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Cite this article: Paterson JT, Rotella JJ, Arrigo KR, Garrott RA. 2015 Tight coupling of primary production and marine mammal reproduction in the Southern Ocean. *Proc. R. Soc. B* **282**: 20143137. http://dx.doi.org/10.1098/rspb.2014.3137

Received: 30 December 2014
Accepted: 17 March 2015

Subject Areas:
ecology

Keywords:
polynyas, primary production, Antarctica, trophic levels, Weddell seal

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Tight coupling of primary production and marine mammal reproduction in the Southern Ocean

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Polynyas are areas of open water surrounded by sea ice and are important sources of primary production in high-latitude marine ecosystems. The magnitude of annual primary production in polynyas is controlled by the amount of exposure to solar radiation and sensitivity to changes in sea-ice extent. The degree of coupling between primary production and production by upper trophic-level consumers in these environments is not well understood, which prevents reliable predictions about population trajectories for species at higher trophic levels under potential future climate scenarios. In this study, we find a strong, positive relationship between annual primary production in an Antarctic polynya and pup production by ice-dependent Weddell seals. The timing of the relationship suggests reproductive effort increases to take advantage of high primary production occurring in the months after the birth pulse. Though the proximate causal mechanism is unknown, our results indicate tight coupling between organisms at disparate trophic levels on a short timescale, deepen our understanding of marine ecosystem processes, and raise interesting questions about why such coupling exists and what implications it has for understanding high-latitude ecosystems.

1. Introduction

High-latitude marine environments are subject to extreme variations in both photoperiod and amount of open water as the extent of sea ice seasonally expands and contracts [1–4]. Primary production (the amount of organic carbon produced by photosynthetic organisms at the base of the food chain) is highly dependent upon the amount of available light [5]. Though localized increases in primary production have been documented under first-year sea ice in the Arctic and Antarctic [6,7], the majority of primary production associated with phytoplankton blooms occurs in areas of open water. The extremes of the photoperiod and changes in the amount of open water exposed to solar radiation in these environments help to explain the large variation in intra-annual primary production. The maximum amount of production occurs during the polar spring and early summer when photosynthetic organisms take advantage of the increase in incident solar radiation and decline in sea-ice cover and form 'blooms' [8,9].

In the sea-ice zones of both polar oceans, polynyas are recurrent regions of open water surrounded by ice [10]. They have long been associated with large numbers of marine mammals and birds and increased amounts of primary production relative to proximal ice-covered areas [11,12]. Many polynyas in the Arctic occur well south of the Arctic Circle and receive sunlight throughout the year and can thereby remain productive. By contrast, all polynyas in the Antarctic occur south of the Antarctic Circle experience minimal sunlight and are non-productive during the polar winter [13]. In both polar oceans, they remain biologically important even as the surrounding sea ice melts in the polar spring. During this time, polynyas are the first areas exposed to the increasing sunlight and are a comparatively localized source of increased primary production in polar oceans [12,14].

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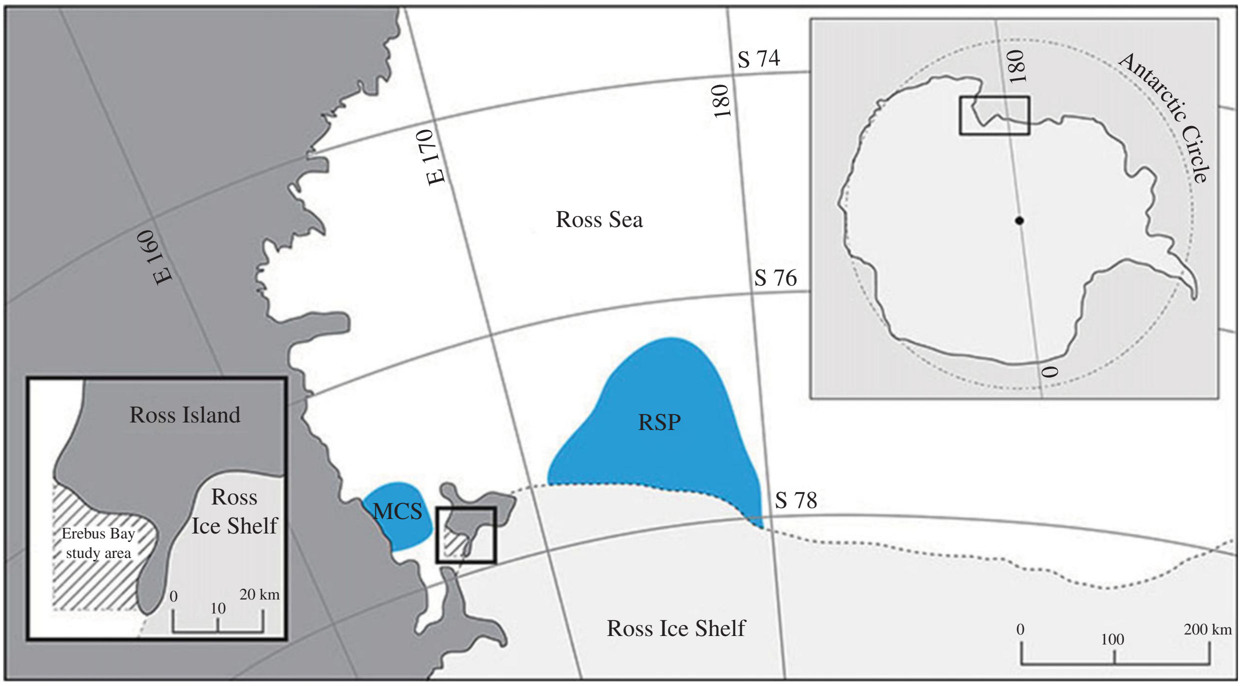

Figure 1. The Ross Sea hosts both the Ross Sea polynya (RSP) and McMurdo Sound polynya (MCS). Locations above are approximate as the areal extent of the polynyas demonstrates significant amounts of interannual variation. The long-term mark–recapture study has focused on the breeding colonies of Weddell seals in Erebus Bay, proximal to the Ross Ice Shelf and Ross Island.

Polynyas form through two, non-mutually exclusive, forcing processes. Mechanically forced polynyas form as a result of wind stress or ocean currents advecting sea ice, whereas localized high-oceanic-heat-flux, or upwelling ocean currents, form convectively forced polynyas [10]. The formation mechanism partially controls primary production in a polynya by influencing factors such as water-column stratification, nutrient availability and temperature [15]. Phytoplankton assemblages vary considerably between polynyas and reflect the diverse interaction of formation mechanisms and environmental conditions [16,17]. Previous work has revealed a rich interplay among regulatory mechanisms that act on these primary producers and influence the timing and magnitude of primary production in polar oceans [18–21]. The strength of connections between primary production and vital rates of upper trophic-level consumers such as birds, seals and whales that are known to take advantage of polynyas remains unclear [22–25] given contrasting results from previous work in Antarctica. For example, one study indicated that enhanced primary production in the Ross Sea polynya does not appear to translate into increased biomass of upper trophic-level predators such as whales and penguins [17], whereas another study using different methods suggested that the colony size of Adélie penguins (*Pygoscelis adeliae*) is positively associated with primary production in polynyas, where penguin rookeries are strongly associated with local polynyas [14].

The Ross Sea overlies the continental shelf in eastern Antarctica (figure 1) and is the most biologically productive area in the Southern Ocean [18,26], though the expansion of sea ice and reduced photoperiod inhibits large-scale primary production during the austral winter. There is debate on the relative contribution of mechanical and convective forcing mechanisms to the formation of the eponymous polynya [27,28]. Recent work suggests both synoptic-scale winds and warm-water upwelling from the Modified Circumpolar Deep Water current contribute to the formation of the Ross Sea polynya [29]. The haptophyte *Phaeocystis antarctica* dominates the phytoplankton assemblage in the Ross Sea polynya, with smaller abundances of various diatoms. The former prefer the comparatively poorly stratified waters of the central Ross Sea, and the latter the well-stratified waters along the edge of the ice [13].

The McMurdo Sound polynya is one of several coastal polynyas that form along the western edge of the Antarctic continent. Like other coastal polynyas in the region, its areal extent and total primary production are much lower than that of the Ross Sea polynya [14]. In general, the coastal polynyas are formed by katabatic winds advecting ice away from the coast [30]. High rates of sea-ice melting in the austral spring and summer induce a strong stratification of the water column later in the season [31]. Previous work has suggested that the stratification in turn favours the dominance of diatoms in the phytoplankton assemblages in many coastal polynyas [14,32–34]. The Ross Sea and McMurdo Sound polynyas form via different forcing mechanisms that differentially influence the phytoplankton assemblages responsible for primary production.

The responsiveness of consumers to variation in primary production in the Ross Sea is relatively poorly known [23]. In general, consumer response to changes in resource abundance is complex and dependent upon a variety of characteristics of both the ecosystem and organism (reviews in [35,36]). A common model for consumer–resource interaction envisions time lags of varying lengths between changes in resource availability and the response of consumers, presumably to allow energy transfer up through trophic levels or the spatial rearrangement of consumers (e.g. [37,38]). Intriguingly, however, studies in several taxa have suggested that consumers use unknown cues to anticipate future resources and increase current reproductive effort to take advantage of anticipated abundances [39–42]. Using a lengthy time series of vital rates for a well-studied carnivore, we report on previously unknown connections between primary productivity in the two Antarctic polynyas studied here and the number of Weddell seal (*Leptonychotes weddellii*) pups born nearby each year during 1997–2012.

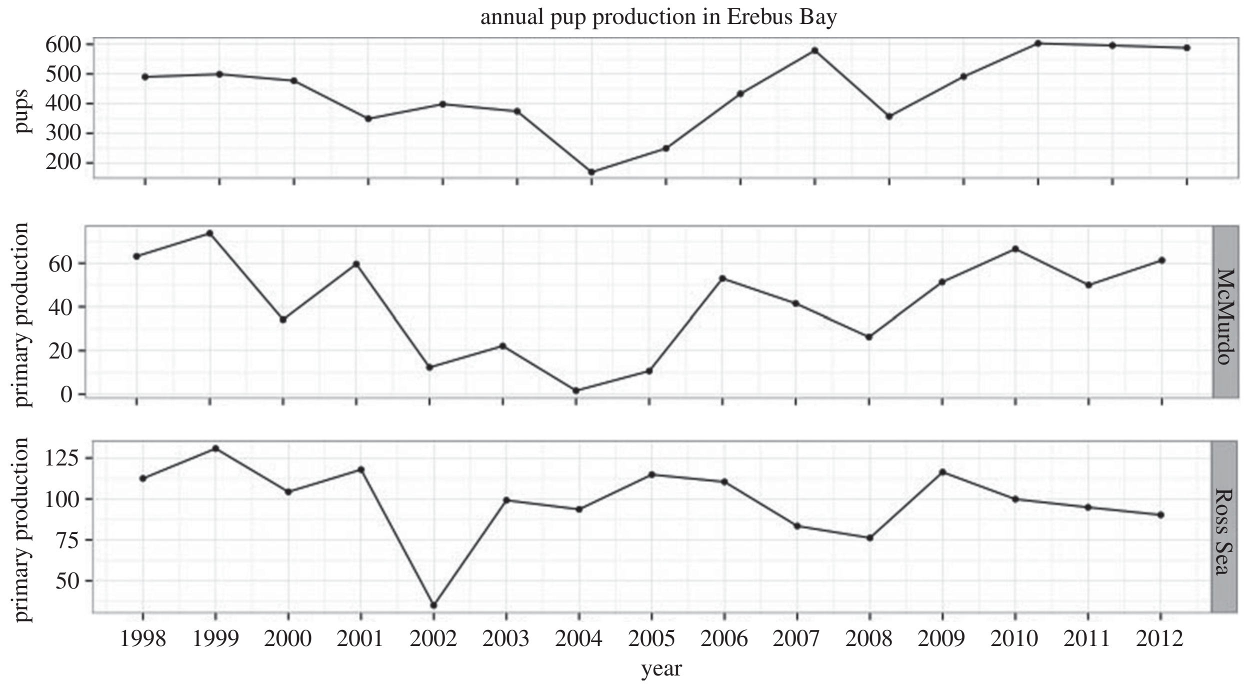

Figure 2. The number of pups born in the Erebus Bay seal colonies between 1997 and 2012 ranges from 169 (2004) to 603 (2007). Primary production (g C m^{-2} yr^{-1}) in both the McMurdo Sound polynya and Ross Sea polynya demonstrates a high degree of interannual variability.

Moreover, we suggest the differential results found for each polynya are due to the different physical forcing mechanisms responsible for the development of each polynya and their influences on assemblages of primary producers. We are the first to investigate a potential connection between a high-trophic-level, fish-eating predator and the magnitude of primary production in different types of polynyas.

2. Material and methods

Primary production was estimated for each polynya from 1997 to 2012 using satellite ocean-colour data from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and MODerate Resolution Imaging Spectrometer (MODIS) [31]. Total primary production per year for each polynya was calculated by first converting chlorophyll a (Chl α) concentrations to primary productivity rates at each pixel [18], and then integrating the rates over the length of the growing season. The estimates of primary production were first standardized to yield values with a mean of zero and unit variance.

Breeding colonies of Weddell seals along the western edge of Ross Island are the subject of a long-term mark–recapture study (1971 to present [43]). Each year during the austral spring (October and November), all pups born are individually marked during repeated visits to the colonies every 2–3 days. Between five and eight complete surveys of the entire area are also conducted each field season. The intense sampling effort allows for a high degree of confidence in the number of pups born into the colonies. For this study, we used the numbers of pups born per year from a subset of the long-term data (1997–2012) that matches the years for which satellite-based estimates of primary production are available in the two polynyas and that also encompassed large annual variation in pup numbers [44].

These two long-term datasets were used to evaluate potential relationships between the number of pups born in Erebus Bay and primary production in the Ross Sea and McMurdo Sound polynyas (figure 2). In the light of the uncertainties regarding the coupling of primary production and the vital rates of upper trophic-level consumers in this system, we developed a series of models (table 1) for the relationship between pup numbers and standardized values of primary production. We proposed models to investigate potential differences in the strength of the association between primary production in either or both of the two polynyas and the number of pups by comparing models using primary production at different time lags. Preliminary analyses of the relationship used a variety of time lags for standardized values of primary production to model the number of pups born each year, and suggested the most support for models with time lags of 0 years (primary production in year t) and 1 year (primary production in year $t - 1$). Accordingly, models with time lags of 0 and 1 year are presented in detail here. Models that regress the number of pups in year t on the magnitude of primary production in year t propose that the number of Weddell seal pups is associated with primary production in the same year, whereas those using primary production in year $t - 1$ propose a 1-year lag in the association.

Interpreting individual coefficients of a model in which collinearity exists between the predictors is a recognized and long-standing problem in ecological modelling [45]. Our study depends on interpreting both the magnitude (to judge the relative strength of the relationship between primary production in the two polynyas and the number of pups born in Erebus Bay) and the sign of the regression parameters. However, collinearity among predictor variables makes a comparative assessment of regression parameters problematic insofar as it inflates the variance of the estimated parameters, potentially obscuring relationships in the data. In this study, primary production in McMurdo Sound and Ross Sea polynyas in the same year were moderately correlated ($\rho = 0.51$) in our data. We addressed the collinearity issue by using a Bayesian perspective on classical ridge regression that shrank our regression coefficients towards zero to appropriately penalize for multicollinearity [46–48]. We assumed exchangeability for the regression coefficients for primary production and assigned the prior distribution: $\beta_i \sim$ Normal (0,rho) and rho ~ Inv-Gamma (0.001, 0.001) for i=1,2,3,4. Model comparison was done using the WAIC (widely applicable information criterion), a fully Bayesian information criterion [49] whose interpretation is similar to AIC, i.e.

lower values indicate a more parsimonious model [50,51]. Relative support for models is based on the comparison of WAIC values to the top model (ΔWAIC = WAIC(model) – WAIC(top model)), similar to the interpretation of ΔAIC values. R^2 values were calculated using the mean of the variance of the (posterior) simulations for residuals to estimate the expected value for the variance of the residuals (proportional to the residual sum of squares in classical regression)

$$R^2 = 1 - \frac{E(\mathrm{Var}\ \boldsymbol{\epsilon})}{\mathrm{Var}\ \boldsymbol{C}},$$

where $\boldsymbol{\epsilon} = \epsilon_1, \ldots, \epsilon_{15}$ and $\boldsymbol{C} = (C_1, \ldots, C_{15})$ are the vectors of residuals and counts of pups for $i = 1–15$ years (1997–2012) [52].

Table 1. Based on the fully Bayesian WAIC (widely applicable information criterion), the data strongly indicate that the number of pups produced in year t is best modelled as a function of primary productivity in the McMurdo polynya (McM) and Ross Sea polynya (Ross) at year t, model 7 (ΔWAIC scores are calculated by subtracting the lowest score from all other scores [$\mathrm{WAIC}_{\mathrm{Model}\ 7} = 178.62$] such that the best-supported model has a ΔWAIC score of 0 and more poorly supported models have larger values).

models: pups$\sim N(\mu, \sigma^2)$	ΔWAIC	R^2	α, intercept	McM_{t-1}, β_1	McM_t, β_2	Ross_{t-1}, β_3	Ross_t, β_4
1: $\mu = \alpha$	12.85	0.00	437.18 (366.65, 504.95)				
2: $\mu = \alpha + \beta_1 \mathrm{McM}_{t-1}$	9.92	0.21	438.53 (372.01, 502.86)	43.03 (−4.18, 121.04)			
3: $\mu = \alpha + \beta_2 \mathrm{McM}_t$	4.84	0.47	440.72 (384.68, 493.23)		79.95 (−0.15, 138.80)		
4: $\mu = \alpha + \beta_3 \mathrm{Ross}_{t-1}$	12.99	0.00	437.12 (363.75, 506.92)			5.00 (−16.78, 56.19)	
5: $\mu = \alpha + \beta_4 \mathrm{Ross}_t$	12.98	0.00	437.67 (366.48, 507.94)				0.83 (−30.58, 37.03)
6: $\mu = \alpha + \beta_1 \mathrm{McM}_{t-1} + \beta_3 \mathrm{Ross}_{t-1}$	11.36	0.09	437.94 (368.34, 505.33)	27.84 (−7.43, 116.94)		−0.36 (−51.05, 43.26)	
7: $\mu = \alpha + \beta_2 \mathrm{McM}_t + \beta_4 \mathrm{Ross}_t$	0	0.62	441.13 (396.54, 483.96)		108.17 (0.07, 163.34)		−49.54 (−101.59, 3.89)
8: $\mu = \alpha + \beta_1 \mathrm{McM}_{t-1} + \beta_4 \mathrm{Ross}_t$	11.21	0.13	438.90 (370.12, 502.04)	27.96 (−5.50, 111.21)			4.74 (−34.05, 56.92)
9: $\mu = \alpha + \beta_2 \mathrm{McM}_t + \beta_3 \mathrm{Ross}_{t-1}$	7.22	0.34	439.90 (383.07, 495.25)		63.60 (−1.74, 129.86)	7.86 (−38.04, 56.66)	

3. Results

The time series used for this model represent a wide range of values for both primary production and the number of pups (figure 3), as well as annual variation in the extent of sea ice (see Discussion). Model-selection results (table 1) strongly suggest that model 7 is the most parsimonious model and much better supported than all other models (ΔWAIC > 4.84 for all other models). Model 7 explained a considerable amount of the variation in the number of pups born in the study area ($R^2 = 0.62$) based on primary production in the McMurdo Sound and Ross Sea polynyas. In model 7, the number of pups in year t has a positive association with the total primary production in the McMurdo Sound polynya in year t and a negative association with total primary production in the Ross Sea polynya in year t (figure 4). Model results suggest that the number of pups for a year with average productivity in both polynyas is approximately 441 (95% credible interval: 396.54–483.96). An increase of 1 s.d. in primary production within the McMurdo Sound polynya is associated with a sizeable increase of 108 pups (95% credible interval: 0.07–163.34); the same increase in primary productivity in the Ross Sea polynya is associated with a more moderate decrease of 49 pups (95% credible interval: −101.59 to 3.88). Thus, it appears that pup production in Erebus Bay is more tightly linked to primary production in the smaller but closer McMurdo Sound polynya than to production in the larger but more distant Ross Sea polynya.

The pattern of positive association between the magnitude of primary production in the McMurdo Sound polynya and the number of pups born in Erebus Bay is consistent across less-supported models (table 1 and figure 4), e.g. the second most-supported model (model 3, ΔWAIC = 4.84, $R^2 = 0.47$), despite being a considerably poorer model than model 7, includes the same positive association for the McMurdo Sound polynya but ignores production in the Ross Sea polynya.

Models that included data on primary production in year $t - 1$ in either or both polynyas performed much worse than did models that included information on primary production in the current year. For example, a model containing information from both polynyas in year $t - 1$ (model 6, table 1) had a ΔWAIC value of 11.36 and explained little of the variation ($R^2 = 0.09$) in annual pup production. Thus, our results provide much stronger support for the hypothesis that current-year production is related to pup production than for the idea that pup production lags primary production by a year.

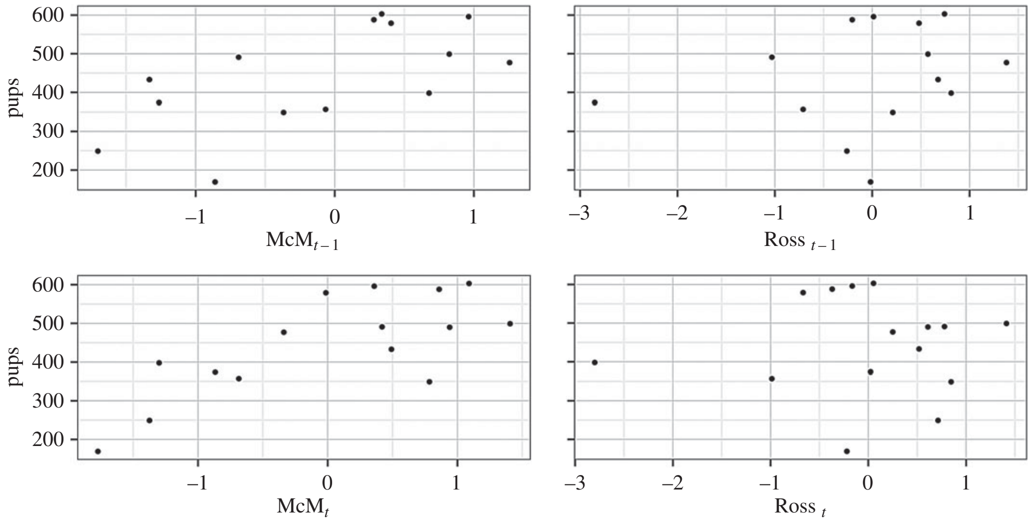

Figure 3. Scatterplots of standardized values of primary production in the McMurdo Sound (McM) and Ross Sea (Ross) polynyas for two time lags (year $t-1$ and t) against the number of Weddell seal pups born in year t.

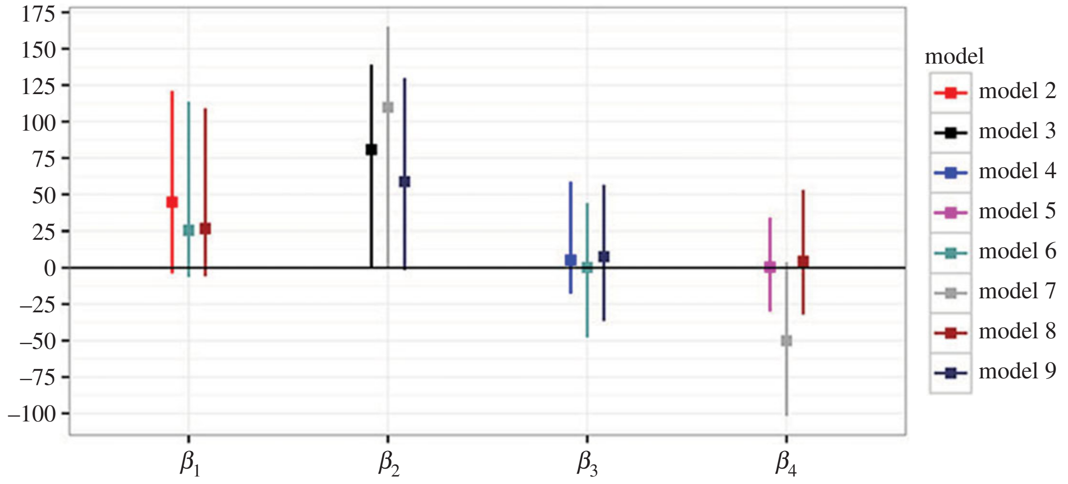

Figure 4. Model results comparing the different 95% credible intervals for the approximate distributions of the regression coefficients suggest a positive association between standardized values of primary productivity in McMurdo at time $t-1$ (β_1) and t (β_2) and the number of pups born in Erebus Bay at time t. There is comparatively little evidence for a relationship between the number of pups born in Erebus Bay and primary production in the Ross Sea polynya in year $t-1$ (β_3) and year t (β_4).

4. Discussion

The difference between the association of primary production in the Ross Sea and McMurdo Sound polynyas to the number of pups born in Erebus Bay is stark. Our results suggest the number of pups is strongly, positively associated with primary production in the McMurdo Sound polynya and less strongly, negatively associated with the Ross Sea polynya. In the Ross Sea polynya, the surge in phytoplankton abundance each spring, which is responsible for increased primary production, is thought to be effectively decoupled from the grazing pressure exerted by zooplankton [32,34]. The phytoplankton assemblage is dominated by *P. antarctica* [34], a species that forms colonies consisting of hundreds of individual cells [53]. Previous work has suggested that zooplankton are incapable of effectively grazing the colonies due either to their large size [54] or their high growth rates [34]. For either hypothesis, the increase in *P. antarctica* may not be matched by an increase in the abundance of consumers such as krill, birds, seals and whales. The various coastal polynyas, including McMurdo Sound, are primarily mechanically forced by intense katabatic winds. These winds are several times stronger than the synoptic-scale wind that drives the Ross Sea polynya. The strength of the katabatic winds in the early spring induces deep mixing of the water column and inhibits phytoplankton blooms [18]. By the time the winds have diminished to the point that melting sea ice can induce stratification, the upper layers of the water column are consistently exposed to increased solar radiation [18,32], which is comparatively inhospitable to the shade-adapted *P. antarctica* [34]. Diatoms dominate these well-stratified waters and prior work has demonstrated that the diatom assemblages are more effectively grazed by zooplankton [55]. The results from our study are partially consistent with a view of ecosystem functioning whereby a high degree of coupling exists between trophic levels in the diatom-dominated McMurdo polynya. However, this traditional description of the ecosystem would also suggest little to no influence of primary production in the *P. antarctica*-dominated Ross Sea polynya on the number of pups due to the decoupling between trophic levels, which is in contrast to the negative association suggested by our top model. Though further work is needed to characterize the coupling of trophic levels in the Ross Sea, our results certainly suggest that primary production is not completely decoupled from the upper trophic levels.

Moreover, model-selection results are somewhat surprising given the timing of pupping (October and November of year t) and the measurements of total primary production (October of year t through March of year $t+1$). Specifically, we find evidence that more pups tend to be born in October and November when primary production at that time and in the following few months is higher in the McMurdo Sound polynya and lower in the Ross Sea polynya (model 7). Because linkages between abiotic and biotic processes in the Ross Sea ecosystem are poorly understood, we currently lack an obvious proximate causal mechanism that could explain the surprising timing of the relationship. Accordingly, we are forced to speculate about the potential mechanisms that are responsible for the strong correlation we detected between primary production in a polynya and reproduction of a high-trophic-level predator. Given the lack of a time lag between variations in primary production and the number of pups born, it seems unlikely that a transfer of primary production upwards through the food chain, *sensu stricto*, within the same season is responsible. Rather, we hypothesize that the relationship is due to spatial rearrangement of the members of the differing trophic levels such that increases in primary production attract fish that are common prey of Weddell seals. When the increase is in the McMurdo Sound polynya, we speculate that individual adult female Weddell seals somehow anticipate the conditions associated with high primary productivity and respond by increasing their probability of producing a pup. Conversely, when primary productivity increases in the much larger Ross Sea polynya the spatial rearrangement of prey items dilutes the relative amount of food available in McMurdo Sound and seals respond by reducing the probability of producing a pup.

This surprising finding is not completely without precedent, as evidence for the so-called anticipatory reproduction [40] has been found in several species including the red fox (*Vulpes vulpes*) [39], squirrels (*Tamiasciurus hudsonicus* and *Sciurus vulgaris*) [40], boreal owls (*Aegolius funereus*) [42] and eastern chipmunks (*Tamias striatus*) [41]. For these studies, actual causal mechanisms are unknown, hypothesized proximate causal mechanism vary and anticipatory reproductive responses to future resource abundance is proposed as an adaptation for increasing juvenile survival (but see [56]). In the case of the Weddell seal, the largest cohorts of pups tend to be produced in years with abundant resources, which ought to increase their chances of avoiding starvation and predation upon gaining nutritional independence several months after being born. Recent work on Weddell seals reported that female pups from the largest birth cohorts have the greatest chance of eventually recruiting to the breeding population and provided evidence that recruitment probability was more tightly associated with environmental conditions experienced by the mothers months earlier when their pups were *in utero* than with conditions during the subsequent period of juvenile independence [57]. The results reported here suggest a possible avenue for extending those findings: specifically, future studies should evaluate whether environmental conditions during the juvenile-independence period, as measured by primary productivity in the McMurdo Sound polynya, relate to survival of young during their first 2 years of life when the majority of deaths occur in a given birth cohort [58]. Whereas analyses that assessed factors associated with eventual recruitment by females, which typically occurs at age 8 [59], integrate processes occurring over multiple years, an analysis aimed specifically at juvenile survival ought, we speculate, to be more powerful for identifying the short-term environmental conditions that are tied more directly to annual variation in juvenile survival rates, which appears to be a key determinant of cohort strength and variation in long-term population trajectories [60]. In order for mothers to reliably place pups into environments with favourable conditions during the juvenile-independence period, females need to have reliable cues to the year's polynya production level many months in advance given the species' long gestation period and the fact that females alter whether they give birth in a given year but not the general location where they give birth. We do not know what cues are available or used but do suspect that seals might gain information on sea-ice conditions during late-summer forays, from sensing the degree of mixing in the water column related to the strength of katabatic winds during late summer–early winter, and/or from some other yet-to-be determined source. However, given that pup production does indeed seem to vary according to the magnitude of primary production in the current year, these results should stimulate future work on the topic.

Trophic-level interactions in the Antarctic are of considerable interest for understanding marine ecosystem processes. Although there are relatively few trophic levels in the food chain in the Ross Sea ecosystem, the temporal responsiveness and the strength/direction of interaction between the trophic levels is comparatively poorly understood [23]. Recent work has found some evidence for the within-season, top–downregulation of prey abundance through predation, e.g. Antarctic toothfish (*Dissostichus mawsoni*) by Weddell seals [61] and fish and krill by Adélie penguins [19,20], and there is evidence for overlap between the trophic levels for some consumers that share prey items [62]. The degree of coupling between variations in primary production and vital rates of upper trophic-level consumers in Antarctic marine ecosystems is comparatively unknown [23]. Penguin colony size has been demonstrated to be associated with the magnitude of primary production in polynyas [14]. By contrast, recent work [25] has suggested a lack of connection between variation primary production in the Ross Sea Polynya and reproductive parameters of Adélie penguin colonies on Ross Island.

High-latitude ecosystems are particularly susceptible to impacts of climate change. We have demonstrated a coupling between primary production in a coastal polynya and vital rates of an upper trophic-level consumer over a comparatively short timescale. The magnitude of primary production in a polynya is largely dependent on the extent of open water and, for coastal polynyas, the extent of open water is partially dependent on the strength of katabatic winds [18]. Conditional on the relationship between the vital rates of Weddell seals and primary production suggested here, changes in the amount of open water in coastal polynyas could have an impact on the population by influencing the number of pups born into the nearby colonies. In March of 2000, an extremely large iceberg calved from the eastern Ross Ice Shelf fragmented, with pieces drifting into the southwestern Ross Sea. The accumulation of iceberg fragments prevented the normal advection of sea ice northward from the Ross Sea, which greatly diminished the amount of open water and reduced the magnitude of primary production for areas in the Ross Sea by as much as 95% [63]. The reduction in primary production is associated with a dramatic drop in the number of Weddell Seal pups born into the same colonies studied here. The regional extent of sea ice and the future of the Ross Ice Shelf in the face of a changing climate are uncertain. Though sea-ice extent has increased in recent years, recent work indicates that the increases are likely short-lived and predicts greatly diminished summer sea-ice extent in the future [64,65]. The impact of reduced sea-ice cover on primary production in polynyas is unique to each polynya as the timing and mechanism of polynya formation influences the degree of water-column stratification, composition of phytoplankton assemblage, and resulting timing and magnitude of primary production. Given the sensitivity of the number of pups to variation in primary productivity, we need to study how polynya productivity might relate (or not) to other aspects of population dynamics such as survival rates, movement in and out of the area, and to other species with different life histories. With such information, we can develop an ecosystem view and make broader predictions about responses to annual changes in ice dynamics, something that will be important to predicting high-latitude marine ecosystem responses to possible climate change.

Ethics statement. Animal handling protocol was approved by Montana State University's Animal Care and Use Committee (Protocol no. 2011-38).

Data accessibility. The datasets supporting this article are available at http://www.montana.edu/rgarrott/antarctica/project_description.htm.

Acknowledgements. Logistical support for fieldwork in Antarctica was provided by Lockheed Martin, Raytheon Polar Services Company, Antarctic Support Associates, the United States Navy and Air Force, and Petroleum Helicopters Incorporated.

Funding statement. This project was supported by the National Science Foundation, Division of Polar Programs (grant no. ANT-1141326 to J.J.R., R.A.G. and Donald B. Siniff) and prior NSF Grants to R.A.G., J.J.R., D.B.S. and J. Ward Testa.

Author contributions. J.J.R. and R.A.G. manage the Weddell seal project. J.T.P. analysed the data and wrote the paper with input from all authors. J.J.R. assisted with the analysis and manuscript preparation. K.R.A. provided primary production estimates.

Competing interests. We have no competing financial interests.

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