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From sea ice to blubber: linking whale condition to krill abundance using historical whaling records

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Abstract Krill (Euphausia superba) are fundamentally important in the Southern Ocean ecosystem, forming a critical food web link between primary producers and top predators. Krill abundance fluctuates with oceanographic conditions, most notably variation in winter sea ice, and is susceptible to environmental change. Although links between local krill availability and performance of land breeding, central place foragers are recognised, the effects of krill variability on baleen whales remain largely unclear because concurrent long-term data on whale condition and krill abundance do not exist. Here, we quantify links between whale body condition and krill abundance using a simple model that links krill abundance to sea ice extent. Body condition of humpback whales (Megaptera novaeangliae) caught in west Australian waters between 1947 and 1963 was estimated from oil yields in whaling records. Annual estimates of krill abundance in the Southern Ocean where those whales foraged $(70^{\circ}-130^{\circ}E)$ were correlated

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significantly with contemporary annual winter sea ice extent. We hindcast sea ice extent for the whaling period from reconstructed temperature data and found that whale body condition was significantly correlated with hindcasted winter sea ice extent, supporting the hypothesis that variations in body condition were likely mediated by associated krill fluctuations. As humpback whales migrate and breed on finite energy stores accrued during summer foraging in the Antarctic, changes in sea ice and concomitant changes in krill abundance have long-term implications for their condition and reproductive success.

Keywords Euphausia superba · Humpback whale · Megaptera novaeangliae · Sea ice dynamics · Energetics · Migration

Introduction

Antarctic krill (Euphausia superba) is a functionally vital species in the Southern Ocean, feeding directly on primary producers and providing food for large numbers of top predators. Annual fluctuations in regional krill abundance have been linked to natural variations in sea ice dynamics, indicating that the krill-centric ecosystem is vulnerable to potential climate-driven ice loss (Chittleborough [1965](#page-6-0); Atkinson et al. [2004](#page-6-0); Nicol [2006](#page-7-0)). Good evidence exists that, on local scales, reproductive success of central place foragers in the Southern Ocean such as penguins, seals, and seabirds (Croxall et al. [1999;](#page-6-0) Reid et al. [2005;](#page-7-0) Atkinson et al. [2008](#page-6-0)) is influenced by fluctuations in krill abundance. However, it remains unclear whether variability in krill abundance affects baleen whales because analyses require long-term data on the condition of whales alongside concurrent data on krill abundance (Atkinson et al. [2008;](#page-6-0) Nicol et al. [2008\)](#page-7-0). Leaper et al. ([2006\)](#page-7-0) found a correlation between the breeding success of southern right whales (Eubalaena australis) in the SW Atlantic and SST anomalies around South Georgia, which have been linked to availability of krill to top predators. Other studies that have been conducted on fin whales (Balaenoptera physalus) in the North Atlantic indicate an association between prey availability and body condition, with repercussions to fecundity and reproduction (Lockyer [1986](#page-7-0); Williams et al. [2013\)](#page-7-0).

Historical whaling records provide a valuable long-term dataset, detailing the number and species of whales caught and, in many cases, the individual lengths and total oil yield. Since the amount of oil extracted from a whale depends in part on its blubber (fat) content (Chittleborough [1965;](#page-6-0) Lockyer [1981\)](#page-7-0), oil yield may provide an indicator of body condition and the variability therein throughout the historical whaling era (1900–1963). An example of how body condition relates to oil yield can be seen in lactating female whales: females are generally fatter to support a growing calf (Lockyer [1986](#page-7-0)) and generate higher oil yields (Chittleborough [1965\)](#page-6-0). Data on krill abundance during the whaling era are, however, scarce, making direct comparisons between food availability and whale condition difficult.

Associations between krill abundance and sea ice extent and duration have been observed in various sectors of the Southern Ocean on a range of scales (Siegel and Loeb [1995;](#page-7-0) Loeb et al. [1997](#page-7-0); Nicol et al. [2000;](#page-7-0) Brierley et al. [2002;](#page-6-0) Atkinson et al. [2004\)](#page-6-0) from local to regional. Whilst the exact mechanisms behind the krill–sea ice relationship remain to be elucidated (Fraser et al. [1992;](#page-7-0) Loeb et al. [1997;](#page-7-0) Nicol [2006](#page-7-0)), it is generally understood that sea ice extent and duration influence krill recruitment because ice provides a feeding habitat and nursery ground for krill (Siegel and Loeb [1995;](#page-7-0) Loeb et al. [1997](#page-7-0); Quetin and Ross [2001;](#page-7-0) Quetin et al. [2007\)](#page-7-0) and possible refuge from airbreathing predators (Brierley et al. [2002\)](#page-6-0). Around the Antarctic Peninsula, elevated krill recruitment is evident following years of heavy ice conditions (Hewitt [2003](#page-7-0); Atkinson et al. [2004](#page-6-0); Flores et al. [2012b](#page-7-0); Fielding et al. [2014\)](#page-7-0).

Associations between krill and sea ice provide an avenue to explore the possible link between whale condition and food availability. Detecting a relationship between whale body condition and sea ice would suggest an association between whale body condition and food availability. This association would be supported if a link between krill abundance and sea ice existed in the same foraging region. Following this line of reasoning, we estimate humpback whale (Megaptera novaeangliae) body condition from historical whaling records and relate this to hindcast sea ice extent (SIE), in order to link whale condition to changing ice conditions via impacts on their food source, krill. Using contemporary krill and sea ice data (1979–2007), we also investigate a temporal relationship between krill abundance and sea ice extent specific to humpback whale foraging areas.

Materials and methods

Humpback whale body condition

We obtained data from the International Whaling Commission (IWC) on total oil yield (tons) per whaling expedition and individual whales [identified to species and length measured (m)] for all southern hemisphere whaling stations. Data were filtered to compile a summary detailing which stations landed humpback whales, the total number of expeditions (returning voyages landing whales) per station per year, and the number of these with corresponding oil yields (75 % of expeditions had associated oil yield data) and a high percentage of humpback whales $(>= 90 \%)$ so that error caused by estimating 'humpback' whale oil yield from multispecies catches was minimised. We restricted the analyses to post-WWII data only (from 1947 to 1963) because of the technological advancements during the war that likely augmented whaling and oil extraction efficiencies (Tønnessen and Johnsen [1982](#page-7-0)). Changes in efficiencies after 1947 are difficult to determine, so we assumed they remained constant. Our study focused on the 'Australia west' (AusW; 35 expeditions) and 'Australia east' (AusE; 20 expeditions) landing regions, as they returned 75 % of the total southern hemisphere humpback whale catch between 1947 and 1963.

Individual length records for all whale species were converted to individual weights (tons) using speciesspecific conversion scaling coefficients (Lockyer [1976](#page-7-0)). In a very small number of expeditions (four expeditions out of 35 for AusW and one expedition out of 20 for AusE), the number of lengths reported was less than the number of humpback whales recorded in the summary, meaning that the total weight calculated from the length data would be underestimated. To adjust for this difference, we approximated the weight for the missing whale records as the average for that expedition, noting that we saw little variation in mean length per year over this time period, and thus length alone was unlikely to have influenced oil yields. Since the number of records missing was very small (nine records out of 14,383 for AusW and 26 out of 6,720 for AusE), any error introduced by assuming average values for these records is likely negligible.

Individual whale weights were then summed by expedition to obtain the total weight of whales caught per species per expedition. Total oil yield per expedition included oil from all baleen whales (sperm whale oil was recorded separately). Catches were comprised exclusively of humpback whales in 46 of the 55 expeditions, and in the remaining nine expeditions, humpback whales made up the majority $(>=)3$ % by number). For multispecies expeditions, the humpback whale oil yield was estimated as the ratio of the weight of humpbacks to all baleen species. For example, if the weight ratio between humpback whales and all other baleen species for a particular expedition was 99:1, then humpback whale oil yield was estimated to be 99 % of the total oil yield. Since other baleen species represented less than 2 % of the total weight per expedition, significant error was unlikely, despite the likely interspecific variation in oil yields per unit body weight (Lockyer [1981](#page-7-0)).

Several parameters have been found to influence the blubber content of baleen whales, including weight, sex, reproductive condition (e.g. pregnant or lactating), age (e.g. mature or immature), position of capture (latitude), and time of year of catch (Chittleborough [1965](#page-6-0)). If these were not consistent between expeditions, then they may have contributed to the variability of oil yield and masked any possible krill-related variability. We investigated this using correlation analysis (see Table S2 for a list of variables considered and associated Pearson's correlation coefficients). Sex composition was assessed as a ratio of females to males in the total catch for each expedition in each region (west and east Australia), with 1 being all females and 0 all males. Where sex was not recorded (35 instances), or recorded as hermaphrodite (1 instance), a sex composition of 0.5 was assigned (equally male or female). Reproductive condition was calculated as the proportion of pregnant or lactating whales in the total catch for each expedition in each region. Maturity (age) was calculated based on length measurements, where males were classified as mature above 38 feet (11.6 m) in length and females above 39.5 feet (12.0 m) (Chittleborough [1965](#page-6-0)). For those instances where sex was not recorded, a value of 38.75 feet (11.8 m) was used to define maturity. The proportion of mature to immature whales was calculated for each expedition in each year. Position of catch for each expedition was calculated as the mean latitude recorded for catches. Time of year of catch was calculated as the median day of year of whales caught in each expedition for each region, to account for any skew in the distribution of catch dates during the expedition. As expedition 4620 in 1951 only recorded eight catch dates out of 574 catches, the day of year of catch was estimated as the mid-point between the expedition start and end date.

Weight and maturity showed a strong correlation with a coefficient of 0.96, so only weight was used in subsequent regression modelling. A multiple regression was fit between mean oil yield per humpback whale per year and catch

variables (mean weight, sex ratio, reproductive condition, position, and median catch day) per year in each region. Mean weight, sex ratio, and catch day were significant factors influencing yearly oil yield ($p < 0.001$, $R^2 = 0.61$, $n = 55$). Remaining variables had little additional explanatory power (reproductive condition $p = 0.36$; position $p = 0.11$) so were excluded from the model. The residuals from the multiple regression relationship (yield $=$ weight $+$ sex ratio $+$ catch day) were used as an indicator of relative humpback whale body condition for a given year: positive residuals indicate years with more 'fat' whales (having higher blubber content), whilst negative residuals indicate years with 'thinner' whales. Residuals were converted to a percentage to control for body size: a $+1$ ton residual for a small whale with a standard yield of, for example, 5 tons equates to a $+20\%$ body condition indicator whereas it equates to $+12.5$ % for a larger whale with a standard yield of, for example, 8 tons.

Krill abundance versus sea ice extent

Data on the abundance of krill in the Southern Ocean coinciding with the whaling era (pre-1963) are scarce, making direct associations between whale body condition and food (krill) availability difficult to investigate. Krill abundance is, however, influenced by sea ice extent (SIE). The relationship between krill abundance and SIE in our study area was established for years post-1979 using standardised krill density measurements obtained from KRILLBASE (Atkinson et al. [2008](#page-6-0)). KRILLBASE is a compilation of data from krill surveys conducted in the Southern Ocean between 1926 and 2003 that has been standardised to account for differences in sampling techniques and catch-ability (Atkinson et al. [2008](#page-6-0)). KRILLBASE therefore provides a uniquely large dataset for the exploration of large-scale spatial and temporal trends and is the only database of krill densities available that spans several years across the east Antarctic region. Data from KRILLBASE were split into 10° sectors around the Southern Ocean. The annual mean krill densities $(no.m^{-2})$ over the austral spring to autumn seasons (between October of previous year and April of the present year) across each of the 10° sectors comprising the foraging zones (AusW: 70° –130 $^{\circ}$ E, AusE: 130E–170W (Donovan [1991](#page-7-0)) were calculated from standardised values of krill density (Table S3). Density is a traditionally used metric to look at population variation in time and/or space (Gaston and McArdle [1994](#page-7-0); Brown et al. [1995](#page-6-0)) and often used to measure variability in krill populations (Pauly et al. [2000;](#page-7-0) Atkinson et al. [2004;](#page-6-0) Flores et al. [2012b](#page-7-0); Fielding et al. [2014](#page-7-0)). Sectors with fewer than five observations were removed from the analysis to reduce potential error from under-sampling. The total number of krill density samples, mean latitude and longitude of

sampling sites, mean net depth, mean Julian day, and mean day or night measurement were also determined for each sector across each year to test for sampling biases. Entries in the database were already categorised as occurring at day (designated one) or night (designated zero). The mean of these day or night values was therefore used as an indicator of whether sectoral means of krill densities were skewed towards day sampling or night sampling.

In the AusE foraging region, there were a total of 16 sector measurements for mean krill density value post-1979, with 65 % (nine of 16 sectors) of these values recorded as zero. We therefore eliminated the AusE region from further analysis, as the zero-inflated, low sample size data were insufficient for robust analysis. In the AusW foraging region, there were 20 sector measurements with no values recorded as zero.

For each sector in the AusW foraging region, we calculated the mean maximum winter SIE between 1979 and 2007 (Raymond [2009\)](#page-7-0) and sea ice duration between 1979 and 2008. To calculate sea ice duration, daily sea ice concentration data were obtained from the National Snow and Ice Data Centre (NSIDC) (Cavalieri et al. [1996\)](#page-6-0) that provides data from October 1978 at a spatial resolution of 25×25 km grid cell. Prior to 8 July 1987, data were generally recorded every other day, with two instances of both one- and three-day gaps between data. From 8 July 1987 onwards, data were recorded every day, with five instances of same day recording, six instances of 2-day gaps between data, and a longer period of 42 days without records between 30 November 1987 and 11 January 1988. Cells with more than 15 % of ocean area covered by sea ice were, by convention, classified as 'ice-covered', a threshold used by the NSIDC (e.g. Stroeve et al. [2007](#page-7-0)). The total area of ice-covered cells for each 10° sector in the 70° -130E region was calculated, resulting in a time series of sea ice advance and retreat in each sector. Data were checked for missing records in the coverage of our study region but none were found. The trend of ice advance/ retreat for each day was calculated as the gradient of ice area change over 7 days, i.e. including three days before and after each day. By taking this seven-day gradient, irregular daily fluctuations could be eliminated and a general trend in ice growth and decay obtained. Sea ice duration is the time between when the ice starts advancing to when it stops retreating. We defined the start of ice advance as the point at which the gradient of change was consecutively positive for at least 5 days, signalling the continual growth of ice (Massom et al. [2013\)](#page-7-0). Likewise, the end of the sea ice retreat was defined as the last point in which the gradient was consecutively negative for 5 days, signalling the end of continual retreat. Sea ice duration was thus the number of days between the start of sea ice advance and the end of sea ice retreat.

Interannual variability in krill density in the AusW foraging region ($n = 20$ sectors) was explored in a multiple linear regression framework with respect to winter SIE and duration from the previous year. Sampling variables (total number of krill density samples, mean latitude and longitude of samples, mean net depth, mean Julian day, and mean day or night measurement) were also included in the multiple linear regression framework to test for sampling bias.

Body condition versus sea ice extent

Empirical SIE data do not exist for the whaling period, between 1947 and 1963. Historical sea ice edge locations have been estimated through direct observations and the use of whaling records (de la Mare [2008](#page-6-0)). However, whaling data are limited to October through April, excluding winter months, during which whaling in the Southern Ocean ceased. As krill abundance variation is thought principally to be connected with winter sea ice dynamics (e.g. Loeb et al. [1997](#page-7-0); Atkinson et al. [2004](#page-6-0)), these summer-only whaling-derived ice edge data were not appropriate for our analysis. Instead, we hindcast winter SIE from sea surface temperature (SST) data, as SIE has been found to be significantly correlated with temperature (Fraser et al. [1992;](#page-7-0) Loeb et al. [1997](#page-7-0)). We split the Southern Ocean into 10° sectors to correspond with the krill data and regressed mean maximum winter SIE across longitudes between 1979 and 2007 for each sector on mean winter (June–August) sea surface temperature for the Southern Ocean region (south of 60° S) using historical SST data reconstructed by the National Oceanic and Atmospheric Administration (NOAA [2007\)](#page-7-0). This relationship enabled us to hindcast winter SIE in each 10° sector of the AusW foraging region to obtain yearly mean winter SIE for each sector. To assess the accuracy of our hindcast SIE data, we compared them to historical sea ice edge positions derived from direct observations and whaling records (de la Mare [2008](#page-6-0)). We calculated the mean ice edge latitude across the west Australian whale foraging area $(70^{\circ}-130^{\circ}E)$ for each available season (October–April), as estimated from whaling records (de la Mare [1999\)](#page-6-0). The resulting seasons spanned from 1931/1932–1939/1940, 1946/1947–1958/ 1959, and 1971/1972–1986/1987.

The relationship between whale body condition and krill density for the AusW foraging region during the whaling era for which oil data were available (1947–1963) was explored using the hindcasted winter SIE as a surrogate for krill density (see Table S3 for summary data). This analysis assumes west Australian humpback whales largely forage in the $70-130$ ^oE area. Whilst a small level of interchange has been found between east and west Australian humpback whale populations (Chittleborough [1965;](#page-6-0) Dawbin

[1966;](#page-6-0) Noad et al. [2000](#page-7-0)), present evidence suggests a relatively low presence of west Australian whales in the neighbouring east Australian foraging region (130°E– 170° W) (Constantine et al. 2014). As sea ice provides an overwintering habitat for krill, there could be a lag between winter SIE and krill abundance, under the hypothesis that spring recruitment may largely be influenced by sea ice extent of the previous winter. Also, as animals experience carry-over effects between seasons that can impact fitness (Harrison et al. [2011](#page-7-0)), body condition in 1 year could be a cumulative effect of sequential high or low food availability. We therefore regressed body condition against winter SIE for the previous year and 2-, 3-, and 4-year running means.

Results

Mean oil extracted per whale was significantly ($R^2 = 0.61$; $F_{3,51} = 26.96; \, p < 0.001$ correlated with the mean weight, sex ratio, and median day of catch of humpback whales caught off Australia, with catches comprising larger whales, a larger proportion of females, and caught earlier in the year containing more oil. Residuals indicate that mean oil yield per whale ranged from -48 to 25 % of expected yield.

In the west Australian humpback whale foraging region, the annual mean density of krill $(no.m^{-2})$ was correlated significantly with the maximum recorded winter SIE of the previous year (Fig. [1](#page-5-0)a; $R^2 = 0.34$; $p = 0.0066$). Longitude and day or night sampling also influenced krill density; however, the influence of these variables was much weaker than SIE (longitude: $R^2 = 0.25$, $p = 0.02$; day or night: $R^2 = 0.20$, $p = 0.50$, and there were no improvements over the just-SIE model with the addition of these variables.

Humpback whale body condition in west Australia catches was significantly correlated with hindcast winter SIE in their Southern Ocean foraging area $(70^{\circ}-130^{\circ}E)$ when considering winter SIE averaged over the previous 2 years (Fig. [1c](#page-5-0); $R^2 = 0.15$, $p = 0.021$) and 3 years $(R^{2} = 0.14, p = 0.025)$, with higher oil yields in years with greater winter SIE in previous years. This relationship was borderline insignificant when considering sea ice extent only from the previous year ($R^2 = 0.11$, $p = 0.052$).

There was a significant positive correlation between the mean hindcast winter SIE from our analysis and the mean ice edge latitude of the preceding spring–autumn season derived by de la Mare [\(2008](#page-6-0)) from historical whaling records across 70°–130°E (Fig. [2](#page-5-0); $R^2 = 0.29$, $p < 0.0001$), so that a reduced sea ice retreat during summer is followed by a greater maximum sea ice extent in winter across this region. The fluctuation in sea ice, as captured by our hindcast winter SIE data, therefore corresponds well to other estimates of sea ice conditions in the west Australian humpback whale foraging area for seasons spanning between 1931/1932 and 1986/1987.

Temperature is a reliable predictor of winter sea ice extent (Fig. [1b](#page-5-0)), and krill abundance is predicted well by winter sea ice extent. It is therefore feasible to make inferences about variability in whale condition as driven by availability of their main food, krill, using sea ice as a proxy for krill abundance (Fig. [3](#page-5-0)).

Discussion

Humpback body condition for whales caught in the west Australian region was significantly correlated with hindcast winter SIE in their Southern Ocean foraging area, suggesting that changing environmental conditions in their foraging area can impact body condition. Within this same foraging area, krill abundance was significantly correlated with observed winter SIE. We therefore propose that the correlation between whale condition and SIE is mediated by fluctuations in abundance of the whales' key food, krill. This temporal relationship between krill abundance and sea ice, although based on smaller samples sizes, is consistent with the large-scale link between SIE and krill abundance exposed for the Atlantic region using KRILLBASE (Atkinson et al. [2004](#page-6-0)). The krill–SIE relationship is also consistent with the concept that sea ice and associated biota provide a source of food and nursery habitat for krill (Nicol et al. [2000](#page-7-0); O'Brien et al. [2011](#page-7-0)), as spatially evident at a broader scale in the west Australian whale foraging region, where krill are more abundant in regions of greater ice cover (Nicol et al. [2000](#page-7-0)). Some regions in the Southern Ocean have greater krill abundance than others despite comparatively low sea ice extent, such as around the Western Antarctic Peninsula (Atkinson et al. [2008](#page-6-0)). Yet, even within these regions, periods of reduced krill abundance are related to periods of reduced sea ice (Atkinson et al. [2004;](#page-6-0) Flores et al. [2012a](#page-7-0)). The relationship between krill and sea ice therefore seems to be driving the relative, rather than absolute, abundance of krill within a region; irrespective of the regional mean krill abundance, when ice is relatively low, krill abundance is regionally low and vice versa.

Our model linking whale body condition to krill abundance, via sea ice extent, exposes the influence of largescale environmental fluctuations on the annual condition of humpback whales. We recognise that factors additional to those considered here contribute to variability in the body condition of humpback whales. For example, sizeable reductions to baleen whale numbers during the whaling era would potentially change the level of inter- and

Fig. 1 a Significant relationship between krill abundance in the 70°– 130E Southern Ocean sector and regional winter sea ice extent (SIE) of the previous year ($R^2 = 0.34$, $F_{1,18} = 9.41$, $p = 0.0066$, $n = 20$, spanning 1981–1996, totalling 611 station measurements). b Highly significant relationship between winter SIE and winter sea surface temperature (June–August) ($R^2 = 0.45$, $F_{1,27} = 21.8$, $p < 0.0001$, $n = 29$, data between 1979 and 2007). c Significant relationship between body condition of whales killed in AusW and the two-year running mean of winter SIE in their foraging region over the previous two years ($R^2 = 0.15, F_{1,33} = 5.92, p = 0.021, n = 35$). Solid circles denote present-day SIE measurements (a, b), open circles represent hindcast SIE values (c). Dashed lines represent the 95 % confidence intervals

intraspecific food competition over time, influencing per capita prey intake: theoretically, the decrease in whale numbers during the whaling era would have resulted in

Fig. 2 Significant relationship between mean hindcast maximum winter sea ice extent (SIE) and mean approximate ice edge latitude of the previous spring to autumn season ($R^2 = 0.29$, $F_{1,35} = 14.14$, $p < 0.0001$, $n = 37$), across the west Australian humpback whale foraging area (70°-130°E). Dashed lines represent the 95 % confidence intervals

Fig. 3 A schematic illustrating the temporal availability of data. Arrows show the relationships investigated, with corresponding linear regression p values

more krill per capita, assuming that competition for prey existed prior to whaling when whale numbers were high. Whilst changes to intraspecific competition during our study period (1947–1963) may factor into determining average body condition, the relevance of interspecific competition is debatable, as competition between foraging baleen whale species is thought to be unlikely (Clapham and Brownell [1996](#page-6-0); Friedlaender et al. [2006](#page-7-0)). Expanding our model to consider further ecosystem influencers would benefit understanding of those factors contributing to changes in whale body condition; however, our simple model of trophic links isolates and quantifies the significant link between body condition, krill, and sea ice for humpback whales and provides a basis for further development.

A large component of the observed variation in recorded oil yield in whaling expeditions was accounted for by differences in composition of landed catch, namely mean weight, the proportion of females in the catch, and the day of year of catch. These variables were amongst those highlighted by Chittleborough (1965) as influencing oil yield. We propose that the remaining variation in annual body condition is, in part, influenced by food availability. The significant relationship between sea ice extent and krill abundance suggests that interannual fluctuations in sea ice extent during the whaling era gave rise to changes in krill abundance, causing variations in feeding conditions and thus oil yield. However, as correlation does not necessarily reflect causation, there may be other explanations for the relationship we found between body condition and hindcast sea ice data. Both hindcast sea ice extent and whale condition show an increasing trend over the time period studied here (1947–1963). If body condition increased over time due to a factor or factors independent of sea ice, such as changes in intraspecific competition or oil extraction efficiencies (which we assumed constant in our analysis), then the correlation between body condition and sea ice could be incidental. Alternatively, the relationship between body condition and sea ice may be related to migration timing. The triggers of migration timing in baleen whales are presently unknown (Lawler et al. [2007](#page-7-0); Visser et al. [2011;](#page-7-0) Santora et al. [2014](#page-7-0)), but if external cues are involved, such as sea surface temperature or prey availability, this may influence body condition: earlier cues mean a shorter foraging period and potentially poorer body condition. Finally, sea ice dynamics may change feeding conditions in other ways than just krill abundance. For example, humpback whales may be better able to forage in loose ice than tightly packed ice, a variable we did not account for in this study. However, evidence that krill abundance links to sea ice (Siegel and Loeb [1995;](#page-7-0) Loeb et al. [1997;](#page-7-0) Nicol et al. [2000;](#page-7-0) Brierley et al. 2002; Atkinson et al. 2004) and that baleen whale body condition links to prey availability (Lockyer [1986;](#page-7-0) Williams et al. [2013\)](#page-7-0) lend strong support to the hypothesis that changes in krill abundance is a plausible explanation for the relationship between body condition and sea ice found here.

This research suggests that in the Southern Ocean foraging grounds of humpback whales that breed off western Australia ($70^{\circ}-130^{\circ}$ E), krill abundance fluctuates with ice extent, as has been demonstrated for other Southern Ocean regions (Nicol et al. [2000;](#page-7-0) Atkinson et al. 2004). Whilst there is a level of uncertainty in our findings due to limitations in the data available for this large-scale trophic analysis, based on the best evidence available, our study indicates a correlative link between humpback whale condition and krill abundance. Whilst it is not surprising that the condition of a predator is linked to abundance of its prey, establishing this link enables predictions to be made and scenarios explored. If ice extent declines in the future,

as predicted under some climate change scenarios, whale food will decline and, in turn, energy acquisition will be hindered. After a sequence of reduced ice/low food years, whales will be migrating and breeding on reduced energy input, potentially impacting their ability to successfully complete the breeding cycle. For example, changes in food availability in the Southern Ocean could be a factor to explain the malnourished condition of whales recently stranded along the west Australian coast (Holyoake et al. [2012](#page-7-0)). If winter SIE in the west Australian foraging region declines in response to a changing climate, we may see future deterioration in whale body condition, fitness, and ultimately, reproductive success.

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