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RESEARCH ARTICLE

A surplus no more? Variation in krill availability impacts reproductive rates of Antarctic baleen whales

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Abstract

The krill surplus hypothesis of unlimited prey resources available for Antarctic predators due to commercial whaling in the 20th century has remained largely untested since the 1970s. Rapid warming of the Western Antarctic Peninsula (WAP) over the past 50 years has resulted in decreased seasonal ice cover and a reduction of krill. The latter is being exacerbated by a commercial krill fishery in the region. Despite this, humpback whale populations have increased but may be at a threshold for growth based on these human-induced changes. Understanding how climate-mediated variation in prey availability influences humpback whale population dynamics is critical for focused management and conservation actions. Using an 8-year dataset (2013–2020), we show that inter-annual humpback whale pregnancy rates, as determined from

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skin-blubber biopsy samples ($n = 616$), are positively correlated with krill availability and fluctuations in ice cover in the previous year. Pregnancy rates showed significant inter-annual variability, between 29% and 86%. Our results indicate that krill availability is in fact limiting and affecting reproductive rates, in contrast to the krill surplus hypothesis. This suggests that this population of humpback whales may be at a threshold for population growth due to prey limitations. As a result, continued warming and increased fishing along the WAP, which continue to reduce krill stocks, will likely impact this humpback whale population and other krill predators in the region. Humpback whales are sentinel species of ecosystem health, and changes in pregnancy rates can provide quantifiable signals of the impact of environmental change at the population level. Our findings must be considered paramount in developing new and more restrictive conservation and management plans for the Antarctic marine ecosystem and minimizing the negative impacts of human activities in the region.

KEYWORDS
Antarctica, climate change, conservation, humpback whale, krill, pregnancy rates

1 | INTRODUCTION

One of the most significant ecological disturbances to occur over the past 200 years was the removal of more than 2 million baleen whales during the 20th century in the Southern Ocean (Rocha et al., 2014). In the 1970s, Laws (1977) proposed that this reduction in whales resulted in a "surplus" of Antarctic krill (*Euphausia superba*). This, in turn, could have allowed remaining krill predators (including other whales, seals, and penguins) to eat more, grow, and reproduce faster. Today, most populations of humpback whales in the Southern Hemisphere have recovered and are at or near their carrying capacity. This recovery has been particularly pronounced for humpback whales along the Western Antarctic Peninsula (WAP; Noad et al., 2019; Pallin, Baker, et al., 2018; Zerbini et al., 2019). However, recent work in the WAP also shows localized krill declines and a southward shift in krill distribution from 1976 to 2016 (Atkinson et al., 2019).

For humpback whales, reproductive success is largely contingent on the accessibility of adequate prey resources on their high-latitude feeding grounds (Lockyer, 1984). As capital breeders, humpback whales and other migratory baleen whales exploit high-latitude prey resources during the summer. They then use this stored energy or "capital" to support their annual migration and breeding activities in low-latitude regions during winter (Baker et al., 1986). Humpback whale feeding rates are highest early in the feeding season when their body condition is at its lowest (Nichols et al., 2022). Pregnant whales, in particular, must store sufficient energy reserves to support gestation and early lactation, when the females are fasting. This contention is supported by data obtained from whales harvested in commercial whaling operations that showed pregnant and/or lactating humpback females taken along the coasts of Australia yielded roughly twice as much oil as non-pregnant females (Dawbin, 1966).

Several studies demonstrate clear connections between whale pregnancy rates, prey availability/quality, and changing oceanic conditions. For example, in grey whales, reproductive rates increased after seasons in which sea-ice conditions allowed more time to access feeding grounds in the Bering Sea (Moore & Huntington, 2008). However, once climatic conditions shifted, and access to these vital feeding regions was truncated, reproductive rates dropped (Moore & Huntington, 2008). Similarly, in North Atlantic right whales, significant increases in reproductive rates during the 1990s were closely related to increases in the availability of their prey. This increase in prey was driven by warming oceanic conditions in the Gulf of Maine (Meyer-Gutbrod et al., 2015). These prey resources declined when a distinct climatic shift flipped the oceanic conditions in subsequent years, followed by a decline in North Atlantic right whale fecundity rates (Meyer-Gutbrod et al., 2015; Meyer-Gutbrod & Greene, 2018). Additional studies have observed a similar phenomenon in Southern Hemisphere baleen whales (Leaper et al., 2006). These studies revealed mechanisms by which whale reproductive rates can respond to varying prey availability and environmental conditions.

Along the WAP, over half a century of environmental change has been documented as part of the Palmer Long-Term Ecological Research (PAL LTER) program. During the austral summer, the breeding stock G (International Whaling Commission management group; Eastern South Pacific) population of humpback whales feeds along the WAP (Gales et al., 2011; Rice, 1998), making one of the longest annual migrations of any mammal (Rasmussen et al., 2007). This region has experienced a rise in winter air temperature of nearly 5°C since the 1950s, resulting in the collapse of ice shelves, the retreat of glaciers, and the exposure of new terrestrial and marine habitats (Meredith & King, 2005; Vaughan et al., 2003). The biological and physical productivity of the WAP marine ecosystem is strongly influenced by the amount of sea ice cover in this region (Massom & Stammerjohn, 2010). Additionally, an overall decline in sea ice has been observed along the WAP, resulting in an annual sea ice extent that is, on average, 80 days shorter than four decades ago

(Ducklow et al., 2013). Thus, the recovery of this humpback whale population is occurring in an environment experiencing some of the fastest climatic warming of any region on the planet (Smith & Stammerjohn, 2001).

Understanding how climate-driven processes influence the population dynamics of humpback whales is critical for prioritizing internationally-developed conservation actions intended to maintain the structure and function of this marine ecosystem. Whales are ecosystem engineers that enhance local primary production, stabilizing their prey base (e.g., Savoca et al., 2021), so understanding the factors that affect their demography is critical to managing these whale stocks and, thus, their contributions to the ecosystem. Ideally, we could forecast periods when ecological conditions are favorable or not for whales and use this knowledge to implement targeted and dynamic management strategies to modify human activities, such as krill fishing, that competes for resources with predators like humpback whales (Reisinger et al., 2022).

The development of non-lethal tissue sampling techniques and methods to isolate and quantify reproductive markers from skin-blubber biopsy samples allow us to assess environmental variability's impact on female humpback whales' pregnancy rates. To investigate this question, we (i) quantified the variation in pregnancy rates in female humpback whales across eight consecutive years and (ii) assessed the variation in annual pregnancy rates as a response to two critical environmental variables (prey availability and sea ice cover) using generalized linear models (GLMs). Our findings illustrate how the availability and variability of resources affect the reproduction of a capital breeder that also has significant ecosystem function. Further, our data provide support for more direct conservation and management actions to mitigate a growing krill fishery in this rapidly changing ecosystem.

2 | METHODS

2.1 | Biopsy collection

We collected skin and blubber samples from female humpback whales during the 2013–2020 austral summers (December–March). This was done in the nearshore waters of the WAP using standard biopsy techniques (Figure 1; Palsbøll et al., 1991). We used a crossbow to project modified bolts and 40 mm stainless steel biopsy tips (CetaDart) to obtain samples from a distance of 10–30 m, targeting the area of the body below the dorsal fin. Samples were collected opportunistically when whales were encountered during prey or visual surveys conducted within ~10 nautical miles of scientific research stations (i.e., Palmer Station, Anvers Island, USA, or Akademik Vernadsky Station, Galindez Island, Ukraine). Dedicated research cruises or platforms of opportunity, including ecotour vessels, were also used. Dependent calves were not sampled during seasons 2013–2019, but all age and sex classes of humpback whales were sampled during 2020. Because of this change in protocol, samples from calves were not included in any analysis. However, the presence of a calf was recorded and identified, as evident by their smaller size (less than half of the presumed mother's length) and close association with an adult, presumed to be the mother. Supplementary data (including location and group size) were recorded at every biopsy event. Samples were stored frozen whole at −20°C until used for analysis.

2.2 | DNA profiling

A standard DNA profile, including sex-specific markers and microsatellite genotypes, was used to identify individual whales. DNA was extracted from the skin-blubber interface using a commercially available kit (DNeasy 96 Blood & Tissue Kit, Qiagen). The sex of each sampled whale was determined by amplification of sex-specific markers following the protocols of Aasen and Medrano (1990) and Gilson et al. (1998). Results were compared to controls for a known male and female using gel electrophoresis.

Samples were genotyped using 10 previously published microsatellite loci to resolve the individual identity of each sampled whale and remove potential duplicates (Table S1; Baker et al., 2013; Berube et al., 2000; Palsbøll et al., 1997; Valsecchi & Amos, 1996; Waldick et al., 1999). Alleles were sized and binned using the software program Genemapper v3.7 (Applied Biosystems). The total number of amplified loci for a given sample was considered as an added quality control threshold, with samples amplifying for <7 loci considered poor quality and repeated or removed from final dataset. Given the estimated probability of identity for these loci from previous studies (Constantine et al., 2012; Pallin, Baker, et al., 2018), we assumed that samples matching at a minimum of seven loci to be recaptures of the same individual. Recaptures of the same individual were removed from the analysis. The expected probability of identity (p_{ID}; the probability that two individuals drawn at random from a population will have the same genotype by chance) for each locus was calculated in GenAlEx v6.5 (Peakall & Smouse, 2006). Cervus 3.0.7 (Kalinowski et al., 2007) was used to compute the number of alleles (K), observed and expected heterozygosity, and the probability of identity for all individual matches.

2.3 | Hormone extraction and quantification

We extracted steroid hormones from the blubber portion of the biopsy samples following standard methods (Kellar et al., 2006; Pallin, Baker, et al., 2018). Briefly, to quantify hormone biomarkers (i.e., progesterone), we sub-sectioned a cross-sectional sub-sample (~0.15 g) spanning from the epidermis-blubber interface to the most internal layer of the biopsy. These sub-samples were then homogenized multiple times using an automated bead mill homogenizer (Bead Ruptor Elite, Omni International). Following the completion of the homogenization process, we isolated progesterone using a series of chemical washes, evaporations, and separations. The final hormone residue was stored at −20°C until analysis.

We quantified the amount of hormone in each extract using a commercially available enzyme immunoassay used extensively in similar studies (Pallin, Baker, et al., 2018; Pallin, Robbins, et al., 2018; Riekkola et al., 2018). Our progesterone EIA kit (EIA kit 900-011, ENZO Life Sciences) had a 100% reactivity with progesterone and an assay detection limit between 15 and 500 pg/ml. Two additional standard dilutions were added to allow for a lower detection limit of the standard curve to 3.81 pg/ml. We determined extraction efficiency by spiking subsamples of blubber from a dead, stranded animal of known pregnancy status, with 150 ng of progesterone and including these with every extraction (Kellar et al., 2006). We calculated the percentage of progesterone recovered after each extraction and adjusted each sample concentration to this efficiency prior to statistical analyses. An extraction efficiency >60% was adequate and is based on the reported range of efficiencies seen using these methods (Kellar et al., 2006). If the efficiency of an extraction set was <60%, the sample extracts were discarded, and the blubber samples were re-extracted and re-analyzed. Each assay was evaluated for color development using a Biotek plate reader Epoch (Gen5™ software [Biotek]) with reading and correction wavelengths of 405 and 630 nm. Blubber hormone concentrations were then transformed into nanograms of progesterone per gram of blubber (wet weight).

2.4 | Pregnancy classification

We assigned pregnancy of female humpback whales following previously published methods (Pallin, Robbins, et al., 2018). Biopsy samples ($n = 29$) were collected from individuals of a known life-history stage from the Gulf of Maine feeding aggregation by the Center for Coastal Studies in Provincetown, MA. Using these control samples from the Gulf of Maine, the pregnancy state relative to blubber progesterone concentrations was modeled using a standard logistic regression model (Kellar et al., 2017). Each WAP humpback sample of unknown pregnancy status was entered into the model, and the model returned a probability of being pregnant for each female sampled (Kellar et al., 2017). If the probability of being pregnant was >99.9%, that female was given an assignment of pregnant. If the probability of being pregnant was <0.1%, that female was assigned as not pregnant. If a biopsied female's probability of being pregnant was between those two bounds, that female was set as undetermined pregnancy.

2.5 | Pregnancy rates

Using this approach, we could estimate the proportion of pregnant females in all samples, including those with an assignment probability between 0.1% and 99.9% (i.e., undetermined pregnancy state). This was accomplished by taking the sum of the estimated probability of pregnancy for all samples and dividing it by the sample size. Additionally, while calves were not included in the analysis, we cannot account for females sampled that are not yet sexually mature. Thus, the pregnancy rates presented here represent an estimate for all females age 1+.

2.6 | WAP environmental data

Biological and environmental variables were used to describe variations in prey and habitat conditions along the WAP during the summer feeding season. The covariates included two environmental factors (i.e., the day of spring ice edge retreat [sIER], and krill abundance). The sIER was generated using previously published methods (Stammerjohn & Maksym, 2017; Stammerjohn et al., 2008, 2012). The sIER was created using the GSFC Bootstrap SMMR-SSM/I Version 3.1 sea ice concentration time series (1979–2020) from the EOS Distributed Active Archive Center at the National Snow and Ice Data Center (the University of Colorado at Boulder, http://nsidc.org; Comiso, 2017). We identified the day of the sIER for each satellite grid cell (25 by 25 km pixel) and for each sea ice year. A regional WAP average was generated by taking the mean of all the satellite pixels within our defined area. Our defined area encompassed, from north to south, the South Shetland Islands to Adelaide Island, including Marguerite Bay, and from east to west, the coast of the WAP to 200 km offshore (Figure 1). The day of the retreat is defined as the day in which sea-ice concentration decreases below the nominal 'ice edge' threshold (here defined at 15% concentration) and remains below for at least five consecutive days. The day of sIER is reported in year-day for the austral spring–summer and typically ranges from year-day ~250 (September 7) to ~370 (January 5).

Krill (*E. superba*) abundance was assessed following previously published methods (Steinberg et al., 2015). Briefly, krill were collected in net tows (typically 0–120 m) on PAL LTER annual research cruises during austral summer (~1 January to 10 February) since 1993 (Steinberg et al., 2015). The PAL LTER study region extends 700 km along the WAP from Anvers Island to Charcot Island and from coastal to slope waters ~200 km offshore (Ducklow et al., 2007). Sampling grid lines are spaced 100 km apart with grid stations every 20 km along each line. To match the spatial distribution of humpback whale sampling, only data from the North sub-region (400–600 sampling lines, Figure 1) were included in the analysis (Steinberg et al., 2015). During the period considered in this analysis (2011–2019), 12–20 net tows were conducted per year in the North sub-region. The abundance at each sampling station was $\log_{10}$-transformed prior to calculating annual mean abundance (Conroy et al., 2020).

Humpback whales utilize the continental shelf and the coastal bays and fjords along the entirety of the WAP for foraging (Weinstein et al., 2017). Additionally, female humpback whales in this region have previously been described to have high pregnancy rates (Pallin, Baker, et al., 2018). Thus, we specifically tested the effects of both a 1- and 2-year lag of each environmental covariate (Chittleborough, 1958b). We did not test the effects of the year of

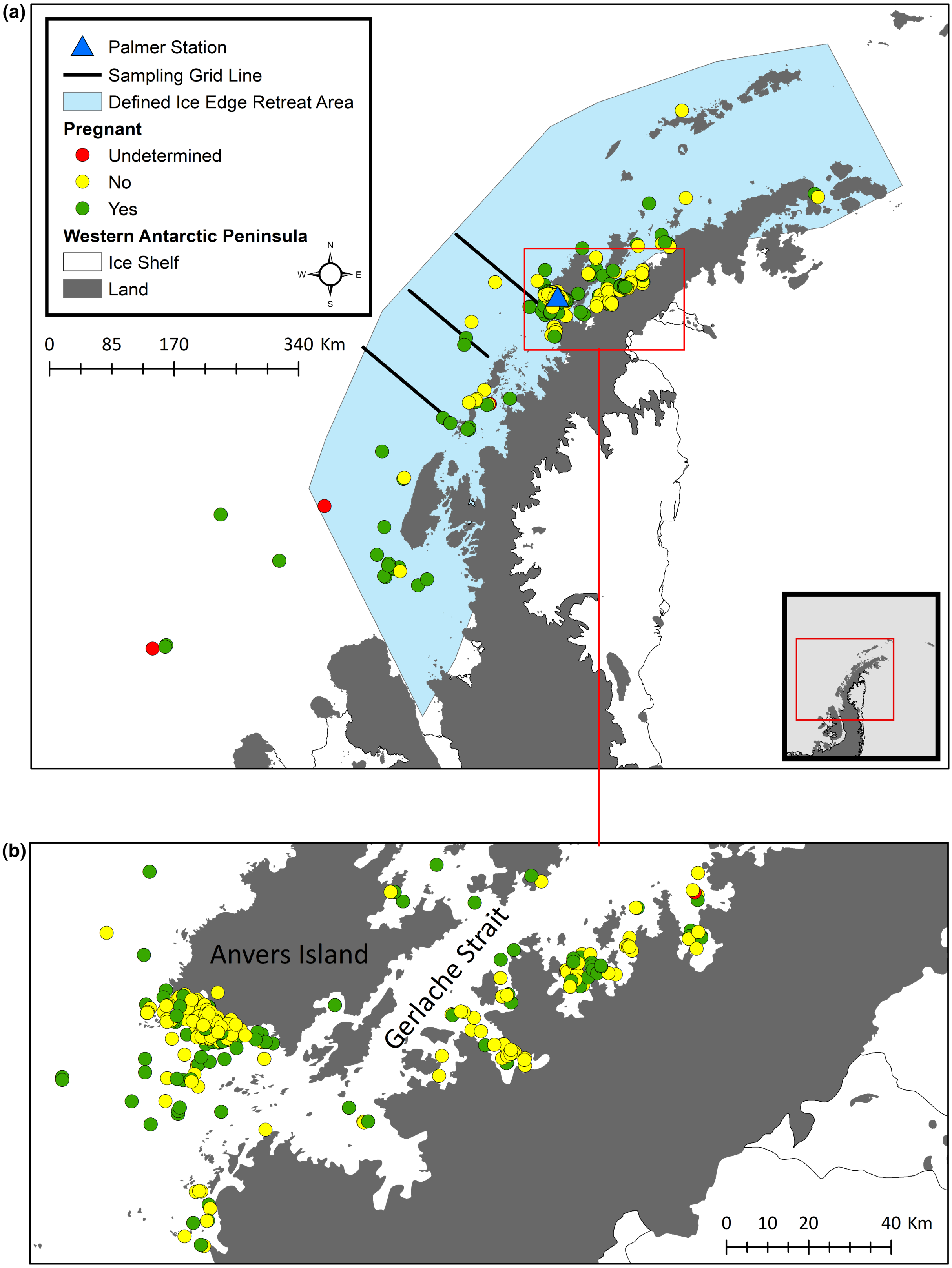

FIGURE 1 Pregnancy status of female humpback whales sampled along the Western Antarctic peninsula (a) and in the Gerlache Strait and adjacent bays (b) during the 2013–2020 field seasons. Maps were created using ArcMap version 10.8.2 (Esri, 2022; https://www.esri.com/en-us/home). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

sampling as we could not account for the time the individual female may have spent along the WAP prior to being sampled.

2.7 | Data analysis

All statistical analyses were performed in R (R Core Team, 2021). We removed all within-year replicates from the data set to avoid re-sample bias in our analyses of interannual variation in pregnancy rates. In this case, the first chronologically collected sample was retained for the analyses. We tested for differences in pregnancy rates across all years by using a χ^2 test of independence. We used a Tukey's post hoc stepwise multiple comparison test to determine if there was a significant difference in pregnancy rates between any two individual years. Lastly, for our analysis of pregnancy rates as a function of environmental covariates, we removed all sample replicates from the analysis, including across-year recaptures. Again, in this instance, the first chronologically collected sample across all 8 years was kept for analysis. We calculated the pregnancy rate anomaly by subtracting the 8-year mean from each year. The normalized values for krill abundance and day of sIER were determined as follows: $y = (x - \min)/(\max - \min)$ to get values between 0 and 1. We considered all statistical tests with a p-value of <.05 significant. All values are expressed as mean ± SD, unless otherwise stated.

We used GLMs with binomial distribution and logit link functions to assess the effects of environmental covariates on humpback whale annual pregnancy rates across 8 years. For all models, variance inflation factors (VIF; >5) and Pearson's correlation coefficients (absolute correlation value >0.7) were calculated for covariates to ensure that correlated covariates were not included together. GLM were optimized using backward selection, accepting the model with the lowest AICc (Akaike Information Criterion corrected).

2.8 | Animal ethics

All research protocols were evaluated and approved under scientific research permits issued by the National Marine Fisheries Service (14,809 and 23,095). The National Science Foundation Antarctic Conservation Act permits (2015-011 and 2020-016) were obtained to conduct biopsy sampling of baleen whales along the Antarctic Peninsula. Oregon State University (OSU) and UC Santa Cruz (UCSC) approved Institutional Animal Care and Use Committee (IACUC) protocols for collecting biopsy samples (OSU permits 4513 & 4943; UCSC permits Friea1706 and Friea2004). Additional sample collection was conducted under the Ministry of Education and Science of Ukraine Permit Series AP No 075-19/2. The samples originating from outside U.S. jurisdiction were imported under the Convention on International Trade in Endangered Species permit numbers 16US50849B/9-19US504849/B, and 20US60410D/9-21US60410D/9. Lastly, all experiments were performed following relevant guidelines and regulations.

3 | RESULTS

3.1 | Individual identification and sex

We collected 669 biopsy samples from age 1+ female humpback whales in the nearshore waters around the WAP in eight field seasons from 2013 to 2020 (Figure 1). On average, 9.96 loci were successfully genotyped per individual. The average PID for any given combination of 7 loci ranged from 1.07×10^{-10} to 6.54×10^{-8}, consistent with previous studies (Pallin, Baker, et al., 2018). Consequently, we considered samples with matching genotype recaptures of the same individual. DNA profiling was sufficient to identify and determine the sex of 584 individual non-calf females from these samples (Table S2). We resampled 54 individuals within the same year (Table S2). Additionally, we recaptured 32 individuals between years (Table S2), with one female recaptured in 2013, 2015, and 2018.

3.2 | Assignment and annual variation in pregnancy

Based on the concentrations observed from the series of spiked controls, our average extraction efficiency was 79.55% ± 14.48% (minimum 61.63%, maximum 129.634). Additionally, our calculated inter-assay and intra-assay coefficients of variation from a series of replicated samples were 6.27% and 8.86%, respectively. We measured progesterone concentrations in 616 samples obtained from 546 individual female humpback whales (Tables 1 and 2, Figure 1). A small number of samples were excluded from the analysis due to within-year re-sampling or insufficient blubber for an extraction. Specifically, 53 of the 669 samples collected did not have blubber for an extraction to take place. Based on the relationship of their progesterone concentration with the reference levels from known pregnant animals (Pallin, Robbins, et al., 2018), 297 samples were assigned as not-pregnant ($p <$.1% pregnant; blubber progesterone: mean = $1.37 \pm 1.35\,\mathrm{ng\,g^{-1}}$;

TABLE 1 Progesterone concentrations ($\mathrm{ng\,g^{-1}}$) of non-calf female humpback whales biopsied along the Western Antarctic Peninsula with a pregnancy assignment

	Mean ($\mathrm{ng\,g^{-1}}$)	SD	Min	Max	N
Not-pregnant	1.37	1.35	0.08	6.86	297
Pregnant	217.20	223.12	19.50	1940.52	306
Undetermined	12.59	2.94	8.88	18.47	13
Total					616

TABLE 2 Summary statistics of pregnancy assignments for non-calf female humpback whales sampled along the Western Antarctic Peninsula during the summer (2013–2020)

			Not-pregnant		95% CL	Pregnant		95% CL
Year	# Samples	# Individuals	*N*	%	Lower-upper	*N*	%	Lower-upper
2013	35	33	18	54.55	36.35–71.89	15	45.45	28.11–63.65
2014	41	40 (39)	7	17.95	7354–33.54	32	82.05	66.46–92.46
2015	48	48	23	47.92	33.29–62.81	25	52.08	37.19–66.71
2016	44	39	18	46.15	30.09–62.82	21	53.84	37.18–69.91
2017	79	75 (72)	10	13.89	6.87–24.06	62	86.11	75.94–93.13
2018	92	86 (83)	38	45.78	34.79–57.08	45	54.22	42.92–65.21
2019	116	109 (105)	56	53.33	43.34–63.13	49	46.67	36.87–56.66
2020	161	140 (139)	98	70.50	62.18–77.93	41	29.50	22.07–37.82
Total	616	570 (558) 546[a]	268	48.03	43.81–52.26	290	51.97	47.74–56.19

Note: Numbers inside parenthesis do not include individuals with an undetermined pregnancy state and are excluded from the following columns. Note this total includes nine females with an undetermined pregnancy state (i.e., the total number of individual females with a definitive pregnancy state used in GLM is 537).

[a] Designates the total number of individual females analyzed for hormones across all 8 years (i.e., across year recaptures have been removed).

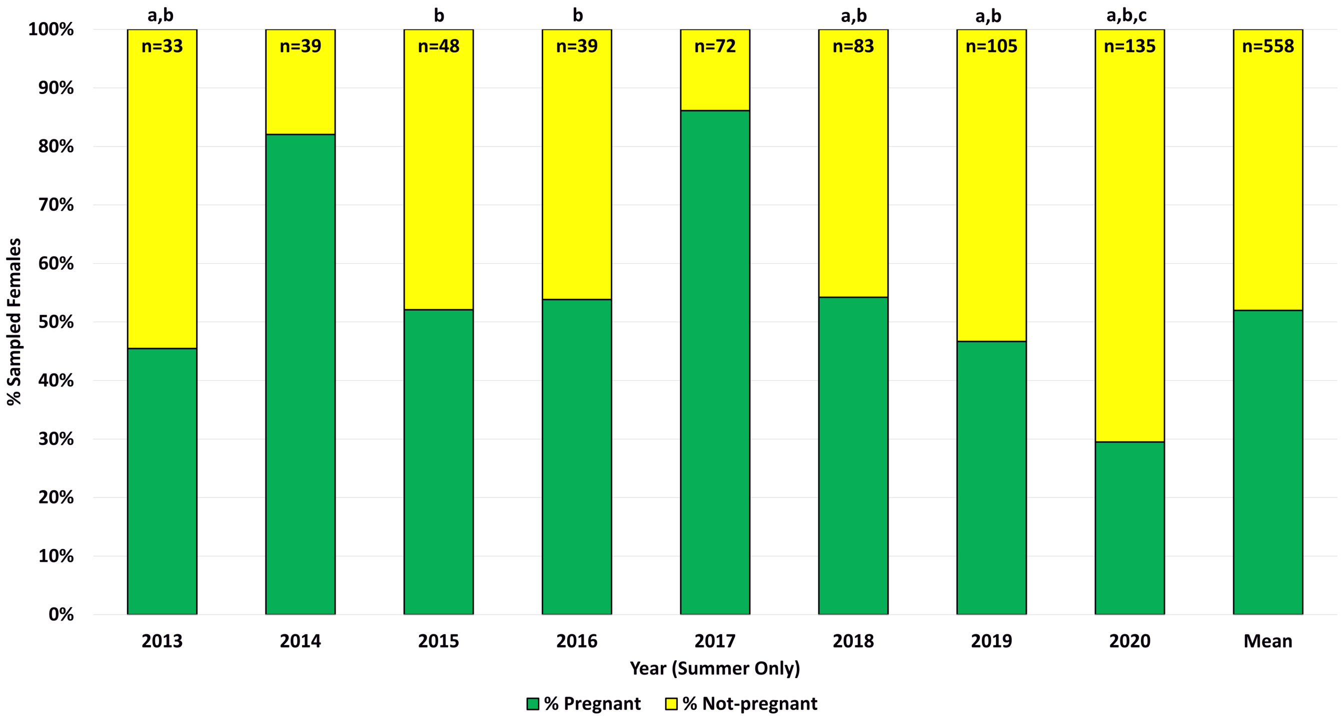

FIGURE 2 Inter-annual variation (summer only) in the proportion of assigned pregnant and not-pregnant (pregnancy rate) non-calf female humpback whales sampled along the Western Antarctic Peninsula based on progesterone concentrations. Within year recaptures have been removed (i.e., n = 558). Post hoc multiple comparisons analysis: a-significantly different from the year 2014; b-significantly different from the year 2017; c-significantly different from the year 2018.

Table 1) and 306 samples were assigned as pregnant ($p > 99.9\%$; blubber progesterone: mean = $217.20 \pm 223.12\,\mathrm{ng\,g^{-1}}$; Table 1). Thirteen samples had a probability of pregnancy between 0.1% and 99.9% (blubber progesterone: mean = $12.59 \pm 2.94\,\mathrm{ng\,g^{-1}}$; Table 1) and were classified as undetermined.

The mean pregnancy rate for all individual females with a definitive pregnancy designation across all 8 years was 51.97% (n = 558, Table 2, Figure 2). Similarly, the estimated proportion pregnant, including females with an undetermined pregnancy state (n = 12), derived from a series of 10,000 bootstrap samples (see Pallin, Robbins, et al., 2018), across all 570 individuals of unknown pregnancy status, was 51.87%. Pregnancy rates varied interannually from 29.50% in 2020 to 86.11% in 2017 (Figure 2). We observed significant variation in pregnancy rates across years ($\chi^2 = 77.85$, df = 7, $p < .001$; $n = 558$, Figure 2). A post hoc multiple comparisons analysis is depicted on Figure 2.

3.3 | Variation in pregnancy rates as a function of regional environmental variation

Of the 546 unique individuals in the entire pregnancy dataset used in this analysis, 537 had a definitive pregnancy state and were used in the model analysis (Table 2). Pearson's correlation coefficients among the four tested environmental variables were <0.7, and the VIF values were <2. Thus, all four variables were included in the model selection process. The time series of pregnancy anomalies and each environmental variable can be seen in Figure 3. GLM models identified that both 1- and 2-year lags of both krill abundance (1-year lag $p < .001$, 2-year lag $p = .044$) and the sIER (1-year lag $p < .001$, 2-year lag $p < .001$) influenced female humpback whale pregnancy rates (Table 3, Figure 4). The deviance explained by the best model was 8.98% (Table 3). Pregnancy rates increased with increasing krill from the previous year (1-year krill lag, *z*-value 4.536; Figure 4) as well as the sIER with both a 1- and 2-year lag (IER 1-year lag, *z*-value 4.222, 2-year lag, *z*-value 3.892). Somewhat surprisingly, pregnancy rates decreased with increasing krill from 2 years prior (2-year krill lag, *z*-value −2.019).

4 | DISCUSSION

This is the first investigation of the relationship between environmental variation and pregnancy rates of baleen whales that feed around the Antarctic. Such information provides a baseline against which effective conservation and management plans can be developed. This is especially relevant because a large-scale krill fishery is rapidly expanding in the region and is in direct competition for krill with baleen whales and other krill predators.

We observed a pregnancy rate of 51.97% across all 8 years of this study; this rate varied from 29.50% in 2020 to 86.11% in 2017. These rates represent an absolute minimum estimate as we cannot differentiate sexually mature and immature females from our samples. Thus, immature females have not been removed from our analyses. Globally, the recovery of humpback whales from 20th-century commercial whaling, especially in the Southern Hemisphere, has been a story of conservation success (Noad et al., 2019; Zerbini et al., 2019). The high pregnancy rates we document here are similar to estimates made for other Southern Hemisphere stocks in the last decade (Noad et al., 2019; Riekkola et al., 2018), as well as the initial estimate of stock G along the WAP between 2010

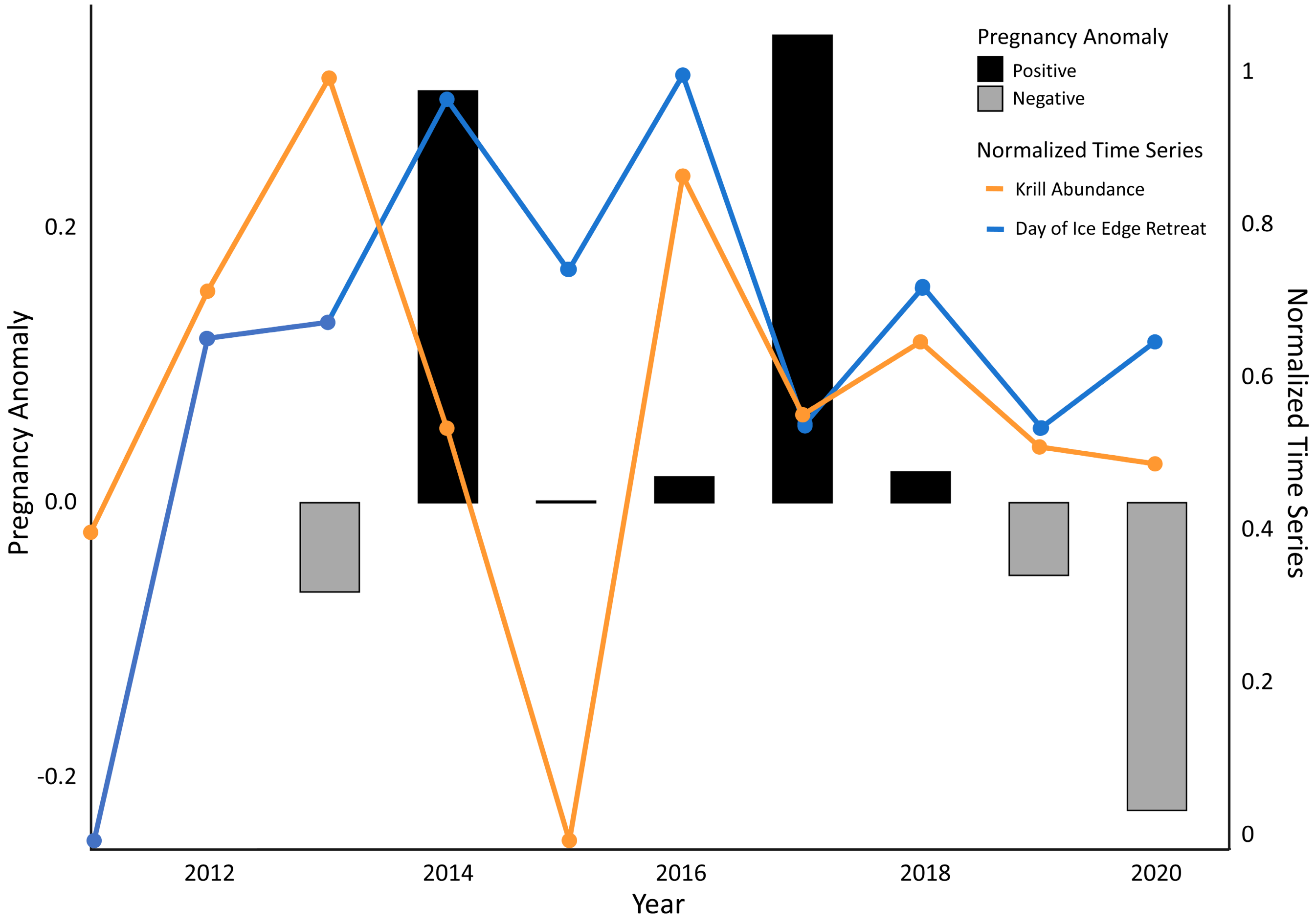

FIGURE 3 Annual time series. Humpback whale pregnancy rate anomalies along the Western Antarctic peninsula from 2013 to 2020 and normalized krill abundance and day of ice edge retreat from 2011 to 2020. See methods for details on anomaly and normalization calculations.

TABLE 3 Results of generalized linear models evaluating variation in annual female humpback pregnancy rates across 8 years as of function of lagged environmental factors (day of spring ice edge retreat (sIER), and krill abundance (krill)) along the Western Antarctic peninsula

	Pregnancy ~	AICc	R^2 adj.	Δ AICc	% dev. Expl.	Weight
1.	**sIER^{-1} + sIER^{-2} + Krill^{-1} + Krill^{-2}**	**687.2**	**0.090**	**0**	**8.98**	**0.747**
2.	sIER^{-1} + sIER^{-2} + Krill^{-1}	689.4	0.084	2.18	8.41	0.251
3.	sIER^{-1} + Krill^{-1}	701.0	0.066	13.82	6.56	0.001
4.	sIER^{-1} + Krill^{-1} + Krill^{-2}	701.5	0.068	14.24	6.79	0.001
5.	sIER^{-2} + Krill^{-1} + Krill^{-2}	703.4	0.065	16.23	6.52	0.000
6.	sIER^{-1} + sIER^{-2} + Krill^{-2}	706.9	0.061	19.68	6.06	0.000

Note: The model in bold is the best fit model. Only the top six models are displayed here. Weight—Relative model support or probability.

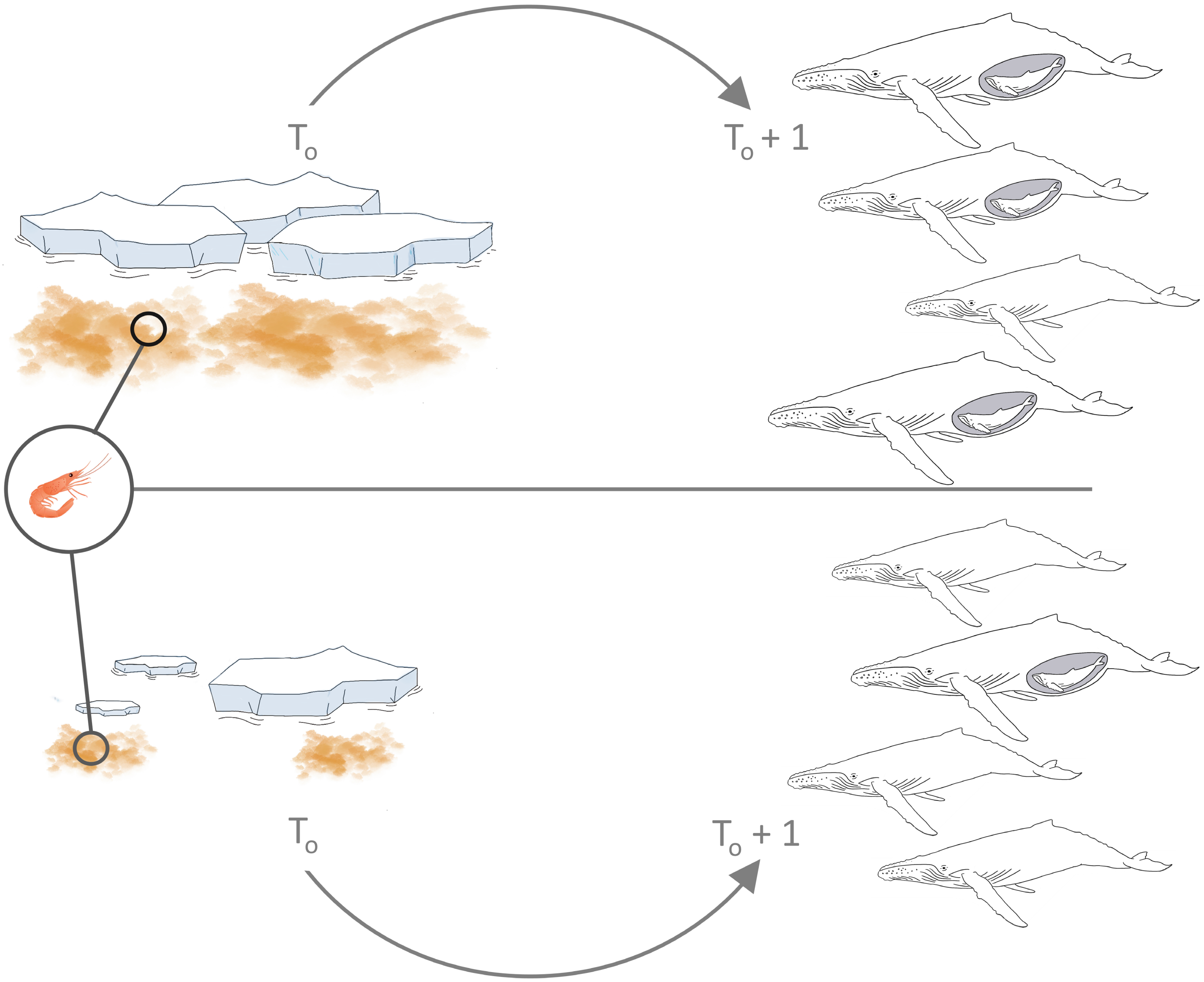

FIGURE 4 Illustration of the results of the generalized linear model showing the effects of krill abundance and the spring ice edge retreat (sIER) on humpback whale pregnancy rates along the Western Antarctic Peninsula. Pregnancy rates were higher in years following high krill and a later sIER (top) and lower in years following low krill and an earlier sIER (bottom). Illustration provided by R. Jones.

and 2016 (Pallin, Baker, et al., 2018). However, we observe significant variability in the 8 years of this study. Similar variation was observed among catches taken during a 6-year period in Antarctic whaling areas IV and V in the early 1950s. However, these latter data are biased because lactating females accompanied by calves were protected by international regulation during this period (Chittleborough, 1958a). It is possible that the inter-annual variation we documented in pregnancy rates could have resulted from temporal match-mismatch among reproductive cohorts, leading to years with heavily inflated or deflated reproductive rates. This variation could also result from sampling bias or spatial heterogeneity in which different reproductive classes distribute preferentially along the WAP. We believe these latter sources of uncertainty to be unlikely in our results because we sampled whales opportunistically over a large portion of their known range in this region (Weinstein & Friedlaender, 2017).

We show that the pregnancy rate of humpback whales was positively related with krill abundance from the previous year but, surprisingly, inversely related with krill abundance from 2 years prior. Previous studies of baleen whales and their reproductive rates show equivalent responses to variation in prey availability and oceanographic and sea ice conditions (Kershaw et al., 2021; Leaper et al., 2006; Meyer-Gutbrod et al., 2015; Meyer-Gutbrod & Greene, 2018). Specifically, a lagged negative relationship between krill availability and the breeding success of southern right whales was observed at South Georgia (Leaper et al., 2006). Similarly, low reproductive rates were observed among female humpback whales within the Gulf of St Lawrence. These were also associated with low prey availability, which led to insufficient energy reserves to maintain pregnancy (Kershaw et al., 2021). Here we show that prey availability in the previous year is the most robust predictor of pregnancy when females are gaining/storing energy for the upcoming pregnancy.

Achieving and maintaining pregnancy is contingent on having access to sufficient prey resources to support the high energetic costs of gestation and lactation. More specifically, an increase in stored energy reserves is required prior to pregnancy (i.e., the feeding season prior to breeding; Miller et al., 2012), followed by a continued accumulation of energy stores to support the development and growth of the fetus throughout the pregnancy (Lockyer, 1981). While migrating and breeding, these whales rely solely on stored energy reserves (Lockyer, 1981). Thus, we observed that higher krill abundances the year prior to sampling led to increased pregnancy rates across the population. What is more challenging to interpret is how higher krill availability 2 years prior results in lower pregnancy rates. We believe this is likely a result of most females breeding once every 2 years (Chittleborough, 1958b), which would be consistent with our observed mean pregnancy rate of around 52%. This 2-year cycle may result in a larger non-reproductive cohort occurring in years of high krill availability 2 years prior, as observed in this study.

We found significant positive relationships between female humpback whale pregnancy rates and the sIER from the 2 years prior. The sIER is a powerful physical force affecting biological processes at all trophic levels within the WAP marine ecosystem (Saba et al., 2014). During a late sIER, many of the dynamic physical oceanographic properties of the WAP ecosystem are stabilized. For example, higher stratification in the water column is created via two mechanisms. First, reduced wind speeds prevent the formation of a deep mixed layer. Second, salinity-driven density gradients are increased because of higher volumes of sea ice meltwater at the surface (Saba et al., 2014). Together, these provide favorable, nutrient-rich conditions high in the water column, triggering intense phytoplankton blooms (Ducklow et al., 2013), supporting the growth and survival of large krill cohorts (Ross et al., 2008). Thus, from an energetic perspective, a later sIER would likely provide female humpback whales the required energy reserves for their upcoming migration and pregnancy via a larger prey base on which to forage.

Responses in the reproductive rates of baleen whales to climate change have been documented previously (Cartwright et al., 2019; Kershaw et al., 2021; Leaper et al., 2006; Simard et al., 2019), and long-term studies are vital to detect such responses. It has been proposed that the rapid recovery of humpback whales in this region is due to a lack of competition due to the slower recovery of other large, krill-consuming predators (Laws, 1977; Pallin, Baker, et al., 2018). In contrast, our study suggests that pregnancy rates of humpback whales are significantly affected by broad-scale ecological variables that directly affect prey abundance and availability. Thus, while this humpback whale population currently has high pregnancy rates, the significant inter-annual variation in these rates (in direct relation to krill availability) shows that this population's trajectory is tightly coupled with prey availability, which can be mediated by environmental change. Therefore, during unfavorable foraging conditions, fewer females will become pregnant (Fleming et al., 2016). Thus, future warming along the WAP that results in a subsequent reduction in prey abundance will likely negatively impact this population of humpback whales and other krill predators in this region (Klein et al., 2018; Watters et al., 2020).

Our results add a critical new facet to a growing body of work regarding cetaceans and competition with the growing krill fishery (Reisinger et al., 2022). We suggest a need for immediate management actions to mitigate the negative impacts to both baleen whales and Antarctic krill stocks. Significant spatio-temporal overlap exists between humpback (and other baleen) whale foraging areas and krill fishing leading to both direct (e.g., entanglements, Welsford et al., 2022) and indirect (e.g., competition, Reisinger et al., 2022) interactions that require attention (Johnson et al., 2022; Weinstein et al., 2017). With the additional stressor that rapid warming is having on krill stocks, it seems prudent to be proactive and remove unnecessary pressure for krill predators. The Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) is responsible for the conservation and maintenance of ecosystem function, krill stocks, and commercial fishing, including implementing conservation measures defining and regulating the total allowable catch, spatial and temporal rules of the fishery, and monitoring of krill dependent species (CCAMLR, 2010, 2021). CCAMLR must utilize this along with other new knowledge on baleen whale foraging ecology and demography (i.e., Bierlich et al., 2022; Pallin, Bierlich, et al., 2022; Pallin, Botero-Acosta, et al., 2022; Pallin, Robbins, et al., 2018; Reisinger et al., 2022), along with the impact that both environmental variability and krill fishing have on this group of krill predators, to improve and modernize current ecosystem-based management plans. This may help push forward CCAMLR's 2011 commitment to implement a Marine Protected Area system in the region (i.e., CCAMLR Conservation Measure 91-04, see https://cm.ccamlr.

org/en/measure-91-04-2011). Other key players have a role in developing and implementing science-based conservation strategies for whales that will influence the outlook of this population, including the International Whaling Commission, International Union for the Conservation of Nature Specialist Groups, Convention on Biological Diversity, Convention on the Conservation of Migratory Species of Wild Animals, the commercial fishing industry and the United Nations Framework Convention on Climate Change. Only with enhanced cooperation, can we ensure this population has the greatest success of recovery from commercial depletion in an environment that is changing rapidly.

We show significant variation in the pregnancy rates of humpback whales feeding along the WAP. Humpback whales are sentinel species of ecosystem health (Bengtson Nash et al., 2018). As such, changes in vital rates (i.e., pregnancy rates) can provide quantifiable signals of the impact of environmental change at the population level. We found a robust relationship between environmental variation and interannual variability in humpback whale pregnancy rates. These relationships align with similar observations among other baleen whales (Kershaw et al., 2021; Leaper et al., 2006) and other Antarctic krill predators such as Antarctic fur seals and gentoo penguins (Reid et al., 2006). This information will assist in monitoring, management, and conservation efforts as changes continue to occur along the WAP. Continued support of long-term ecological programs is critical to understanding the population dynamics of long-lived species relative to environmental trends occurring over long time scales. Our data are in marked contrast to the argument that krill stocks are in surplus and overabundant for the needs of krill predators. On the contrary, we found that variation in krill availability in this region are tightly coupled with the reproductive rates of some of the largest krill predators in the region. As a result, continued warming and increased fishing along the WAP which continue to reduce krill stocks, will likely impact this humpback whale population, and other krill predators in the region. Humpback whales are sentinel species of ecosystem health, and changes in pregnancy rates can provide quantifiable signals of the impact of environmental change at the population level. This study was fundamental in its methodological approach to a wild species that has a global distribution. A number of populations of related species are experiencing similar changes in their environment and this study can act as a template for similar comparison in those systems.

AUTHOR CONTRIBUTIONS

Logan J. Pallin and Ari S. Friedlaender assisted in the project concept and design, assisted in data collection, and analyses. David W. Johnston, Doug P. Nowacek, Andrew J. Read assisted in project concept and design and data collection. Nick M. Kellar, Oscar M. Schofield, Sharon E. Stammerjohn, Deborah K. Steinberg and Daniel P. Costa assisted in project concept and design and data analysis. Chris M. Johnson assisted in project concept and design. Ross C. Nichols and Oksana Savenko assisted in data collection. Natalia Botero-Acosta, Debbie Steel, Charles S. Baker, Jack A. Conroy assisted in data analysis. All authors participated in drafting the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no competing interests.

DATA AVAILABILITY STATEMENT

The datasets supporting this article have been placed in a dryad repository and can be found at https://doi.org/10.5061/dryad.9zw3r22j7.

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SUPPORTING INFORMATION

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