CONTRIBUTED PAPER

High-speed chases along the seafloor put Bryde's whales at risk of entanglement

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Abstract
Recent changes in the South African marine ecosystem and the introduction of an experimental octopus fishery have resulted in an unsustainable high rate of fatal Bryde's whale entanglements. Using suction-cup attached bio-loggers, we identified a previously undescribed feeding behavior used by Bryde's whales to catch prey, and this behavior may make them susceptible to entanglement and mortality in bottom-mounted fishing gear. As they chase down their prey, inshore Bryde's whales sprint and maneuver along the seafloor for extended periods of time, making multiple direction changes, and reaching extraordinarily high swimming speeds. These findings assisted in the implementation of mandatory changes to octopus fishing gear that have drastically reduced the number of entanglements. The novel finding that Bryde's whales use high-speed chases near the seafloor to catch their prey highlights the value of using species-specific, behavioral information for making conservation recommendations.

KEYWORDS
Balaenoptera edeni brydei, Bryde's whales, entanglement, kinematics, South Africa
1 | INTRODUCTION

Although baleen whales were nearly hunted to extinction during the industrial whaling era, many species have made strong recoveries in the years since the international ban on commercial whaling went into effect (Thomas et al., 2016). Recently, there have been several high-profile success stories, with large aggregations of whales returning to historical territories they have not occupied for years (Hucke-Baetge et al., 2004; Jackson et al., 2020). However, baleen whales now face a different set of threats that include changing ocean dynamics, increased ship traffic, and entanglement in fishing gear (Moore, 2019; Record et al., 2019; Silber et al., 2012; Tulloch et al., 2019). These growing anthropogenic threats disproportionately impact small, genetically distinct populations in areas densely occupied by humans, and many of these populations remain vulnerable (Caswell et al., 1999; Mate et al., 2015). To complicate matters, the ecology, behavior, and habitat use patterns of small and threatened whale populations tend to be poorly understood (Thomas et al., 2016). Therefore, conservation measures that are urgently implemented during times of crisis are often based on knowledge of better-known species or populations, and this may hamper their effectiveness (Van Der Hoop et al., 2013). Baleen whales are dynamic animals that exhibit regional cultural differences, adaptable foraging strategies, and complex habitat use patterns, and therefore effective conservation measures must take into account the biology of the target population (Brakes et al., 2021; Thomas et al., 2016).

In the past 30 years, South African marine ecosystems and patterns of human use have undergone substantial changes, with fluctuations in small pelagic fish stocks, a geographical shift in their distribution from west to east, a growth in coastal fisheries (Cockcroft et al., 2008; Coetzee et al., 2008; Moloney et al., 2013; Roy et al., 2007), and a national drive to expand the ocean economy (“Operation Phakisa,” www.operationphakisa.gov.za). Consequentially, the only resident baleen whale population in South African waters has come under increased pressure. In South Africa, the Bryde’s whale (Balaenoptera edeni brydei) has two distinct, allopatric forms, recently confirmed as separate subspecies (Best, 1977; Penry et al., 2018). The offshore form inhabits pelagic waters beyond the continental shelf and performs protracted seasonal migrations. The smaller inshore form resides year-round in shallow waters on the continental shelf, makes limited alongshore movements, and regularly forages in sheltered bays.

The inshore population comprises ~600 individuals (Best et al., 1984; Penry et al., 2016) who mostly feed on small pelagic fish such as anchovy (Engraulis capensis) and sardine (Sardinops sagax) (Best, 1977; Best et al., 1984). Like most rorquals, Bryde’s whales are primarily lunge-feeders that forage by accelerating into aggregations of prey, opening their mouths, and engulfing prey-laden water. Yet, Bryde’s whales also show considerable variation in their feeding strategies. Lunging behaviors vary based on prey-type and location in the water column, and some Bryde’s whales use unique foraging behaviors that are distinct from lunges (Iwata et al., 2017). Unlike other rorqual species, Bryde’s whales are neither specialists nor generalists; instead, different populations exhibit highly localized prey preferences and foraging strategies (Constantine et al., 2018; Freitas & Penny, 2021). South African Bryde’s whales follow the annual northwards sardine migration along the east coast, where high prey densities provide a valuable foraging opportunity (Penry et al., 2016). However, given the cryptic and solitary nature of Bryde’s whales (Constantine et al., 2018), little is known about their foraging strategies during the rest of the year, when these whales primarily inhabit sheltered bays with lower prey densities, and where they are likely to encounter human activity. Understanding the foraging ecology, behavior, and habitat use patterns of inshore Bryde’s whales is critical for implementing effective conservation measures designed to reduce human-caused mortality.

Given their small numbers, genetic isolation, and proximity to humans, the inshore South African Bryde’s whale population is highly susceptible to human activities and was classified as Vulnerable in the National Red List Assessment (Penry et al., 2016). At the time of assessment, there were few instances of entanglements (Meýer et al., 2011; Penry et al., 2016). However, recent changes in the existing west coast rock lobster (Jasus lalandii) fisheries (Cockcroft et al., 2008) and the introduction of an experimental octopus (Octopus vulgaris) fishery (started to explore economic viability on a commercial scale; proposed in Oosthuizen, 2004) have resulted in an unexpectedly high rate of fatal Bryde’s whale entanglements. Between 2014 and December 2021, 17 Bryde’s whales were observed entangled in fishing gear, and at least 10 entanglements were fatal (Table 1). The fishing gear involved in these entanglements was primarily used for trapping common octopus (seven confirmed, one suspected) and rock lobster (four) and was identified on both live and dead whales. All of these entanglements occurred near the seafloor (based on the position of the gear on the animal) and likely happened while the whales were feeding (in most instances a rope was caught in the mouth, Table 1 and Figure 1). Any rope that rises into the water column is a potential entanglement hazard for large whales (Moore, 2019). However, certain species are more susceptible to entanglement in the groundlines that run between traps, while other species are more at
risk from marker lines that extend to the surface. Factors such as species-specific behavioral patterns, habitat use, and fishing gear configuration play a significant role in the risk, severity, and outcomes of entanglement (Johnson et al., 2005; Meÿer et al., 2011). The octopus fishery has only been operating for a few years and at a very limited capacity; however, the high rate of entanglements suggest that octopus fishing gear poses an extreme hazard for inshore Bryde’s whales.

The increasingly common entanglement of South African inshore Bryde’s whales in bottom-mounted fishing gear has become an urgent conservation issue. This is exacerbated by the small size of this genetically distinct population, the poorly understood ecology and behavior of the species, and the potential for rapid commercial expansion of the experimental octopus fishery. Therefore, the goals of this study were: (1) to use whale-born multisensor bio-loggers to determine if inshore South African Bryde’s whales use specific foraging strategies that put them at high risk for entanglement with bottom-mounted fishing gear; and (2) to recommend policy interventions that could mitigate the risk of entanglement-related mortality. In 2019, the results of this study informed the decision to place restrictions on octopus fishing gear. The South African government worked quickly and decisively to make data-driven policy changes, and there have been fewer entanglements since the new regulations were implemented. It remains to be seen whether this success can be maintained as the octopus fishery continues to expand and as the whales adapt their behaviors to a changing environment.

### METHODS

In April of 2018 and 2019, we deployed suction-cup attached bio-logging tags on 12 inshore Bryde’s whales in Plettenberg Bay, South Africa (34°04’S, 23°27’E). The whales were approached in a rigid-hulled inflatable boat and tags were deployed using a long pole (Goldbogen et al., 2019). The bio-loggers were outfitted with depth sensors (10 Hz), accelerometers (400 Hz), magnetometers (50 Hz), Global Positioning System (GPS), and cameras (Customized Animal Tracking Solutions; Goldbogen et al., 2017). After the tags were recovered, the accelerometer and magnetometer signals were aligned with the body axis of the whale (Cade et al., 2021; Johnson & Tyack, 2003), were smoothed with a low-pass filter (forward-backward Butterworth filter, cutoff frequency = 0.15 Hz; Segre et al., 2016), designed to isolate the movement of the body

<table>
<thead>
<tr>
<th>Date (month/year)</th>
<th>Gear type</th>
<th>Components involved</th>
<th>Entanglement</th>
<th>Result</th>
</tr>
</thead>
<tbody>
<tr>
<td>April 2014</td>
<td>Octopus</td>
<td>Groundline</td>
<td>Mouth and body</td>
<td>Died</td>
</tr>
<tr>
<td>May 2016</td>
<td>Octopus</td>
<td>Marker line</td>
<td>Unknown</td>
<td>Freed itself</td>
</tr>
<tr>
<td>June 2016</td>
<td>Possible octopus</td>
<td>Unknown</td>
<td>Mouth</td>
<td>Broke free with rope</td>
</tr>
<tr>
<td>June 2016</td>
<td>Octopus</td>
<td>Marker line</td>
<td>Mouth and body</td>
<td>Died</td>
</tr>
<tr>
<td>September 2016</td>
<td>Rock lobster</td>
<td>Marker line</td>
<td>Tail</td>
<td>Broke free with rope</td>
</tr>
<tr>
<td>May 2017</td>
<td>Octopus</td>
<td>Groundline</td>
<td>Mouth and body</td>
<td>Died</td>
</tr>
<tr>
<td>January 2018</td>
<td>Rock lobster</td>
<td>Marker line</td>
<td>Mouth and body</td>
<td>Disentangled</td>
</tr>
<tr>
<td>March 2018</td>
<td>Octopus</td>
<td>Groundline</td>
<td>Mouth and body</td>
<td>Died</td>
</tr>
<tr>
<td>April 2018</td>
<td>Illegal gill net</td>
<td>Net</td>
<td>Caught in net</td>
<td>Died</td>
</tr>
<tr>
<td>October 2018</td>
<td>Unidentified rope</td>
<td>Unknown</td>
<td>Mouth and body</td>
<td>Died</td>
</tr>
<tr>
<td>March 2019</td>
<td>Octopus</td>
<td>Groundline</td>
<td>Mouth and body</td>
<td>Died</td>
</tr>
<tr>
<td>March 2019</td>
<td>Muscle seeding line</td>
<td>Horizontal line</td>
<td>Mouth</td>
<td>Broke free with rope</td>
</tr>
<tr>
<td>July 2019</td>
<td>Octopus</td>
<td>Marker line</td>
<td>Mouth and body</td>
<td>Died</td>
</tr>
<tr>
<td>November 2019</td>
<td>Purse seine net</td>
<td>Net</td>
<td>Caught in net</td>
<td>Died</td>
</tr>
<tr>
<td>January 2020</td>
<td>Anchor chain</td>
<td>Chain</td>
<td>Mouth and body</td>
<td>Disentangled</td>
</tr>
<tr>
<td>May 2020</td>
<td>Rock lobster</td>
<td>Marker line</td>
<td>Tail</td>
<td>Disentangled</td>
</tr>
<tr>
<td>October 2020</td>
<td>Rock lobster</td>
<td>Marker line</td>
<td>Mouth and body</td>
<td>Died</td>
</tr>
</tbody>
</table>

Note: Most entanglements involved octopus fishing gear (seven confirmed, one suspected). In November 2019, new regulations on octopus fishing gear designed to mitigate entanglement were implemented (Table 3). Since then, there have been no Bryde’s whale entanglements involving the octopus fishery. Data collected by the South African Whale Disentanglement Network.
from the movement caused by the fluke strokes, and were used to calculate the body orientation of the whale (pitch, roll, heading; Johnson & Tyack, 2003). An unsmoothed version of the pitch was filtered with a band-pass filter (forward-backward Butterworth filter, cf $= 0.15, 0.40$ Hz; Segre et al., 2019) to obtain a nondimensional representation of the fluke stroke. The speed was calculated by calibrating the background, high-frequency accelerometer vibrations (400 Hz) against the orientation-corrected depth rate (Cade et al., 2018). To remove sampling error, speed and depth were smoothed with a low-pass filter (cf $= 0.40$ Hz).

Using the depth, speed, and body orientation, we identified trajectories where the whales descended, swam at high speeds along the seafloor, and performed a feeding lunge (Figure 2a). The chases were primarily identified by looking for U-shaped dives, where the depth at the bottom remained constant for $>15$ s (long enough to ensure that the whale was swimming along the seafloor), where the lunging maneuver occurred at the same depth as the chase, and where the speeds were higher than the average Bryde's swimming speed (1.7 m/s; Gough et al., 2019). Lunges were identified by a rapid acceleration followed by a dramatic decrease in speed (Figure 2a; Cade et al., 2016; Goldbogen et al., 2006). We broadly confirmed the seafloor depth by matching GPS data recorded while the whale was at the surface with the bathymetry. From each event, we measured the duration of the trajectory (starting when the whale arrived at the seafloor; ending immediately after engulfment), the distance traveled along the seafloor (Figure 2b; calculated using the speed and the heading; Ware et al., 2006), and the top speed (Figure 2a).

Examinations of entangled Bryde's whales were conducted with a permit from the South African Department of Forestry, Fisheries, and Environment (DFFE) as part of the efforts of the South African Whale Disentanglement Network (SAWDN). All entangled whales were examined by MAM or GSP (in person or using detailed
photographs) to determine the type of fishing gear involved, the configuration of the ropes on the body, and the outcome of the entanglement (Table 1).

3 | RESULTS

We identified 27 high-speed seafloor chases performed by five Bryde’s whales (Table 2). The predatory chases ranged in depth from 18 to 98 m; had an average duration of 35 s (range: 15–95 s); an average top speed of 5.3 m/s (range: 3.8–7.4 m/s); and an average distance traveled of 86 m (range: 42–253 m). Most of the chase trajectories (n = 17) ascribed simple arcs with only a single-direction change (heading change range: 42°–299°). Many of the chase trajectories (n = 10) included two or more direction changes. Although we identified several other types of feeding behaviors present in the bio-logger data, the seafloor chasing behavior was present in multiple animals and in both years of the study. Our estimates of the prevalence of this behavior are conservative given that we did not include failed chases that ended without

FIGURE 2 Bio-logger data reveal that South African Bryde’s whales use high-speed chases to catch low-density schools of fish. (a) A Bryde’s whale descends to the seafloor (blue line) and swims in high-speed arcs (purple line) before accelerating to catch its prey (red line). Once it finishes filtering (A, yellow circle) it descends to the seafloor again for another chase. (b) A side view, top-down view, and three-dimensional view of the seafloor chase that lasts 37.7 s and covers 94 m. (c) Swimming and turning at high-speed near the seafloor, for extended distances puts Bryde’s whales at risk for encountering and getting entangled in poorly anchored fishing gear.

<table>
<thead>
<tr>
<th>Whale</th>
<th>Year</th>
<th># Chases</th>
<th>Max speed (m/s)</th>
<th>Duration (s)</th>
<th>Distance (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2018</td>
<td>3</td>
<td>4.6 (4.1, 4.9)</td>
<td>56 (34, 95)</td>
<td>141 (75, 253)</td>
</tr>
<tr>
<td>2</td>
<td>2018</td>
<td>5</td>
<td>4.7 (3.9, 5.6)</td>
<td>32 (22, 47)</td>
<td>91 (48, 166)</td>
</tr>
<tr>
<td>3</td>
<td>2018</td>
<td>11</td>
<td>5.7 (4.9, 7.4)</td>
<td>28 (15, 56)</td>
<td>75 (42, 148)</td>
</tr>
<tr>
<td>4</td>
<td>2019</td>
<td>5</td>
<td>5.7 (5.1, 6.1)</td>
<td>31 (42, 25)</td>
<td>66 (53, 82)</td>
</tr>
<tr>
<td>5</td>
<td>2019</td>
<td>3</td>
<td>4.5 (3.8, 5.1)</td>
<td>48 (36, 64)</td>
<td>100 (66, 141)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>27</td>
<td>5.3 (3.8, 7.4)</td>
<td>35 (15, 95)</td>
<td>86 (42, 253)</td>
</tr>
</tbody>
</table>

Note: The average maximum speed, duration, and distance are shown for each whale, with minimum and maximums displayed in parenthesis. The complete dataset is available in the Supporting Information.
Mitigation measures designed to reduce entanglement of large whales in octopus fishing gear

**Regulations:**
1. The bottom line should consist of entirely of sinking ropes.
2. The chain on the buoy line must be moved from the top of the line to the bottom.
3. There must be sheathing of the top 2 m of the buoy line with PVC piping/tubing.
4. The buoy must be mounted on the bottom with timed released mechanisms.

The octopus fishery will be halted if there are:
1. Two or more entanglements of southern right whales or humpback whales in 3 months.
2. One Bryde’s whale entanglement.
3. One mortality from any of these three species.

**Note:** The regulations were implemented on November 15, 2019 by the Department of Forestry, Fisheries, and Environment.

South African Bryde’s whales sprint and maneuver along the seafloor to catch schools of fish, and this unique behavior may make them susceptible to entanglement in bottom-mounted fishing gear. The seafloor chases often lasted for extended periods of time (up to 95 s), with the whales traveling long distances (up to 253 m), making multiple direction changes, and reaching high swimming speeds (up to 7.4 m/s; compared to cruising speeds of 1.9 m/s; Gough et al., 2019). These movement patterns, followed by a terminal lunge, suggest that the whales were actively chasing fleeing prey. Although the whales changed heading, they mostly remained rolled upright and neutrally pitched throughout the trajectory (Figure 2a), suggesting that the whales were maintaining close contact with the seafloor and not swimming in the vertical dimension (Segre et al., 2019). Our findings agree with previous observations: extensive scratching found on the underside of inshore Bryde’s whale flukes led to the hypothesis that these whales often forage in shallow water, where they make frequent contact with the seafloor (Best, 1977). Extended chasing behaviors have not been documented in other rorqual species and may be unique to inshore Bryde’s whales. The onboard videos suggest the whales were feeding on low-density schools of fish, and this prey-type and abundance may compel the use of these complex predatory maneuvers. The act of locking onto, chasing down, and capturing small schools of fish represents a different feeding style than rorqual whales normally employ.

Swimming, turning, and lunge-feeding at high-speed near the seafloor puts Bryde’s whales at risk of encountering and becoming entangled in bottom-mounted fishing gear. Octopus fishing gear consists of ~30 traps spaced 10–20 m apart with 16 mm diameter floating groundline, and anchored to the seafloor. The lines connecting the traps float, forming loops between traps (some arching up to 4 m above the seafloor; Figures 1 and 2c) that are an entanglement risk to whales chasing fish near the seafloor. Between 2014 and 2021, four Bryde’s whales were entangled in the groundlines of octopus gear. Vertical buoy marker lines also represent an obstacle that can catch a whale’s mouth or tail as it swims by, and many of the buoy marker line entanglements occurred near the seafloor (three Bryde’s entanglements involved vertical lines). Given the eight entanglements that occurred in the last 7 years, and the small size of the experimental octopus fishery, it is apparent Bryde’s whales are vulnerable to entanglement in octopus gear. Furthermore, entanglements involving the heavy traps and extensive 16 mm groundlines of octopus gear are often fatal for the relatively small (<15,000 kg) Bryde’s whales, who become anchored below the surface and die before they can be freed by disentanglement teams. The seafloor chasing behavior provides an explanation for how Bryde’s whales encounter both the groundlines and the vertical lines of octopus fishing gear.

In contrast, the majority of gear used for catching rock lobster consists of single traps attached to 12 mm diameter vertical marker lines. Lobster traps are often set in clusters that form thickets of vertical ropes, which present an entanglement hazard for many whale species (Meýer et al., 2011). However, the west coast rock lobster fishery is considerably larger than the experimental octopus fishery (in 2021, 983 permits were issued for west coast rock lobster and four for octopus), but has historically accounted for a smaller number of Bryde’s entanglements (four individuals). This suggests that either Bryde’s whales are less susceptible to entanglement in rock lobster traps, or they are separated (spatially or behaviorally) from the trapping activities. The chasing behaviors we documented occurred along a sandy seafloor: the type of substrate used for trapping octopus. Meanwhile, the rocky seafloors where lobster occur may be less conducive to extended chases. More recently (in 2020), two Bryde’s whales were entangled in rock lobster gear, and it remains to be seen if changes to fishing gear reduce entanglements or if entanglements become more frequent as the shifting ecosystem alters the behaviors and distributions of the...
whales, small schooling fish, rock lobsters, and the respective fisheries (Moloney et al., 2013).

Since the 2006 establishment of the SAWDN, 240 known large whale entanglements have occurred in South African waters. Most of these involved the two migratory species: southern right whales (Eubalaena australis) and humpback whales (Megaptera novaeangliae). These species are primarily susceptible to entanglement in shark exclusion nets and vertical lines (Meÿer et al., 2011), and most entanglements did not appear to be linked to feeding behaviors (unlike with Bryde’s whales). However, there is evidence that recent changes in the ecosystem have altered historic foraging patterns of these two migratory species (Findlay et al., 2017), which could increase the future risk of entanglements in all types of fishing gear.

For the small, genetically distinct population of inshore Bryde’s whales the current rate of fishing gear entanglement is considered likely to be unsustainable. In 2019, after three whales were killed within a few weeks, a large public outcry ensued and a temporary moratorium was placed on the octopus industry. Following this, an emergency meeting was called by the Minister of Forestry, Fisheries, and the Environment in which preliminary results from this study were presented. Initial discussions at the first committee meeting explored the viability of spatial and temporal closures to the fishery, however these were based on the timing and distributional knowledge of the better-known migratory species (humpback and southern right whales) and would have done little to limit the risk to the resident Bryde’s whale population. In subsequent discussions, the results of this study and the necropsy data assisted in the decision to prioritize the implementation of mandatory changes to the octopus fishing gear rather than imposing spatial or temporal closures to the fishery (SADFFE, 2019). The gear must now include sinking groundlines, redesigned vertical lines, and acoustic or time release mechanisms on sunken buoys (Table 3). Grappling can be used to recover gear, as an alternative to vertical lines and bottom mounted buoys. Additionally, the octopus fishery will be temporarily halted if there are two additional non-fatal entanglements of humpback or right whales, or a single entanglement of a Bryde’s whale. The fishery will be permanently halted following a fatality from any of the three species. Since the new regulations went into effect on November 15, 2019, there have been no Bryde’s whale entanglements in octopus fishing gear. The South African government worked decisively to make data-driven policy changes and should be commended for their swift action. While these are steps in the right direction, it remains to be seen whether they will be effective in reducing whale entanglement, and if they will allow for the large-scale expansion of the octopus fishery. This will require long-term monitoring (Ebdon et al., 2020) and a willingness to adapt if changing conditions (behavioral, environmental, or political) decrease the effectiveness of these mitigating strategies (Davies & Brillard, 2019; Record et al., 2019). The novel finding that Bryde’s whales use high-speed chases near the seafloor to catch their prey highlights the value of using species-specific, behaviorally based information for making conservation and management recommendations.

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CONFLICT OF INTEREST
The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS
Conceptualized the manuscript: Paolo S. Segre, Gwenith S. Penry, and Jacopo di Clemente. Conducted the field work: Paolo S. Segre, Gwenith S. Penry, Jacopo di Clemente, Shirel R. Kahane-Rapport, and William T. Gough. Conducted the necropsies: Michael A. Meÿer and Gwenith S. Penry. Supervision: Amanda T. Lombard and Jeremy A. Goldbogen. Wrote the manuscript: Paolo S. Segre and Gwenith S. Penry. All of the authors edited and provided comments.

DATA AVAILABILITY STATEMENT
Data are available in the supplementary materials.

ETHICS STATEMENT
This study was conducted under permits issued by the Department of Forestry, Fisheries, and the Environment (RES 2018/632019/57) and ethics approval from Nelson Mandela University (A19-SCI-ICMR-001) and Stanford University.

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