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La Niña conditions influence interannual call detections of pygmy blue whales in the eastern Indian Ocean

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Oceans across the globe are warming rapidly and marine ecosystems are changing as a result. However, there is a lack of information regarding how blue whales are responding to these changing environments, especially in the Southern Hemisphere. This is because long term data are needed to determine whether blue whales respond to variability in environmental conditions. Using over 16 years of passive acoustic data recorded at Cape Leeuwin, we investigated whether oceanic environmental drivers are correlated with the migration patterns of eastern Indian Ocean (EIO) pygmy blue whales off Western Australia. To determine which environmental variables may influence migration patterns, we modelled the number of acoustic call detections of EIO pygmy blue whale calls with broad and fine scale environmental variables. We found a positive correlation between total annual whale call detections and El Niño Southern Oscillation (ENSO) cycles and the Indian Ocean Dipole (IOD), with more whale calls detected during La Niña years. We also found that monthly whale call detections correlated with sea surface height around the hydrophone and chlorophyll-a concentration at a prominent blue whale feeding aggregation area (Bonney Upwelling) where whales feed during the summer before migrating up the west Australian coast. At the interannual scale, ENSO had a stronger relationship with call detections than IOD. During La Niña years, up to ten times more EIO pygmy blue whale calls were detected than in neutral or El Niño years. This is likely linked to changes in productivity in the feeding areas of the Great Australian Bight and Indian Ocean. We propose that in lower productivity years whales either skipped migration or altered their habitat use and moved further offshore from the hydrophones and therefore were not detected. The frequency and intensity of ENSO events are predicted to increase with climate change, which is likely to impact the productivity of the areas used by blue whales. These

changes in productivity may affect the physical condition and reproductive success of individual whales. A reduction in reproductive success could have a significant impact on blue whale recovery from historical whaling and their ability to adapt to a changing environment.

Introduction

Global temperatures have been steadily increasing over the past few decades due to the burning of fossil fuels and the emission of greenhouse gases such as carbon dioxide and methane. The ecological impacts of climate change are evident in terrestrial and marine systems, spanning from the warm tropics to the cold polar regions (Walther et al., 2002; Parmesan, 2006). Overall, marine environments are changing at a much faster rate than terrestrial systems (Burrows et al., 2011). Ocean circulation has changed considerably due to increased water temperatures and changes to major ocean currents. Poleward western boundary currents are strengthening, bringing warmer water further south towards mid to high latitude regions (Wu et al., 2012; Yang et al., 2016). In the Southern Ocean, the Antarctic Circumpolar Current is predicted to strengthen and shift its overall position southward (Saenko et al., 2005). At the same time, other abiotic climate stressors in temperate and southern oceans (e.g., shifts in sea surface temperature and acidification, and decreases in winter sea-ice cover) have been found to drive change for marine fauna (Kroeker et al., 2013; Post et al., 2013; Stuart-Smith et al., 2015). To date, abiotic factors have resulted with biotic changes at lower trophic levels. These include decreases in primary productivity and changes in phytoplankton community structure (Montes-Hugo et al., 2009), which in turn influence the structure of grazer communities such as krill and salps (Atkinson et al., 2004). Some of these changes have transferred to higher trophic level species. However, a better understanding of how these lower trophic changes will impact higher trophic levels in the context of climate change is necessary, especially for conservation efforts.

Climate change can increase the risk of extinction of already endangered megafauna with depleted populations. The change in environmental conditions can disrupt the reproductive success of large whales, by affecting resource availability, survival, and growth (Post and Forchhammer, 2008; Molnár et al., 2010; Auer and Martin, 2013). Food availability is strongly correlated with body condition and fecundity in female fin, humpback, and sperm whales (Lockyer, 1986; Wiley and Clapham, 1993; Whitehead, 1996; Braithwaite et al., 2015), as well as in odontocetes, pinnipeds, and sirenians (Read and Gaskin, 1990; Boyd, 1996; Learmonth et al., 2006). A reduction in prey availability can result in increased competition for resources and a decrease in body condition and fecundity during periods of low productivity. Thus, climate change can indirectly threaten the recovery of large whales by influencing their prey. Some of these greatly depleted whale populations have recovered since the banning of commercial whaling, while others have shown little to no signs of recovery (Magera et al., 2013).

Long-term data is required to identify the historical and potential future impacts of climate change on higher trophic marine species (Rosenzweig et al., 2008). This is because cyclic/periodic climatic events such as the El Niño-Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD) can mask the underlying effects of long-term climate change. These large-scale, ocean basin-wide environmental drivers influence climatic factors such as rainfall and temperature to the point of affecting the likelihood of extreme events such as heatwaves, droughts, and floods. In the ocean, ENSO events can lead to marine heatwaves, changes in primary productivity, and the excessive runoff of nutrients, sediments, pollutants (McPhaden et al., 2006). Few studies have examined how the interannual climatic variability caused by ENSO and the IOD affects marine megafauna, because long-term studies at decadal scales are expensive and logistically difficult to conduct.

Antarctic blue whales, in particular, are likely to be vulnerable to environmental change in the Southern Ocean (Atkinson et al., 2004; Montes-Hugo et al., 2009; Mulvaney et al., 2012; Wijffels et al., 2016; Yang et al., 2016; Turney et al., 2017) because they feed predominantly in the euphausiid-rich waters for a relatively brief period (three to four months) each year in the austral summer. (Branch et al., 2007; Gill et al., 2011). During this time, a high rate of fat layer development is essential for the whales to prepare for long-distance migration to and from low-latitude breeding grounds, a journey which may require fasting for months at a time (Brodie, 1975). Pygmy blue whales, on the other hand, may not be able to build up large blubber stores like Antarctic blue whales as they do not feed in

the euphausiid-rich waters surrounding Antarctica. As their reproductive success in linked with their migration, tracking the movement of these animals can reveal how they are responding to environmental changes. The primary methods of studying the movement patterns of whales include visual surveys, satellite tagging, acoustic tracking, and more recently satellite imagery. Visual surveys require high levels of effort, are restricted to daylight hours, and are hindered by adverse weather conditions. Satellite tagging provides precise movement tracks but is expensive and tags only work for a limited duration before falling off. More recently, with improved resolution, satellite imagery has been used to survey whales, but this method requires high levels of image processing and computing power. Passive acoustic monitoring (PAM), on the other hand, provides a relatively cost-effective method and can be effective for monitoring vocal species. PAM can be used to generate long-term data and requires less effort than other methods as the data are collected passively. Therefore, PAM could be used to detect variability in biological signals due to environmental changes.

Blue whales are ideal candidates for using PAM because they produce stereotypical, simple, and low frequency calls (McDonald et al., 2006). In addition, their cryptic nature and distribution in remote areas means that visual surveys are ineffective. Blue whales are traditionally thought to move each year between mid-to-high latitude productive feeding grounds in summer and low-latitude oligotrophic breeding areas to overwinter (Branch et al., 2007). Eastern Indian Ocean (EIO) pygmy blue whale calls are detected across mid-latitude southern Indian Ocean waters, including off the Crozet Islands (Samaran et al., 2010), Amsterdam Island, Reunion Island (Samaran et al., 2013), and in southern Australian waters. Within Australian waters, blue whale aggregations have been observed feeding in the Great South Australian Coastal Upwelling System (GSACUS) near the Bonney coast in the eastern Great Australian Bight (Figure 1, Gill, 2002; Gill et al., 2011), as well as in the subtropical convergence zone (Garcia-Rojas et al., 2018). The GSACUS is a wind-driven coastal upwelling system active from November to May during which upwelling of nutrient-rich water makes the area an important marine biodiversity hot spot (Ward et al., 2006; Kämpf, 2010). The EIO pygmy blue whales are present within the GSACUS from November to May, coinciding with the period that upwelling occurs (Gill, 2002; Gill et al., 2011; Balcazar et al., 2015; Tripovich et al., 2015). Satellite-tracking studies show EIO pygmy blue whales migrate from the south of Australia (starting their migration in March/April), moving past the West Australian coast to reach Indonesia from June after which they return south between the months of October and December (Double et al., 2014; Möller et al., 2020; Thums et al., 2022).

The aim of this study is to investigate the environmental drivers that are correlated with, and therefore potentially influence, the migration patterns of EIO pygmy blue whales detected off Cape Leeuwin, Western Australia. We use acoustic detections of pygmy blue whales calls as a proxy for whale presence and analyse large-scale oceanic climate drivers such as ENSO and IOD. We hypothesise that fewer whales migrate (indicated by fewer acoustic detections) during years of low

FIGURE 1
Map of the Australian Bight. The hydrophone H01W1 is located approximately 105 km from the shore at Cape Leeuwin, Western Australia (blue square). The Bonney Upwelling (red square) is the largest and most predictable upwelling location and also a known blue whale feeding aggregation area within the Great South Australian Coastal Upwelling System (GSACUS; highlighted in green).

productivity in known feeding areas. We examined whether environmental variables such as chlorophyll and ocean temperature and height correlate with changes in whale presence. Establishing a link between environmental variables and whale presence could be used to predict the occurrence of baleen whales in the future and provide valuable information for the conservation and management of these threatened species.

Methods

Acoustic data collection

Passive acoustic data from a hydrophone recording station at Cape Leeuwin was obtained from January 2003 to December 2018. The monitoring station is maintained by the Comprehensive Nuclear Test Ban Treaty Organisation (CTBTO) and forms part of the International Monitoring System. The hydrophones at Cape Leeuwin are moored to the bottom of the ocean in a triplet array with the hydrophones positioned at a depth of 1,063 m. Acoustic data were recorded continuously with a sampling rate of 250 Hz for a flat frequency range of 1-100 Hz. The noise floor of the hydrophones was ≤ 60 dB per µPa (1-Hz band) and ≤ 81 dB per µPa (wide band). Data from a single hydrophone (H01W1; Figure 1; 34.9° S, 114.2° E) were analysed in this study. H01W1 is located approximately 72 km from the nearest point of land at Cape Leeuwin.

To detect EIO pygmy blue whale calls, we used an automated detector with the spectrogram correlation method in the bioacoustics analysis program Ishmael 3.0 (Mellinger et al., 2018). The EIO call typically consists of three units that are repeated, as described in McCauley and Jenner (2010). Our spectrogram correlation detector targeted the third harmonic (66 – 71 Hz) of the second unit of the EIO call using the same parameters described in Truong and Rogers (2021). Variations in the three-unit call have been described recently for this population, with some of the units being either excluded or inserted into the song, leading to different song structures and detection rates (Jolliffe et al., 2019). The second unit was the only unit present in all the song variations described, which is why it was targeted for detection. The proportion of the song variations differed slightly between years that were sampled, but overall, the relative proportions of each song variant were mostly consistent across years (Jolliffe et al., 2019).

Individual calls were verified visually using Raven Pro 1.6 and false positives were removed. False negative rates were quantified by randomly selecting a subset of recordings and manually counting the calls. Our detector was designed to be conservative by using a relatively high detection threshold. This resulted with low false positive rates (0.84%) and high false negative rates (81.35%) as we targeted loud calls produced by whales closer to the hydrophone and excluded fainter calls produced by whales further away. We analysed the whale

detection data for EIO pygmy blue whale calls at two temporal scales: an annual scale to assess the relationship between ENSO and whale call detections; and a monthly time series to examine the link between environmental covariates and whale call detections at a finer temporal scale.

Environmental data

The southern oscillation index (SOI) quantifies the atmospheric pressure difference between Tahiti and Darwin and is used as an indicator of ENSO status. Monthly SOI values between 2003 and 2018 were obtained from the Australian Bureau of Meteorology (http://www.bom.gov.au/climate/enso/soi/) and yearly averages were calculated for the interannual analysis. The strength of the IOD is measured using the Dipole Mode Index (DMI). The DMI is represented by an anomalous sea surface temperature (SST) gradient between the western and eastern Indian Ocean. DMI values were obtained from the Global Climate Observing System Working Group on Surface Pressure (https://psl.noaa.gov/gcos_wgsp/Timeseries/DMI/). Satellite-derived environmental variables included SST, sea surface height (SSH), and sea surface chlorophyll-a (SSC), all of which were obtained for 2003 to 2015. SST data were from the NOAA Optimum Interpolation SST V2 from NOAA's Physical Sciences Lab based in Boulder, Colorado, USA (https://psl.noaa.gov/). SSH data were obtained from the AVISO multi-satellite mission and SSC data from MODIS-Aqua, both acquired from the NOAA Ocean Watch – Central Pacific program (https://oceanwatch.pifsc.noaa.gov/). SSC was measured at the location of the hydrophone (SSC.HP) and at a major upwelling and feeding location, the Bonney Upwelling (SSC.BU) (Figure 1). We wanted to test SSC as it is a proxy for primary productivity which would then likely influence krill abundance. The Bonney Upwelling (37.2° S, 139.5° E) was selected as it is one of the most prominent upwelling locations within the GSACUS in the Great Australian Bight and also a known blue whale feeding aggregation area (Ward et al., 2006). All environmental variables were sampled monthly and averaged over a 1° x 1° latitude and longitude grid (approximately 10,000 km^2).

Data analysis

Yearly models

We analysed the interannual variability of whale call detections and yearly average SOI and DMI. In our yearly models, the response variable was the total number of EIO pygmy blue whale detections within each year and the explanatory variables were SOI and DMI. We used a generalised linear model (GLM) with a negative binomial distribution as part of the analysis at a yearly scale to assess the correlation between the interannual variability of whale call detections and yearly averaged SOI values for data up to and including 2018. SST, SSH and SSC were not analysed at the yearly

scale as they are highly seasonal and averaging at an annual scale would result in the loss of seasonal variation.

Monthly models

At the monthly scale, we assessed the relationship between environmental covariates and the number of monthly call detections, examining data up to and including 2015. Total monthly detections were used as the response variable in the monthly models. To determine which environmental variables were correlated with the detection of EIO pygmy blue whale calls we used a time series analysis with count data following generalised linear models using the tscount package (Liboschik et al., 2017) in R version 4.0.2 (R Core Team, 2020). The environmental variables used in the models included SOI, SST, SSH, SSC.HP, and SSC.BU. A variance inflation factor was used to check for collinearity and none of the variables were highly correlated (i.e., no values exceeded ten). The time series approach accounted for possible serial dependence (autocorrelation) with past observations. The highly cyclic, seasonal nature of whale call detections and the potential increase in the number of whale calls through time (since this is a recovering population) meant time was an important consideration for this analysis. To account for autocorrelation in the data a first order autoregressive term ($\beta 1$) was used to capture short-range serial dependence, whereas a 13th order autoregressive term ($\alpha 13$) was used to capture the annual seasonality. The models were fitted using a negative binomial distribution and a "log" link function due to high overdispersion of the data where the variance far exceeded the mean. Model selection was used to identify the best fitting model using a forward stepwise selection approach. The best fitting models were assessed using AIC values.

Results

Interannual and monthly variability in call detections

A total of 74,812 EIO pygmy blue whale calls were detected from Cape Leeuwin between 2003 and 2018, with the highest number of calls being detected in 2008 (Figure 2). The number of calls detected per year between 2008 and 2012 was 9,112 ± 1,324 (mean ± SE). This was substantially higher than in the preceding and following years, where an average of 1,164 ± 403 calls were detected each year between 2003 and 2007 and an average of 3,906 ± 746 calls were detected each year between 2013 and 2018. The monthly whale call detections were seasonal in nature, with calls peaking in April for most years and occasionally peaking in March or May in other years (Figure 3A). The highest monthly detection occurred in June 2011 with 5,950 calls, despite the highest yearly call detections being in 2008. The high number of yearly call detections between 2008 and 2012 was due to increased call detections during the peak months in those years (Figure 3A). Monthly time series of the environmental variables are presented in Figures 3B, C, 4.

Statistical analysis

Yearly models

The negative binomial GLM showed a positive relationship between yearly-averaged SOI values and yearly EIO whale call detections (Figure 5; Coefficient estimate = 0.08, SE = 0.03, p = 0.0078, R^2 = 0.567), where more calls were detected in years of higher SOI values corresponding to La Niña conditions. There was also a positive relationship with DMI and yearly call detections (Figure 6; Coefficient estimate = 2.85, SE = 1.24, p = 0.02, R^2 = 0.124).
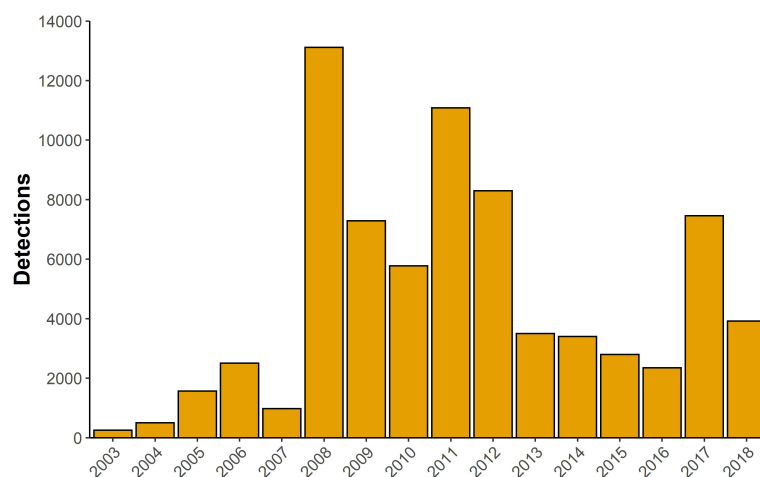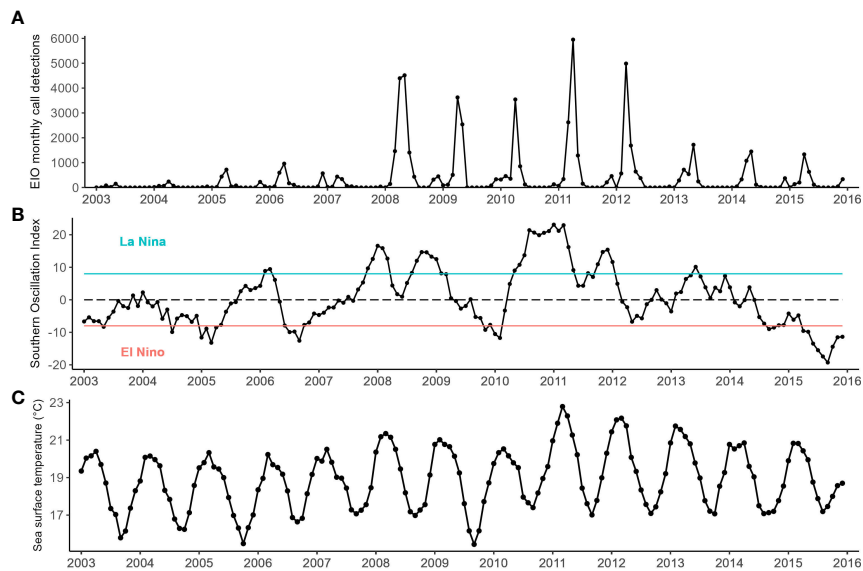

FIGURE 2
Total yearly number of eastern Indian Ocean (EIO) pygmy blue whale calls detected between 2003 and 2018 at Cape Leeuwin.
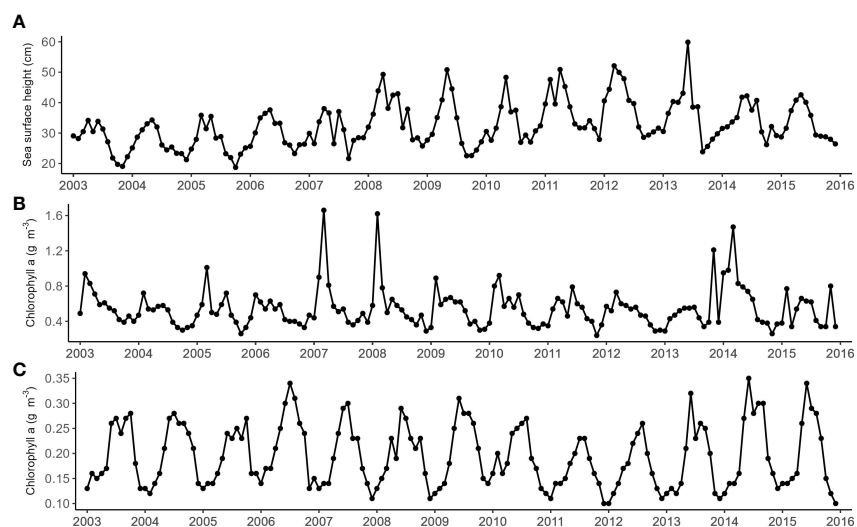
FIGURE 3

Monthly time series of **(A)** eastern Indian Ocean (EIO) pygmy blue whale call detections between 2003 and 2016 at Cape Leeuwin, Western Australia, **(B)** Southern oscillation index (SOI) obtained from the Australian Bureau of Meteorology calculated as a three-month running average between 2003 and 2016 SOI values above the green line indicate La Niña conditions; SOI values below the red line indicate El Niño conditions, **(C)** mean sea surface temperature measured across a 1° x 1° latitude and longitude grid centred around the Cape Leeuwin hydrophone.

Monthly models

The time series analyses accounted for possible autocorrelation with observations through time due to seasonality and possible population increase. The univariate models identified SOI as the best explanatory variable (Table 1). The multivariate model with the best fit included the variables SOI, SSH, SSC.HP, and SSC.BU (AIC = 1558.8, Table 2), with SST dropped from the final model. The next best model contained SSH, SSC.HP and SSC.BU (AIC = 1561.2,

FIGURE 4

Monthly time series of **(A)** Sea surface height measured at Cape Leeuwin obtained from the AVISO multi-satellited mission. Chlorophyll-a obtained from Modis Aqua from the NOAA Ocean Watch - Central Pacific Program **(B)** measured at Cape Leeuwin, and **(C)** measured at the Bonney Upwelling. All variables were averaged from a 1° x 1° latitude and longitude grid at each location.
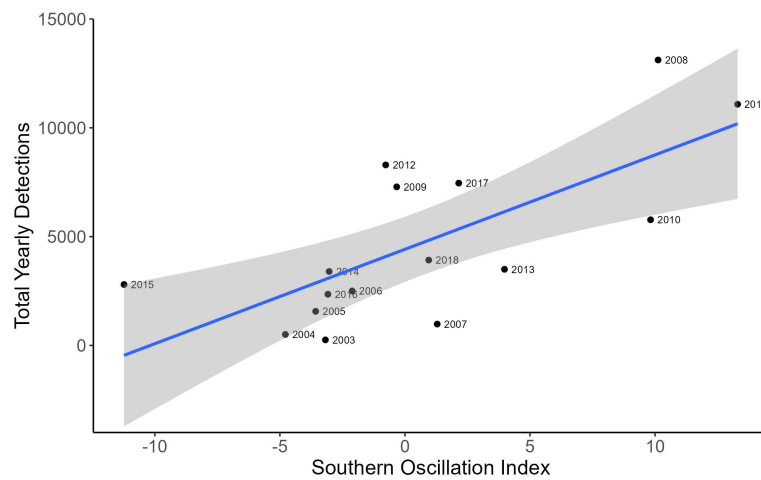
FIGURE 5
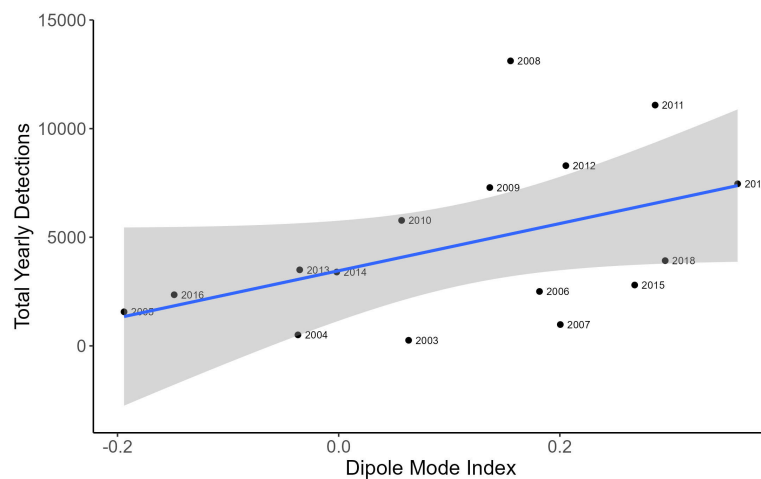A scatterplot showing the correlation between the total yearly EIO pygmy blue whale call detections and yearly average southern oscillation index. The blue line represents line of best fit and the grey shaded area is estimated 95% confidence interval.

Table 2). Under the principle of parsimony, the second model with three explanatory terms would be the better model as the difference in AIC is only 2.4. Based on the second model SSH (Figure 7A, Coefficient estimate = 0.08, SE = 0.05) and SSC.BU (Figure 7B, Coefficient estimate = 1.15, SE = 1.0) were positively correlated with monthly whale call detections, while SSC.HP (Figure 7C, Coefficient estimate = -10.4, SE = 5.2) was negatively correlated with monthly whale call detections.

Discussion

ENSO events were correlated with, and so likely had influence on, the number of EIO pygmy blue whale calls detected in the southeast Indian Ocean. The IOD was also correlated with the total number of yearly pygmy blue whale detections. Increased numbers of detected whale calls between 2008 and 2012 coincided with La Niña events over multiple consecutive years, with the highest number of calls detected in

FIGURE 6
A scatterplot showing the correlation between the total yearly EIO pygmy blue whale call detections and yearly average dipole mode index. The blue line represents line of best fit and the grey shaded area is estimated 95% confidence interval.

TABLE 1 Univariate models obtained from the monthly time series analysis with whale call count data.

Variable	AIC	β1	α13	Coefficient estimate	σ²
SOI	**1582.6**	0.55 ± 0.21	-0.07 ± 0.28	0.04 ± 0.05	7.79
SSC.BU	1589.2	0.54 ± 0.22	-0.05 ± 0.28	1.20 ± 1.54	8.46
SSC.HP	1609.7	0.52 ± 0.10	-0.04 ± 0.16	-10.57 ± 3.71	2.47
SST	1634.7	0.33 ± 0.34	0.06 ± 0.21	0.66 ± 0.59	16.82
SSH	1644.6	0.37 ± 0.13	-0.14 ± 0.19	0.08 ± 0.04	2.21

Models are ranked by AIC values. AIC is the Akaike information criterion, β1 and α13 are measures of autocorrelation, and σ2 is a measure of overdispersion. Values are coefficient estimates ± SE.

2011 during the strongest La Niña event. The 2010/2011 La Niña, one of the strongest on record, was associated with unprecedented warming and strengthening of the Leeuwin Current (Feng et al., 2013). If we use the number of whale calls as a proxy for the number of migrating whales, the greater number of whale calls detected suggests that more whales migrate past the west coast of Australia during La Niña years, as our study area represents a corridor through which whales move between feeding areas and low-latitude breeding grounds. We propose that the tenfold increase in the number of blue whale calls detected from 2007 to 2008 and sustained through to 2012 is due to more whales migrating during this period. The increase in the number of whale calls detected after 2008 suggests that the whales change their behaviour, responding quickly to shifts in climatic conditions. The IOD is also correlated with blue whale call detections, but the relationship is not as strong as ENSO. There was no lag observed between the timing of increased whale call detections and the onset of the sustained La Niña conditions which commenced in 2008.

Although the EIO population is believed to be recovering (McCauley et al., 2018), the increased number of call detections is likely not due to an increase in EIO blue whale population numbers, as a shift of this magnitude over such a short period is unrealistic. Rather, it likely represents a higher proportion of the whale population migrating past Cape Leeuwin.

La Niña and El Niño conditions likely affect ocean productivity and food availability within the southern Indian Ocean feeding grounds of EIO pygmy blue whales as it affects other oceanic regions (Wang and Fiedler, 2006; Messié and Chavez, 2012). Therefore, we speculate that there are at least two possible explanations for the change in the number of blue whale calls detected during La Niña years. The first is that more whales underwent the yearly migration from the Great Australian Bight past Cape Leeuwin during highly productive La Niña years, while fewer whales migrated during years of lower productivity. Monthly chlorophyll-a concentrations at the important GSACUS foraging location of the Bonney Upwelling were

TABLE 2 Multivariate model selection with all variables and whale call detection counts as the dependent variable using a count time series analysis.

Model	AIC	β1	α13	σ2	SST	SSH	SOI	SSC.HP	SSC.BU
SSH + SOI + SSC.HP + SSC.BU	**1558.8**	0.39 ± 0.2	0.08 ± 0.3	3.5	–	0.06 ± 0.06	0.02 ± 0.04	-9.3 ± 5.5	1.26 ± 1.0
SSH + SSC.HP + SSC.BU	1561.2	0.36 ± 0.2	0.09 ± 0.3	3.3	–	0.08 ± 0.05	–	-10.4 ± 5.2	1.15 ± 1.0
SOI + SSC.HP + SSC.BU	1571.2	0.56 ± 0.2	0.04 ± 0.3	7.1	–	–	0.04 ± 0.05	-7.03 ± 6.9	1.58 ± 1.5
SSH + SOI + SSC.BU	1583.9	0.41 ± 0.2	-0.06 ± 0.2	3.6	–	0.05 ± 0.06	0.03 ± 0.03	–	1.1 ± 1.0
SST + SSH + SOI + SSC.HP	1584.6	0.3 ± 0.3	0.05 ± 0.2	9.6	0.53 ± 0.8	0.03 ± 0.1	0.01 ± 0.06	-0.54 ± 14.4	–
SST + SSH + SOI + SSC.HP + SSC.BU	1604.9	0.32 ± 0.4	0.07 ± 0.2	11.9	0.46 ± 0.9	0.03 ± 0.1	0.01 ± 0.07	-1.76 ± 16.9	0.73 ± 2.0
SST + SSH + SSC.HP + SSC.BU	1621	0.3 ± 0.4	0.06 ± 0.2	14.1	0.52 ± 1.0	0.03 ± 0.1	–	-1.47 ± 18.2	0.61 ± 2.1
SST + SSH + SOI + SSC.BU	1626.8	0.3 ± 0.4	0.06 ± 0.2	14.8	0.53 ± 0.6	0.02 ± 0.1	0.013 ± 0.08	–	0.64 ± 2.1
SSH + SOI + SSC.HP	1630.1	0.38 ± 0.1	-0.003 ± 0.2	1.8	–	0.08 ± 0.04	0.02 ± 0.03	-8.95 ± 4.1	–

Models are ranked in order of AIC values, with better fitting models having lower AIC values. AIC is the Akaike information criterion, Beta1 and alpha13 are measures of autocorrelation and σ2 is a measure of overdispersion. Values are coefficient estimates ± SE.
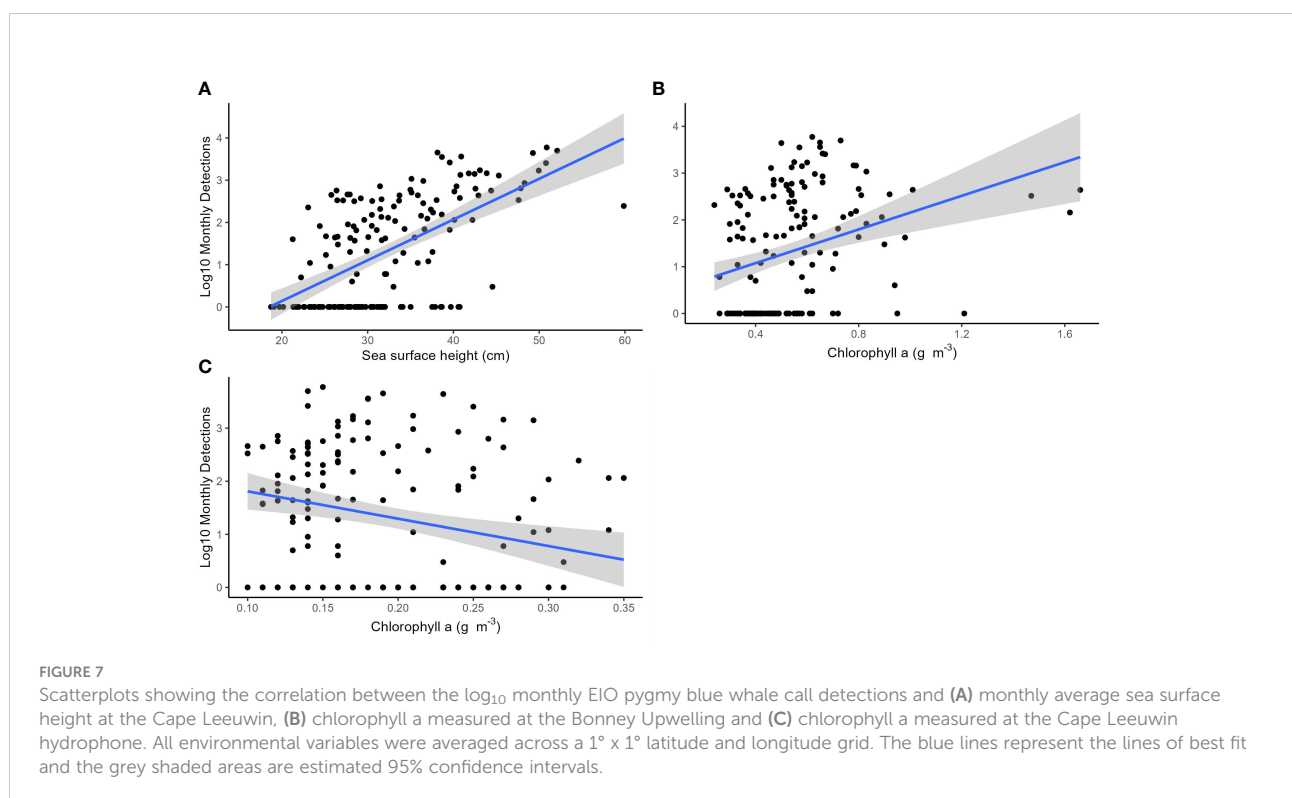
seasonal, which reflected the seasonal call detections of EIO whale calls at Cape Leeuwin. Chlorophyll-a concentrations at the hydrophone location were also seasonal, but out of sync with the number of whale call detections, explaining the observed negative relationship. Sea surface height at the hydrophone was also higher during La Niña conditions due to the strengthening of the Leeuwin Current. The variability in chlorophyll-a suggests that changes in food availability affect blue whale migratory behaviour. Firstly, the blue whales likely use partial migration strategies (Širović et al., 2004; Širović et al., 2009; Thomisch et al., 2016), typical of other migratory species (Chapman et al., 2011), so that only a proportion of the population migrates each year. Moving away from productive feeding grounds where krill are in high densities can be a risky strategy, as blue whales require large amounts of food to sustain their large body size and high energetic requirements (Goldbogen et al., 2011). The great distances that blue whales travel during migration are assumed to be energetically demanding. Therefore, individuals that are not in good body condition may skip migration altogether. In this case, the larger number of whale call detections suggests that a higher proportion of whales may have developed better body condition and underwent migration during La Niña years.

A second possible explanation is that a higher proportion of whales foraged within the GSACUS and subtropical convergence regions south of Australia during La Niña years, while during lower productivity years they foraged in areas away from Australia. Alternatively, EIO pygmy blue whales that typically feed in other regions within the Indian Ocean (Samaran et al., 2010; Samaran et al., 2013) may shift to feed in the Great Australian Bight in years when there are strong, sustained La Niña conditions, resulting in more whales migrating past the Cape Leeuwin hydrophone. Conditions within the Indian Ocean in La Niña years may make the GSACUS in the eastern Great Australian Bight a more favourable feeding site. Conversely, when conditions are not favourable and productivity is low, the whales may move to feed in other areas of the Indian Ocean (as far west as Amsterdam Island) and would therefore not be detected as they no longer pass by Cape Leeuwin during their northbound migration. A recent study of EIO pygmy blue whales in the central Indian Ocean showed an increase in the number of call detections from 2012 to 2016 near Amsterdam Island (Torterotot et al., 2020). This complements our results, where the number of call detections decreased after 2012 following the period of sustained La Niña conditions. This suggests that a higher number of EIO pygmy blue whales may have moved away from the Great Australian Bight towards the central Indian Ocean after 2012, potentially because of ENSO driven environmental conditions and altered prey availability. Further studies are needed to determine whether the whales detected in the central Indian Ocean are from the same population as those found in the GSACUS.

The monthly covariates that were examined had varied degrees of seasonality which to an extent was correlated with

FIGURE 7
Scatterplots showing the correlation between the $\log_{10}$ monthly EIO pygmy blue whale call detections and **(A)** monthly average sea surface height at the Cape Leeuwin, **(B)** chlorophyll a measured at the Bonney Upwelling and **(C)** chlorophyll a measured at the Cape Leeuwin hydrophone. All environmental variables were averaged across a 1° x 1° latitude and longitude grid. The blue lines represent the lines of best fit and the grey shaded areas are estimated 95% confidence intervals.

the seasonality of EIO pygmy blue whale call detections. SST had the most regular and predictable seasonality. SST and SSH peaked in autumn and were lowest in early spring. These patterns reflected the seasonal dynamics of the Leeuwin Current (Feng et al., 2009). During La Niña years, the Leeuwin Current experiences warming, and the southward flow strengthens (Feng et al., 2013). This too is reflected in the SST and SSH measured off Cape Leeuwin, where the annual peak temperature and height are elevated during La Niña years. Despite SSH and SST being influenced by La Niña conditions, models containing SST did not perform very well. A possible reason for SST not being a good predictor could be due to its highly predictable seasonality which does not correlate well with the less seasonally predictable blue whale calls. SSH is unlikely to directly influence blue whale movement patterns but may have an indirect relationship. SSH at Cape Leeuwin is largely driven by the strength of the Leeuwin Current, but SSH can also be influenced by upwelling and eddies which can change the availability of nutrients. Chlorophyll was also seasonal in nature, albeit not as regularly so as SST. Overall, chlorophyll levels at the Bonney Upwelling exceeded the levels measured at Cape Leeuwin. This supports the idea that feeding was more likely to occur along the Bonney coast then it was to occur at Cape Leeuwin. Furthermore, chlorophyll at Cape Leeuwin peaked during winter when the whales were further north, while chlorophyll peaked during summer at the Bonney Upwelling which is when the whales would be feeding. We used chlorophyll as a proxy for productivity, however it may not necessarily translate to krill availability or abundance. Satellite-measured chlorophyll also only reflects what is on the surface, so *in-situ* measurements at other depths could improve our models. The Bonney coast is not the only known feeding aggregation area within the GSACUS. Pygmy blue whales have also been observed feeding in the subtropical convergence zone (Garcia-Rojas et al., 2018). However, the subtropical convergence covers a large area and is highly variable in terms of upwelling and productivity, therefore analysis using the subtropical convergence was too broad and out of the scope for this study.

There are limitations in using acoustics to infer population level changes in migration patterns, as it can be difficult to differentiate whether calls come from multiple vocalising whales or a single, highly vocal individual. In addition, only singing individuals (i.e., males) are represented, as non-singing whales cannot be detected (Croll et al., 2002; Oleson et al., 2007). This means that the sampling could be biased towards male individuals and may not reflect the behaviour of female and non-vocalising whales. The conservative detector with a high detection threshold that we used meant that a substantial proportion of calling animals were missed. This was intentional, since we took a conservative approach for this study and aimed to capture whales closer to the hydrophone, rather than detecting faint calls from individuals much further away. To identify if there were changes in whale behaviour through time, our sampling design sampled in a standardised, continuous fashion, using a conservative acoustic detector that would be less influenced by changes in ambient sea noise. Whales were also only sampled as they migrate past the Cape Leeuwin hydrophone site, decreasing the likelihood of resampling the same animals over extended periods which would increase if we had also sampled within a feeding or breeding site. Additionally, it is also possible for individual whales to migrate further offshore and be out of range of the hydrophone. However, studies using satellite telemetry to track pygmy blue whales have shown that tagged individuals migrated close to the Cape Leeuwin hydrophone (Double et al., 2014; Möller et al., 2020).

ENSO events are predicted to become more intense under further climate change (Cai et al., 2014). The feeding success of baleen whales is dependent on synchronisation with planktonic production, which often occurs in pulses (Edwards and Richardson, 2004). Marine plankton has shown varied responses to climate change at different levels, leading to either a temporal or spatial mismatch between different trophic levels and their functional groups (Edwards and Richardson, 2004). Small animals with short life cycles and large population sizes will probably adapt to the longer growing seasons and be able to persist. However larger animals with longer life cycles and smaller population sizes are more likely to experience population decline (Bradshaw and Holzapfel, 2006). Extreme climatic events are predicted to disrupt phenotypic plasticity in marine birds (Lescroël et al., 2014), which means that the adaptability and resilience of other marine vertebrates should be called into question. Rates of observed shifts in the distribution and phenology (timing) of marine species are comparable to, or greater than, those for terrestrial systems (Poloczanska et al., 2013). The recovery of endangered whale populations would be influenced by their ability to adapt to these environmental changes.

This study of 16 years of whale acoustic presence, though covering a small subset of time in comparison to climate modelling studies, suggests that large-scale changes in environmental variability due to ENSO are potentially influencing the migration behaviour of blue whales. This period contained only two La Niña events and further sampling of additional La Niña events would provide a clearer picture of the impacts of ENSO events on whale migration. Our study highlights the importance of capitalising on archived, calibrated, long-term acoustic data (such as the CTBTO data) to examine the influence of periodic climatic signals such as ENSO in addition to long-term warming trends on whale migratory behaviour.

Data availability statement

Ethics statement

Ethical review and approval was not required for the animal study because acoustic data was obtained passively with no direct impact on the animals.

Author contributions

Both authors conceived and designed the project, revised, and approved final manuscript. GT conducted blue whale acoustic analysis, statistical analysis and wrote the first draft of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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