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[4931]-
Received: 4 February 2020 | Accepted: 16 February 2021

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NOTE

Influence of krill (*Euphausia superba*) availability on humpback whale (*Megaptera novaeangliae*) reproductive rate

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Food abundance influences the distribution of living organisms and is essential to their vital activities, including reproduction (Costa, 2009). Global climate variation has influenced prey availability, through changes in environmental factors, with cascading effects in marine ecosystems (Doney et al., 2012).

Some effects of climate variability have been observed in the western Antarctic Peninsula (WAP) region. Changes in species composition at the base of the food web, with an increase in the abundance of the small cryptophytes to the detriment of the larger diatoms, have been observed in tandem with warming in the region and consequent changes in ice coverage area and timing of the seasonal cycle (e.g., Mendes et al., 2018; Moline et al., 2004; Schofield et al., 2017). These changes may cascade up the food web and negatively affect the recruitment and abundance of Antarctic krill (*Euphausia superba*, hereafter krill) as it does not have the capacity to feed on the small cell size cryptophytes (e.g., Moline et al., 2004). Krill has a vital role in Southern Ocean ecosystem (e.g., Laws, 1985), as it is the main prey item of many species of penguins, seals, and whales in the region (e.g., Botta et al., 2017; Herr et al., 2016; Nowacek et al., 2011; Reid et al., 2005). Therefore, it is expected that variations in the food web, and particularly in krill abundance, will have consequences for many predator species and the ecosystem as a whole (e.g., Doney et al., 2012; Loeb et al., 2009; Montes-Hugo et al., 2009; Schofield et al., 2017; Seyboth et al., 2017).

For marine mammals, changes in their prey distribution and abundance due to climate shifts are expected to affect nutrition and therefore reproductive success and survival (Simmonds & Isaac, 2007). The link between low prey availability and reproductive success in cetacean species explains the importance of nutrition at the population level (Braithwaite et al., 2015; Christiansen et al., 2018; Leaper et al., 2006; Murphy et al., 2007; Paterson et al., 2015; Seyboth et al., 2016). Poor nutrition may cause reproductive failure due to absence or delay of ovulation, decrease in female fertility, low sperm production, pregnancy loss, and neonatal mortality (Reeves et al., 2001).

One species of baleen whale that relies on the high productivity of the Antarctic Peninsula region during summer is the humpback whale (*Megaptera novaeangliae*), a cosmopolitan species (Bastida et al., 2007) with seven recognized stocks that feed in the Southern Ocean (International Whaling Commission, 2006). The WAP region is the main feeding ground of so-called Breeding Stock G, which typically migrates seasonally between the WAP and breeding grounds located in the southeast Pacific (off the coasts of northern Peru, Ecuador, Colombia, Panama, and Costa Rica), where the species mainly occurs during the austral winter (e.g., Acevedo et al., 2017; Albertson et al., 2017; Dalla Rosa et al., 2008; Félix & Haase, 2001a).

The aim of this paper is to contribute to an understanding of the interactions between krill, krill-dependent predators, and krill fisheries to improve management strategies for the latter (Commission for the Conservation of Antarctic Marine Living Resources, 2017a), by investigating the relationship between krill density at the WAP and the breeding success of humpback whales from Breeding Stock G. Our work aligns with priorities identified by the Working Group on Ecosystem Monitoring and Management (WG-EMM) from the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which recently encouraged further work to study the reproductive success of baleen whales and variability in krill abundance (CCAMLR, 2017b).

Data on the occurrence of humpback whales were collected from 2004 to 2010 during opportunistic surveys on board whale-watching vessels operating at Salinas, Santa Elena Peninsula, in the southwest region of Ecuador (2°12′S, 80°56′W; Figure 1). This area was considered representative of the breeding and calving grounds of Breeding Stock G (Félix & Haase, 2001a; IWC, 2006). Trips occurred between June and October, however, only data collected in August were included, as this corresponds to the peak of birthing and abundance in the area and is also the period when survey effort was most concentrated (Félix & Botero-Acosta, 2011).

The number of observers on board the vessels varied from one to four (*M* = 2). Surveys were conducted under favorable sea states (i.e., Beaufort ≤ 4) and good visibility (minimum of 3 nautical miles). The trajectories of the trips were nonsystematic being guided by sightings of whales in the area. Nevertheless, the area covered, and the lengths of the trips were relatively consistent, hence, the number of trips was used as a measure of effort. Whale groups were generally found within about 10 km of the tip of the Santa Elena Peninsula (Félix & Botero-Acosta, 2011).

Individuals were classified as adults, juveniles, or calves based on relative body size (see Félix & Haase, 2001a). Groups of two individuals in close association, one being significantly smaller (i.e., about one third) than the other, were considered mother-calf pairs (Félix & Botero-Acosta, 2011). Resighted individuals, detected by photo-identification of either flukes or dorsal fins, were subtracted from the total number of whales observed (Table 1). The annual relative birth rate (RBR) was calculated as the ratio of the numbers of calves to noncalves counted per trip in August of each year.

Krill density was estimated from annual acoustic monitoring undertaken by the United States Antarctic Marine Living Resources Program (U.S. AMLR) around the Antarctic Peninsula annually from January to March (Hewitt et al., 2003). These data derived from calibrated acoustic backscatter collected at three frequencies (38, 120, and 200 kHz). Acoustic backscatter was integrated over depths from about 10–15 m down to the bottom or 250 m (whichever was shallower) and averaged over 1 nm segments of the survey grid. Mean krill density (g/m^2) was estimated using the three-frequency stochastic distorted-wave Born approximation (SDWBA) (e.g., Reiss et al., 2008) following standard protocols (CCAMLR, 2010). Only data collected in the Bransfield Strait were considered for our analysis, assuming that it is representative of the whole feeding ground of the species, as this is an area where humpback whales are very abundant during summer months (e.g., Herr et al., 2016; Secchi et al., 2011). In most years mean krill density was estimated from data collected during two survey legs (in January and February).

To assess the effect of food availability on the reproductive success of humpback whales, we estimated the cross-correlation between RBR of whales and weighted krill density (i.e., the mean krill density was multiplied by the inverse of its coefficients of variation). We weighted krill density values as data are overdispersed (i.e., its variance is higher than its mean), so that using the mean in the analysis would probably lead to a misinterpretation of the correlation between variables being tested. Cross-correlation method allow the identification of the time lag that maximizes the correlation between the explanatory and the response variables (Legendre & Legendre, 1998) and was run in PAST software version 3.0 (Hammer et al., 2001). The result was later used in a regression model run in R software version 4.0.2 (R Core Team, 2020) to test the relationship between krill biomass and RBR weighted by effort (number of trips of each year). We considered a 0.05 level of significance in the analysis.

Relative birth rates of humpback whales were computed from data collected during 278 whale-watching trips ($M = 39.7 \pm 7.9$ per year) (Table 1). A total of 127 calves ($M = 18.1 \pm 13.2$ per year) and 1,637 noncalves ($M = 233.8 \pm 130.4$ per year) were recorded, excluding resights. The RBR ($M = 0.07 \pm 0.03$) was significantly correlated with krill density data of the previous year (i.e., lagged by 1 year; $r^2 = 0.90$, $p = .02$; Figure 2). The relationship between RBR and krill density in the previous year balanced by the number of trips was positive and significant ($r^2 = 0.78$, $p = .02$).

This is the first time that the relationship between environmental conditions around the Antarctic Peninsula and the calf production by humpback whales from Breeding Stock G has been investigated. The only previous information regarding variation in reproduction was a brief comparison of crude birth rates between a neutral year (1996) and an El Niño year (1997) (Félix & Haase, 2001b). A significant difference in birth rates during these years was not detected, possibly reflecting the time lag we found in the present study using a longer data set. Unfortunately, our estimates of krill density in the Bransfield Strait did not include the years 1995 and 1996.

The effects of climate change on top predators are difficult to quantify and understand, given the nonlinearities of physical and biological processes and the time lags of the relationships involved (Doney et al., 2012; Leaper et al., 2006; Seyboth et al., 2016). The significant correlation between the RBR and krill density in the WAP feeding ground one year earlier indicates how humpback whales may be affected by climate variability and then can help us to understand such effects. The 1-year lag we found corresponds to a period of 12–23 months and points to possible effects during different phases of the whales’ reproductive cycle. Females experience an estrous period and become receptive to mating in winter, in synchrony with the period of testosterone peak production and spermatogenesis for males (Chittleborough, 1965). The generalized female reproductive cycle lasts from two to three years and consists of two main phases: gestation and lactation. Gestation takes about 12 months, with most births occurring by midwinter (e.g., Chittleborough, 1958). Lactation also lasts about 12 months, with a mean birth interval of two years, although parturition in consecutive years has been recorded previously (Clapham & Mayo, 1990). In general, female humpback whales produce a calf every 2.38 years over their reproductive life spans (Barlow & Chapman, 1997), as resting phases may be included in the cycle (Chittleborough, 1958). Our findings indicate that the influence of climate variability on nutritional condition affects the pregnancy rate of humpback whales. This may occur because females need to build fat reserves during the summer to withstand the ongoing demands of gestation (Lockyer, 1984) or the forthcoming demands of lactation. A female’s nutritional condition may determine whether she can bear and raise a calf. The fact that some females may not migrate at all (Clapham, 2009) supports this possibility.

Previous studies (e.g., Braithwaite et al., 2015; Leaper et al., 2006; Murphy et al., 2007; Seyboth et al., 2016) have shown that an adequate nutritional condition is achieved based on circumstances found during consecutive years, in accordance with other research demonstrating that nutrition affects cetaceans during different phases of the reproductive cycle (Lockyer, 1986, 1987; Reeves et al., 2001). A single feeding season with poor food availability may make it impossible for a female to sustain her own energetic requirements during migration and may therefore compromise gestation, birth, lactation, and hence, calf survival. For example, if the mother’s nutritional state is poor, she may not provide milk in sufficient quantity or quality for calf survival (Reeves et al., 2001), or the fetus may be terminated before birth, as shown to happen for other marine mammals as the Antarctic fur seal (*Arctocephalus gazella*) (e.g., Lea et al., 2006). In addition to food availability, carry-over effects may influence the reproductive success of whales (e.g., Braithwaite et al., 2015). Specifically, for humpback whales in the Bransfield Strait, such effects may result from changes in the local carrying capacity of krill and/or from an increase in competition with fin whales (*Balaenoptera physalus*), which have increased in density within our study area during recent decades,[1] and with krill fisheries.

It is important to note though that apart from such recognized effects, breeding stocks of humpback whales in general have been growing considerably (e.g., Bortolotto et al., 2016; Félix et al., 2011; Pavanato et al., 2017). This would potentially require an increase of krill for natural predators in the area, and relatively high pregnancy rates were found for individuals of the species using the Antarctic Peninsula during summer 2010–2016 (Pallin et al., 2018). Nevertheless, pregnancy rates varied from 36% and 86% during this time (Pallin et al., 2018), which may be an indication of the influence of varying food availability and potential competition with increasing population of other species using the feeding area. Krill stocks can overcome years of poor recruitment with 2–3 years of favorable conditions (Siegel et al., 1998). However, such recoveries may be threatened by periodic climate events such as

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[1] EcoMega (unpublished data).

strong ENSOs (El Niño Southern Oscillation), which are expected to become more frequent in coming decades (Cai et al., 2014), and to influence the timing and magnitude of spring blooms (Reiss et al., 2015). Given the short length of our data set, we were unable to test for possible relationships between RBR and climate variables such as the Oceanic Niño Index (ONI), the Southern Oscillation Index and the Antarctic Oscillation. It is necessary to have at least two complete cycles of the explanatory variable to test for cross-correlation with potential response variables (Legendre & Legendre, 1998). However, it is an assumption of this work that variation in krill density, potentially impacting the two to three years reproductive cycle of female humpback whales (as previously detailed), would be detected during the 7-year period of investigation.

Our results suggest that the Antarctic food web needs to be continuously and carefully studied so that the demography of krill-dependent predators in the Southern Ocean can be better understood and incorporated into precautionary management of the ecosystem. New methods to investigate adiposity in cetaceans, such as adypocite area and lipid-percent, measured from biopsied tissues (Castrillon et al., 2017), progesterone levels in blubber to estimate pregnancy rates (Clark et al., 2017), and drone surveys of body condition (Christiansen et al., 2016) can all complement such work. Further investigation of the effects of climate variability and food availability on humpback whale population dynamics can benefit from the continued monitoring of whales in their breeding and feeding grounds, as well as the surveys to estimate krill density in the WAP during the austral summer.

This study also suggests that CCAMLR, which aims to take the requirements and conservation status of krill predators into account while managing the krill fishery, may need to consider data collected outside the Southern Ocean. As suggested in previous studies (e.g., Hinke et al., 2017; Weinstein et al., 2017), the overlap of krill predators and krill fisheries can pose risks to predator populations that rely on krill as their main food resource. We have shown that the outcomes of changes in krill availability may not be apparent in the Antarctic since many predators leave the Southern Ocean during the austral winter and thus data from the whole home range of such species might be needed.

ACKNOWLEDGMENTS

We thank the whale watching operators off Salinas that offered their boats as research platforms, and all volunteers and colleagues who helped with data collection and photographs. The

U.S. AMLR Program provided data on krill density, and we thank all crew and researchers involved in such data collection. Marcelo Pinho and Michael Sumner helped with data visualization. This article is part of E.S.’s Ph.D. Thesis in Biological Oceanography (FURG, Brazil) under the supervision of E.R.S., L.D.R., and M-A.L., the latter during a period of research undertaken at IMAS (Institute for Marine and Antarctic Studies)/UTAS (University of Tasmania). Financial support was provided by CNPq (National Council for Research and Development) and CAPES (Coordination for the Improvement of Higher Education Personnel) to the development of this research. CNPq provided research fellowships to E.R.S. (PQ 310597/2018-8) and L.D.R. (PQ 309548/2019-5) and a Ph.D. scholarship to E.S, who received a CAPES scholarship (PDSE/88881.133669/2016-01) for the period at UTAS. CAPES also provided free access to many relevant journals through the portal “Periódicos CAPES.” This work is a contribution of the *Grupo de Oceanografia de Altas Latitudes* – GOAL/High Latitudes Oceanography Group activities in the Brazilian Antarctic Program (PROANTAR) and the research group *Ecologia e Conservação da Megafauna Marinha*-EcoMega/CNPq. The study was conducted as part of the Antarctic Research Projects ECOPELAGOS and Baleias (CNPq grant numbers 442637/2018-7 and 408096/2013-6, respectively) and is within the scope of the

Capes PrInt Program (public notice 041/2017) and the Whales and Climate Research Program.

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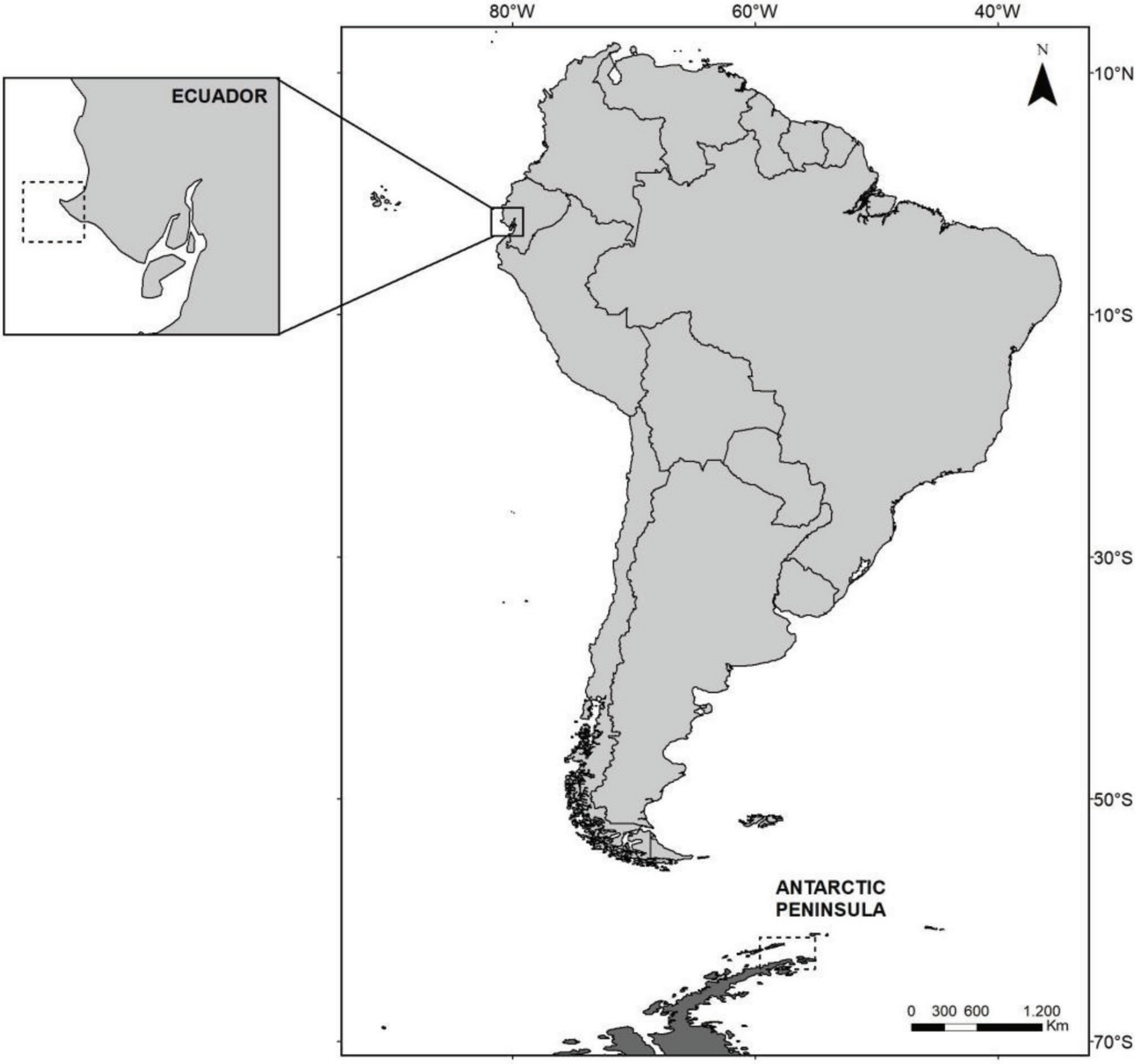
TABLE 1 Data used in the analysis. Number of trips in each year during August from 2004 to 2010, sightings of humpback whales in the breeding ground off Ecuador, relative birth rate (RBR), and acoustic estimates of krill density in the Bransfield Strait (mean ± standard deviation, and weighted).

Year	Calves	Noncalves	Trips	RBR	Krill density (g/m^2)	Weighted krill density
2004	5	79	28	0.06	17.9 (± 48.7)	6.62
2005	5	150	29	0.03	30.8 (± 109.9)	8.61
2006	13	217	45	0.06	41.6 (± 144)	12.05
2007	11	206	42	0.05	110.4 (± 168.1)	72.85
2008	26	277	47	0.09	123.3 (± 230.34)	65.36
2009	27	214	45	0.13	72.9 (± 133.9)	40.10
2010	40	494	42	0.08	54.6 (± 123.8)	24.02

FIGURE 1 Map of the studied areas. Dashed rectangles indicate areas where data on humpback whales and krill were respectively collected off the southwest coast of Ecuador (Santa Elena Peninsula, Salinas) and in the Bransfield Strait, Antarctic Peninsula.

FIGURE 2 Humpback whales breeding success versus krill biomass. Correlation between the relative birth rate of humpback whales breeding off Ecuador (balanced per number of fieldwork trips performed each year) and weighted krill density in the Bransfield Strait lagged by 1 year ($r^2 = 0.90$, $p = .02$).



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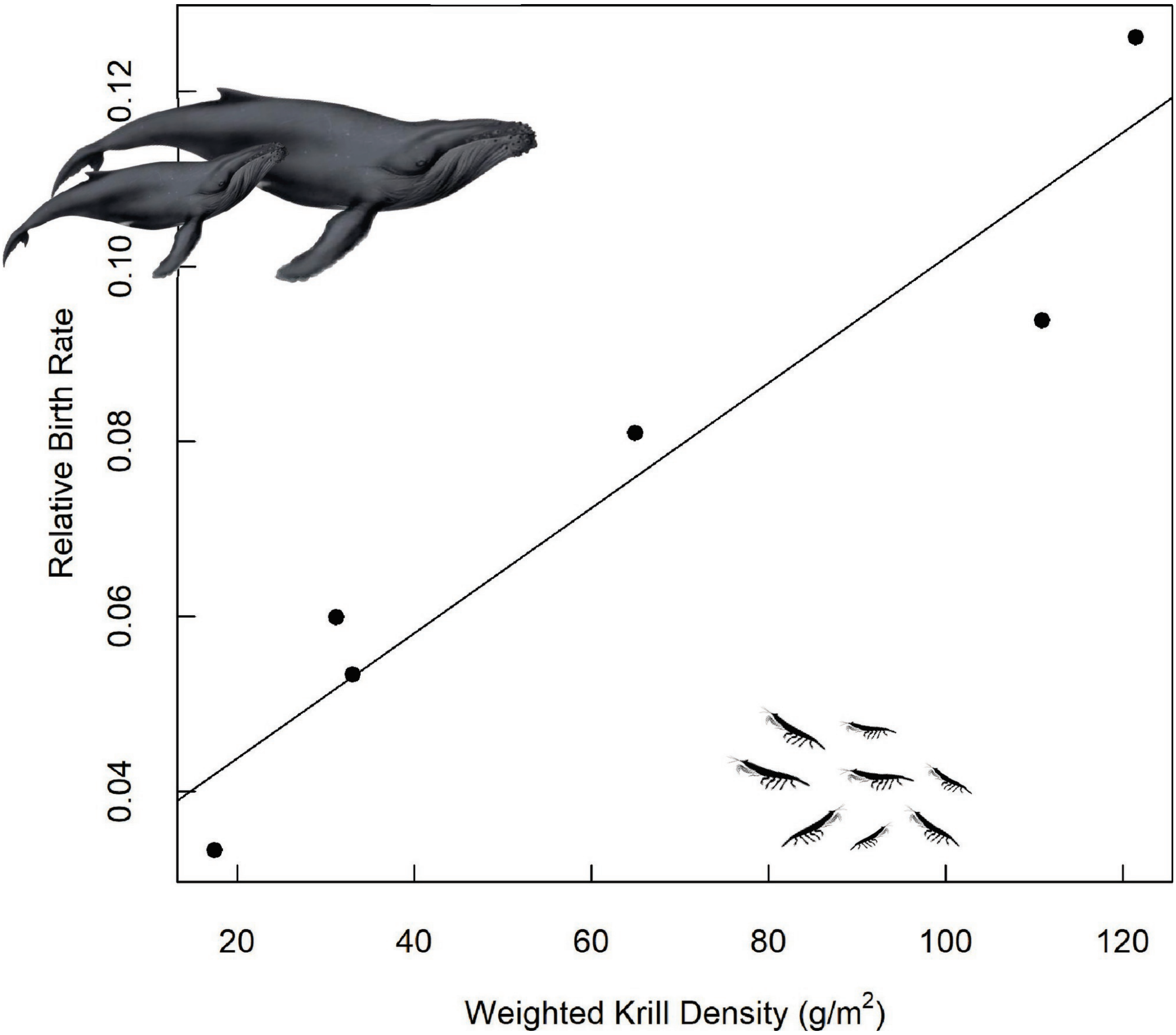

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