvest if minke whales had very high individual site fidelity to specific regions of the coast. Such site fidelity is not likely for a species that has shown large-scale redistributions of abundance in the North Atlantic (NAMMCO, in press). Moreover, a site-fidelity hypothesis is in conflict with recent aerial survey results off West Greenland that found minke whales to be most abundant in the SW (Heide-Jørgensen *et al*., 2009), whereas the SW region should have been highly depleted relative to the NW if the sex-ratio trend followed from site fidelity and a female-biased harvest (Brandão and Butterworth, 2009).

Finally, our sensitivity analysis demonstrated that the decline in female proportion was driven by the final 5 years of data. The temporal synchrony with large-scale environmental changes along the West Greenland coast leads us to conclude that these changes have played a role in the patterns observed in the catch.

Potential biases

In this study, it has been assumed implicitly that sex has been determined and reported correctly. Most of the sexes in the Greenland time-series were provided by hunters. The reported female proportion was estimated to be the same (67%) for animals caught by Greenlanders and by the Norwegian whaling vessels (Kapel, 1980). An independent estimate for 1982 and the period 1996–1998 of 77% females available from genetic analysis

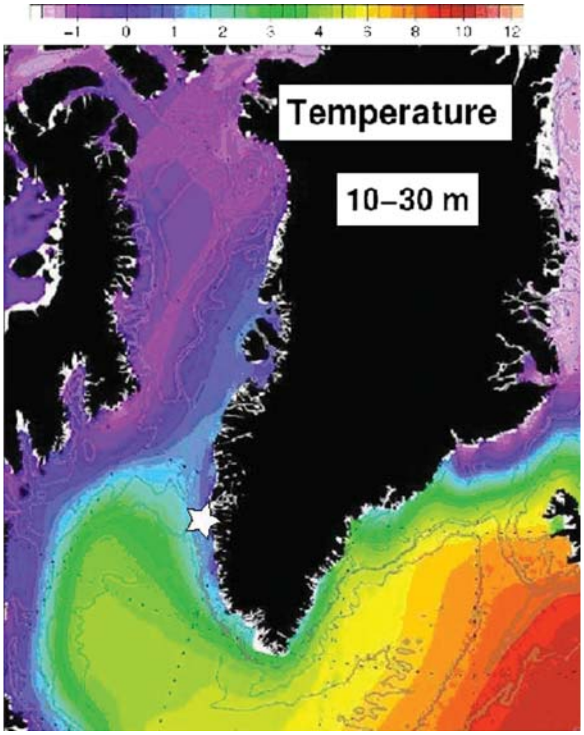

Figure 11. Temperature interpolation (°C) at 10–30 m around Greenland from the World Ocean Atlas. Note the warm water moving around the southern tip of Greenland from East Greenland, driven by the Irminger Current. The white star shows the location of the temperature station used in this study. Image adapted from Ribergaard *et al.* (2006).

(Andersen *et al.*, 2003) showed that of 166 samples from minke whales off West Greenland, only three males were incorrectly reported as females, and two females incorrectly as males.

Sex-specific selectivity in the harvest is not a reason for the dominance of females in the catches. Surfacing minke whales spend on average 2–3 s at the surface (Heide-Jørgensen and Simon, 2007), and the only visible feature during that short period is a portion of the back and the dorsal fin. There is no difference between the dorsal fin and the size of adult male and female minke whales, or in the behaviour of either sex when surfacing (Horwood, 1990). Therefore, it is not possible for hunters to distinguish a male and female whale before it is shot, and the potential for sex-specific harvest selectivity is negligible. Moreover, harvesting strategies for the Norwegian and Greenland catch were similar, the only difference being that whales were flensed and processed on board large ships offshore in the Norwegian period.

Conclusions

Minke whales along West Greenland display pronounced sexual segregation. Females tend to occur farther north off West Greenland, whereas most males remain off SW Greenland or along the east coast. It does not seem likely that minke whales residing on either side of Greenland in summer alone constitute separate functioning populations. Comparison with commercial catches taken offshore by Norwegian vessels suggests divergent patterns in the densities of whales, sex ratios, and temporal trends. Trends over time in the sex ratio of inshore catches indicate few changes off northern and central West Greenland, whereas recent catch data (2002–2006) from southwest Greenland show a decline in the sex ratio. This period coincides with higher values of SST than over the previous 30 years. Increased sea temperatures off West Greenland may have initiated a redistribution of females along the coast, possibly supplied by the movement of whales from east to west. Therefore, we suggest that the changes observed in the sex ratio in the inshore catch may be related to large-scale oceanographic changes along the coast of West Greenland. Detailed examination of the trends in sex ratio in future minke whale catches analysed in conjunction with higher spatial and temporal resolution environmental data, including perhaps prey distributions, would likely provide further insight into the mechanisms proposed.

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