



Bryde's whale seasonal range expansion and increasing presence in the Southern California Bight from 2000 to 2010

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ABSTRACT

Bryde's whales (*Balaenoptera edeni*) are commonly found in tropical and subtropical regions of the Pacific Ocean, but few studies have explored the presence of Bryde's whales at the boundary of their distribution range. Such studies are increasingly relevant as climate impact models predict the range expansion of warm water species towards the poles in response to ocean warming. Like other baleen whales, Bryde's whales produce distinct low frequency (< 60 Hz) calls, which can be used for long-term acoustic monitoring of whale presence in an area. Autonomous passive acoustic recorders deployed at five sites in the Southern California Bight (SCB) were used to investigate the presence of Bryde's whales in temperate waters from 2000 to 2010. Calling Bryde's whales were observed in the SCB from summer to early winter, indicating a seasonal poleward range expansion. There was a significant increase in the presence of calling Bryde's whales in the SCB between 2000 and 2010, but no significant correlation was found between Bryde's whale presence and local sea surface temperature. Bryde's whale occurrence is likely driven by prey availability within the California Current ecosystem, which is affected by seasonal and inter-annual changes in climate and oceanographic conditions. Continued monitoring of Bryde's whales and their prey in the eastern North Pacific is needed to provide a longer time series and determine the full effect of climate variability and ocean warming on the distribution of this species.

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1. Introduction

Bryde's whales (*Balaenoptera edeni*) are commonly found in the warm waters of the eastern tropical Pacific (ETP) (Leatherwood et al., 1988), an oceanographic region bounded by Mexico to the north (30°N), Hawaii to the west (155°W), and Peru to the south (15°S). While Bryde's whales are not known to undertake long distance migration observed for some baleen whales (Corkeron and Connor, 1999; Barlow, 2006), limited seasonal poleward range expansion has been observed during summer in populations off South Africa and within the Gulf of California, Mexico (Tershy, 1992; Best, 2001). As a warm-water species, Bryde's whales are predicted to gradually expand their range poleward with long-term ocean warming (MacLeod, 2009). To date, very little is known about Bryde's whales in the Southern California Bight (SCB), the northern boundary of their distribution in the eastern North Pacific (Privalikhin and Berzin, 1978; Leatherwood et al., 1988), but more information on the existing

seasonal and inter-annual dynamics of Bryde's whale distribution is needed to identify their response to long-term trends.

The SCB is defined as the coastal and offshore region extending from Point Conception (34°26'53"N, 120°28'17"W) in southern California, to Ensenada, Mexico (31°51'28"N, 116°36'21"W), on the west side of the northern Baja California peninsula. Historically, Bryde's whales were rare visitors to the SCB (Leatherwood et al., 1988). The first reported sighting of a Bryde's whale off California was in 1963 (Nicklin, 1963; Morejohn and Rice, 1973). Extensive ship and aerial surveys conducted in the eastern North Pacific in the last two decades have produced just a handful of confirmed Bryde's whale sightings, notably in 1991, 2006, 2008, and 2010 (Smultea et al., 2012). Two Bryde's whale strandings have been recorded in southern California in the last few decades: in Corona del Mar, Orange County in 1982, and at Pt. Mugu, Ventura County, in 2004 (Table 1). Visual surveys have yielded only a few Bryde's whale sightings north of the SCB (Privalikhin and Berzin, 1978; Smultea et al., 2012). Records from 20th century whaling (1911–1971) indicate two Bryde's whales were harvested at the Richmond, California station in 1966 (Table 1), although it is possible these whales were misidentified (Morejohn and Rice, 1973). More recently, in 2010, two unprecedented

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Table 1
Dates and coordinates of previous Bryde's whale sightings, strandings, and whaling harvests in the eastern North Pacific, excluding two Bryde's whale strandings in southern Puget Sound, Washington (Huggins et al., 2011).

Year	Date	Event	Coordinates	Source
1963	8 January	Sighting/entangled whale	32°51'36"N, 117°16'12"W ^a	Nicklin (1963), Morejohn and Rice (1973)
1966	31 July	Whaling harvest	38°00'N, 123°40'W	International Whaling Commission, msecretariat@iwcoffice.org
1966	2 August	Whaling harvest	38°00'N, 123°42'W	International Whaling Commission, msecretariat@iwcoffice.org
1982	29 November	Stranding	33°35'30"N, 117°52'30"W	James P. Dines and David S. Janiger, Natural History Museum of Los Angeles County
1991	5 October	Sighting	36°6'58"N, 125°8'59"W	Smultea et al. (2012)
2004	22 July	Stranding	34°01'N, 119°00'W	National Strandings Network, MMHSRP.NationalDB@noaa.gov
2006	17 August	Sighting	32°53'60"N, 119°10'53"W	Smultea et al. (2012)
2006	18 August	Sighting	32°45'5"N, 118°56'4"W	Smultea et al. (2012)
2008	19 October	Sighting	33°7'6"N, 118°19'52"W	Smultea et al. (2012)
2010	24 September	Sighting	32°55'40"N, 118°54'23"W	Smultea et al. (2012)
2010	25 September	Sighting	32°51'N, 119°05'W	Smultea et al. (2012)

^a Estimated coordinates based on descriptions of the encounter from listed sources.

Bryde's whale strandings were reported in Washington State, along with several other sightings and strandings of tropical cetaceans anomalous to the region (Huggins et al., 2011).

Intermittent Bryde's whale sightings in the eastern North Pacific over the last 50 years suggest a possible link between Bryde's whale distribution and climate oscillations. In fact, shifts in Bryde's whale prey distributions in the eastern North Pacific have been correlated to seasonal and inter-annual climate variability (Brinton and Townsend, 2003; Chavez et al., 2003; Keister et al., 2011; Salvadeo et al., 2011). Targeted, long-term monitoring would elucidate the dynamics of Bryde's whale presence in this region, and aid in determining a relationship to varying ecological and oceanographic conditions. Visual identification of Bryde's whales is challenging in the eastern North Pacific where similar-looking species, such as sei whales (*B. borealis*) and fin whales (*B. physalus*), commonly occur (Leatherwood et al., 1988). However, baleen whales are known to produce species-specific vocalizations. Long-term passive acoustic monitoring of known whale vocalizations can be used to determine whale presence and observe temporal and spatial dynamics of acoustically-distinct species and populations (Thompson and Friedl, 1982; Stafford et al., 2001; Širović et al., 2004; Oleson et al., 2007b). Bryde's whales in particular have a geographically varying acoustic repertoire consisting of pulses, downsweeps, and moans (Cummings et al., 1986; Oleson et al., 2003; Heimlich et al., 2005). There are at least six distinct Bryde's whale call types described in the ETP and the Gulf of California, Mexico, but only one call, termed Be4 per Oleson et al. (2003), has been exclusively documented north of approximately 15°N, including off the west coast of the Baja California peninsula (Cummings et al., 1986; Edds et al., 1993; Oleson et al., 2003; Heimlich et al., 2005).

In this study, we report the presence of Bryde's whale calls in passive acoustic data from the SCB alongside sea surface temperature (SST) from 2000 to 2010. Our objective was to investigate the seasonal and inter-annual changes in Bryde's whale presence at the boundary of their distribution range, and correlate their presence to SST. Given that these whales are typically distributed in tropical waters, we tested the hypothesis that the presence of Bryde's whale calls is linked to warmer SST.

2. Materials and methods

2.1. Passive acoustic data

Autonomous, seafloor-mounted Acoustic Recording Packages (ARPs) and High-frequency Acoustic Recording Packages (HARPs) (Wiggins, 2003; Wiggins and Hildebrand, 2007) were deployed at five locations in the SCB (Fig. 1) between August 21, 2000 and

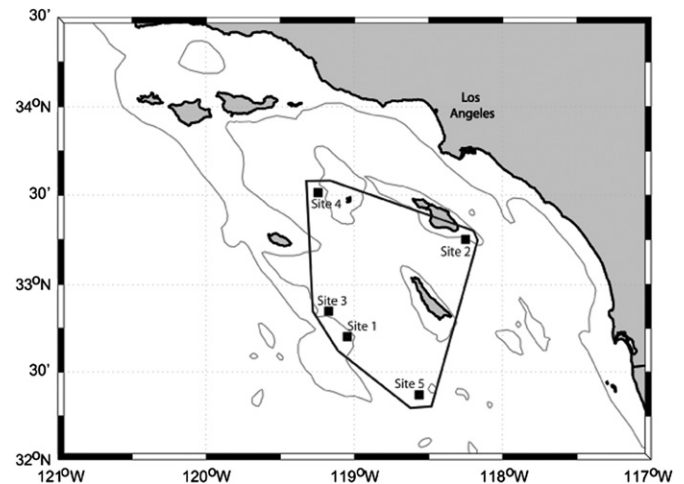


Fig. 1. ARP (Site 1) and HARP (Sites 2–5) deployment locations (black squares) in the Southern California Bight. Site 1 recorded in 2000, 2001, and 2003; Site 2 recorded in 2005, 2006, and 2007; Site 3 recorded in 2007 and 2008; Sites 4 and 5 recorded in 2009 and 2010. Thin gray lines mark 500 m bathymetric contour. The black polygon denotes the area used for basin-scale sea surface temperature data extraction.

December 31, 2010 (Table 2). ARPs recorded continuously at 500 Hz or 1 kHz during deployments from 2000 to 2003; HARPs were used in subsequent deployments, from 2005 to 2010, and recorded continuously at 200 kHz. HARP data were decimated using an eighth-order, low-pass Chebyshev type I filter to reduce the data to 2 k Samples/s (new effective bandwidth: 10–1000 Hz) which lessened computational requirements for all subsequent analyses.

There was one deployment per year, during the summer and fall of 2000, 2001, 2003, 2005, 2006, and 2008 with average deployment duration 60 day. Concurrent data were collected at Sites 2 and 3 in 2007 (67 day total effort; 41 day concurrent), and Sites 4 and 5 in 2009 (586 day total effort; 228 day concurrent) and 2010 (617 day total effort; 300 day concurrent) (Table 2). HARPs deployed at Sites 4 and 5 in 2009 and 2010 recorded continuously throughout the year with occasional short gaps (3–29 day) in the data between deployments.

Year-long recordings from Sites 4 to 5 in 2009 to 2010 allowed us to determine seasonal patterns in Bryde's whale presence, while data from Sites 1 to 3 (2000–2008) allowed us to investigate inter-annual trends. Although the absence of a whale call does not necessarily mean a whale is not present in the area, the presence of the Be4 call type (Oleson et al., 2003) was used in this study as a proxy for Bryde's whale presence in the SCB. While we encountered one other Bryde's whale call type, the Be2, or high

Table 2

Deployment information (year, instrument site, latitude, longitude, depth, recording start and end dates, and number of recording days) for all acoustic data used in the analysis of Bryde's whale call presence in the Southern California Bight.

Deployment year	Site	Coordinates	Depth (m)	Instrument type	Recording start date	Recording end date	Number of recording days
2000	1	32°42'7"N, 119°2'26"W	300	ARP	21 August	15 October	56
2001	1	32°42'5"N, 119°3'14"W	254	ARP	27 August	23 October	58
2003	1	32°41'58"N, 119°3'7"W	245	ARP	1 August	31 October	92
2005	2	33°15'8"N, 118°15'2"W	318	HARP	13 August	27 September	45
2006	2	33°15'8"N, 118°15'8"W	335	HARP	1 September	25 October	54
2007	2	33°15'2"N, 118°14'59"W	339	HARP	11 July	3 September	54
2007	3	32°50'49"N, 119°10'36"W	1013	HARP	24 July	16 September	54
2008	3	32°50'50"N, 119°10'29"W	1018	HARP	4 August	27 September	54
2009	4	33°30'35"N, 119°15'17"W	977	HARP	13 January	31 December	292
2009	5	32°22'12"N, 118°33'55"W	1304	HARP	14 January	31 December	293
2010	4	33°30'53"N, 119°14'50"W	910	HARP	1 January	31 December	305
2010	5	32°22'11"N, 118°33'48"W	1281	HARP	1 January	31 December	312

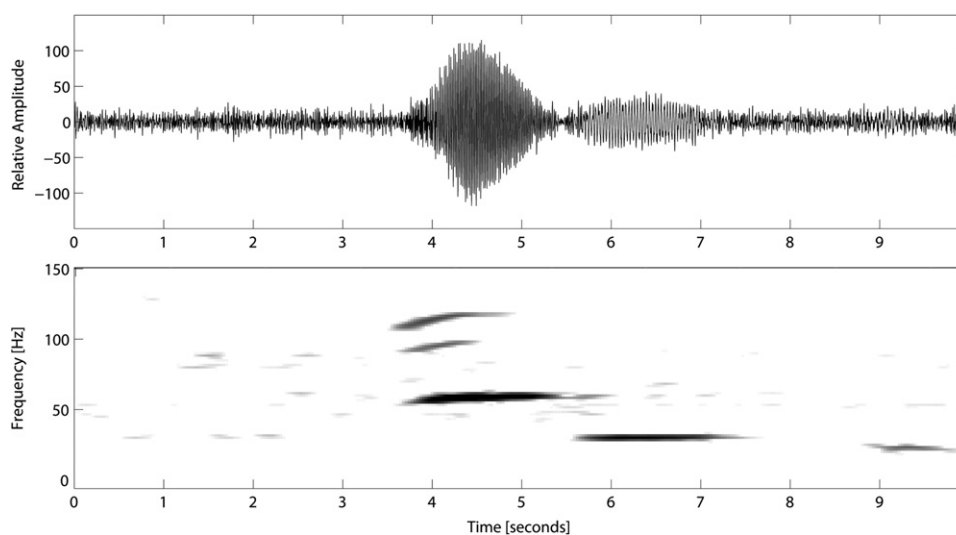


Fig. 2. Waveform and spectrogram of Bryde's whale Be4 call recorded at Site 1 in the Southern California Bight in September 2003. The spectrogram was created from data sampled at 500 Hz, using 300-point fast Fourier transform, Hanning window, and 95% overlap.

burst-tonal (Oleson et al., 2003; Heimlich et al., 2005), in recordings from the SCB, this call type was extremely rare (less than 3% of total number of hours with manually-detected Bryde's whale calls) and in those cases the Be4 call type was generally also present. Thus, to have sufficient data for robust statistical analysis and avoid confounding due to multiple call types, we only used the Be4 call as an indicator of Bryde's whale acoustic presence in the SCB. While estimating density and abundance from calls is non-trivial (Marques et al., 2011), evidence suggests that Be4 calls recur at a reasonably constant rate (Oleson et al., 2003), and that Bryde's whales typically travel alone or in very small groups (Leatherwood et al., 1988). Therefore, we assume constant call rates for individuals and that a higher rate of calling is indicative of an increased presence of whales.

Manual and automated detections were used for finding Bryde's whale Be4 calls in the data (Fig. 2). Trained human analysts manually scanned all recorded data from 2000, 2001, 2003, and 2010, and a subset of data from 2009. Presence of Bryde's whale calls during each hour was determined from long-term spectral averages (Wiggins and Hildebrand, 2007). For data collected between 2005 and 2009, spectrogram correlation was used to automatically determine call presence within each hour of data (Mellinger and Clark, 2000). A three-segment kernel representing the Be4 call was developed by modifying MATLAB (Mathworks, Natick, MA) spectrogram correlation software code provided by D. Mellinger (Oregon State University). The kernel

was based on the measurement of 30 independent calls, each call separated by at least one day of recording to decrease likelihood the calls were from the same individual. The kernel consisted of a 1 s upsweep from 55 to 57.5 Hz, a more gradual 1 s upsweep from 57.5 to 57.6 Hz, and finished with a 1 s tone (57.6 Hz). A 3 Hz bandwidth was applied to the kernel to account for frequency variability. For the purposes of this study, the detection threshold was adjusted to minimize missed calls since the goal was to detect all hours of call presence (Munger et al., 2005). The final automatic detector had 10% missed cues and 50% false positives based on a predefined test data set. The high false positive rate was due to ship noise in the Be4 frequency band. All detections were manually verified and all false positives were removed from the data before subsequent analysis.

We define call-hour rate as the number of hours with Be4 calls present per day, normalized by the total number of hours per day with acoustic data (effort). We averaged these daily rates into weekly bins for plotting.

2.2. Sea surface temperature

To investigate the relationship between Bryde's whale calling presence and temperature, we used the remotely-sensed daily 4 km AVHRR Pathfinder version 5 data set (<http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/>) described by Casey et al. (2010). Daytime quality-controlled SST data were obtained for

years with passive acoustic data (2000, 2001, 2003, 2005–2009). Version 5 data were not available for 2010. We used Windows Image Manager (WIM) and WIM Automation Module (WAM) software developed by M. Kahr (Scripps Institution of Oceanography) to reduce global data to the areas of interest and to extract daily means. Area of interest was defined as an area around each recording instrument where Bryde's whale calls may be detected and which can provide consistent, good quality SST data. We expect Bryde's whale calls to be detected at a range of several tens of km, thus, daily SST values were calculated from a 40 km radius around each acoustic recording site. These values were averaged into 7-day bins to plot against weekly call-hours for qualitative analysis. For basin-scale analysis, a polygon with corners around each of the five acoustic recorder sites was extracted (Fig. 1). A single SST mean value was averaged from the daily means within this polygon between August 15 and October 15 for years with passive acoustic and SST data available to correlate with Bryde's whale call-hour rates.

2.3. Statistical analyses

To correlate Bryde's whale call presence with sea surface temperature, we first determined the number of independent call and SST samples for the respective data. We calculated the integral time scale (ITS) from the daily SST time series for each site and year with passive acoustic data (Emery and Thomson, 1998). We also calculated the ITS for Bryde's whale daily call-hour presence for each site and deployment period. We used the average of all the SST ITS, which was 51 day, for determining the number of degrees of freedom for subsequent statistical analyses using SST, as it was the more conservative measure between the SST and Bryde's whale call-hour ITS results.

Bryde's whale calling presence for each year was determined by calculating an average call-hour rate over a continuous 45-day period with available data within the peak calling season (13 August to 16 October). We used 45 day because that was the duration of the shortest instrument deployment over the August–October period (in 2005). For 2007, 2009, and 2010, which had overlapping data from two acoustic recording sites, we ran a Wilcoxon signed-rank test to confirm that call-hour rates within 45-day periods between sites did not differ significantly ($W=7$, $P>0.05$). In these cases, we pooled data from both sites within the 45-day window to calculate the Bryde's whale call-hour rates during peak presence for each year. Additionally, we used the pooled data for calculating weekly call-hour rates in the region.

We calculated a least-squares linear regression from the call-hour rates to check if there was a trend in Bryde's whale call rates over time. We tested whether there was an increase in Bryde's whale call-hour rate over our study period using t-test for slope of the line. To investigate the effects of basin-scale variations on the presence of calling Bryde's whales in the SCB, we calculated Pearson's correlation coefficient between the overall Bryde's whale call-hour rates and SST means. We tested the hypothesis that there is a positive correlation between Bryde's whale call-hour rate in SCB and temperature. All statistical analyses were conducted using SigmaStat 3.11 for Windows (Aspire Software International, Ashburn, VA).

3. Results

Bryde's whale Be4 calls were not present in 2000 or 2001, but they were present in all analyzed years of acoustic recordings onward from 2003 (Fig. 3). From the data collected in 2009 and 2010, the period with year-round recordings, a distinct seasonality in the presence of Bryde's whale calls in the SCB is evident,

with calls detected in both years between August and December (Fig. 3, top two panels). There was variation in weekly call rates, as well as in the date of the first call detection. In 2009, the first Bryde's whale calls were detected in mid-June, while in 2010 the first calls were detected in August.

While year-long recordings were not available from 2000 to 2008, the time periods analyzed fell within the periods of seasonal presence of Bryde's whales in the SCB. Peaks in calling in 2003, 2007, and 2008 occurred in late August. In 2006 and 2010, peaks occurred in October. There was no clear peak in 2005, and there was also considerably less calling presence that year than in other analyzed years between 2003 and 2010. Despite variability in calling presence, there was a significant overall increase in Bryde's whale call-hour rate during the peak calling period between 2000 and 2010 ($t(7)=2.74$, $P=0.029$; Fig. 4), with a rate of increase of 0.014 call-hours/year. Although Bryde's whale calls were generally more prevalent during the warmer summer months, there was no significant relationship between call-hour rates and sea surface temperature ($r=0.159$, $P=0.353$).

4. Discussion

Major findings of this study are two-fold: (1) Bryde's whale calls are present in the SCB between summer and early winter, suggesting a seasonal poleward range expansion of this typically warm-water species; (2) Bryde's whale seasonal presence in the SCB has been increasing over the last decade. This increasing trend does not correlate to local SST, but could relate to larger-scale climate variability and long-term climate trends.

4.1. Seasonal poleward range expansion

Our results indicate that Bryde's whales are present in the SCB between summer and early winter. This finding corroborates the timing of all previous sightings, strandings, and whaling harvests of Bryde's whales in the region (Table 1). Seasonal poleward range expansion of Bryde's whales into the SCB corresponds with observed seasonal movements of Bryde's whales in other geographic regions (Tershy, 1992; Best, 2001). The presence of the Be4 call in the SCB indicates these whales may belong to a population of Bryde's whales distributed on the west coast of the Baja California peninsula, where the Be4 call type was first recorded (Oleson et al., 2003).

Traditionally, Bryde's whale distribution worldwide has been marked by waters warmer than 20 °C (Leatherwood et al., 1988). In this study, Bryde's whale calls were generally found in the SCB during months with high SST; however, we found no direct correlation between temperature and whale presence. Our results show that the whales remained in the SCB at least through the end of December in 2009 when the SST was 15 °C, confirming previous studies that have questioned the association of Bryde's whales with the 20 °C isotherm (Gallardo et al., 1983; Wiseman et al., 2011). Since lower temperatures alone do not appear to limit Bryde's whale distribution, it is likely that the whales are responding to a more complex convergence of physical, environmental, and biological conditions.

Aside from temperature, Bryde's whale occurrence has been linked to regions of strong upwelling and high productivity (Gallardo et al., 1983; Palacios, 2003; Pardo and Palacios, 2006). In the SCB, strong seasonal upwelling stimulates phytoplankton blooms in the spring and early summer, which in turn feed zooplankton aggregations that attract higher trophic level feeders, including baleen whales, to the region in the summer months (Fiedler et al., 1998; Burtenshaw et al., 2004; Mann and Lazier, 2006; Barlow et al., 2008). Since zooplankton account for 40% of

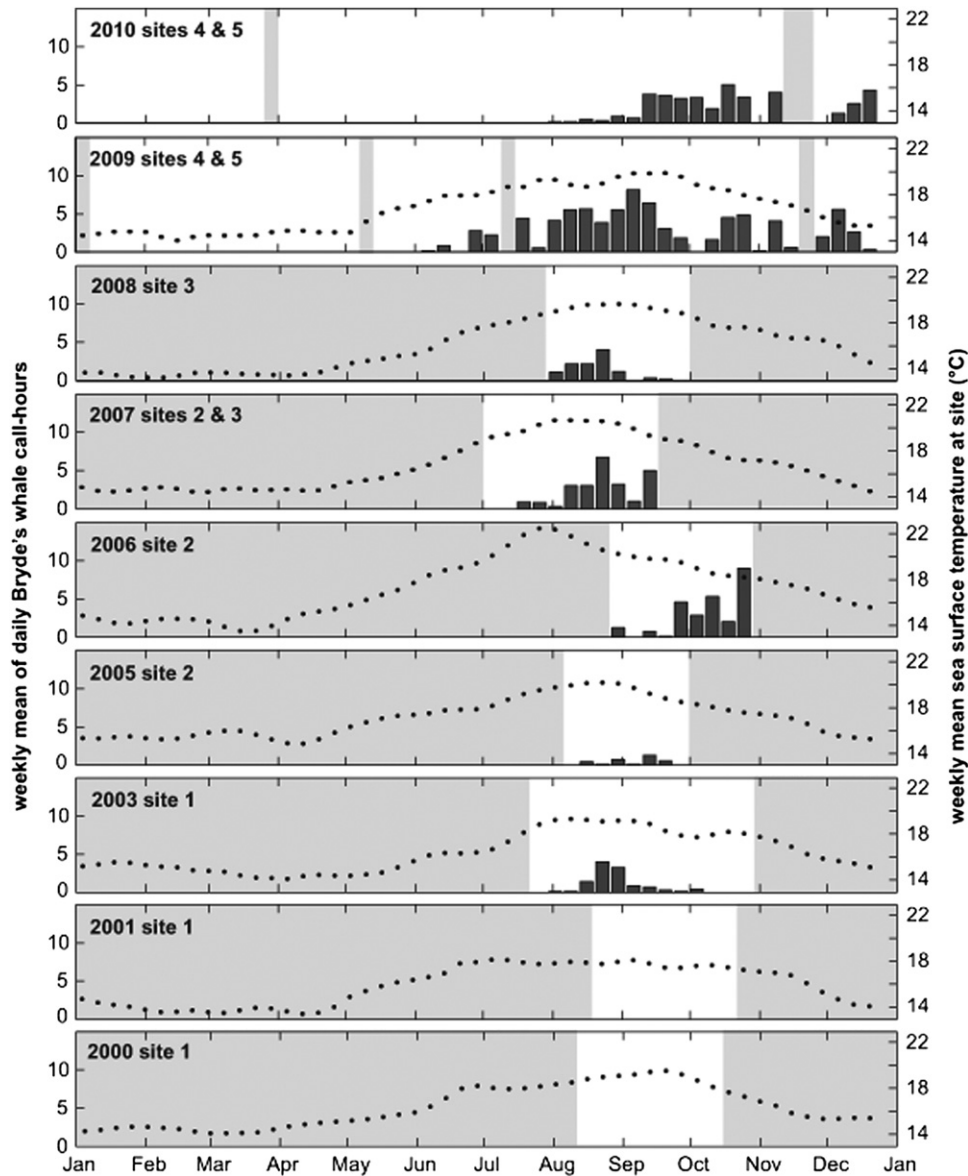


Fig. 3. Weekly mean of daily count of the hours with Bryde's whale calls (black bars) and average weekly sea surface temperature (SST) from a 40 km radius around the recording site (dotted line) over each year. Shaded areas represent times when data were not available. Note that SST data for 2010 were not available.

Bryde's whale diet composition (Pauly et al., 1998), it is possible that Bryde's whales are seasonally exploiting aggregations of zooplankton in the SCB.

The timing of Bryde's whale presence in the SCB also coincides with the seasonal presence and movement of other Bryde's whale prey species. Small schooling fish constitute the majority of Bryde's whale diet (Leatherwood et al., 1988; Tershy, 1992; Pauly et al., 1998); while anchovy (*Engraulis mordax*) are present in the SCB year-round (Mann and Lazier, 2006), one particular stock of sardine (*Sardinops sadax*) migrates north along the west coast of the Baja California peninsula into the SCB between July and December (Felix-Uraga et al., 2004). This timing also coincides with a seasonal transition to poleward dominated flow (Lynn and Simpson, 1987; Bray et al., 1999; Lluch-Belda et al., 2003a; Melton et al., 2009), which transports another Bryde's whale prey species, pelagic red crab (*Pleuroncodes planipes*) (Leatherwood et al., 1988), north along the west coast of the Baja California peninsula (Lluch Belda et al., 2005). If the Be4 call found in the SCB in fact belongs to the same population of Bryde's whales that occupies the west coast of the Baja California

peninsula, these whales could be following the seasonal poleward movement of their prey.

4.2. Increasing presence

Bryde's whale calling presence has increased significantly in the SCB in the last decade. An increase in the number of hours with calls present could signify an increase in the number of whales in the SCB, but it could also mean the same number of whales is remaining in the SCB longer. Either way, this results in an increase in Bryde's whale presence in the SCB. Alternatively, an increasing call-hour rate could signify a shift in behavior. In other words, it is possible that the same number of whales is present for the same amount of time from year to year, but the whales are vocalizing more often. Call types have been associated with certain behaviors, such as feeding or mating, in other baleen whales (Oleson et al., 2007a; Stimpert et al., 2007); however, there are no studies linking the Be4 call to a particular behavior to date. Furthermore, there is currently no evidence to suggest that baleen whales are drastically changing their behavior from year

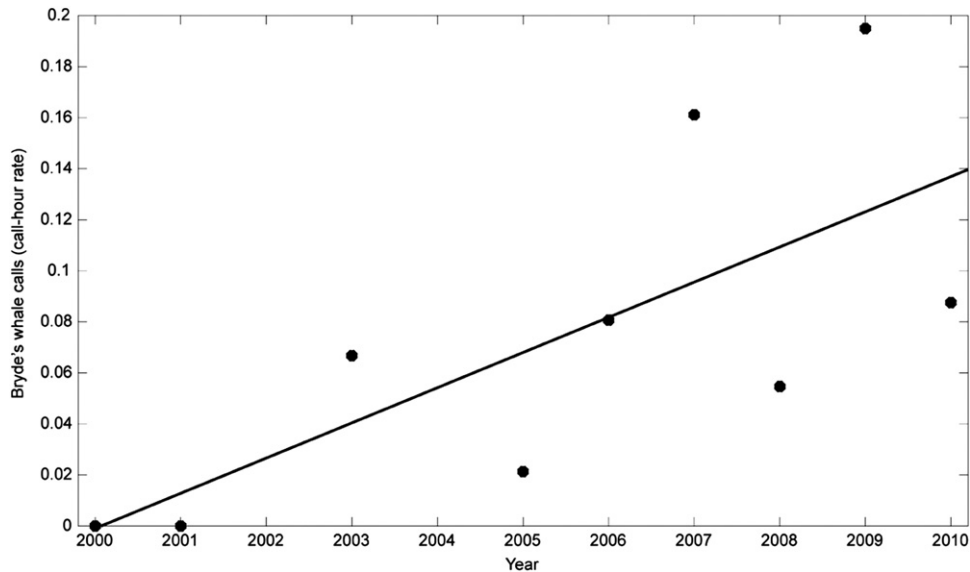


Fig. 4. Average Bryde's whale call-hour rate calculated over a 45-day period between 13 August and 16 October for each year (black dots). Black line is the linear least-squares fit ($t(7)=2.74$, $P=0.029$).

to year to include more call production. Using the law of parsimony, we assume that a long-term increase in call-hour rate is best explained by the increasing presence of Bryde's whales.

One explanation for an increase in Bryde's whale presence in the SCB may be an increase in Bryde's whale abundance in the ETP. Although confounded by changes in visual survey effort, estimates show an increase in Bryde's whale abundance in the ETP (Gerrodette and Forcada, 2002). Increasing seasonal presence of Bryde's whales in the SCB may reflect a 'spillover' of animals from the ETP (Holt, 1987). The call type monitored in this study, however, was identified and only recorded in a small, northerly portion of the entire area of the ETP surveyed in Oleson et al. (2003) and Heimlich et al. (2005) studies. This suggests that the Bryde's whales in this study may be an acoustically distinct population, which makes it less likely that the increasing presence of this call type in the SCB is a 'spillover' of animals from the greater ETP.

There is stronger ecological and oceanographic evidence to support an increasing trend in Bryde's whale presence in the SCB within the last decade. In the Pacific Ocean, warm and cool climatic events of the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) drive most inter-annual physical and ecological changes (McGowan et al., 1998; Bograd and Lynn, 2003; Lluch-Belda et al., 2003b; Di Lorenzo et al., 2005). Although we did not find a significant correlation between SST and Bryde's whale presence in the SCB, northerly range expansion during warm ENSO and PDO events has been observed in the California Current for several Bryde's whale prey, such as zooplankton (Keister et al., 2011), small schooling fish (Salvadeo et al., 2011), and red crab (Lluch Belda et al., 2005). In La Paz Bay, in the southern Gulf of California, Mexico, Salvadeo et al. (2011) found a decrease in Bryde's whale presence corresponding to warm ENSO events, and hypothesized that the whales were following prey aggregations to higher latitudes. This corroborated an observed increase in Bryde's whale abundance in the central Gulf of California during a warm ENSO event in 1984 (Tershy et al., 1991). It is conceivable that, on the west coast of the Baja California peninsula, Bryde's whales and their prey are also expanding their ranges in response to inter-annual climate fluctuations. This would explain the inter-annual variability in Bryde's whale presence shown herein (Fig. 3).

Northerly range expansion has also been observed within the last decade for Humboldt squid (*Dosidicus gigas*) (Field et al., 2007), which share prey species with Bryde's whales (Leatherwood et al., 1988;

Tershy, 1992; Markaida and Sosa-Nishizaki, 2003). Interestingly, Humboldt squid have been increasing in abundance in the California Current since 2003 (Bjorkstedt et al., 2010), the same year Bryde's whales were first detected in this study. Humboldt squid presence in the California Current also parallels the seasonality in Bryde's whale presence reported here; both species are absent from the region from spring until early summer (Bjorkstedt et al., 2010). It has been proposed that the northerly range expansion of Humboldt squid is related to changes in oceanographic conditions and warm ENSO events (Zeidberg and Robison, 2007).

In the last decade, there has been considerable fluctuation between warm and cool events affecting the California Current ecosystem, but the effects were not always observed within the SCB (Bjorkstedt et al., 2010). To test for statistically significant association between Bryde's whale presence in the SCB and climate fluctuation, we would need a longer time series to account for regional variability within large-scale oceanographic patterns.

4.3. Long-term climate trends

The anomalous presence of Bryde's whales and other tropical cetaceans as far north as Washington State in 2010 and 2011 (Huggins et al., 2011), along with the increasing trend in Bryde's whale presence at the boundary of their distribution range presented here, suggest significant ecosystem changes may be occurring within the eastern North Pacific. Recent projections of global ocean warming impacts forecast the gradual range shift of cetacean species and their prey towards the poles (Parmesan and Yohe, 2003; Learmouth et al., 2006; MacLeod, 2009; King et al., 2011). Our study shows the seasonal and inter-annual dynamics of Bryde's whales in the SCB using the longest time series for an acoustic study of this species to date, but continued monitoring is necessary to elucidate the persistence of Bryde's whale presence in the SCB, and further explore the relationship between Bryde's whales and long-term climate trends.

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