Signals from the South; Humpback Whales Carry Messages of Antarctic Sea-ice Ecosystem Variability

Running head: *Humpback Whales as Antarctic Sentinels*

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Abstract

Southern hemisphere humpback whales (*Megaptera novaeangliae*) rely on summer prey abundance of Antarctic krill (*Euphausia superba*) to fuel one of the longest-known mammalian migration on the planet. It is hypothesised that this species, already adapted to endure metabolic extremes, will be one of the first Antarctic consumers to show measurable physiological change in response to fluctuating prey availability in a changing climate; and as such, a powerful sentinel candidate for the Antarctic sea-ice ecosystem. Here we targeted the sentinel parameters of humpback whale adiposity and diet, using novel, as well as established, chemical and biochemical markers, and assembled a time trend spanning eight years. We show the synchronous, inter-annual oscillation of two measures of humpback whale adiposity with Southern Ocean environmental variables and climate indices. Further, bulk stable isotope signatures provide clear indication of dietary compensation strategies, or a lower trophic level isotopic change, following years indicated as leaner years for the whales.

The observed synchronicity of humpback whale adiposity and dietary markers, with climate patterns in the Southern Ocean, lend strength to the role of humpback whales as powerful Antarctic sea-ice ecosystem sentinels. The work carries significant potential to reform current ecosystem surveillance in the Antarctic region.

Introduction

Southern hemisphere (SH) humpback whales (*Megaptera novaeangliae*) undertake one of the longest migrations known for any mammal on the planet (Rasmussen et al., 2007). These migrations between Antarctic feeding grounds and equatorial breeding grounds are associated with voluntary fasting and represent a period of intensive energy utilisation. Males engage in competitive breeding behaviour, whilst migrating females are predominantly pregnant and/or nursing young calves. This extreme migratory behaviour allows these populations to exploit the dense annual swarms of Antarctic krill (*Euphausia superba*) that form in the Southern Ocean through summer months, whilst also satisfying the physiological needs of newborn calves, born without a substantial blubber layer and therefore the ability to adequately thermo-regulate in polar waters. Lunge feeding in rorqual whales (Balaenopteridae) has been posed as only being energetically viable at certain prey densities (Goldbogen et al., 2011), pointing to the co-evolution of SH populations with Antarctic krill through iron feed-back loops in the iron-limited Southern Ocean ecosystem (Nicol et al., 2010; Smetacek, Assmy, & Henjes, 2004). Recently, this long-assumed principal contribution of Antarctic krill to the energetic budget of SH humpback whales has been evidenced for the east coast of Australia migrating breeding stock (E1, as designated by the International Whaling Commission) through a variety of biochemical investigations (Eisenmann et al., 2016; Eisenmann et al., 2017; Waugh, Nichols, Noad, & Bengtson Nash, 2012).

Antarctic krill undergo 12 larval stages before assuming their pelagic adult life-stage (George, 1982; Poulsen, Kawaguchi, Kukkonen, Leppanen, & Bengtson Nash, 2011). The first three of these are non-feeding stages that undertake the larval ascent to reach the underside of the sea-ice, where they commence feeding upon ice-algae associated microbes to fuel further development (Nicol, 2006). This species therefore relies on the sea-ice ecosystem as a nursery ground, with the implication that larval recruitment is often reported as being closely tied to sea-ice extent e.g. (Loeb et al., 1997). Under this hypothesis, a decrease in suitable sea-ice habitat would result in reduced recruitment success, which in turn translates to reduced prey availability for baleen whales and other higher order Antarctic consumers, in subsequent years (Flores et al., 2012). More recently, the proximate role of sea-ice extent in cyclical krill biomass fluctuations was found to be secondary to inter-cohort competition for food resources (Ryabov et al., 2017). Nonetheless, climatic conditions defined by cryosphere loss and changing ocean pH are predicted to have a devastating impact on this sympagic species, with ocean acidification forecasted to result in a complete collapse of Antarctic krill populations by 2300 if current CO₂ emissions are left unmitigated, (Kawaguchi et al., 2013).

The pivotal role of Antarctic krill in the Antarctic sea-ice ecosystem forewarns that even a marginal decrease in krill stocks could produce ripple effects at higher trophic levels (Fountain et al., 2012; Gross, 2005). Direct monitoring of Antarctic krill biomass is, however, complicated by the cost and logistics of broad-scale Antarctic field surveys and the limitations of accurately monitoring a swarming species (patched abundance). An alternative approach for estimating krill biomass is to focus on the integrated response that changed krill availability might elicit in a dependent, higher trophic level species. The flat structure of the Antarctic sea-ice ecosystem, and the highly specialised krill diets of many Antarctic consumers, makes a top-down biomonitoring approach particularly suitable. The concept of

using marine predators as “sentinel organisms” or “messengers” of oceanic ecosystem health relies on the identification of an indicator species in which defined and measurable parameters (sentinel parameters) serve as reliable and cost-effective indicators of environmental change.

The Convention for the Conservation of Antarctic Marine Living Resources’ (CCAMLR) Ecosystem Monitoring Programme employs seals, penguins, and other sea-birds as ecological sentinel species (CCAMLR, 2004). The absence of easily quantifiable, validated sentinel parameters, have to date prevented the inclusion of baleen whales into the Programme.

However, a number of characteristics render, specifically humpback whales, a particularly attractive Antarctic sentinels. Their reliance on Antarctic krill for the bulk of their annual energy budget dramatically simplifies food web forensic investigations. Secondly, Adaptive obesity has enabled these populations to operate at metabolic extremes. These metabolic adaptations, combined with a reliance on a single prey species (Laird et al. 2008) has, however, also placed these populations in a precarious trophic position. In response to unfavourable feeding conditions, it is expected that this highly mobile species will avoid the threat of starvation through dietary diversification. As such, humpback whale homeostasis is likely to be highly responsive to environmental oscillations. Finally, the extensive migrations of SH populations facilitate sampling at temperate latitudes. Temperate sampling removes the logistical and financial challenges associated with Antarctic travel, which in turn enhances the feasibility of realising co-ordinated, long-term, circum-polar surveillance.

Recently, two novel markers of “adiposity”, or lipid reserves, were developed for humpback whales and incorporated into the Southern Ocean Persistent Organic Pollutant Program’s (SOPOPP) long-term monitoring of the E1 breeding population. This monitoring also included the sentinel parameter of “diet”, evaluated by traditional carbon and nitrogen Bulk Stable Isotope (BSI) measures. The first adiposity marker, the adipocyte index (AI)

(Castrillon, Huston, & Bengtson Nash, 2017), is based upon the principle that adipocyte number is set early in mammalian development and remains constant throughout adulthood and fluctuating weight (Faust, Johnson, Stern, & Hirsch, 1978). Any change in lipid stores is therefore a result of a change in the volume of existing adipocytes, rather than adipogenesis. The AI is a histological measure defined as the ratio of inter-vacuole area to adipocyte area. A larger adipocyte area (denominator) yields a smaller AI. Conversely, a higher AI suggests an individual with lower lipid reserves.

The second measure of adiposity incorporated into long term monitoring, is the novel use of lipophilic Persistent Organic Pollutant (POP) burdens in the outer blubber layer of migrating adult male individuals. The toxicokinetics of lipophilic POPs are governed by lipid dynamics (Yordy et al., 2010), and tissue POP partitioning is strongly impacted during times of negative energy balance. Recent research within the author team demonstrated that just a few months of the seasonal fast can result in up to a 500-fold increase in average population outer blubber POP concentration (Bengtson Nash, Waugh, & Schlabach, 2013). The apparent increase in chemical burden with weight loss arises as rapid lipid depletion is not accompanied by corresponding chemical metabolism and elimination (Chevrier et al., 2000; Imbeault et al., 2002; Pelletier, Doucet, Imbeault, & Tremblay, 2002; Tremblay, Pelletier, Doucet, & Imbeault, 2004). Rather, chemicals are merely mobilised and seek dynamic equilibrium among the body's remaining lipid stores (Cropp, Bengtson Nash, & Hawker, 2014). As the body's lipid stores are diminished, each remaining lipid reservoir receives additional input of POPs mobilised from depleted lipid stores. The outer blubber layer of cetaceans performs a number of other physiological functions, aside from lipid storage (e.g. thermoregulation and buoyancy). As such, lipids associated with this layer are to a degree conserved as excessive lipid depletion would compromise these ancillary roles and individual survival. Consequently, as overall lipid depletion occurs, the outer blubber layer starts to

represent an increasing proportion of the individual's remaining lipid stores and thus accumulates proportionately greater pollutant loads (Figure 1). Observation of the responsiveness of outer blubber humpback whale POP burdens to migration-associated weight-loss led authors to postulate that longitudinal monitoring of population outer blubber POP burdens, at set time-points, may provide an indication of this population's inter-annual adiposity (Bengtson Nash, 2011; Bengtson Nash et al., 2013).

In this study, we investigated the inter-annual variability of humpback whale adiposity and diet in relation to climatic conditions in their corresponding Antarctic feeding grounds during the summer preceding winter sampling. The sampled breeding population of humpback whales has been associated with the Antarctic feeding areas IV (70-130oE) and V (130oE-170oW) as classified by the International Whaling Commission (Chittleborough (1965); Schmitt et al. (2014) (Figure S1)). These areas fall within the Food and Agricultural Organization (FAO) of the United Nations sub-areas 58.4.1 and 88.1 respectively. The responsiveness of chosen sentinel parameters to climate variability is discussed in the context of the application of SH populations as powerful new sentinels of the Antarctic sea-ice ecosystem, and the need for continued efforts to elucidate proximate environmental drivers.

Materials and Methods

Sample collection

Skin and blubber biopsies were collected from free swimming individuals in Moreton Bay Marine Park, North Stradbroke Island, south-east Queensland, Australia (approximately 27° 26 S, 153° 34 E). Individuals moving along this migration path are representative of the International Whaling Commission categorised breeding stock, E1. Remote biopsies were

collected from free-swimming animals as described in detail elsewhere (Waugh, Huston, Noad, & Bengtson Nash, 2011). Bulk stable isotope data was derived from both northward migrating cohorts, traveling to their equatorial breeding grounds (sampled during the last week of June/first week of July), as well as during the southward leg of the migration journey as whales were returning to Antarctic feeding grounds (sampled last week of September/first week of October). Adiposity markers (AI and POP) analysis was performed only on samples derived from the southward migration. Shallow biopsies (4 cm) were obtained from the dorsal region of the whale, slightly posterior and ventral to the dorsal fin, as advocated by (Lambertsen, Baker, Weinrich, & Modi, 1994). Upon collection, blubber was separated from the skin and stored at -20° C until time of analysis. Animal work was conducted under the approvals of the University of Queensland and Griffith University Animal Research Ethics Committees (Approval Numbers NRCET/309/08/SBN, NRCET/273/07/SBN, ENTOX/207/09/SBN, ENV/17/10/AEC).

Lipid Determination

Approximately 30 mg of each blubber sample was used for lipid analysis. Individual samples were extracted using a modified Bligh and Dyer methanol-chloroform-water extraction method as described in detail elsewhere (Bligh & Dyer, 1959; Waugh, Nichols, Noad & Bengtson Nash (2012); Waugh, Nichols, Schlabach, Noad, & Bengtson Nash, (2014); Bengtson Nash, Schlabach, & Nichols, 2014). Lipid class profiles were determined by an Iatroscan Mark V TH10 thin layer chromatograph coupled with a flame ionization detector (Volkman & Nichols, 1991). The total blubber percent lipid was calculated by summing the individual lipid class percentages.

Chemical Analyses

Only organochlorine data from adult males, as determined through genetic sexing (Palsbøll, Vadder, Bakke, & El-Gewely, 1992), was used for this study to avoid the confounding factors associated with pregnancy and lactation in females.

All samples were analysed for thirty-two polychlorinated biphenyls (PCBs) (IUPAC numbers -18, 28, 31, 33, 37, 47, 52, 66, 74, 99, 101, 105, 114, 118, 122, 123, 128, 138, 141, 149, 153, 156, 157, 167, 170, 180, 183, 187, 189, 194, 206 and 209), and the organochlorine pesticides; hexachlorobenzene (HCB) and the dichlorodiphenyltrichloroethane (DDT) group (o,p'-DDE, p,p'-DDE, o,p'-DDD, p,p'-DDD, o,p'-DDT, p,p'-DDT). Contaminant values are reported on a lipid weight basis (l.w.) in nanograms per gram (ng/g).

The blubber extraction, clean-up, analysis and quality assurance procedures are published elsewhere in full (Bengtson Nash, Poulsen, Kawaguchi, Vetter, & Schlabach, 2008). In brief, 0.3 g of blubber was homogenised with sodium sulphate and cold column extracted with cyclohexane/ethyl acetate (1:1). The extract underwent further clean-up by gel permeation chromatography, alumina and silica columns before injection on high-resolution gas chromatography/high-resolution mass spectrometry (HRGC/HRMS) using a Hewlett-Packard 5890II (1990–2003) or 6890N (2003–2006) gas chromatograph coupled to an AutoSpec mass spectrometer (Micromass Waters, Manchester UK). ¹³C-labelled isomers were used as internal standard for each group. Chemical data for individual animals included in the current investigations are summarised in Table S1.

Histology and Image Analysis

The Adipocyte Index was derived as described elsewhere (Castrillon, Huston, & Bengtson Nash, 2017). Five to twenty-seven animals per sampling period were used for AI metrics. As there were no significant differences observed between genders (Table S1), both males and

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females were used for AI calculations. In brief, c.a. 100 mg blubber tissue was embedded in paraffin and treated with increasing concentrations of alcohol (70, 80, 95, and 100%), cleared with xylene and then penetrated with 100% paraffin. The paraffin blocks were sectioned at 5 μm using a rotary microtome and mounted on glass microscope slides. The slides were subsequently stained with hematoxylin and eosin (H&E). Slides were viewed with an Olympus BX41 microscope. Digital images were taken with a QImaging MicroPublisher 3.3RTV camera, using QCapture Pro software. A representative area of the slide was captured at 10X magnification and analysed using the threshold tool in ImageJ (Abràmoff, Magalhães, & Ram, 2004), a public domain, Java-based image processing program. From a grey scale, thresholding was used to create binary images (Shapiro, Stockman, & C., 2002) allocating white to lipid-filled adipocyte area and black to inter-vacuolar space. The AI is defined as the ratio of inter-vacuolar area to adipocyte area within the image. This approach assumes that, the larger the adipocyte area, the lower the inter-vacuolar space. In this manner, the higher the AI, the lower the energy reserves of the individual.

Bulk Stable Isotope Analysis

Between ten and sixty-two animals per sampling period were used for BSI Analysis. No differences were observed between genders (Table S1), hence both male and female individuals were included in BSI calculations. Protocols for BSI analysis are published elsewhere (Eisenmann et al., 2016). In brief, blubber samples were extracted overnight in a 2:1 chloroform:methanol solution to remove any oils and lipids (Caraveo-Patiño, Hobson, & Soto, 2007; Hobson & Schell, 1998) and oven-dried at 58°C. 1-2 mg of clean sample material were weighed into tin capsules for isotope analysis (Caraveo-Patiño et al., 2007).

All stable isotope abundances are calculated in ‰ using the following formula:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000 \quad (1)$$

where $X = {}^{13}\text{C}$ or ${}^{15}\text{N}$, and $R =$ the respective ratio ${}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. The international reference standards for carbon and nitrogen are respectively Vienna Pee Dee Belemnite and N_2 in air. International standards IAEA-CH₆ for carbon and IAEA N1 for nitrogen were used for calibration of laboratory standards KHP and $(\text{NH}_4)_2\text{SO}_4$ for sample runs. The preparation system was a Europa EA-GSL interfaced to a SERCON Hydra 20-20 isotope ratio mass-spectrometer (IRMS). Based on analysis of replicate standards, the standard deviation for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively averaged 0.1‰ and 0.15‰.

Source prediction and trophic fractionation

BSI values were compared to literature-derived estimates as per (Eisenmann et al., 2016), to compare against predicted values for a consumer feeding exclusively on a low Antarctic trophic level prey item, such as Antarctic krill. Literature-derived estimates were adjusted to account for trophic fractionation (TF; predicted range = TF + prey value $\pm$ standard deviation). We included the standard deviation of all values in the defined prey isotope ranges to account for possible sub-regional variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Environmental Data

Historical Sea-ice concentration data were obtained from the National Snow and Ice Data Centre (NSIDC) <https://nsidc.org/> (Cavalieri, Parkinson, Gloersen, & Zwally, 1996). Average annual summer sea-ice concentrations were calculated from daily measurements between 1st November and the 30th April each year. Historical Southern Annular Mode (SAM) data was obtained from the British Antarctic Survey website <http://www.nerc-bas.ac.uk/icd/gjma/sam.html> whilst El-Niño Southern Oscillation (ENSO) data was obtained from the National Ocean and Atmospheric Administration (NOAA) http://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/SOI/. Chlorophyll *a* (CHL) data was

obtained by remote sensing. The mean monthly CHL concentration product based on the combined record of Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and Moderate Resolution Imaging Spectroradiometer (MODIS) satellite data was obtained from the National Aeronautics and Space Administration (NASA) hosted Oceancolor website. The geographical area constrained for CHL and Sea-ice concentration data corresponded to the IWC feeding area V between 130°E and 170°W, south of 60°S.

Statistical Analysis

Time trends of blubber POP concentrations were derived using statistical Plot and Image Analysis (PIA), based on the work of Nicholson and Fryer (Nicholson & Fryer, 1991) and adopted by the Arctic Monitoring and Assessment Program (AMAP).

The differences between genders for BSI and AI data was assessed by student-t test calculations.

Pearson product moment correlation coefficients were calculated to explore the strength of the association between population adiposity (AI), and selected environmental variables, namely; summer sea-ice concentration, ENSO index and CHL.

Results

Adiposity Markers

When longitudinal POP monitoring records were constrained by the variables of; sampled migration time-point (population targeted within the same 2 weeks of consecutive calendar years); gender (males), and age group (adults), four years of comparable POP data was available, namely; 2008, 2009, 2011 and 2013 (Table S1). Within this record, 2011 appeared as a spike in POP contaminant burdens, a trend that was consistent across compounds/compound groups, of which hexachlorobenzene (HCB), polychlorinated biphenyl

(PCB) congeners and dichlorodiphenyltrichloroethane (DDT) isomers were the dominant categories, and thus the compounds included in this study (Figure 2).

Similarly, when the AI of animals sampled in the respective years were compared, the highest AI values (i.e. the thinnest cohort) were observed in 2011 (Figure 2; Table S2).

Dietary Tracers – Bulk Stable Isotope Analysis

In order to evaluate the two dimensional ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) positioning of BSI profiles, the grey shaded areas of Figure 3 depict the isotopic range where values are expected to fall within, if an individual is feeding exclusively on a first order Antarctic consumer, such as Antarctic krill. In the earlier sampling years; 2008 (with the exception of a few animals that fell below this space), 2009, as well as 2011, which represented the lean year for the whales, both nitrogen and carbon isotopic signals indicate adherence to the expected low trophic level Antarctic signal. In 2013 and 2014, however, the population shows greater heterogeneity in both trophic level ($\delta^{15}\text{N}$) and food web origin as indicated by $\delta^{13}\text{C}$. This heterogeneity in feeding signal returns to a tighter clustering around the expected Antarctic low trophic signal again in 2015 (Figure 3; Table S3).

Antarctic Climate Indicators

Sea-Ice Concentration Sea ice is expected to be the dominant integrated driver of Antarctic ecosystem productivity as it is governed by temperature, winds and ocean circulation (A. G. Fountain et al., 2016). When sea-ice concentration records from Antarctic feeding Area V were scrutinized, a negative relationship ($r=-0.85$; $p=0.068$) between sea-ice concentration in the summer preceding sampling, and adiposity markers was observed (Figure 4; Table S3).

El-Niño Southern Oscillation and Southern Annular Mode The leading mode of atmospheric variability in Antarctica is the Southern Annular Mode (SAM) (Thompson & Wallace, 2000) which describes the north to south movement of the westerly wind belt that surrounds the Antarctic continent. Similarly, the ENSO index describes atmospheric pressure and sea surface temperature differences between the eastern and western Pacific. Both empirical functions move between positive and negative phases. A positive SAM is associated with a higher pressure blanket over the mid-latitudes and lower pressures covering high latitudes (Thompson & Wallace, 2000). The opposite is true for negative SAM. Similarly, positive ENSO events, or La- Niña events, describe a relative warming of sea surface temperatures in the western Pacific combined with increasing wind pressures in the eastern Pacific. The counterpart of La Niña events are the negative El-Niño phases.

Investigation of the inter-annual climate indices over the monitoring period revealed that both SAM and ENSO were in positive modes in the summer preceding 2011 sampling (Figure 5; Table S4), with the La Niña event of 2010/2011 representing one of the strongest La Niña events on record. ENSO indices were found to be positively correlated with population adiposity ($r=0.70$; $p=0.188$).

Chlorophyll-*a* When the average summer primary productivity between 2008 and 2015, as indicated by satellite CHL data from feeding Area V, was examined, the austral 2010/2011 summer is depicted by an apparent increase in primary productivity. This pattern again oscillates with the adiposity indicators ($r=0.55$; $p=0.34$) (Figure S2; Table S4).

Temporal Trend Analysis

POP data, as the most data-limited measure used in this monitoring effort, was subjected to power analysis to provide insight into the monitoring duration required to detect a long-term directional change of 5% per year with an 80% power. Based on the coefficients of variation

of the current POP data, and a sample size of on average 11 specimens per year, it was calculated that 12, 15 and 18 years' of annual sampling would be required for HCB, Σ DDE and Σ PCB data respectively, emphasizing the importance of long-term monitoring.

Discussion

Information regarding the adiposity and dietary utilisation of migrating humpback whale populations carries explicit information regarding their summer foraging success and therefore the productivity of their Antarctic feeding grounds. The direct covariance of the two selected adiposity markers lend strong support that 2011 represented a lean year for this population of whales, and therefore that they likely encountered poor Antarctic feeding conditions in the austral summer of 2010/11. Examination of dietary tracers as explanatory variables behind the observed change in energy reserves revealed signs of foraging diversification following the 2011 lean year, as demonstrated by the departure of individual BSI values from the predicted low Antarctic trophic level signal in 2013 and 2014, before returning to a tighter clustering around the expected isotopic space in 2015 (Figure 4).

In order to further explore and validate the connection between the targeted sentinel parameters and environmental conditions in the corresponding Antarctic feeding ground, potential underlying ecological parameters in this region were explored. Candidate parameters of the observed variability in population energy reserves and diet include; krill biomass and availability, as well as indirect abiotic parameters. Although krill monitoring is performed throughout certain areas of the Southern Ocean (Atkinson et al., 2017), no inter-annual krill monitoring data is available from the Antarctic sector corresponding to this populations' feeding ground. By contrast, remote satellite monitoring provides spatially resolved data-sets concerning sea-ice concentration and ocean productivity, whilst meteorological monitoring provide insight into regional climatic cycles.

Summer sea-ice concentrations in feeding area V over the monitoring period revealed a marked drop in the 2010/2011 austral summer preceding the anomalous 2011 sampling year (Figure 4). This observation is consistent with reduced sea-ice contributing to the leaner migrating whales observed in 2011. The classical mechanistic hypothesis for how reduced sea-ice is expected to exert an influence on krill biomass i.e. through reduced larval recruitment, however, would not predict immediate responsiveness of krill consumers. Rather, a lag-phase associated with reduced larval numbers maturing into their adult pelagic life-stage is expected. Such a lag-phase was not observed in the available timeline; rather, the temporal alignment of lower sea-ice concentration and lower population adiposity was direct. This observation suggests that the classical view may be an over-simplification of the sympagic interaction and indeed is in line with new contrary evidence suggesting a higher sensitivity of krill larvae to inter-cohort resource competition, than availability of sea-ice habitat (Ryabov, de Roos, Meyer, Kawaguchi, & Blasius, 2017).

The observation that both SAM and ENSO were in positive modes in the summer preceding sampling (Figure 5), and notably that the La Niña event of 2010/2011 was one of the strongest La Niña events on record, suggests that a broad climatic influence upon the eastern Antarctic feeding ground was linked to the leaner whales observed in 2011. Interestingly, (Fountain et al., 2016) report that when La Niña events co-occur with positive SAM, the sea level pressure response can be enhanced. It is known that ENSO conditions have a strong relationship with Antarctic sea-ice, resulting in a cyclical increase and decrease which has often confounded long-term trends (Curran, van Ommen, Morgan, Phillips, & Palmer, 2003; Meehl, Arblaster, Bitz, Chung, & Teng, 2016). The majority of investigations, however, have focused on the relationship between ENSO conditions and the Antarctic Peninsula and the western Antarctic regions. By comparison, very little is known about how ENSO events are

expected to influence the eastern Antarctic sector. Notably, Welhouse et al. (Welhouse, Lazzara, Keller, Tripoli, & Hitchman, 2016) recently found a robust signal of cooling over East Antarctica during La Niña years. Further, phytoplankton community responses to ENSO mediated environmental conditions were investigated by (Zhang et al., 2014) in Prydz Bay, East Antarctica. A distinctive pattern was observed in La Niña years, which resulted in a shift from diatom-dominated assemblages to an increase in brown algae and blue-green algae. CHL values were also elevated in La Niña years, despite lower species diversity. Such patterns may be expected to carry significant consequences for ecosystem dynamics.

This uncoupling between CHL data and system biodiversity during La Niña years may also have contributed to the negative association observed between system CHL and whale energy reserves (Figure S2). When summer primary productivity, as indicated by CHL data from the corresponding Antarctic feeding area were compared, the austral 2010/2011 summer is depicted by relatively high CHL values, which again show a similar trend to adiposity indicators. This observed pattern may be a function of greater ice-free areas, as indicated by sea-ice concentration; a direct product of changed pigmentation signal from an altered phytoplankton assemblage, or alternatively, be reflective of a release from grazing in the absence of preferred phytoplankton assemblages and/or krill biomass in the photic ocean layer (Ainley et al., 2015; Behrenfeld, 2014).

Krill biomass is known to undergo five to six year population cycles, with large variation between population minima and maxima (Ryabov et al., 2017). These oscillations have been postulated to be driven by periodic climatological factors (Ryabov et al., 2017). It is possible that our current data set captured the transition between two such cycles, leading to a temporary (2010/2011) constriction of energy flow along this Antarctic sea-ice ecosystem food chain. Under this scenario, altered dietary signals of the whales in years following the

constriction may be attributed to changed feeding behaviour (i.e. adaptation and cognitive learning based on environmental conditions) by the whales in response to lower 2010/11 feeding success. Such adaptations may have entailed a diversification in either, or both of, feeding ground and prey choice, as indicated by dietary signals in the 2013 and 2014 sampling years.

In addition to the krill cycle hypothesis it is, however, worthwhile to consider alternate scenarios that may have elicited the same trophodynamic response in the whales. For example spatial “unavailability” of krill to the whales, rather than biomass decline. Great interest, as well as uncertainty, surrounds krill movement e.g. (Cresswell et al., 2009; Siegel, 2016), and spatial (including vertical) migration of krill should be considered in the context of these findings. Regional migration of krill, or earlier seasonal onset of migration of krill further inshore to under-ice habitats to avoid diving predators (Curtice et al., 2015) may have impacted 2010/11 summer foraging success of the whales. This scenario would have produced similar trophodynamic responses in the whales to the krill cycle hypothesis. On the other hand, a recent observation by (Clarke & Tyler, 2008) of krill at abyssal depths, presents another possibility. Whilst the bulk of the post-larval Antarctic krill population is typically confined to the upper 150 m of depth, Clarke et al. documented the presence of krill, including gravid females, at up to 3500 m depth. Large-scale, temporary vertical migration of krill to abyssal depths would inherently have entailed increased omnivory and a diet higher in $\delta^{15}\text{N}$ (Cresswell et al., 2009). The signal of a benthic diet would be carried forward to whales in subsequent years when krill stocks and optimal whale foraging depths again showed improved spatial alignment.

Finally, Antarctic oceanography can be expected to be influenced by regional climate oscillations (Martinson, Stammerjohn, Iannuzzi, Smith, & Vernet, 2008), which in turn may impact upwelling and isotopic baselines in the region. Whilst a baseline isotopic change (i.e.

variations in factors influencing the lowest levels of the food web) does not explain the poor nutritional condition of the whales, such a contribution cannot be ruled out in the observation of individual animals below the expected $\delta^{15}\text{N}$ space in 2008, and the apparent trophic level rise of the whales in 2013 and 2014.

Further environmental forensic and inter-disciplinary work is required to define key Antarctic environmental factors driving the trophodynamic response in SH humpback whales, particularly during anomalous years. Nonetheless, despite unresolved uncertainties surrounding whale movement, krill distribution, isotopic turn-over and baselines; the combination of our findings suggest the existence of a closely coupled relationship between the energetic reserves of a high-fidelity Antarctic krill consumer, SH humpback whales, and underlying climatic conditions in their eastern Antarctic feeding ground. Similar connections have previously been reported for other baleen whale krill consumers (Leaper et al., 2006; Seyboth et al., 2015). This is the first time, however, that non-lethal, chemical and biochemical biomarkers of the core sentinel parameters of diet and adiposity have been targeted. These were found to be sufficiently sensitive to signal oscillations in climate variables in the corresponding Antarctic feeding area over the eight-year monitoring period.

In light of the pivotal global influence of the Southern Ocean, any climatic change in this region carries global ramifications. Long-term time series of physico-chemical environmental parameters; such as ocean salinity (van Wijk & Rintoul, 2014), temperature (Gille, 2002), sea-level (Kusuhara, 2015) and CO_2 uptake (Le Quéré et al., 2007) all point to directional change, with an increase in extreme La Niña events also predicted (Capotondi, 2015). There is also evidence of change within the biological system, for example the influence of decreasing sea-ice extent on salp and krill populations in the Antarctic Peninsula region (Loeb et al., 1997). Biological responses to climate change are much more challenging to

capture and interpret and frequently require resource intensive investment, however, they hold the key to understanding the ecological impact of change, and evaluating ecosystem resilience.

The implications of this study's findings are a strong basis for the implementation of SH humpback whale populations as standardised sentinels of the Antarctic sea-ice ecosystem for the purpose of long-term, and circumpolar ecosystem surveillance. Humpback whales have a circum-Antarctic distribution and, their annual migrations afford sampling opportunity at temperate latitudes, removing the need for Antarctic travel. Novel, non-lethal, chemical and biochemical quantification of sentinel parameters offers a distinct financial and logistical advantage to *in-situ* Antarctic monitoring, providing a time-integrated signal of population trophodynamics.

Long-term, circumpolar records may further help to explain and predict unusual baleen whale mortality events such as those described for Western Australia and South American migrating humpback whale populations (Coughran, Gales, & Smith, 2013; Fulgencio de Moura et al., 2010), and South American right whale (*Eubalaena australis*) populations recorded in recent periods (Rowntree et al., 2015).

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Figure Captions

Figure 1 Schematic representation of the weight-loss associated concentration effect of lipophilic POPs (indicated as green markers) occurring in blubber adipocytes over the course of the migration journey. Double-ended arrows on the whales indicate the decreasing blubber thickness between sampling time-points **A** (post summer feeding) and **B** (fasted)

Figure 2 Average annual outer blubber burdens of hexachlorobenzene (HCB), dichlorodiphenyltrichloroethane (DDT) isomers and polychlorinated biphenyl (PCB) congeners in adult, southward migrating males, depicted alongside the population's annual average AI. Error bars represent the standard errors of the means.

Figure 3 Annual austral winter BSI measures, where the grey shaded area corresponds to predicted isotope ranges of an individual feeding entirely on a first order Antarctic consumer, such as Antarctic krill. The colour of the markers depict the time-point at which an individual was sampled. Black markers indicate that an individual was sampled on the northward leg of the migration, when animals are travelling to their equatorial breeding grounds. White markers indicate animals that were sampled three months later in the year, on the southward leg of the migration when animals are returning to Antarctic feeding grounds.

Figure 4 Average summer sea- ice concentration in feeding area V measured in the summer preceding winter sampling, displayed with the annual population AI. The displayed year is the AI sampling year i.e. 2008 is the 2007/8 austral summer sea-ice signal. Error bars represent the standard error of the means.

Figure 5 Average climate indices measured in the summer preceding winter sampling, displayed with annual population AI measures. The displayed year is AI sampling year i.e. 2008 is the 2007/8 summer climate indices. Error bars represent the standard error of the means.