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An Update on the Occurrence of Humpback Whale (*Megaptera novaeangliae*) Super-Groups on the West Coast of South Africa

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ABSTRACT

Humpback whale (*Megaptera novaeangliae*) super-groups, comprising 20+, tightly aggregated, feeding individuals, form during the austral summer in the southern Benguela ecosystem off the west coast of South Africa. This phenomenon, observed since 2011, is thought to be linked to increased productivity from positive chlorophyll-a anomalies associated with reduced water export in the area, and possible changes in associated trophic structures. Oceanographic conditions vary over time and space, so that super-groups occurrence can also be highly spatially variable. In this study, we investigate the spatiotemporal patterns of super-groups by compiling records from scientific surveys, whale-watching operators, and citizen science reports between July 2015 and June 2022. In total, sightings of 239 humpback whale super-groups were collated for this period, considering sighting with best estimate group size of 20 individuals or more. Super-groups appeared from August to April, peaking between October and January, and the seasonality of their occurrence seems to have expanded in comparison to previously published data. Although the effect of inconsistent effort throughout the study is unknown, results identify the overall regularity and spatiotemporal patterns of super-group formations, while highlighting the need for improved, collaborative and systematic data collection to gain deeper insights into this mid-latitude feeding phenomenon.

1 | Introduction

Humpback whales (*Megaptera novaeangliae*) have a broad global distribution and are considered a cosmopolitan species (Clapham and Mead 1999). However, there is some evidence that those occurring in the three main geographically distinct areas of the North Pacific, North Atlantic, and Southern Hemisphere could be considered subspecies (Jackson et al. 2014). In most regions, the presence of humpback whales is highly seasonal, as individuals migrate between high-latitude summer feeding grounds and mid- to low-latitude winter–spring breeding and calving grounds (Dawbin 1966). In the Southern Hemisphere,

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the International Whaling Commission (IWC) has identified seven geographically separate breeding stocks (BSs) (labeled A to G) that winter along the coastlines of continents or islands for calving and mating (IWC 1998) and migrate to the Southern Ocean summer feeding areas, where mixing of breeding stocks is known to occur (for example IWC 2009; Marcondes et al. 2021). Breeding stock B (BSB) uses the African west coast, while breeding stock C (BSC) uses the east coast of Africa and the islands of the western Indian Ocean during the breeding season (IWC 1998). Both of these stocks are further divided into sub-stocks based mainly on their area of distribution, as follows: sub-stock B1 breeds off equatorial west Africa (mainly Angola and Gabon); sub-stock B2 is formed by whales using the migratory corridor and feeding ground off the Namibian and the western South African coasts, with a breeding ground that is still undetermined; sub-stock C1 breeds along the east African continental shelf; sub-stock C2 around the Comoros Archipelago and the Central Mozambique Channel Islands; sub-stock C3 uses the coastal waters of Madagascar during the breeding season; and sub-stock C4 breeds within the Mascarene Islands of Mauritius and Réunion (IWC 2007; Figure 1).

A key and unique characteristic of the South African west coast is the regular presence of feeding humpback whales at a latitude more commonly used as a migration corridor or breeding ground (Findlay et al. 2017). The geographical extent of sub-stock B2 using the coasts of Namibia and western South Africa remains poorly defined in the literature, with different studies using different boundaries. However, it is broadly accepted that its range overlaps with the Benguela upwelling system, mainly the southern Benguela off the west coast of South Africa (Barendse et al. 2011; Elwen et al. 2014). The Benguela ecosystem is one of the most productive and nutrient-rich areas of the world's oceans (Flynn et al. 2020). Although humpback whales from sub-stocks B1 (Gabon) and B2 (west South Africa) are genetically distinct (Rosenbaum et al. 2009), such differentiation has been found to be weaker than initially postulated (Kershaw et al. 2017), with photographic and genetic evidence of individuals moving between these geographical areas (Barendse et al. 2011; Carvalho et al. 2010).

One of the limitations of the breeding-ground-based model to underpin whale population structure, which is that individuals of a particular stock may migrate across multiple breeding grounds. This is the case for animals mainly using Mozambique, Madagascar, and the Mascarene Islands grounds, for example (Cerchio et al. 2008; Dulau et al. 2017; Dulau-Drouot et al. 2011). In addition, more recent lines of evidence, including genetic (Kershaw et al. 2017) and photographic matches (Marcondes et al. 2021; Ramos et al. 2023; Tree et al. 2024; Kalashnikova et al. 2024), suggest that there may be more dynamic processes at play. Indeed, connectivity between these breeding stocks is yet to be fully understood, with boundaries that can be more porous than previously believed, and it is likely that their definition or boundaries will need re-assessing.

Humpback whales have been documented feeding on the west coast of South Africa for decades. The first evidence arose from observations of feeding on "herring-like" fish during whaling operations in the early 1900s (Matthews 1938), followed by stranded and entangled individuals with prey items in their stomachs (Findlay and Best 1995). Observations of lunge-feeding

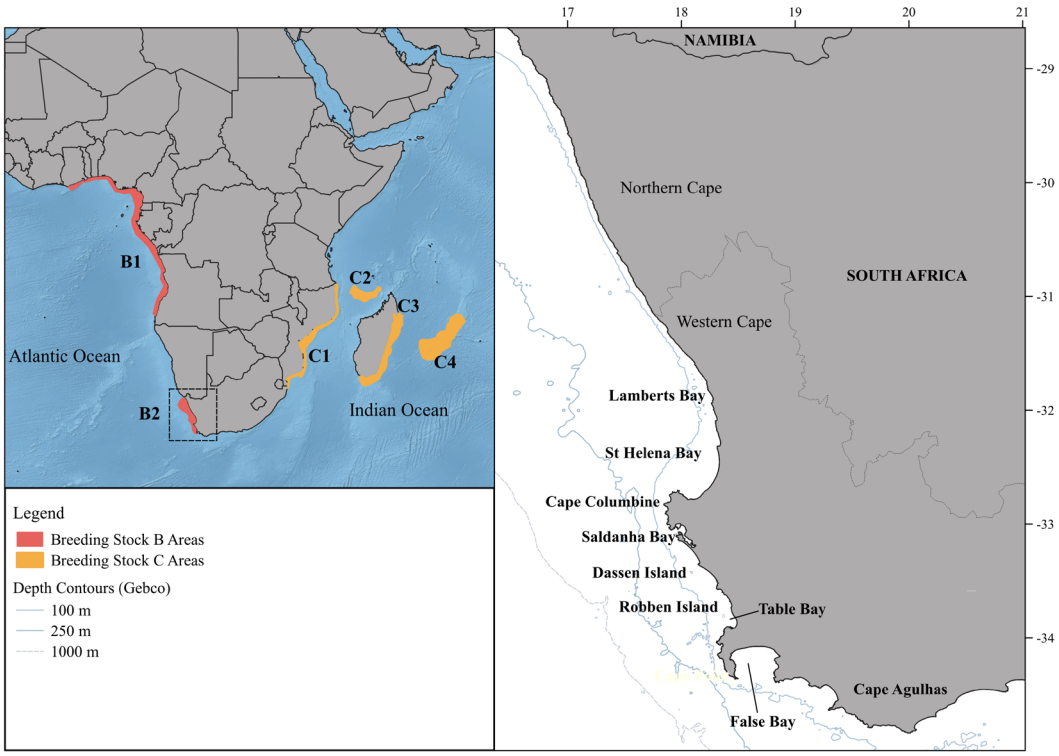

FIGURE 1 | Map indicating the main areas used by humpback whale sub-stocks on the west (Breeding Stock B sub-stocks) and east coast of Africa and the western Indian Ocean (Breeding Stock C sub-stocks) (left side of the map) and the localities mentioned throughout the text (right side of the map). The area zoomed in on the west coast of South Africa encompasses the area used by super-groups.

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behavior off Cape Columbine were associated with defecation, with individuals producing feces containing *Euphausia* species (Best et al. 1995). Also, small groups of humpback whales (of two to three individuals) and loose aggregations of up to 20 individuals feeding on crustaceans were made in Saldanha Bay, where sighting rates peaked from austral mid-spring (October) to late summer (February), in contrast to the normal migratory peaks of early and late winter/spring (Barendse et al. 2010). The timing, behavior, movement patterns, and scarring patterns of the observed animals (Barendse et al. 2010; Elwen et al. 2014) suggest that the animals seen feeding within this region were from sub-stock B2 (western South African coast) and suspended their southward migration to the Southern Ocean from an unknown breeding ground farther north, taking advantage of the productive waters of the Benguela upwelling system to build up energy stores on abundant food before heading south (Barendse et al. 2010; Best et al. 1995). Previous records of stomach content and feeding behavior in the area indicate that prey items targeted by the humpback whales in the area seem to include mantis shrimp (*Pterygosquilla armata capensis*) (Findlay and Best 1995), *Euphausia lucens* (Barendse et al. 2010; Best et al. 1995), hyperiid amphipods (*Themisto gaudichaudii*), and small pelagic fish (Barendse et al. 2010). However, from 2011 onwards groups of densely aggregated feeding humpback whales, forming so-called "super-groups" (defined as "groups of 20 or more individuals estimated to be within five body lengths of their nearest neighbor" by Findlay et al. 2017) have been observed on the west coast of South Africa. Four potential scenarios for the development of such behavior were suggested by the authors: (i) changes in prey availability leading to a novel feeding strategy; (ii) increasing whale abundance elsewhere resulting in the exploration of alternative feeding strategies or areas; (iii) a historically unobserved behavior or strategy that became apparent as populations recovered from whaling; and (iv) the probability of super-group feeding detection increased as a result of population recovery (Findlay et al. 2017). Which of these scenarios better explains the formation or detection of super-groups, as well as which breeding stocks and sub-stocks are involved in such feeding aggregations remain open questions. The importance of this feeding ground for the sub-stocks that frequent it, the scale of feeding, or the timing and occurrence of super-groups also remain poorly understood.

Based on the data provided by Findlay et al. (2017), the spatiotemporal pattern of the formation of these super-groups has been linked to oceanographic conditions (Dey et al. 2021). Specifically, a relatively high chlorophyll-a concentration in the month prior to the observation of super-groups, combined with the decrease in the water export from the area, seems to provide favorable conditions for the development and concentration of prey species, triggering the formation of super-groups on the west coast of South Africa (Dey et al. 2021). As such oceanographic conditions have a spatiotemporal variation, especially considering climate variabilities, variations in the formation of humpback whale super-groups can be expected. To assess the continued occurrence and variation of this phenomenon in a dynamic and changing ocean, as a follow up from Findlay et al. (2017), we investigated the spatiotemporal occurrence of humpback whale super-groups in South Africa since 2015.

2 | Materials and Methods

2.1 | Data Collection

Sightings of groups of humpback whales on the South African west coast, from False Bay to Lambert's Bay (between 32°–35° S and 16°–20° E) (Figures 1 and 2) were collated from July 2015 to June 2022. Data sources included boat-based and aerial surveys performed by three research groups (Cape Peninsula University

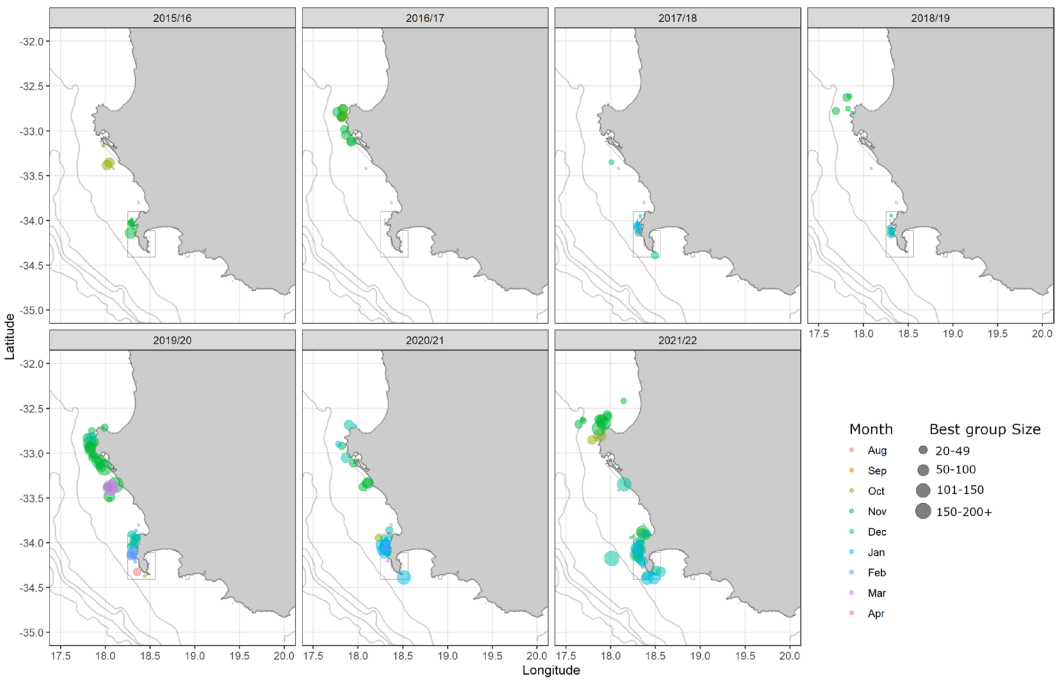

FIGURE 2 | Maps showing the location and size class of humpback whale super-groups on the southwestern coast of South Africa season between 2015 and 2022. Sightings are represented by points, with each month of the year shown in different colors.

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of Technology, University of Pretoria, and Sea Search Research and Conservation), sightings from whale-watching companies operating in the area (Simon's Town Boat Company and Captain Jack's Ocean Safaris), and a citizen science database (Seafari sighting reporting app and a gyrocopter pilot (JT) who performs voluntary conservation photography flights within the study area—all such flights remain at a minimum altitude of 300 m from whales).

2.2 | Data Processing

The compiled dataset was ordered chronologically, standardized, and filtered to avoid duplicates. Confidence in species identification was high as all records were collected by experienced marine mammal observers and/or accompanied by photographs.

Most opportunistic records provided only a single minimum or best estimate or a range of group size (for example "at least 20 whales", "30–50 whales in the area"). Where a range was provided, the arithmetic mean was used as the best estimate (for example 40 whales for a provided range of "30-50 whales in area"). In the Seafari app, sightings of groups larger than nine individuals are recorded in ranges of 10–30, 50–100, and >100 individuals, and users are encouraged to provide exact numbers in the comments field if they are confident of doing so. All sightings from the Seafari app were manually checked and additional details from the comments field were used to improve the precision of the group size and geographic position information of the sightings.

As feeding super-groups occur mainly in the summer months in the focal area (Findlay et al. 2017), data were split across calendar years so that a season is considered from July 1 of each year to June 30 of the following year. The number of super-groups per season and their period and area of occurrence were investigated.

3 | Results

Records of 239 unique humpback whale super-groups were combined from July 2015 to June 2022, with estimated group sizes ranging from 20 to 200 individuals. Citizen scientists contributed 60% of these data, while 40% were from research data. The spatial super-group distribution is shown in Figure 2. Within a season, reports occurred from August to April, with most sightings between late October and January. Only one group was reported for August (August 22, 2019 of 40 to 50 whales off Cape Point); none was ever recorded in September, and only one was recorded in the first half of October. All other records occurred after October 18. The last sighting of super-groups within a year was found to be more variable, ranging from mid-November (November 15, 2015) to early April (April 4, 2018).

The number of records per season increased over time, varying from 10 in 2015/16 to a maximum of 66 in 2019/20 (Figure 3), likely as a result of increased observer effort in the last three years of the dataset.

Most groups ($n = 106$) had a best estimate of between 20 and 29 individuals. Twenty-two groups were reported with a best group estimate of 100 or more individuals (Table 1). The largest overall group was recorded as "three super-groups of approximately 100-300 animals each plus another three groups of 20–30 animals each" on November 28, 2019 in the Seafari app, followed by "Feeding supergroups. Small groups of 10

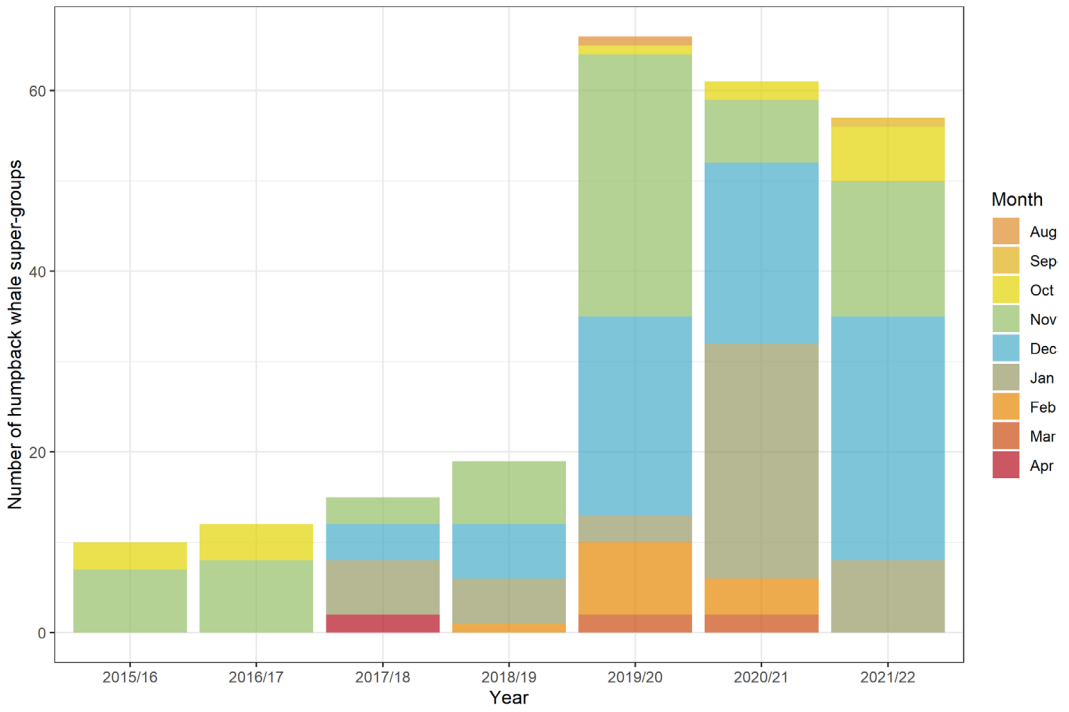

FIGURE 3 | Barplot of the number of humpback whale super-groups reported in each season (calendar years split to encompass a whole summer feeding season from July 1 of 1 year to June 30 of the following year) between 2015 and 2022 on the west coast of South Africa.

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up to groups of 200 whales. About 500 whales in the area" on March 3, 2020. Each of these entries was treated as one record of a super-group, considering that their formation seems to be very dynamic, with individuals getting together and spreading out within a relatively short time (for example hours ~ a day). Calves within the super-groups were only recorded on four occasions, November 2017, November 2018, and October and November 2021.

The mean latitude of super-groups occurrence per calendar month over the season is presented visually as a box and whiskers plot in Figure 4. Super-groups seem to move southward from October–November to December, then stay around the same area until the end of the season.

TABLE 1 | The number of humpback whale super-groups observed in each group size category (considering the best-estimated group size), based on data between 2015 and 2022.

Best group size (number of individuals)	Number of observations
20–29	106
30–39	12
40–49	38
50–99	61
100–200	22

4 | Discussion

The collated dataset provides updated information on the spatiotemporal distribution of humpback whale super-groups on the west coast of South Africa between 2015 and 2022. The data used indicate an annual occurrence of super-groups, with an occurrence restricted to a relatively small area in the southern Benguela ecosystem. Results may be influenced by observer effort to some extent, as most research survey effort is restricted to this part of the coast, and observer interest and effort increased substantially over more recent years, with dedicated research surveys becoming more regular, and an expansion of reporting tools and networks for citizen scientists.

Despite substantial observer effort from different data sources, no super-groups have ever been reported to the east of ~18.5° E (effectively Cape Point), although sporadic feeding events by single animals or small groups are reported by whale-watching operators along the south coast of South Africa. Feeding humpback whales have been regularly reported in areas to the west (offshore) and north of St Helena Bay (~32.5° S) and along the coast of Namibia, although also not forming super-groups (SE, TG, unpublished data). These areas were not covered by research surveys considered here and might also be less covered by citizen science, as they are less populated. Therefore, the occurrence of super-groups in areas beyond the one identified here cannot be completely discounted. For instance, the lack of super-groups reported in the central part of the study area, around Yzerfontein/Dassen Island, is likely a reflection of the stretch being relatively underrepresented in the collated data set. This is supported by

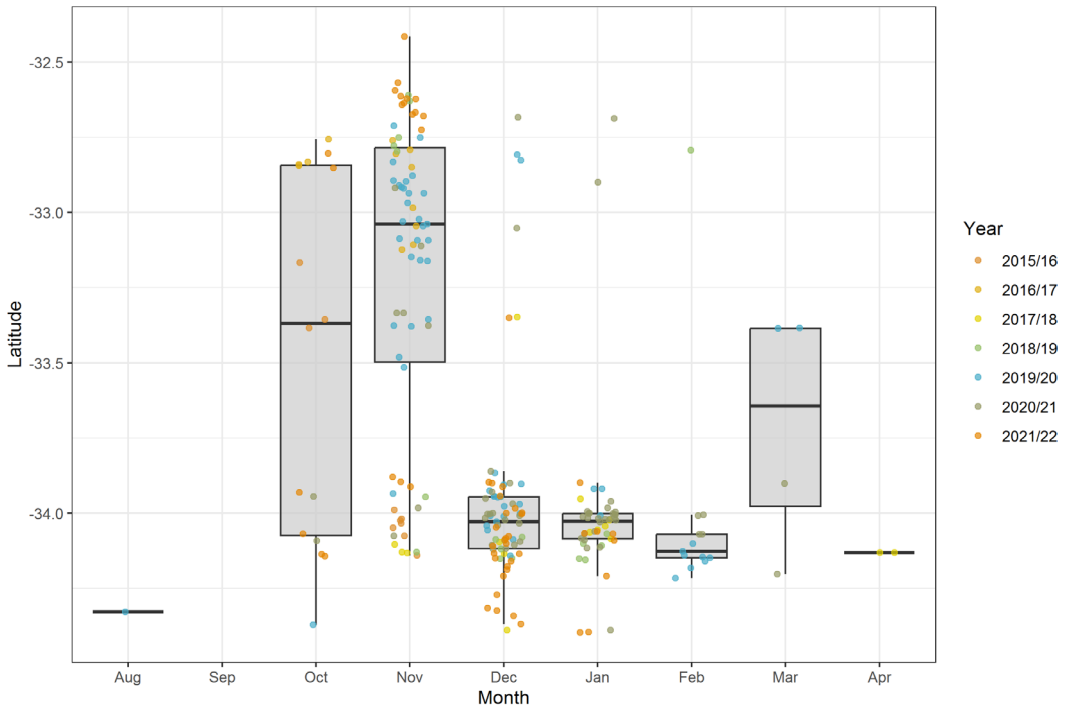

FIGURE 4 | Boxplots indicating the latitudinal range of the reported humpback whale super-groups reported in each month of their occurrence between July 2015 and June 2022. The years refer to calendar years split to encompass a whole summer feeding season from July 1 of 1 year to June 30 of the following year. Dots indicate the latitude of the super-groups location (different colors used by year), black lines represent monthly median latitude, gray areas indicate the range of the middle 50% of the monthly data, while the whiskers extend to the most extreme latitude positions (minimum and maximum values) there are not considered outliers for each month.

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the fact that most super-groups reported by Findlay et al. (2017) were in that area, and by recent reports from a licensed whale-watching operator in the area since late 2022 (Ash Appleby, Pers. Comm.). Although the Benguela ecosystem is considered to extend as far south as Cape Agulhas (~150 km southeast of Cape Point), upwelling is strongest, and associated productivity is highest west and north of Cape Point, where the predominant offshore wind direction creates strong upwelling cells. As per the findings described in Dey et al. (2021), such conditions of high and stationary productivity are important for the formation of super-groups.

The timing of the onset of super-groups from around October every year during the study period seems to align with an increase in upwelling favorable winds and associated increases in phytoplankton and zooplankton densities in the southern Benguela, which typically starts in that month (Dufois and Rouault 2012; Hutchings et al. 2012; Rouault et al. 2010; Verheye et al. 2016). However, it is important to note that significant interannual changes in this upwelling and associated productivity have been found in the area, driven by large-scale oceanographic features such as El Niño and La Niña climatic phenomena, as well as a general decadal-scale increase in wind conditions favorable to upwelling (Hutchings et al. 2012; Rouault et al. 2010; Verheye et al. 2016). The influence of such changes on primary and secondary productivity in the area is complex (Dey et al. 2021) and might vary in time and space along the coast of South Africa (Rouault and Tomety 2022) with a yet unknown impact on humpback whale feeding behavior. Extreme climatic events are predicted to become stronger and more frequent (Cai et al. 2014), so further changes in the ecosystem of the Benguela upwelling system can be expected, with potential impacts on the occurrence of whales in the area, and also on the spatiotemporal formation of super-groups. In turn, the presence of whales in the area could enhance local productivity through the whale pump (Roman and McCarthy 2010; Gilbert et al. 2023). However, although the role of animal-driven nutrient cycling in ecosystems is increasingly recognized (for example Lavery et al. 2010, 2014; Ratnarajah et al. 2018; Gilbert et al. 2023; Roman et al. 2025), the specific contribution of super-groups to this process requires localized assessment.

Supporting earlier observations by Findlay et al. (2017) for the distribution of the super-groups between 2011 and 2015, we observed a southward shift in super-groups during the season, with most groups reported north of Dassen Island early in the season while those off the Cape Peninsula near Cape Town mostly only occurred from December onwards. However, observer bias may affect this result to some extent. Most observations registered through the Seafari app relate to the Cape Peninsula area, leading to reasonable confidence in the low number of super-group observations in this region early in the season (October/November). However, as field efforts by research teams in the area from Saldanha to St Helena Bay tended to be mostly in October–November, the presence of super-groups to the north later in the season may be underestimated. Indeed, Barendse et al. (2010) showed continued feeding of humpback whales off Saldanha Bay from mid to late summer (January–February). Increased observer coverage across the feeding season would help untangle these patterns and reveal the true extent of feeding and super-group occurrence on the coast of South Africa.

The low occurrence of mother-calf pairs in super-groups, despite the post-breeding season timing of their occurrence, also corroborates previous observations and may be evidence that super-groups are formed predominantly by non-breeding individuals (Findlay et al. 2017). In fact, young males, probably yearlings, have been identified during whaling operations in the area throughout the whole austral summer (Olsen 1914).

Aside from South Africa, humpback whale super-groups have been observed off eastern Australia where a few isolated cases were reported in September–October 2020 (Pirotta et al. 2021), although these records seem to be of rather less predictable feeding aggregations. In the Southern Ocean, large feeding aggregations for fin whales (*Balaenoptera physalus*) that could be described as super-groups have been observed in recent years, with groups of up to 150 tightly packed animals engaged in lunge feeding on Antarctic krill (*Euphasia superba*) (for example Burkhardt and Lanfredi 2012; Herr et al. 2022). Pygmy right whales (*Caperea marginata*), the smallest and most elusive of the baleen whales, have also been reported in groups of 8 to 100 individuals feeding on krill near the subtropical convergence (Frainer and Elwen 2024). With the recovery of baleen whale species from commercial whaling, such phenomena might become more common in classic high-latitude feeding grounds, but also in mid-latitudes, with individuals taking advantage of high-productivity areas during migration.

Although there is currently no relative abundance estimate for humpback whales on the west coast of South Africa, the group sizes of the data presented here alone indicate a high density of individuals in the study area during spring and summer. Such numbers would likely be substantially higher than the estimate of 500 individuals in the area for summer between 1983 and 2008 (Barendse et al. 2011). At the same time, it is important to highlight that to date it is not clear if individuals joining super-groups use the west coast (i) as a stopover for opportunistic feeding in the Benguela upwelling system for a short time while/before migrating further south to classic feeding grounds; (ii) as a feeding ground, as known for sub-stock B2, with an unknown breeding ground; or (iii) as residents, exploring its resources year-round. Discussion on this topic was initially raised by Barendse et al. (2011), who found evidence indicating that individuals seem to have a long-term fidelity to the area and some level of residency. However, more in-depth investigations are needed to understand the use of the area by the species, ideally with the association of individuals forming super-groups with specific sub-stocks.

While citizen science data has its limitations and biases, the value of such data cannot be underestimated and is increasingly being used in the field of marine science (for example Kelly et al. 2020; Potts et al. 2021). In the present work, citizen science increased the data available, reinforcing its importance in the generally funding-limited research field in South Africa (Tulloch et al. 2013; Potts et al. 2021). Contributions to the open-access humpback whale fluke matching platform Happywhale (Cheeseman et al. 2017) by researchers and citizen scientists alike have also revealed movements of humpback whales between South Africa and Brazil (Ramos et al. 2023). Efforts for the increased development of citizen science datasets are therefore encouraged.

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In addition, dedicated and systematic research is critical to further our understanding of the formation of humpback whale super-groups, as many research gaps remain in place. These include but are not limited to:

i. The prey items targeted by the super-groups;

ii. The age and social structure of super-groups;

iii. The connectivity of the super-groups to recognized breeding sub-stocks and Antarctic feeding areas.

iv. Abundance estimates and further distribution analyzes to better understand factors that might influence the habitat use of super-groups.

v. The dynamics of formation and stability of the super-groups;

vi. The potential impact of the presence of super-groups on the local ecosystem based on their nutrient cycling contribution.

vii. The assessment of a potential increasing human-wildlife conflict in the area. The large number of whales feeding in the study area can be considered a conservation success story; however, the individuals are using an area of high anthropogenic activities and one of the busiest shipping lanes in southern Africa (for example Cape Town and Saldanha Bay ports) likely increasing human-wildlife conflict. Such spatial overlap needs urgent management and research attention.

Author Contributions

Elisa Seyboth, Ken Findlay, Simon Elwen: conceptualization. **Elisa Seyboth, Simon Elwen:** formal analysis, visualization, and writing – original draft. All authors: data curation and writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

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