Signals from the south; Humpback whales as the new Southern Ocean sentinel

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Southern hemisphere humpback whales (*Megaptera novaeangliae*) are high-fidelity Antarctic krill (*Euphausia superba*) predators that rely on the summer biomass abundance to fuel the longest-known migrations for any mammal on the planet. It is postulated that this species, already adapted to endure metabolic extremes, will be one of the first Antarctic predators to show measurable physiological change in response to fluctuating principal prey availability in a changing climate. Here we show the synchronous, inter-annual oscillation of two measures of adiposity, namely the adipocyte index (AI) and lipophilic contaminant burdens, with Southern Ocean environmental variables and climate indices. Further, bulk stable isotope signatures provide strong indication of dietary compensation strategies following years indicated as leaner years. The clear synchronicity of humpback whale dietary and adiposity signals with climate patterns in the Southern Ocean lend strength to their role as powerful Antarctic sea-ice ecosystem sentinels. The work carries significant potential to reform long-term and circum-Polar ecosystem surveillance in the region.

Southern hemisphere (SH) humpback whales (*Megaptera novaeangliae*) undertake the longest migrations known for any mammal on the planet.[1] These migrations between Antarctic feeding grounds and equatorial breeding grounds are associated with voluntary fasting and represent a period of intensive energy utilisation. Males undertake competitive breeding behaviour, whilst migrating females are predominantly pregnant and/or nursing young calves. This extreme migratory behaviour allows these populations to exploit the 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 thermoregulate in polar waters. Lunge feeding in rorqual whales (Balaenopteridae) has been posed as only being energetically viable at certain prey densities,[2] pointing to evolution of SH populations in apparent mutualism with Antarctic krill through iron feed-back loops in the iron-limited Southern Ocean ecosystem.[3,4]

Antarctic krill undergo 12 larval stages before assuming their adult morphology.[5] The first three of these are non-feeding stages that undertake the larval ascent to reach the underside of sea-ice where they commence feeding upon ice-algae associated microbes to fuel further development.[6] This sympagic species therefore relies on the sea-ice ecosystem as a nursery ground with the implication that larval recruitment is closely tied to sea-ice extent.[7] With a decrease in suitable sea-ice habitat, krill populations may experience reduced recruitment success which translates to reduced krill biomass, and hence prey availability for baleen whales and other higher trophic Antarctic predators in subsequent years.[8]

It is postulated that SH humpback whales, on account of their specialized diet[9] and adaptation to endure metabolic extremes,[10] will be one of the first Antarctic predators to show measurable physiological change in response changing abundance of Antarctic krill.

Temporal monitoring of the east coast of Australia migrating humpback whale breeding population since 2008 has revealed significant inter-annual variability in blubber Persistent Organic Pollutant (POP) burdens. Following author demonstration that just a few months of the seasonal fast results in a dramatic, up to 500-fold, increase in average blubber concentration of lipophilic POPs, it was postulated that longitudinal monitoring of population POP burdens, may provide an indication of the population's inter-annual lipid reserves, or "adiposity".[11] The increase in apparent body lipophilic chemical burden arises as rapid lipid depletion during this time, is not associated with corresponding chemical metabolism and elimination.[12-17] Whole-of-body lipid depletion is reflected through the re-distribution of lipophilic chemical burdens among the body's remaining lipid stores. As the outer blubber layer of cetaceans plays an important role in physiological functions aside from lipid storage, such as buoyancy and thermoregulation, it is conceivable that there exists a threshold under which lipid depletion cannot occur without compromising functioning of these ancillary roles and therefore individual survival. Consequently, as whole-of-body lipid depletion occurs, the outer blubber layer represents an increasing proportion of the individual's remaining lipid stores and accumulates proportionately greater pollutant loads (Figure 1).

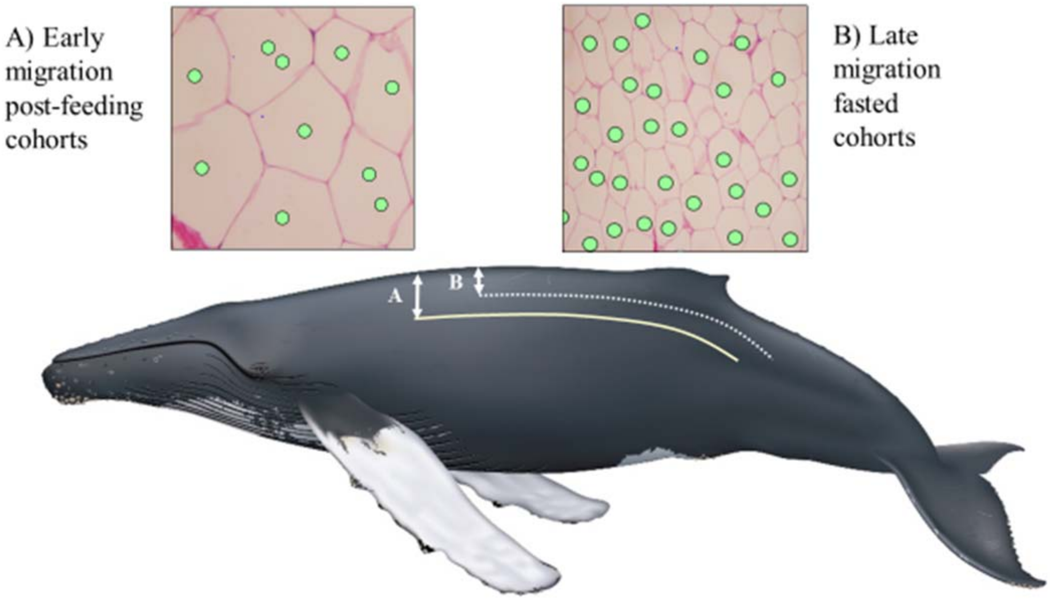
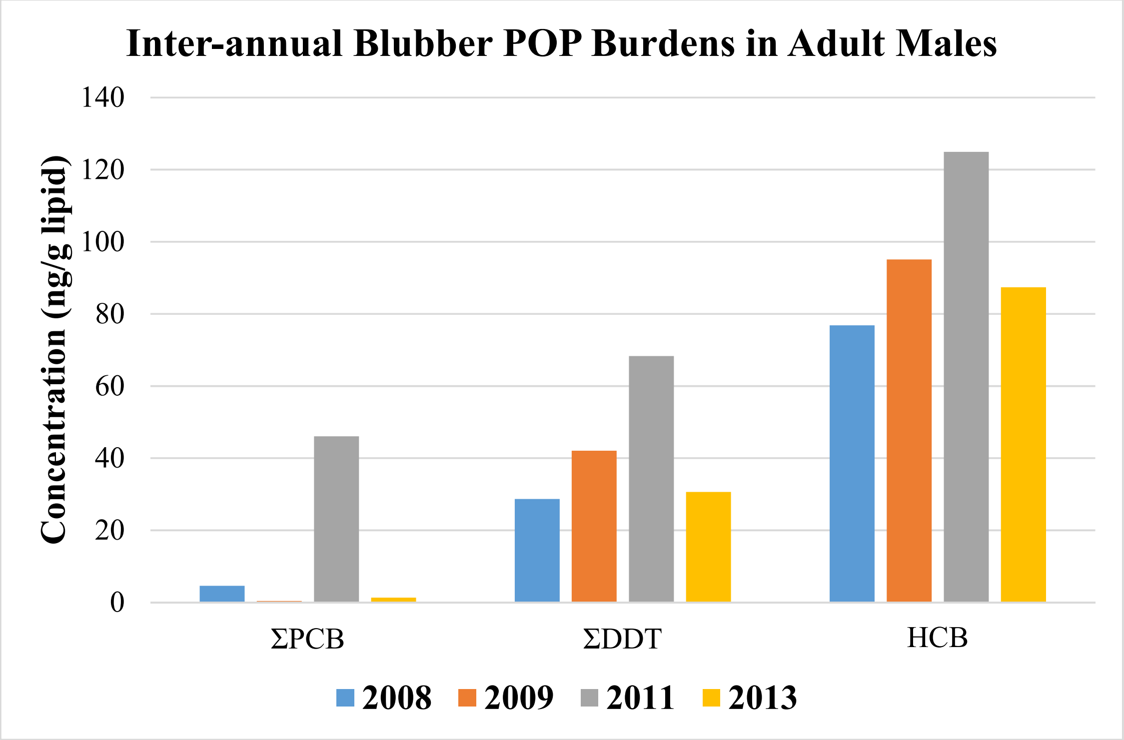


Figure 1 Schematic representation of lipophilic POP redistribution and concentration during rapid lipid depletion

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), 2011 appeared to represent a spike in the most frequently detected contaminant burdens (Figure 2).



Similarly, when the adipocyte index (AI), a histological measure of adiposity as indicated by relative adipocyte area,[18] of animals sampled in the respective years are compared, we observe a direct correlation (r=0.94) with blubber POP concentrations (Figure 3). Co-variance of these two measures lend strong evidence that 2011 represented a "lean" year in this population, with lower lipid reserves driving the elevated blubber POP concentrations.

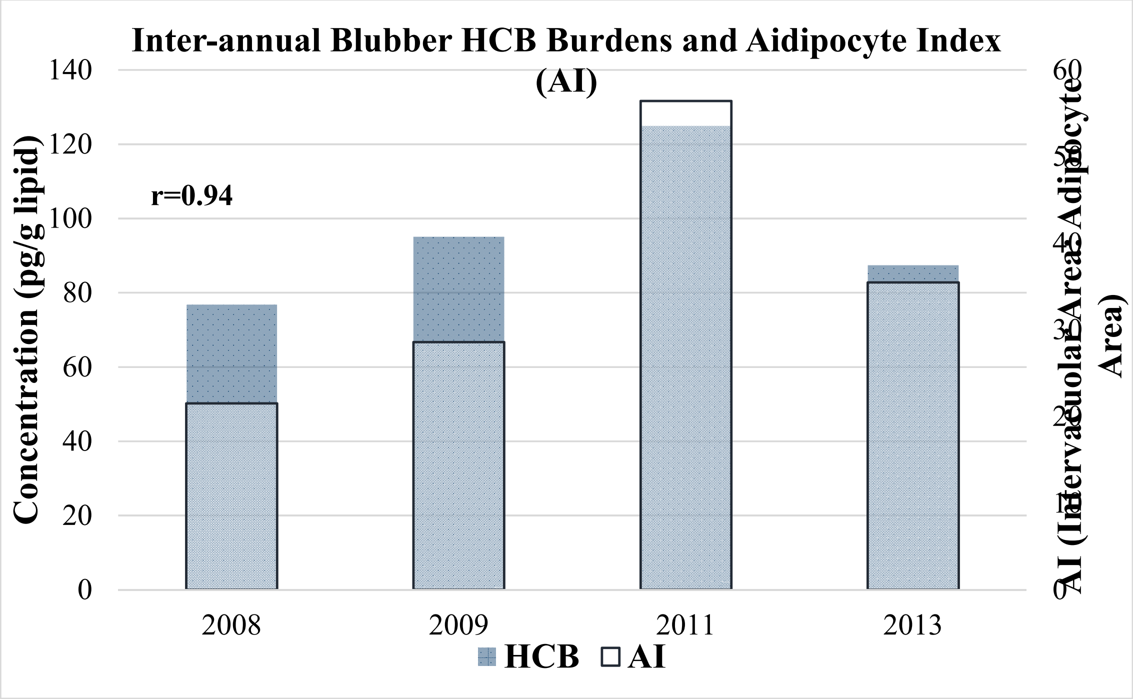


Figure 3 **Inter-annual correlation between the AI and the dominant POP compound, hexachlorobenzene (HCB)**

Further investigation of diet tracers, as explanatory variables behind the observed change in energy reserves, revealed evidence of prey and/or feeding diversification following the anomalous 2011 lean year (Figure 4).[19] In the earlier sampling years; 2008, 2009, as well as the anomalous 2011, both nitrogen and carbon isotopic signals indicate adherence to the expected low trophic level Antarctic signal. In 2013, however, the population shows greater heterogeneity in both trophic level ($\delta^{13}N$) and food web origin as indicated by $\delta^{13}C$. This enhanced heterogeneity in feeding signal returns to a tighter clustering around the Antarctic low trophic signal again in 2015. It remains to be found whether the altered feeding signal is can be directly attributed to changed feeding behaviour by the whales in response to lower feeding success in 2011 i.e., a change that involved adaptation and cognitive learning based on environmental conditions. Alternatively, in the absence of changed whale feeding behaviour, a similar signal might be expected if krill were unavailable to the whales in the same numbers in 2011 due to, for example, vertical migration to avoid higher ocean temperatures[20]. Migration to the deep ocean by the krill would also involve an altered diet, the signal of which would be carried forward to whales in subsequent years when krill stocks and whale feeding depths again showed improved alignment. Bulk stable isotope analysis alone is unable to detangle these two, potentially overlapping, scenarios although compound specific isotope analysis may provide further clues.

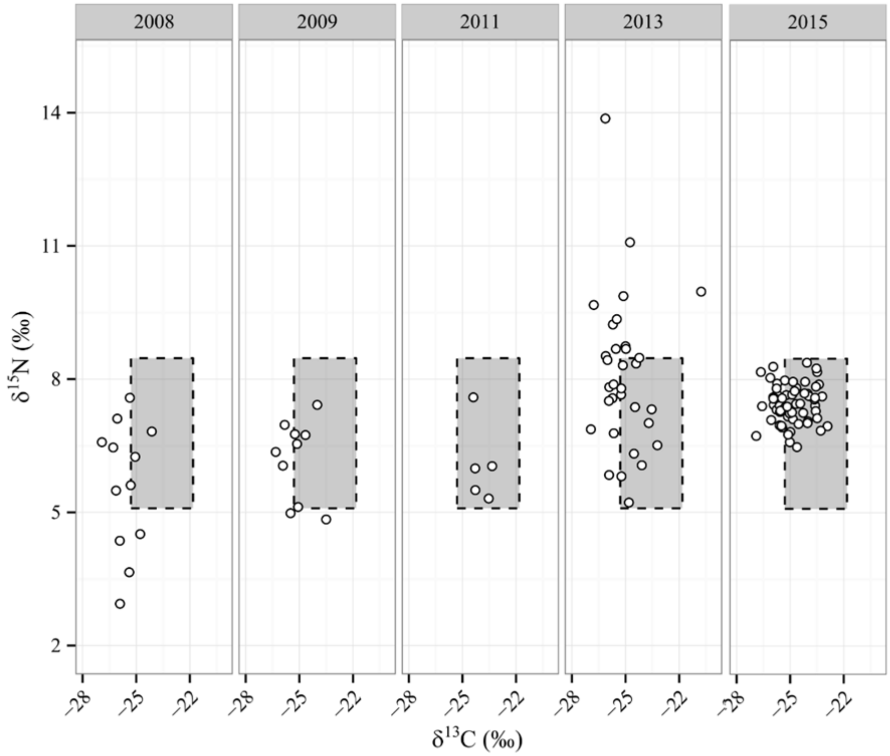
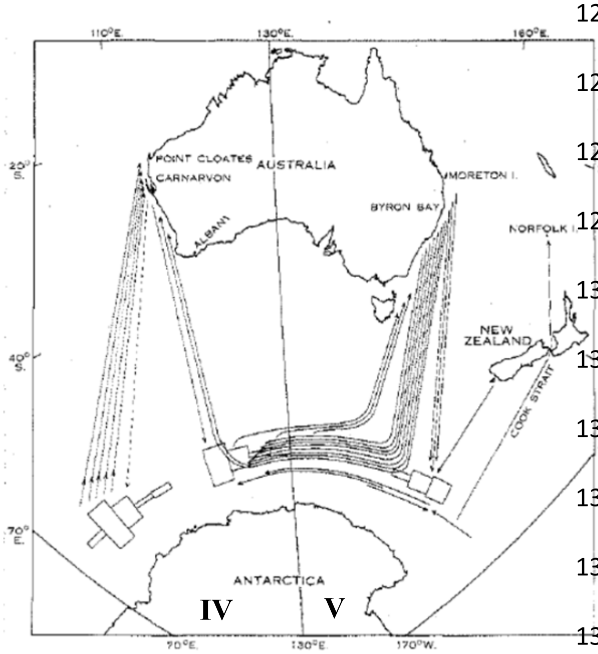


Figure 4 **Inter-annual Bulk Stable Isotope Analysis, where the grey shaded area corresponds to predicted isotope ranges of an individual feeding entirely on a low trophic level Antarctic prey species, such as Antarctic krill**

The sampled breeding population of humpback whales have been associated with the Antarctic feeding areas IV and V as classified by the International Whaling Commission[21,22]

(Figure 5) Extended Data. These areas fall within the Food and Agricultural Organization (FAO) of the United Nations sub-areas 58.4.1 and 88.1 respectively.



Extended Data Figure 5 Feeding Sampling Location X area of the study population (Image from Chittleborough, 1965)[21]

Information regarding population adiposity and dietary utilisation therefore carries explicit information regarding the summer productivity of this Antarctic region.

In order to further establish and validate this connection, investigations into potential underlying ecological parameters in this region were performed. Candidate causal parameters of the observed variability in population energy reserves include krill biomass and access/availability as a function of environmental variables. Although krill monitoring is performed throughout certain areas of the Southern Ocean,[23] no inter-annual krill monitoring data is available from the concerning feeding areas IV or V.

Sea ice is expected to be the dominant integrated driver of ecosystem productivity as it is driven by temperature, winds and ocean circulation.[24] When sea-ice concentration records from the relevant feeding area in the summer preceding sampling are scrutinized, a strong negative correlation with blubber POP concentrations (r=-0.95, -0.93 and -0.85 for HCB, ΣDDT and ΣPCB respectively) is observed (Figure 6). This observation is consistent with underlying environmental parameters contributing to the leaner migrating whales observed in 2011.

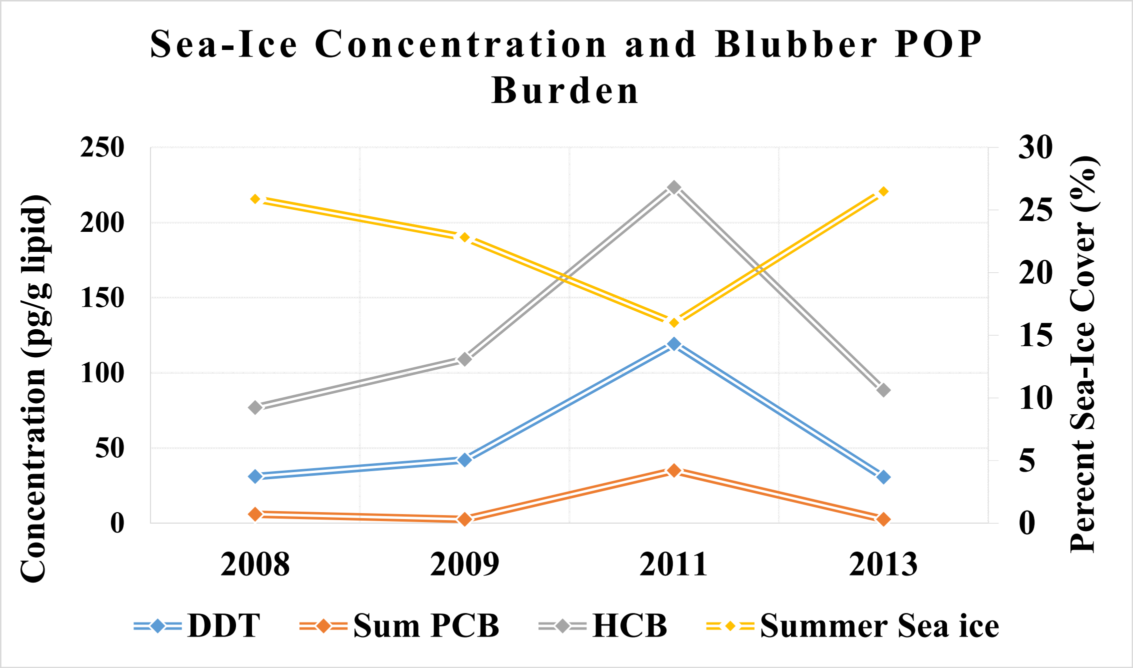
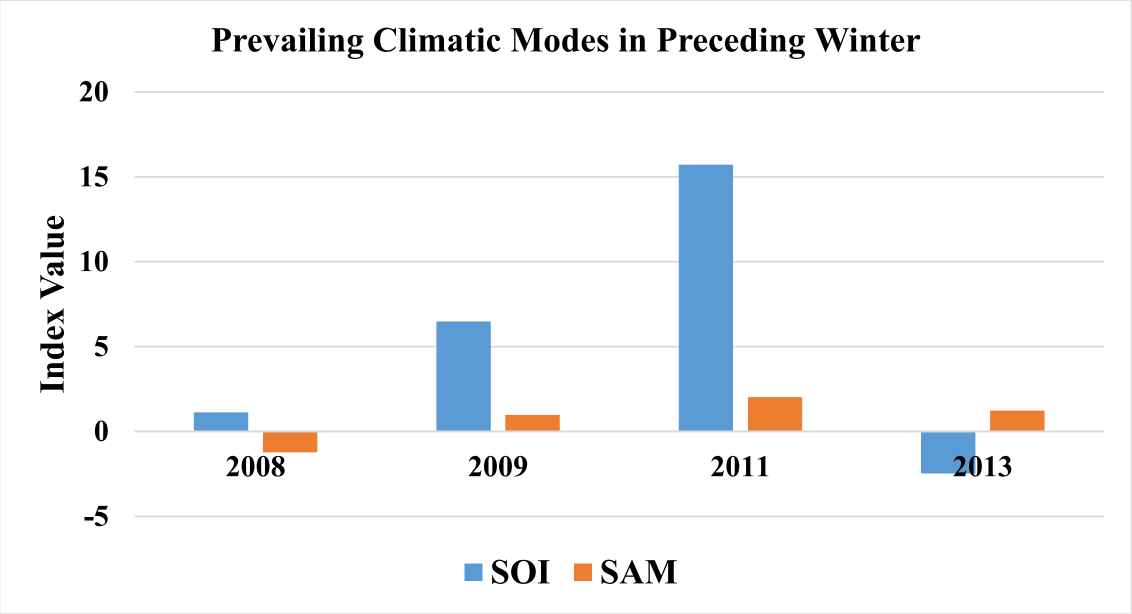


Figure 6 **Percent summer sea- ice and blubber POP burden**

The leading mode of atmospheric variability in Antarctica is the Southern Annular Mode (SAM)[25] which describes the north to south movement of the westerly wind belt that surrounds the Antarctic continent. Similarly, the El-Nino Southern Oscillation (ENSO) index describes atmospheric pressure and sea surface temperature differences between the eastern and western Pacific and are known to impact the Antarctic climate. 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.[24] The opposite is true for negative SAM. Similarly, positive ENSO events, or La-Nina 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 Nina events are the negative El Nino phases.

Investigation of the inter-annual climate indices reveals that both SAM and ENSO were in positive modes in the winter preceding sampling (Figure 7) Extended Data with the La Nina event of 2010/2011 representing one of the strongest La Nina events on record. Fountain et al. (2016)[24] report that when La Nina events co-occur with positive SAM, the sea level pressure response can be enhanced.[24]



Extended Data Figure 7 Inter-annual climate indices

ENSO conditions have a strong relationship with Antarctic sea-ice, resulting in a cyclical increase and decrease which has often confounded long-term trends.[26,27] Whilst previous investigations of the relationship between ENSO conditions and the Antarctic climate have focused on the Antarctic Peninsula and the western Antarctic regions, comparatively little is known about how ENSO events are expected to influence the eastern Antarctic sector. Recently, Welhouse et al (2016)[28], however, found a robust signal of cooling over East Antarctica during La Nina years. Phytoplankton community responses to ENSO mediated environmental conditions were further investigated by Zhang et al. (2014)[29] in Prydz Bay, East Antarctic. A distinctive pattern was observed in La Nina years which resulted a shift from diatom dominated assemblages to an increase in brown algae and blue-green algae. Chlorophyll *a* (Chl *a*) values were also elevated in La Nina years, despite a lower species diversity. Such patterns would in turn carry significant consequences for ecosystem dynamics.

When inter-annual summer satellite Chl *a* data from the corresponding Antarctic area of interest are compared, the austral 2010/2011 summer is depicted by an apparent increase in primary productivity, as indicated by Chl *a* (Figure 8). This trend again oscillates closely with adiposity indicators (r=0.99 for blubber HCB burdens and 0.88 for AI respectively). This observation may be a function of greater ice-free areas, as indicated by sea-ice concentration, or alternatively be reflective of a release from grazing in the absence of preferred phytoplankton assemblages and/or lower zooplankton biomass.[30,31]

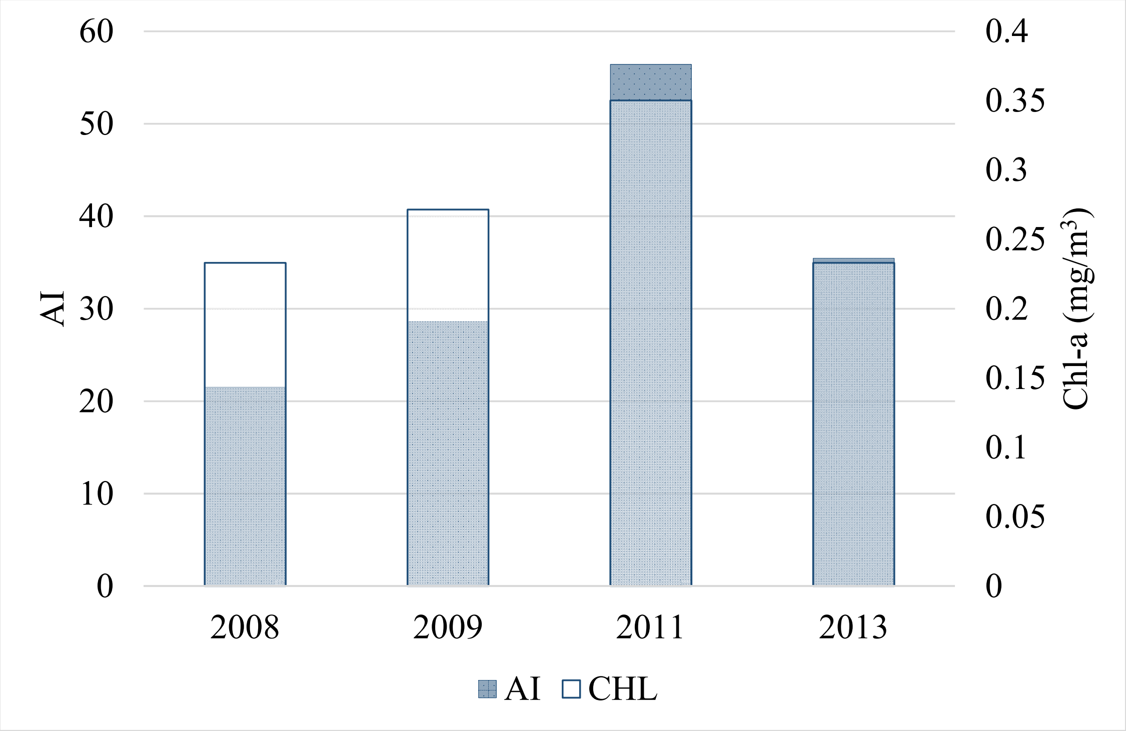


Figure 8 **Inter-annual mean summer Chl-*a* measurements presented together with inter-annual mean AI**

Further inter-disciplinary work is required to define key physical driving factors in the corresponding Antarctic region. Nonetheless, the combination of our findings demonstrate a closely co-varying relationship between the energetic reserves a high-fidelity Antarctic krill predator and underlying climatic conditions in the corresponding eastern Antarctic feeding area. Similar connections have previously been observed for other krill predators in the Antarctic Peninsula region.[32] [33] Our investigations further show that relative inter-annual blubber POP burdens, in a distinct population of polar biota, can be applied as indicators of adiposity and that combined, the biomarkers of diet and adiposity of humpback whales were sufficiently sensitive to signal oscillations in climate variables in the corresponding Antarctic feeding area.

Given the pivotal 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,[34] temperature,[35] sea-level[36] and CO_2 uptake, [37] all point to directional change with an increase in extreme La Nina events also predicted.[38] There is also some evidence of change within the biological system e.g.[7] Biological responses to climate change are, however, much more challenging to capture and interpret. Whilst such data-sets hold the key to understanding the ecological impact of change and system resilience, robust parameter sets remain rare and elusive without resource intensive investment. The pivotal role of Antarctic krill in the Antarctic sea-ice ecosystem forewarns that even a marginal decrease in krill stocks is likely to produce ripple effects at higher trophic levels.[39] Direct monitoring of Antarctic krill biomass is complicated by the cost and logistics of broad-scale Antarctic field surveys and the limitations of accurately monitoring a swarming species. The flat structure of the Antarctic ecosystem lends itself to a sentinel approach to biomonitoring[40]. The implication of our findings is a strong basis for implementing Southern hemisphere humpback whale populations as standardised “sentinels” of the Antarctic sea-ice ecosystem for the purpose of long-term, and circum-polar ecosystem surveillance. Humpback whales have a circum-Antarctic distribution. In contrast to current sentinel programs in the region[41], their annual migrations afford temperate sampling opportunity without the need for Antarctic travel. Finally, author advances in chemical and biochemical quantification of sentinel parameters offer a distinct financial and logistical advantage to *in-situ* Antarctic monitoring of population behaviours and dynamics.

Based on the coefficients of variation (CVs) of the current POP data, and a sample size of on average 11 specimens per year, it is estimated that 12 and 15 years' of annual sampling is required to detect a long term directional change of 5% a year with an 80% power for HCB and DDE respectively. Importantly, temporal trend analyses highlighted the importance of annual sampling at the standardised sampling time points as a two year sampling frequency results in a requirement for more than 10 times the number of specimens in order to maintain the same power of the data.

Long term, circum-Polar records may further help to explain and predict unusual humpback whale mortality events described for western Australia and south American migrating populations and[42,43] and South American right whale (*Eubalaena australis*) populations in recent periods.[44]

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. Skin and blubber biopsies were collected from free-swimming animals as described in detail elsewhere [45]. Sampling was performed on the southward leg of the migration journey as whales were returning to Antarctic feeding grounds (sampled last week of September/first week of October). Upon collection, blubber was separated from the skin and stored at -20^{o} C in furnaced, amber glass vials until time of analysis. Animal work was conducted under the University of Queensland and Griffith University Animal Research Ethics Committee (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 extraction. Individual samples were extracted using a modified Bligh and Dyer methanol-chloroform-water extraction method [46] as described in detail elsewhere.[45] Lipid class profiles were determined by an Iatroscan Mark V TH10 thin layer chromatograph coupled with a flame ionization detector.[47] The total blubber percent lipid was calculated by summing the individual lipid class percentages.

Chemical Results

Only chemical data from adult males, as determined through genetic sexing, were used for this study to avoid the confounding factors associated with pregnancy and lactation in females.

Analytes

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).

Chemical Data

The blubber extraction, clean-up and quality assurance procedures have been described elsewhere in full.[11] Individual animal chemical data included in the current investigations are summarised in Table 1. Extended Data

Extended Data **Table 1 Blubber chemical burdens of individual animals (ng/g lipid) to two significant figures. Outliers are indicated by italics. Shaded areas indicate analytical results not available. Blank cells denote concentrations under the method level of detection**

Sampling Year and Animal ID	HCB	ΣPCB	ΣDDT
2008			
3S08	180	9.1	79
4S08	74	3.8	23
6S08	74	4.1	27
7S08	10	0.85	4.3
13S08	61	5.9	31
17S08	86	8.9	59
18S08	57	3.8	19
21S08	71	*24*	21
22S08	57	2.9	
24S08	190	9.7	66
25S08	60	7.0	15
27S08	26	2.9	12
28S08	66	0.74	
30S08	59		16
Arithmetic mean	77	5.9	29
SD	49	5.8	23
Arithmetic Mean Outliers Removed		4.6	
SD Outliers Removed		3.2	
2009			
9S09	178	*13*	80
10S09	130	0.55	32
12S09	110		60
13S09	46		7.0
14S09	13		
21S09	78	1.4	31
Arithmetic mean	95	2.5	42
SD	74	4.8	25
Arithmetic Mean Outliers Removed		0.39	
SD Outliers Removed		0.54	
2011			
1S11	54	3.5	13
4S11	*1000*	130	320
5S11	33	2.5	66
6S11	82	12	28
7S11	300	26	*680*
8S11	210	150	95
9S11			16
10S11			37
11S11	170	23	67
21S11	42	110	38
22S11		0.21	36
26S11	111	4.3	33
Arithmetic mean	220	46.0	120
SD	290	56.0	190
Arithmetic Mean Outliers Removed	125		68
SD Outliers Removed	89		84
2013			
2S13	51	0.48	15
3S13	81	0.60	27
5S13	51	1.0	15
8S13	160	2.2	54
11S13	83	1.3	27
13S13	100	0.96	31

14S13	29	0.17	7.3
17S13	110	1.4	33
18S13	150	3.1	50
22S13	44	1.4	15
25S13	110	1.8	44
30S13	79	1.7	30
33S13	110	1.7	34
34S13	85	1.8	57
35S13	71	0.55	19
36S13	79	1.1	31
Arithmetic mean	87	1.3	31
SD	35	0.71	14

Histology and Image Analysis

The adipocyte Index was derived as described elsewhere.[18] Five to twenty-seven animals (mixed gender) per sampling period were used for AI metrics. 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. Subsequently the slides were 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.[48] a public domain, Java-based image processing program. From a grey scale, thresholding was used to create binary images,[49] 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.

Stable Isotope Analysis

Protocols for bulk stable isotope analysis are published elsewhere.[50] Stable isotope results for between five and sixty-two (mixed-gender) animals were used per sampling cohort. In brief, blubber samples were extracted overnight in a 2:1 chloroform:methanol solution to remove any oils and lipids[51,52] and oven-dried at 58°C. 1-2 mg of clean sample material were weighed into tin capsules for isotope analysis.[52]

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

$$\delta X = \left[\left(\frac{Rsample}{Rstandard}\right) - 1\right] x\ 1000 \quad (1)$$

where X = ^{13}C or ^{15}N, and R = the respective ratio ^{13}C/^{12}C or ^{15}N/^{14}N. The international reference standards for carbon and nitrogen are respectively Vienna Pee Dee Belemnite and N_2 in air. International standards IAEA-CH_6 for carbon and IAEA N1 for nitrogen were used for calibration of laboratory standards KHP and $(NH_4)_2SO_4$ 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 δ^{13}C and δ^{15}N respectively averaged 0.1‰ and 0.15‰.

Source prediction and trophic fractionation

Bulk stable isotope values were compared to literature-derived estimates as per Eisenmann et al. (2016)[19], to compare against predicted values for a predator 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 ± standard deviation). We included the standard deviation of all values in the defined prey isotope ranges to account for possible sub-regional variations in δ^{13}C and δ^{15}N.

Environmental Data

Historical Sea-ice concentration data were obtained from the National Snow and Ice Data Centre (NSIDC) https://nsidc.org/.[53] Average annual summer sea-ice concentration was calculated from daily measurements between 1st October and the 31st March 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 ENSO data was obtained from the National Ocean and Atmospheric Administration (NOAA) http://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/SOI/. Chlorophyll *a* 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

Grubb's test for outliers was performed on each annual POP data-set and outliers removed from further calculations. Pearson product moment coefficient was applied for correlation investigations. Time trends of blubber POP concentrations were derived using statistical Plot and Image Analysis (PIA), based on the work of Nicholson and Fryer [54] and adopted by the Arctic Monitoring and Assessment Program (AMAP).

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Author Contributions

SBN is responsible for: Conception and leadership of inter-related research programs and investigations; funding acquisition; data synthesis and interpretation; led field aspects and performed writing of the manuscript; JC participated in a field event and is responsible for production and interpretation of data aspects related to adipocyte metrics; PE participated in a field event and is responsible for production and interpretation of data aspects related to bulk stable isotope analysis; BF is responsible for joint student supervision and interpretation of data aspects related to bulk stable isotope analysis; JS, RC and AD are responsible for remote sensing data handling and contributed to remote sensing data interpretation whilst AD also participated in a field event; AB is responsible for PIA analyses; PBN supported chemical analysis aspects. CW participated in two field events and undertook sample extractions for chemical analysis for two years' worth of data. BP co-led a field event, undertook sample extractions and contributed to various aspects of manuscript production; GDL participated in a field event and undertook chemical extractions associated with one years' worth of sampling; DM undertook chemical extractions associated with one years' worth of sampling. JC, PE, JS, RC, AD, AB and PBN further contributed to the editing of various drafts of the manuscript.