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Seasonal fluctuations in occurrence of inshore Bryde's whales in Plettenberg Bay, South Africa, with notes on feeding and multispecies associations

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Seasonal fluctuations in the occurrence of inshore South African Bryde's whales *Balaenoptera edeni* were investigated between November 2005 and June 2008. Sighting data were collected in Plettenberg Bay on the south-east coast of South Africa. Bryde's whale occurrence was modelled in relation to the following environmental covariates: sea surface temperature, chlorophyll *a* concentrations and wind speed. Seasonal increases in encounter rates (sightings per day) were observed during summer and autumn, with a peak in April that corresponded to increased feeding activity and above average aggregation sizes. All three environmental covariates were significant factors in terms of explaining variability in the occurrence of whales. Multispecies associations with common dolphins *Delphinus capensis* and Cape gannets *Morus capensis* were most common in summer and autumn, when feeding activity was highest.

Keywords: *Balaenoptera edeni*, chlorophyll *a*, generalised linear models, multispecies associations, seasonality, SST

Introduction

In the marine environment, seasons are usually characterised by fluctuations in oceanographic features such as sea surface temperature (SST) and primary productivity (chlorophyll *a* concentration) (Burtenshaw et al. 2004). Associations between cetaceans and such covariates have previously been identified (e.g. Jaquet et al. 1996, Moore et al. 2002) and help to explain temporal variability in occurrence, especially when data on prey distribution are not readily available. For example, the distributions of four rorqual species were strongly correlated with SST fronts in the Gulf of St Lawrence (Doniol-Valcroze et al. 2007). Sei whale *Balaenoptera borealis* and North Atlantic right whale *Eubalaena glacialis* abundance, distribution and foraging patterns have also been shown to vary between years in response to changing environmental conditions and prey availability (Payne et al. 1990, Kennedy et al. 2001, Bannister 2002).

Wind speed can be an important factor affecting detection of cetaceans, particularly in the case of inconspicuous species such as the harbour porpoise *Phocoena phocoena* (Barlow 1988, Palka 1996). Wind strength has also been identified as a mechanism for wind-induced upwelling events, which create favourable conditions for prey species (e.g euphausiids and shoaling fish) of many baleen whales (Croll et al. 2005, Doniol-Valcroze et al. 2007).

A consequence of variability in the availability of resources for cetaceans is the need to move between regions within their home range (Stern 2002). Temporal disparities in occurrence are obvious for most baleen whale species because of the pronounced spatial partitioning of their respective high-latitude feeding and low-latitude calving grounds (Stern 2002). Moving between these two areas requires large-scale migrations, which may, however, be suspended when sufficient prey is available in lower latitude areas, e.g. humpback whales *Megaptera novaeangliae* on the west coast of South Africa (Best et al. 1995, Barendse et al. 2011). Exceptions to the typical patterns of large-scale migrations of baleen whale populations are exhibited in fin whales *Balaenoptera physalus* in the Mediterranean Sea (Forcada et al. 1996), humpback whales in the Arabian Sea (Whitehead 1985, Mikhalev 1997), and the global populations of Bryde's whales *Balaenoptera edeni*, which have limited spatial migrations (Best 2001, Kato 2002, Stern 2002). Bryde's whales have undefined or disparate reproductive cycles and feed intensively and opportunistically throughout the year. These characteristics, unusual for baleen whales, lessen the need for these animals to migrate to particular feeding or breeding areas (Best 1977, Bannister 2002, Kato 2002).

Until recently, the discovery of two forms of Bryde's whale off South Africa was thought to be unique (Best 1977). However, there is increasing evidence for the occurrence of allopatric forms elsewhere, e.g. south-west Japan, Oman and Angola (Kato et al. 1996, Mikhalev 2000, Weir 2007). Consensus on the number of species or subspecies of Bryde's whales and the correct nomenclature for each *Balaenoptera edeni/brydei/*ssp. is yet to be established (Rice 1998, Bannister 2002). In our study, all Bryde's whales were referred to as *B. edeni*, according to the Society for Marine Mammalogy Committee on taxonomy. However, two forms were distinguished, namely 'inshore' and 'offshore'. Best's (1977) comparison of the two forms off South Africa provided baseline information on morphology, diet, reproductive cycles and distribution (Table 1), all of which support the year-round occurrence of the inshore form within South African coastal waters (Best 1977, 2001, Kato 2002, IUCN 2008).

For the few known inshore populations of Bryde's whales, alongshore movements are most likely driven by the movements of their prey (Gaskin 1977, Kato 1996, Zerbini et al. 1997, Best 2001). Inshore Bryde's whales feed mainly on pelagic shoaling fish such as sardine *Sardinops sagax* and anchovy *Engraulis* spp. (Best 1977, Zerbini et al. 1997). Feeding events along the south-eastern coast of Brazil occur during the austral summer and autumn, coinciding with the spawning of sardine in the shallower coastal waters (Siciliano et al. 2004). Bryde's whales are commonly seen feeding on sardine or juvenile tuna *Thunnus* sp. in summer off the coast of south-west Japan (Kato 2002) and on anchovy *Engraulis japonicus* in the western North Pacific in late summer (Murase et al. 2007). In the waters around the north-eastern Maldivian archipelago, large concentrations of Bryde's whales apparently feed in nearshore waters in April (autumn) (Ballance et al. 2001). These habits are consistent with those reported from the Gulf of California (Tershy 1992) and for the South African inshore form (Best 1977).

The majority of the South African inshore population of Bryde's whales occurs between Cape Agulhas and East London in summer (Best et al. 1984). Off the west coast of the country, there appears to be a seasonal shift in distribution with an influx in winter (Best et al. 1984). It is likely that animals move north along both the east and west coasts of South Africa during autumn and winter and return to the central Agulhas Bank during spring (Best 2001). These movements coincide with those of pelagic shoaling fish (sardine and anchovy), their main prey (Best 2001). Both fish species are critically important ecologically and economically, and serve as an important food source for many predators in South African waters (Cockcroft and Peddemors 1990, van der Lingen and Durholtz 2005, O'Donoghue et al. 2010b). Anchovy and sardine recruits are abundant along the inshore nursery areas of the West Coast in autumn and winter during the annual southward recruit migration (Hampton 1992, Hutchings 1992, Barange et al. 1999). Similarly, sardine movements close inshore up the East Coast during autumn and winter (an annual event known as the 'sardine run') are well documented (Baird 1971, Crawford 1981, Armstrong et al. 1991), although the reasons for the migration and the conditions and mechanisms driving it have only recently begun to be understood (O'Donoghue et al. 2010a, Fréon et al. 2010). During the past decade, sardine and anchovy adults have occurred predominantly over the central and eastern Agulhas Bank, between Cape Agulhas and Port Elizabeth (Roy et al. 2007, Coetzee et al. 2008), where spawning peaks mainly during spring and summer.

Bryde's whales are currently classified as 'data deficient' by the International Union for the Conservation of Nature (IUCN) and obtaining information to assess the true conservation status of the many populations of this species is considered a high priority (IUCN 2008). This is because of the increasing molecular evidence that numerous genetically isolated populations, possibly subspecies, of Bryde's whale exist and may require management at a local rather than only at a global scale (Pastene et al. 1997, Yoshida and Kato 1999, Wada et al. 2003, Sasaki et al. 2006, Kanda et al. 2007). The South African inshore population is relatively small and appears to be genetically isolated from other Bryde's whale populations (Penry 2010). Best et al. (1984) estimated the population size to be 582 (SE 184) individuals in 1983, but Penry (2010) estimated a smaller population of between 130 and 250 animals (CV = 0.07–0.38) during the period 2005–2008 on the south-east coast of South Africa. Although these studies are not directly comparable because of differences in survey methods, spatial coverage and analysis, it appears that the population could be in decline. It has been suggested that insufficient prey resources off South Africa has contributed to observed declines in

Table 1: Summary of biological differences between the inshore and offshore Bryde's whales from South Africa from Best (1977, 2001)

		Inshore	Offshore
Appearance	Length at maturity (m): Male	12.8–13.1	13.7
	Female	13.7–14.0	14.3–14.6
	Scarring: Oval pits	Few or none	Extensive over body
	Ventral scratches	Common	Absent
	Baleen shape	Narrow	Broad
Distribution	Habitat	Coastal	Pelagic
	Distance from coast	<20 nautical miles	>50 nautical miles
Life history	Prey	Small schooling fish (e.g. sardine, anchovy)	Mostly euphausiids; some mesopelagic fish
	Reproductive season	Aseasonal	Year-round, peaks in autumn
	Ovulation rate (y^{-1})	2.35	0.42
	Migrations	Local, longshore movements	North–south movements, towards the equator in winter and to 34° S in summer

populations of seabirds that depend on some of the same prey species as that of Bryde's whales (Crawford 1998, Crawford et al. 2007).

No new data on Bryde's whales have been collected in South Africa in over 25 years. Basic information such as abundance estimates, genetic identity and an understanding of how environmental conditions influence the temporal dynamics of this population are currently lacking. Such knowledge is essential to understanding their role in the marine ecosystem and how other components (e.g. fluctuating prey stocks, competing predators, climate change and commercial activities) may affect their survival. An understanding of the effects of environmental factors can assist in the management and conservation of cetaceans (MacLeod et al. 2004).

A study on the inshore population of South African Bryde's whales was undertaken with the following objectives: to investigate seasonal and monthly patterns in their occurrence within the study area; to identify environmental variables associated with temporal variability in whale occurrence; to explore temporal variability in feeding activity; and to describe their associations with other species and when these occur.

Material and methods

Study area

The study area included approximately 50 km of coastline and up to 6 nautical miles offshore in and around Plettenberg Bay on the south-east coast of South Africa (Figure 1). The bay is situated at the eastern margin of the Agulhas Bank between a wide continental shelf to the west (Central Bank) and a narrow shelf to the east. The 100 m and 200 m isobaths lie at 19 km and 90 km respectively south of Plettenberg Bay. Water depth does not generally exceed 50 m inside the bay and tidal range is about 1.5–2 m. The southern and western side of the bay has a gradual gradient whereas towards Nature's Valley (the eastern border of the bay) the drop-off is steeper.

In and around the study area westerly winds dominate throughout the year, with the percentage of easterlies increasing during summer; autumn being the calmest period (Schumann 1998). Sea surface temperatures along the south-east coast of South Africa range from 9.6 to 24.8 °C, with averages of 16–17 °C in winter and 20–21 °C in summer. The combination of a shallow mixed layer and abrupt topography allows weak summer winds to cause rapid changes in SST along the South Coast, although the water temperature rarely falls below 10 °C (Schumann 1999). Intense thermoclines that occur over the inner shelf during summer are a result of the combination of warm easterly winds in summer and cold, turbulent westerly winds in winter (Schumann and Beekman 1984).

Data collection

Data were collected daily between November 2005 and June 2008. Platforms for data collection included commercial vessels from three different whale-watching companies (Ocean Safaris, Ocean Blue Adventures, and The Explorer) and a research vessel (*Delphinus*) that was primarily used for the collection of biopsy samples. These vessels were all power-driven catamarans, each fitted with two outboard motors (85–200 hp), ranging in length from 6.3 m to 10.7 m. Eye-height from aboard the vessels was approximately 2.5 m above sea level and the observers scanned out to the horizon in front and to the sides of the vessel using the naked eye. Numbers of observers varied between three and eight, and included the primary author (GSP), interns and vessel crew. All trips conducted, and thus all encounters with whales, were in sea conditions equivalent to Beaufort sea states ≤3 (<5.4 m s^{-1} or 7–10 knots). If sea conditions deteriorated, equipment was stowed and the vessel was returned to shore. A one-nautical mile area around the Robberg Peninsula (Figure 1) was closed to whale watching; however, vessels could enter to approach the seal colony on the peninsula. The research vessel was permitted to approach whales within this area for data collection.

The searching protocol was similar on both types of vessel. However, surveys did not follow a formal design or achieve uniform coverage of the study area. Instead, the aims were to achieve the maximum possible number of encounters for the collection of photo-identification data and biopsy samples (from the research vessel) or the maximum possible number of encounters with all cetacean species and other wildlife (from the whale-watching vessels). Figure 1 shows a typical route taken by the commercial whale-watching vessels. Southern right whales *Eubalaena australis* are present in the bay during the winter, usually in shallow waters, and they are targeted by the whale-watching vessels. The potential biases associated with this are addressed below.

Trips were approximately of 2 h duration and there could be up to three trips in any one day (Croll et al. 2005, O'Callaghan and Baker 2005). Global positioning system (GPS) coordinates for sightings were plotted on a digital map in ArcMap™ 9.3. Identification photos were used to ensure that individual whales were not double-counted as a result of successive trips on one day. The number of trips conducted each month and season was used as a measure of effort. The seasons were defined as follows: spring (September–November), summer (December–February), autumn (March–May) and winter (June–August). Encounter rate (sightings per day) was used to explore seasonal and monthly variation in the occurrence of Bryde's whales.

Feeding was recorded when lunges were observed or when whales were associating with other predator species feeding on small shoaling fish (c.f. Tershy 1992). An event refers to feeding activity on a concentration of prey, its duration lasting until the prey was eaten or predators satiated. The proportion of encounters during which feeding events occurred was determined. Solitary Bryde's whales were differentiated from aggregations of Bryde's whales during feeding events and whilst travelling (surfacing regularly and moving in one direction). An aggregation was defined as more than one Bryde's whale within a maximum radius of 1 nautical mile from another whale.

A multispecies association was classified when more than one species was involved in a feeding frenzy or when travelling together as a coordinated group. Associations of Bryde's whales with common dolphins *Delphinus*

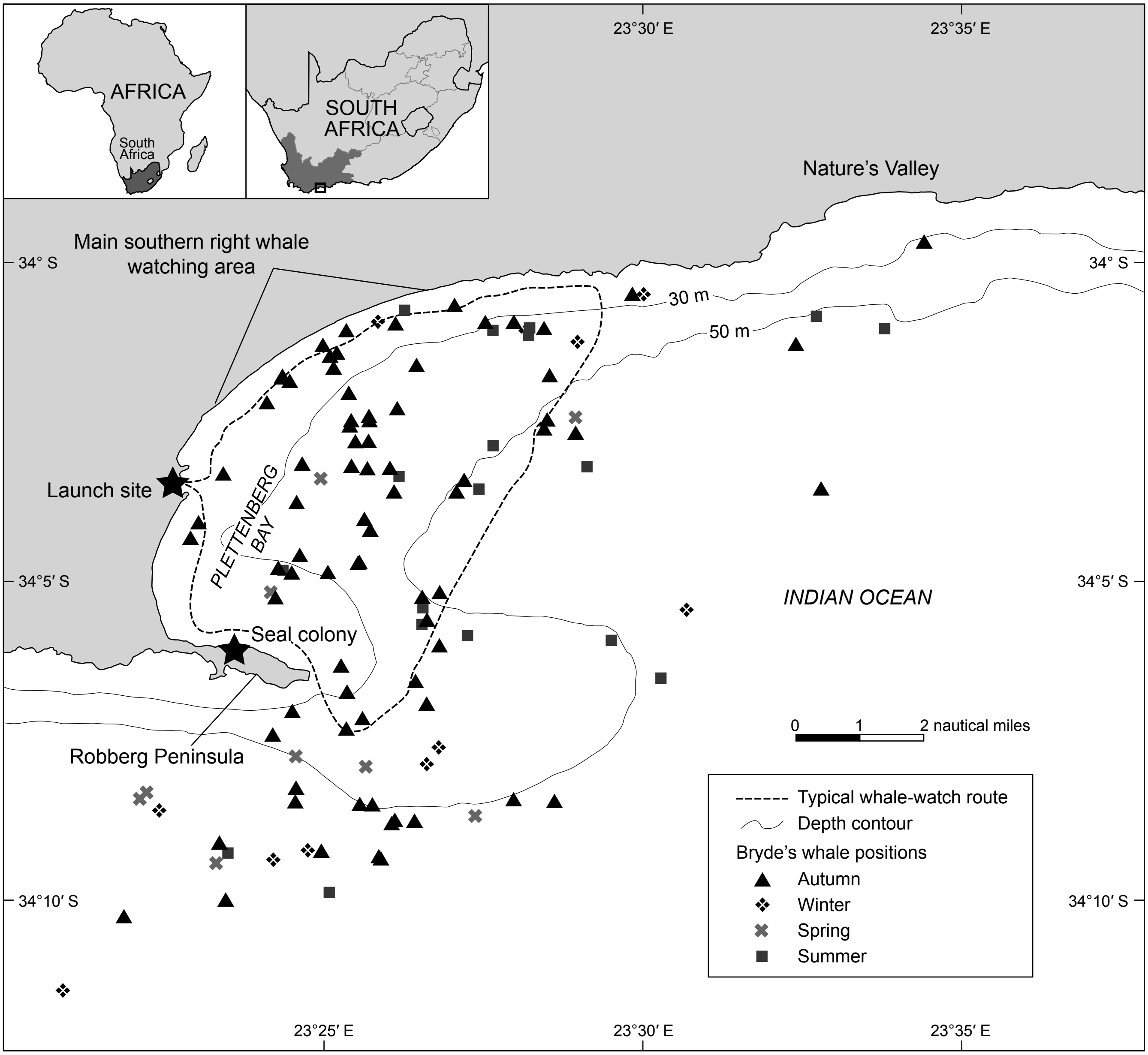

Figure 1: Map of Plettenberg Bay showing positions of Bryde's whales encounters per season during the study period and the typical route taken by the whale-watching vessels

capensis, Cape gannets *Morus capensis*, Cape fur seals *Arctocephalus pusillus pusillus* or 'other cetaceans' were systematically recorded for each encounter. Seasonal variation in the proportion of encounters during which each of these species was associated with Bryde's whale, and the relative occurrence of feeding or travelling associations, were investigated.

Chlorophyll *a* concentrations (8-day averages) recorded by the sea-viewing wide field-of-view spectro-radiometer (SeaWiFS) ocean-colour sensor were extracted from the NASA archives for the area between 34°–34.2° S and 23.4°–23.7° E. Daily SST measurements were extracted for a grid square (1 km^2) centred on the study area (34.125° S, 23.625° E), from data recorded with a spatial resolution of 0.25° and a temporal resolution of one day by the NASA Earth Observing System satellite using the advanced very high resolution radiometer (AVHRR) and advanced microwave scanning radiometer (AMSR) (Reynolds et al. 2007). Weather data, additional to those recorded at sea (and including daily wind speeds), were obtained from the South African Weather Service.

Data analysis

Generalised linear models

Statistical models can be fitted to relate whale occurrence to predictor variables in order to identify the spatial and temporal use of critical habitats (Gregr and Trites 2001, Doniol-Valcroze et al. 2007, Panigada et al. 2008). In the

Table 2: Summary of the number of trips conducted (above the diagonal line) and the number of Bryde's whale encounters (below the diagonal line) during each month from November 2005 to June 2008

Year	Season/month											
	Summer		Autumn			Winter			Spring			Summer
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
2005	–	–	–	–	–	–	–	–	–	–	5 / 5	14 / 9
2006	6 / 5	4 / 0	10 / 7	9 / 9	9 / 6	13 / 4	28 / 2	15 / 1	16 / 1	12 / 3	11 / 5	12 / 4
2007	13 / 8	9 / 7	9 / 6	11 / 7	9 / 5	8 / 0	11 / 2	10 / 3	10 / 1	12 / 2	7 / 1	4 / 2
2008	10 / 4	4 / 3	10 / 6	13 / 13	13 / 12	3 / 3	–	–	–	–	–	–

absence of data on prey availability within the study area, the environmental factors known to affect the distribution of shoaling fish (SST, chlorophyll *a* and nutrient input through wind-induced coastal upwelling) (Cury and Roy 1989, Schumann 1999, Croll et al. 2005) were used as covariates to potentially explain variation in Bryde's whale encounter rates. Wind speed was included on account of its possible effect on the detectability of cetaceans (Palka 1996, Buckland et al. 2001). Variation in the encounter rate of Bryde's whales was modelled as a function of different explanatory variables (SST, chlorophyll *a*, wind speed, month, season) using generalised linear models (GLMs) implemented in program R (R Development Core Team 2005). The error structure of the response variable was assumed to be Poisson-distributed and modelled through a log link. The number of trips conducted was used as an offset to account for varying effort. Models were fitted through a backwards–forwards stepwise selection procedure, starting with a fully saturated model containing all explanatory variables. Retention or removal of variables was governed by the Akaike's information criterion (AIC), with the lowest AIC value indicating the best fit to the data. Models assuming a quasi-Poisson distribution were used to estimate the scale of the relationship between the mean and variance of the data, and thus to determine whether or not the data were overdispersed. Month and season were treated as factor variables.

The fitted relationships were plotted using the model that best explained the variation in the data. To illustrate the independent relationships between encounter rate and each covariate, the other variables were kept constant at their mean values. The results for April and August are shown here as these months corresponded to the highest and lowest number of encounters respectively.

Results

During a total of 330 trips conducted between November 2005 and June 2008, 146 Bryde's whale encounters were recorded (Table 2).

Seasonal and monthly patterns

There was significant variation in encounter rate between seasons (ANOVA, $F_{3,279} = 15.3$, $p < 0.05$), which peaked in autumn (0.67) and declined throughout winter and spring (0.10 and 0.12 respectively). Mean chlorophyll *a* concentrations were highest in autumn (4.4 mg m^{-3}) and lowest in summer (1.6 mg m^{-3}). In contrast, mean SST was highest in summer (>20 °C) and lowest in winter (17 °C), with temperatures between 18 and 19 °C during spring and autumn. Mean wind speed varied little between spring and summer (4.1 vs 4.2 m s^{-1}), but was lowest in autumn (3.6 m s^{-1}).

Variation in encounter rate between months was also significant (ANOVA; $F_{11,271} = 6.13$, $p < 0.05$). The mean monthly encounter rate was considerably higher in April (0.98) than in all other months (<0.6) (Figure 2a). The highest mean chlorophyll *a* concentration (8 mg m^{-3}) was also found in April, and thereafter declined by about 50% and remained consistently low throughout the rest of the year, with a small peak in September (Figure 2b). Mean monthly wind speed values were highest in October and lowest in July (Figure 2c). Mean SST generally remained above 20 °C from December to March and then dropped in April to 18 °C (Figure 2d), coinciding with increases in the encounter rate and chlorophyll *a* concentrations. The highest encounter rate of whales was between November and May when SST was >18 °C.

Factors affecting Bryde's whale encounter rate

Diagnostics of the modelling to investigate which variables best explained variation in encounter rate are shown in Table 3. There was no evidence of co-linearity between the explanatory variables, each having a variance inflation factor (VIF) of <5. The best model (Model 1) included month, SST, chlorophyll *a* and wind speed (Table 3). All variables were significant except chlorophyll *a* (Table 4). Variation in encounter rate of Bryde's whales was better explained by month than by season. The fitted relationships between encounter rate and each environmental variable for the best fitting model (Model 1; Figure 3, Table 3) showed a positive relationship with chlorophyll *a* (all months) and SST (more variation during August than April and generally less variation at low temperatures). A negative relationship between encounter rate and wind speed was predicted. Lower wind speeds had wider confidence intervals, reflecting higher variation in encounter rate during such conditions.

Feeding events

During the study period, there were 33 Bryde's whale encounters when feeding events were observed. Feeding

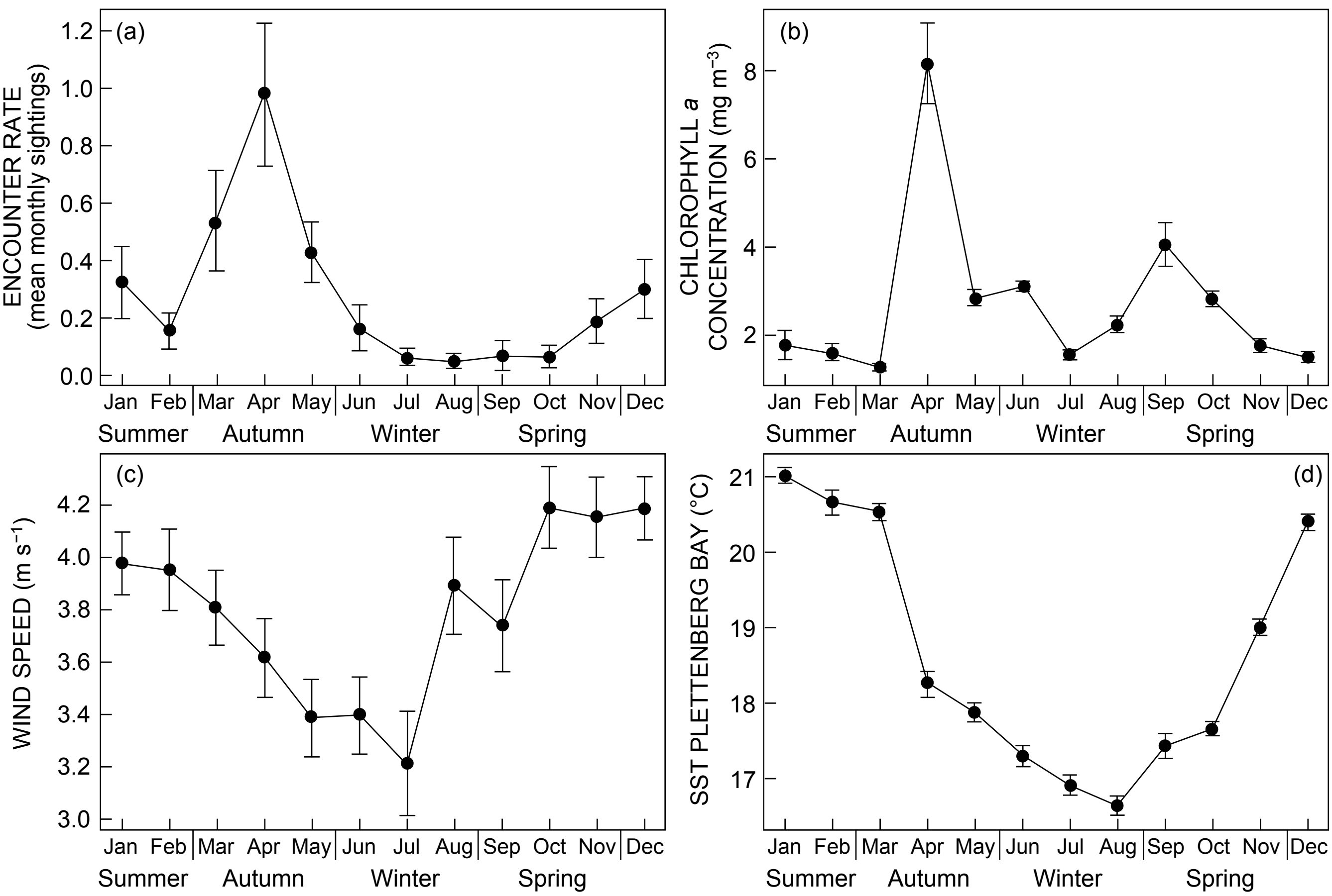

Figure 2: (a) Encounter rate per month of Bryde's whales at Plettenberg Bay, (b) mean monthly chlorophyll *a* concentration, (c) mean monthly wind speed and (d) mean monthly SST. Error bars denote SE

Table 3: Model diagnostics for generalised linear models for Poisson-distributed data. Sea surface temperature (SST), chlorophyll *a* concentration (Chl *a*), wind speed, season and month were included in the models. The best three models are shown; all others had ΔAIC > 12. Covariates with a significant ($p < 0.05$) effect on the number of encounters per month or season) are shown

Model	Variables included in the model	AIC	ΔAIC	Significant variables
1	Month, SST, Chl *a*, wind speed	1 024.2	0.0	SST** Wind speed*** Month***
2	Month, Chl *a*, wind speed	1 029.5	5.3	Month*** Wind speed***
3	Season, SST, Chl *a*, wind speed	1 035.4	11.2	Season*** SST*** Wind speed***

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

Table 4: Summary results of the best model in Table 3: encounter rate ~ SST + chlorophyll *a* + wind speed + as.factor (month), family = Poisson, offset = log(trips + 1)

Coefficients	Estimate	SE	*Z*-value	*p*
(Intercept)	−3.137212	1.166338	−2.690	0.007
SST	0.139787	0.051949	2.691	0.007
Chlorophyll *a*	0.002311	0.013907	0.166	0.868
Wind speed	−0.262356	0.059764	−4.390	<0.001
Month (Feb)	0.604100	−0.202272	−1.730	0.084
Month (Mar)	0.309625	0.258564	1.197	0.231
Month (Apr)	0.893574	0.275935	3.238	0.001
Month (May)	0.081021	0.326398	0.248	0.804
Month (Jun)	−0.670142	0.402420	−1.665	0.096
Month (Jul)	−1.716009	0.588955	−2.914	0.004
Month (Aug)	1.640039	0.655703	−2.501	0.012
Month (Sep)	−1.458646	0.569379	−2.562	0.010
Month (Oct)	−1.389587	0.566856	−2.451	0.014
Month (Nov)	−0.393016	0.331823	−1.184	0.236
Month (Dec)	−0.202272	0.274597	−0.737	0.461

activity was higher in summer/autumn than in winter/spring; only one winter feeding event was recorded throughout the study period (Figure 4a). Aggregation size at feeding events was similar in autumn (mean = 3.8; SD 1.19), summer (mean = 3.8; SD 1.09) and spring (mean = 3.3; SD 0.44); the single feeding event recorded for winter involved only two Bryde's whales (Figure 4b).

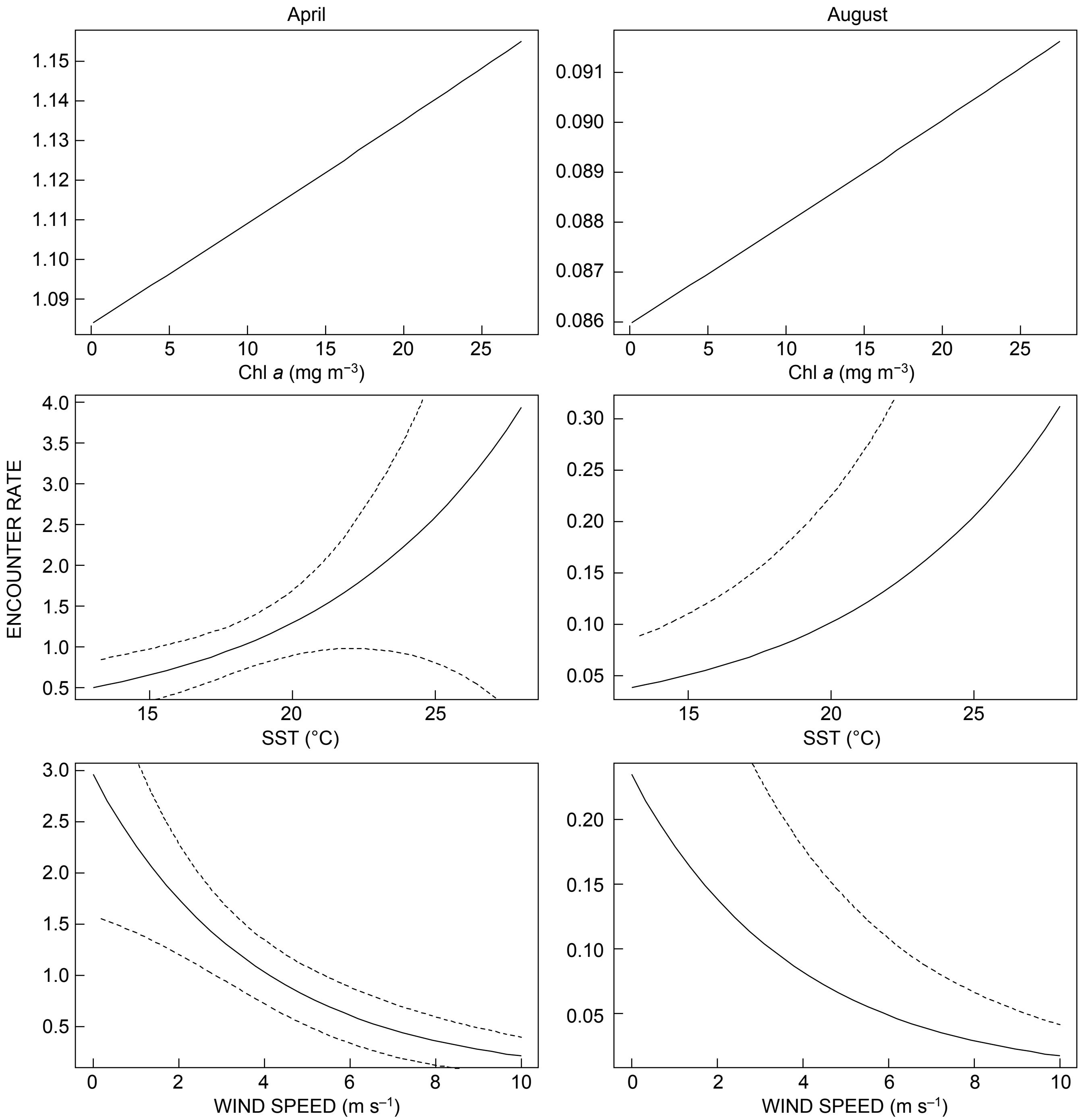

Figure 3: Predicted relationships (solid line) and upper and lower 95% CI (broken lines) for encounter rate in relation to each covariate (when other covariates are at mean values) for April and August, corresponding to periods of highest and lowest encounter rates respectively

Multispecies associations

The species most commonly associated with Bryde's whales were Cape gannets (23%), Cape fur seals (18%) and common dolphins (16%). Bottlenose dolphins *Tursiops aduncus* were involved in <3% of the mixed-species associations and only while travelling. Bryde's whales were seen feeding most frequently in association with common dolphins and Cape gannets (>55% of all associations) and infrequently (8%) fed alone (Figure 5). Solitary animals were usually travelling (92%) (Figure 5).

Solitary whales were encountered more often than conspecific aggregations, except in summer (Figure 6). Associations with common dolphins were highest in spring, whereas in summer common dolphins and Cape gannets were associated with Bryde's whales in approximately equal proportions (Figure 6). In autumn, Cape fur seals and Cape

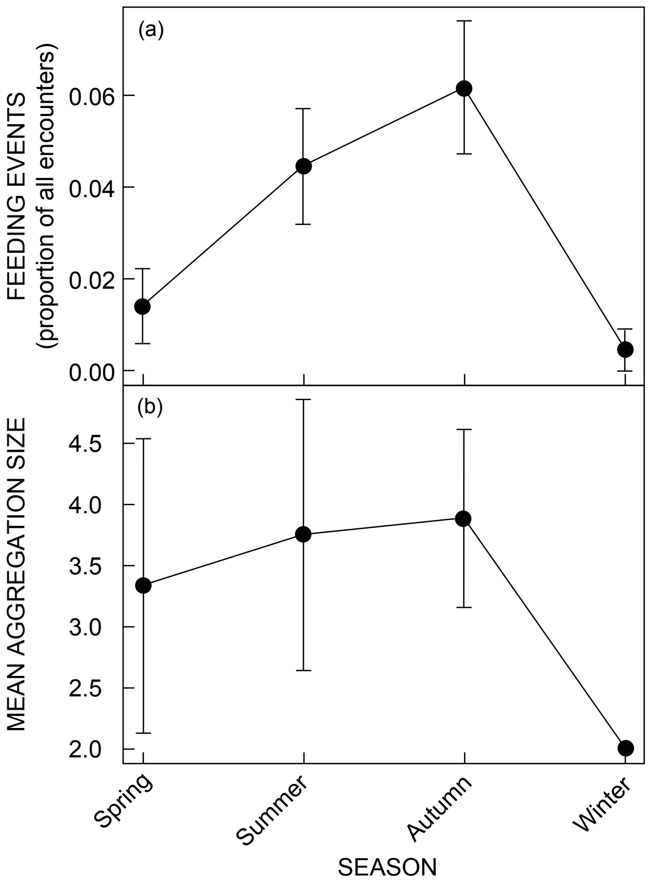

Figure 4: (a) Mean daily number of encounters where feeding was observed per season and (b) the mean aggregation size during feeding activity per season. Error bars denote SE. The frequency of feeding events was corrected for effort using the number of trips conducted during each season

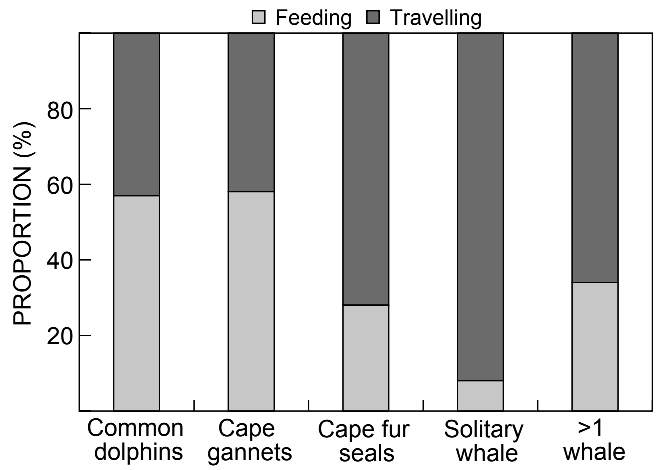

Figure 5: The proportion of encounters for which feeding or travelling behaviour were recorded, for a solitary Bryde's whale, a group of Bryde's whales, or one or more Bryde's whales associated with other species (common dolphins, Cape gannets or Cape fur seals)

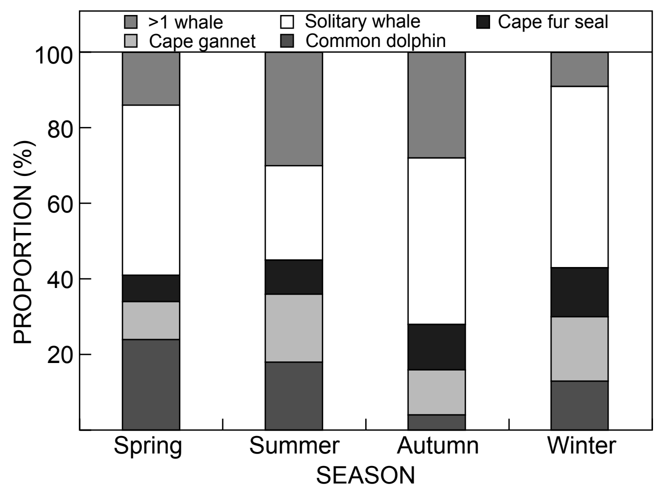

Figure 6: Seasonal differences in the proportion of encounters that were of a solitary Bryde's whale, a group of Bryde's whales, or one or more Bryde's whales associated with other species (common dolphins, Cape gannets or Cape fur seals)

gannets were associated with Bryde's whales more often than were common dolphins, and in similar proportions (Figure 6). Multispecies associations and aggregations of Bryde's whales were infrequent in winter, a period when the overall encounter rate was low (Figure 6).

Discussion

Using platforms of opportunity such as whale-watching vessels is common for cetacean research, not least owing to the high cost of conducting dedicated surveys at sea. Imperfect sampling design that frequently characterises such research, including restricted spatial and temporal coverage, bias towards one or more particular species, and time limitations set by the length of trips, can profoundly influence results. However, as long as adequate spatial and temporal coverage is achieved and a range of habitats are included in surveys, bias in the results can be minimised (Evans and Hammond 2004). The effects of areal restriction of the whale-watching vessels could potentially have been confounding in this study, especially considering that they preferentially targeted southern right whales in the shallow waters during winter. Such effects could not be assessed quantitatively because survey effort data were not collected. However, the tour vessels were not wholly confined to shallow waters or certain areas of the bay during winter. During each trip, the vessels visited the Cape fur seal colony situated on the western side of the bay, some 6 nautical miles from the right whale and dolphin focal areas on the northern side. In so doing, they undertook a searching leg across the outer area of the bay. These offshore legs often resulted in Bryde's whale sightings (Figure 1).

Nonetheless, it cannot be ruled out that reduced areal coverage of the bay during winter may have contributed to reduced encounter rates of Bryde's whales during this period. It is, however, unlikely that this could explain the smaller aggregation sizes encountered during this period and the lower incidence of multispecies associations and feeding events, relative to other times of the year.

Aggregation size of Bryde's whales was positively correlated with the occurrence of feeding behaviour in this study. This was similar to the situation in the Gulf of California, where solitary individuals were usually travelling, whereas aggregations of comparable sizes to those found in this study during summer and autumn were associated with feeding (Tershy 1992). During winter there are increased sightings of Bryde's whales farther north along the East Coast, frequently in groups with common dolphins and Cape gannets (Best et al. 1984, Best 2001, O'Donoghue et al. 2010b). This appears to coincide with the annual north-eastward migration of sardine into KwaZulu-Natal waters (Fréon et al. 2010). Thus, movements of animals away from the study area in pursuit of prey during the sardine run could have contributed to the observed temporal differences in encounter rates, aggregation size, interspecific interactions, and feeding behaviour of Bryde's whales in our study.

Cape gannets have been shown to be the best indicators of sardine presence along the south-east coast of South Africa (O'Donoghue et al. 2010c). They were also associated with Bryde's whales more often than any other species in our study. Observations of multispecies associations offer strong support for cooperative feeding, especially between common dolphins, Cape gannets and other marine predators (sharks and seals) that appear to work together in herding and corralling fish into tightly packed 'bait balls'. It has previously been noted that individual Bryde's whales act independently of conspecifics during feeding (Tershy 1992). However, it is not known how successful feeding is in the absence of the other species, the activities of which enable Bryde's whales to lunge through high densities of fish, engulfing maximum amounts of prey with minimal effort. Multispecies feeding events involving Bryde's whales have previously been documented for waters off south-east Brazil, New Zealand, Venezuela and the Gulf of California (Notarbartolo di Sciara 1983, Breese and Tershy 1993, Zerbini et al. 1997, Siciliano et al. 2004, Baker and Madon 2007, Stockin et al. 2009, Wiseman et al. 2011). The associations identified in this study were in accordance with those of other populations of Bryde's whales and with those previously reported by Best et al. (1984) for the South African inshore form.

Bryde's whale encounter rate was negatively related with wind speeds, positively related with SST and poorly related with chlorophyll *a* concentrations. Generally these are not what may have been expected if the whale encounters were associated with conditions in space and time that were conducive to productivity (e.g. wind-induced upwelling). These relationships may have been obscured by the fact that data were collected only during low to moderate wind speeds (approximately ≤10 knots). However, Grémillet et al. (2008) observed spatial match-mismatch patterns in the occurrence of phytoplankton, zooplankton, forage fish and Cape gannets in the southern Benguela and advised caution be applied when interpreting spatial overlap between primary productivity and top predators. It has been shown that Bryde's whale occurrence is mainly related to changes in the distribution of their prey (Nemoto 1959, Best 1960, Gaskin 1977, Tershy 1992, Zerbini et al. 1997, Best 2001); given both the temporal fluctuations in their encounter rates and weak relationships with environmental variables, this is most likely also the case for the study animals. Similar weak relationships between SST-related variables and commercial catches of anchovy and sardine by the fishing industry (Agenbag et al. 2003) suggest that linking the occurrence of Bryde's whale to the presence of forage fish through environmental data is probably not feasible.

Foraging Bryde's whales need to forage frequently to satisfy their daily consumption needs (Best et al. 1984); therefore, they are unlikely to remain in one place for long periods of time (entire seasons) if their prey is on the move. This notion is supported here by the fact that encounter rate varied more between months than seasons. Prey dynamics (abundance and availability) have been shown to affect the behaviour, seasonality and abundance of Bryde's whales in coastal waters off south-east and southern Brazil, Venezuela and the Gulf of California (Notarbartolo di Sciara 1983, Tershy 1992, Zerbini et al. 1997).

The most recent (2005–2008) abundance estimate for the inshore Bryde's whale population (Penry 2010) is indicative of a decline in numbers since 1983 when the last estimate was made (Best et al. 1984). This difference could be a result of differences in methods used and spatial coverage, but changes in prey availability over the past 25 years could also be a contributing factor. Estimates of anchovy and sardine biomass derived from annual acoustic surveys suggest an increase in prey availability in the area east of Cape Agulhas (within which our study area is located) over the past 10–15 years (Coetzee et al. 2008). These surveys do not, however, provide indices of prey abundance at a smaller temporal resolution and therefore make it impossible to link estimates of Bryde's whale to forage fish abundance. Fluctuations in marine mammal abundance and distribution have been used as indicators of ecosystem change or as tools for ecosystem management (Hooker and Gerber 2004, Sergio et al. 2008). However, not all marine mammals are easy to monitor, so by understanding their relationship with other marine predators, such as Cape gannets in the case of Bryde's whales in South Africa, inferences can be made regarding the availability of prey within the ecosystem.

There appear to be no obvious threats to the South African inshore population of Bryde's whales. The biggest potential risk is most likely its small size and restricted home range, making it vulnerable to changes in the environment (Clapham et al. 1999, Elwen et al. 2011). Small populations (e.g. North Atlantic right whales, western gray whales *Eschrichtius robustus*) are particularly susceptible to human impacts such as incidental mortality and habitat degradation (Clapham et al. 1999). Future planned studies on South African Bryde's whales include further investigations of their abundance and the use of stable isotope analysis to determine whether they are capable of adapting to new prey species in response to possible future reduced availability of their main prey species. If the results show that they do not exploit other prey species, then conservation measures may need to be implemented in order to conserve this small population.

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