

Migration redefined? Seasonality, movements and group composition of humpback whales *Megaptera novaeangliae* off the west coast of South Africa

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The migration of Southern Hemisphere humpback whales *Megaptera novaeangliae* between their feeding and breeding areas has thus far been considered a highly predictable and seasonal event. However, previous observations on the humpbacks that pass through the nearshore waters of the west coast of South Africa have revealed deviations from the behaviour and seasonality expected during a typical migration. This ‘anomaly’ is hypothesised to be associated with prey availability in the region. Shore-based observations between July 2001 and February 2003 from North Head, Saldanha Bay, in the Western Cape province, yielded relative abundances that again did not support a classical migration pattern, with the highest sighting rates from mid-spring through summer. Movement parameters (actual swimming speed, direction and linearity) of humpback groups tracked by theodolite showed mid-spring to be a turning point in their behaviour, after which we observed a significant reduction in actual swimming speed, an increase in ‘non-directional’ movement, and a distribution farther from shore than in other seasons. Additional data on group composition and sex collected between 1993 and 2008 showed a significantly female-biased sex ratio during mid-spring, the first such recorded for any region. Direct observation of feeding on crustacean prey during spring and summer further supports the notion that humpbacks may have more flexible foraging habits than previously appreciated, and that the southern Benguela upwelling region may function as an important feeding area for these whales.

Keywords: Benguela upwelling, Breeding Stock B, feeding, group composition, humpback whale, migration, Pythagoras software, seasonality, sex ratios, shore-based survey, South Atlantic, theodolite tracking

Introduction

Humpback whales *Megaptera novaeangliae* in general are believed to undertake extensive and predictable migrations from polar feeding grounds in summer to tropical overwintering areas, displaying high fidelity to the same breeding and feeding areas (Clapham et al. 1993, Clapham 2000, Stevick et al. 2003, Rasmussen et al. 2007). These migrations frequently follow nearshore migration corridors in the Southern Hemisphere (Dawbin 1966, Bryden 1985). Although behaviour associated with reproduction, e.g. male–male competition (Brown and Corkeron 1995) and singing (Clapham and Mattila 1990), is often observed during migration, feeding behaviour during transit is only seen occasionally, and very rarely in the Southern Hemisphere (Best et al. 1995, Stockin and Burgess 2005, Stamation et al. 2007). The bulk of feeding is thought to occur in the areas of high productivity at high latitudes where the whales spend their summers

(Clapham and Mead 1999) with the exception of the unique Arabian Sea population that is apparently resident year-round (Mikhalev 1997, Rosenbaum et al. 2009, Minton et al. in press).

The division of different populations of humpback whales in the Southern Hemisphere reflects their associated feeding and breeding areas and has been based on their previously assigned summer feeding regions or Antarctic Areas numbered I–VI (Donovan 1991) and the more recently designated Breeding Stocks labelled A–G (IWC 1998). Whales from Breeding Stock B (BSB) found off the west coast of Africa are thought to feed in Areas II (60° W–0°) and III (0°–70° E). In some Breeding Stocks there has been some evidence for substructuring of stocks based generally on ongoing mitochondrial DNA analyses (e.g. Rosenbaum et al. 2009). In the case of BSB, the stock has been separated

into B1 and B2 (IWC 2001) with the former located in the Gulf of Guinea (north of 18° S), whereas the humpback whales that migrate past the west coast of South Africa are presumably part of B2, found south of 18° S (see IWC [in press] for details of most recent BS subdivisions).

Historical catches from shore-based whaling stations in the Saldanha Bay region have hinted that the whales there conform more or less to a classic migration pattern with two distinct seasonal peaks of abundance, thought to correlate with the northward (July/August) and southward (October/November) migrations (Olsen 1914, Harmer 1931). On the other hand, Olsen (1914), based on his observations from 1912 to 1913, commented that the whaling season at Saldanha Bay was relatively long, lasting till mid-December. More recent and mounting evidence has added further support that this area does not function as a typical migration corridor, and that there may be other contributory factors that influence the timing and duration of visits of humpback whales to this region (Best et al. 1995, Findlay and Best 1995).

This study was conducted to examine trends in humpback whale relative abundance, occurrence, and movement across seasons in the Saldanha Bay region, based mainly on shore-based observations. As such, it represents the most extensive research effort to date on the species in this region, and, apart from a six-week long pilot study in 1993 (Best et al. 1995), the first since the *Discovery* investigations of the 1920s (Matthews 1938). Furthermore, data on group composition were obtained from the most comprehensive genetic collection available for the region, collected during boat intercepts of humpbacks between 1993 and 2008.

Material and methods

Description of study area and study period

The study was carried out from North Head, Saldanha Bay (33°02' S, 17°55' E), located on the west coast of South Africa, approximately 100 km north of Cape Town (Figure 1). This is some 30 km south of Cape Columbine, the westernmost headland in the Western Cape province of South Africa, and the site of an earlier pilot study (Best et al. 1995). The region has a Mediterranean-type climate (Kruger 2004) with an average rainfall of 298 mm per annum recorded mostly during winter (Zucchini et al. 2003, Zucchini and Nenadić 2006). The wind blows from a predominantly southerly direction in summer and westerly in winter. Saldanha Bay was the site of two modern whaling stations, Donkergat and Salamander, which operated sporadically between 1909 and 1967 (Best 1994, Findlay 2000).

The highly exposed coastline has an approximate north-westerly/south-easterly orientation (330°–150° True) and is characterised by a rocky shore, broken by a number of small bays with sandy or boulder beaches, and a few small nearshore islands and rocks. The tidal cycle is semi-diurnal with an average tidal range of about 1.2 m. The bathymetry of the area is shown in Figure 1.

In an attempt to gather data across all seasons, a shore-based watch was kept from North Head during two periods of fieldwork: the first for five months, from 24 July to 20 December 2001, and the second for nine months, from 6 May 2002 to 15 February 2003.

Observations of environmental and sighting conditions

A number of environmental observations were made at the lookout every hour in order to assess the sighting (searching and tracking) conditions. The following variables were recorded:

- (a) Surface windspeed (in knots) and direction (magnetic bearing): measured with a hand-held anemometer (analogue at first and digital from 25 August 2001 onward) and compass
- (b) Cloud cover: expressed as a fraction of eight (0/8 = no cloud, 8/8 = complete cover) over observation area only (i.e. over the sea)
- (c) Sea-state: judged according to the Beaufort Scale over the entire observation area
- (d) Glare: magnetic bearing and estimated extent of reflection of sun off the water, expressed as percentage of total search area affected
- (e) Swell: estimated by judging the height of the average swell rising against a rocky islet (Schooner Rock) with a known height of 9 m above sea level (ASL)
- (f) Visibility at the midline: the midline was set perpendicular to the coastline, at a bearing of 240° True from the lookout. The visibility at this line was the radial distance from the tower to the fix, calculated from the maximum vertical angle at which individual wavelets could clearly be distinguished through the theodolite eyepiece. This distance was assumed to be equivalent to the distance at which a whale could still be accurately tracked. This measurement was not made when the theodolite was being used for tracking whales
- (g) Sightability: a subjective index on a scale of 1–5 (1 = very poor, 5 = very good) that summarised how good overall conditions were for spotting whales, and taking into account factors (a)–(f) above

Search effort was classified into one of three categories, based on prevailing sighting and weather conditions:

- (a) Optimal watch: full search effort during suitable conditions over the entire search area, with at least one person searching with binoculars and another with naked eye
- (b) Suboptimal watch: equivalent to whale vessel surveys where masthead watch discontinued. Conditions were considered suboptimal at average windspeeds >20 knots for extended periods, Beaufort sea-states of 5 or more, or when more than one half of the search area was obscured by mist or clouds. In practice, this was when the sightability was estimated to be 2 or less (poor to very poor). During a suboptimal watch, searching would be carried out as described above, but sightings would only really be possible within the visible area or within a certain distance from shore. Both optimal and suboptimal efforts were considered in the calculation of sighting rates
- (c) Standby: this mode was entered into under the following conditions: when a suboptimal watch continued for longer than two hours with no visible signs of improvement; at the sudden onset of extreme weather conditions, e.g. continuous rain, thick mist, windspeeds >30 knots, swell height >7 m; or where such extreme conditions already existed at the start of a day. During standby, the team would remain at the lookout for some time to assess whether conditions were improving to acceptable levels

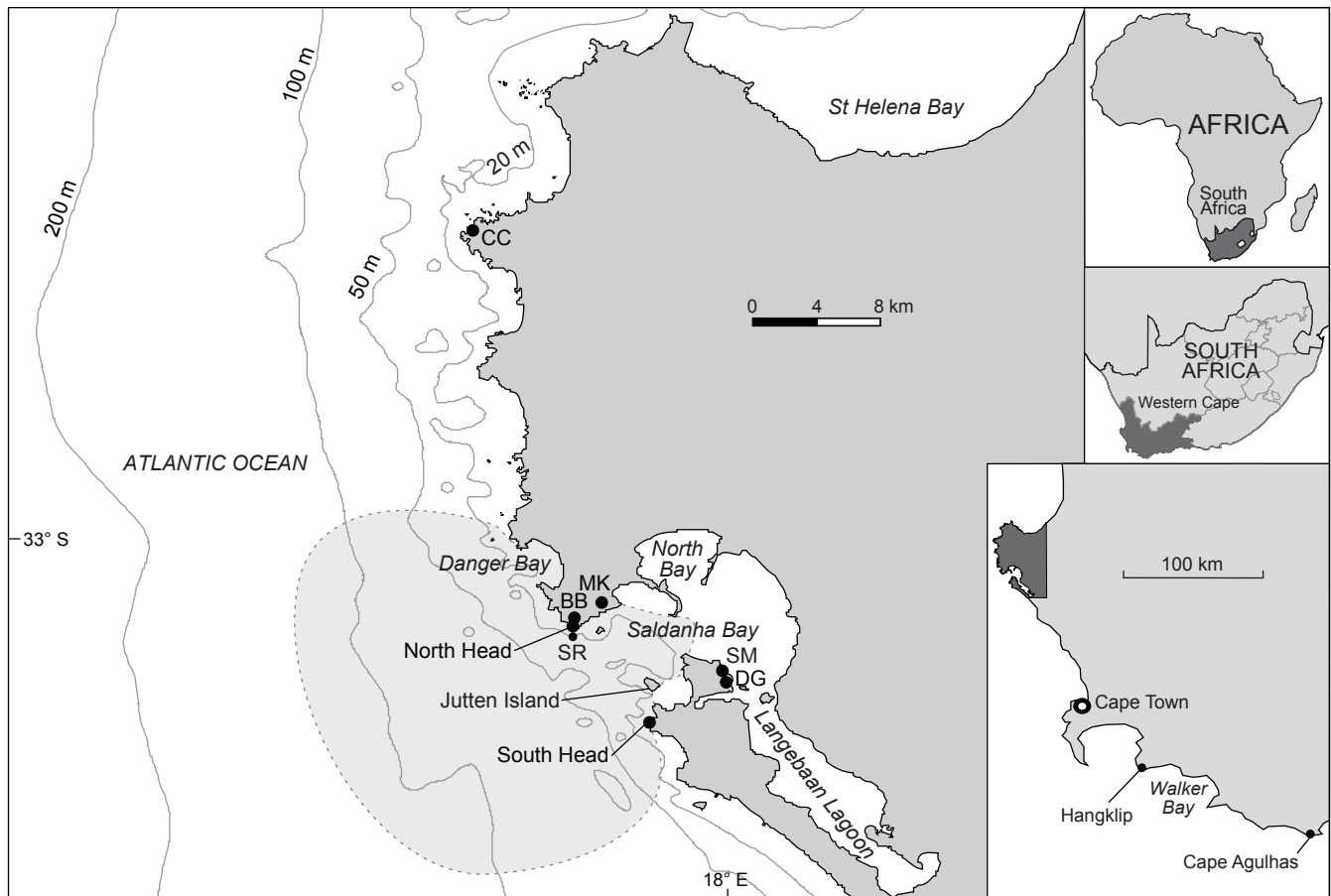


Figure 1: Location of the study area on the west coast of South Africa (BB = Baviaansberg, MK = Malgaskop, CC = Cape Columbine, DG = Donkergat, SM = Salamander, SR = Schooner Rock). Approximate extent of the search area is indicated by lightly shaded area

or not. No searching with binoculars was attempted and any whales sighted during this time were regarded as incidental sightings and excluded from trackline analysis

Climatic data

Further environmental measurements (daily minimum and maximum air temperatures [$^{\circ}\text{C}$], twice daily air pressure [kPa]) were obtained from the South African Weather Services as recorded at the nearest coastal weather station, Cape Columbine lighthouse ($32^{\circ}49'36''\text{S}$, $17^{\circ}57'30''\text{E}$, 68 m ASL). Hourly tidal measurements (m), as recorded by a tide meter situated in Saldanha Bay, were obtained from the South African (SA) Naval Hydrographer's Office (<http://www.sanho.co.za>). These were all required for calculating the correction for the effect of refraction during trackline analysis (see below).

Data collection: shore-based observations

The primary lookout (or tower) was at Baviaansberg, a hill 72.8 m ASL about 700 m (at 240°) from the shoreline on the North Head of Saldanha Bay. The lookout position was located within a military small-arms firing range, and on the rare occasion when the range was active, a secondary observation post at Malgaskop (111.8 m ASL), another hill set 2.65 km farther inland, was used (Figure 1).

The search area was defined as the area of open ocean to the south, west and north of the lookout, stretching as far as visibility allowed (Figure 1). Although Saldanha Bay, Danger Bay and visible parts of Langebaan Lagoon were also searched from time to time, they were not considered as part of the primary search area, but groups of whales that entered these bays were still tracked. Only small sections of the search area were obscured by land, e.g. behind Jutten Island or extremely close inshore.

Teams of 2–4 observers searched for whales for alternating two-hour shifts, starting approximately one hour after sunrise and ending an hour before sunset, weather permitting. Half of the team searched by the naked eye and the other half with $7\times$ or $8\times$ wide-angle binoculars, alternating roles every 10 minutes. At least one experienced observer (who could also operate the theodolite) was always included with novices. The entire search area was searched by all on watch, regardless of the number of observers.

When a whale or group of whales was spotted, the first cue (i.e. blow, body, splash, breach, slick) was recorded, the species identified if possible and the group size estimated. The most experienced observer would then track the group, using a Wild T1 manual theodolite (equipped with a $22\times$ telescope) that was mounted and levelled on a fixed base. The height of the focal plane at each lookout was calculated

through triangulation using a geographically referenced orthophoto (1:10 000) produced by the South African Chief Directorate: Surveys and Mapping, and two reference points of known height and position in the field of view: a trigonometric beacon situated at North Head Lighthouse, and the highest tip of Schooner Rock. The latter was also used as the fixed reference point of known position and bearing on which the horizontal azimuth was calibrated every day. The aim of the tracking was to obtain an accurate 'fix' on the group on at least three different surfacing events, where an event was defined as a number of short-spaced surfacings bracketed by a longer submergence. A fix consisted of the recorded behavioural cue (body, blow, breach, splash or slick), an estimate of group size, the time (to the nearest second) and the vertical and horizontal angles (to the nearest second) as measured by the theodolite. A series of such fixes was termed a 'track'. Searching would resume once a reliable fix was made on the group being tracked. Although groups were tracked for a minimum of three fixes, tracking could continue for several hours if no other groups were seen, or up to an interception by the boat (see below). Revised group size estimates were made as tracking progressed. The group size recorded at the first fix was considered the minimum estimate, whilst the number at the final fix (excluding any feedback from the boat if the group was intercepted) was taken as the best group size estimate available. In the event of a group splitting, the two resultant groups would be treated as new groups. During tracking, the search area was still scanned for new sightings by watchers not operating the theodolite, and although the search effort during this time could be considered somewhat reduced, it was assumed during analyses that search effort remained constant during both searching and tracking.

Spatial analyses

Tracks were inspected and for each surfacing event a single fix was selected based on the type of cue recorded at the fix, in the following order of priority: body, splash, and blow. In the few instances where no fixes on such cues were available, a fix on a breach or slick would be used. The horizontal and vertical angles and time recorded at the selected fixes were imported into and analysed using the software program Pythagoras (Gailey and Ortega-Ortiz 2000, 2002). The algorithm used is based on the work of Lerczak and Hobbs (1998), and takes into account tidal height (in m, measured at the nearest hour) and a refraction correction (G Gailey, Department of Wildlife and Fisheries Science, Texas A&M University, pers. comm., Leaper and Gordon 2001); the latter was based on the air temperature (°C) and pressure (kPa) measured daily at 14:00 at Cape Columbine. The refraction correction was applied to all fixes from both tracks and midline visibility measurements.

The coordinates (latitude and longitude) of each fix were calculated by Pythagoras, and these positions along with associated sighting data were imported into a global information system (GIS) (ESRI® ArcMap™ 9.2 and ESRI® Arcview™ 3.3). Accurate digital versions of the coastline, depth soundings and depth contours of the study area were obtained from the SA Naval Hydrographer's Office (as used for marine navigational chart SAN 117, scale 1:150 000). Due to its irregular nature, it was necessary to create an 'idealised'

version of the coastline before calculating the distance of a fix from the shore. This was done by joining the heads of bays within the search area, thus essentially 'removing' these bays to provide a more accurate estimate of the distance from this 'smoothed' coastline. In the few cases in which whale groups were inside these bays, the distance from the shoreline would be indicated as a negative measurement. At least one reliable fix was taken for 259 groups of humpback whales and the position of this first fix (in some cases the only reliable fix) was used to calculate the distance of the group to the nearest shoreline in a GIS, using a Transverse Mercator Projection with central meridian set at 17.9° E.

Seasonality

Conventional austral seasons, viz. autumn (March–May), winter (June–August), spring (September–November) and summer (December–February) were considered. The prefixes 'early', 'mid-', or 'late' were added to the season name for the first, middle and last month in a season respectively (e.g. mid-spring = October). Where observations were carried out in the same month in different years, these duplicate months were combined into a single seasonal sample, e.g. October 2001 and 2002 formed the mid-spring sample. Sample sizes of tracked whale groups varied considerably between months due to the timing of study periods, variability in sighting rates, and associated effort. Some months/seasons with very low sample sizes (<15) were therefore combined in order to increase the available sample size, resulting in seven seasonal groupings: late autumn to mid-winter = May 2002, June 2001/2002, July 2001/2002 ($n = 23$); late winter = August 2001/2002 ($n = 25$); early spring = September 2001/2002 ($n = 16$); mid-spring = October 2001/2002 ($n = 55$); late spring = November 2001/2002 ($n = 31$); early summer = December 2001/2002 ($n = 36$); mid- to late summer = January 2003, February 2003 ($n = 26$). The term 'season' is used herein to refer to these seasonal groupings, unless stated otherwise.

Trackline analysis

Three or more reliable fixes at different surfacings could be obtained for 212 groups and these were used in trackline analyses in Pythagoras (Gailey and Ortega-Ortiz 2002), and separated according to the seasons described above.

For each trackline the following parameters were calculated:

- (a) Actual swimming speed (= 'leg' speed): the unweighted mean of the swimming speeds calculated for each leg (the distance travelled between two consecutive fixes in a track) by dividing the distance covered between a pair of fixes, by the time it took to travel between them
- (b) Linearity: a form of migration index, calculated by dividing the net distance covered by a track (i.e. the direct measurement between the first and last fix) by its cumulative distance (the sum of all legs). Linearity values range between 0 and 1, with values close to 1 representing a straight track-line, whereas a value close to 0 represents a track with no constant direction
- (c) Net course: the true bearing in degrees of a track, calculated between the first and last fixes
- (d) Net speed: calculated by dividing the linear 'distance made good' between the first and last fixes of a track by the time it took to travel between them (i.e. total duration of track)

Data collection: boat-based observations

For the duration of the study, when weather and personnel availability permitted, whale groups were intercepted using a 6 m semi-rigid inflatable boat powered by twin outboard motors. The boat was directed from its mooring inside Saldanha Bay to whale groups by the land-based observers via VHF radio, as soon as they had made an accurate fix on the group. The boat was dispatched to any sighting that appeared to be within reasonable range of a small boat (about 15 km) and that, based on its direction and speed, would not disappear from the search area or field of visibility before the boat could reach it. Groups would generally be intercepted in the order of being spotted; in the case of simultaneous sightings, priority would be given to groups that were most likely to be lost (i.e. farther away or faster moving). If other groups were spotted by the boat crew during an intercept, these groups would be visited after data collection was completed.

Intercepts were used to confirm group size, take individual identification photographs and collect skin biopsies using a Paxarms biopsy rifle (Krützen et al. 2002). Skin samples were placed into individual cryogenic tubes filled with a NaCl-saturated, 20% dimethylsulfoxide (DMSO) solution. At the end of each day all skin samples were stored in a domestic freezer (-5°C) until they could be transferred to a -15°C freezer at the laboratory in Cape Town.

At periodic intervals while the boat was at sea during or between humpback sightings, a hydrophone would be deployed and an acoustic watch maintained for approximately 10 minutes at a time.

Group composition and behaviour

A group was considered to be one or more animals that displayed noticeable coordinated movement or behaviour and where individuals were no further than an estimated 100 m from each other (after Whitehead 1983, Corkeron et al. 1994). Cow–calf pairs were defined as two whales, one of which was less than half the length of the other.

All humpback whale groups from which genetic skin and photo-identification samples were collected during other boat-based cetacean studies of the Mammal Research Institute (MRI) in the same region (between 1993 and 2008) were included in the group composition analyses.

Total genomic DNA was extracted from the epidermal layer of biopsies using proteinase K digestion followed by a standard phenol/chloroform extraction method (Sambrook et al. 1989) or using DNAeasy tissue kit (Qiagen). Sex determination was carried out by polymerase chain reaction (PCR) amplification followed by *TaqI* digestion of the ZFX/ZFY region of the sex chromosomes (Palsbøll et al. 1992), or using multiplex PCR amplification of the ZFX/ZFY sex linked gene (Bérubé and Palsbøll 1996).

Behavioural observations made from the shore were limited to estimating group size and recording overall group behaviour (such as travelling, milling, surface activity, breaching, and possible feeding). Group size, behaviour and composition were also recorded during all boat intercepts. Any incidents of defecation were noted and a faecal sample was collected when possible.

Results

Sightings, search effort and sighting conditions

Shore-based observations were carried out on 102 (or 68%) of the available days between 24 July and 20 December 2001 and on 177 (61.9%) of the available days between 6 May 2002 and 15 February 2003 for a total of 1 802.18 hours. A total of 1 197 groups of baleen whales was sighted, the majority being southern right whales *Eubalaena australis* (669) followed by humpback whales (289), four mixed species (humpback and right whale) groups, and a single blue whale *Balaenoptera musculus*. Positive species identification was not possible for 234 other groups of large whales, although 15 of these were recorded as 'like-humpback', 16 as 'like-right whale' and 12 as Bryde's *B. brydei* or minke *B. bonaerensis* whales. Only groups that were positively identified as comprising solely humpback whales were considered in the analyses.

Effort during both field seasons was very discontinuous, with gaps of up to seven days with no watch, mainly due to poor sighting conditions. In order to create approximately equivalent subsamples to calculate mean sighting rates and measures of variance during a month or season, daily search effort for days 1–7, 8–14, 15–21 and 22 to month end were summed; this resulted in four subsamples in a full month. Sightings per unit effort (SPUE) was calculated by dividing the number of whale groups seen by the total number of hours watched (including both optimal and suboptimal effort) in a subsample, and transformed to groups per 10 hours of searching (Figure 2). The SPUE, as calculated here, is not an absolute measure of humpback whale abundance, because *inter alia* it includes all sightings within the search area, not only those that crossed the midline during the watch period, and does not exclude the possibility that a group may have been resighted on more than one occasion on or between days. Furthermore, the number of groups passing through the search area when there was no search effort, or at night, is unknown. A between-season comparison of the mean daily sightability index (calculated by dividing the sum of hourly sightability estimates by the number made on that day) showed a slight decrease in mean sightability from autumn/mid-winter (2.95 ± 0.102 SE) through to late summer (2.46 ± 0.14 SE), although this difference was not significant (ANOVA, $df = 6$, $F = 2.69$, $p = 0.0163$). Sightability therefore appeared to be constant enough across seasons to allow the use of SPUE as an index of relative abundance.

In general, effort levels were higher and more consistent during the first part (autumn and winter) of both study periods, but the SPUE was low with only slight peaks in late July/August. During both study periods, search effort became more variable from September onwards, mainly due to the frequent occurrence of unfavourable weather conditions that interrupted or prevented searching. Prominent peaks in SPUE occurred at the end of October in both years (peaks A and C in Figure 2), and both times these stretched into November. The highest overall SPUE was recorded during the fourth week of October 2002 (peak C) when at least one group was seen per hour. Other above-average peaks in SPUE occurred in December 2002 (peak B), and at the end of January/beginning February 2003 (peak D) despite low and very discontinuous search effort (Figure 2).

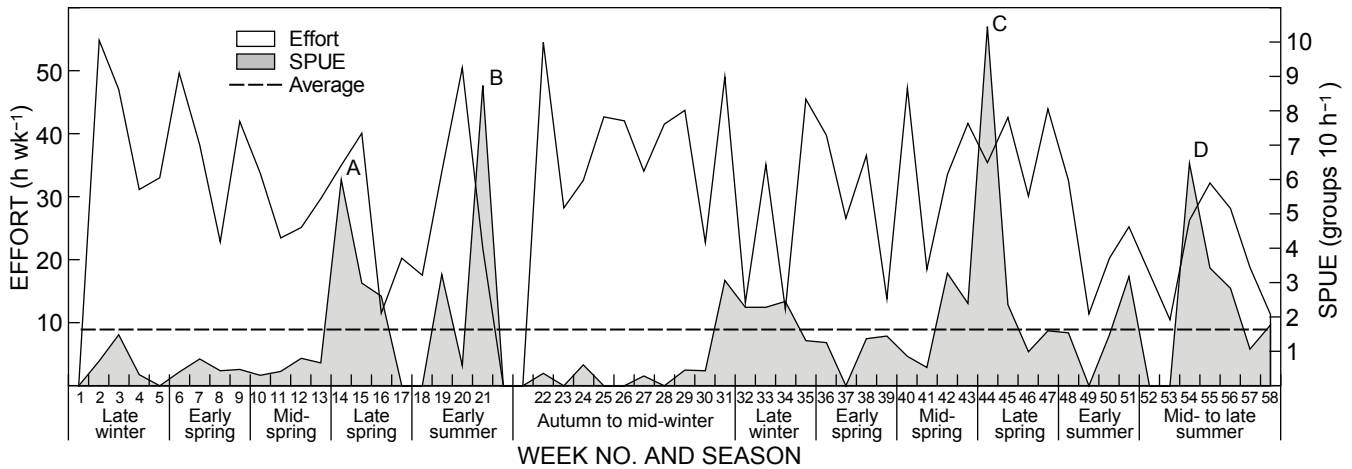


Figure 2: Sightings per unit effort (SPUE) of humpback whale groups and search effort per week for two field seasons 24 July–20 December 2001 (weeks 1–21) and 6 May 2002–15 Feb 2003 (weeks 22–58). Dashed line is average SPUE (1.63) over the entire study period. Peaks marked A–D are referred to in the text

Table 1: Summary of mean sightings per unit effort (SPUE, whale groups per 10 h of search effort), range and search effort by seasonal grouping based on monthly subsamples (four per month)

| Season | <i>n</i> | Mean SPUE (groups 10 h ⁻¹) ± SE | Range SPUE (min–max) | Total hours on watch | Days on watch | Daily hours on watch |
|---------------------------|----------|--|-------------------------|-------------------------|------------------|-------------------------|
| Late autumn to mid-winter | 12 | 0.69 ± 0.28 | 0–3.06 | 459.08 | 69 | 6.65 |
| Late winter | 8 | 1.19 ± 0.32 | 0–2.46 | 293.30 | 46 | 6.38 |
| Early spring | 8 | 0.71 ± 0.18 | 0–1.45 | 260.80 | 38 | 6.86 |
| Mid-spring | 8 | 3.07 ± 1.25 | 0.43–10.46 | 242.23 | 42 | 5.77 |
| Late spring | 8 | 1.51 ± 0.40 | 0–2.99 | 238.63 | 35 | 6.81 |
| Early summer | 7 | 2.46 ± 1.16 | 0–8.73 | 180.95 | 32 | 5.65 |
| Mid- to late summer | 6 | 2.59 ± 0.92 | 0–6.48 | 127.18 | 20 | 6.36 |
| All seasons | 57 | 1.63 ± 0.28 | 0–10.46 | 1 802.18 | 282 | 6.35 |

The mean SPUE by season showed an apparent increase in whale availability from mid-spring onwards, despite a strongly decreasing trend in total hours watched from winter to summer (Table 1). There were fewer suitable watching days from late spring onward. All seasons, with the exception of mid-spring, experienced weeks with no sightings (min SPUE = 0), and despite higher mean sighting rates in mid-spring and summer (Table 1), no significant difference was detected between seasons (Kruskal-Wallis statistic = 10.05229, $n = 57$, $p = 0.1225$). Given the small and variable sample sizes and the large difference in range between minima and maxima of the seasonal groupings (Table 1), the median may be a more appropriate measure of central tendency than the mean (Zar 1996), and the multisample median test showed a significant difference between seasons ($\chi^2 = 12.62920$, $df = 6$, $p = 0.0493$). When samples were combined into only two seasonal blocks, namely autumn/winter (mean SPUE = 0.96 ± 0.22 SE, $n = 20$) and spring/summer (2.03 ± 0.40 SE, $n = 37$), a *t*-test showed a significantly higher SPUE for the latter grouping ($p = 0.0477$, t -value = -2.0252).

Visibility at midline and spotting distance of whale groups

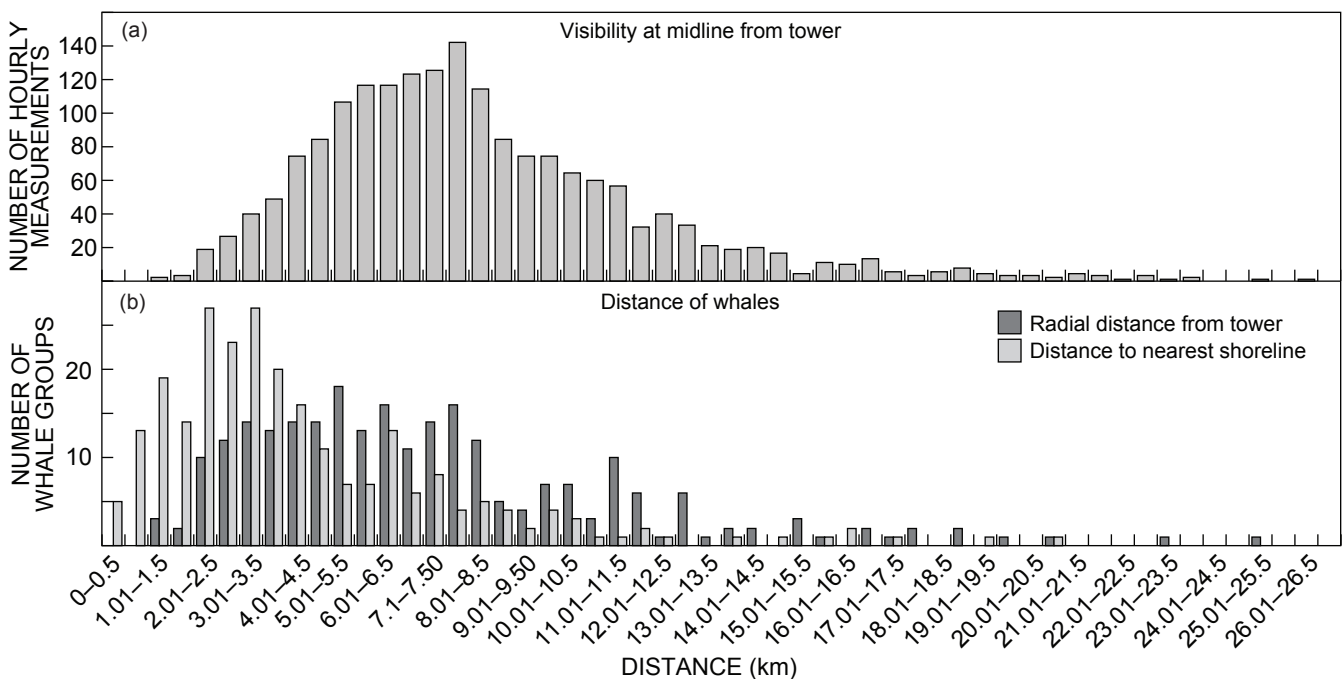
Overall, 1 834 hourly theodolite readings were taken at the midline as indicative of the theoretical maximum visibility

during periods of optimal and suboptimal watch. The average visibility from the tower over the entire period was 8.21 ± 0.08 km (SE) ranging from 1.29 to 26.46 km. The average distance from the tower (the 'sighting distance') for all 251 humpback groups on which a reliable fix was made (excluding the eight sighted and fixed inside Saldanha Bay) was 7.24 ± 0.26 SE and ranged between 1.24 and 25.11 km (Table 2). A comparison of the frequency distribution of all midline visibility measurements and radial sighting distances to all humpback groups (placed in 0.5 km bins) showed similarly shaped distributions, with the highest number of visibility observations recorded in the 7.5–8.0 km bin, although there was an extended peak from about 5.5–8.5 km (Figure 3). The distribution of whale sighting distance showed a much flatter peak with a wider range of 2–8.5 km, the 5–5.5 km bin containing most groups. Whale groups, in general, appeared to be seen at shorter distances from the tower than the recorded visibilities (Figure 3), with a fairly abrupt fall-off of sighting distances beyond 8.5 km, whereas visibility measurements showed a much steadier decrease from 8.5 km and farther. To determine whether the theoretical visibility limited our ability to spot and track whales, we compared the distance at which a group was sighted with the visibility taken at the nearest hour to the time of the fix at which the group distance was calculated (the 'prevailing

Table 2: Seasonal mean radial sighting distance from the tower to humpback groups on which a reliable theodolite fix was made ($n = 251$, shaded columns), and mean hourly visibility measured at the midline. Eight whale groups sighted within bays were excluded from this analysis

| Season | Mean \pm SE (km) | | n | | Minimum (km) | | Maximum (km) | |
|---------------------------|--------------------|-----------------|--------|------------|--------------|------------|--------------|------------|
| | Whales | Visibility | Whales | Visibility | Whales | Visibility | Whales | Visibility |
| Late autumn to mid-winter | 7.46 \pm 0.74 | 8.20 \pm 0.16 | 27 | 496 | 2.68 | 1.28 | 18.98 | 23.46 |
| Late winter | 8.61 \pm 0.74 | 9.22 \pm 0.21 | 25 | 293 | 2.16 | 2.02 | 16.62 | 26.46 |
| Early spring | 5.29 \pm 0.82 | 8.94 \pm 0.26 | 16 | 256 | 1.77 | 2.98 | 11.46 | 25.00 |
| *Mid-spring | 8.67 \pm 0.55 | 8.18 \pm 0.22 | 71 | 237 | 1.24 | 2.14 | 23.28 | 21.51 |
| Late spring | 6.40 \pm 0.60 | 8.18 \pm 0.22 | 32 | 233 | 1.34 | 2.50 | 13.89 | 23.80 |
| *Early summer | 6.18 \pm 0.56 | 7.20 \pm 0.27 | 49 | 185 | 2.21 | 1.50 | 25.11 | 19.63 |
| Mid- to late summer | 6.22 \pm 0.59 | 6.20 \pm 0.23 | 31 | 134 | 2.25 | 2.18 | 17.47 | 14.68 |
| All seasons | 7.24 \pm 0.26 | 8.21 \pm 0.08 | 251 | 1 834 | 1.24 | 1.29 | 25.11 | 26.46 |

* Seasons between which sighting distances from tower to whales were significantly different ($p < 0.05$, Tukey's HSD test for unequal sample sizes)

**Figure 3:** Frequency distributions of (a) all hourly midline visibility measurements ($n = 1\ 834$) and (b) all radial sighting distances from tower, and calculated distances to nearest shoreline, of whale groups fixed by theodolite ($n = 251$, excluding eight groups sighted within bays)

visibility'). These measurements were sorted into 1 km bins according to the prevailing visibility, and the mean distance from the tower for whale groups within each bin calculated. A plot of mean sighting distance against prevailing visibility showed that up to about 7 km from the tower, sighting distances were on average higher than the visibility, but beyond this, whale groups were seen at distances well below the prevailing visibility (Figure 4). However, the mean distances of whale groups to the nearest shoreline (i.e. perpendicular distance) at prevailing visibility were considerably less compared with prevailing midline visibility (Figure 4).

Seasonal variations of visibility at the midline were tested and showed a highly significant difference (ANOVA, $df = 6$, $F = 14.4918$, $p < 3.24 \times 10^{-16}$) with significant differences in mean visibility between a number of seasons shown by Tukey's HSD test for unequal n (Table 3). The best visibility was measured in late winter with a clear decreasing trend in

visibility from late spring to late summer; the poorest mean visibility being recorded in mid-late summer (Table 2).

Distance distribution of whales from the shore

Whale groups were seen beyond 15 km from the shore on only six occasions, once in both late winter and early summer, and four times in mid-spring. For all seasons, except late winter and mid-spring, groups were closer to shore than the overall mean (Table 4). Between-season ANOVA showed a highly significant difference of distance of groups from shore ($df = 6$, $F = 4.41$, $p < 0.0003$) and Tukey's HSD test for unequal sizes indicated that this difference was between mid-spring (highest) and early summer (lowest) ($p < 0.004$). A quarter of the number of whale sightings was within 2 km from the shore, including the eight sightings within Saldanha Bay (negative distances). More than half the groups were seen in the range 2–6 km and the remaining

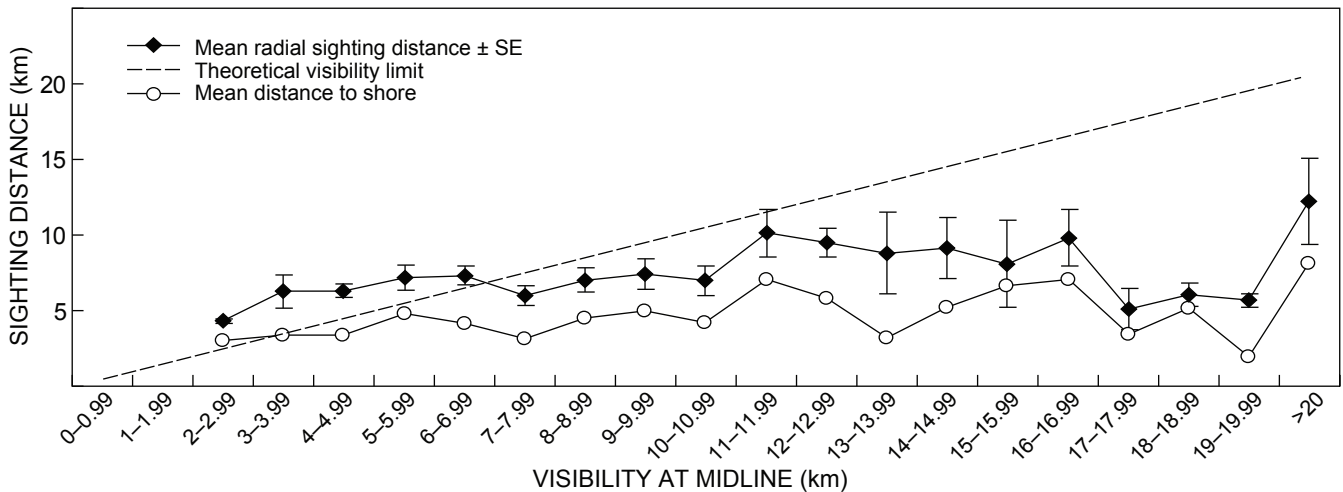


Figure 4: Mean radial sighting distances (km \pm SE) from tower, and calculated distances to nearest shoreline, of whale groups at prevailing visibility at the midline (per 1 km bin) as measured by theodolite. Dotted line indicates theoretical visibility limit

Table 3: Between-season comparison of visibility measurements at midline using Tukey's HSD test for unequal sample sizes (shading indicates $p < 0.05$)

| Season | Autumn/ mid-winter | Late winter | Early spring | Mid-spring | Late spring | Early summer | Mid- to late summer |
|---------------------|-----------------------|----------------|-----------------|------------|----------------|-----------------|------------------------|
| Autumn/mid-winter | | 0.010203 | 0.592470 | 0.999879 | 1.000000 | 0.091302 | 0.000111 |
| Late winter | | | 0.752770 | 0.010471 | 0.025587 | 0.000026 | 0.000026 |
| Early spring | | | | 0.409064 | 0.581084 | 0.000538 | 0.000026 |
| Mid-spring | | | | | 0.999984 | 0.186617 | 0.000309 |
| Late spring | | | | | | 0.113501 | 0.000147 |
| Early summer | | | | | | | 0.259254 |
| Mid- to late summer | | | | | | | |

Table 4: Seasonal mean distance from position of first reliable theodolite fix on whale groups to nearest the coastline and minimum and maximum distances of whales from shore

| Season | Mean \pm SE (km) | <i>n</i> | Minimum | Maximum |
|---------------------------|--------------------|----------|---------|---------|
| Late autumn to mid-winter | 3.69 \pm 0.35 | 27 | 0.48 | 9.34 |
| Late winter | 5.58 \pm 0.75 | 25 | 1.34 | 15.65 |
| Early spring | 3.35 \pm 0.58 | 16 | 0.58 | 9.93 |
| *Mid-spring | 5.81 \pm 0.48 | 71 | 0.37 | 19.01 |
| Late spring | 3.74 \pm 0.43 | 32 | 0.37 | 7.73 |
| *Early summer | 3.36 \pm 0.45 | 49 | 0.04 | 20.75 |
| Mid- to late summer | 3.86 \pm 0.56 | 31 | 0.58 | 14.55 |
| All seasons | 4.42 \pm 0.21 | 251 | 0.37 | 20.75 |

* Seasons when groups were seen at significantly different mean distance from shore ($p < 0.05$, Tukey's HSD test for unequal sample sizes)

25% farther than 6 km and up to a maximum of 20.75 km. There was a rapid fall-off in number of sightings from 10 km onward with only about 6% of groups recorded in this zone (Figure 3b). When groups were sorted into four distance zones, viz. inside bays to 5 km, 5–10 km, 10–15 km, and farther than 15 km, a seasonal pattern in distance offshore became evident (Figure 5). The majority of groups were seen within 5 km from the shore in all seasons, and the hypothesis that the proportion of groups within and beyond 5 km did not differ significantly (χ^2 test) was rejected for all except late winter, mid- and late spring (Figure 5).

Group size and composition

The size of 289 groups observed from shore ranged between one and six, with the notable exception of the maximum group size recorded of 15 individuals, and another of 10. These apparent outliers were probably loose association of several smaller groups rather than single groups. The most frequent group size ($n = 122$) was two animals (10 of which were identified as cow-calf pairs by the boat crew) followed by singletons ($n = 83$). The mean group size based on these best estimates was 2.2 ± 0.08 SE ($n = 289$) and excluding the outliers mentioned above, 2.12 ± 0.06

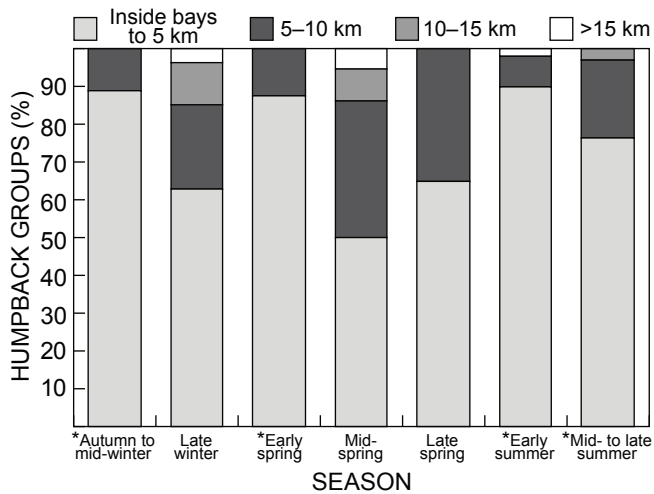


Figure 5: Seasonal breakdown of distance from shore of humpback groups ($n = 259$). Seasons where numbers of groups within and beyond 5 km zones differ significantly (χ^2 , $p < 0.05$) are indicated by an asterisk

($n = 287$). The largest mean group sizes were recorded in mid-spring (2.44 ± 0.12) and early summer (2.5 ± 0.19) and the smallest in late winter (1.69 ± 0.15) and late spring (1.75 ± 0.11), with an overall significant difference between seasons (Kruskal-Wallis $H = 25.5825$, $df = 6$, $p = 0.0003$). Dunn's multiple comparison *post hoc* test showed late winter (August) to have a significantly smaller mean group size than both mid-spring ($z = 3.540$, $p < 0.0084$) and early summer ($z = 3.1402$, $p < 0.036$), whereas the mean of mid-spring was also significantly higher than late spring ($z = 3.1903$, $p < 0.03$) (Figure 6).

Group sizes recorded during the 116 boat intercepts ranged from one to seven, except for one grouping recorded as 20, which in reality was a dynamic aggregation of several smaller groups. Excluding this grouping, the mean group size encountered was 1.97 ± 0.084 SE ($n = 115$). Group size was recorded for the same group by both shore observations and boat intercepts 85 times; of these 61 were identical, in six cases boat estimates were higher than corresponding land estimates and in 18 cases land estimates were higher than boat-based ones. Although the mean size of these groups estimated from land (2.09 ± 0.12) was larger than that made during boat intercepts (1.85 ± 0.086), the difference was not significant (*t*-test, independent variables, two-sided, $df = 168$, *t*-value = -1.7145 , $p = 0.08843$).

Genetic analysis

Sex determination was attempted for 216 skin biopsies collected between 1993 and 2008. The majority of samples (104) were taken at Saldanha Bay during the principal study, followed by 92 taken during a St Helena Bay study on southern right whale feeding (2003–2006). The balance was made up of six samples collected at Cape Columbine in 1993, a single sample from Walker Bay (1999) and 13 taken during boat transects for Heaviside's dolphins *Cephalorhynchus heavisidii* along the coast (1999–2000, 2008). Overall, 119 females and 91 males were identified but six samples did not yield results. Three duplicate samples of

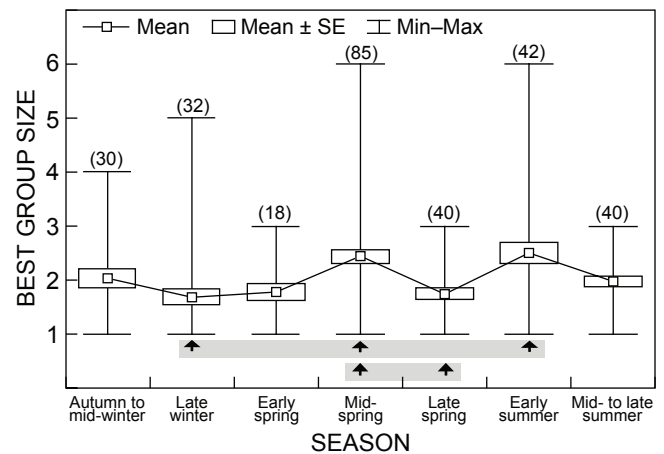


Figure 6: Seasonal mean (range = whiskers and SE = boxes) of best estimates for group size (sample sizes in parentheses) as observed from land, excluding two outlier groups ($n = 287$). Shaded rectangles below plot summarise significant results from multiple comparison *post hoc* test with arrows indicating significantly different seasons

the same individual on the same day and/or from the same sighting were identified from genotyped individuals (using 10 microsatellite loci) (Pomilla 2005, Carvalho et al. 2009) and these were removed, leaving a total of 207 sexed samples. The overall female (56.5%) to male (43.5%) ratio, including cow-calf pairs, did not vary significantly from parity ($n = 207$, $df = 1$, $\chi^2 = 3.521739$, $p > 0.06057$). A total of 32 groups was identified as cow-calf pairs and, from these, 20 cows and 12 calves were biopsied: the calves were comprised of nine males and three females. A possible bias may exist towards the sampling of cow-calf pairs due to their generally slower movement (Noad and Cato 2007) and more time spent at the surface. Cows and calves that were sampled (32 out of 64 animals) were therefore removed from the overall sample to test this, but the remaining female (53.7%) to male (46.3%) ratio still did not deviate significantly from an 1:1 ratio ($n = 175$, $df = 1$, $\chi^2 = 0.965714$, $p > 0.32575$). Following this, the 20 cows were retained in the sample, but the 12 calves were excluded. The reasons for this were that the presence of calves was presumably dependent on their mothers, and that whaling data on gender included only mature whales. This resulted in a significant female bias in the overall sex ratio (1.407 females:1 male, $n = 195$, $\chi^2 = 5.584615$, $p < 0.01812$).

Other possible biases in selection of intercepted groups

Cows with calves have also been shown to prefer areas closer to shore in a breeding area (Ersts and Rosenbaum 2003), perhaps introducing another source of bias, although this has not been illustrated during migration. To test this, we compared the mean distance from shore of all cow-calf pairs to other groups intercepted by boat between 1999 and 2006 at Saldanha Bay/St Helena Bay, during months when cow-calf pairs were sighted (Figure 7). Distance (calculated using a GIS) was measured between the GPS position of the boat at the time of the intercept, and the nearest coastline. The mean distance to shore of cow-calf

pairs ($n = 30$; 3.49 ± 0.713 km SE) did not differ significantly from non-cow-calf groups ($n = 137$; 4.98 ± 0.359 km) (t -test, independent variables, two-sided, $df = 165$, t -value = -1.77487 , $p = 0.07776$).

To test whether group size affected the likelihood of being intercepted, thus introducing a bias through the selection of larger groups, the mean of the best estimates of group size made from land was compared for whale groups that were intercepted ($n = 85$; 2.094 ± 0.115) and not intercepted ($n = 104$; 2.23 ± 0.101). There was no significant difference between the means of these groupings (t -test, independent variables, two-sided, $df = 287$, t -value = 0.7877 , $p = 0.4315$).

In terms of a selection bias of humpback groups intercepted during the other studies, these were all incidental sightings (excepting the six samples from Cape Columbine) during effort directed at other target species, and thus we have to assume that these encounters were random.

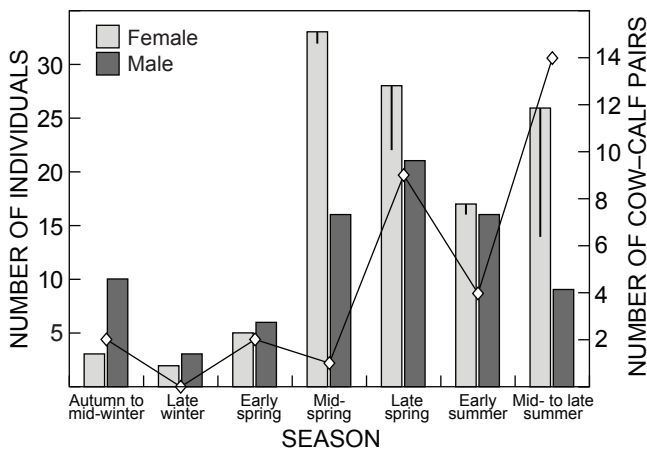


Figure 7: Numbers of male and female whales (including 20 cows, as indicated by the solid lines within the bars) per season as determined genetically ($n = 195$). Calves ($n = 12$) were excluded, but total number of cow-calf pairs seen per season is indicated by line plot

A seasonal plot of the numbers of females and males (including cows with calves but excluding the calves themselves, Figure 7) suggests that during autumn, winter and early spring, slightly more males than females were sampled, bearing in mind that sample sizes were very small. For the rest of spring and summer, more females were available, and for mid-spring and mid- to late summer, this bias was significant (Table 5). The number of cow-calf pairs seen during boat intercepts increased from late spring onwards with most seen from December to February (Figure 7).

Genetic samples of 76 complete groups of whales (132 individuals) were collected and the overall sex ratio (excluding eight calves but including cows) did not deviate significantly from parity (53 males, 71 females; $\chi^2 = 2.612903$, $p < 0.106$). Identical numbers (13) of males and females were recorded for lone animals. Most pairs (excluding cows with calves) consisted of a male and female (18) followed by female-only pairs (14), and then male only (6). The eight cow-calf pairs included six male and two female calves, whereas two of the pairs were accompanied by single male escorts. Apart from these cow-calf pairs with escorts, groups of three individuals were completely sampled only another four times; one all-male, two with more males and one with more females. A seasonal breakdown of the gender composition of groups that were completely sampled (Figure 8) shows a decrease in the occurrence of single males after early spring, with none recorded in mid-spring. Female-biased groups were found in all seasons except late winter (however, note the low sample size). Male-female pairs and cow-calf pairs (including those with escorts) were only seen from mid-spring onwards. No single females were recorded after late spring. Mid-spring was the only season where there was a significant (female) biased sex ratio of 2.88:1 (Figure 8, $\chi^2 = 7.258$, $p = 0.00706$).

Swimming speed

Actual swimming speed (= leg speed) ranged from 0.55 to 10.68 km h⁻¹ (Table 6), with an overall mean of

Table 5: Seasonal sex ratios in humpback whales biopsied in the region of Saldanha Bay, South Africa, 1993–2008 (shading indicates $p < 0.05$)

| Season (month[s]) | Female (%) | Male (%) | n | χ^2 | p |
|--|------------|----------|-----|----------|---------|
| <i>Including cows and calves (n = 207)</i> | | | | | |
| All seasons combined | 56.52 | 43.48 | 207 | 3.522 | 0.06057 |
| Autumn/mid-winter (March–July) | 21.43 | 78.57 | 14 | 4.570 | 0.03251 |
| Late winter (August) | 40.00 | 60.00 | 5 | 0.200 | 0.65472 |
| Early spring (September) | 45.45 | 54.55 | 11 | 0.091 | 0.76303 |
| Mid-spring (October) | 66.00 | 34.00 | 50 | 5.120 | 0.02365 |
| Late spring (November) | 57.69 | 42.31 | 52 | 1.231 | 0.26726 |
| Early summer (December) | 51.43 | 48.57 | 35 | 0.029 | 0.86577 |
| Mid- to late summer (January, February) | 65.00 | 35.00 | 40 | 3.600 | 0.05778 |
| <i>Excluding calves (n = 195)</i> | | | | | |
| All seasons combined | 58.46 | 41.54 | 195 | 5.585 | 0.01812 |
| Autumn/mid-winter (March–July) | 23.08 | 76.92 | 13 | 3.769 | 0.05221 |
| Late winter (August) | 40.00 | 60.00 | 5 | 0.200 | 0.65472 |
| Early spring (September) | 45.45 | 54.55 | 11 | 0.091 | 0.76303 |
| Mid-spring (October) | 67.35 | 32.65 | 49 | 5.898 | 0.01516 |
| Late spring (November) | 57.14 | 42.86 | 49 | 1.000 | 0.31731 |
| Early summer (December) | 51.52 | 48.48 | 33 | 0.030 | 0.86181 |
| Mid- to late summer (January, February) | 74.29 | 25.71 | 35 | 8.257 | 0.00406 |

4.6 ± 0.15 km h⁻¹ SE. An examination of leg speed by season revealed a strong decrease in mean swimming speed from autumn through to late summer, and Kruskal-Wallis analysis of variance showed a highly significant difference between seasons (Kruskal-Wallis statistic = 59.21, *p* < 0.0001). Dunn's multiple comparison between the seasons showed significantly higher swimming speeds in autumn to winter compared with mid-spring to late summer

(*p* < 0.05) (Table 6). Overall, net speed averaged 3.91 km h⁻¹ and ranged from 0.091 to 10.47 km h⁻¹ (Table 6). Seasonal mean net speed was always lower than actual swimming speed, with the smallest difference between these parameters observed during autumn to late winter, whereas the difference increased from early spring onwards, and was the greatest in mid- to late summer (Table 6).

Direction and linearity of movement

Net course and linearity of movement were calculated for all groups with three or more fixes made at different surfacing events (*n* = 212). A frequency distribution plot of net course (Figure 9) showed a bimodal distribution, with the larger mode at 100–200° and a second smaller peak at 280–360°. Taking into account that the orientation of the coastline is at approximately 330–150°, it may be assumed that the first mode (100–200°) represents predominantly southbound and the second (280–360°) northbound animals. For linearity, the highest number of groups observed (Figure 10) had an index in the 0.7–1.0 range (where 1 = a straight line) with a definite peak between 0.9 and 1.0. Although there was some variation between 0 and 0.7 levels, the number of observations across this range remained relatively constant and much lower than the peak. It was therefore assumed that a linearity index of 0.9 and greater indicated migration-like movement (swimming in a more-or-less straight line) whereas indices of <0.9 represented non-migrating groups.

A plot of cumulative frequency of direction of movement by season, with three directional groupings based on the two modes (north and south), and another containing all groups heading in other directions, shows predominantly southwards movement in autumn to late winter (Figure 11). The null hypothesis that mean angles of movement by groups were distributed uniformly each season (i.e. no directionality) was tested using the Rayleigh's test for circular uniformity (Zar 1996). This was rejected (*p* < 0.05) for autumn/mid-winter (*n* = 23, average degrees = 155.14,

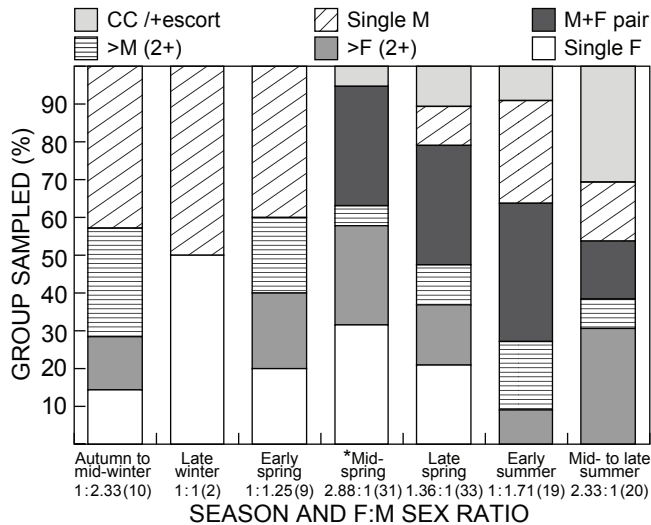


Figure 8: Seasonal composition of humpback whale groups that were completely sampled genetically, 2000–2006. Female:male sex ratio and total number of individuals (in parentheses) are indicated below each season. Asterisk = significant female bias ($\chi^2 = 7.258$, *p* < 0.05). Key to legend: CC = cow-calf pairs, including two with (male) escorts; M + F pair = male and female; >F = all-female duos and groups of three or more with female bias; >M = all-male duos and groups of three or more with male bias; single male (M) and single female (F)

Table 6: Mean actual swimming speed (leg speeds) and net speed by season, with Dunn's multiple comparison post-test on actual swimming speeds (shading indicates *p* < 0.05)

| Season | Actual swimming speed and net speed (in parentheses) (km h ⁻¹) | | | | Dunn's multiple comparison of actual swimming speeds between seasons: z-value (<i>p</i> -value) | | |
|---------------------|--|------------------------------|-----------------|------------------|--|---------------------------------|---------------------------------|
| | <i>n</i> | Mean ± SE | Min. | Max. | Autumn/mid-winter | Late winter | Early spring |
| Autumn/mid-winter | 23 | 6.07 ± 0.35 (5.80 ± 0.42) | 1.68 (0.94) | 8.47 (8.55) | – | ns | ns |
| Late winter | 25 | 6.53 ± 0.29 (6.04 ± 0.36) | 3.46 (2.09) | 9.32 (9.29) | ns | – | ns |
| Early spring | 16 | 5.77 ± 0.61 (5.18 ± 0.71) | 1.89 (0.64) | 9.62 (10.47) | ns | ns | – |
| Mid-spring | 55 | 4.14 ± 0.33 (3.30 ± 0.34) | 0.55 (0.16) | 10.68 (9.18) | 3.19 (0.0031) | 4.71 (0.53 × 10 ⁻⁴) | ns |
| Late spring | 31 | 4.23 ± 0.37 (3.60 ± 0.40) | 0.91 (0.091) | 8.62 (8.77) | 3.13 (0.0367) | 3.92 (0.0018) | ns |
| Early summer | 36 | 4.28 ± 0.31 (3.31 ± 0.33) | 1.04 (0.41) | 8.37 (7.85) | 3.09 (0.0417) | 3.91 (0.0019) | ns |
| Mid- to late summer | 26 | 2.67 ± 0.20 (1.90 ± 0.21) | 1.01 (0.13) | 5.28 (4.10) | 5.5 (0.1 × 10 ⁻⁵) | 6.31 (0.6 × 10 ⁻⁶) | 4.24 (4.78 × 10 ⁻⁴) |
| All seasons | 212 | 4.61 ± 0.15 (3.91 ± 0.17) | 0.55 (0.091) | 10.68 (10.47) | | | |

ns = not significant

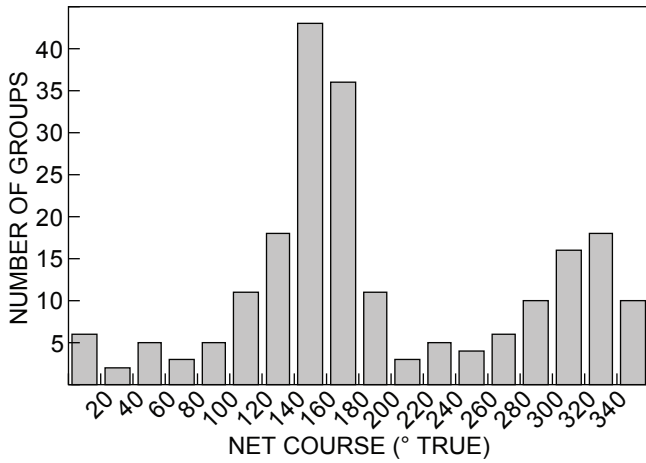


Figure 9: Frequency distribution of net course of 212 humpback whale groups tracked from North Head, Saldanha Bay

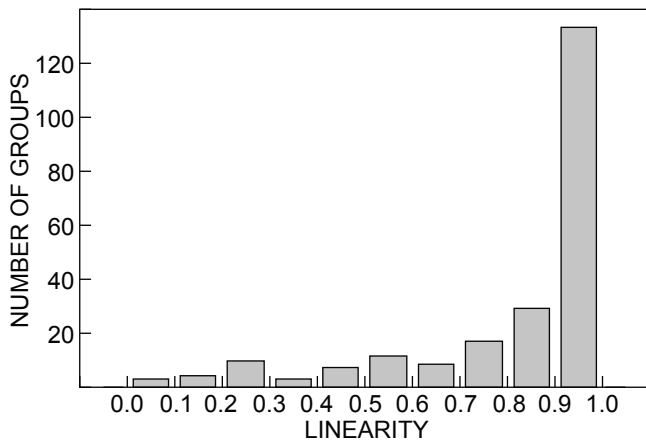


Figure 10: Frequency distribution of linearity of movement of 212 humpback whale groups tracked from North Head, Saldanha Bay

Rayleigh's $R = 19.78$, Rayleigh's $z = 17.012$) and late winter ($n = 25$, average degrees = 158.52 , $R = 16.61$, $z = 11.03$) as well as late spring ($n = 31$, average degrees = 148.51 , $R = 14.77$, $z = 7.04$). Thus, in these seasons, distribution of the mean angle was not distributed uniformly and there was definite directionality in a predominantly southerly direction (Figure 11). In the other seasons there were more or less equal numbers of groups moving both north and south, although there were ever-increasing numbers of groups moving in other directions from early spring onwards.

Non-directionality reached its peak in mid- to late summer, when the number of groups moving north, south or in other directions each made up roughly one-third of the total groups tracked (Figure 11). The incidence of 'migration-like' movement predominated from autumn to early spring after which there were more or less equal numbers of 'migrators' and 'non-migrators' for the remaining spring months (October/November), and a marked decline in groups moving in straight lines (Figure 11). Throughout summer, non-migrating groups predominated.

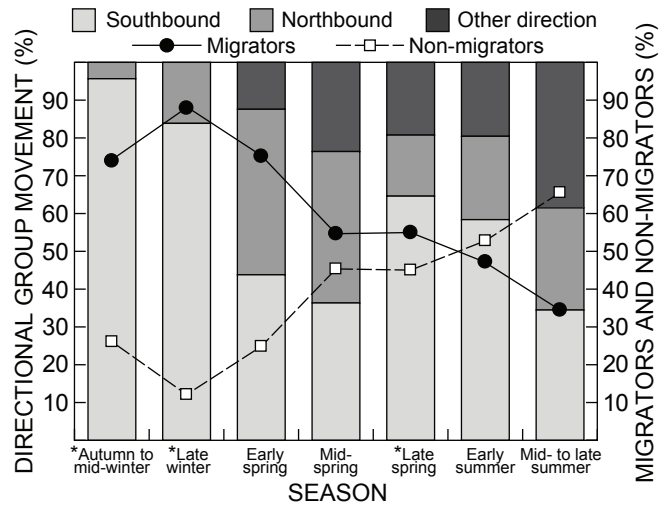


Figure 11: Directionality (net course) and linearity of movement of humpback whales groups ($n = 212$) by season. Bars show cumulative frequency of occurrence of groups that were southbound ($100\text{--}200^\circ$), northbound ($280\text{--}360^\circ$) or heading in other directions, based on net course ($^\circ$ True). Asterisk indicates seasons with significant ($p < 0.05$) directionality as determined by Rayleigh's test. Line plots show percentage of migrating (linearity ≥ 0.9) or non-migrating (linearity < 0.9) groups seen

Relationships between trackline parameters and other variables

The relationships between the various trackline parameters (linearity, leg speed and direction) and other variables (season, distance from shore and group size) were not always clear. There was no relationship between group size and leg speed ($r^2 = 0.0059$, $r = -0.0768$, $p = 0.2655$), nor between distance from the shore and linearity ($r^2 = 0.006$, $r = 0.078$, $p = 0.258$); but there was a significant and positive correlation between leg speed and distance offshore (Figure 12a, $r^2 = 0.0433$, $r = 0.2081$, $p = 0.0023$) with groups farther offshore travelling at higher speeds. A separation of groups into nearshore (within 5 km from land and inside bays, $n = 156$) and offshore (beyond 5 km, $n = 56$) showed the latter to move significantly faster, at a mean leg speed of 4.99 km h^{-1} compared to the nearshore mean of 4.47 km h^{-1} (t -test, t -value = -1.4928 , $df = 210$, $p = 0.04775$). Leg speed also showed a significant and positive correlation with linearity (Figure 12b; $r^2 = 0.2103$, $r = 0.4586$, $p < 0.00005$), but there was no significant correlation between speed and net course ($r^2 = 0.0076$; $r = 0.0874$, $p = 0.2049$). A significant and negative correlation between linearity and group size suggests that larger groups tended to display non-migratory movement (Figure 12c; $r^2 = 0.0228$, $r = -0.1511$, $p = 0.0278$).

Seasonal patterns in movement

Whereas the various trackline parameters considered independently showed seasonal differences between winter and summer, a movement pattern was more difficult to define for combined parameters. To test for seasonal patterns in movement, a *post hoc* multivariate approach was attempted using the software PRIMER v6 (Clarke

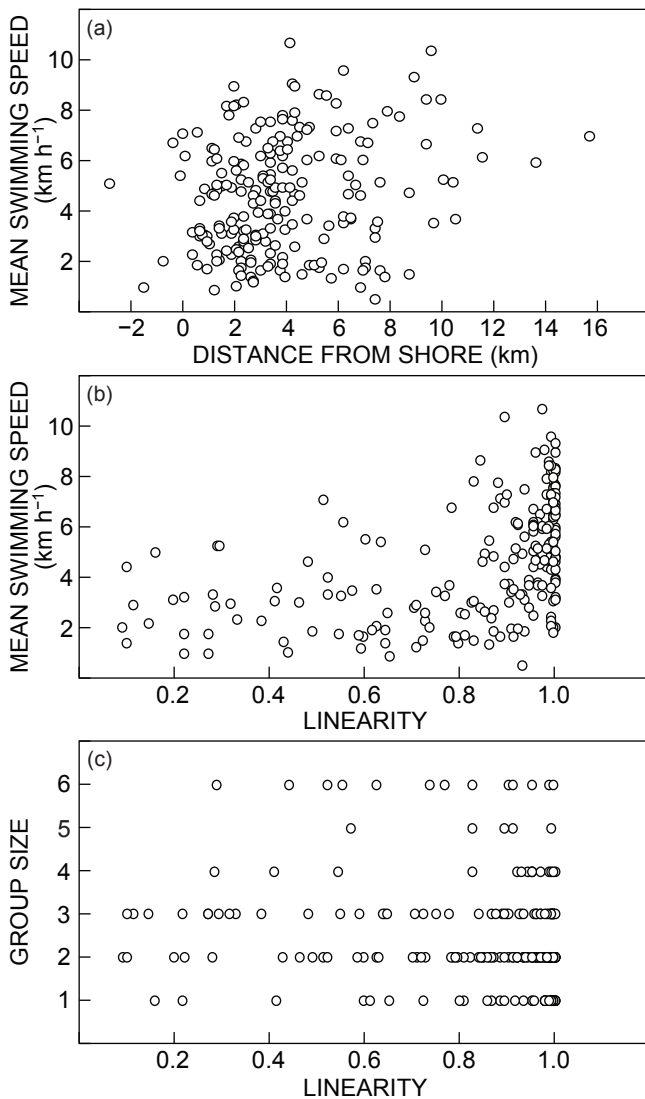


Figure 12: Relationship between mean swimming speed and (a) distance of whale groups from the shoreline, (b) linearity of movement of humpback groups and (c) relationship between size of humpback groups and linearity of movement

1993, Clarke and Warwick 2001, Clarke and Gorley 2006). Each whale group was considered a 'sample' with values for the three parameters: leg speed, course and linearity. Parameter values were normalised (the mean subtracted from each value and divided by the standard deviation) and the similarity between every pair of samples calculated based on Euclidian distance. In a non-metric multi-dimensional scaling (MDS) ordination of whale groups (Figure 13a; stress-value = 0.1 indicating a good two-dimensional representation), with season selected as the identifying feature (or 'factor', see Clarke and Gorley 2006), the first marked feature is the major grouping of samples into the top and bottom halves of the plot. The second major feature is the clustering of most autumn/winter samples into the bottom right of the lower group. Mid-spring samples are the most dispersed, and more or less equally distributed between the top and bottom clusters. While the

summer samples are also found in both clusters, they are located more to the left of the plot, particularly the mid- to late summer samples (Figure 13a, all to the left of line A). A one-way analysis of similarities (ANOSIM) was applied to samples according to the seven seasonal groupings. This is a non-parametric permutation procedure applied to a resemblance (= similarity) matrix based on the rank similarity of each sample. It calculates a global R -value and overall p -value, as well as a measure of significance of similarity for pairwise tests between sample groups. The ANOSIM showed an overall significant difference (global $R = 0.055$, $p = 0.005$) between seasonal groupings. The pairwise comparison between seasons (Table 7) showed no difference between groups from the two autumn/winter seasons. Late winter and early spring stood out as the least similar to any other seasons, differing significantly from all (including each other) except mid-spring. The latter (October) was the only season that did not differ from any other season. The similarity between late spring and early summer, and the significant difference between both these seasons with mid- to late summer, is also noteworthy. To establish which of the three parameters were responsible for the groupings, a principal component analysis (PCA) was carried out on the data, and the two factors responsible for most of the patterning (in the MDS ordination) shown as an XY-scatterplot with the parameters overlaid (Figure 13b). From this, we can conclude that differences in course were mostly responsible for the separation of the top (northbound) and bottom (southbound) clusters, accounting for 33.1% of the variation, whereas the strong grouping of winter samples was due to speed and linearity (49% of variation).

Migrators vs non-migrators

In order to show up possible differences in the movement patterns of migrators and non-migrators according to their linearity of movement, the groups were plotted in an MDS ordination (as described above), but this time including the parameters leg speed, course and distance from shore, and using linearity as distinguishing factor (migrators ≥ 0.9 and non-migrators < 0.9). The plot (Figure 14a; stress-value = 0.15 showing a fairly reliable two-dimensional representation, Clarke 1993) shows some degree of separation, firstly between the two groupings (group A = non-migrators, group B = migrators), and secondly within migrators (groups B1 and B2). The PCA (Figure 14b) showed distance from shore and leg speed to be responsible for the separation between migrators and non-migrators, whereas the two migratory subgroups separated out mainly due to differences in course, B1 containing northbound and B2 southbound groups (Figure 14a). Migrators and non-migrators were found to be significantly different when an ANOSIM was applied (global $R = 0.133$, $p = 0.001$).

Feeding behaviour

From land, eight groups were observed to display apparent feeding behaviour, which included milling about (slow movement of indeterminate direction) and faster erratic movement with frequent directional changes. Nine groups intercepted by boat also appeared to be engaged in feeding, although actual feeding behaviour (lunges at surface) was directly observed during only five

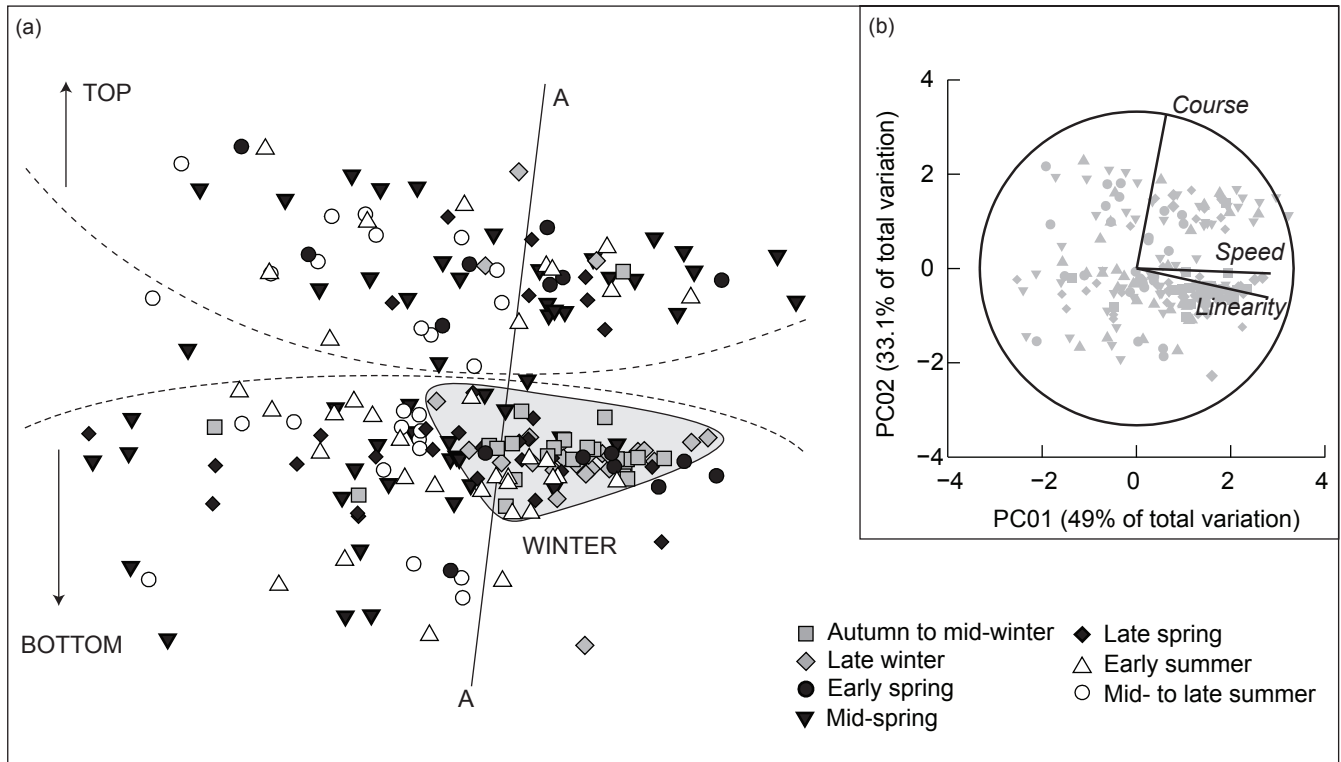


Figure 13: (a) Non-metric MDS ordination plot of seasonal samples based on the combination of movement parameters (normalised, Euclidian distance, stress-value = 0.1). Dashed lines indicate the top and bottom groupings and shaded shape encloses the majority of autumn/winter samples. Line A represents the right-hand limit of all mid- to late summer samples; and (b) PCA of seasonal samples of whale movement parameters with those responsible for most variation (speed and linearity horizontally and course vertically) overlaid onto the scatterplot

Table 7: Summary results from ANOSIM of pairwise, between-season comparisons based on the trackline parameters speed, course and linearity (shading indicates $p < 0.05$)

| Season | Autumn to mid-winter | | Late winter | | Early spring | | Mid-spring | | Late spring | | Early summer | |
|---------------------|----------------------|-------|-------------|--------|--------------|-------|------------|-------|-------------|-------|--------------|-------|
| | R | p | R | p | R | p | R | p | R | p | R | p |
| Late winter | -0.023 | 0.937 | | | | | | | | | | |
| Early spring | 0.189 | 0.003 | 0.174 | 0.007 | | | | | | | | |
| Mid-spring | 0.014 | 0.352 | 0.059 | 0.106 | 0.017 | 0.371 | | | | | | |
| Late spring | 0.061 | 0.054 | 0.115 | 0.003 | 0.188 | 0.038 | -0.038 | 0.878 | | | | |
| Early summer | 0.061 | 0.075 | 0.114 | 0.009 | 0.118 | 0.031 | -0.014 | 0.681 | -0.018 | 0.814 | | |
| Mid- to late summer | 0.014 | 0.352 | 0.478 | 0.0001 | 0.256 | 0.005 | -0.009 | 0.545 | 0.101 | 0.005 | 0.065 | 0.033 |

of these (Table 8). Fourteen groups were observed to engage in surface activity other than feeding, including repeated breaching and competitive behaviour such as flipper slapping. Defecation was observed 37 times for 23 groups intercepted during nine months from 2001 to 2006. All defecating groups were seen during the months of October 2002/04 (five times), November 2001/04/05/06 (11), December 2001/04 (5) and January 2003 (3). The total number of defecating groups seen from the boat, expressed as a fraction of the total humpback groups intercepted during these nine months (94 groups), results in a defecation incidence of 24.47%. The groups included two of the TOP groups observed to be feeding (Table 8). The

stools ranged in colour from dark/bright pink to brick red, presumably indicating crustacean prey. Most of the faecal samples collected (preserved in 95% ethanol) were highly diluted and consisted of whitish to pink paste in emulsion or as a particulate suspension. Four samples that contained slightly larger particles were examined through a stereomicroscope and yielded unidentifiable crustacean (possibly euphausiid) exoskeleton remains, with the exception of one collected on 29 November 2006 that contained fairly intact specimens of a hyperiid amphipod.

The possible relationship between observed/suspected feeding behaviour (including defecation) and whale movement patterns and distribution was explored by labelling

all groups tracked on the days in which such behaviour was recorded (all groups 30 October 2001–26 January 2003 in Table 8) as ‘feeding’ groups, and all groups on other days as ‘non-feeding’. Using the same MDS plot (Figure 14, based on the parameters leg speed, course and distance from shore), but with feeding/non-feeding as distinguishing factor, there was a strong similarity between the grouping based on linearity (Figure 14a) and feeding behaviour (Figure 14c).

Acoustic stations

In all, 33 acoustic stations were surveyed, for a minimum of 10 minutes each, from 2001 to 2003 during August, September, October, November, December and January. During a total time of 141 minutes monitored, no humpback vocalisations were detected.

Discussion

Despite variable and, at times, discontinuous search effort, the summer seasonal coverage of this study meant across-year effort was more extensive than during any previous attempt at shore-based monitoring of southern humpback whales. All seasons, with the exception of autumn, were well surveyed. This allowed us to compare whether the observation of a ‘suspended migration’ reported by Best et al. (1995) during spring was indeed unusual, or whether the observed whale availability and behavioural patterns were applicable to other seasons and years.

Sighting conditions, visibility and distance of whales from shore

On days when searching occurred, the mean sightability, based on the various environmental observations, appeared to have been constant enough to allow comparison of sighting rates across seasons. The significant seasonal variation of mean visibility at the midline between some seasons may raise concerns about whether whale groups were missed in the search area due to limited visibility. Such conditions were most prevalent during summer months when not only the lowest visibility was recorded but also the maximum distances at which whales were tracked exceeded visibility maxima estimates. This suggests that visibility was difficult to judge during these months, in all likelihood as a result of the frequent occurrence of coastal fog, persistent south-easterly winds, or strong refraction due to the strong gradient between high air and low sea temperatures. Despite this, some of the highest sighting rates were still recorded during summer.

Compared to the radial sighting distances to whales, the overall mean visibility was always greater, except for mid-spring and mid- to late summer. However, when the mean sighting distance was compared to the mean visibility measurement prevailing at the time of sighting, it was greater than the visibility up to about 7 km. This apparent contradiction might be the consequence of the visibility measurements being taken on the midline, whereas most sightings were made well away from the midline. If alongshore visibility should be greater than offshore visibility in times of moderate–poor visibility (for instance, owing to the majority of haze being over the sea rather than the

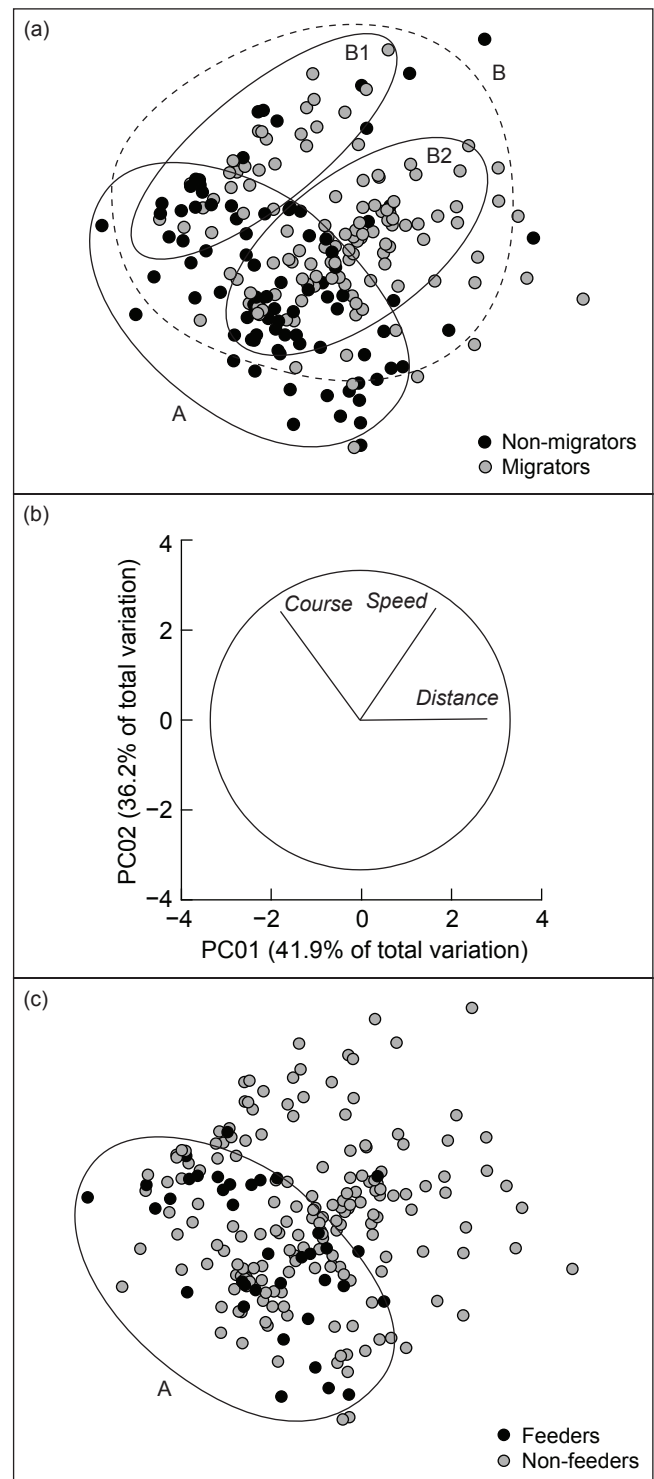


Figure 14: (a) Non-metric MDS ordination of migrators (linearity ≥ 0.9) and non-migrators (linearity < 0.9) based on the parameters speed, course and distance from shore (normalised, Euclidian distance, stress-value = 0.15). Group A (enclosed by the solid line) indicates non-migratory grouping, and group B (dashed line) migrators; shape B1 includes the northbound ($280\text{--}360^\circ$) groups and B2 the southbound ($100\text{--}200^\circ$) groups; and (b) shows the PCA axes and parameters that best explain the clustering seen in (a); (c) shows the same MDS plot with feeding and non-feeding as the distinguishing factor

Table 8: Description of groups showing feeding or feeding-like behaviour seen from land and/or boat

| Date ¹ | Sighted from | Group size | Def. ² | Description of behaviour |
|-------------------|--------------|------------|-------------------|---|
| 30 October 2001 | Land | 2 | N | Milling about, apparently feeding |
| 03 November 2001 | Boat | 3 | Y | Dark pink defecation |
| 10 November 2001 | Boat | 2 | Y | Bright pink defecation |
| 06 December 2001 | Land | 3 | N | Slowly moving south, apparently feeding. Associated with seven dusky dolphins <i>Lagenorhynchus obscurus</i> |
| 16 December 2001 | Boat | 2 and 2 | Y | Two groups seen defecating |
| 17 December 2001 | Land/boat | ±20 and 3 | Y | Large, loosely associated group identified as 11 smaller groups from land. Milling and suspected feeding behaviour. Defecation seen in this group and during a later sighting of three animals |
| 19 December 2001 | Land | 15–20 | N | At least two subgroups of animals scattered over large area, milling about |
| 11 September 2002 | Land/boat | 1 | N | Small animal with erratic movements, long dives, spending brief time at the surface. Cape fur seals <i>Arctocephalus pusillus</i> , seabirds and unidentified dolphins displaying feeding behaviour nearby |
| 17 October 2002* | Boat | 8 | Y | Combination of seven earlier sightings. Pairs of animals doing side-ways coordinated surface lunges, mouths open and ventral grooves distended. Jellies, euphausiids and mysids seen in water. Defecation seen |
| 29 October 2002 | Land | 2 and 3 | Y | Two separate groups, one milling and possibly feeding and the second active on the surface. Defecation seen |
| 30 October 2002 | Boat | 6 and 2 | Y | Defecation seen in first group that was made up of a cow–calf pair and escort, later joined by another pair and singleton. Later sighting of two, also defecated |
| 13 December 2002* | Land/boat | 2 | N | Milling and feeding lunges, erratic movement in circles, apparently along thermal divide (16 °C on one side and 17 °C on the other) |
| 10 January 2003 | Boat | 2 and 1 | Y | Cow–calf pair and later single animal. Bright, brick-red defecation by both groups |
| 26 January 2003* | Land/boat | 3 and 2 | Y | One group seen from land to be lunging, also surface active and milling about. A different group seen from boat also lunged. Bright pink defecation seen during intercept. Blue whale <i>Balaenoptera musculus</i> sighted displaying suspected feeding behaviour, swimming along a foam line parallel to shore |
| 12 October 2004 | Boat | 5 | Y | Two humpbacks and three southern right whales. Defecation seen |
| 08 November 2004 | Boat | 2 and 2 | Y | Defecation seen in two groups |
| 29 November 2004 | Boat | 1 | Y | Individual travelling slowly while defecating. Later resighted and defecated whilst lobtailing (five stools produced in five minutes) |
| 02 December 2004 | Boat | 9 | Y | Single humpback with eight southern rights, defecation by both species |
| 23 March 2005* | Boat | 2 | N | Lunge feeding |
| 24 November 2005 | Boat | 3 | Y | One animal slightly separate from others and evasive. Defecation seen |
| 12 October 2006* | Boat | 3 | N | Two humpbacks and one southern right both apparently feeding. Humpbacks made sideways lunges through 'mysid' patch. Plankton sample collected |
| 19 November 2006 | Boat | 1 and 5 | Y | Single animal, later resighted as part of larger group. Defecation seen both times |
| 22 November 2006 | Boat | 2 | Y | Defecation seen |
| 26 November 2006 | Boat | 2 | Y | Evasive group. Defecation seen |
| 29 November 2006 | Boat | 1 | Y | Evasive pair, apparently feeding. Defecation seen |
| 14 November 2007 | Boat | 14–20 | N | Large association of several subgroups, apparently feeding, associated with feeding seabirds |

¹ * indicates direct observation of feeding

² Def. = defecation seen; yes (Y) or no (N)

land), this could account for the apparent discrepancy. When visibility was good, i.e. 7 km and farther, this effect seemed to disappear. Considering that the seasonal mean distance from shore of whale groups never exceeded 6 km, and was <4 km in all but two seasons (see below), and

assuming that north- or southbound whales would remain at a more or less constant distance from the shore as they travel through the search area, it seems likely that the majority of whales would have passed within the visibility range at some stage. This is apparent when comparing the

mean radial distance at which whales were sighted to the calculated distance to the nearest shoreline. Groups were evidently sighted well before they passed the nearest point to the tower. Visibility as measured through the theodolite is probably a conservative estimate of the distance at which whales may be sighted (but not necessarily tracked), given that cues such as blows are visible with the naked eye, and not only at a 22× magnification.

The mean distance of whales from the shore was fairly similar (at around 3.5 km) for most seasons, with the notable exceptions of late winter and mid-spring when it was about 5.5 km. Not surprisingly, these two seasons exhibited a greater proportion of groups in the 5–10 km range. Generally, the majority of whales were still seen in the 'inshore' zone (<5 km) with very few beyond 10 km, and this was unlikely to be as a result of restricted visibility offshore. This is compatible with observations by Best et al. (1995) at Cape Columbine during mid- to late spring, although the mean offshore distance of 3.1 ± 0.2 km recorded in that study was lower than both our overall mean (4.41 ± 0.21 km) and that of the same season (5.78 ± 0.48 km). This may be because Cape Columbine is situated slightly more to the west than Saldanha Bay and so possibly acts as a headland that coastally migrating whales have to navigate around.

Seasonality of occurrence and movement patterns

Mid-spring (October) stands out in more than one respect as a seasonal 'turning point'. First, the highest sighting rate was recorded at this time of year and it remained relatively high from then onwards, despite the decreased search effort and reduced visibility. Second, there were also noticeable changes in the whale movement parameters from autumn to early spring, and the remaining seasons. Mean actual swimming speed started decreasing significantly from mid-spring onwards, from more than 6 km h^{-1} in winter to $<3 \text{ km h}^{-1}$ in late summer. The corresponding mean net swimming speeds are well within the range of 'migration' speeds of humpback whales recorded off the east coast of South Africa (Findlay 1994), and elsewhere (Noad and Cato 2007, Lagerquist et al. 2008). However, the low actual and net speeds recorded in mid- to late summer certainly fall in the lower end of the range and are very similar to the low speeds recorded at Cape Columbine (Best et al. 1995).

Sightings in mid-spring were distributed almost evenly between the near- and offshore zones, recording the overall highest mean distance from shore. This was also the period when non-directionality in movement became a prominent feature and where almost equal numbers of groups either milled around or moved in near-straight lines, in all major directions. Multivariate representation of the movement variables in combination confirms mid-spring as a period where whale movement was less distinctive than in any other season, sharing similarities with both the preceding and following seasons. This is in strong contrast with groups from the winter months that all displayed movement patterns that were, with few exceptions, very alike in terms of speed, course and linearity. From this, it could be speculated that mid-spring represents a period when we observed an overlap of two behaviourally distinctive 'subgroups' of humpbacks: one component migratory, although judging by the observed direction both north- and southbound, and the other distinctly

non-migratory, and each perhaps occurring at different distances from the shore. Olsen (1914) reported similar 'anomalous' behaviour off Saldanha during 1912/1913, and speculated that there may be two components to humpbacks moving past during their northern migration. One consisted of animals that moved straight to the north, and had empty stomachs when caught, while the other was seen to move 'wildly back and forth' along the coast, apparently in search of food (see later discussion on feeding).

Olsen (1914) also reported on whales frequently seen by vessels farther offshore, which presumably met the coastline north of South Africa on their northward migration. Reeves et al. (2004) made similar inferences during an estimate of historical seasonal distributions of humpbacks and blue whales from 18th and 19th century logbooks of catches in the North Atlantic. They concluded that the humpbacks migrated over an extended period making use of both nearshore and offshore routes, and that sporadic feeding took place well south of 'traditional' feeding grounds, a behaviour that may persist to the present. Our finding that groups farther offshore moved slightly faster may support this, although the distance that Olsen (1914) refers to was presumably well beyond the visibility range of our station. It therefore remains difficult to distinguish different 'components' of the population based on movement patterns alone.

Defining migrators/non-migrators

High availability or relative abundance of whales in an area, whether based on direct observations or historical catches, is not necessarily conclusive evidence of a migration peak, but could represent a local feeding aggregation. The multivariate comparison of migrators vs non-migrators did show a difference between these groupings on the basis of actual swimming speed and distance from shore. Furthermore, within the 'migratory' group, two subgroups separated out on the basis of their course; this suggests the existence of two migrational streams heading in opposite directions. Although there was a definite increase in the proportion of groups showing non-migratory (non-linear) movement from autumn through to late summer, linearity alone can thus not be considered a reliable indicator of migrational behaviour without taking into account direction of movement, and speed. For example, in early spring more groups showed linearity >0.9 , but the number of groups heading south and in other directions were about equal.

Our observations in October/November (mid- to early spring) are consistent with those made earlier at Cape Columbine (Best et al. 1995) during the same months, in that the groups showed both southerly and northerly directionality. Perhaps more difficult to explain is the dominance of southbound groups, moving at higher speed during the winter, at a time when we would expect to observe at least the tail end of a northern migration (Olsen 1914). It would appear that, although groups that displayed both strong directionality and linearity were present during almost all the seasons, there was a shift in movement pattern from October/November onwards when both strong directed movement (both north and south) were observed, as at Cape Columbine, but also an increase in the 'non-migrating' and slow-swimming components. Whether the 'fast-and-straight' swimmers were actually migrating or simply moving up or

down the coast, perhaps between Cape Columbine and Saldanha, in a determined manner (as suggested by Olsen 1914), remains uncertain. What is clear is that the dominant movement pattern changed between winter and summer; fast movers became fewer towards summer, especially those heading south, and by mid- to late summer almost all groups moved slowly. This is supported by the significantly low average speed of 2.9 km h⁻¹ and the virtual disappearance of the fast-moving and straight-swimming component that characterised groups sighted during winter.

Other behaviours observed elsewhere during migration have included singing (Clapham and Mattila 1990) and non-acoustic means of communication such as breaching, tail-slapping and other surface behaviour (Dunlop et al. 2007, 2008). Although surface active behaviour was observed, we did not detect any vocalisations, but we received a reliable report of singing on 29 December 2003 from an observer in a steel-hulled yacht near Dassen Island, about 50 km south of Saldanha Bay (P Evans, pers. comm.).

Group size, sex ratio and composition

The changes observed in mid-spring were not limited to movement patterns alone. Group sizes recorded were larger than average, and it was the only season where the overall sex ratio varied significantly from parity, with a strong female bias of about 2:1, even when cow–calf pairs were excluded. This is in marked contrast to the findings of Brown et al. (1995) who described a migration (both north- and southward) off the eastern Australian coast from May to October that was overall highly skewed towards males. Similar apparent male-dominated sex ratios have been observed on breeding grounds (Craig and Herman 1997, Palsbøll et al. 1997). With no evidence for any stock-level deviations from an approximate 1:1 sex ratio (see discussion in Clapham and Mead 1999), it has been speculated that male bias during migration may be a result of some females possibly remaining in ‘feeding’ areas (presumably at high latitudes) throughout winter. On the breeding grounds, such a bias might be explained by a longer residence time of males (Craig and Herman 1997). Our discovery of a region with a significant female bias may offer a plausible explanation as to where the ‘missing’ females go while males complete the full migration, with mid-spring falling roughly between the northward and southward migrations. Compared to ours, the study site of Brown et al. (1995) was situated much closer to the Group V northern destination (breeding area), but unfortunately they did not provide a seasonal (monthly) breakdown of recorded sex ratios, which prevents more detailed comparisons. A number of questions thus still remain: (1) Where were these females during winter? Did they spend time in an unknown area or merely travel at a more leisurely pace from the feeding grounds, compared to males, to reach the coast of Saldanha during mid-spring? (2) Do male-biased sex ratios occur at localities farther up the west coast of Africa? Whaling data from the former Congo (now Gabon) at about 1° S indicated that, in 1949, males made up nearly 65% of all catches, 47.55% in 1950 and about 50% in 1951 (Budker and Collignon 1952), implying that the situation is not markedly different than in the breeding grounds for humpbacks. More recently, however, Pomilla and Rosenbaum (2006) reported

a male-biased sex ratio at breeding grounds off Gabon, as well as Madagascar.

Apart from the sex ratio at any given site, a number of authors have commented on differential timing of migrating humpbacks based on sex, age and reproductive state (see summaries in Clapham 1996, 2000), as well as group composition (Brown and Corkeron 1995). Typically, for Southern Hemisphere humpbacks, lactating females with ‘yearling’ calves are believed to head north from the feeding grounds first. They are followed by immature whales of both sexes; then mature males and resting females, and finally pregnant females (Dawbin 1997). Resting and recently impregnated females are the first to leave on the southward migration, followed by immature whales and mature males. The last to leave breeding areas are cows with new-born calves (Chittleborough 1965, Dawbin 1966). Bearing in mind that we could not assess the reproductive condition of female whales, except when they were accompanied by small calves, we did observe seasonal changes in composition of completely sampled groups, suggesting some staggering in migrational timing. The proportion of singletons (both males and females) decreased from winter to summer, with single females disappearing altogether after late spring. Again, mid-spring stands out with the first appearance of male/female pairs; this was also the most commonly recorded grouping off East Australia (Brown and Corkeron 1995), especially during the northward migration. The decrease in singletons of both sexes and increase in mixed gender pairs from mid-spring may be evidence of increased breeding interactions. This may be due to ‘mate guarding’, as suggested by Brown and Corkeron (1995), a notion supported by Clapham’s (1993) finding of male–female dyads on feeding grounds (also see discussion in Valsecchi et al. 2002). We did not test for the relatedness of pairs, so males accompanying females could conceivably include some large male yearlings not identified as calves.

From late spring onwards the number of cows accompanied by calves was highest, although some cow–calf pairs were sighted in most months. The peak birth month for Southern Hemisphere humpbacks is early August (Matthews 1938, Chittleborough 1958, 1965). Although not explicitly measured, the size of calves observed off Saldanha (estimated relative to the size of the accompanying female) ranged from about new-born size in a few instances (3.96–4.57 m) to the suggested size at independence (between 8 and 10 m; Clapham et al. 1999), with the majority falling in roughly ‘half the mother’s length’; or between 5 and 6 m. This suggests considerable variation in the departure time from breeding areas, and arrival at, or transit through the study area, or may reflect some yearlings or second-year animals still accompanied by their mothers. There is some support for the latter possibility from the records of adult female humpback whales accompanied by calves/juveniles, as described in a Norwegian Whaling Statistics form (obtained from S Burkett, International Whaling Commission), annotated by the manager of the Hangklip whaling station (K Bernsten) in 1913 (Table 9). Between 21 October and 19 November, eight small whales were landed that were described as being accompanied by their mothers (or whales assumed to be their mothers) at the time they were taken, seven of which were also killed and proved to be females

Table 9: Details of humpback whales accompanied by 'calves' taken at Hangklip whaling station, South Africa, in 1913 (length data converted from whole feet or inches), from notes by the manager of the station, K Bernstein

| Date | Length of adult female (m) | Accompanying 'calf' | | Notes on records (translated from Norwegian) |
|-------------|----------------------------|---------------------|-----|--|
| | | Length (m) | Sex | |
| 21 October | | 8.53 | F | In company of mother that escaped |
| 31 October | 14.33 | 8.53 | M | These two animals together so assumed to be mother and calf |
| 01 November | 14.63 | 7.32 | M | As above |
| | 12.80 | 7.01 | F | As above |
| 10 November | 15.24 | 8.84 | M | Young one shot first then the mother. Adult pregnant with 12.7 cm foetus |
| 15 November | 14.02 | 8.53 | F | These two animals together so assumed to be mother and calf |
| 18 November | 14.02 | 8.84 | M | As above |
| 19 November | 14.63 | 8.84 | M | As above |

of adult size (12.8–15.24 m). Six of the small whales were 8.53–8.84 m long, or about the size of humpback whales at 10–11 months of age (8–10 m, Clapham et al. 1999). These were presumable calves from the previous year. The other two were considerably smaller (7.0–7.3 m), and may represent calves-of-the-year, about three months old, a finding not inconsistent with some estimates of early growth in humpback whales (Stevick 1999).

Feeding behaviour

Humpback whales have been observed to shift their feeding areas as a response to changes in prey availability in the Gulf of Maine, North Atlantic, over a period of <10 years (Weinrich et al. 1997). At traditional feeding grounds in the Southern Ocean, Murase et al. (2002) showed that humpback whales associate strongly with high concentrations of euphausiids and that their distribution was determined by the availability and location of prey species. They suggested that humpbacks should be able to feed equally efficiently during migration in high-density euphausiid swarms. Such swarms of the dominant euphausiid species in the southern Benguela, *Euphausia lucens*, do occur periodically off Saldanha (Stuart 1986, Pillar et al. 1989, 1992), although numerous other meso- and macrozooplanktonic crustaceans (other euphausiids, amphipods, mysids) and small pelagic fish are found in the area that could be potential humpback prey (Hutchings et al. 1991, Gibbons et al. 1995, Gibbons and Hutchings 1996). Historical records of humpback stomach contents from the region (Olsen 1914) include copepods ('rodaate' in Norwegian) and fish: a stomach full of 'herrings' from a humpback whale taken at Donkergat in 1912 or 1913 was illustrated by Olsen (1914), whereas the stomach contents of four humpbacks examined there in 1926 were empty (2) or contained fish (2). One of the latter, taken on 25 June was crammed with fish noted as 'clupeoids', while the other (taken on 20 September) was filled with a pasty mass of fish scales and bones (Matthews 1938). However, four stomachs examined at Donkergat in 1962 and 1963 in June (1), July (2) and August (1) were all empty (Best 1967).

Feeding by humpbacks during migration has thus far been considered opportunistic, such as the surface feeding on small 'baitfish' by a single humpback associated with bottlenose dolphins *Tursiops aduncus* observed off Queensland, Australia (Stockin and Burgess 2005), and the more recent description of a 'supplemental' feeding ground by

Stamation et al. (2007), also for the Area V stock. However, Dawbin (1956) suggested that feeding opportunities could cause deviations or interruptions in the southward migration of humpback whales past New Zealand, recently confirmed by satellite telemetry (Gales et al. 2009), and a similar situation seems to occur off the west coast of South Africa. Although we observed actual feeding only five times, defecations were observed in almost a quarter of all groups, during months when defecation was recorded. In many cases we saw movements and concentrations of whales that suggested feeding, similar to observations at Cape Columbine in 1993 (Best et al. 1995). These groups almost always consisted of two or more animals, and on several occasions these smaller 'sub'-groups formed loose aggregations of up to 20 animals that moved around in a fairly large general area. Such aggregations were first seen in December 2001, and again in October 2002 and November 2007. The strong correspondence of groups seen or suspected to be feeding (based on behavioural observations) and 'non-migratory' groups (based on movement parameters), as shown by multivariate analysis, suggests that most groups in the general area were probably engaged in feeding.

The regular incidence of defecations seems to support the fact that feeding occurred over a number of days in the vicinity (following the reasoning of Danilewicz et al. 2008). We observed swarms of euphausiids, mysids and gelatinous organisms at the surface on at least one occasion next to feeding humpback whales (17 October 2002). Massive swarms of *E. lucens* were also found washed up on the beach of North Bay, inside Saldanha Bay, during October 2002 and 2006. A plankton haul carried out near a feeding group on 26 January 2003 contained *E. lucens* and the amphipod *Themisto gaudichaudi* (Gibbons 1999). These findings, along with the amphipod remains found in one faecal sample, and an earlier record by Findlay and Best (1995) of an entangled juvenile humpback that had fed on stomatopods before its death, suggests that crustacean prey is not confined to euphausiids.

As in October/November 1993 (Best et al. 1995), an examination of humpback movement patterns off the South African west coast failed to provide strong supporting evidence for a conventional bi-directional humpback migration, this despite longer seasonal coverage and clear seasonal peaks in relative abundance during early spring and summer. These peaks, when considered in combination with the observed movement pattern, pointed to activities

other than migration, in particular localised feeding. In the light of this, it seems that Olsen's (1914) observations nearly a century ago, as well as those of Best et al. (1995), were not anomalous for the region, and that a significant component of humpback whales may make use of the area as a feeding ground. This occurs at least from October to February/March, well beyond the expected peak of the southern migration. The prevalence of this behaviour during the time when the southward migration should take place may relate to the nutritional condition of the animals, as suggested by the much lower oil yields of southward migrating humpbacks compared to northbound ones off West Australia (Chittleborough 1965). Specifically, females that are either pregnant or nursing are likely to have a greater urgency to feed at the first available opportunity. Male humpbacks would presumably also have expended considerable energy in the breeding areas, as demonstrated for sei whales *Balaenoptera borealis* heading south that had significantly reduced testis mass compared to during the northern migration (Best and Lockyer 2002).

The spatial extent of this feeding/non-migratory behaviour remains unclear. If we assume it to be associated with upwelling cells of high productivity in the southern Benguela system (Weeks et al. 2006), the range could span for about 1 000 km from Lüderitz in the north to Cape Point in the south. Some historical observations in summer of humpback whales off the Namibian coast at Hollam's Bird Island (see John Keeler's 1830 account reported in Best and Shaughnessy 1979), and catches in the 19th century off Walvis Bay up to January (Townsend 1935), may support this. There are notable differences in the nature of these upwelling cells: Cape Columbine and the Cape Peninsula cells are synchronous but seasonally variable, with highest upwelling in spring and summer, whereas the Namaqua cell at Lüderitz is more perennial and extends farther offshore (Weeks et al. 2006). Movement between different cells could explain the determined northerly and southerly directionality seen from mid-spring through summer.

The movement patterns and behaviour observed in this study do not exclude the presence of a strictly migratory population component, but make it virtually impossible to identify it from these data. Grey whales *Eschrichtius robustus* that feed opportunistically in 'pockets' along their migration route in the eastern Pacific (Moore et al. 2007) are now considered to be flexible foragers. The putative migration of humpbacks appears to represent not only a continuum in terms of breeding behaviour as suggested by Brown and Corkeron (1995), but also includes a component of foraging. Based on our findings, as well as an ever-growing number of records of feeding during migration (e.g. Stamation et al. 2007), in traditional 'wintering' areas (Danilewicz et al. 2008, de Sá Alves et al. 2009) and 'rediscoveries' of previously unknown feeding grounds (Gibbons et al. 2003), 'flexible forager' is a label that seems equally appropriate for humpback whales.

It is possible that such feeding behaviour may occur at other mid-latitude locations with similar oceanographic conditions to the southern Benguela, provided that suitable prey organisms are present at sufficiently high densities. The resident population of humpback whales in the Arabian Gulf certainly proves that they are able to subsist off the monsoon- and upwelling-driven productivity found off Oman

(Mikhalev 1997). A better understanding of the scale of this behaviour off the west coast of South Africa may only be achievable through satellite telemetry or a subregion-wide survey (ship or aerial) during the spring to summer peak, similar to the study by Moore et al. (2007) on grey whales.

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