The environmental factors determining temporal distributions of cetaceans in Mossel Bay, South Africa

By

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PLAGIARISM DECLARATION

I, David Levy, declare that the dissertation, which I hereby submit for the degree of MSc (Biological Sciences) at the University of Cape Town, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature:

Date:

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ABSTRACT

A variety of cetacean species make use of the bays along the South African coast for different purposes, including feeding, mating and calving. Sightings of five species of cetaceans were recorded from shore based locations between February 2010 and August 2014 in Mossel Bay, Western Cape. In this study, we aimed to examine the underlying environmental variables: sea surface temperature (°C), chlorophyll *a* concentration ($mg.m^{-3}$) and moon brightness (as % of full) that potentially affect presence patterns within the bay, and several temporal scales (diurnal, monthly, seasonal, annual). The study focused on three whale species: the southern right whale (*Eubalaena australis*), humpback whale (*Megaptera novaeangliae*) and Bryde's whale (*Balaenoptera brydei*); and two dolphin species: the Indo- Pacific bottlenose dolphin (*Tursiops aduncus*), and the Indian Ocean humpback dolphin (*Sousa plumbea*). Generalized additive models (GAM) were used to model the sighting rate of the common cetacean species in the area, by relating sighting rate to the environmental variables. Cow-calf groups and adults-only groups were modelled separately for humpback and southern right whales. Chlorophyll *a* concentration is commonly indicative of high trophic productivity, and sea surface temperature is indicative of biophysical processes that influence cetacean distribution, as well as cetacean migration preferences. Change in sea surface temperature (over the study period) was a significant contributing factor to the sighting rate of cow-calf paired groups and adults-only groups of both right whales and humpback whales, underlying their greater sighting rate during the winter and spring months annually; thus conforming to the seasonal migration from Antarctica for breeding and calving. Chlorophyll *a* concentration was a significant factor contributing to Bryde's whale, bottlenose and humpback dolphin distribution. These species reside along the South African coast all year round, but are more frequently seen when trophic productivity is high. During 2011, sea surface temperature values were lower and chlorophyll *a* concentrations greater than average in Mossel Bay, due to the La Niña effect. This was found to positively correlate with the use of Mossel Bay by the cetacean species in the area. This paper highlights the importance of biophysical processes on cetacean distribution at various temporal scales (diurnal, monthly, seasonal and annual), and the information it provides may be used for conservation planning management.

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INTRODUCTION

Understanding biodiversity distribution patterns has long been an important focus of interest for ecologists. In more recent decades, motivation for this focus includes the concern over the status of global biodiversity, and the need to determine the current status, in order to predict the impacts of global environmental change (species invasion, climate change, pollution and habitat destruction) on biodiversity in the future (Gaston, 2000; Robinson *et al.,* 2011). Advances in remote-sensing technology, species occurrence recording methods and analytical tools for collecting and analyzing data have allowed for the development of various models for quantifying taxa distribution, e.g. rule-based, literature review based and empirical statistical models.

Species distribution models (SDM) are an example of empirical statistical models that provide practical information on the spatial distribution of species. They can be used in conservation planning, biosecurity (species invasion and disease), climate change adaptation, and the testing of hypotheses from theoretical ecology that relate to the processes driving biogeographic patterns (Robinson *et al.,* 2011). Many different SDMs have been developed including correlative, coupled correlative and process-based models. While each model has advantages and disadvantages, most studies have used correlative models (Robinson *et al.,* 2011). The correlative model consists of relating species occurrence records (presence-absence and/or presence only) with environmental data in order to explain or predict species distributions at spatial and/or temporal scales. For example, sighting counts of a species (groups/individuals) observed over a period of time in a defined study area are correlated with seasonal (or diel, yearly or other time scale) environmental factors, in order to predict their use of the area.

Over the past two decades, the use of SDMs has increased rapidly to explain terrestrial animal distribution (Robinson *et al.,* 2011); even though there has been a growing interest in SDM use for marine mammal distribution (Redfern *et al.,* 2006), it has not been widely utilized until the last decade.

Most SDMs for the marine environment have been applied in conservation planning, e.g. the design of marine protected areas to include essential fish habitats (Leathwick *et al.,* 2008; Maxwell *et al.,* 2009; Robinson *et al.,* 2011; Valavanis *et al.,* 2008). While there have been numerous applications of SDMs to marine species, concern has been raised on the appropriateness of SDMs for marine systems regarding climate change and species invasion, largely because physiological and ecological factors differ in importance between terrestrial and marine realms and some of the knowledge for marine systems has yet to be adequately incorporated into SDMs (Elith and Leathwick, 2009; Kearney and Porter, 2009; Pearman *et al.,* 2008; Pearson and Dawson, 2003; Robinson *et al.*, 2011; Skelly *et al.,* 2007). For example, the dispersal of terrestrial organisms is usually considered an important factor. Conversely, since dispersal is more frequent in the marine realm, dispersal would be less of a concern for marine SDM applications. Ontogenetic shifts and feeding are considered to be important ecological factors in the application of marine SDMs when compared to terrestrial SDMs. And therefore, it was suggested that marine SDMs be compared with different types of SDMs and other types of models (e.g. coupled correlative and process based SDMs; spatial population dynamic models), especially for applications regarding climate change and species invasion (Robinson *et al.*, 2011).

Marine ecosystems are dynamic and are therefore subject to variability that operates on multiple distribution scales e.g. spatial (meters to thousands of kilometers) and temporal (days to decades) scales (Redfern *et al.*, 2006). This could lead to spatial or temporal lags between physical processes and biological response (Grémillet *et al.*, 2008). Consequently, the challenges may be greater when developing species-habitat models for the marine environment, compared to the terrestrial environment. The ability of such models to explain or predict marine animal distribution depends on them being sufficiently flexible to accommodate a variety of potential explanatory variables (Redfern *et al.,* 2006). However, species distribution models of marine mammals are becoming common. Many cetaceans are wide-ranging, and their distribution patterns respond to entire marine ecological changes rather than to short-term variability in reproduction and survival (Forney, 2000).

As a result, models that predict and explain cetacean habitat suitability and distribution are essential in order to inform management of anthropogenic activities that threaten cetacean populations (Redfern *et al.,* 2006). Cetacean-habitat models (distribution models) have already been used to relate distributions to environmental factors, including investigating and mapping distributions and habitat preference (Au and Perryman, 1985; Baumgartner *et al.*, 2003; Davis *et al.*, 2002; Elwen *et al.*, 2010; Kaschner *et al.*, 2006; Moses and Finn, 1997; Selzer and Payne, 1988; Tynan *et al.*, 2005; Waring *et al.*, 2001; Yen *et al.*, 2004). They have also been used in management such as the improvement of sighting rate estimates (Forney, 2000), the development of marine protected areas (Cañadas *et al.,* 2002; Hooker *et al.,* 1999) and understanding cetacean-fisheries interactions (Kaschner, 2004; Torres *et al.,* 2003). Despite this, cetacean-habitat modelling is still in its infancy. Habitat variables used to model cetacean distributions include oceanographic data such as water column properties, surface water conditions, and ecosystem characteristics such as competitor, prey and predator densities. Physical oceanographic data (e.g. sea surface temperature, chlorophyll *a* concentration) represent proxies for prey sighting rate or availability, which are expected to influence cetacean distributions directly (Redfern *et al.,* 2006). Since the nature of marine ecosystems is patchy, it is challenging to apply prey distribution indices and sighting rate to a broad geographic area. Variables commonly used for cetacean-habitat models include sea surface temperature and chlorophyll α concentration (Baumgartner *et al.,* 2003; Davis *et al.,* 2002; Smith *et al.,* 1986).

Along the southern coast of South Africa, a number of whale and dolphin species occur and make use of Mossel Bay for different purposes, including mating and feeding (James, 2014). Cetacean species commonly found in the area include the southern right whale (*Eubalaena australis*), humpback whale (*Megaptera novaeangliae*), Bryde's whale (*Balaenoptera brydei*), Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) and the Indian Ocean humpback dolphin (*Sousa plumbea*).

Since southern right and humpback whales are known to migrate over long distances between continental waters, they are referred to as migratory species throughout this thesis. South African populations of Bryde's whales, humpback dolphins and bottlenose dolphins reside in South African waters (Best, 2007). Even though some individuals in these populations may cover large distances and show some seasonality in different areas along the coast (Barros and Cockcroft, 1991; Karczmarski *et al.,* 2000; Penry *et al.*, 2011), they are not known to make extended, annual migrations from one area to another like humpback and southern right whales. Therefore, Bryde's whales, humpback dolphins and bottlenose dolphins are all referred to as non-migratory species in this thesis for convenience. Groups of cow-calf pairs of animals are referred to as 'cow-calf' groups throughout the thesis. Groups of adult humpback whales and southern right whales may have included juveniles, but these can be difficult to distinguish at a distance from land-based observation platforms. Juvenile animals have been included in 'adults-only' groups throughout the thesis. Although common bottlenose dolphins (*T. truncatus*) occur off South Africa, they are exclusively seen off the continental shelf (Best, 2007), and were thus highly unlikely to be seen from the shore-based platforms used in this study. Thus, we have assumed all bottlenose dolphins seen were *Tursiops aduncus*.

Southern right whales are known to use sheltered coastal areas off South Africa for mating and calving in winter (Best, 2007). During other times of the year, the majority of animals migrate to high latitudes (Southern Ocean) to feed, with a small proportion remaining off Saldanha and St Helena Bays (Barendse *et al.,* 2010; Best, 2007). Winter and spring distribution patterns of right whales along the coast of South Africa are non-uniform with certain preferred areas consistently used for calving and mating (Elwen and Best*,* 2004a). Although the current study area provides potentially suitable habitat for right whales, and is used regularly by them, it has never been recorded as one of the high density areas for this population since surveys began in 1969 (Elwen and Best, 2004a). During the winter breeding season, there is a general westward movement of animals along the South African coast (Best, 2011; Mate *et al*., 2011). Mossel Bay lies to the east of the right whales' main habitat along the SA coast and we might thus expect numbers to peak in the earlier half of the 'whale season' (June-November). Since the 1970s at least, the southern right whale population using the South African coast has increased at approximately 7% per annum as it has recovered from over-exploitation by commercial whaling activities, which ended in 1923 (Brandão *et al.*, 2011).

In 2008, the population was estimated to be 4600 individuals, which is approximately 23% of the original estimated population size (Brandão *et al*., 2011). Although the number of cow-calf pairs observed during annual aerial counts of right whales continue to increase at a similar rate since 2008, the number of adults unaccompanied by calves has decreased markedly since 2010 (Roux *et al.,* 2015). A decrease in groups of these animals (shown in this study) was found in Mossel Bay during the study period. Though the reason for these declines is currently not known, a possible reason for changes in distribution and composition of right whales in South Africa could be due in part to a re-establishment process for this population, since historical catches were dominated by females (Best*,* 2011; Best and Ross, 1986).

The general pattern of humpback whale movements around southern Africa is to move between summer feeding grounds in higher latitudes and winter breeding grounds in tropical lower latitudes on both the east (e.g. Mozambique, Madagascar) and west coasts (E.g. Angola, Congo and Gabon), with South African coastal waters forming part of the migration route (Barendse *et al.*, 2010; Barendse *et al.*, 2011; Findlay *et al*., 2011). Humpback whales are expected to occur in Mossel Bay between May and February (Banks, 2013; Findlay *et al*., 2011).

Three distinct populations of Bryde's whales have been described in the southern African region with only the inshore stock resident to the continental shelf of southern South Africa, likely to be encountered in this study (Best*,* 2001). Although resident to the continental shelf, the inshore stock of Bryde's whales shows some seasonal movement, and has been known to undertake excursions following prey such as schools of fish up the west and east coasts of South Africa (Best, 2007; Penry *et al*., 2011). In Plettenberg Bay (141.2 km east of Mossel Bay), inshore populations of Bryde's whales occur all year round, with greater encounter rates in autumn, and a decline throughout winter and spring (Penry *et al*., 2011).

Indo-Pacific bottlenose dolphins have been sighted as far west as False Bay and have a continuous distribution from Cape Agulhas eastwards into the Indo-Pacific region (Saayman *et al.,* 1972). They are opportunistic predators that prey on reef dwelling animals and sandy benthic prey (Best, 2007). There could be bottlenose dolphin seasonal movement along the eastern South African coast associated with the migrating pilchards known as the 'sardine run' (Barros and Cockcroft, 1991). Indo-pacific bottlenose dolphin distribution varies seasonally (mainly winter and summer) in Algoa Bay (380.4 km east of Mossel Bay), in positive correlation with the abundance and distribution of inshore prey resources (Reisinger and Karczmarski, 2010).

Indian Ocean humpback dolphins occur in the near-shore coastal zone of South Africa, off estuarine systems, coral reefs and seagrass beds (Karczmarski *et al.,* 2000). Most of the knowledge on the biology of humpback dolphins has mainly come from South African populations, even though research gaps remain on their natural history and status off the South African coastline (Plön *et al.*, 2015). They are usually restricted to shallow waters (less than 30 m deep) and feeding/foraging is more intensive near shallow reefs and relatively sheltered areas, whereas travelling is more prevalent along open stretches of coastline, sandy shores and areas with high human activity (Karczmarski *et al.,* 2000). Humpback dolphin survival is threatened by anthropogenic activity in the near-shore waters of the Indian Ocean (Braulik *et al.*, 2015).

Predator-prey associations between the species of cetaceans investigated in this study may play a role in cetacean distribution in Mossel Bay (James, 2014). Hunting associations between Bryde's whales, long-beaked common dolphins and other predatory species, such as Cape fur seals (*Arctocephalus pusillus pusillus)* and various shark species have been found to occur (Best, 2007; Penry *et al.*, 2011). Bottlenose and Humpback dolphins feed on various prey species, including benthic reef species (Barros and Cockcroft, 1991). Great white sharks (*Carcharodon carcharias*) are known to also prey on bottlenose dolphins (James, 2014).

The aim of this thesis is to build on the findings of James (2014) using a longer time series, to generate information on the presence, seasonality and sighting rate of cetaceans in Mossel Bay from 2010-2014, and relate this to environmental factors to try and determine underlying causes of temporal patterns. My thesis addresses the following questions: 1) Are there seasonal patterns in the use of Mossel Bay by the cetacean species? 2) Has sighting rate in Mossel Bay changed during 2010-2014? 3) Are there any environmental factors that may be driving the use of Mossel Bay, and if so, at what temporal scale (monthly, seasonal)?

METHODS

Study area

Mossel Bay (34°11'S; 22° 8'E) is located on the south coast of South Africa. It is a semi-enclosed shallow bay, approximately 30 km in width, with a 20 m depth contour, at 1.2 km from the shore (Figure 1). Cape St Blaize headland causes the bay to be relatively sheltered from the prevailing swell, and is where the town of Mossel Bay is located. Sand and exposed near-shore reefs are characteristic of the bay.

The prevalent wind during winter and autumn blows from west-north-west, whereas during summer and spring, the wind mostly blows from the east and east-south-east. The swell enters Mossel Bay predominantly from the south west and therefore, western Mossel Bay has calmer waters than the rest of the bay (James, 2014).

Mossel Bay is home to about 4000 Cape fur seals on Seal Island, great white sharks and various cetacean species. The bay is impacted by commercial and recreational boat traffic, and since the beginning of its operations in November 2011, a desalination plant (construction finished on May 2011). The Mossel Bay area has been subjected to industrialization in the last 33 years, which may have negatively impacted the marine environment in the bay (James, 2014).

Cetacean data

Cetacean sightings data of migratory (southern right and humpback whales) and non-migratory species (Bryde's whale, bottlenose and humpback dolphins) were collected daily from six shore-based observation stations in Mossel Bay, South Africa, between February 2010 and August 2014 (Figure 1) by MSc students (E Mertz 2010-2011, B James 2011-2013, M Betts 2013-2014, University of Pretoria) with assistance from staff and interns from Oceans Research, Mossel Bay. Animal location was recorded using a theodolite (a Wild T16, then a Sokkisha SET 2B); data not included in this study. There were gaps in the data collection during that period of time and these are detailed in Table 1, and site 3 was not used after 2013.

Shore based searches for cetaceans were conducted during watch periods at 2-3 sites each day for a minimum of 2 hours per site (weather permitting). A watch period was defined as the observation effort (number of scans) conducted at one site during a field day. Searching was conducted continuously with Minolta binoculars (10X50), a Nikon field scope (20x) and the naked eye, with species identity confirmed using the theodolite scope when necessary (20 X magnification) and cetacean groups found were tracked using the theodolite for focal follows, data not presented here (James, 2014). Cetacean presence, including species and number of groups (as well as group size and presence of calves) in the search area was assessed during 5-minute scans, collected at half hourly intervals throughout watch periods. The number of individual animals as well as number of groups were counted during a watch and recorded as counts of individuals/groups respectively.

In-between scans, observers kept watch with the naked eye for animals moving into the survey area with the Minolta binoculars and the Nikon field scope, starting from opposite directions. Groups of animals sighted in-between scans were tracked, but not included in the sighting rate calculations unless they were still present during the next watch; in which case, a watch was extended to allow continued group tracking until group was lost or weather deteriorated. Calves were identified as animals approximately 2/3rds or less the size of adult animals. Due to the distance at which animals were observed it was not possible to differentiate juveniles and thus, these animals are included in this study as adults-only.

Environmental data were collected during the surveys, including: cloud cover, swell height, wind strength and direction and sea state. The sea state index was based on the Beaufort scale, ranging from 0-6 (calm to stormy waters).

An evaluation of an effective sighting radius (search area) was made for each site, taking into account the elevation platform above sea level at each site, as well as sighting probability of humpback dolphins and bottlenose dolphins from shore (data not presented here; James, 2014). Humpback and Southern right whales were searched within 1.2 km from shore and at the maximum 20 m depth contour of the bay, due to the species sheltered area preferences (Bridget James pers.comm, Sea Search). A similar effective radius was estimated for the search of Bryde's whales since beyond the 20 m depth contour in Mossel Bay, swell may deteriorate sighting ability (Bridget James pers.comm, Sea Search). Sighting ability (or 'sightability') "is a subjective 'all inclusive' parameter (Hammond *et al.,* 2002) used as an overall index of the ease with which a cetacean can be sighted by an observer relative to all the environmental conditions prevalent at the time" (James, 2014, pp. 40). The index for sightability ranged from 0-5 (poor to excellent). The ability to see animals is reduced in poor weather conditions (Bailey *et al.,* 2013; Redfern *et al.,* 2008). Thus, searching was ended if weather factors such as rain or mist occurred or increased wind (>15 knots).

Environmental data

The environmental variables chosen for the data analyses included: chlorophyll *a* concentration (mg.m^{-3}), sea surface temperature (°C), and moon brightness (expressed as % of full). They represent proxies for prey abundance or availability (Redfern *et al.*, 2006) and have previously been used in cetacean habitat modelling as they are expected to influence cetacean sighting rate (Baumgartner *et al.,* 2003; Davis *et al.,* 2002; James, 2014; Smith *et al.,* 1986). SST anomalies were previously found to correlate with temporal distribution of whales (Ramp *et al.,* 2015) and dolphins (Sprogis *et al.,* 2015), and moon brightness was hypothesized to affect sighting rates by affecting the vertical migration of micronekton, which controls the diel movements of prey of various species of dolphins (Benoit-Bird *et al.,* 2009; Elwen *et al.,* 2009). Chlorophyll *a* is often used as a proxy for biological productivity, and is used as a variable for cetacean habitat modelling as an indication of cetacean prey availability (Redfern *et al.*, 2006).

Tide height is used as an indicator of possible prey availability when modelling cetacean sighting rates (James, 2014). Tide height has been shown to influence dolphin feeding in areas of strong tides (Bailey *et al.*, 2013). The study area has small tides (0.2-2.3m [http://www.tides4fishing.com/af/south-africa/mossel-bay]) and no areas of strong flow (e.g. restricted passages), so there is little reason to expect an influence. Time of day wasn't explored since this study concentrated on seasonal and monthly patterns.

Monthly average chlorophyll *a* concentration and SST were obtained from the Giovanni portal of NASA (http://disc.sci.gsfc.nasa.gov/giovanni), covering an area of 651 km^2 in Mossel Bay from Cape St. Blaize to the Groot Brak River. Sea surface temperature (SST) was incorporated into all models as an SST anomaly (dSST) and this was calculated by subtracting the monthly SST values from the long-term (2010-

2014) monthly mean. A chlorophyll *a* anomaly (dCHL) was calculated in the same way and incorporated into all models. Seasons were defined based on mean monthly rainfall (mm) and average midday temperature (°C) over the study period as follows; summer: December-February, autumn: March-May, winter: June- August, spring: September-November (http://www.saexplorer.co.za/south-africa/climate/mossel_bay_climate.asp). Moon brightness was expressed as a percentage of full moon (100%).

Whale migration and dolphin occurrence in Mossel Bay may be affected by factors outside the study area such as large scale oceanographic factors. The Southern Ocean waters mix with warmer sub Antarctic waters as these flow northward, thus affecting water temperature and oceanographic processes in the bays along coastal South Africa, such as Mossel Bay (Peterson and Stramma, 1991). Consequently, a Southern Oceanic Niño Index (ONI; Table 2) for 2010-2014 was chosen in order to investigate SST anomalies in the Southern Ocean, and compare them to SST data of this study. A word of guidance to the information presented in Table 2, is taken from NOAA website**:** "Because of the high frequency filter applied to the ERSSTv4 data (Huang *et al*., 2015), ONI values may change up to two months after the initial "real time" value is posted. Therefore, the most recent ONI values should be considered an estimate. DESCRIPTION: Warm (red) and cold (blue) periods based on a threshold of +/- 0.5^{o}C for the Oceanic Niño Index (ONI) [3 month running mean of ERSST.v4 SST anomalies in the Niño 3.4 region (5^{o}N-5^{o}S, 120^{o}-170^{o}W)], based on centered 30-year base periods updated every 5 years. For historical purposes, periods of below and above normal SSTs are colored in blue and red when the threshold is met for a minimum of 5 consecutive overlapping seasons. The ONI is one measure of the El Niño-Southern Oscillation, and other indices can confirm whether features consistent with a coupled ocean-atmosphere phenomenon accompanied these periods."

(http://www.cpc.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml).

Statistical analysis

Statistical analyses, including data exploration and modelling were conducted using the software R and RStudio, version 0.98.1091 (2009-2014 RStudio, Inc.). R Packages 'mgcv' (Wood, 2006), 'MASS' (Venables and Ripley, 2003) and 'gplots' (Bolker *et al.,* 2010) were used during analyses.

Sightings recorded at a sea state higher than 4, and a sightability index lower than 3 were filtered out due to the known impact of poor weather conditions on the ability to observe, identify and estimate group size of cetaceans (Evans and Hammond, 2004; Mandleberg, 2004; James 2014). Sea state and weather conditions from land were not found to significantly influence sightings of humpback dolphins and bottlenose dolphins in the study area (James, 2014).. Sighting records were filtered for each species for the entire bay (records from all six sites).

Survey effort was randomly split between sites within the bay on a daily basis. Differences in survey effort (number of 5-minute scans conducted) between the six sites of observation were tested over the entire study period, as well as annually, seasonally, monthly and daily using a Kruskal-Wallis test using R STUDIO software. The survey effort did not differ significantly between all six sites throughout the study period (χ^2 =5, *df* = 4, *p-value* = 0.41). The survey effort did not differ significantly among sites annually (χ^2 =6, *df* = 5, *p-value* = 0.29). The survey effort did, however, differ significantly among all six sites at a seasonal (χ^2 =6, *df* = 5, *p-value* < 0.01) and monthly (χ^2 =29, *df* = 5, *p-value* < 0.01) scale. The difference in survey effort among sites at a daily scale (χ^2 =99, *df* = 5, *p-value* < 0.01) was expected, since only 2-3 sites were used per day. Sighting data from all six sites around the bay were merged in order to investigate sighting rate of the cetacean species in comparison to broad scale oceanographic and environmental processes. Potential flaws in this method are discussed later on.

Records were filtered to obtain the recorded number of groups of each species per watch for the entire sighting period. Right whales would often remain for extended periods in small areas and the watch would be extended to allow further tracking until the group was lost; subsequently, this was recorded and the watch ended. In order to avoid counting the same groups of right whales, only the first count of a watch was used in this analysis.

For each species, the daily number of groups was divided by the daily number of scans conducted at all six sites combined, in order to calculate the search per unit effort (SPUE) for the entire bay. Mean SPUE was then calculated at monthly, seasonal and yearly time scales.

Autocorrelation

Correlation between predictor variables (including temporal variables) was calculated in order to see whether a variable was too strongly correlated with another, so as to aid with elimination of a variable from the model, thus increasing model explanatory power. However, temporal variables that were correlated e.g. *month* and *season*, were still both included in the model to help detect potential monthly shifts. All predictor variables that might be correlated (e.g. *dSST* and *dCHL*, *season* and *month*) were tested for correlation using the Pearson Product-Moment correlation test. A significant correlation was considered to be one in which the correlation coefficient r was ≥ 0.4, or ≤ -0.4 and the p-value was < 0.05. If a correlation had a p-value of <0.05 but r was between -0.4 and 0.4, it was not considered a significant correlation (H. Winker, SANBI pers. comm.) Correlation results are shown in Table 3.

A positive correlation was found between season and month ($r = 0.62$, p-value=$2.2\text{x}10^{-16}$). However, since seasonal patterns are expected for migrating whales, a subtle inter-seasonal (monthly) pattern is of interest and therefore, both *season* and *month* variables were included in the models for these species. Variables *dSST* and *dCHL* had a negative correlation ($r = -0.43$, p-value = $2.2\text{x}10^{-16}$). Variables *year* and *dSST* had a positive correlation ($r = 0.42$, p-value = $2.2\text{x}10^{-16}$).

SST anomalies in the Southern Ocean (*dSST* [ONI] values) were compared to SST anomalies in Mossel Bay (*dSST* values) over the study period. *dSST* [ONI] values during 2010 and 2011 were most anomalous when compared to *dSST* [ONI] values during 2012, 2013 and 2014 (Table 2). A Pearson product-moment correlation coefficient was calculated between *dSST* values (ONI) during 2010-2014 and *dSST* values (Mossel Bay) during 2010-2014, and a positive correlation was found (r = 0.37, p-value = 0.006). A positive correlation was found between *dSST* (ONI) values and *dSST* values during 2010-2011 (r = 0.51, p-value=0.01).

Evaluation of sighting rate data

SPUE data were tested for differences across *year*, *season* and *month* using a Kruskal-Wallis test in R STUDIO software by year, season and month for each cetacean group over the study period, in order to explore temporal trends in the sighting rate.

Statistical Models

Generalized additive models (GAMs) were used to model cetacean sighting rate, since they deal with data that have no constant variance, and allow for interaction between variables and the smoothing of variables. Given that the data were counts per unit of time and considered rare events, a Poisson distribution was used with a log-link function. In order to model sighting rate, the response variable was chosen to be sighting rate (count data) and the underlying factor 'effort' (number of scans), was modeled using a 'log (offset)' function. The offset term was chosen to allow effort to be taken into account. By ignoring effort, there is a bias risk that involves getting a greater sighting rate of a species simply because of more watch periods per scans at a site (Zuur, 2009). For variables *dSST*, *dCHL* and *Mbright*, penalized splines (natural cubic smoothing splines) were used [and denoted by *s*, e.g. *s(dSST)*], since they are highly non-linear and trend more as curves over time (Zuur, 2009).

Since there were differences in sighting rate between cow-calf and adults-only groups (these two groups generally respond to different cues; Elwen and Best, 2004a; Smultea, 1994), I chose to create a separate model for each group for both species of migrating whales (southern right and humpback whales). Environmental variables used for modelling the sighting rate of cow-calf and adults-only groups of migrating whales (right and humpback whales) in the area included: *dSST*, *year*, *month*, *season* and *year-*

season interaction. Since the seasonal migration patterns conformed to the known winter calving and breeding trend, there was an interest to find within year/season cue changes in migration patterns. Variables used for modelling the sighting rate of Bryde's whales and dolphin species included: *year*, *season*, *day*, *Mbright* and *dCHL*. Separate SST models were made for these species, since *dCHL* and *dSST* were negatively correlated (Table 3). The variables used in these SST models were: *dSST*, *year*, and *season*.

Model selection

Candidate models were selected by using a backwards stepwise model selection method, with the least significant variable removed at each step (Crawley, 2007). The Akaike Information Criterion (AIC) was used to decide between candidate models based on a balance of explanatory power of a variable against the decrease in model degrees of freedom; a reduction in the AIC value greater than the number of additional variables indicates an improvement in explanatory power (Keller *et al.,* 2012). The coefficient of determination (R^2 (adj.)) denotes the variability in the data explained by the model. An ANOVA Chi-square test between candidate models showed no significant difference between candidate models (p-value>0.05). The candidate model that included all its factors to be significant contributors and had the smallest AIC value was considered the best model.

RESULTS

Sea surface temperature anomalies indicated lower than normal sea surface temperatures in Mossel Bay during the summer and spring months of 2010, as well as the summer months of 2011 (Figure 2a). Sea surface temperature anomalies indicated above normal sea surface temperatures during the autumn months of 2012, spring months of 2013 and summer months of 2014. Chlorophyll *a* concentration anomalies indicated lower than normal chlorophyll *a* concentrations in Mossel Bay during the months of 2010 and 2012 (especially during autumn 2012), as well as the spring months of 2013 (Figure 2b). Chlorophyll *a* concentration anomalies indicated above normal chlorophyll *a* concentrations during the months of 2011, winter months of 2013 and autumn months of 2014 (Figure 2b).

A total of 9236 5-minute scans were conducted between February 2010 and August 2014 around Mossel Bay, during which 8465 scans animals were observed and 6833 were conducted during suitable sighting conditions. Mossel Bay was not surveyed during the spring months of 2014. Inter-annual survey gaps are detailed by site, month and season in Table 1. Adults-only southern right whales had the largest sighting rate (SPUE) of all cetacean species in the Mossel Bay area (2010-2014), followed by the bottlenose dolphins, humpback dolphins, cow-calf groups of southern right whales, adults-only humpback whales, cow-calf groups of humpback whales and Bryde's whales (Table 4).

Southern right whales

Adults-only groups of southern right whales were the groups of cetaceans most frequently seen in Mossel Bay between February 2010 and August 2014 (Table 4). Right whales were seen throughout all years during the study period, although the sighting rate of adults-only groups has generally declined since 2010 (Figure 3a) and differed significantly between years 2010-2014 of the study period (χ^2=12.81, *df* = 4, *p-value* = 0.01). Mean seasonal sighting rates of adults-only groups also differed significantly (χ^2 =219.43, *df* = 3, *p-value* < 0.01) and adults-only groups were mostly seen during winter and spring months (June-October; Figure 3b). Mean monthly sighting rates of adults-only groups differed significantly between months (χ^2 =337.79, *df* = 11, *p-value* < 0.01), with sighting rates greatest during June-August of 2010 and 2014, and August-September of 2011, 2012 and 2013 (Figure 3c). The best fitting general additive model included the variables: *year*, *season*, *year-season interaction* and *smoothed SST anomaly* (*s(dSST)*; Table 5a). The variable *year* explains the annual decrease over the study period, while the variables *s(dSST)*, *season* highlight the annual winter-spring preference, indicative of the annual migration into the area. The *year-season* interaction highlights the fact that the timing of maximum sighting rate varies among years (early in 2010, late in 2011-2013).

Overall, groups of adults-only right whales were much more abundant than cow-calf groups over the study period. Mean annual sighting rates of cow-calf groups differed significantly between years (χ^2 = 11.93, *df* = 4, *p-value* = 0.02) with a clear declining trend across the study years. Cow-calf groups were not abundant in 2010, but sighting rates increased almost four times in 2011 and 2012, after which they declined again (Figure 4a). Both mean seasonal and mean monthly sighting rates of cow-calf pairs differed significantly across season ($\chi^{2=}$ 102.24, *df* = 3, *p-value* < 0.01) and months (χ^2 = 173.26, *df* = 11, *p-value* < 0.01) respectively. Cow-calf groups were only seen in the winter and spring months (Figure 4b), mainly between August and October (early spring; Figure 4c), which was generally later than adults-only groups (June-September; Figure 2b). The best fitting general additive model for cow-calf groups included the variables: *s(dSST)* and *season* (Table 5b). Although this model had the largest AIC of 509.5, it only included significant variables and the adjusted R^2 was very similar to the other candidate models (0.21 vs. 0.22) and the percentage deviance explained varied little more than 1% (Table 5b). The significant variable *season* highlights the annual winter-spring preference, indicative of the annual migration into the area. The significant *s(dSST)* variable accounts for differences in SST anomalies in the area between years 2010-2013 (Figure 2).

Humpback whales

Adults-only groups of humpback whales also declined slightly over the study period (Figure 5a), although mean annual sighting rates of adults-only groups were not significantly different across years ($\chi^2 = 1.24$, *df* = 4, *p-value* = 0.87). Mean seasonal sighting rates of these groups differed significantly across seasons ($\chi^{2} = 65.51$, *df* = 3, *p-value* < 0.01) and months ($\chi^2 = 72.79$, *df* = 11, *p-value* < 0.01) and were mostly seen during the winter and spring months (Figure 5b), during September and November (Figure 5c). The best fitting general additive model for adults-only groups of humpback whales included the variables: *month* and *season* (Table 5c). Mean annual sighting rates of cow-calf groups differed significantly across years ($\chi^2 = 16.06$, *df* = 4, *p-value* < 0.01), declining from 0.015 (groups/scan) in 2010 to 0 in 2014 (Figure 6a). Mean seasonal sighting rates of cow-calf groups differed significantly across seasons ($\chi^{2} = 55.74$, *df* = 3, *p-value* < 0.01) and months ($\chi^2 = 82.78$, *df* = 11, *p-value* < 0.01), and they were seen mostly in spring, predominantly during spring 2010 and 2012 (Figure 6b), particularly during November (Figure 6c). These monthly and seasonal trends were expected given the migration patterns of these species. The best fitting general additive model for cow-calf groups of humpback whales included the variables: *year*, *month* and *season*, all of which were significant (Table 5d). AIC scores and adjusted R^2 values showed little change between the candidate models (Table 5d), and therefore I chose the model that included only significant variables.

Bryde's whales

Mean annual sighting rates of Bryde's whale groups differed significantly across years ($\chi^2 = 45.65$, *df* = 4, *p-value* < 0.01), although sightings of groups of Bryde's whales was rare, with all years having small SPUE values, except 2011, suggesting they were more sighted in that year (Table 4; Figure 7a). Bryde's whales sighting rates were particularly low in 2012 and 2013 (Table 4; Figure 7a), and no cow-calf pairs were recorded during the study period. Mean seasonal sighting rates of Bryde's whale groups differed significantly across seasons (χ^2 = 13.49, *df* = 3, *p-value* < 0.01), with SPUE greatest in autumn, followed by summer and winter and a relatively low SPUE in spring (Figure 7b). Mean monthly sighting rates of Bryde's whale groups also differed significantly across months (χ^2 = 31.55, *df* = 11, *p-value* < 0.01) and sighting rates peaked in April 2014, but were more consistent during summer and autumn months in 2011 (Figure 7c). The best fitting general additive model for groups of Bryde's whales included the variables: *year*, *season* and *Chlorophyll a* anomaly (*s[dCHL]*; Table 5e), all of which contributed significantly to the model. When *s(dSST)* was included in the model instead of *s(dCHL)*, the AIC increased from 307.5 to 318.8 and percentage deviance explained decreased from 27.0 % to 22.4% (Table 5e).

Indian Ocean Humpback dolphins

Humpback dolphin occurrence declined considerably during the study period, (Figure 8a) and was significantly different across years (χ^2 = 27.16, *df* = 4, *p-value* < 0.01). Mean SPUE was greatest in winter and summer and declined slightly in spring and autumn (Figure 8b), but was not found to be significantly different across seasons (χ^2 = 2.50, *df* = 3, *p-value* = 0.47) or months (χ^2 = 10.06, *df* = 11, *p-value* = 0.52).The best fitting general additive model for humpback dolphins included the variables: *year* and *chlorophyll a* - *s[dCHL]* and *s[dSST]* (Table 5f). The chlorophyll *a* model suggests reduced sighting rates at higher levels of chlorophyll *a* concentration, although there was a low number of sightings in these conditions (Figure 8c). The sea surface temperature model suggested increased sighting rate during both warmer and colder than normal sea surface temperatures (winter and summer, and the 2011 La Niña months; Figure 8d), although this is partially driven by a low number of sightings in these conditions.

Bottlenose dolphins

Groups of bottlenose dolphins were frequently seen during the study (Table 4) and mean annual sighting rates differed significantly across years ($\chi^2 = 19.17$, *df* = 4, *p-value* < 0.01), being greatest in 2011, with no discernable difference in occurrence between the other years (Figure 9a). Mean seasonal sighting rates of bottlenose dolphin groups differed significantly across seasons ($\chi^2 = 8.02$, *df* = 3, *p-value* = 0.04) and months ($\chi^2 = 12.36$, *df* = 11, *p-value* = 0.34) being generally greater during the summer and spring months (Figure 9b). The best fitting general additive model for these groups included the variables: *s(dCHL)* and *year* (Table 5g), which were significant. Other variables such as *season*, *moon brightness* (*Mbright*) and *day* did not contribute significantly to the model. A model with *s(dSST)* instead of *s(dCHL)* had a slightly greater AIC (1287.1 vs 1283.1; Table 5g). Although the number of sightings was low, the chlorophyll *a* model suggested that sighting rate was generally greater (over the study period) when chlorophyll *a* concentration was greater than average, (Figure 9c). The SST model suggested that there were sinusoidal trends for sea surface temperature preferences during the study, with greater sighting rate at both sea surface temperature extremes, but particularly for colder than average waters (Figure 9d).

DISCUSSION

All five cetacean species observed in Mossel Bay during this study showed significant variation in sighting rates between years and/or seasons, as well as with several of the environmental variables examined. The strongest patterns observed for the two migratory species examined (right and humpback whales) were those pertaining to season (month, year-season, and season), overwhelming any potential links to more local environmental conditions such as temperature or chlorophyll. Notably, a significant annual variation in sighting rate was detected for adult-only groups of right whales, which may be related to a general decline in the numbers of this component of the population along the South African coast (Roux et al. 2015). Non-migratory species (Bryde's whale, bottlenose dolphin and humpback dolphin) also showed significant yearly variations in sighting rate, and also showed significant (but not necessarily linear) influence from local Chlorophyll conditions.

Data collection on free ranging marine mammals is challenging and costly. Shore based data collection offers a significantly cheaper option than boat-based surveys, but has a number of limitations. Foremost amongst these is that any shore based observation site has a limited field of view and that groups cannot be approached to confirm identity (e.g. juvenile identification) and number of individuals. Furthermore, among the three field observers, Bridget James was the most proficient in shore-based observational surveying as a result of her expertise at Sea Search. The other surveyors had mostly boat-based surveying proficiency. Greater shore-based surveying proficiency from the other surveyors may have resulted in more accurate results. For example, increased observational proficiency could have led to observe fewer/more animals accurately over the study period, and thus allow for the calculation of more realistic SPUE data for the models.

To minimize the impact of a limited field of view, multiple sites were used across the bay and short watch periods conducted at two to three sites per day to increase the area of the bay's scanned area in a day. When compared to boat-based techniques, shore-based observations have no influence on the movements and behavior of cetaceans, which makes them preferable for the recording of animal sightings (Würsig *et al*., 1991).

Autocorrelation in the sighting data is also a problem. It is very likely that the recorded data included duplicate observations (e.g. the same group of animals seen more than once during a day at one or more different sites), and therefore methods were employed, where possible, to remove possible duplicate data in the data processing. This removal in turn allowed me to assume that the groups seen at each site were different. Another method used to account for autocorrelation of cetacean sightings is photo-identification of individuals (Elwen *et al.*, 2010). However, it is not possible for land-based observations. It was deemed safer to use the recorded number of groups of animals (as opposed to individual cetaceans) when accounting for the autocorrelation of sightings among sites.

The merging of SPUE data from the six sites of observation was made for the purpose of investigating cetacean sighting rate in the bay as a whole, and placed in the larger context of cetacean sighting rate in South Africa.

However, there are potential flaws in merging these data. Firstly, although annual survey effort was not significantly different between sites, monthly and seasonal survey effort did differ between sites. Secondly, differences in water depth and distance from shore between the six sites could potentially impact the sighting rates of cetaceans much more than the environmental factors used in the models of this study, due to potentially different depth preferences among the cetacean species (Redfern *et al*., 2006; Robinson *et al.*, 2011). Thirdly, the varying substrate characteristics (sandy bottoms and exposed near-shore reefs) off the six survey sites is likely to be different and could also impact the sighting rate of cetaceans more than merely the environmental factors explored in this study, with regard to substrate preferences due to foraging e.g. by the dolphin species (James 2014; Karczmarski *et al.*, 2000).

Distance from shore wasn't deemed an important factor with regard to depth in Mossel Bay, since depth increases gradually with distance from shore around the bay (James, 2014). Humpback dolphins were previously found to occur at a “critical depth” of the 25 m isobath, with a preferential use of water depths of less than 15-20 m in Algoa Bay and KwaZulu-Natal (Karczmarski *et al.*, 2000). During the study period, all humpback dolphins were found in Mossel Bay at water depths of less than 20 m, and bottlenose dolphins were observed at water depths of up to 40 m. It is likely that bottlenose dolphins occurred in deeper waters than humpback dolphins during periods of cutting across Mossel Bay from the observed area off the Saint Blaize lighthouse Point to the observed area off Groot Brak, instead of swimming through near-shore shallow areas (James, 2014); a behavior which was also observed in Algoa Bay and Richard’s bay (Ross *et al.*, 1987).

As for substrate preferences, both humpback dolphins and bottlenose dolphins were previously found to prefer reef systems and the vicinity of river mouths for feeding (Barros and Cockcroft, 1991; Bearzi, 2005; Cockcroft and Ross, 1990; Karczmarski *et al.*, 2000); and thus likely to occur more frequently off survey sites in the vicinity of reef systems in Mossel Bay, between Klein Brak and Groot Brak estuaries, between Seal Island and the Cape St. Blaize Point (James and Harrison, 2008). The inshore populations of Bryde’s whales are opportunistic predators that prey on reef dwelling animals and sandy benthic prey (Best, 2007); thus, they could potentially occur around both sandy and reef substrates in Mossel Bay. As for the migrating humpback and southern right whales, they were previously shown to prefer the more sheltered areas in bays for mating, as well as shallow sandy bottoms for calving (Best, 2007; Elwen and Best, 2004a) and thus it is likely that they would occur more frequently in the vicinity of the survey site off Cape St. Blaize point (Site 1; Figure 1), where the headland offers sheltered waters from the prevailing swell, and possibly off survey sites in the vicinity of fine grained sandy bottom.

Had the same survey effort been conducted for each survey day during the study period at each one of the six shore-based sites of observation around the bay, more information could have been generated about the impact of the depth and substrate factors on the sighting rate of cetacean species in Mossel Bay, and a comparison of cetacean sighting rate between survey sites could have been established. This is something worth thinking about in future studies.

Chlorophyll *a* and SST values available for this study during the study period were monthly averages for the entire bay and therefore, too coarse, both spatially and temporally, for making more accurate model predictions that could have otherwise yielded a better understanding of the distribution of the cetacean species in the bay and over the study period.

Migratory species

The decline in sighting rate of adults-only groups of right whales in Mossel Bay (2010-2014) may be partially due to a westward shift (towards Namibia) in the populations of adults–only right whales (Roux et al., 2015). This decline may also represent part of an overall decrease of adults-only groups off the South African coast between 1979-2010 (Best, 2011; Roux *et al.,* 2015). Furthermore, changes in group composition (adults-only groups; cow-calf groups) of this population may be due to a recovery process from female dominated historical catches (Best, 2011; Best and Ross, 1986). Results of this study also show seasonal differences in the use of Mossel Bay between adults-only groups, which peaked in winter and cow-calf groups, which peaked in spring. These results were similar to the trends found in another study conducted further west (off Dyer Island) for these species (Vinding *et al*., 2015), as cow-calf groups peaked later than adults-only groups during winter and spring (July-December). Whale aggregation sites are known to occur elsewhere in the world e.g. Southern Australia (Burnell and Bryden, 1997) and a preference for the protected waters of bays was previously reported for right whales (Elwen and Best, 2004ab). De Hoop and St Sebastian Bay (west of Mossel Bay) were previously established as main cow-calf pair congregation sites, or "nursery areas" with Walker Bay (further west) as a main congregation area of adults-only groups (Elwen and Best, 2004ab). Even though males, females and juveniles all move along the coast with near-term females, these aggregation sites have remained consistent over time (Elwen and Best, 2004ab).However, exceptions do occur, an example being the increase of relative cow-calf group density in Walker Bay since the early 1990s, a main congregation area of adults-only groups (Best *et al.,* 2005). Mossel Bay has not been classified as a main congregation site for either group type.

SST was a significant factor underlying the sighting rate of both groups of southern right whales in Mossel Bay (2010-2014). The austral winter and spring months of 2010, and the spring months of 2011 had lower than normal sea surface temperatures, due to a La Niña effect.

La Niña anomalies cause the extension of the upwelling characteristic of the Agulhas current over the Agulhas bank (Jackson *et al.,* 2012), and thus result in increased chlorophyll *a* concentration, followed by enhanced productivity and thus availability of cetacean prey species on the south-eastern coast of South Africa. One example of such a phenomenon include the effect of temperature on the dispersion and recruitment of chokka squids (*Loligo vulgaris reynaudii*) on the Agulhas Bank (Martins *et al.,* 2010). Adults-only group occurrence is greater during the austral winter and spring months of 2010, and the spring months of 2011. Since the presence of adults-only groups in the area is mainly for mating purposes, it is not clear whether higher prey availability during these months could be a reason for greater occurrences of adults-only groups in the area. La Niña SST anomalies may also influence the distribution of cetacean species in other areas around the world (Aliaga- Rossel and Quevedo*,* 2011; De vos *et al.*, 2014; Salvadeo, 2011).

Cow-calf sighting rate was found to be particularly low during the years 2010 and 2013 of the study period. This could be either random, related to avoidance of males and/or possibly reinforce a previously described 3-year cow-calf pair cycle occurrence, associated with a pattern of returning lactating females (Best *et al.,* 2005). Essentially, females are thought to breed quite consistently every 3 years as there has been a greater sighting rate of cow-calf pairs every third year (compared to the first two years of the cycle) on the breeding grounds since the 1980s (Best *et al.,* 2005). This could be the case in Mossel Bay, with years 2010 and 2013 being the first years of this cycle respectively, and perhaps the 3rd year (2012 in this case) represents the returning larger groups of lactating females, which is characteristic of this 3-year breeding cycle.

Shallow sandy beaches and calm water preferences for cow-calf pairs suggest that the main reason for group differential distribution may be due to segregation from males implying that harassment of lactating females by males or juveniles represent an important issue (Elwen and Best*,* 2004ab). In addition, great white sharks in the area may prey on or harass right whale calves (James, 2014; Taylor *et al.*, 2013). Even though their occurrence in the Bay is rare, Orcas (*Orcinus orca*) are also potential predators of right whale calves (Sironi *et al.*, 2008).

Humpback whales migrate from the Southern Ocean to coastal waters off South Africa, as they move along their migratory route to their breeding grounds further north (Banks*,* 2013). Only *year*, *month* and *season* were significant variables that explained their sighting rate in the GAM suggesting their presence in Mossel Bay is driven largely by broad scale factors related to the timing of their migration and not local environmental conditions. Sighting rates of both cow-calf pairs and adults-only groups of humpback whales in Mossel Bay peaked in spring. This seasonal pattern was also previously found off Dyer Island and Plettenberg Bay (Banks*,* 2013; Vinding *et al.,* 2015). However, there were a few occurrences of both groups in Mossel Bay during the summer months. A seasonal extension into spring and summer in the presence of humpback whales along the west coast of South Africa has been reported and is linked to feeding in the productive upwelling in that region (Barendse *et al.,* 2010). No such pattern was observed in Mossel Bay, confirming that the dominant behavior of humpback whales in Mossel Bay is migration.

Mean monthly sighting rate of cow-calf pairs in Mossel Bay peaked in November, later than adults-only group occurrence, which peaked in September. This conforms to the highly structured migration patterns of this species' social groups, given the last group to leave the coast and return back to Antarctica's feeding grounds is usually made up of females in early lactation (i.e. cow-calf pairs; Best*,* 2007). This structured pattern was also found during a study off Dyer Island (south-west coast), where adults-only whales peaked during the winter months and cow-calf pairs peaked during late spring and early summer months (Vinding *et al.,* 2015). Group segregation in the temporal use of bays by humpback whales was also studied in other parts of the world. Adults-only and cow-calf groups of humpback whales make use of coastal waters at different times, off the coast of Hawaii (Smultea, 1994). Adults-only and cow-calf groups of humpback whales also make use of the bays off coastal New Zealand and Brazil, at different times (Gibbs and Childerhouse, 2000; Martins *et al.*, 2001).

Non-migratory species

There was no smooth increase or decrease in sighting rate of Bryde's whales over the study period (2010-2014) in Mossel Bay (Figure 7).Aggregation of groups in the bay would be expected to vary in time with respect to feeding conditions (Penry *et al.*, 2011); this was the case in Mossel Bay as occurrence fluctuated annually (Figure 7). The rate of occurrence was low compared to other cetaceans in the area. This was also the case in a separate study off Dyer Island between the years 2002-2012, where the occurrence rate of Bryde's whales was low compared to other cetacean species in the area (Vinding *et al.,* 2015). The reason for this is not known. However, the impact of anthropogenic shore-based and harbor activity on these species could be one reason but is difficult to quantify since little is known about regional populations (Penry *et al.*, 2011).

The seasonal trend over the entire study period consisted of a maximum peak of occurrence in autumn, followed by summer. This trend is similar to the seasonal and monthly peak encounter rate found in Plettenberg Bay (Penry *et al.,* 2011), in which the April distribution peak corresponded to increased feeding activity and larger than average aggregation sizes. In the Dyer Island area, Bryde's whales were encountered year round, but mostly seen between March and May (autumn), and rarely between July and December (winter and spring; Vinding *et al*., 2015). The more consistent peaks of occurrence during the autumn and summer months of 2011 in Mossel Bay might also correspond to increased feeding, since a greater than usual chlorophyll *a* concentration anomaly during these months was a significant factor explaining whale distribution around the bay, and thus may increase the probability of observing whales.

The year 2011 showed greater occurrences of Bryde's whales in the bay, and especially during autumn. La Niña SST anomalies enhancing productivity during this time may have increased prey availability and consequently feeding, resulting in a higher probability of observing these animals.

Humpback dolphins, though generally uncommon (Penry *et al.*, 2011) in coastal waters off South Africa, were frequently seen in Mossel Bay. In this study, SPUE declined annually from 2010-2014, similarly to the negative annual trend of humpback dolphin occurrence observed during a previous study (2002-2012) off Dyer Island, along the south-west coast (Vinding *et al.,* 2015). Temporal prey sighting rate has been suggested to drive seasonal movements of dolphins between coastal bays (Karczmarski *et al.,* 1999). Summer and winter were found to be more concentrated in chlorophyll *a* than usual over the study area. This may be related to greater prey availability in the area, which suggests that humpback dolphins may get closer to shore while looking for prey, and therefore easier to sight (B. James pers. comm., Sea Search). . Since humpback dolphins are vulnerable and range widely off the southern Cape coast, it has been suggested that a conservation plan be implemented on a large scale to provide protection from anthropogenic activities (James, 2014). It is only once information regarding meta-population of humpback dolphins on the Cape south coast is achieved, that a better risk assessment of their population as a whole could be made, based on the IUCN red list criteria (James, 2014).

Bottlenose dolphins (*Tursiops aduncus*) prefer reef-associated habitats and habitats in the vicinity of river mouths, but they are considered opportunistic feeders and would thus utilize a wide variety of habitat types (Bearzi*,* 2005; Cockcroft and Ross, 1990; Kiszka *et al.,* 2011; Stensland *et al.,* 2006). The greater sighting rates during the lower than usual La Niña SST anomalies suggest more prey availability in the area. And consequently, better chances for the animals to be observed. However, there were great sighting rates at both ends of the sea surface temperature range, and this may indicate that the occurrence of bottlenose dolphins in Mossel Bay may only be partly influenced by the La Niña effect. A previous study on bottlenose dolphin distribution in South Western Australia has shown dolphin occurrence to be significantly attributed to Southern Ocean El Niño/La Niña oscillations (Sprogis *et al.,* 2015).

Moon brightness was not a significant predictor of any of the dolphin species' sighting rate in this study. Moon brightness was used as a proxy for tidal height, given that the fullness of the moon would affect the tidal height, which may affect access to some parts of the reef for foraging during the day (James, 2014); and time of day can affect the movement of dolphin prey (Karczmarski *et al.*, 1999) and thus dolphin movement (James, 2014). Due to time constraints, I did not include these variables in the model; however, this is something that warrants further investigation in future studies.

The shore-based method used in this study allowed for the simultaneous study of multiple cetacean species' sighting rate in Mossel Bay, which is valuable for conservation initiatives, as well as a better understanding of whale migration routes. Temporal movements of cetaceans along the Cape south coast can be more clearly defined by combining methods of population size and group composition estimations, such as multi-site mark-recapture techniques, satellite tracking of individuals and the simultaneous collection of data from multiple study sites. Cetacean distribution is also influenced by various anthropogenic activities in Mossel Bay. Desalination plant discharges may have negatively influenced bottlenose and humpback dolphin distribution in the area between October

2011 and May 2012, and may influence bio-physical processes by impacting SST and chlorophyll *a* concentration (James, 2014). Mossel Bay is also subject to other anthropogenic impacts such as urban runoff and boat traffic, including fishing vessels and vessels associated with the Petroleum South Africa (PetroSA) liquid gas refinery (James, 2014). The information provided here is necessary for the conservation management of the area. Marine mammals are apex predators at the top of the food chain and therefore influence marine biodiversity and marine biophysical processes.

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TABLES

Table 1: Missing months and corresponding seasonal gaps in cetacean data collection, during the study period (2010-2014), in Mossel Bay.

Site	Year	Missing months	Seasonal gap
1-5	2010	Jan	Part of summer
6	2010	Jan, Feb	Part of summer
2	2011	Jun-Dec	Most of winter
3	2012	Aug	Part of winter
3	2013	Jun-Dec	Winter, Spring, part of summer
1	2014	Sep-Dec	Spring, part of summer
2	2014	Mar-Jun; Aug-Dec	Autumn, part of winter, spring
3	2014	Jan-Dec	All four seasons
4	2014	Sep-Dec	Spring, part of summer
5-6	2014	Feb-Dec	Most of summer, autumn, winter, spring

Table 2: Oceanic Niño Index (ONI), a Southern Ocean oscillation Index of average monthly SST during the study period. Red colored values represent periods of above normal SST anomalies. Blue colored values represent periods of below normal SST anomalies.

Year	Summer (DJF)	Autumn (MAM)	Winter (JJA)	Spring (SON)
2010	1.3	0.5	-0.8	-1.4
2011	-1.3	-0.6	-0.3	-0.9
2012	-0.7	-0.4	0.1	0.4
2013	-0.4	-0.2	-0.2	-0.2
2014	-0.5	-0.2	0	0.4

Table 3: Pearson product-moment correlation values of environmental variables used for Generalized Additive Modelling of the sighting rate of dolphins and whales in Mossel Bay. dSST = sea surface temperature anomaly, dCHL = chlorophyll *a* anomaly and *Mbright* = moon brightness. Significant correlations (values >0.4 or <-0.4) between variables are in bold (p-values were < 0.05 respectively).

Variables	year	season	month	day	dSST	dCHL
Year	-	-	-	-	-	-
Season	-0.11	-	-	-	-	-
Month	-0.15	**0.62**	-	-	-	-
Day	-0.08	0.04	0.03	-	-	-
dSST	**0.42**	0.04	0.04	-0.06	-	-
dCHL	0.03	-0.01	-0.02	0.005	**-0.43**	-
Mbright	-0.02	0.01	-0.002	0.20	0.02	-0.02

Table 4: The number of cetacean groups observed and SPUE during the study period in Mossel Bay, 2010-2014

Year	Number of scans	Bryde's whale		Humpback whale (adults; cow-calf)		Humpback dolphin		Bottlenose dolphin		S. right whale (adults; cow-calf)	
2010	1456	5	0.003	24; 22	0.016; 0.015	53	0.036	50	0.034	146; 9	0.100; 0.006
2011	2482	37	0.015	30; 16	0.012; 0.006	68	0.027	122	0.049	129; 54	0.052; 0.021
2012	1094	1	0.0009	10; 8	0.009; 0.007	22	0.020	28	0.025	32; 19	0.029; 0.017
2013	2059	1	0.0004	28; 2	0.013; 0.0009	33	0.016	56	0.027	156; 17	0.076; 0.008
2014	1374	3	0.002	12; 0	0.009; 0	18	0.013	32	0.023	40; 15	0.029; 0.010
Total	8465	47	0.005	104; 48	0.012; 0.006	194	0.022	288	0.034	503; 114	0.059; 0.013

Table 5: Candidate Generalized Additive Models fitted to sighting rates of cetacean species groups in Mossel Bay, as follows: (a) Adults-only groups of Southern right whales; (b) cow-calf groups of Southern right whales; (c) Adults-only groups of humpback whales; (d) cow-calf groups of humpback whales; (e) groups of Bryde's whale; (f) groups of humpback dolphins; (g) groups of bottlenose dolphins. The table summarizes the number of field days (n), degrees of freedom (df), AIC (Akaike Information Criterion) and AICc (penalized AIC) values, percentage of deviance in the data explained by the model (Dev %), and the coefficient of determination (adjusted R^2). The candidate model in bold represents the best model and variables in italics represent variables that contributed significantly ($p<0.05$) to the model. 'Y' is sighting rate (number of groups). Effort is SPUE. A * denotes an interaction between variables.

(a) Southern right whale (adults-only) Model (*n*=709)	**df**	**AIC**	**AICc**	**Dev %**	**R^2 (adj.)**
Y ~ offset(log(Effort)) + *year* + *year*season* + month + *season* + *s(dSST)*	13.4	1441.2	1441.7	41.30	0.32
Y ~ offset(log(Effort)) + *year* + *year*season* + *season* + *s(dSST)*	12.4	1440.7	1441.1	41.20	0.32
(b) Southern right whale (cow-calf) Model (*n*=709)	***df***	**AIC**	**AICc**	**Dev %**	**R^2 (adj.)**
Y ~ offset(log(Effort)) + year + year*season + month + *season* + *s(dSST)*	10.0	508.6	508.9	38.70	0.22
Y ~ offset(log(Effort)) + year + year*season + *season* + *s(dSST)*	9.3	507.5	507.8	38.70	0.22
Y ~ offset(log(Effort)) + year + *season* + *s(dSST)*	8.1	509.3	509.5	37.90	0.21
Y ~ offset(log(Effort)) + *season* + *s(dSST)*	7.0	509.5	509.7	37.50	0.21
(c) Humpback whale (adults-only) Model (*n*=709)	***df***	**AIC**	**AICc**	**Dev %**	**R^2 (adj.)**
Y ~ offset(log(Effort)) + year + year*season + *month* + *season* + s(dSST)	6.1	559.5	559.6	21.40	0.08
Y ~ offset(log(Effort)) + year + *month* + *season* + s(dSST)	5.3	558.0	558.1	21.40	0.08
Y ~ offset(log(Effort)) + *month* + *season* + s(dSST)	4.4	556.5	556.6	21.30	0.08
Y ~ offset(log(Effort)) + *month* + *season*	3.0	555.7	555.7	20.90	0.08
(d) Humpback whale (cow-calf) Model (*n*=709)	***df***	**AIC**	**AICc**	**Dev %**	**R^2 (adj.)**
Y ~ offset(log(Effort)) + *year* + year*season + *month* + *season* + s(dSST)	6.7	283.7	283.9	38.50	0.14
Y ~ offset(log(Effort)) + *year* + year*season + *month* + *season*	5.0	283.0	283.1	37.70	0.13
Y ~ offset(log(Effort)) + *year* + *month* + *season*	4.0	283.4	283.5	37.00	0.13
(e) Bryde's whale Model (*n*=709)	***df***	**AIC**	**AICc**	**Dev %**	**R^2 (adj.)**
Y ~ offset(log(Effort)) + *year* + *season* + day + *s(dCHL)* + s(*mbright*)	13.5	311.1	311.7	27.10	0.06
Y ~ offset(log(Effort)) + *year* + *season* + *s(dCHL)* + s(*mbright*)	12.5	309.2	309.6	27.10	0.06
Y ~ offset(log(Effort)) + *year* + *season* + *s(dCHL)*	11.5	307.5	307.9	27.00	0.06
Y ~ offset(log(Effort)) + *year* + *season* + *s(dSST)*	10.7	318.8	319.2	22.40	0.09
(f) Humpback dolphin Model (*n*=709)	***df***	**AIC**	**AICc**	**Dev %**	**R^2 (adj.)**
Y ~ offset(log(Effort)) + *year* + season + day + *s(dCHL)* + s(*mbright*)	9.1	1069.9	1070.1	9.73	0.09
Y ~ offset(log(Effort)) + *year* + day + *s(dCHL)* + s(*mbright*)	8.0	1067.9	1068.1	9.72	0.10
Y ~ offset(log(Effort)) + *year* + day + *s(dCHL)*	7.0	1066.2	1066.4	9.67	0.10
Y ~ offset(log(Effort)) + *year* + *s(dCHL)*	6.1	1067.2	1067.3	9.28	0.09
Y ~ offset(log(Effort)) + *year* + season + *s(dSST)*	5.3	1074.6	1074.7	8.04	0.08
Y ~ offset(log(Effort)) + *year* + *s(dSST)*	4.2	1072.9	1073.0	7.99	0.08
(g) Bottlenose dolphin Model (*n*=709)	***df***	**AIC**	**AICc**	**Dev %**	**R^2 (adj.)**
Y ~ offset(log(Effort)) + *year* + season + day + *s(dCHL)* + s(*mbright*)	11.0	1286.1	1286.5	8.57	0.13
Y ~ offset(log(Effort)) + *year* + season + *s(dCHL)* + s(*mbright*)	10.0	1284.1	1284.4	8.57	0.13
Y ~ offset(log(Effort)) + *year* + season + *s(dCHL)*	8.4	1283.7	1283.9	8.26	0.13
Y ~ offset(log(Effort)) + *year* + *s(dCHL)*	7.3	1283.1	1283.3	8.08	0.13
Y ~ offset(log(Effort)) + *year* + season + *s(dSST)*	10.7	1288.1	1288.4	8.29	0.11
Y ~ offset(log(Effort)) + *year* + *s(dSST)*	9.6	1287.1	1287.4	8.16	0.11

FIGURES

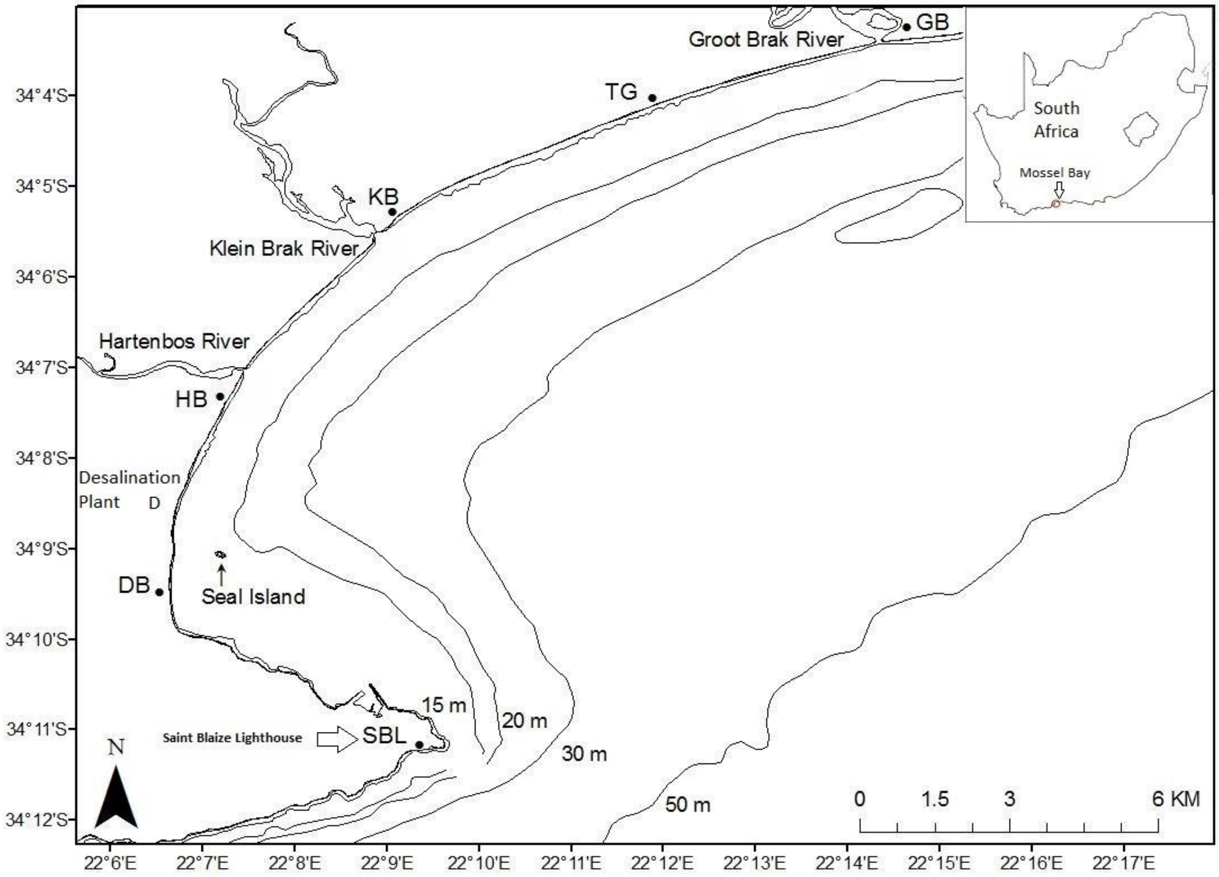

Figure 1: Location of land-based survey sites in Mossel Bay. Sites 1-6 were located as follows: 1. St. Blaize Lighthouse (SBL), 2. Diaz Beach (DB), 3. Hartenbos (HB), 4. Klein Brak (KB), 5. Tergniet (TG) and 6. Groot Brak (GB). Three estuaries are present in Mossel Bay, The Hartenbos, Klein Brak and Groot Brak River. The desalination plant (D) is located between Diaz Beach and Hartenbos River.

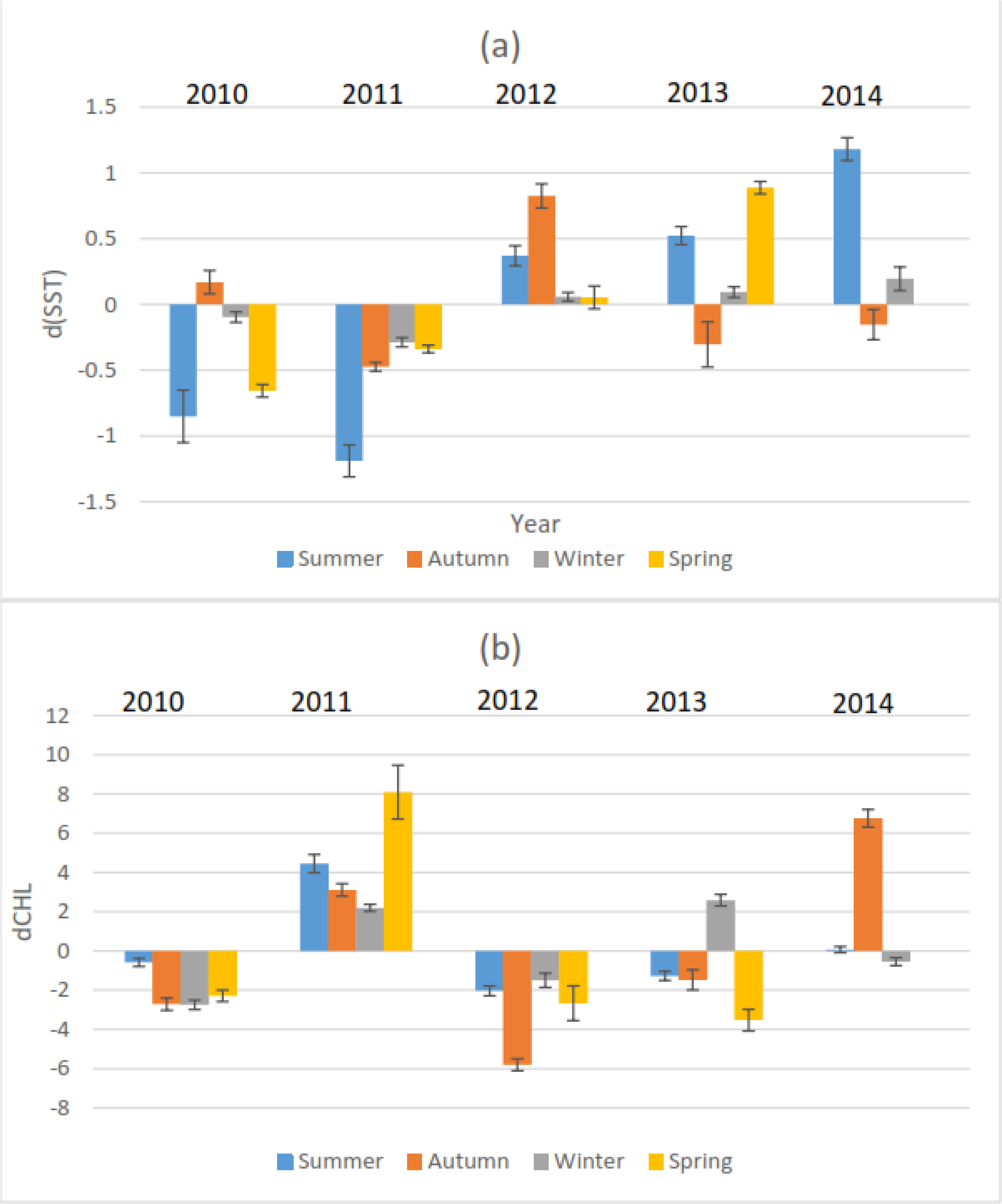

Figure 2: (a) Mean inter-annual SST anomalies (dSST) per season in Mossel Bay, over the study period (2010-2014), (b) Mean inter-annual CHL anomalies (dCHL) per season in Mossel Bay, over the study period (2010-2014).

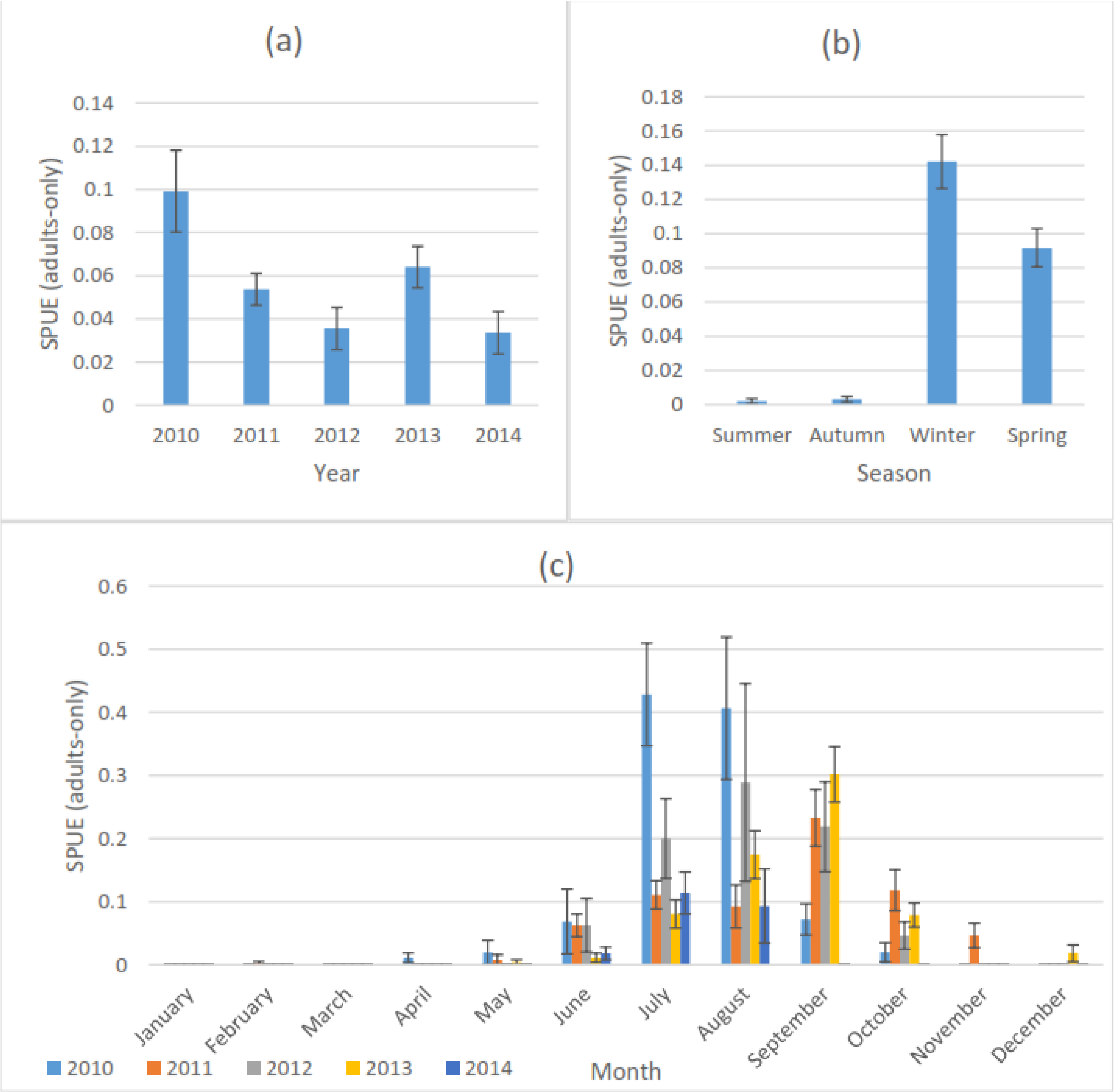

Figure 3**:** Mean sighting rates (SPUE ± standard error) of adults-only groups of southern right whales in Mossel Bay for the period 2010-2014. (a) Annual means, (b) seasonal means, (c) inter-annual monthly means.

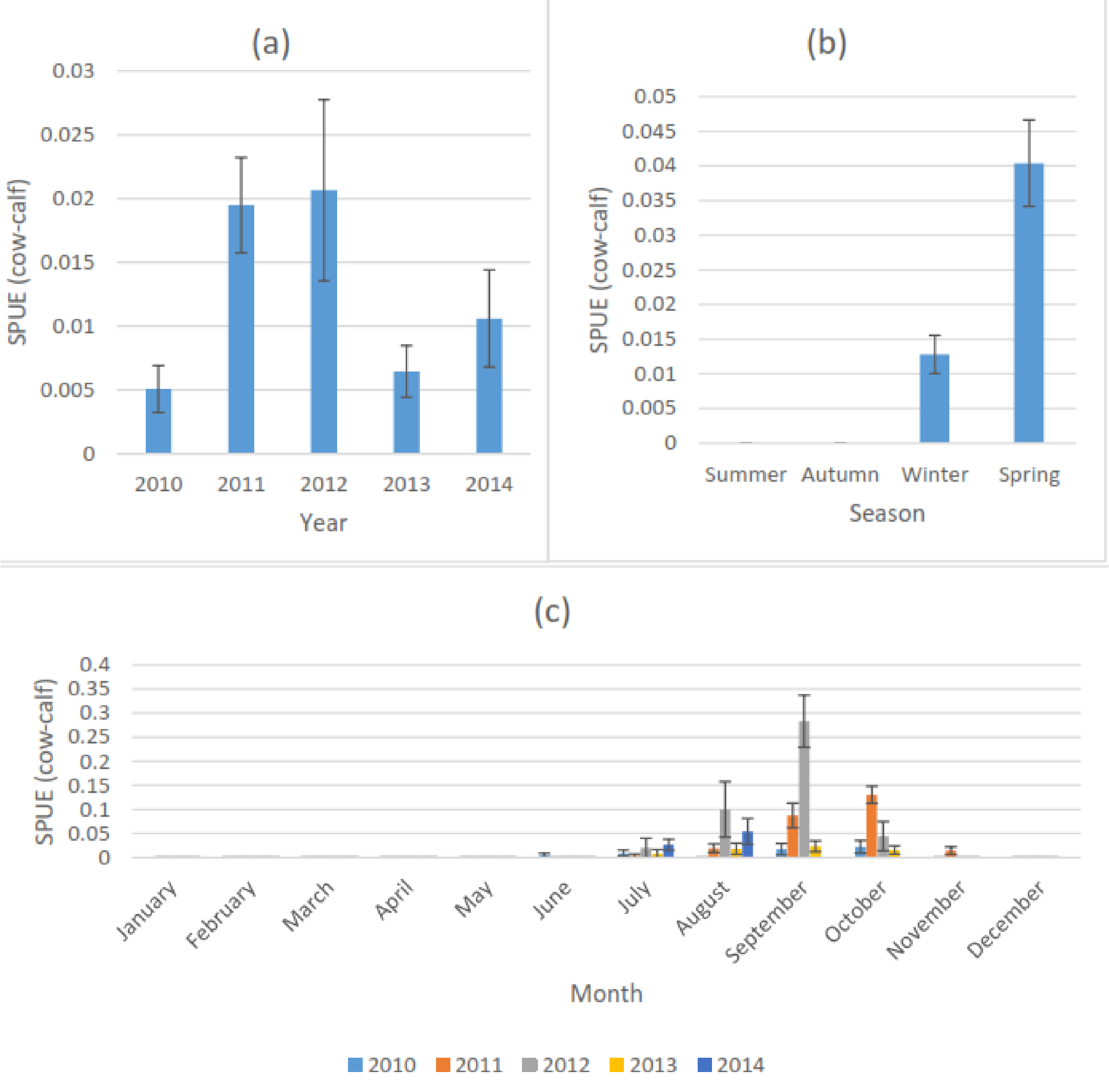

Figure 4: Mean sighting rates (SPUE ± standard error) of cow-calf groups of southern right whales in Mossel Bay for the period 2010-2014. (a) Annual means, (b) seasonal means, (c) inter-annual monthly means.

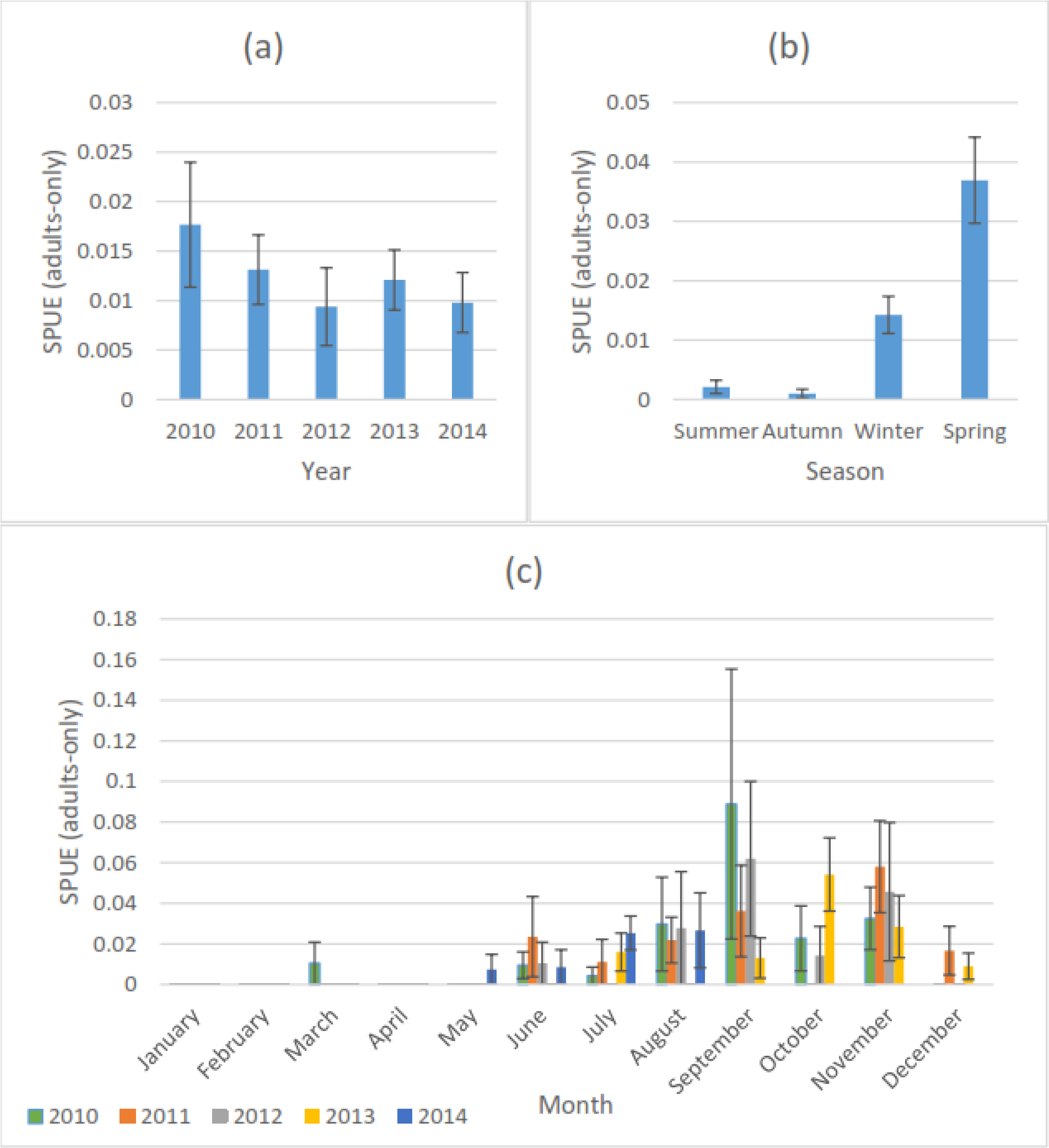

Figure 5: Mean sighting rates (SPUE ± standard error) of adults-only groups of humpback whales in Mossel Bay for the period 2010-2014. (a) Annual means, (b) seasonal means, (c) inter-annual monthly means.

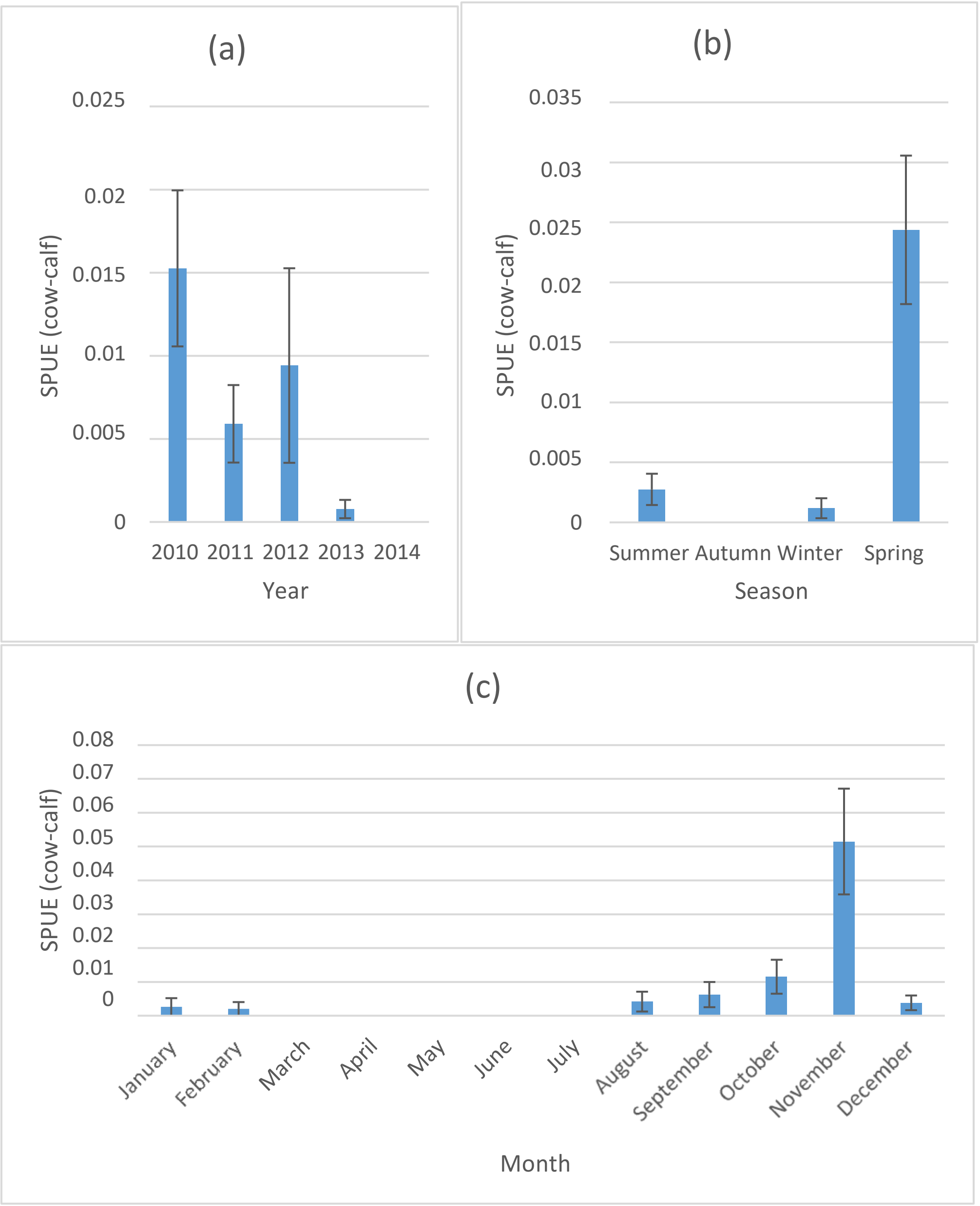

Figure 6: Mean sighting rates (SPUE ± standard error) of cow-calf groups of humpback whales in Mossel Bay for the period 2010-2014; (a) Annual means, (b) seasonal means, (c) inter-annual monthly means.

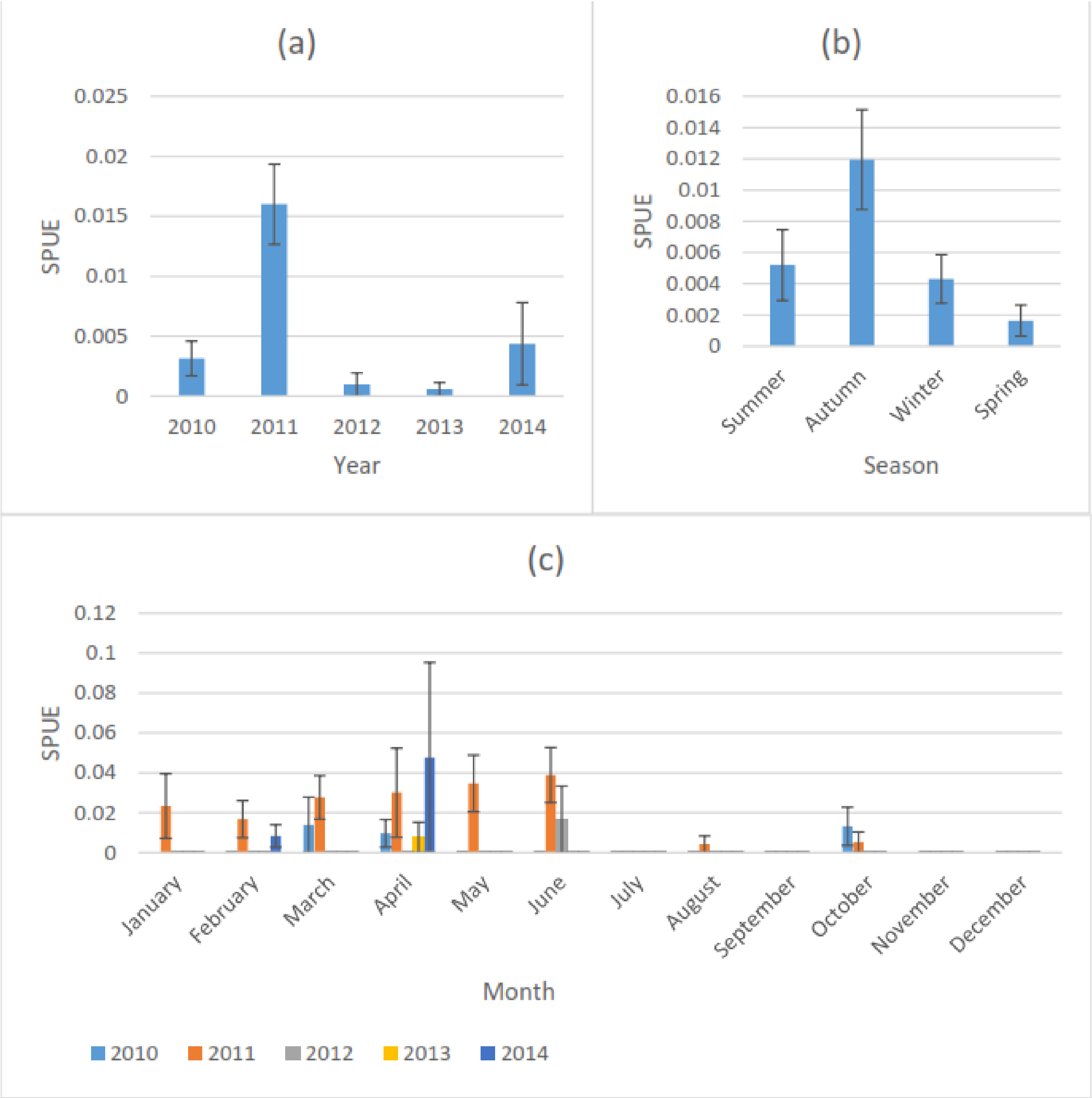

Figure 7: Mean sighting rates (SPUE ± standard error) of groups of Bryde's whales in Mossel Bay for the period 2010-2014. (a) Annual means, (b) seasonal means, (c) inter-annual monthly means.

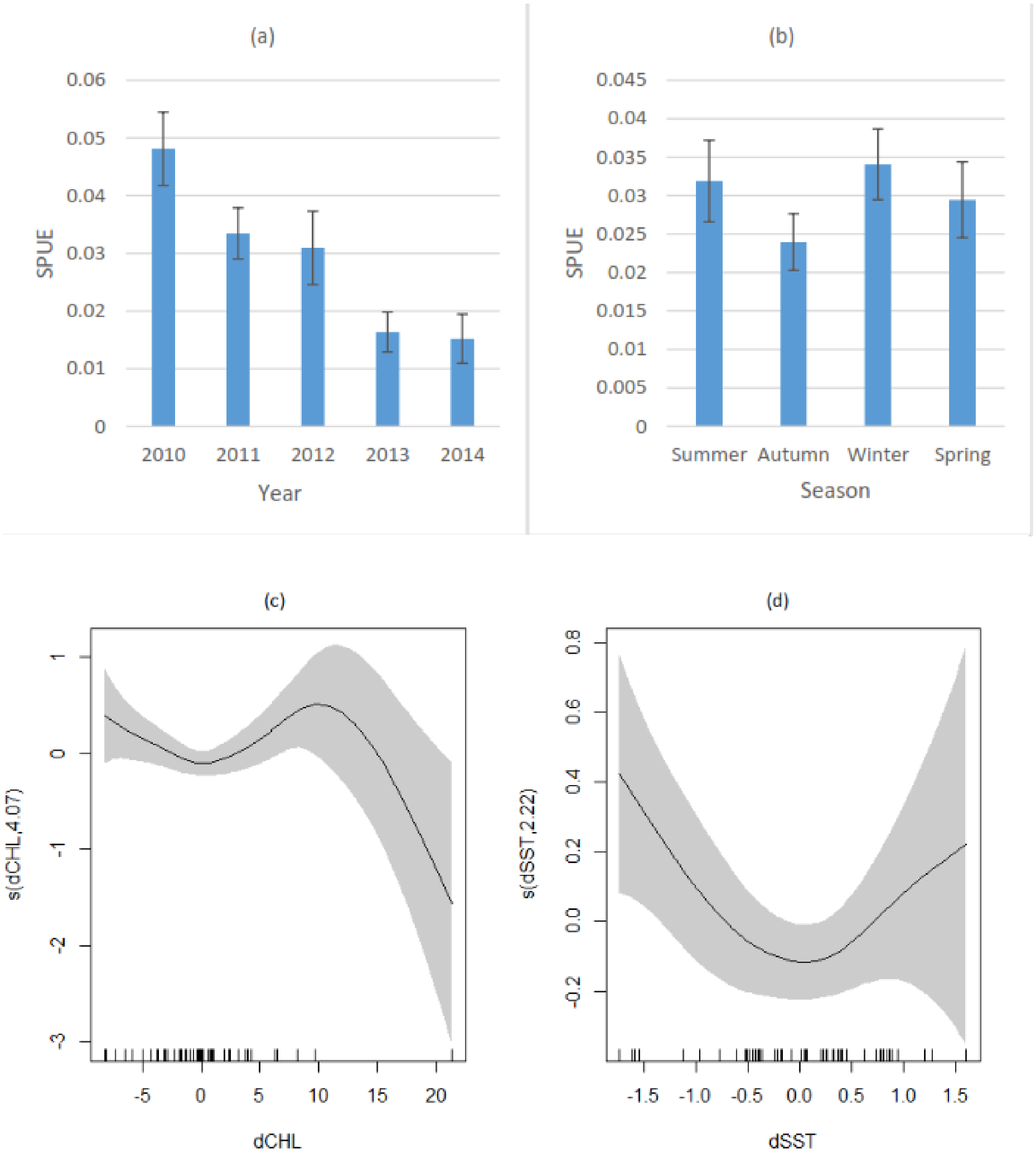

Figure 8: Mean sighting rates (SPUE ± standard error) of groups of humpback dolphins in Mossel Bay for the period 2010-2014. (a) Annual means, (b) seasonal means. (c) GAM response curve showing the smoothed fit of the relationship between chlorophyll *a* anomalies over the study period and the sighting rate of humpback dolphins in the area; (d) GAM response curve showing the smoothed fit of the relationship between sea surface temperature anomalies over the study period and the sighting rate of humpback dolphins in the area; *Note: the y-axis in each of the GAM graphs represents the smoothed change in *dCHL* and *dSST* over the entire study period and is on the scale of the link function, not the measured variable. The area in grey shows the 95% confidence interval.

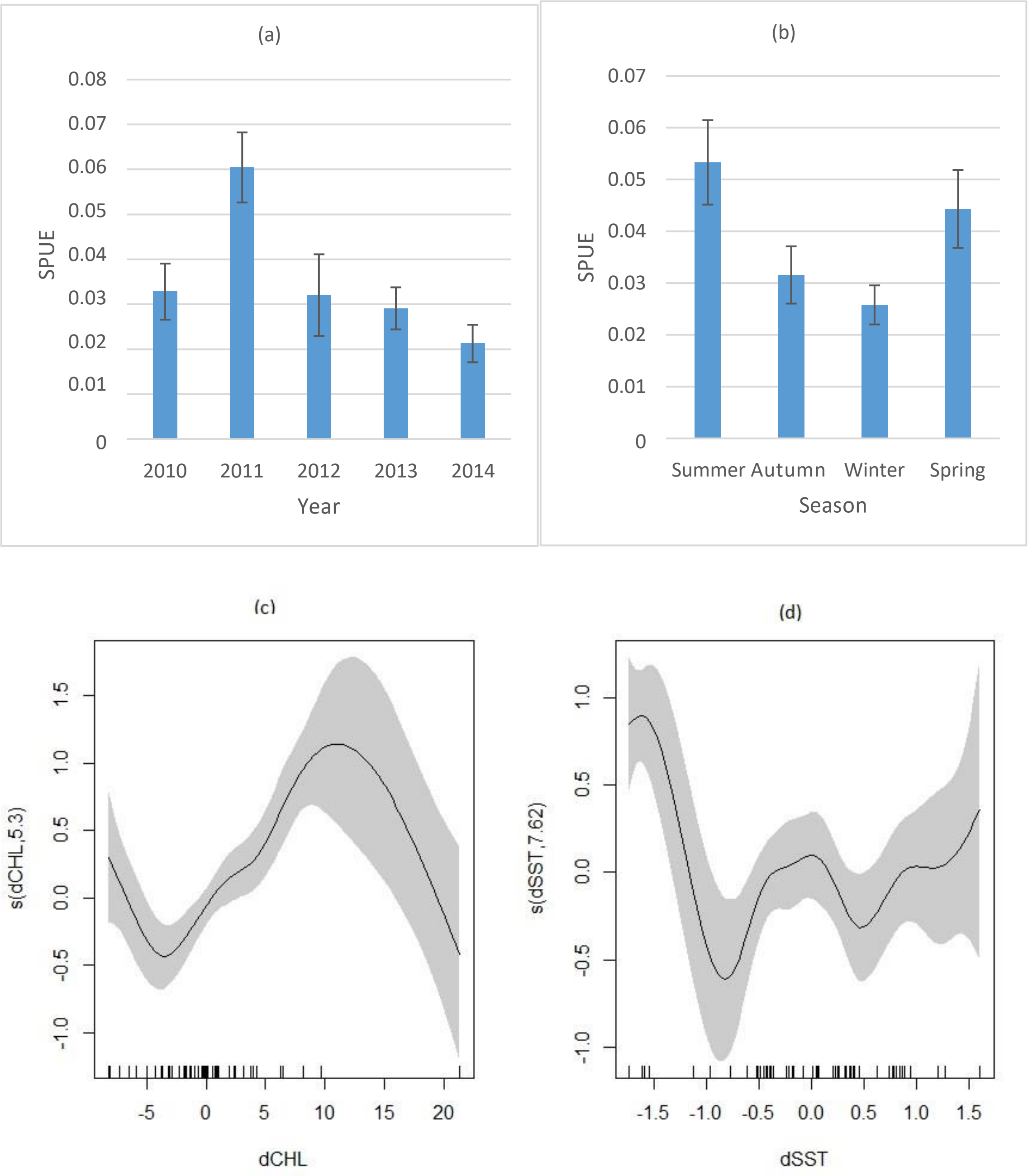

Figure 9**:** Mean sighting rates (SPUE ± standard error) of groups of bottlenose dolphins in Mossel Bay for the period 2010-2014. (a) Annual means, (b) seasonal means. (c) GAM response curve showing the smoothed fit of the relationship between chlorophyll *a* anomalies over the study period and the sighting rate of bottlenose dolphins in the area; (d) GAM response curve showing the smoothed fit of the relationship between sea surface temperature anomalies over the study period and the sighting rate of bottlenose dolphins in the area; *Note: the y-axis in each of the GAM graphs represents the smoothed change in *dCHL* and *dSST* over the entire study period and is on the scale of the link function, not the measured variable. The area in grey shows the 95% confidence interval.