Importance of seasonal ice zone for blue and fin whales in the Southern Ocean feeding ground

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ABSTRACT

Blue and fin whales were major krill predators in the Southern Ocean but intensive whaling industry dramatically reduced the populations by 99% and 95% respectively. We have used whaling dataset in a new analysis on circumpolar abundance of these whales relatively to environmental (sea surface temperature (SST), seasonal ice zone (SIZ)) and trophic parameters (summer oceanic primary production (SOCC) and krill densities). Most of whale catches was located in the Atlantic - West Indian sector. SIZ encompassed most of these whale catches and fin whale distribution corresponds to a wider SST range than blue whale's. This global circumpolar analysis shows that historical abundances of whales were highly correlated to SIZ extent and only marginally related to the available densities of their krill prey. No relationship is found with the SOCC. Although circumpolar assessment of krill biomasses remain uncertain possibly leading to an unreliable relationship between whales and krill abundance, sea ice acts as a major feature for krill-eating whales in the Southern Ocean. Large SIZ provides favourable feeding ground throughout summer sought by blue and fin whales migrating in these high latitudes due to their large energy requirements.

INTRODUCTION

The oceanographic context largely influences the spatial distribution of the Southern Ocean productivity which in turn drives the at-sea distribution of many Antarctic marine top predators such as whales (Tynan 1998; Nicol et al. 2000; Thiele et al. 2000). Several whale species feed every summer on vast quantities of their chief prey Antarctic krill, Euphausia superba (Brown & Lockyer 1984; Kawamura 1994).

Antarctic whales were the largest krill predators and among them, blue (*Balaenoptera musculus*) and fin (*Balaenoptera physalus*) whales represented the largest consumers of krill biomass before the whaling era (Laws 1977). Indeed Antarctic blue and fin whales consumed every year an estimated 200 million tonnes of krill annually, 1000 time greater than the current krill fishery (Nicol & Endo 1997). Whale stocks depletion was thought to be responsible for the "Krill surplus" in the 1960s (Laws 1977; Lubimova et al. 1985). Historical data on whale distribution could bring a pertinent contribution to our understanding of environment-krill interactions.

The distribution of Antarctic whales was shown to exhibit a strong heterogeneity (Kasamatsu et al. 1996) but to date the relationships with their environment at the global Southern Ocean scale remain largely circumstantial. Tynan (1998) reported the major influence of Southern Boundary of Antarctic Circumpolar Current (SBACC; Orsi et al. 1995) in explaining latitudinal whale distributions. However, this circum-Antarctic structure does not explain the longitudinal differences in blue and fin whale abundance. Sea ice and primary production are two major driving features reported to locally influence both whales and krill abundance (Nicol et al. 2000; Thiele et al. 2000). Sea ice was found to have a profound effect on krill recruitment however conflicting evidence has subsequently been reported on the spatial influence of sea ice extent on krill density (Nicol et al. 2000; Constable & Nicol 2003;

Atkinson et al. 2004). Regionally, whales and krill were found within area of greater sea ice extent (Nicol et al. 2000; Thiele et al. 2000) but it was purported to not apply at circumpolar scale (Constable & Nicol 2003; Atkinson et al. 2004).

Effective sighting sampling of whales is difficult to realize at the whole Southern Ocean scale (Murase et al. 2002). However past floating factories caught 190,000 (95%) blue whales and 510,000 (90%) fin whales in the Southern Ocean during extensive industrial whaling from 1931 to the mid sixties (see also Clapham & Baker 2001). The extent of the exploitation over such a long period of time in association with strong whale philopatry (Clapham & Seipt 1991) advocates for this catch dataset to represent an unbiased view on the historical global distribution of whales in the Southern Ocean (Tynan 1998).

In this paper we intend to use this unequalled database to investigate the influence of oceanic parameters (sea surface temperature and sea ice extent) and primary production on the past circum-Antarctic distribution of blue and fin whales, and their relationship with the past estimates of krill densities.

MATERIALS AND METHODS

(a) Whales, krill and oceanographic data

Whaling data were provided by the International Whaling Commission. Monthly catch data of blue and fin whales from industrial floating factory whaling operations in the Southern Ocean from 1931-1966 were used to estimate the summer (December-January-February) spatial distribution of these species.

We used 1°-grid monthly sea surface temperature (SST) climatology based on data collected between 1951 and 1980 (Bottomley et al. 1990) and monthly sea ice climatology, averaged over 1903-1994, from a mixture of few ship measurements and mainly satellite sources since the early 1970s (Rayner et al. 1996), to estimate sea ice extent (both available on http://iridl.ldeo.columbia.edu). We defined the Seasonal Ice Zone (SIZ) like the area delimited by the winter maximum (September) and the summer minimum (February) sea ice extent.

Whales and Chlorophyll *a* distribution data are not contemporaneous. We constructed a synoptic summer climatologic distribution (December to February) of surface chlorophyll *a* concentration from 1998 to 2003 using the SeaWIFs monthly global coverage dataset. Summer offshore Chlorophyll *a* concentration (SOCC) was estimated for oceanic waters (i.e. depth >1000 m).

Global estimates of krill biomass were extracted from the historical densities of krill in the Southern Ocean throughout the summers of 1926-1951 (from Atkinson et al. 2004). We used this unique historical dataset because of its global Antarctic coverage compared to the 1976-2003 dataset mainly restricted to West Atlantic and higher latitude of Indian sector. Moreover, the surveys between 1926 and 1951 were carried out contemporaneously with whaling activities.

(b) Data analysis

Because the SST distribution varies over the austral summer, we firstly extracted the SST corresponding to the frequency of whale catches for each month, and we then compiled the SST range from December to February. We applied a Pearson chi-square test in order to compare the range of SST between blue and fin whales.

For the circumpolar analysis, we splitted the longitudinal abundance of whales and krill, SIZ extent and SOCC of the entire Southern Ocean into 24 sectors of 15° in order to remove the effect of the spatial autocorrelation between bins which existed at higher resolutions. Since data were not normally distributed (Shapiro-Wilk tests, all $p<0.05$), we used the GENMOD procedure (GLM analysis) in SAS with a log-link function and a negative binomial (blue and fin whales, krill and SIZ) and a Poisson (SOCC) distribution (see Cotté et al. submitted, for details of the analysis).

RESULTS

Most of the circumpolar catches of blue (98.9%) and fin whales (93.5%) were located within the SIZ. Both whales show a heterogeneous abundance around the Antarctic continent with a greater abundance in the Atlantic and west Indian sector, and north of the Ross Sea (Fig. 1). Few whales were caught in the eastern part of the Indian sector of the Southern Ocean and the lowest abundance was observed over the Pacific sector (Bellingshausen-Amundsen area). Blue and fin whales show a similar circumpolar pattern except in the West Atlantic sector where fin whales are more abundant relatively to the blue whale abundance. However this difference can be due to the fact that the dataset we used begin in 1931, while blue whale was actively hunted earlier on Land Station (especially at South Georgia), leading in a probable under-estimation of the catches in this area.

Figure 2 shows the SST range corresponding to the catches frequency of blue and fin whales. The SST distributions are significantly not uniform (chi-square: $\chi^2=38507$, $p>0.05$, $df=13$, the high χ^2 value is due to the high number of whale catches, N are indicated in the Figure 2). The SST range exhibited by the catches frequency of fin whale is larger than the blue whales. While blue whales were exclusively found in waters cooler than 2°C, 15% of fin whales corresponds to warmer waters.

Whales were globally more abundant in sectors where the SIZ extent was the largest (Fig. 1): Atlantic-west-Indian Ocean and the Ross Sea sector. Low abundance of whales was observed in the eastern part of Indian and Pacific sector of the Southern Ocean, where the SIZ is minimal. An exception is noticed in the area at the west of the peninsula, where high abundance of fin whales was found. Note also that the use of a climatology of the sea ice edge is responsible of the whales catches carried out south of the mean ice edge in February. Sea ice extent is inter-annually highly variable and the catches located in the summer pack ice in Figure 1 were certainly conducted in year of low sea ice extent.

The SOCC is high north of the Weddell and Ross Seas and in the Kerguelen heard area (Moore and Abbott 2000). Most of krill stocks are located in the Atlantic sector (Atkinson et al. 2004), however west and middle area of the Southern Indian Ocean and Ross Sea sector contains regionally high krill biomass. We found a positive relationship between krill densities and SOCC ($\chi^2=8.68$, $p<0.01$). However, consistently with the results of Constable et al. (2003) and Atkinson et al. (2004) krill densities were unrelated to the SIZ ($\chi^2=0.01$, $p>0.05$). Because of the relationship between krill and SOCC, these factors will be tested in separate models. From all models (4), blue and fin whale circumpolar abundances are strongly related to the SIZ (χ^2 comprised between 7.4 and 19.2, all $p<0.013$). No significant relationship was found with the SOCC for both whales, and the correlation with krill densities is at the limit of the significativity, once the Bonferroni correction applied.

DISCUSSION

The SST range we described in the previous section is essentially related to the latitudinal distribution of whale catches. This latitudinal distribution is effectively larger in fin whale than in blue whale, especially in the southern Atlantic sector (Fig. 1). Kasamatsu (2000) described sighting data derived from systematic survey in Antarctic waters with similar SST ranges we report here from historical data. This SST range is also a reflectance of the sea ice influence on the SST. Blue whale was therefore found closer to ice edge (i.e. low SST). But despite this strong association between blue whale distribution and the ice edge, catches locations were strangely far from the ice edge in the sector between 30°W and 30°E. Tynan (1997) described the influence of the SBACC on the ecosystem of the Southern Ocean, and particularly the effect of this feature on the latitudinal distribution of whales. The reconstruction of historical sea ice extent from whaling (de la Mare, 1997) and the strong inter-regional variability in sea ice extent around Antarctica showing a major sea ice retreat in the Weddell sector in the 1960s (Cotté et al. submitted) could be responsible of the discrepancy between blue whale distribution and ice edge in this sector. Indeed, major blue whaling period occurred well before 1960 and the distribution of these whales was probably limited to the South by an ice edge located north of the current ice edge.

From our analyses we proposed an explanation on the heterogeneous longitudinal distribution of whales overall the Southern Ocean. These results highlight the strong relationship with the SIZ while it was unexpected that the larger krill predators was only marginally related to their prey, although whales undertake long migration, from their tropical winter breeding ground to their austral summer feeding ground, to consume vast amounts of krill. The relationship with krill could be biased by a lack of an accurate assessment at a global scale. We use the most synoptic dataset of krill contemporaneous with the whaling period, but whereas the new techniques, such as hydroacoustics, improve the regional estimates of stocks (west Atlantic sector for Hewitt et al. 2004; east Indian sector for Nicol et al. 2000), the circumpolar abundance is still uncertain (Stemacek and Nicol, 2005).

The hypothesis our results on the SIZ support could be that both species were mainly targeting their krill prey in relation to sea ice habitat, and not only to their overall abundance. Whales are known to follow the receding of ice edge, followed by the whaling fleets (Hjort et al, 1933), where they found large densities of krill. Krill swarms provided by this predictable feature allow a highly efficient foraging for large whales (Nemoto 1970). A large SIZ ensure therefore an efficient feeding ground over their summering time in the Southern Ocean. Moreover the sea ice habitat is important for krill, especially through the sea ice algae which provides the only suitable food resource for krill larvae, the most sensitive stage of starvation in the whole krill life cycle (Ross et al. 2000). However the area of South Georgia seems to make exception to the mechanism we depict here. High abundance of whales (especially fin whales, although blue whale was also hunted in this region from the South Georgia land station before 1930) occurs in this dynamic sector where the krill population is essentially driven by advection, where the process is known as the “krill conveyor belt” (Murphy et al. 1998). Therefore, although SIZ is important for krill-eating whales in the Southern Ocean, other factors are probably in action at regional scale like in the highly dynamic South Georgia area

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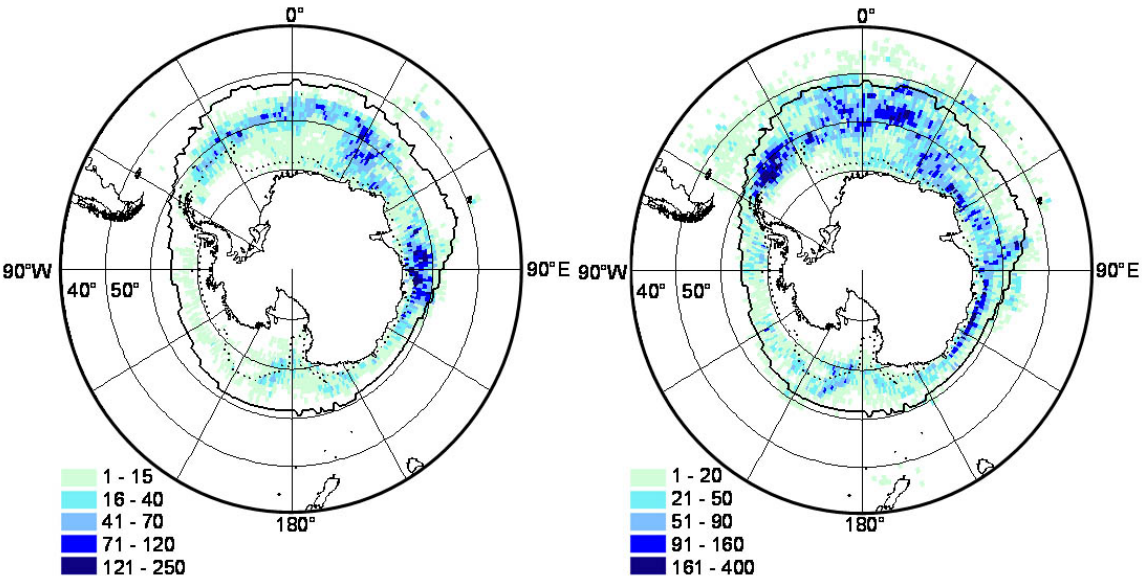

Figure 1. Distribution of blue whale (left map) and fin whale (right map) catches with winter (continuous line) and summer (dotted line) sea ice extent.

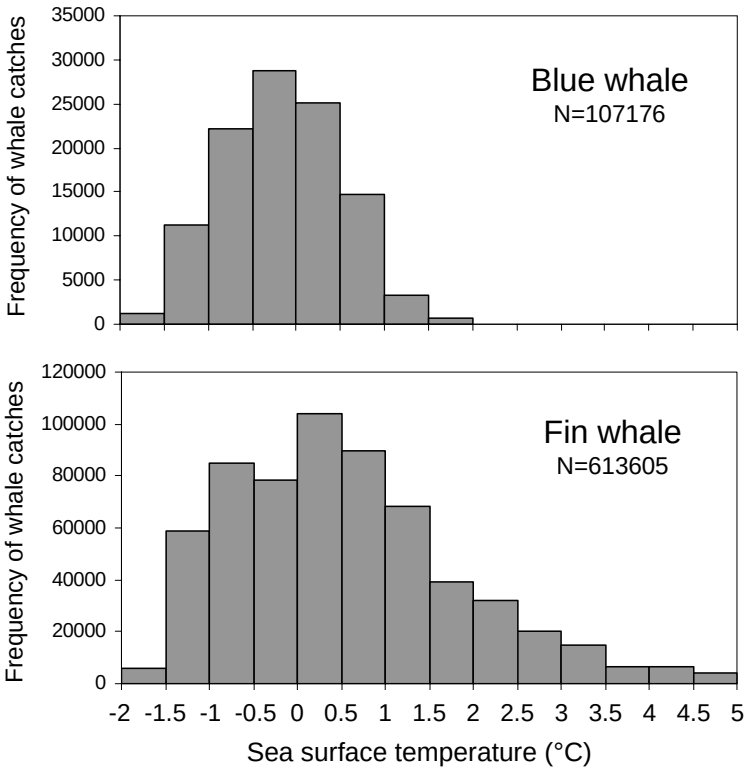

Figure 2. Frequency of whale catches by sea surface temperature in the Southern Ocean.