

Human disturbance impact on shorebirds at Muizenberg Beach, South Africa, during and prior to the COVID-19 lockdown

Jemma Elizabeth Lewis (LWSJEM001)

Supervised by Associate Professor Deena Pillay, Department of Biological Sciences,
University of Cape Town



Minor dissertation presented in partial fulfilment of the requirements for the degree of MSc in
Applied Ocean Sciences

Department of Biological Sciences

University of Cape Town

Rondebosch, 7701

South Africa

March 2021

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

PLAGIARISM DECLARATION

I understand that plagiarism is to copy another's ideas or work (word-for-word or by paraphrasing) and pretend it is one's own, and that this is wrong. I personally produced this report and verify that it contains only my own work, unless otherwise indicated using the referencing and citations. This work has not previously been submitted to or published by any other entity. To my knowledge, no one else has copied the work presented in this report. No one will be allowed to copy this work in future and present it as their own.

Signed: Date: 30/03/2021

ABSTRACT

The impact of humans on the natural environment has been so extensive that the scientific community has defined a new geological era: the Anthropocene. Coastal ecosystems rank amongst the most threatened of global habitats due to high urban human population density and demand for socio-ecological services provided by the coast. Sandy beach ecosystems are prominent constituents of coastal regions and sought after for their recreational value, but these systems are understudied relative to more charismatic marine habitats such as coral reefs and kelp forests. Human disturbance has been identified as one of the most serious threats to sandy beach ecosystems, but several knowledge gaps prevail, including its effects on shorebirds. The 2020 global COVID-19 pandemic resulted in a period of abnormally limited human mobility that has been coined the ‘anthropause’. In South Africa, a national lockdown commenced on 27 March 2020 and consisted of five levels to combat the pandemic. Specifically, lockdown levels 5, 4, and 3 did not permit human presence in public areas, including beaches. The aim of this study was to understand the impact of human disturbance during and prior to the COVID-19 lockdown on shorebird abundance and community structure on Muizenberg Beach, South Africa ($34^{\circ}06.3'S$ $18^{\circ}28.3'E$), using two approaches. The first approach used photographic data to compare shorebird numbers across five lockdown levels in 2020 with equivalent periods in 2019 (prior to the pandemic) to determine the effects of contrasting levels of human abundance on shorebirds. Results from this component indicated that shorebird abundance was negatively related to human abundance and year, but positively associated with the lockdown levels. Most importantly, greatest shorebird abundance across the study were recorded under lockdown levels 5 and 4, when there were virtually no humans on the beach. Similarly, the lowest bird abundance was recorded under lockdown level 1, when human abundance was greatest for 2020. The second approach implemented in this study was based on *in situ* counts of shorebirds on Muizenberg Beach between lockdown levels 3 and 1 in 2020,

to understand how intermediate to moderate levels of lockdown influenced shorebird community structure. PERMANOVA analysis indicated that while a significant difference in the shorebird community structure among lockdown levels was detected, it was secondary relative to zonal variation. SIMPER analysis showed *Larus dominicanus* (Kelp Gull) to be the dominant shorebird species, contributing the most to community structure within all three lockdown levels. Significant differences in community indices and *L. dominicanus* abundance were detected between zones but not lockdown levels, apart from the Shannon-Wiener diversity metric. In general, the minor effects of lockdown levels 3 to 1 on the shorebird community were attributed to high human numbers on the beach and low species variation across the respective lockdown levels. Overall, results indicate a strong negative relationship between shorebird and human abundance on Muizenberg Beach over a two-year period prior to, and including, periods of enforced lockdown. At intermediate to moderate levels, however, lockdown had minimal effects on community structure. In a global context, findings provide valuable information on human impacts on sandy beach shorebirds and suggest that closure for two months may positively impact bird communities within urban beach ecosystems.

ACKNOWLEDGMENTS

I would like to acknowledge and express my appreciation to the University of Cape Town, Postgraduate Funding, for the funding provided to complete my Coursework Master's degree. On a personal level, I would like to give my sincere gratitude to my supervisor, Associate Professor Deena Pillay, for his continued support, availability and guidance during an extremely difficult period brought about by the COVID-19 pandemic. This study would not have been possible without the photographic library of Muizenberg Beach supplied by Associate Professor Coleen Moloney and her student Casha De Vos, for which I am extremely grateful. I would like to extend my appreciation to Jayden Collison for his help analysing the *in situ* data component of my dissertation. Additionally, I would like to thank Jayden, Alexandra Azevedo, and Matthew Germishuizen for their help with the *in situ* data collection. Lastly, I would like to thank my family and friends for their unwavering support and invaluable input throughout my MSc studies.

CONTENTS

1. INTRODUCTION.....	1
1.1 The anthropocene and increasing human population along the coast	1
1.2 Sandy beaches and ecosystem functions.....	2
1.3 Impact of human disturbance on shorebirds.....	3
1.4 COVID-19 and the South African lockdown.....	9
1.5 Aims and hypotheses.....	10
2. METHODOLOGICAL APPROACH.....	12
2.1 Study site.....	12
2.2 Data collection.....	12
<i>2.2.1 Photographic data: 2019 vs 2020</i>	
<i>2.2.2 <u>In situ</u> data collection (lockdown levels 3, 2 & 1) in 2020</i>	
2.3 Statistical analysis.....	18
<i>2.3.1 Photographic data: 2019 vs 2020</i>	
<i>2.3.2 <u>In situ</u> data collection (lockdown levels 3, 2 & 1) in 2020</i>	
3. RESULTS.....	20
3.1 Statistical analysis.....	20
<i>3.1.1 Photographic data: 2019 vs 2020</i>	
<i>3.1.2 <u>In situ</u> data collection (lockdown levels 3, 2 & 1) in 2020</i>	
4. DISCUSSION.....	30
4.1 Photographic data: 2019 vs 2020.....	31

4.2 *In situ* data collection (lockdown levels 3, 2 & 1) in 2020.....34

5. CONCLUSION.....37

6. REFERENCES.....39

7. APPENDIX 1.....53

1. INTRODUCTION

1.1 The Anthropocene and increasing human population along the coast

The extraordinary ability of humankind to engineer ecosystems has long distinguished us from other species and has led to unprecedented population growth over the past half a century (Vitousek et al., 1997; Ellis and Ramankutty, 2008). The impact of humans on the natural environment has been so extensive that the scientific community has established a new geological era: the Anthropocene (Lewis and Maslin, 2015; Monastersky, 2015). This era is characterised by the concurrent ‘twin environmental crises of our time’ (Corlett et al., 2020): an unprecedented rate of biodiversity loss and a notable change of the Earth’s climate (Díaz et al., 2019; Intergovernmental Panel on Climate Change, 2019a). These interconnected global crises are eliciting immense ecological, economic and social impacts, highlighting the unsustainable nature of modern urbanisation and habitation (Biggs et al., 2011; Díaz et al., 2019; Coll, 2020).

Anthropogenic activities have altered at least 70% of the land surface (Watson et al., 2016; Intergovernmental Panel on Climate Change, 2019b) and increasing cumulative impacts are also being experienced by 66% of the ocean surface (Halpern et al., 2015). Coastal ecosystems, which are unique ecotonal interfaces between the land and ocean, are among the most threatened of ecosystems by anthropogenic activities (Neumann et al., 2015). Human population density is significantly higher in coastal than non-coastal regions (Small and Nicholis, 2003), and in relation to other ecosystems, coastal ecosystems are showing some of the most rapid and largest recent declines in species (Díaz et al., 2019). Coastal ecosystems provide access points for marine trade and transport, are rich in subsistence resources, and facilitate recreational and cultural activities (Neumann et al., 2015) – factors

which have long attracted people and continue to facilitate human settlement (Small and Nicholis, 2003).

Of further concern is that development and utilisation within coastal regions have greatly increased in the past decade, with continued trends of coastal immigration being observed (Hugo, 2011; Neumann et al., 2015). Population growth and development place high pressure on coastal ecosystems and natural resources through pollution and utilisation, and are therefore critical drivers of change in these habitats (Crossland et al., 2005; Patterson and Hardy, 2008).

1.2 Sandy beaches and ecosystem functions

Coastal regions are dominated by sandy beach ecosystems, which experience high human disturbance in relation to other coastal ecosystems (McLachlan and Brown, 2006; Defeo et al., 2008). Sandy beaches are important socioeconomic resources, supporting extensive tourism, and recreation economies (Pendleton et al., 2001). Additionally, sandy beaches provide essential ecosystem services that drive multifunctionality within the larger coastal ecosystem, while supporting unique biodiversity (Schlacher et al., 2008; Schooler et al., 2019). The most important ecological functions provided by sandy beaches include: provision of critical foraging areas for higher vertebrates such as birds and fish; provision of nesting and nursery areas for birds and turtles; mineral recycling and water filtration, and the linking of terrestrial aquifers with coastal waters through nutrient rich groundwaters (Schlacher et al., 2008).

Sandy beach ecosystems face additional stressors since they are caught between both rising sea levels on the marine side and expanding human populations and coastal development on the land side (Schalcher et al., 2008). Sandy beaches are being modified and negatively affected by a wide range of human activities including the destruction of dune and beach habitats by

coastal development (Defeo et al., 2008), beach nourishment (Jones et al., 2008), shoreline armouring (Dugan et al., 2008), wildlife disturbance (Yasué and Dearden, 2006), pollution (Junoy et al., 2005), rigorous beach maintenance regimes (Schooler et al., 2019), and increased demand of their ecosystem services from a growing coastal population (Gül and Griffen, 2020).

The abovementioned human impacts have cumulatively led to a decline in biotic abundance and diversity in sandy beach ecosystems (Schlacher et al., 2008; Gül and Griffen, 2020) and an alteration in interspecific interactions (Maxwell et al., 2013). Due to the detrimental shifts sandy beach ecosystems are experiencing, it is of great importance to understand how these ecosystems and the species utilising them will respond to the increasing pressures from a growing human population.

1.3 Impact of human disturbance on shorebirds

In sandy beach ecosystems, shorebirds are one of the biotic assemblages impacted by human disturbance. In fact, human disturbance has been identified as one of the most serious threats to shorebird assemblages (Atlantic Flyway Shorebird Initiative, 2016; Mengak and Dayer, 2019). Nevertheless, it is still unclear what constitutes human disturbance, and what the associated impacts are, and a better understanding of these issues is vital to conserve and sustainably manage shorebird populations.

Mengak and Dayer (2019), conducted an extensive study that brought together managers and scientists to co-produce a shared definition of what constitutes human disturbance relative to shorebirds. The final consensus reached was that: human disturbance changes the normal behaviour of shorebirds. This conclusion is in line with several other definitions (Fox and Madsen, 1997; Nisbet, 2000; Frid and Dill, 2002; Stillman et al., 2009), importantly however,

it is expanded to include the finding that such disturbance will lead to additional energy expenditure by shorebirds. The behavioural changes and additional energy expenditure may result in reduced productivity and survival rates. Resident birds are thought to be more tolerant of disturbance as they may become habituated to predictable and non-threatening events (Baudains and Lloyd, 2007). By having a clear definition of what constitutes human disturbance to shorebirds, it is easier to identify how they will be affected by the disturbance and how to mitigate the impact on shorebird populations.

Numerous studies have shown human disturbance to negatively impact shorebird populations and communities. A summary of these studies is reviewed in detail in Table 1. Direct impacts of human disturbance on shorebirds include decreased abundance, behavioural changes, a reduction in foraging time and increased energy expenditure (Thomas, Kvitek and Bretz, 2003; Burger et al., 2004; Yasué, 2006; Rogers, Piersma and Hassell, 2006; Yasué, Dearden and Moore, 2008; Glover et al., 2011; Martin et al., 2015; Murchison, Zharikov and Nol, 2016; Navedo et al., 2019). These impacts in turn can sometimes negatively impact shorebird body-condition, true-annual survival rate, fecundity and breeding success (Beale and Monaghan, 2004; Weston et al., 2012; Gibson et al., 2018). Additionally, human impacts influence shorebird community structure, habitat selection at a local and landscape scale, prevent access to feeding areas and limit population sizes (Thomas, Kvitek and Bretz, 2003; Rogers, Piersma and Hassell, 2006; Meager et al., 2012; Ryan, 2013).

Nevertheless, human disturbance does not always result in negative impacts on shorebird communities, with some studies indicating negligible to favourable effects (Peters and Otis, 2006; Baudains and Lloyd, 2007; Yasué, Dearden and Moore, 2008). As is evident in Table 1, the majority of studies regarding human disturbance and sandy beach shorebirds have been conducted in the Northern hemisphere, and of the remaining studies, four were in Australia,

two in South Africa and one in Chile. This highlights the need for additional research on human disturbance impacts on shorebirds in the Southern hemisphere and in third world countries, such as South Africa and Chile.

The studies reviewed in Table 1 have employed different methodological techniques to quantify the impact of human disturbance on shorebird communities and populations. Studies have also varied temporally (duration) and spatially (number of sites) and comparisons were made using one or both approaches. The reviewed studies typically made use of spatio-temporal comparisons of shorebird responses to lower and higher levels of human disturbance on shorebirds (Table 1). However, due to logistical reasons, none were able to assess the impact of no human disturbance on shorebirds for an extended period of time. Some studies made use of temporal exclusion of human disturbance around nesting areas regularly frequented by humans (Weston et al., 2012), but at a limited spatial scale. The 2020 global COVID-19 pandemic has however allowed human exclusions to be possible at scales in space and time that would otherwise have been difficult to achieve, thereby facilitating a meaningful study of the impact of human absence on shorebird communities.

Table 1: Review of global studies on the impact of human disturbance on shorebirds between 2003 and 2019. Included are the study location, methodology used, organisational level at which shorebird responses were tested and the main conclusions of the study.

Location	Method	Organisational level	Conclusions	Reference
California, North America	-Study period: 1 yr. -Temporal comparison (spring and fall migrations) -Spatial comparison (2 sites varying in human disturbance)	Population and individual	-The number and activity of humans significantly reduced the foraging time of <i>Calidris alba</i> . - <i>C. alba</i> was negatively impacted most by free running dogs.	Thomas, Kvitek and Bretz, 2003
East Lothian Scotland	-Study period: 1 yr. -Experimental (manipulation of food and human disturbance)	Population and individual	-Birds in better condition responded sooner to human disturbance and were more alert, whereas birds in poor condition showed the least behavioural response. -Results suggest behavioural indexes of disturbance are flawed.	Beale and Monaghan, 2004
Delaware Bay, North America	-Study period: 20 yrs. -Temporal comparison (1982, 1987, 1992, 2002)	Community and individual	-Human disturbance in 58% of the cases resulted in birds flying away. -Foraging was disrupted by the presence of people and dogs.	Burger et al., 2004
South Carolina, North America	-Study period: 4 yrs. -Temporal comparison (23 surveys)	Community	-Roost-site selection for most species was not influenced by human disturbance (boating). -Roost-site selection was determined by environmental factors.	Peters and Otis, 2006
North-western Australia	-Study period: 4 yrs. -Spatial comparison (5 sites, varying in tidal height and disturbance)	Population and individual	-Human disturbance and predation induced marked energetic costs on roosting birds. -Disturbance at roost sites and roost availability limited access to feeding areas and limited population size.	Rogers, Piersma and Hassell, 2006
Vancouver Island, Canada	-Study period: 1 month -Spatial comparison (habitat choice and environmental factors)	Community and individual	-Bird responses to human disturbance depends on associated energetic or predation risk costs. -Birds responded more to human disturbance when foraging costs are lower.	Yasué, 2006

Table 1 continued.

Location	Method	Organisational level	Conclusions	Reference
Gulf of Thailand	-Study period: 1 yr. -Spatial comparison (4 sites varying in habitat type and human density)	Population and individual	- <i>Charadrius peronii</i> selected beaches with low human disturbance. -The chance of hatching clutches and fledging chicks was greater in areas with lower human disturbance.	Yasué and Dearden, 2006
Cape Peninsula, South Africa	-Study period: 8 yrs. -Temporal comparison (1998 vs. 2005)	Population and individual	-Incubating birds had greater nest attentiveness at the more disturbed site. -Chick mortality was significantly higher in disturbed sites. -Fecundity was notably higher in disturbed sites.	Baudains and Lloyd, 2007
New Jersey, North America	-Study period: 1 month -Observational (behaviour) -Spatial comparison (habitat type)	Community and individual	-Gulls are less impacted by human disturbance than other birds. -Dogs caused the highest disturbance to birds.	Burger et al., 2007
Gulf of Thailand	-Study period: 3 yrs. -Spatial comparison (5 sites with varying shorebird densities)	Community and individual	-Humans did not temporarily displace birds but did decrease their foraging rate. -Human disturbance was unlikely to impact bird fitness in the National Park because of available high-quality habitats.	Yasué, Dearden and Moore, 2008
Victoria, South-eastern Australia	-Study period: 6 months -Spatial comparison (restricted and non-restricted areas)	Community and individual	-Large-bodied birds had longer flight initiation distance (FID) -FID was significantly influenced by the starting distance of human approach, flock size, type of disturbance and habituation.	Glover et al., 2011
Moreton and North Stradbroke Island, Eastern Australia	-Study period: 1 yr. 4 months -Spatial comparison (25 ha and 250 ha, habitat type)	Community	-Human use of beaches influenced habitat selection of birds at a local (25 ha) and landscape (250 ha) scale.	Meager et al., 2012
Southern Australia	-Study period: 4 months -Experimental (human exclusion around nests)	Community and individual	-Temporary beach closures around nests in high- and low-use recreational beaches benefited breeding birds.	Weston et al., 2012

Table 1 continued.

Location	Method	Organisational level	Conclusions	Reference
Western Cape, South Africa	-Study period: 30 yrs. -Temporal comparison (1980/81 vs 2010/11)	Community	-Marked differences in bird community structure were recorded over a 30-year period with increased human disturbance. -Large-bodied birds were less susceptible to human disturbance than small-bodied birds.	Ryan, 2013
Tarifa, Southern Spain	-Study period: 8 yrs. -Temporal comparison (weekly basis)	Community and individual	-Increase in human numbers caused a marked decreased bird numbers. -Human presence significantly reduced foraging time.	Martin et al., 2015
Vancouver Island, Canada	-Study period: 4 yrs. -Temporal comparison (spring and fall migrations)	Community and individual	-Increasing human numbers were associated with bird absence -Bird disturbance increased with proximity of humans, activity speed, and presence of dogs.	Murchison, Zharikov and Nol, 2016
Southern Atlantic Coast, North America	-Study period: 6 yrs. -Spatial comparison (4 regions consisting of 2 sites with varying levels of recreation)	Population and individual	- In disturbed sites <i>Charadius melodus</i> was 7% lighter than in less disturbed sites. -True-annual survival was less in more disturbed sites.	Gibson et al., 2018
Chiloé island, Southern Chile	-Study period: 3 yrs. -Spatial comparison (disturbed and non-disturbed sites)	Population and individual	- <i>Limosa haemastica</i> density and foraging was higher in non-disturbed bay. - <i>L. haemastica</i> density significantly decreased with an increase in human abundance.	Navedo et al., 2019

1.4 COVID-19 and the South African lockdown

The 2020 global COVID-19 pandemic has severely impacted the human population, resulting in nationwide lockdowns and the restriction of human movement and contact (Coll, 2020), temporarily halting entire economic sectors and social interactions (Coll, 2020). This period of abnormally limited human mobility has been coined the ‘anthropause’ (Rutz et al., 2020) and has afforded scientists the opportunity to quantify and understand the extent of human impacts on various biological and ecological processes at a global scale previously unattainable through experimental and comparative approaches (Larson et al., 2016; Gaynor et al., 2018; Tucker et al., 2018; Jones, 2019; Rutz et al., 2020).

In South Africa, a national state of disaster was declared by the president, Cyril Ramaphosa, on 15 March, as a result of the global COVID-19 pandemic (South African Government, 2020a). On 27 March, a national lockdown commenced consisting of five lockdown levels (Figure 1), with level 5 imposing the highest restriction on human movement and level 1 the least. Restrictions of importance for this study was the public closure of beaches during levels 5, 4, and 3, after which they were formally reopened to the public (South African Government, 2020a, b, c).

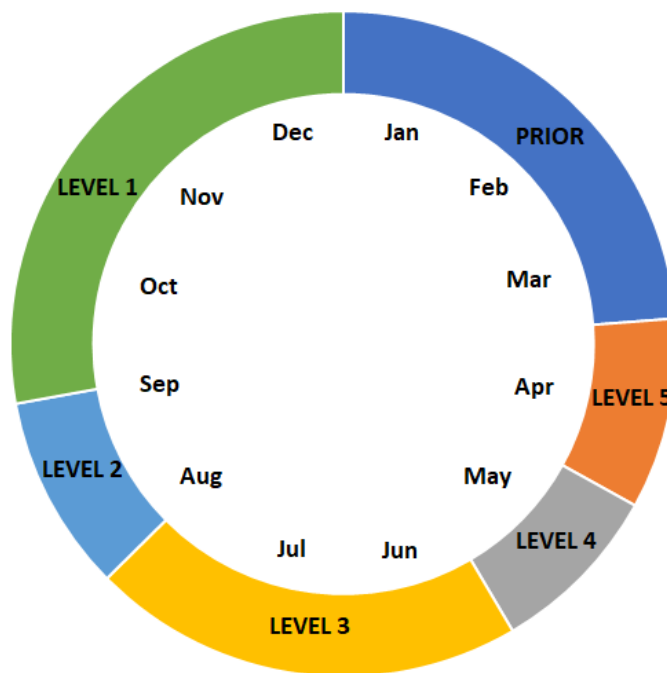


Figure 1: Duration of the South African COVID-19 lockdown levels in the year 2020.

1.5 Aims and hypotheses

This study seeks to quantify effects of variation in human abundance on shorebird communities through temporal analysis over a two-year period that includes the COVID-19 lockdown period on Muizenberg Beach, South Africa. The study makes use of two approaches to achieve its goals and test hypotheses, as indicated below.

The first approach utilises a photographic library, spanning April 2019 to November 2020, to quantify shorebird and human abundance on the beach. This approach is used due to the imposed restrictions prohibiting beach access during lockdown levels 5, 4, and 3, and due to an existing photographic library of Muizenberg Beach. It was hypothesised that shorebird abundance would be negatively influenced by human abundance and consequently that a positive relationship between the relevant lockdown level and shorebird abundance would

occur. Additionally, it was hypothesised that mean shorebird abundance between the years would be highest in 2020 due to the imposed lockdown restrictions. This hypothesis was based on the assumption that enforced lockdown levels would be extended for a significant proportion of the sampling period. The second approach involves *in situ* counts and shorebird identification along four zones of the beach, during lockdown levels 3, 2 and 1. This approach was adopted due to an ease in restrictions from level 3, allowing for community analyses to be carried out under moderate to low levels of human disturbance. It was hypothesised that shorebird community structure would differ between the lockdown levels 3, 2 and 1. More specifically, it was expected that community indices and the abundance of the dominant shorebird species would decrease from lockdown levels 3 to 1, under the assumption that a substantial gradient of increasing human abundance would occur during this period.

2. METHODOLOGICAL APPROACH

2.1 Study site

The study was conducted on Muizenberg Beach in Cape Town, South Africa (34°06.3'S 18°28.3'E; Figure 2), and spanned the period April 2019 through to November 2020. Muizenberg Beach is surrounded by extensive urban developments and recreational businesses. The beach is one of the most popular local recreational centres, supporting activities such as fishing and swimming. Additionally, it is considered Cape Town's primary surfing locality and supports a large and growing surfing community.

The study comprised two components that broadly aimed to test the hypotheses posed. Firstly, to determine effects of the five COVID-19 lockdown levels on shorebird abundance, photographic data were used to compare shorebird numbers across five lockdown levels in 2020 (during the COVID-19 pandemic) with equivalent periods in 2019, prior to the pandemic. Secondly, *in situ* counts of shorebirds on Muizenberg Beach were undertaken in 2020 between lockdown levels 3 and 1, to understand how intermediate to moderate levels of lockdown influenced shorebird community structure.

2.2 Data collection

2.2.1 Photographic data: 2019 vs 2020

The rapid onset of the nation-wide lockdown in South Africa precluded *in situ* sampling to test hypotheses pertaining to impacts of COVID-19 lockdown on shorebirds. However, pre-existing photographs of Muizenberg Beach (Figure 3) collected in a separate study focusing on diatom aggregations, provided an ideal platform to understand lockdown effects on shorebirds. This is due to a standardised methodology (outlined below) used to collect the photographs

prior to the COVID-19 pandemic (2019) and during strict lockdown levels (levels 5 and 4) in 2020, thus providing a photographic dataset of shorebird community structure before and during the lockdown. Photographs continued to be collected by researchers in the diatom aggregation study, during less strict lockdown levels 3, 2 and 1 in 2020, completing the photographic library that provided the basis for assessing COVID-19 lockdown effects on shorebirds of Muizenberg Beach.

All photographs between 2019 and 2020 (and among different lockdown levels therein) were taken using a Nikon D300 SLR (single lens reflex) camera mounted on a tripod (50 cm), with a Tokina AF 20-35mm lens, using a polarising filter. Photographs were taken daily every 12 minutes, through a glass window from a fixed position from the residence of the lead researcher on the diatom aggregation study, overlooking Muizenberg Beach.

To assess effects of COVID-19 lockdowns on shorebirds, only photographs taken on three successive days around a spring low tide were analysed, with the dataset being further constrained by using photographs over a four-hour period around the low tide (interval = 30 min). This methodology generated a total of nine photographs per day per spring low tide. In each photograph only shorebird abundance could be accurately determined as identification of birds to genus or species level could not be achieved. From these photographs, the number of humans could also be recorded to relate bird numbers to those of humans on the beach. Shorebird and human numbers were quantified only within the first 191 m of the beach within each photograph, starting from the point known as Surfer's Corner (Figure 2). Beyond the 191 m mark, identification of birds was difficult due to resolution decline in photographs. Analysis of 2020 and 2019 photographs were temporally randomized to ensure random interspersions of photograph selection during the analysis and to prevent temporal bias.

The analysis of photographs only around the spring low tide was based on a preliminary study that monitored fixed mounted Muizenberg Beach web cameras from the start of lockdown level 5 through to level 4 (27 March to 23 May 2020). Photographs from two independent cameras overlooking different sections of Muizenberg beach (Surf Emporium, [Muizenberg Web Cam | Surf Emporium](#); Wavescape, [Muizenberg 2 - Tools - Webcams \(wavescape.co.za\)](#)) were downloaded every hour during daylight hours for a week. From these photographs, frequency histograms of bird numbers per hour of daylight time were created, which identified peak bird occurrence at spring low tide and few shorebirds at approaching high tide (intertidal space limitation). A second preliminary study was initiated involving photographs being downloaded every 30-min, two hours before to two hours after spring low tide. This study indicated that analysis of photographs at 30-min over a 4-hour period straddling spring low tide over three days was adequate to answer the central question posed in the main study.

2.2.2 *In situ* data collection (lockdown levels 3, 2 & 1) in 2020

From June 2020 onwards, level 3 lockdown allowed for *in situ* counts and identification of shorebirds to be undertaken to supplement photographic data collected between 2019 and 2020. Counts were conducted on three successive days straddling spring low tides from June to November of 2020. Muizenberg Beach was divided into four spatial zones from Surfer's Corner to the Zandvlei Estuary mouth (Figure 2). Each zone comprised 191 m of a total 764 m stretch of the beach (Figure 2). Shorebird identification and counts were conducted on foot at low tide, starting at Surfer's Corner (zone 1) and ending at the estuary mouth (zone 4). Counts were performed 5 m above the high-water mark while walking parallel to the water mark and having a clear view of the intertidal zone. For the purpose of this study 'shorebird' was defined as any bird present on the sandy substrate of the beach. The number and species of shorebird were recorded and counted by eye for each zone with only shorebirds on the substrate being

recorded and shorebirds in flight excluded from the count. By differentiating the beach into zones, a finer spatial understanding of lockdown levels 3 to 1 on the shorebird community could be gained mainly in the context of habitat heterogeneity. The shorebird species-pool was limited and common species were easily identifiable in the majority of cases. Photographs of unidentifiable, rarer species were taken for identification at a later stage using an appropriate field guide (Branch et al., 2017).



Figure 2: Google Earth image showing a 764 m stretch of Muizenberg beach (black line) from Surfers Corner to the Zandvlei estuary mouth. The beach was divided into four zones (between the black dots) of 191 m each. These zones formed the basis of the second component of this study, which aimed to understand spatial variability in *in situ* shorebird communities across lockdown levels 3, 2 and 1. Inset: approximate location of Muizenberg Beach (red dot) within South Africa.



Figure 3: **A** Photograph of Muizenberg Beach, taken on 06/03/2020 at 09:46. Black arrows indicate the extent of zone 1 (191 m) and the region where birds and humans were counted for the 2019-2020 study. **B** A zoomed-in section (300%) of **A** denoted by a red arrow in the photograph indicating a portion of the counted birds.

2.3 Statistical analysis

2.3.1 *Photographic data: 2019 vs 2020*

Shorebird and human count data for 2019 and 2020 were averaged per day over the two-year period. A GLM model was used to determine whether bird numbers in Muizenberg Beach were affected by year (2019 vs 2020), and human numbers. A separate GLM model was run on the 2020 data, to assess effects of lockdown level (5 to 1) on shorebird abundance. The GLM models were constructed in RStudio (RStudio Team, 2019) using the ‘dplyr’ package (Wickham et al., 2021) and the model structure was as follows: a Poisson distribution and identity link function was specified, with bird abundance set as the response variable and human abundance and year specified as the predictor variables for the 2019-2020 dataset, and lockdown level as an predictor variable for the 2020 dataset. A Poisson distribution was used as the data were non-negative, numeric count values. Residual analyses were used to confirm the Poisson distribution.

2.3.2 *In situ data collection (lockdown levels 3, 2 & 1) in 2020*

Multivariate analyses were conducted on the *in situ* count data in PRIMER v6 with the PERMANOVA+ add-on package (Clarke and Warwick, 2001; Clarke and Gorley, 2006; Anderson, Gorley and Clarke, 2008). The data were 4th- root transformed to downweigh a disproportionate contribution of dominant species (Field et al., 1982). The Bray-Curtis measure of similarity was used to generate underlying similarity matrices, with a dummy variable of 1 to account for zero values.

Non-metric multidimensional scaling (MDS) plots (999 permutations) were used to visualise differences in shorebird assemblages among lockdown levels (3 to 1) and zones (1 to 4). A

two-way crossed design (factors: lockdown level, zone and lockdown level x zone) was created to test, using a permutational multivariate analysis of variance (PERMANOVA), among- and within-factor effects on shorebird assemblages. A sum of squares type III and permutation of reduced residuals under a reduced model with 999 permutations was specified for the PERMANOVA. If a significant factor effect was identified, a pairwise test was run to determine within-factor differences. A two-way crossed similarity of percentages (SIMPER; factors: lockdown level, zone and lockdown level x zone) analysis was performed to identify diagnostic species that contributed most to assemblage differences across factors tested, with a cut-off level of 90%. DIVERSE analysis was used to estimate species richness (S), number of individuals (N), and Shannon-Wiener diversity index (H') of the shorebird assemblage across lockdown levels and zones.

Analysis of variance (ANOVA) was used to test if lockdown level, zone and their interaction significantly affected estimated diversity measures. A residual analysis was performed for each ANOVA test to check for normality. If the residuals were not normally distributed, the data were log-transformed and an ANOVA was run on the transformed data. An additional ANOVA was performed on *Larus dominicanus* (Kelp Gull) abundance using the above-mentioned approach and rationale, given that it was the most dominant shorebird species encountered. Post-hoc Tukey tests were performed to identify within-treatment differences where relevant. All univariate tests were conducted in RStudio (RStudio Team, 2019).

3. Results

3.1 Statistical analysis

3.1.1 Photographic data: 2019 vs 2020

Shorebird abundance had a significant negative relationship with human abundance (Z -value = -19.72 , $p < 0.0001$) and with year (Z -value = -15.36 , $p < 0.0001$; Table 2). For the 2020 dataset, shorebird abundance was significantly and positively related to lockdown level (Z -value = -24.19 , $p < 0.0001$; Table 2) (Figure 4). Shorebird abundance was greatest in April 2020 (74.56 ± 6.23 SE per photograph; lockdown level 5), where humans were virtually absent from the beach (0.13 ± 0.08 SE shorebirds per photograph; Figure 4B). Although the highest average shorebird abundance was recorded in April 2020, overall, shorebird abundance was higher in 2019 (Table 2). This is visually shown by a higher average shorebird abundance over the winter period (May through to August) in 2019, relative to the same time period in 2020, with the highest shorebird abundance occurring in July (57.46 ± 14.20 SE shorebirds per photograph; Figure 4A). In contrast, this trend was not recorded in 2020, where, following April and May abundance peaks, decreasing trends are observed. (Figure 4B). The decreasing trend of shorebird abundance shown in 2020 also illustrates the significant positive relationship observed between lockdown level and shorebird abundance (Figure 4B, Table 2).

Table 2: Generalized linear model (GLM Poisson distribution and identity link function) of shorebird abundance in response to human abundance, year and lockdown level (LDL) on Muizenberg beach. The Z-value test statistic is displayed with the associated standard error (\pm SE) value. Significant p -values are shown emboldened ($p < 0.0001$ ****).

Dataset	Predictor	Estimate	SE	Z-value	<i>p</i>-value
2019-2020	(Intercept)	4.15	0.04	106.06	<0.0001 ****
	Humans	-0.05	0.00	-23.33	<0.0001 ****
	Year 2020 (2019 as reference var.)	-0.41	0.04	-9.44	<0.0001 ****
2020	(Intercept)	0.48	0.11	4.21	<0.0001 ****
	LDL	0.78	0.03	28.32	<0.0001 ****

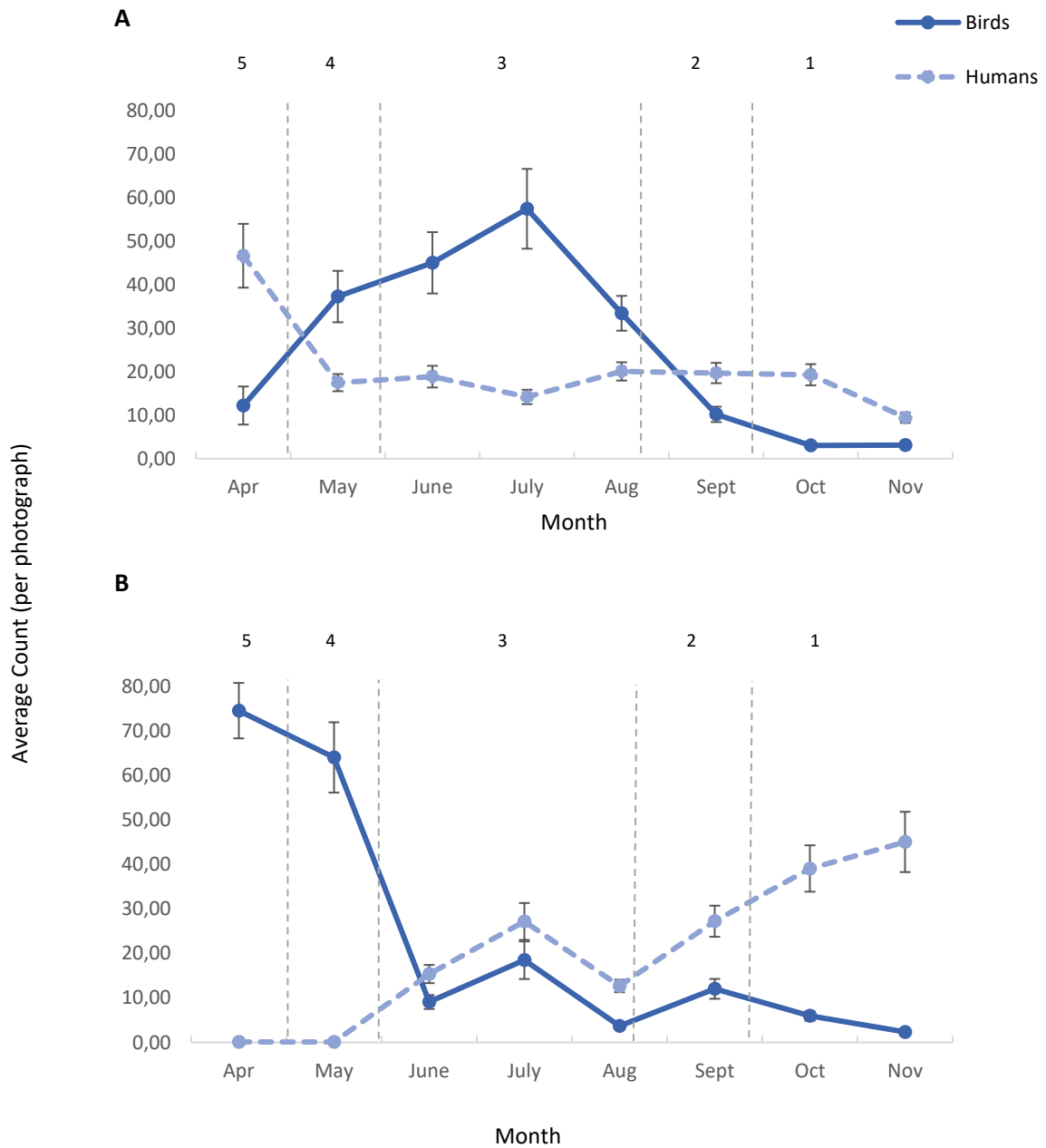


Figure 4: Total average count (\pm SE) of shorebird and human abundance on and around spring low tides at Muizenberg each during the respective lockdown levels (5 to 1), spanning a period of eight months of the years **A** 2019 and **B** 2020.

3.1.2 *In situ* data collection (lockdown levels 3, 2 & 1) in 2020

During the five-month period of data collection that constituted lockdown levels 3, 2, and 1, a total of seven shorebird species were identified (Appendix 1), with the majority of birds being gull species. PERMANOVA analysis indicated a significant difference in the shorebird community structure between lockdown levels (df = 2; Pseudo-F = 3.114; $p = 0.015$) and between zones (df = 3; Pseudo-F = 8.268; $p = 0.001$) over a five-month period in 2020 (Table 3). A pairwise test indicated that for lockdown level, a significant difference occurred between levels 3 and 2 ($p = 0.009$; Table 4). This is visually evident in an MDS ordination, which shows the spatial separation of levels 3 and 2 (Figure 5A), although there is also some overlap of these samples. Significant differences for zone were detected between zones 1 and 2 ($p = 0.001$), zones 1 and 3 ($p = 0.001$), zones 1 and 4 ($p = 0.010$), and zones 2 and 4 ($p = 0.050$) (Table 4). A separation of zone 1 from the other zones is evident in the MDS ordination, with some overlap (Figure 5B).

Table 3: Multivariate PERMANOVA analysis of shorebird community structure within lockdown levels (LDL), zones and their interaction. Test statistics include degrees of freedom (DF), sum of squares (SS), mean of squares (MS), pseudo-F statistic and the p -value. Significant p -values are shown emboldened ($p < 0.05$ *, $p < 0.001$ ***).

Predictor	DF	SS	MS	Pseudo-F	p -value	Unique number of permutations
LDL	2	3 835	1918	3.114	0.015 *	999
Zone	3	15 274	5 091	8.268	0.001 ***	998
LDL X Zone	6	1 393	232	0.377	0.973	999

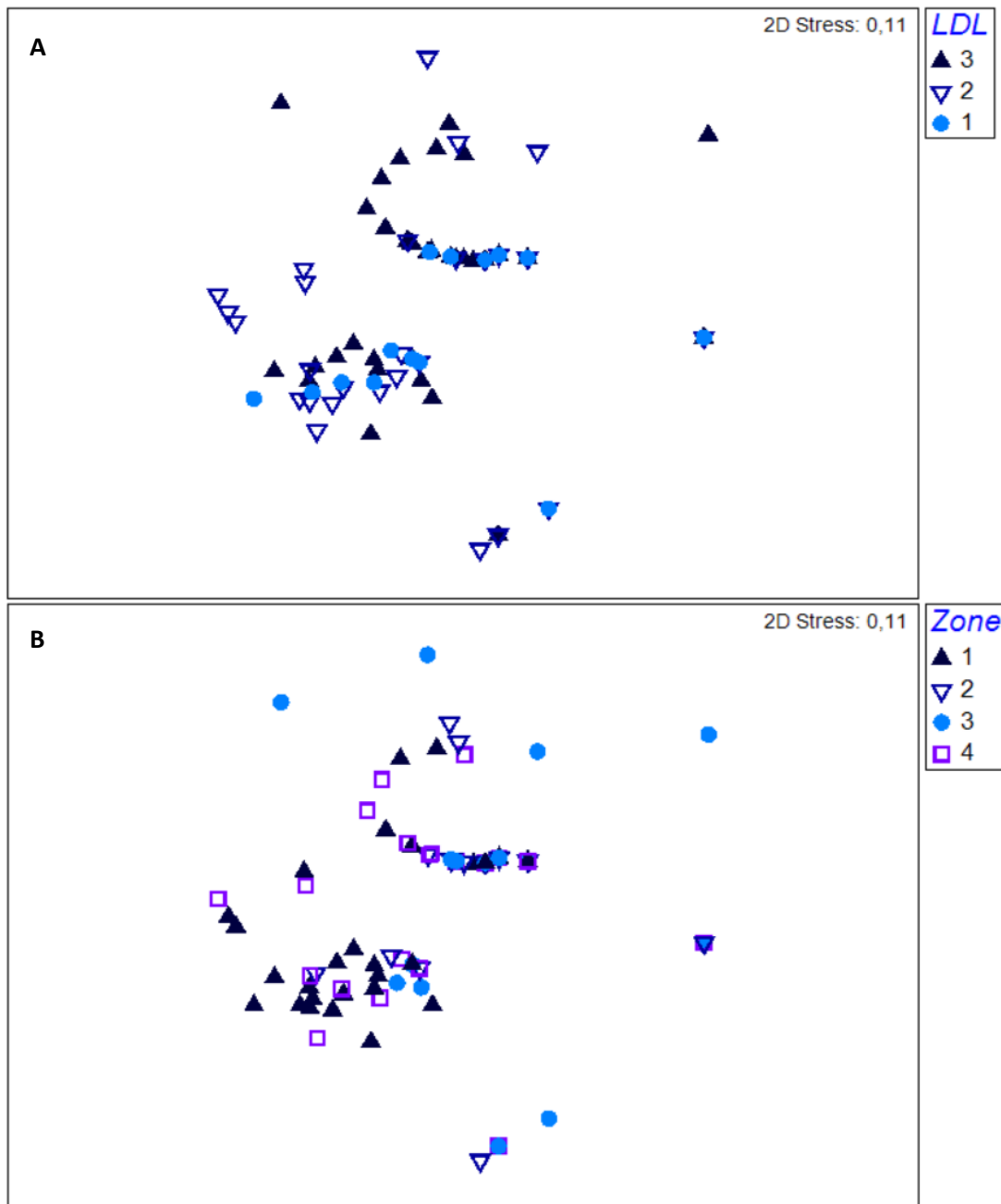


Figure 5: Non-metric MDS showing variation in shorebird community structure (4th-root transformed) along Muizenberg beach for a five-month period of 2020 at different **A** lockdown levels (LDL) and **B** zones (1 to 4).

Table 4: Pairwise test statistics for multivariate PERMANOVA analysis of differences in lockdown level (LDL) and zone shorebird community structure on Muizenberg beach over a five-month period during 2020. Significant p -values are shown emboldened ($p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***).

Predictor	t-value	p-value	Unique number of permutations
LDL			
3, 2	2.12	0.009 **	998
3, 1	1.39	0.155	998
2, 1	1.59	0.090	999
Zone			
1, 2	5.27	0.001 ***	999
1, 3	3.83	0.001 ***	999
1, 4	2.55	0.002 **	999
2, 3	0.63	0.695	999
2, 4	2.26	0.012 *	999
3, 4	1.18	0.248	999

SIMPER analysis showed *Larus dominicanus* (Kelp Gull) to be the dominant shorebird species, contributing the most to community structure within all three lockdown levels (Table 5). *Chroicocephalus hartlaubii* (Hartlaub Gull) contributed 26.17 % to the community within level 2 and 12.85 % within level 1 (Table 5). As with lockdown level, *L. dominicanus* was again the dominant species of the shorebird community across all spatial zones (Table 6). *C. hartlaubii* only made substantial contributions to dominant species in zone 1 (21.67 %; Table 6).

Table 5: SIMPER results representing species contributions to average similarity within lockdown levels (LDL) over a five-month period, after a 4th-root transformation on shorebird community structure data. Species contributing up to 90% Bray-Curtis similarity were included. Similarity is divided by the standard deviation (SD).

Species	LDL	Average Abundance	Average Similarity	Similarity/ SD	Contribution (%)	Cumulative (%)
<i>L. dominicanus</i>	3	1.23	45.94	1.33	93.08	93.08
<i>L. dominicanus</i>	2	1.12	30.21	1.10	72.03	72.03
<i>C. hartlaubii</i>	2	0.80	45.94	0.60	26.17	98.20
<i>L. dominicanus</i>	1	1.23	45.94	0.95	87.15	87.15
<i>C. hartlaubii</i>	1	1.23	45.94	0.38	12.85	100.00

Table 6: SIMPER results representing species contributions to average similarity within zone over a five-month period, after a 4th-root transformation on shorebird community structure data. Species contributing up to 90% Bray-Curtis similarity were included. Similarity is divided by the standard deviation (SD).

Species	Zone	Average Abundance	Average Similarity	Similarity/ SD	Contribution (%)	Cumulative (%)
<i>L. dominicanus</i>	1	1.69	51.16	3.70	77.15	77.15
<i>C. hartlaubii</i>	1	1.02	14.37	0.79	21.67	98.82
<i>L. dominicanus</i>	2	0.81	39.16	0.97	99.10	91.10
<i>L. dominicanus</i>	3	0.79	25.85	0.74	92.99	92.99
<i>L. dominicanus</i>	4	1.29	46.36	1.32	92.97	92.97

ANOVA showed that the three shorebird community indices differed significantly among zones ($p < 0.0001$; Table 7). A post-hoc Tukey test indicated a significant difference in all three metrics between zones 1 and 2 ($p < 0.001$), and zones 1 and 3 ($p < 0.001$; Figure 6). Additionally, a significant difference in total shorebird abundance (S) and the Shannon-Weiner index (H') between zones 1 and 4 occurred ($p < 0.010$; Figure 6). The Shannon-Weiner index (H') also differed significantly between lockdown levels ($p < 0.010$; Table 7), with significant differences occurring between levels 2 and 3 (Tukey test, $p < 0.050$; Figure 6). Additionally, ANOVA results identified a significant difference ($p < 0.0001$) in *L. dominicanus* abundance for zone only (Table 7), with significant differences occurring between zones 3 and 2 ($p < 0.001$), zones 4 and 2 ($p < 0.001$), and zones 1 and 4 ($p < 0.010$; Figure 6) according to Tukey tests.

Table 7: ANOVA results testing the influence of lockdown level (LDL), zone and their interaction on three diversity indices (Species richness (S), species abundance (N) and Shannon-Weiner index (H')) and *L. dominicanus* abundance. Test statistics include degrees of freedom (DF), sum of squares (SS), F-value statistic and *p*-value. Significant *p*-value are shown emboldened ($p < 0.01$ **, $p < 0.0001$ ****).

Predictor	DF	SS	F-value	<i>p</i> -value
S				
LDL	2	0.74	2.61	0.0780
Zone	3	4.97	11.70	<0.0001 ****
LDL X Zone	6	0.81	0.96	0.4570
N				
LDL	2	4.18	1.98	0.1430
Zone	3	48.00	15.17	<0.0001 ****
LDL X Zone	6	4.01	0.63	0.7030
H'				
LDL	2	0.50	5.40	0.0100 **
Zone	3	1.56	11.23	<0.0001 ****
LDL X Zone	6	0.21	0.75	0.6080
<i>L. dominicanus</i>				
LDL	2	1.76	0.95	0.3890
Zone	3	37.99	13.70	<0.0001 ****
LDL X Zone	6	0.60	0.60	0.7300

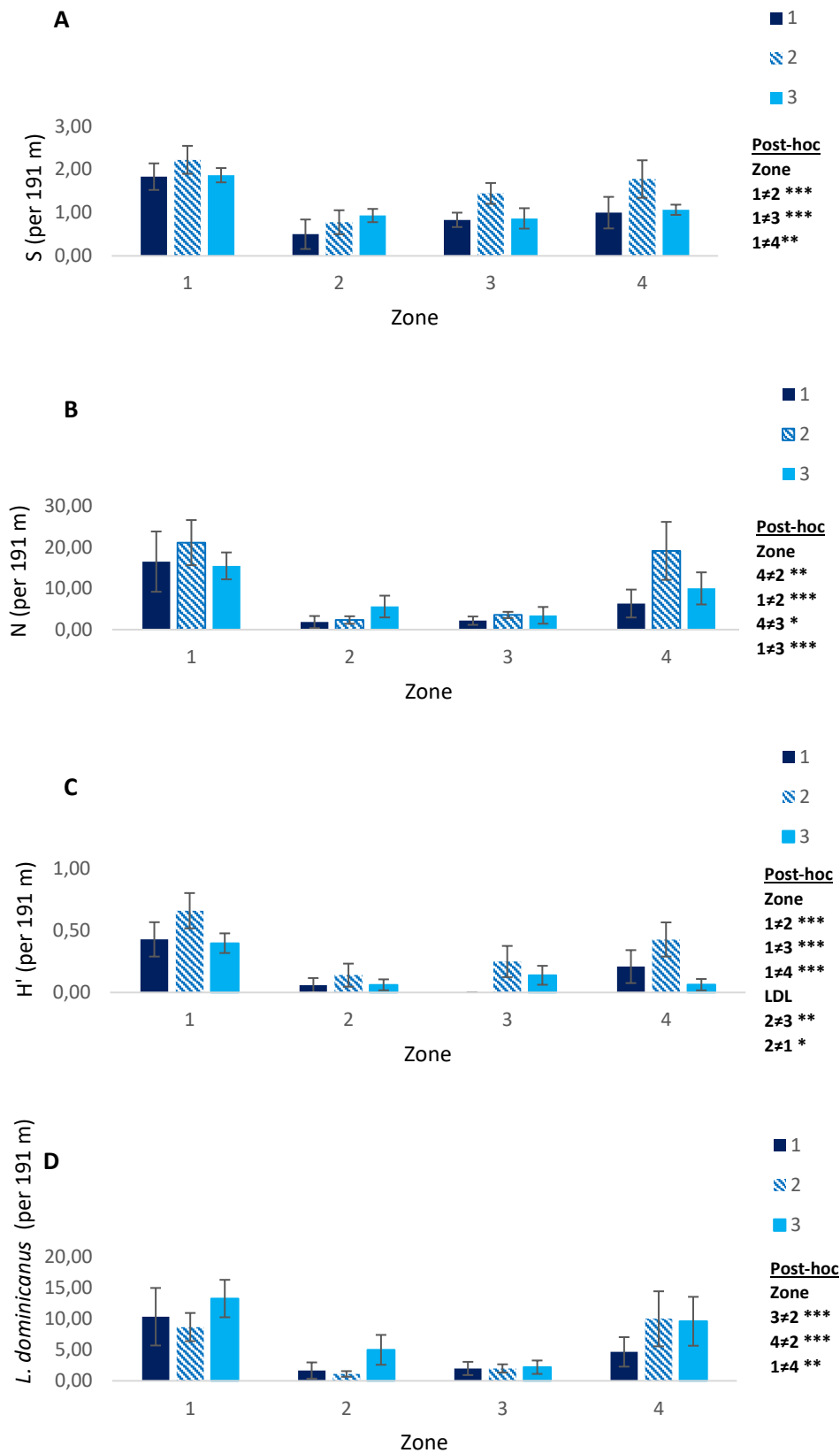


Figure 6: Variation of three diversity measures (mean \pm SE) **A** species richness (S), **B** species abundance (N), **C** Shannon-Weiner index (H') and **D** the average abundance of *L. dominicanus* (\pm SE) for four zones on Muizenberg beach during lockdown levels 3 to 1. Results for a post-hoc Tukey test are shown where a significant difference occurred between the zones or lockdown levels.

4. Discussion

The global 2020 COVID-19 pandemic has resulted in an unparalleled reduction in human mobility across the planet (Coll, 2020), leading to what has been described as the anthropause (Rutz et al., 2020). This has allowed scientists to opportunistically address the previously intractable question of how the natural environment is impacted by modern human presence, lifestyle and activities (Coll, 2020; Rutz et al., 2020). The human population has and continues to cause unprecedented environmental change, increasing the risk of environmental catastrophe (Rockström et al., 2009a, b). In marine ecosystems alone, drivers of change include loss of coastal and marine habitat, intense pressure of fishing and aquaculture, alien invasive species invasions, increasing pollution, and climate change (Sala et al., 2000; Pauly et al., 2003; Lotze et al., 2006; Worm et al., 2006; Poloczanska et al., 2013; Mengerink et al., 2014; Levin and Le Bris 2015; McCauley et al., 2015; Ramírez et al., 2017; Halpern et al., 2019; Food and Agriculture Organisation (FAO), 2020). The mitigation of these driver effects on ecological systems is closely coupled with the appropriate management of human activities within the context of social acceptance, implementation and compliance with regulations (Mora et al., 2009; Coll et al., 2013; Bundy et al., 2017).

Assessments of the potential impacts of human activities on the natural environment have previously been based on local-, or at most, regional-scale studies (Coll, 2020). The anthropause has provided opportunities to understand these impacts from a global perspective (Coll, 2020), at spatial and temporal scales that previously would have been impossible to achieve through conventional experiments and comparative sampling alone (Rutz et al., 2020). This is evident in the present study where shorebird abundance was monitored on Muizenberg Beach over an eight-month period with varying levels of human abundance, including a two-month period of virtual-human exclusion. This was afforded by lockdown levels imposed by

the government and would previously not have been feasible, experimentally or comparatively, over the spatial and temporal scales employed in the present study.

However, like all temporal comparative studies, a central question underpinning interpretation of data regarding anthropause effects, is the quality of baseline data. This, in turn, is fundamental to understanding causal versus spurious processes related to seasonality (Rutz et al., 2020). Fortuitously, the present study was able to build on pre-existing data, allowing for meaningful comparisons between the anthropause period (2020) and the previous year (2019). This has considerably strengthened the study (Rutz et al., 2020) by helping to distinguish human presence from seasonal effects (April through to November) in influencing shorebird abundance.

To understand the impacts of the anthropause on shorebird communities at Muizenberg Beach, two separate approaches were used. The first used a two-year photographic library spanning April 2019 to November 2020 to quantify and relate shorebird and human abundance. The second approach made use of *in situ* counts and shorebird identification along four zones of the beach, spanning six-months that included lockdown levels 3, 2 and 1. Here the goal was to understand how moderate to low lockdown levels influence shorebird community structure.

4.1 Photographic data: 2019 vs 2020

It was hypothesised that shorebird abundance would be negatively influenced by human abundance and consequently, that shorebird numbers would be positively influenced by increasing lockdown level, with highest shorebird abundance occurring during level 5 and the lowest in level 1. Additionally, a difference in shorebird abundance was hypothesised between sampling years, with greater shorebird abundance predicted in 2020 than in 2019. This

hypothesis was based on the assumption that the enforced lockdown levels (levels 5 to 3) would be extended for a significant proportion of the sampling period in 2020.

In general, results conformed to the proposed hypotheses. Shorebird abundance was negatively related to human presence, and positively to increasing lockdown level for the 2020 data. Additionally, the greatest average shorebird abundance recorded between both years occurred during level 5 in April 2020 (74.56 ± 6.23 SE shorebirds per photograph), when humans were virtually absent from the beach (0.13 ± 0.08 SE humans per photograph; Figure 4B). Additionally, the lowest average shorebird abundance recorded between both years occurred during lockdown level 1 in November 2020 (2.36 ± 0.53 SE shorebirds per photograph), when average human abundance was greatest in 2020 (45.06 ± 6.78 SE humans per photograph; Figure 4B). It is noteworthy that in 2019 the relationship between shorebird and human abundance with pseudo-lockdown level was not as strong as with lockdown level in 2020, where an obvious decreasing trend in shorebird abundance with decreasing lockdown level and increasing human numbers was evident (Figure 4).

Results indicate that human presence generally, negatively impacts shorebird abundance on Muizenberg Beach, and align with findings of other studies (Table 1). Shorebird populations on Los Lances Beach in southern Spain for example, were shown to be influenced by human presence, which negatively affected behaviour and abundance in urban sectors of the beach and within the Natural Park (Martin et al., 2015). Additionally, the impact of human disturbance was negative for all shorebird species over the study period, indicating no habituation towards human disturbance and resulting in long-term declines in shorebird populations (Martin et al., 2015). Previously, the spatial distribution of shorebirds has also been shown in separate studies to be negatively correlated with human disturbance (Pfister et al., 1992; Tarr et al., 2010).

The higher average shorebird abundance recorded over the 2019 winter period (May through to August) is a trend previously recorded in the literature. *Larus dominicanus* (Kelp Gulls), which dominated the Muizenberg Beach shorebird community (see section 3.1.2 of results), have been recorded in greater numbers during the winter months relative to summer months (September and December) on sandy beaches in the Eastern Cape of South Africa, the Swartkops estuary and Algoa Bay (McLachlan et al., 1980; Martin and Baird, 1987; Spearpoint et al., 1988). Interestingly, the 2019-winter increase in shorebird abundance was not evident in 2020. This leads to the question whether the observed winter-peak in 2019 may not be purely seasonal, but rather, is due to decreased human abundance in winter relative to summer (Figure 4A). While answering this question is beyond the scope of the current study, it does raise interesting possibilities regarding effects of human abundance on shorebirds more broadly.

It was hypothesised that shorebird abundance would be greater in 2020 than 2019, but this did not materialise – abundance was in fact significantly less in 2020 than in 2019 (Table 2), despite a lockdown being implemented in 2020. This can, however, be explained by the assumption that qualified the hypothesis posed viz. that if lockdown levels would be extended for a significant proportion of time, then shorebird abundance would be greater in 2020. In reality, humans were effectively excluded from the beach for a total of two months (April and May) during levels 5 and 4 (Figure 4B) out of the eight-month sampling period. It was expected at the onset of the study that humans would also have been excluded from the beach during lockdown level 3 (South African Government, 2020c), which would have resulted in an additional two and a half months of human exclusion from the beach, and potentially in a higher mean shorebird abundance for 2020 (Figure 4B). However, humans were not excluded from the beach during level 3 and a high average human abundance was recorded during this period accompanied by a sharp decrease in shorebird abundance (Figure 4B). This may have resulted

from a lack of compliance (Schneider et al., 2020), confusion around the lockdown regulations and/or 'covid fatigue', which describes the tendency of humans to grow tired of the rules and regulations put in place to prevent the spread of COVID-19 (Harvey, 2020).

The strong negative relationship between shorebird and human abundance is likely a result of multiple mechanisms operating individually or interactively. Coastal areas are used for a variety of human activities that vary in their impact on shorebird populations (Davidson and Rothwell, 1993). Muizenberg Beach is no exception and is utilised by surfers, bait-collectors and recreational visitors, all of whom influence resources required by shorebirds in different ways. At high numbers, humans can limit physical space for shorebirds, thereby rendering the beach less suitable as a substrate for birds (Martin et al., 2015; Schneider et al., 2020). This, allied with noise pollution and interference by dogs, represent additional stresses/disturbances for shorebirds, decreasing habitat suitability (Colwell, 2010; Schlacher et al., 2015). Trampling of sediment macrofauna along with associated changes in sedimentary biogeochemical processes (e.g. increased anoxia), may reduce trophic resource availability to shorebirds, with benthic bait-collecting compounding this effect (Wynberg and Branch, 1994, 1997; Schlacher et al., 2016). All of these processes may contribute to explaining the largely negative association between shorebird and human numbers recorded in this study. More broadly, out of the 12 types of disturbance that can impact shorebird assemblages (Mangak and Dayer 2019), four (dogs, direct harassment by people/dogs, shell fishing and recreational fishing) are pervasive on Muizenberg Beach, constituting moderate to high disturbance on shorebirds (Mangak and Dayer, 2019).

4.2 *In situ* data collection (lockdown levels 3, 2 & 1) in 2020

It was hypothesised that shorebird community structure would differ from lockdown levels 3 to 1. More specifically, it was expected that community indices and abundance of *Larus dominicanus* (Kelp Gull) – the dominant shorebird species, would decrease from lockdown levels 3 to 1, under the assumption that a substantial gradient of increasing human abundance would occur from levels 3 to 1.

Results support the first section of the hypothesis posed by virtue of a significant difference in community structure occurring between lockdown levels (Table 3), but specifically between levels 3 and 2 (Table 4). These results can be explained by examining contributions of dominant shorebird species that characterised each of the lockdown levels. *L. dominicanus* was the most dominant species across all three lockdown levels and contributed most to dissimilarity between the lockdown levels (Table 5). However, the contribution of *Chroicocephalus hartlaubii* (Hartlaub's Gull) increased during level 2 from level 3, with the opposite occurring for *L. dominicanus* (Table 5). This change in dominance is the most likely explanation for the observed difference in shorebird community structure between levels 3 and 2.

Although a change in the contribution of species to the community was detected (Table 5), significant differences in community indices and *L. dominicanus* abundance were not detected between lockdown levels using univariate testing (Table 7), thus leading to the refutation of the second section of the hypothesis. The exception was the Shannon-Wiener diversity metric, which did vary among lockdown levels (Table 7). The broad disagreement between hypothesis and the observation may be explained through the assumption qualifying the hypothesis, namely that a continuous substantial gradient of increasing human abundance would occur between levels 3 to 1, including a phase of virtual human exclusion at lockdown level 3. This assumption was not met as the gradient in human abundance was not as strong from levels 3 to

1, as it was for levels 5 to 3, with no exclusion of humans occurring under level 3 (Figure 4B) as expected given government regulations. Level 3 regulations did not permit the re-opening of beaches (South African Government, 2020c) however, this period saw an increase in human numbers on the beach of almost double the 2019 levels (Figure 4).

Interestingly, Shannon-Wiener diversity indices were higher in level 2 than in level 3, which is counter expectation (Figure 6). This discrepancy can be explained by the high dominance of *L. dominicanus* in level 3 (93.08%), its subsequent contribution decreased during level 2 (72.03%) and a greater contribution of *C. hartlaubii* in the latter phase. Given that the Shannon-Wiener index incorporates evenness in its estimation of diversity and downweights dominance, it is not surprising that values for this index were greater in level 2 than level 3. The causes of greater dominance of *L. dominicanus* under level 3 lockdown are difficult to identify, but the rapid increase in human abundance is a likely driver (Figure 4B). Large gulls from the *Larus* family are known to be opportunistic foragers that exploit a wide range of food resources of multiple origins (Duhem et al., 2003; Yoda et al., 2012; Reusch et al., 2020). Since the 1970s, an increase in population sizes of many *Larus* species has occurred because of their ability to forage on anthropogenic food resources (Lisnizer et al., 2011; Oro et al., 2013). As an opportunistic forager, *L. dominicanus*, may have benefitted from additional food resources with the increased human abundance during level 3.

Additionally, high *L. dominicanus* abundance may have been influenced by large amounts of beach kelp observed in level 3. Under normal circumstances, washed-up kelp is removed and harvested from beaches by the City of Cape Town and private entities (Department of Agriculture, Land Reform and Rural Development, 2020), however, it was observed that these activities were temporarily halted between lockdown levels 5 to 2. Beach kelp hosts a wide variety of invertebrate species (Blankley and Grindley, 1985) and both *L. dominicanus* and *C.*

hartlaubii have been known to forage on these invertebrates (Steele, 1992). Accumulation of beach kelp is thus likely to have contributed to the high *L. dominicanus* abundance seen in level 3. Personal observation indicated a resumption of kelp removal in level 1 that could have contributed to decreasing *L. dominicanus* abundance, which in turn may have resulted in greater contribution of *C. hartlaubii* (Table 5) through decreased competition for space and food resources (Burger, 1981; Burger et al., 2007).

While temporal differences in shorebird assemblages were minor, spatial differences were prominent (Table 3). At a community level, assemblage structure was predominantly unique in zone 1 (Table 4), which was the only zone where *L. dominicanus* (77.15 %) and *C. hartlaubii* (21.67 %) jointly contributed to 90% of community structure (Table 6). Given that shorebird community structure is influenced by abiotic factors such as beach slope, distance from estuaries and beach kelp (Lafferty, Rodriguez and Chapman 2013), the unique shorebird community structure in zone 1 is likely due to unique features of this zone. On a similar note, differences in community metrics, mainly due to greater levels in zones 1 and 4, are also likely to be due to characteristic environmental features. Zone 1 is located near a rocky intertidal area, while zone 4 is situated near an estuary mouth. Rocky intertidal areas within a sandy beach environment (zone 1) have been shown to increase shorebird abundance in relation to the surrounding areas, mainly due to an increase in trophic resource availability (Lafferty, 2001). Similarly, shorebird abundance and richness have been reported to increase with proximity to estuaries (zone 4), mainly due to increased trophic resource availability (Colwell and Sundeen, 2000; Neuman et al., 2008, Lafferty, Rodriguez and Chapman, 2013).

5. Conclusion

The COVID-19 anthropause is the greatest large-scale ‘experiment’ in modern history, allowing for assessments of drastic, global reductions in human activities on the natural environment (Rutz et al., 2020; Coll, 2020). Collectively, data gained from anthropause studies provide a unique, quantitative perspective on human-nature interactions, while shedding light on causal driving mechanisms (Bates et al., 2020; Rutz et al., 2020; Coll, 2020)

The results of this study indicate a strong negative relationship between shorebird and human abundance on Muizenberg Beach over a two-year period prior to, and including, phases of enforced lockdown. This relationship was evident across both years, but was particularly striking in 2020, during enforced COVID-19 lockdown. In the latter year, periods of virtual human exclusion had the highest shorebird numbers recorded across both years, with a near seven-fold increase in shorebird abundance in 2020 relative to 2019 at the start of the study. Periods of highest human numbers were associated with lowest shorebird numbers in 2020. These findings are rendered more significant given that (1) the sampled shorebird community was situated in a highly urbanised environment and that (2) studies have shown urbanised bird populations to be more tolerant to human disturbance than rural or suburban populations (Samia et al., 2015). Findings thus indicate that urban shorebird populations may be more sensitive to human disturbance than previously thought, but such effects may not be easily detectable without periodic human exclusion from beaches, as afforded by the anthropause. Findings also suggest that lockdown levels 3 to 1, minimally impacted shorebird community structure, likely because the expected human exclusion under level 3 did not occur on Muizenberg Beach.

In a global context, findings indicate a need to reassess the human impacts on shorebird communities within urban beach ecosystems. This becomes even more pertinent in view of an exponentially increasing human population and the concurrent ‘twin environmental crises of our time’ (Corlett et al., 2020). Findings from this study also indicate that beach closures for a short duration of only a few weeks can have a marked impact on shorebirds, which in turn suggests that periodic closure of beaches, particularly during periods of vulnerability such as breeding and migration seasons, may be beneficial to shorebird populations and beach ecosystems more broadly.

6. References

Anderson M.J., Gorley R.N., Clarke K.R., 2008. PERMANOVA+ for PRIMER: guide to software and statistical methods. *Plymouth, UK: PRIMER-E*.

Atlantic Flyway Shorebird Initiative (AFSI), 2016. Atlantic Flyway Shorebird Initiative Business Plan. [ONLINE] Available at: <https://atlanticflywayshorebirds.org/>. [Accessed 19 February 2021].

Bates, A.E., Primack, R.B., Moraga, P., and Duarte, C.M., 2020. COVID-19 pandemic and associated lockdown as a “Global Human Confinement Experiment” to investigate biodiversity conservation. *Biological Conservation*, 248, p.108665.

Baudains, T.P. and Lloyd, P., 2007. Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. *Animal Conservation*, 10(3), pp.400-407.

Beale, C.M. and Monaghan, P., 2004. Human disturbance: people as predation-free predators? *Journal of Applied Ecology*, 41(2), pp.335-343.

Biggs, D., Biggs, R., Dakos, V., Scholes, R.J. and Schoon, M., 2011. Are we entering an era of concatenated global crises? *Ecology and Society*, 16(2), p.27.

Blankley, W. O., and J. R. Grindley. 1985. The intertidal and shallow subtidal food web at Marion Island. In *Antarctic nutrient cycles and food webs*, pp. 630-636. Springer, Berlin, Heidelberg, 1985.

Branch, G., Griffiths, C., Branch, M., Beckley, L., 2017. Two oceans: a guide to the marine life of southern Africa. *Penguin Random House South Africa*.

Bundy, A., Chuenpagdee, R., Boldt, J.L., de Fatima Borges, M., Camara, M.L., Coll, M., Diallo, I., Fox, C., Fulton, E.A., Gazihan, A. and Jarre, A., 2017. Strong fisheries management and governance positively impact ecosystem status. *Fish and Fisheries*, 18(3), pp.412-439.

Burger, J., 1981. Feeding competition between laughing gulls and herring gulls at a sanitary landfill. *The Condor*, 83(4), pp.328-335.

Burger, J., Jeitner, C., Clark, K. and Niles, L.J., 2004. The effect of human activities on migrant shorebirds: successful adaptive management. *Environmental Conservation*, 31(4), pp.283-288.

Burger, J., Carlucci, S.A., Jeitner, C.W. and Niles, L., 2007. Habitat choice, disturbance, and management of foraging shorebirds and gulls at a migratory stopover. *Journal of Coastal Research*, 23(5 (235)), pp.1159-1166.

Clarke K.R., Gorley R.N., 2006. *PRIMER v6: User Manual/Tutorial*. Plymouth, UK: PRIMER-E.

Clarke K.R., Warwick R.M., 2001. *Change in marine communities: an approach to statistical analysis and interpretation*. 2nd edn. Plymouth, UK: PRIMER-E.

Coll, M., Libralato, S., Pitcher, T.J., Solidoro, C. and Tudela, S., 2013. Sustainability implications of honouring the Code of Conduct for Responsible Fisheries. *Global Environmental Change*, 23(1), pp.157-166.

Coll, M., 2020. Environmental effects of the COVID-19 pandemic from a (marine) ecological perspective. *Ethics in Science and Environmental Politics*, 20, pp.41-55.

Colwell, M.A., 2010. *Shorebird ecology, conservation, and management*. University of California Press.

Corlett, R.T., Primack, R.B., Devictor, V., Maas, B., Goswami, V.R., Bates, A.E., Koh, L.P., Regan, T.J., Loyola, R., Pakeman, R.J. and Cumming, G.S., 2020. Impacts of the coronavirus pandemic on biodiversity conservation. *Biological Conservation*, 246, p.108571.

Crossland, C.J., Baird, D., Ducrotoy, J.P., Lindeboom, H., Buddemeier, R.W., Dennison, W.C., Maxwell, B.A., Smith, S.V. and Swaney, D.P., 2005. The coastal zone—a domain of global interactions. *Coastal fluxes in the Anthropocene*. Heidelberg, Berlin: Springer, pp. 1-37.

Department of Agriculture, Land Reform and Rural Development (DALRRD), 2020. Description of the Commercial Seaweed Sector. [ONLINE] Available at: https://www.nda.agric.za/daDev/sideMenu/fisheries/03_areasofwork/Resources%20Research/Seaweed%20main%20web%20page.pdf. [Accessed 15 February 2021].

Defeo, O., McLachlan, A., Schoeman, D.S., Schlacher, T.A., Dugan, J., Jones, A., Lastra, M. and Scapini, F., 2009. Threats to sandy beach ecosystems: a review. *Estuarine, Coastal and Shelf Science*, 81(1), pp.1-12.

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H., Chan, K.M. and Garibaldi, L.A., 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*, 366(6471), p.eaax3100.

Dugan, J.E., Hubbard, D.M., Rodil, I.F., Revell, D.L. and Schroeter, S., 2008. Ecological effects of coastal armoring on sandy beaches. *Marine Ecology*, 29, pp.160-170.

Duhem, C., Vidal, E., Legrand, J. and Tatoni, T., 2003. Opportunistic feeding responses of the yellow-legged gull *Larus michahellis* to accessibility of refuse dumps. *Bird Study*, 50(1), pp.61-67.

Ellis, E.C. and Ramankutty, N., 2008. Putting people on the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment*, 6(8), pp.439-447.

Field, J.I., Clarke, K.R. and Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series*, 8(1), pp.37-52.

Food and Agriculture Organisation (FAO), 2020. The state of world fisheries and aquaculture. *FAO*, Rome.

Fox, A.D. and Madsen, J., 1997. Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. *Journal of Applied Ecology*, 34(1), pp.1-13.

Frid, A. and Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, 6(1), p.11.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H. and Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. *Science*, 360 (6394), pp.1232-1235.

Gibson, D., Chaplin, M.K., Hunt, K.L., Friedrich, M.J., Weithman, C.E., Addison, L.M., Cavalieri, V., Coleman, S., Cuthbert, F.J., Fraser, J.D. and Golder, W., 2018. Impacts of anthropogenic disturbance on body condition, survival, and site fidelity of nonbreeding Piping Plovers. *The Condor: Ornithological Applications*, 120(3), pp.566-580.

Glover, H.K., Weston, M.A., Maguire, G.S., Miller, K.K. and Christie, B.A., 2011. Towards ecologically meaningful and socially acceptable buffers: response distances of shorebirds in Victoria, Australia, to human disturbance. *Landscape and Urban Planning*, 103(3-4), pp.326-334.

Gül, M.R. and Griffen, B.D., 2020. Diet, energy storage, and reproductive condition in a bioindicator species across beaches with different levels of human disturbance. *Ecological Indicators*, 117, p.106636.

Halpern, B.S., Frazier, M., Afflerbach, J., Lowndes, J.S., Micheli, F., O'Hara, C., Scarborough, C. and Selkoe, K.A., 2019. Recent pace of change in human impact on the world's ocean. *Scientific Reports*, 9(1), pp.1-8.

Halpern, B.S., Longo, C., Lowndes, J.S.S., Best, B.D., Frazier, M., Katona, S.K., Kleisner, K.M., Rosenberg, A.A., Scarborough, C., and Selig, E.R., 2015. Patterns and emerging trends in global ocean health. *PloS one*, 10(3), p.e0117863.

Harvey, N., 2020. Behavioural fatigue: real phenomenon, naïve construct, or policy contrivance? *Frontiers in Psychology*, 11, p.589892.

Hugo, G., 2011. Future demographic change and its interactions with migration and climate change. *Global Environmental Change*, 21, pp.S21-S33.

Intergovernmental Panel on Climate Change (IPCC), 2019a. Special Report on the Ocean and Cryosphere in a Changing Climate. [ONLINE] Available at: <https://www.ipcc.ch/srocc/>. [Accessed 8 February 2021].

Intergovernmental Panel on Climate Change (IPCC), 2019b. Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse Gas Fluxes in Terrestrial Ecosystems. [ONLINE] Available at: <https://www.ipcc.ch/srocc/>. [Accessed 8 February 2021].

Jones, A.R., Murray, A., Lasiak, T.A. and Marsh, R.E., 2008. The effects of beach nourishment on the sandy-beach amphipod *Exoediceros fossor*: impact and recovery in Botany Bay, New South Wales, Australia. *Marine Ecology*, 29, pp.28-36.

Jones, N., 2019. Ocean uproar: saving marine life from a barrage of noise. *Nature*, 568(7751), pp.158-161.

Junoy, J., Castellanos, C., Viéitez, J.M., De la Huz, M.R. and Lastra, M., 2005. The macroinfauna of the Galician sandy beaches (NW Spain) affected by the Prestige oil-spill. *Marine Pollution Bulletin*, 50(5), pp.526-536.

Lafferty, K.D., 2001. Birds at a Southern California beach: seasonality, habitat use and disturbance by human activity. *Biodiversity and Conservation*, 10(11), pp.1949-1962.

Lafferty, K.D., Rodriguez, D.A. and Chapman, A., 2013. Temporal and spatial variation in bird and human use of beaches in southern California. *SpringerPlus*, 2(1), pp.1-14.

Larson, C.L., Reed, S.E., Merenlender, A.M. and Crooks, K.R., 2016. Effects of recreation on animals revealed as widespread through a global systematic review. *PloS one*, 11(12), p.e0167259.

Levin, L.A. and Le Bris, N., 2015. The deep ocean under climate change. *Science*, 350(6262), pp.766-768.

Lewis, S.L. and Maslin, M.A., 2015. Defining the anthropocene. *Nature*, 519(7542), pp.171-180.

Lisnizer, N., Garcia-Borboroglu, P. and Yorio, P., 2011. Spatial and temporal variation in population trends of Kelp Gulls in northern Patagonia, Argentina. *Emu-Austral Ornithology*, 111(3), pp.259-267.

Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H. and Jackson, J.B., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*, 312(5781), pp.1806-1809.

Martin, A.P. and Baird, D., 1987. Seasonal abundance and distribution of birds on the Swartkops estuary, Port Elizabeth. *Ostrich*, 58(3), pp.122-134.

Martín, B., Delgado, S., De la Cruz, A., Tirado, S. and Ferrer, M., 2015. Effects of human presence on the long-term trends of migrant and resident shorebirds: evidence of local population declines. *Animal Conservation*, 18(1), pp.73-81.

Maxwell, S.M., Hazen, E.L., Bograd, S.J., Halpern, B.S., Breed, G.A., Nickel, B., Teutschel, N.M., Crowder, L.B., Benson, S., Dutton, P.H. and Bailey, H., 2013. Cumulative human impacts on marine predators. *Nature Communications*, 4(1), pp.1-9.

McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H. and Warner, R.R., 2015. Marine defaunation: animal loss in the global ocean. *Science*, 347(6219), pp.236-247.

McLachlan, A., Wooldridge, T., Schramm, M. and Kühn, M., 1980. Seasonal abundance, biomass and feeding of shore birds on sandy beaches in the Eastern Cape, South Africa. *Ostrich*, 51(1), pp.44-52.

McLachlan, A. and Brown, A.C., 2006. *The Ecology of Sandy Shores*. Burlington, MA: Academic Press.

Mengak, L. and Dayer, A.A., 2020. Defining human disturbance to shorebirds using manager and scientist input. *Environmental Management*, 65(1), pp.62-73.

Mengerink, K.J., Van Dover, C.L., Ardron, J., Baker, M., Escobar-Briones, E., Gjerde, K., Koslow, J.A., Ramirez-Llodra, E., Lara-Lopez, A., Squires, D. and Sutton, T., 2014. A call for deep-ocean stewardship. *Science*, 344(6185), pp.696-698.

Monastersky, R., 2015. Anthropocene: The human age. *Nature News*, 519(7542), p.144.

Mora, C., Myers, R.A., Coll, M., Libralato, S., Pitcher, T.J., Sumaila, R.U., Zeller, D., Watson, R., Gaston, K.J. and Worm, B., 2009. Management effectiveness of the world's marine fisheries. *PloS Biol*, 7(6), p.e1000131.

Murchison, C.R., Zharikov, Y. and Nol, E., 2016. Human activity and habitat characteristics influence shorebird habitat use and behavior at a Vancouver Island migratory stopover site. *Environmental Management*, 58(3), pp.386-398.

Navedo, J.G., Verdugo, C., Rodríguez-Jorquera, I.A., Abad-Gómez, J.M., Suazo, C.G., Castañeda, L.E., Araya, V., Ruiz, J. and Gutiérrez, J.S., 2019. Assessing the effects of human activities on the foraging opportunities of migratory shorebirds in Austral high-latitude bays. *PloS one*, 14(3), p.e0212441.

Neuman, K.K., Henkel, L.A. and Page, G.W., 2008. Shorebird use of sandy beaches in central California. *Waterbirds*, 31(1), pp.115-121.

Neumann, B., Vafeidis, A.T., Zimmermann, J. and Nicholls, R.J., 2015. Future coastal population growth and exposure to sea-level rise and coastal flooding-a global assessment. *PloS one*, 10(3), p.e0118571.

Nisbet, I.C., 2000. Disturbance, habituation, and management of waterbird colonies. *Waterbirds*, 23(2), pp.312-332.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S. and Martínez-Abraín, A., 2013. Ecological and evolutionary implications of food subsidies from humans. *Ecology Letters*, 16(12), pp.1501-1514.

Patterson, M. and Hardy, D., 2008. Economic drivers of change and their oceanic-coastal ecological impacts. *Ecological Economics of the Oceans and Coasts*. Edward Elgar Publishing, pp.187-209.

Pauly, D., Alder, J., Bennett, E., Christensen, V., Tyedmers, P. and Watson, R., 2003. The future for fisheries. *Science*, 302(5649), pp.1359-1361.

Pendleton, L., Martin, N. and Webster, D.G., 2001. Public perceptions of environmental quality: a survey study of beach use and perceptions in Los Angeles County. *Marine Pollution Bulletin*, 42(11), pp.1155-1160.

Peters, K.A. and Otis, D.L., 2006. Shorebird roost-site selection at two temporal scales: is human disturbance a factor? *Journal of Applied Ecology*, 44(1), pp.196-209.

Pfister, C., Harrington, B.A. and Lavine, M., 1992. The impact of human disturbance on shorebirds at a migration staging area. *Biological Conservation*, 60(2), pp.115-126.

Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T. and Duarte, C.M., 2013. Global imprint of climate change on marine life. *Nature Climate Change*, 3(10), pp.919-925. Ramírez, F., Afán, I., Davis, L.S. and Chiaradia, A., 2017. Climate impacts on global hot spots of marine biodiversity. *Science Advances*, 3(2), p.e1601198.

Reusch, K., Suárez, N., Ryan, P.G. and Pichegru, L., 2020. Foraging movements of breeding Kelp Gulls in South Africa. *Movement Ecology*, 8(1), pp.1-12.

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F.S., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J. and Nykvist, B., 2009a. A safe operating space for humanity. *Nature*, 461(7263), pp.472-475.

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin III, F.S., Lambin, E., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J. and Nykvist, B., 2009b. Planetary boundaries: exploring the safe operating space for humanity. *Ecology and Society*, 14(2).

Rogers, D.I., Piersma, T. and Hassell, C.J., 2006. Roost availability may constrain shorebird distribution: exploring the energetic costs of roosting and disturbance around a tropical bay. *Biological Conservation*, 133(2), pp.225-235.

RStudio Team, 2019. *RStudio: Integrated Development for R*. RStudio, Inc., Boston, MA. URL <http://www.rstudio.com/>.

Ryan, P.G., 2013. Medium-term changes in coastal bird communities in the Western Cape, South Africa. *Austral Ecology*, 38(3), pp.251-259.

Rutz, C., Loretto, M.C., Bates, A.E., Davidson, S.C., Duarte, C.M., Jetz, W., Johnson, M., Kato, A., Kays, R., Mueller, T. and Primack, R.B., 2020. COVID-19 lockdown allows

researchers to quantify the effects of human activity on wildlife. *Nature Ecology & Evolution*, 4(9), pp.1156-1159.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A. and Leemans, R., 2000. Global biodiversity scenarios for the year 2100. *Science*, 287(5459), pp.1770-1774.

Samia, D.S., Nakagawa, S., Nomura, F., Rangel, T.F. and Blumstein, D.T., 2015. Increased tolerance to humans among disturbed wildlife. *Nature Communications*, 6(1), pp.1-8.

Schlacher, T.A., Carracher, L.K., Porch, N., Connolly, R.M., Olds, A.D., Gilby, B.L., Ekanayake, K.B., Maslo, B. and Weston, M.A., 2016. The early shorebird will catch fewer invertebrates on trampled sandy beaches. *PloS one*, 11(8), p.e0161905.

Schlacher, T.A., Schoeman, D.S., Dugan, J., Lastra, M., Jones, A., Scapini, F. and McLachlan, A., 2008. Sandy beach ecosystems: key features, sampling issues, management challenges and climate change impacts. *Marine Ecology*, 29, pp.70-90.

Schlacher, T.A., Weston, M.A., Lynn, D., Schoeman, D.S., Huijbers, C.M., Olds, A.D., Masters, S. and Connolly, R.M., 2015. Conservation gone to the dogs: when canids rule the beach in small coastal reserves. *Biodiversity and Conservation*, 24(3), pp.493-509.

Schneider, T.J., Maguire, G.S., Whisson, D.A. and Weston, M.A., 2020. Regulations fail to constrain dog space use in threatened species beach habitats. *Journal of Environmental Planning and Management*, 63(6), pp.1022-1036.

Schooler, N.K., Dugan, J.E. and Hubbard, D.M., 2019. No lines in the sand: Impacts of intense mechanized maintenance regimes on sandy beach ecosystems span the intertidal zone on urban coasts. *Ecological Indicators*, 106, p.105457.

Spearpoint, J.A., Every, B. and Underhill, L.G., 1988. Waders (Charadrii) and other shorebirds at Cape Recife, Algoa Bay, South Africa: seasonality, trends, conservation, and reliability of surveys. *Ostrich*, 59(4), pp.166-177.

Small, C. and Nicholls, R.J., 2003. A global analysis of human settlement in coastal zones. *Journal of Coastal Research*, 19(3), pp.584-599.

South African Government, 2020a. Disaster Management Act: Regulations to address, prevent and combat the spread of Coronavirus COVID-19: Amendment. [ONLINE] Available at: <https://www.gov.za/documents/disaster-management-act-regulations-address-prevent-and-combat-spread-coronavirus-covid-19>. [Accessed 11 January 2021]

South African Government, 2020b. Disaster Management Act: Regulations: Alert level 4 during Coronavirus COVID-19 lockdown. [ONLINE] Available at: <https://www.gov.za/documents/disaster-management-act-regulations-29-apr-2020-0000>. [Accessed 11 January 2021].

South African Government, 2020c. Disaster Management Act: Regulations: Alert level 3 during Coronavirus COVID-19 lockdown. [ONLINE] Available at: <https://www.gov.za/documents/disaster-management-act-regulations-alert-level-3-during-coronavirus-covid-19-lockdown-28> [Accessed 11 January 2021].

Steele, W.K., 1992. Diet of Hartlaub's Gull *Larus hartlaubu* and the Kelp Gull *L. dominicanus* in the Southwestern Cape Province, South Africa. *Ostrich*, 63(2-3), pp.68-82.

Stillman, R.A., Cox, J., Liley, D., Ravenscroft, N., Sharp, J. and Wells, M., 2009. *Solent disturbance and Mitigation Project: Phase I report*. Report to the Solent Forum.

Tarr, N.M., Simons, T.R. and Pollock, K.H., 2010. An experimental assessment of vehicle disturbance effects on migratory shorebirds. *The Journal of Wildlife Management*, 74(8), pp.1776-1783.

Thomas, K., Kvitek, R.G. and Bretz, C., 2003. Effects of human activity on the foraging behavior of sanderlings *Calidris alba*. *Biological Conservation*, 109(1), pp.67-71.

Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T. and Bartlam-Brooks, H., 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 359(6374), pp.466-469.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. and Melillo, J.M., 1997. Human domination of Earth's ecosystems. *Science*, 277(5325), pp.494-499.

Watson, J.E., Shanahan, D.F., Di Marco, M., Allan, J., Laurance, W.F., Sanderson, E.W., Mackey, B. and Venter, O., 2016. Catastrophic declines in wilderness areas undermine global environment targets. *Current Biology*, 26(21), pp.2929-2934.

Weston, M.A., Dodge, F., Bunce, A., Nimmo, D.G. and Miller, K.K., 2012. Do temporary beach closures assist in the conservation of breeding shorebirds on recreational beaches? *Pacific Conservation Biology*, 18(1), pp.47-55.

Wickham, H., François, R., Henry L., and Müller k., 2021. *dplyr: A Grammar of Data Manipulation*. R package version 1.0.3. URL <https://CRAN.R-project.org/package=dplyr>.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B., Lotze, H.K., Micheli, F., Palumbi, S.R. and Sala, E., 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science*, 314(5800), pp.787-790.

Wynberg, R.P. and Branch, G.M., 1994. Disturbance associated with bait-collection for sandprawns (*Callinassa kraussi*) and mudprawns (*Upogebia africana*): long-term effects on the biota of intertidal sandflats. *Journal of Marine Research*, 52(3), pp.523-558.

Wynberg, R.P. and Branch, G.M., 1997. Trampling associated with bait-collection for sandprawns *Callinassa kraussi* Stebbing: effects on the biota of an intertidal sandflat. *Environmental Conservation*, pp.139-148.

Yasué, M., 2006. Environmental factors and spatial scale influence shorebirds' responses to human disturbance. *Biological Conservation*, 128(1), pp.47-54.

Yasué, M. and Dearden, P., 2006. The potential impact of tourism development on habitat availability and productivity of Malaysian plovers *Charadrius peronii*. *Journal of Applied Ecology*, 43(5), pp.978-989.

Yasué, M., Dearden, P. and Moore, A., 2008. An approach to assess the potential impacts of human disturbance on wintering tropical shorebirds. *Oryx*, 42(3), pp.415-423.

Yoda, K., Tomita, N., Mizutani, Y., Narita, A. and Niizuma, Y., 2012. Spatio-temporal responses of black-tailed gulls to natural and anthropogenic food resources. *Marine Ecology Progress Series*, 466, pp.249-259.

7. Appendix 1

Table A1: List of observed shorebird species recorded in *in situ* counts during lockdown levels 3 to 1.

Common name	Scientific name
Hartlaub's gull	<i>Chroicocephalus hartlaubii</i>
Kelp gull	<i>Larus dominicanus</i>
Common pigeon	<i>Columba livia</i>
Common starling	<i>Sturnus vulgaris</i>
Cormorant	<i>Phalacrocorax capensis</i>
Oyster catcher	<i>Haematopus bachmani</i>
White fronted plover	<i>Charadrius marginatus</i>