Estimating population changes in humpback whales *Megaptera novaeangliae* migrating past Cape Vidal, South Africa

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Shore-based surveys of humpback whales *Megaptera novaeangliae* were performed from Cape Vidal, on the east coast of South Africa (iSimangaliso Marine Protected Area, Indian Ocean), from two independent platforms between 27 June and 7 August in 2018 and 2019, to estimate the relative abundance and growth rate of the C1 breeding substock of the species. Observed whale groups were tracked by analogue survey theodolites, and observed numbers were adjusted to account for daily sighting effort and the proportions of groups missed by observers. Daily sighting frequency was aggregated across the season to result in annual relative abundance estimates of 10 499 (2018) and 11 009 (2019) individuals, with peak frequencies from 28 July to 3 August in both years. When compared with previous estimates from the same study area, we estimated an average annual increase rate of 7.4% to 8.8% over 31 years from 1988. These results indicate a slowing of the rate of increase from previous estimates, which could suggest that the population is approaching pre-exploitation numbers or that yet unidentified threats are negatively impacting the growth rate. Continued monitoring of the recovering humpback whale stocks is critical to identify any possible effects of Southern Ocean ecosystem changes on the stock health of these whales.

Keywords: abundance estimate, analogue theodolite, carrying capacity, mark-recapture, migration, shore-based survey, sightability, whale stock

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Introduction

Annual migrations of most baleen whale species (order Cetacea, suborder Mysticeti) involve seasonal movements between high-latitude summer feeding grounds and medium-latitude to low-latitude breeding grounds during winter months (Kellogg 1929; Norris 1967; Stone et al. 1990; Zerbini et al. 2006; Acevedo et al. 2022). Such journeys include some of the longest annual migrations by any mammal globally (Stone et al. 1990; Rasmussen et al. 2007; Acevedo et al. 2022). The knowledge accumulated from whaling records and the associated research identified a need to manage whale stocks for whaling purposes (e.g. the 'Discovery' investigations: Rayner 1940). Together, these data provide valuable information on different population aspects and the behaviour of whales, including their migrations and seasonal abundances.

The rate at which populations change is a fundamental demographic parameter used to assess wildlife populations (Skalski et al. 2005); the rate of increase (increase rate) of a population is often an essential parameter for population assessments for conservation management and viability studies in ecosystem modelling (Mori and Butterworth 2006; Zerbini et al. 2010). Since the international protection of humpback whales *Megaptera novaeangliae* from commercial whaling was first enforced in 1963 (Gambell 1993), the population has recovered steadily (Zerbini et al. 2010).

Humpback whales in the Southern Hemisphere are stratified into seven ocean-basin breeding stocks (BS) (designated A–G, corresponding to the east and west coasts of the major continents in the Southern Hemisphere and including the Pacific islands). Estimates of breeding stock increase rates are available for almost all seven recognised humpback whale stocks (Jackson et al. 2015), including the C1 substock (Findlay et al. 2011), which utilises the coasts of South Africa, Mozambique and southern Tanzania during the austral breeding season (IWC 2011). However, the estimates of the C1 substock are based on data collected between 1988 and 2002 (Findlay and Best 1996a; Findlay et al. 2011), which warranted an update to provide current information for conservation management. Given that the comprehensive assessment of humpback whales by the International Whaling Commission (IWC) suggested that, in 2011, the C1 substock was approaching 65%–98% of its pre-whaling population size, a decelerating rate of increase might be expected (IWC 2011; Jackson et al. 2015). Additionally, as anthropogenic factors are increasingly shown to affect the environmental conditions on breeding and feeding grounds (Trathan et al. 2007), up-to-date information on population trends is critical to monitor population responses to environmental change.

Findlay and Best (1996a, 1996b) conducted dedicated daily shore-based observations from an elevated platform (south tower) using theodolites. The south tower was specifically built for shore-based whale monitoring that was conducted at Cape Vidal, on the northeastern coast of South Africa (Indian Ocean) (Figure 1), in June, July and August from 1988 to 1989. These authors then introduced a second platform (i.e. north tower, 22 m from the south tower) for the 1990 and 1991 surveys, allowing for simultaneous independent observations to determine observer effectiveness through independent mark-recapture analyses of the sightings data. In 2002, the shore-based surveys were repeated by Findlay et al. (2011) using the same platforms, equipment and sampling protocols. The number of passing humpback whales estimated during the 1988–2002 surveys (17 days in each year, 6–22 July) and during the 1990, 1991 and 2002 surveys (25 days each year, 6–30 July), revealed increase rates of 11.5% and 9%, respectively.

Although the results of these studies have been used in an assessment of this species (IWC 2011) and helped to better understand the status of the C1 substock as it recovers from whaling, the continuation of data collection is essential for an updated evaluation of their population dynamics and conservation status, and to better understand potential threats to their recovery. This will also support effective transboundary management strategies for humpback whales that migrate seasonally along the east coast of Africa.

This study aimed to estimate the current rate of increase of the Southern Hemisphere humpback whale C1 breeding substock as an indicator of population-level and ecosystem changes. To achieve this, the specific objectives were to:

(i) estimate the current relative abundance of the C1 breeding substock migrating past Cape Vidal from land-based observations in 2018 and 2019; and
(ii) determine the rate of increase of the population by comparing the abundance estimates from this study with those made previously.

The results may be used to update the International Union for Conservation of Nature (IUCN) global conservation status assessment for the C1 substock, update the IWC's comprehensive stock assessment of humpback whales, and highlight potential changes in the Southern Ocean ecosystem, the feeding grounds of the study population.

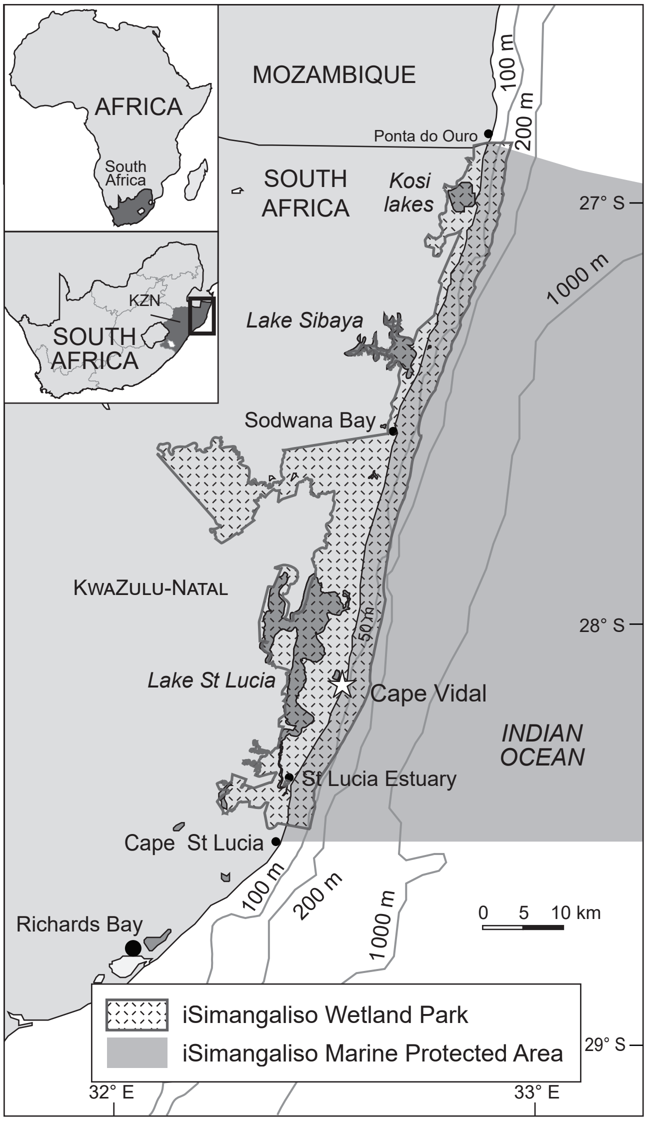

Figure 1: Map of the study area, which encompasses the coastal area around Cape Vidal, South Africa. The block around the study area indicates the iSimangaliso Marine Protected Area

Materials and methods

Study area

Shore-based visual monitoring of the northwards migration of humpback whales was undertaken from Cape Vidal (28°07' S, 32°33′ E) on the northeastern coast of South Africa (Indian Ocean) in 2018 and 2019 (Figure 1). The observation sites were the same as those used previously in 1988, 1989, 1990, 1991 and 2002 for similar investigations (Findlay and Best 1996a, 1996b; Findlay et al. 2011). The location was chosen by these authors as it is a headland, has a high vantage above sea level, and the orientation of the coastline relative to the general south-to-north migration results in the concentration of whales into a migratory corridor. Adequate infrastructure was also available as the area forms part of the iSimangaliso World Heritage Site, managed by the iSimangaliso Wetland Park Authority and Ezemvelo KwaZulu-Natal (KZN) Wildlife.

Data collection

Field surveys were carried out from 27 June to 7 August in both 2018 and 2019. This period coincides with the peak of the northwards migration of humpback whales along the east coast of southern Africa, as identified from historic whaling data from the Durban Whaling Station and from previous studies on this species in the area (Findlay and Best 1996b; Findlay et al. 2011).

Observations

Observations were conducted by teams of two observers on each platform (the north and south towers) during daylight hours (between 07:00 and 17:00), each day whenever weather and observation conditions permitted (i.e. wind speed <20 knots, Beaufort sea state ≤5). Both observers in each team searched the entire field of view, with one observer using 8 × 50 Nikon wide-angle binoculars to search for new groups of whales entering the monitoring area, while also scribing. The second observer operated the theodolite (see below) while also searching for new groups with the naked eye. The observers chose the role that they were most comfortable with and maintained that role throughout the study period.

Theodolite tracking

Analogue one-second-resolution theodolites (Sokkisha TM20H; Sokkia Co. Ltd, Japan) were used throughout the surveys to track whale movements. These were the same theodolites as were used in the previous surveys, thereby contributing to the comparability of the datasets. Observers were trained to set up, calibrate and operate the theodolites before each survey period. Once sighted, whale groups were tracked using the theodolite, and positional fixes of the horizontal and vertical angles of successive bouts of surface-active behaviour were recorded. Vertical angles to groups provided the radial distance between them and the observers, while horizontal angles provided the bearing from the north as the theodolites were referenced on known-bearing landmarks each day. Estimated positions were immediately plotted on charts, which allowed possible errors in the fixes to be immediately identified and for discrimination between groups that were close together. Additionally, this real-time plotting helped the observers to predict where the whales would surface next. Time was measured to the nearest second using timepieces synchronised across both towers.

Parameters recorded

Collected data were divided into: (i) search effort data (including start and end time of activities, and observer team changeovers); (ii) encounter data (time, position and group size), combined with the theodolite tracks measuring whale behaviour (speed, distance and direction of migration); and (iii) weather condition data, which were recorded hourly, on the hour (i.e. wind speed and direction, cloud cover, sea state, swell height and visibility [maximum distance offshore that the theodolite could accurately record a vertical angle, in kilometres]). The sightability at the towers was evaluated and scored hourly during the observations. These data were then meaned, producing a daily sightability score. Group sizes from each surfacing were also meaned to provide the estimated number of whales per group.

Data analyses

Data conversions

Data were digitised and analysed through custom Python-coded applications (Spyder 4.14 running Python 3.8.3 64-bit | Qt 5.9.7 | PyQt5 5.9.2). In initial analyses, the horizontal and vertical theodolite angles were converted into the distances and bearing from the platform, taking both a refraction correction factor and the curvature of the Earth into consideration (Findlay and Best 1996a). These were subsequently converted into GPS coordinates on a Cartesian plane (as positional fixes) (Findlay and Best 1996a).

As observations were only recorded during daylight hours under good sighting conditions, and whales were assumed to continue their migration at night, the daily frequency of migrating whales (over 24 h) was extrapolated from the number of groups sighted during the watch periods each day. Such extrapolation required an assumption that the migration speeds of whales are constant across the 24 h (Findlay and Best 1996b).

Estimations of daily frequency

For a whale group to be included in the estimations of daily frequency, it had to have crossed the midline of the observation area within the observation period, to avoid daily frequencies being inflated. Groups not seen crossing the midline of the observation area were projected forwards or backwards using their measured speed and bearing to calculate their projected time of midline crossing. Such groups were only included in the analyses if the projected time of their projected intersection fell within the observation period.

Mark-recapture analyses

It is important to note that observers may miss detections of whale groups owing to both availability and perception biases (Marsh and Sinclair 1989). Therefore, to accurately estimate the number of groups missed using mark-recapture analyses, several assumptions need to be made (Seber 1982; Findlay and Best 1996b). These assumptions were adopted in this study (see Discussion) from Findlay and Best (1996b).

Recaptures for the mark-recapture analyses were defined as ‘the time and position of the midline crossing of each sighting made from the south tower (i.e. marking of a whale group) compared with the equivalent time and position parameters from the north tower (i.e. the recapture of a whale group).’ For groups to be identified as matches, the crossing time and position had to fall within a spatial and temporal threshold. Three spatial and temporal threshold combinations were tested and included: 10 min and 500 m, 15 min and 1 000 m, and 20 min and 2 000 m. The 20-min and 2 000-m threshold combination was adopted for this study.

Chapman estimation

The Chapman-modified Peterson estimate (Chapman 1974) for small populations was used to estimate the population size of marked groups in the second sample and the proportion of marked groups in the population. The total number of groups (N) recorded each year from the north tower (Nn) and the south tower (Ns), as well as the number of matched group sightings between towers (M), were tallied in each of three distance bins (near, mid, and distant) and three sightability conditions (good, fair, and poor) (see ‘Data stratification’, below, for the definitions of these categories) for each day’s observations to estimate the total number of groups in the area.

The use of Chapman’s method is similar to Gentleman and Zeh’s (1987) method, which compares samples of tracks rather than groups. Consequently, it includes additional variances arising from the uncertainty of linking sightings into tracks.

The proportion of groups missed

The proportion of total tracks recorded by observers on a particular tower was evaluated by the proportion of tracks matched between towers against those seen by the individual tower. The reciprocal of this value results in the proportion of groups missed by the respective tower.

Data stratification

The total number of groups (N) crossing the midline on each day was tallied in three interval bins (i) of perpendicular distance from the coast, as follows:

$i = 1$, between 0 and 2.99 km offshore (referred to as the 'near' distance bin);
$i = 2$, between 3 and 5.99 km offshore (referred to as the 'mid' distance bin);
$i = 3$, greater than 6 km offshore (referred to as the 'distant' distance bin).

The proportion of missed groups by each tower in each of the distance intervals (i) was estimated by mark-recapture under different sightability conditions (w):

$w = 1$, poor sightability, rating 0–1.99;
$w = 2$, fair sightability, rating 2–3.99;
$w = 3$, good sightability, rating 4–5.

Data heterogeneity

The classification of i and w accounted for heterogeneity in sighting probabilities as noted by Findlay and Best (1996a), who indicated that distance from the observer (or distance offshore), sightability, whale behaviour and group size can influence these probabilities. The last two factors were excluded from the analyses because: (i) evaluation of behaviour can be highly subjective; and (ii) some groups were recorded by both towers as having different group sizes (given the distances of observers from the whale groups).

On days when no observations were conducted owing to poor weather conditions, the number of whale groups was averaged from the days before and after to produce a representative count for that day.

Daily tallies

Daily tallies of the number of whale groups (N) recorded in each distance bin ($_{d,i}$) were adjusted for the proportion (P) missed in each distance bin under the day's weather conditions. Adjusted tallies in each distance bin ($a_{d,i}$) were calculated using the formula devised by Findlay and Best (1996a):

$$a_{d,i} = N_{d,i}(1 + P_{w(d),i}) \tag{1}$$

Adjustment for observation conditions

Adjusted counts within the three distance bins were summed and divided by the total observation effort (e) for that day to give an estimate of sighting frequency (J_d) of groups sighted per hour, using the formula devised by Findlay and Best (1996a):

$$J_d = \left(\sum_{i=1}^{3}(a_{i,d})\right) / e_d \tag{2}$$

Converting to 24-h estimates

Hourly estimates were multiplied by 24 to produce a daily adjusted tally (D_d) using the formula devised by Findlay and Best (1996a); the migration rate was assumed to be consistent throughout the day and night so that hourly tallies could be extrapolated:

$$D_d = J_d \times 24 \tag{3}$$

Converting from whale groups to the number of individuals

Tallies of individuals per day (I_d) were determined as the product of daily group sighting frequency, and the mean group size recorded in that year (S), using the formula devised by Findlay and Best (1996a):

$$I_d = D_d S \tag{4}$$

Estimating the total number of whales

The total estimated number of whales passing the survey area during the study period (N) each year was estimated by summing the daily tallies recorded for each day, using the formula devised by Findlay and Best (1996a):

$$N = \sum_{d=1}^{h}(i_d) \tag{5}$$

Comparison of abundance between years

Because of logistical and timing constraints, the timing of the previous surveys did not occur over the exact 42-day period as this 2018/2019 study. To mitigate this, total numbers of humpback whales were calculated for periods that overlapped with those of previous surveys. All available values for 6–22 July, 1–22 July, 27 June–22 July, and 6–30 July across all available survey years were plotted using exponential regression to obtain a rate of increase for each period. These results will be reported as a range of increase rates.

Statistical analyses

Humpback whale group sizes and frequency data (hereafter referred to as data) were of a sample size between 0 and 2 000. A Shapiro–Wilk normality test was run to indicate whether the data were normally distributed. If so, a parametric test (t-test) was used; otherwise, a nonparametric Wilcoxon signed-rank test was used.

Results

Observation effort

In 2018 the observers surveyed for 289 h from each tower, while in 2019 the effort increased to 312.5 h for each tower over the equivalent 42-day monitoring period (Figure 2; Table 1).

The number of hours of survey effort per day varied from 0 to 10 owing to variable weather conditions (Figure 2). During the 2018 season, only 5 days (12%) had no observation effort, while 19 days had >9 h of observation (45%). This was similar in 2019 when there were also 5 days of no observation effort (12%), but 23 days (54%) with observations for >9 h. Data were not normally distributed ($p \leq 0.05$) for both years. There was no significant difference in survey effort in 2018 (median [Md] = 8, $n = 42$) when compared with in 2019 (Md = 9.5, $n = 42$) (Wilcoxon signed-rank test, $T = 335$, $z = -0.977$, $p = 0.329$).

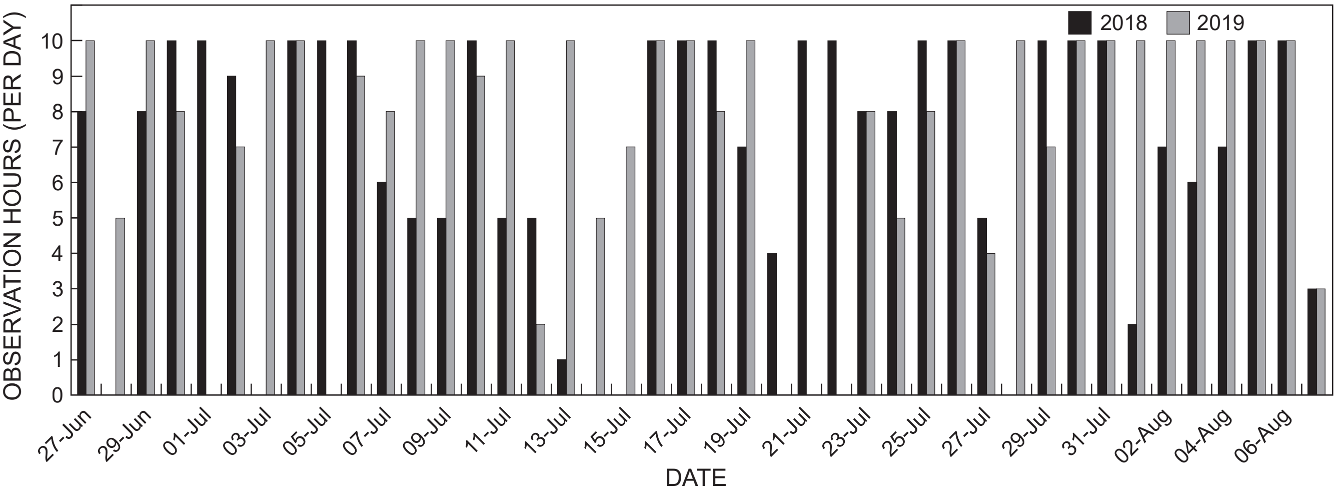

Figure 2: Distribution of daily observation effort (hours) carried out during independent surveys of humpback whales in 2018 and 2019 at Cape Vidal, South Africa

Table 1: Summary of the observation effort and the number of humpback whale groups observed during shore-based surveys undertaken at Cape Vidal, South Africa, during 2018 and 2019

Year	Observation effort (h)		Number of humpback whale groups observed	
	South tower	North tower	South tower	North tower
2018	289.0	289.0	1 100	1 281
2019	312.5	312.5	1 306	1 271

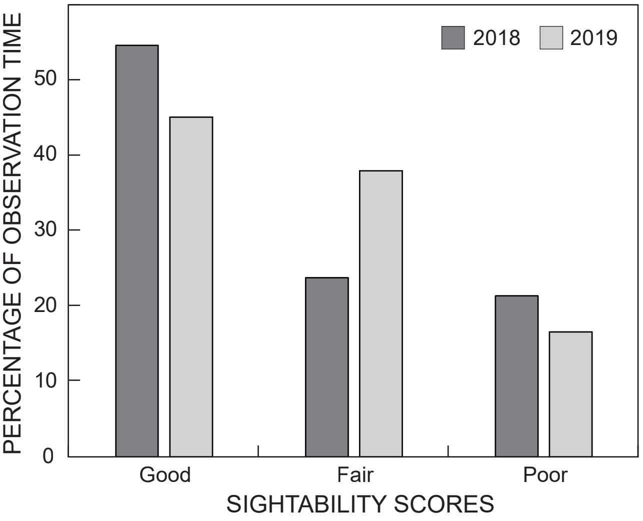

Figure 3: Frequency of mean daily sightability ratings of humpback whales, observed from the north and south towers combined, over the surveys conducted in 2018 and 2019 at Cape Vidal, South Africa

Sightability

For most days, sightability was rated (see 'Data stratification', above) as 'good' (55% in 2018; 45% in 2019), followed by 'fair' (24% in 2018; 38% in 2019) and then 'poor' (21% in 2018; 17% in 2019), as illustrated in Figure 3. The mean sightability rating over the survey period was not normally distributed ($p \leq 0.05$). There was no significant difference in mean sightability between 2018 (Md = 4.14, $n = 42$) and 2019 (Md = 3.96, $n = 42$) (Wilcoxon signed-rank test, $T = 391$, $z = -0.512$, $p = 0.609$).

Whale group sighting frequency

Table 1 shows the number of humpback whale groups recorded from the north and south towers in each year of this study.

Whale group frequency data (i.e. the number of migrating humpback whale groups per hour per day) are shown in Figure 4. In both years, whale group numbers increased over the season, peaking during the week from 28 July to 3 August. The highest numbers of groups per hour that were recorded on a single day was nine (90 groups in 10-h effort) in 2018 (31 July) and 12 (36 groups in 3 h) in 2019 (7 August) (Figure 4).

The whale group frequency data were normally distributed for the north tower in 2018 ($p = 0.397$) and 2019 ($p = 0.016$), as well as for the south tower in 2018 ($p = 0.2180$) and 2019 ($p = 0.018$), and a paired-samples *t*-test was conducted. The frequency of whale groups recorded as observed from the north tower was not significantly different between 2018 (sample mean [*M*] = 3.856 [SD 2.333]) and 2019 (*M* = 3.555 [SD 2.692]) ($t(42) = 0.718$, $p = 0.477$), and likewise as observed from the south tower between 2018 (*M* = 3.363 [SD 2.151]) and 2019 (*M* = 3.689 [SD 2.814]) ($t(42) = 0.714$, $p = 0.480$).

Group size estimates and proportion of groups missed

A median of two whales per group was recorded in both 2018 (north tower SD = 1.142; south tower SD = 1.180) and 2019 (north tower SD = 0.948; south tower SD = 1.230).

When considering unstratified data from both years (Table 2), it was estimated that observers at the north tower missed 41% of groups and those at the south tower missed

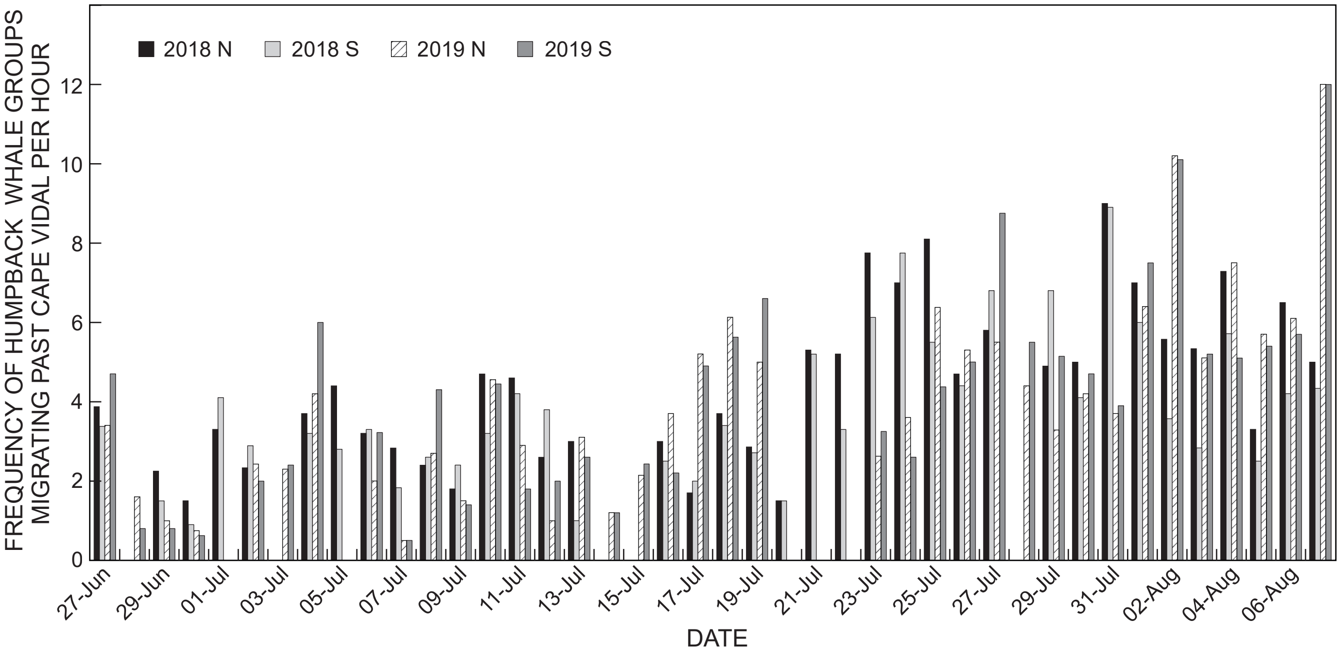

Figure 4: Daily number of humpback whale groups migrating per hour past Cape Vidal, South Africa, observed from the north (N) and south (S) towers in the 2018 and 2019 surveys

Table 2: Independent sightings, matches, and proportions missed, based on observations from the north and south towers, during the survey period at Cape Vidal, South Africa, in 2018 and 2019. Results are presented as both unstratified and stratified into the different distance and sightability bins and a combination of both. *N*n = number of humpback whale group sightings from the north tower; *N*s = number of humpback whale group sightings from the south tower; *M* = number of matched humpback whale groups; *N* = total number of humpback whale groups whales calculated by Chapman's estimation; SD = standard deviation; *P*n = proportion of humpback whale groups missed by observers at the north tower; *P*s proportion of humpback whale groups missed by observers at the south tower

Year	Stratification	*N*n	*N*s	*M*	*N*	SD	*P*n	*P*s
2018/2019	Unstratified	2 552	2 406	1 417	4 332.62	49.17	0.41	0.44
2018/2019	Distance bins							
	Near (0–2.99 km)	1 241	1 026	777	1 638.50	17.68	0.24	0.37
	Middle (3–5.99 km)	844	849	525	1 364.49	22.56	0.38	0.38
	Distant (>6 km)	394	433	112	1 516.08	103.25	0.74	0.72
	Discarded (inaccurate)	73	98					
	Total	2 552	2 406					
2018/2019	Sightability bins							
	Good (mean rating 4–5)	1 577	1 550	880	2 777.07	40.86	0.43	0.44
	Fair (mean rating 2–3.99)	866	767	476	1 394.92	26.36	0.38	0.45
	Poor (mean rating 0–1.99)	109	89	61	158.68	7.41	0.32	0.45
	Total	2 552	2 406					
2018/2019	Combined bins							
	Poor / Near	56	49	43	63.77	1.60	0.14	0.25
	Poor / Middle	30	29	14	61.00	7.87	0.53	0.55
	Poor / Distant	20	9	4	41.00	10.58	0.60	0.81
	Fine / Near	502	404	307	660.41	11.47	0.24	0.39
	Fine / Middle	268	252	154	438.08	14.24	0.39	0.43
	Fine / Distant	79	85	14	457.67	93.91	0.84	0.83
	Good / Near	683	573	427	916.33	13.66	0.26	0.38
	Good / Middle	546	568	357	868.39	16.42	0.37	0.35
	Good / Distant	295	339	94	1 058.37	75.63	0.72	0.68
	Discarded (inaccurate)	73	98					
	Total	2 552	2 406					

44% of groups passing through the monitored area. Under stratified conditions whale groups farthest offshore in the 'distant' bin accounted for most of the misses (74% from the north tower and 72% from the south tower, for 2018 and 2019 combined). Within the different sightability conditions, more whale groups were missed during 'good' weather conditions (43% from the north tower and 44% from the south tower for 2018 and 2019 combined) than during either 'fair' conditions (north tower 38%; south tower 45%) or 'poor' conditions (north tower 32%; south tower 45%).

Sighting matches

During the 2018 and 2019 field seasons, a total of 4 332.62 humpback whale groups were estimated or projected to cross the midline during the combined survey periods at the north and south towers. On days when no observations were made, the mean number of groups recorded on the day before and the day after were used, thus resulting in the decimal amount. Using the threshold combination of a 20-min time interval and 2 000-m crossing resolution, a total of 1 417 whale groups were matched between towers. Results indicate that 59% of groups were observed from the north tower and 56% from the south tower. The sighting probability of whale groups was proportionate to the number of matches between both towers. The distance bin with the highest sighting probability was the 'near' bin with 777 matches (Table 2), whereby the north tower recorded 76% and the south tower recorded 63% of whale groups within this bin. Concerning the sightability bins, the one denoting 'good' weather conditions recorded the highest matches at 880. In the combined bins (distance and sightability), the 'poor/near' bin included most of the matches (*n* = 43), whereby the north tower recorded 86% and the south tower 75% of the whale groups.

Relative abundance estimates

After accounting for the proportion of matches missed, the data from the south tower were used for relative abundance estimations, as per Findlay et al. (2011).

Relative abundance estimated in 2018

In 2018, the number of whale groups sighted per day (corrected by the proportion missed) ranged from 36.72 (13 July) to 292.32 (31 July) (Figure 5). The daily relative abundance estimates were extrapolated over 24 h and combined for the 42-day survey period, resulting in an estimated 5 096.42 humpback whale groups. Considering that the mean whale group size for 2018 was 2.06 (SD 1.18*)*, a resulting estimate of 10 498.61 humpback whales migrated past Cape Vidal during the survey period in that year.

Relative abundance estimated in 2019

In 2019, the number of whale groups sighted per day (corrected by the proportion missed) ranged from 4.05 (7 July) to 384.8 (7 August) (Figure 5). Note that the effort was low on 7 August owing to logistical constraints. Approximately 5 825.04 humpback whale groups were estimated to have crossed the survey area during the 2019 survey period. Considering that the mean group size for 2019 was 1.89 (SD 1.23*)*, 11 009.32 humpback whales were estimated to have migrated past Cape Vidal during the 42-day survey period in 2019.

Temporal changes in relative abundance estimates

The 2018 and 2019 estimates of the number of individual humpback whales migrating past Cape Vidal were compared with those of historical surveys (Findlay and Best 1996a, 1996b; Findlay et al. 2011) (Table 3; Figure 6). Available values across all survey years were used to estimate the relative increase rate of the humpback whale population

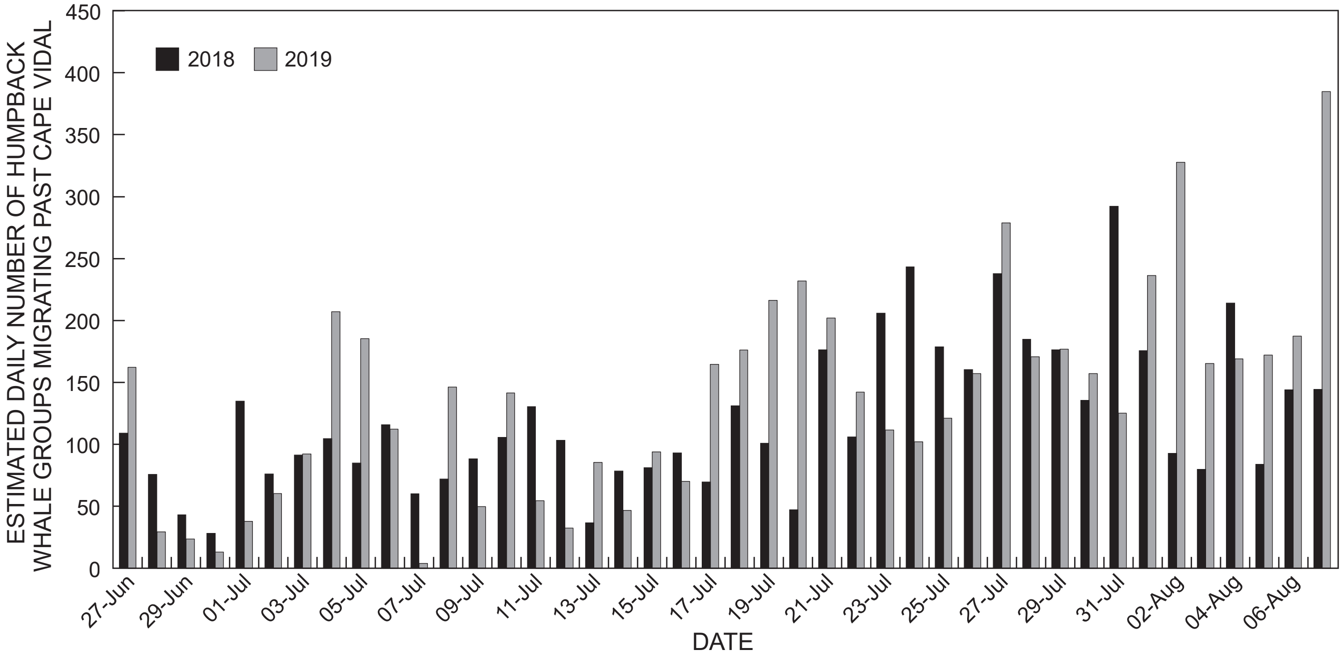

Figure 5: Daily estimates of humpback whale groups passing Cape Vidal, South Africa, in the 2018 and 2019 survey period

migrating past Cape Vidal. Results showed that the population size was still increasing, but the rate of increase had declined from 11.5% for the period 1988–2002 to between 7.4% and 8.8% for the period 1988–2019 (Figure 6).

Discussion

The coastal migratory routes of Southern Hemisphere humpback whales, which once made them highly susceptible to shore-based whaling in mid-latitude and low-latitude waters, have made them a prime candidate for shore-based monitoring of their migrations in more recent years. The specific survey methodology applied in this study was consistent with previous surveys at Cape Vidal (Findlay and Best 1996a, 1996b; Findlay et al. 2011) to ensure data comparability and accurate identification of population trends. More specifically, the use of theodolites allowed precise measures of

Table 3: Abundance estimates of humpback whales migrating past Cape Vidal, South Africa, from all available survey periods, with overlapping dates from 1988–1991, 2002 (data from Findlay et al. [2011]), and 2018–2019

Year	Period					
	6–22 July	1–22 July	27 June–22 July	6–30 July	17 June–6 August	27 June–6 August
1988	358					
1989	249	296	302			
1990	359	420	420	695	1 000	
1991	587	734	831	1 093	1 777	
2002	1 673			2 406		
2018	3 893	4 550	5 105	6 801		10 498.61
2019	4 532	5 928	6 457	7 378		11 009.32

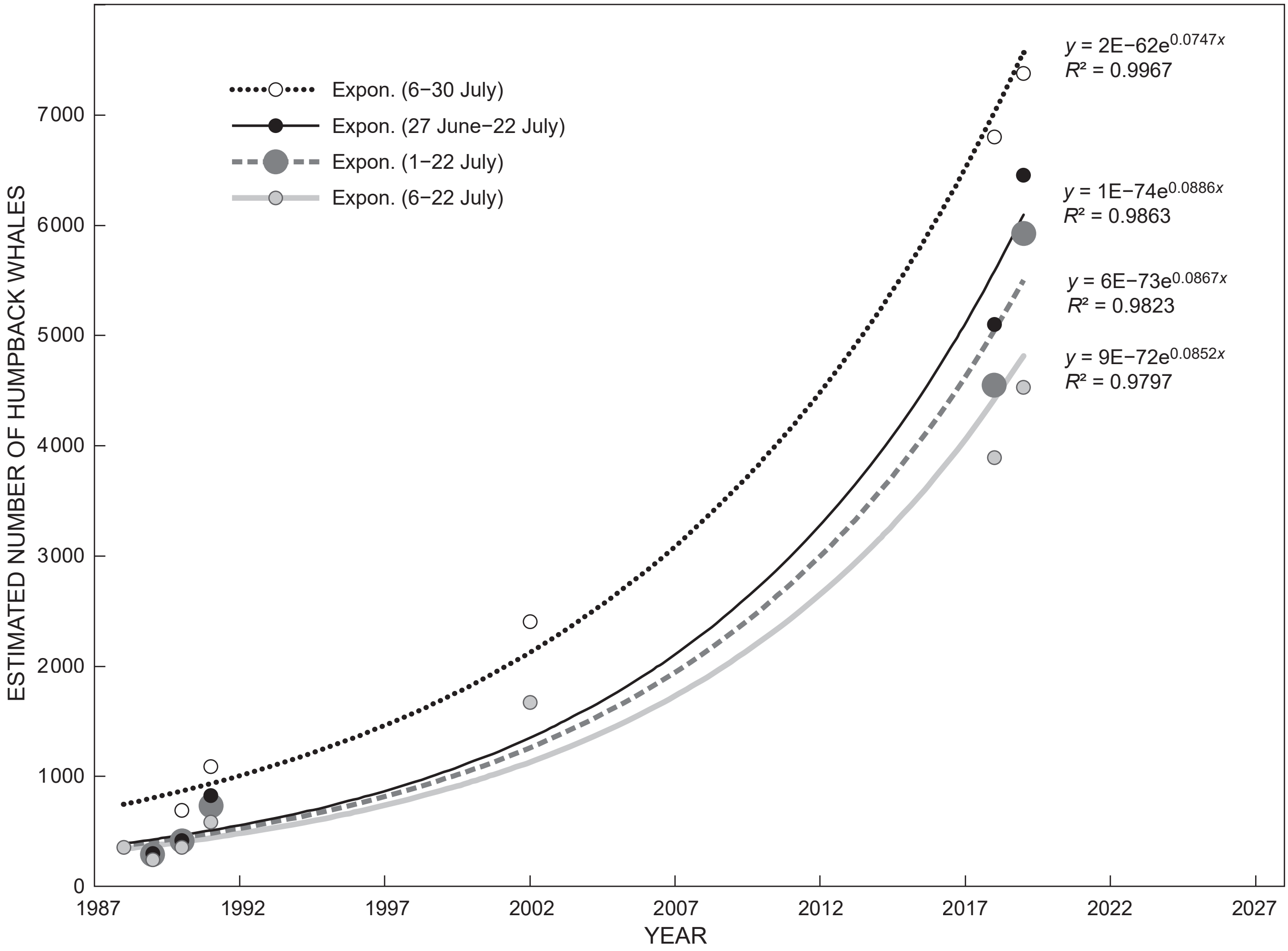

Figure 6: Increase in the number of humpback whales migrating northwards past Cape Vidal, South Africa, during the dates 6–22 July, 1–22 July, 27 June–22 July, and 6–30 July, from all available survey years (data from Findlay et al. [2011] and the present study)

the whales' distance from shore, heading and speed, whereas the application of two observer platforms allowed the proportions of whales missed by each tower to be determined, which were then accounted for in the final abundance estimates.

Overall, the survey was considered successful in addressing the objectives of the study, in part owing to a high percentage of observation days with >8 h of monitoring effort. This reflects the good weather conditions during the surveys, resulting in fair to good sightability for reliable observations.

The survey methods used in this study required volunteers, many of whom participated in both years, ensuring the pairing of experienced with inexperienced observers in the second year. Owing to the high density of whales throughout the survey period, more handling time for obtaining and recording fixes off the theodolite was required; therefore, less effort time was available to search for new groups, especially at the limits of what could be observed. Notably, Buckland et al. (1993) reported that when performing two-platform shore-based surveys, the detection rates of whales were higher when observers were motivated by viewing many whales. Therefore, every attempt was made to encourage observers to continuously search and detect whales and keep enthusiasm high, especially on low-density days.

Although no differences were found in sightability conditions between years, early in the 2019 survey the observers had to contend with low grey haze caused by the burning of sugarcane inland. This was also experienced by Findlay (1994) in previous surveys, but owing to the lower magnification of the theodolite (than the binoculars) it was sometimes impossible to track whales in the haze. These conditions improved when the wind strength increased throughout the day and was no longer a limiting factor by the first week of July, and optimal tracking of whale groups was possible throughout the rest of the survey. During hazy periods whales could only be detected by the white water left after a breach. Although this may have impacted accurate measurements of some migration characteristics (the whale group's speed, distance offshore, and migration direction), this limitation was accounted for by the proportion of groups missed when estimating the daily whale frequencies and the mean distance offshore.

The lack of a significant difference in the sightability conditions between years was attributed to the surveys being undertaken over the same time each year, and therefore seasonal weather patterns were similar across all surveys. The two-platform method aided estimation of the proportions of whales missed because of glare, and observations of whales in the early morning. This was because the platforms faced east, allowing for whale blows to be backlit by the sun. Paterson and Paterson (1989) found that sun glare before 06:00 was a significant factor influencing humpback whale sightings off east Australia, resulting in a higher sighting rate between 06:00 and 08:00 as observers could see whales that had moved out of the glare and were within the visible limits.

In this study, the observed peak in the number of northward-migrating humpback whales throughout the survey period corresponds to the peak period identified by Findlay and Best (1996b). Those authors described the local density peaks as waves occurring throughout July, implying a link between migrations and the reproductive cycle of humpback whales, as the waves might reflect different ages, sex, and reproductive classes in the order that they arrived at the breeding grounds. Lactating females with young calves would arrive first, followed by sexually immature individuals, mature males, resting females, and finally pregnant females (Dawbin 1956; Chittleborough 1965). The peaks identified by Findlay (1994), from 1988 to 1991, were not as pronounced in the present study. This change might be attributable to successive waves becoming less defined with the higher number of whales in the migration stream. Noad et al. (2008) observed a similar change and reported a delayed first peak in the number of northward-migrating humpback whales off the east coast of Australia, suggesting that the first two peaks had converged, leading to a sustained single peak that was both longer and higher. More-detailed studies (including genetic studies) are needed to confirm this in the C1 substock.

Owing to the present study being land-based, it was not possible to assign sex or age class to individual whales, which would have allowed temporal segregation by age and reproductive classes to be assessed, as was found for humpback whales in the North Atlantic (Stevick et al. 2003). However, we did observe an unusual pattern of newborn calves in the migration stream, higher than previously reported by Findlay and Best (1996a) and Findlay et al. (2011). This increased presence of newborn calves may indicate that whales are leaving their Southern Ocean feeding grounds later than usual, suggesting that pregnant females might be spending longer on the feeding grounds to ensure they acquire sufficient body condition to support their energy requirements for migration, calving and nursing of young. This may also be linked to reduced prey availability in the feeding grounds (van den Berg 2020). Studies have shown that reproductive performance in baleen whales is linked to body condition, given the influence of food availability on individuals (e.g. Christiansen et al. 2018; Seyboth et al. 2021; Pallin et al. 2023). Studies assessing the body condition and age of the migrating humpback whales, in conjunction with a detailed analysis of their hormones, would aid in understanding any temporal segregation by age and reproductive class during the migrations. This would expand our understanding of the timing, segregation and trophic ecology of migrating humpback whales observed from Cape Vidal.

The probability of detecting and tracking humpback whales decreased as distance from shore increased, contrary to the findings of Findlay and Best (1996a) and Rugh (1989) for gray whales *Eschrichtius robustus*. This could be confounded in the present study under the conditions of decreased sightability caused by glare or haze, especially in 2019, as hazy conditions offshore on most days forced observers to focus on the 'mid' and 'near' bin. Additionally, differences in whale group behaviour at varying depths could have led to more cues for the observers. Whales are likely to protect young and will become discreet in shallower waters ('near' bins) (based on anecdotal evidence), whereas breaching occurs farther from shore in deeper water ('mid' and 'distant bins') but is more noticeable. This in turn correlates with the increased sighting probabilities in deteriorating weather conditions. The increased surface activity (including fin slapping, tail slapping and breaching) of humpback whales related to conditions of strong winds (Findlay and Best 1996a) may have influenced this result. Furthermore, whales can be increasingly difficult to spot when they are relaxed (resting or traveling slowly) in calm conditions, because their blows are less frequent and less intense.

Consistency in effort and methods between years is required to accurately identify a population trend across years through estimates of relative abundance. Both the levels and efficacy of effort need to be considered at different whale frequencies (e.g. sightings per hour), which led Findlay et al. (2011) to adopt the assumptions below when comparing previous humpback whale estimates from surveys at Cape Vidal:

(i) The proportion of the population passing beyond the spatial and temporal limits of the observations is consistent across years.
(ii) Depending on the distance and weather conditions, detection probabilities remain constant throughout the time-series or need to be accounted for, so that the efficacy of effort can be somewhat standardised.
(iii) Observer accuracy and precision is constant throughout the survey series.
(iv) The diel pattern of migration remains constant throughout the survey period.

In the present study, these assumptions were met by: (i) setting a temporal and spatial threshold limit for observations (20 min, 2 000 m); (ii) defining distance and sightability categories which were analysed separately to measure detection probabilities in different conditions; (iii) ensuring effort and methods remained constant throughout all surveys, including the use of the same theodolite equipment, observation towers and survey dates as those used in the previous studies; and (iv) extrapolating the daytime frequencies over 24 h to maintain consistency and comparability with the previous studies.

Results of this study indicate that the relative abundance of the C1 humpback whale substock is increasing steadily (increase rate = between 7.4% and 8.8% for the period 1988–2019), but at a slower rate in comparison with the period 1988–2002 (increase rate = 11.5%: Findlay et al. (2011). Considering that the current size of the C1 substock is assumed to be close to pre-exploitation levels (IWC 2011), the lower rate of increase identified in this study suggests that it may be reaching carrying capacity.

Contrary to these findings, a comparable study from eastern Australia on the E1 substock has shown a consistent increase rate of approximately 11% over 24 years, with no evidence of slowing (Noad et al. 2019). As this stock size is near pre-exploitation levels (Noad et al. 2019), a stable high increase rate (close to the maximum biologically possible for the species: Zerbini et al. 2010) was believed to be related to intrinsic growth combined with temporary immigration from other substocks on the breeding grounds, in that individuals from low-density stocks may be temporarily drawn to larger aggregations in breeding grounds, before moving south to their native feeding grounds (Zerbini et al. 2010; Clapham and Zerbini 2015). The present study assumes that any immigration into the migration stream of the C1 substock from neighbouring substocks was negligible, as suggested by Rosenbaum et al. (2009) and through a photo-identification study by Cerchio et al. (2006).

The question of whether a reduction in the rate of increase indicates that carrying capacity is being approached, or is a result of anthropogenic impacts, remains unknown. Both Smetacek and Nicol (2005) and Constable et al. (2014) identify the difficulty of disentangling such drivers. However, the global increase in humpback populations across the Southern Hemisphere, and the results of models suggesting that current abundance estimates are approaching pre-exploitation levels (regardless of changes in carrying capacity: see Jackson et al. 2015), indicate that humpback whales have a potential for stock recovery once a particular pressure (in this case whaling) has been reduced. Current research suggests humpback whale numbers are approaching pre-whaling numbers; however, there are several increasing anthropogenically driven changes to the ocean environment—with the increase in ocean noise (Kunc et al. 2016) and climate change being the most pressing (Constable et al. 2014)—which might impact the recovery of the species.

The impacts of climate and environmental change on marine ecosystems are complex to unravel (Constable et al. 2014) and identifying animals that are useful for monitoring such impacts, and that allow for future predictions of the responses of top marine predators, is deemed critical (Fleming et al. 2016). Indicator species are those that can be easily monitored and whose status reflects the environmental condition of their habitat (Landres et al. 1988; Cairns and Pratt 1993; Bartell 2006; Burger 2006; Siddig et al. 2016). The ease of monitoring humpback whales on their migration and breeding grounds and their dependence on seasonal foraging success for their breeding success make them an ideal indicator species for the Southern Ocean ecosystem (Siddig et al. 2016; Bengtson Nash et al. 2018). The findings from this study represent an important update on the recovery of the C1 substock and should be considered when assessing the status of the species by the IWC and IUCN. A multidisciplinary approach should be adopted to better understand the effects of climate change on humpback whales in the Southern Hemisphere, and the response by the species to the multiple threats they currently face.

Overall, this study has shown that shore-based observations from Cape Vidal and monitoring using theodolite tracking remains a cost-effective and accurate method of estimating the relative abundance of humpback whales off the east coast of South Africa. Considering the findings of the current study, it is possible to conclude that, for the period investigated:

(i) the location of Cape Vidal, on the east coast of South Africa, remains an excellent vantage point to monitor the breeding stock C of migrating humpback whales; and
(ii) the relative abundance of the humpback whale C1 substock is still increasing, although the rate of increase has slowed over the last two decades.

The present study used shore-based monitoring of Southern Hemisphere humpback whales to provide an updated estimate of their relative abundance and an average annual rate of population increase. Importantly, these data reflect the number of humpback whales migrating past Cape Vidal, a migration corridor, and do not necessarily represent the abundance of humpback whales at a specific breeding or calving ground. It is recommended that this new information is taken into consideration by global decision-makers (such as the IUCN and IWC) as well as local authorities (such as managers of marine protected areas and spatial planners).

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