1 **Population abundance of recovering humpback whales (*Megaptera***

2 ***novaeangliae*) and other baleen whales in the Scotia Arc, South Atlantic**

3

4 **Mick Baines[1]*, Natalie Kelly[2], Maren Reichelt[1], Claire Lacey[3,9], Simon Pinder[4], Sophie**

5 **Fielding[5], Eugene Murphy[5], Phil Trathan[5], Martin Biuw[7], Ulf Lindstrøm[7,8], Bjørn A. Krafft[6]**

6 **and Jennifer A. Jackson[5]**

7 [1]Wildscope, El Cuartón, Tarifa, Cádiz, Spain

8 [2]Australian Antarctic Division, Department of Agriculture, Water and the Environment, Kingston,

9 Tasmania 7050, Australia

10 [3]SMRU, Scottish Ocean Institute, University of St Andrews, St Andrews, Fife, KY16 8LB, UK

11 [4]Leuchars, St Andrews, KY16 0HR, UK

12 [5]British Antarctic Survey, NERC, High Cross, Cambridge CB3 0ET, UK

13 [6]Institute of Marine Research, Nordnes, Bergen, Norway

14 [7]Institute of Marine Research, Framsenteret, Tromsø, Norway

15 [8]UiT Norges Arktiske Universitet, Tromsø, Norway

16 [9]Marine Mammal Research Program, Hawaii Institute of Marine Biology, University of Hawaii at

17 Manoa, HI 96744

18

19 *Corresponding author: mickbaines@gmail.com

20

21 **ABSTRACT**

22 Following the cessation of whaling, South Atlantic populations of humpback (*Megaptera*

23 *novaeangliae*) and some other baleen whale species are recovering, but there has been

24 limited monitoring of their recovery in the Scotia Arc, a former whaling epicentre and a

25 hotspot for Antarctic krill (*Euphausia superba*). To inform the management of krill fisheries,

1   up to date assessment of whale biomass and prey consumption is essential. Using a model-

2   based approach, we provide the first estimates of whale abundance and krill consumption for

3   South Georgia and the South Sandwich Islands, and total abundance of humpback whales

4   across their southwest Atlantic feeding grounds, using data collected in 2019. Humpback

5   whale abundance was estimated at 24,543 (CV = 0.26; 95% CI 14,863 – 40,528), similar to that

6   measured in Brazil on the main wintering ground for this population. The abundance of baleen

7   whales in South Georgia and the South Sandwich Islands, including those not identified to

8   species level, was estimated at 43,824 (CV = 0.15; 95% CI 33,509 – 59,077). Based on the

9   proportion of humpback whales identified during the surveys (83%), the majority of these are

10   likely to be humpback whales. Annual krill consumption by baleen whales was estimated to

11   be in the range 4.8 – 7.2 million tons, representing 7 - 10% of the estimated krill biomass in

12   the region. However, there is a need to better understand feeding rates in baleen whales, and

13   further research into this field should be a priority in order to improve the accuracy and

14   precision of prey consumption rate estimation.

15

16   **KEY WORDS**

17   HUMPBACK WHALE; BALEEN WHALE; ABUNDANCE; KRILL CONSUMPTION; SOUTH GEORGIA;

18   SOUTH SANDWICH ISLANDS

19

20   **1.   INTRODUCTION**

21   Baleen whales are important predators of krill, but were decimated by modern whaling during

22   the 20th century (Rocha et al. 2014). In the South Atlantic, whaling was initially very intense in

23   the vicinity of sub-Antarctic South Georgia island, and latterly spread across the Scotia Arc via

24   offshore factory ships working with catcher vessels. Species were successively targeted, with

1   humpback whales (*Megaptera novaeangliae*) hunted initially, followed by blue

2   (*Balaeonoptera musculus*), fin (*B. physalus*), and sei whales (*B. borealis*). There was only

3   limited exploitation of southern right whales (*Eubalaena australis*) in the 20th century, as this

4   species was already very rare following heavy exploitation in the early 19th century (IWC

5   2001). Since whaling ended, the abundance of some cetacean species has been increasing.

6   The southwest Atlantic population (referred to by IWC (1998) as Breeding Stock A) of

7   humpback whales is thought to have recovered to a level similar to that in the 19th century,

8   before its exploitation on an industrial scale (Bortolotto et al. 2016, Ward et al. 2011, Zerbini

9   et al. 2019). In the light of the increasing size of this humpback whale population, and of other

10   species in the region such as the blue whale (Branch et al. 2004, Calderan et al. 2020), fin

11   whale (Viquerat & Herr 2017) and southern right whales (Best et al. 2001, Groch et al. 2005,

12   Crespo et al. 2019), re-assessment of whale abundance and krill consumption rates by whales

13   on their high latitude South Atlantic feeding grounds is urgently needed for inclusion in krill

14   fishery management models (e.g. Trathan et al. in press).

15   Antarctic krill (*Euphausia superba*) is a critical species in Southern Ocean food webs and

16   constitutes the main prey of a wide range of taxa, including species of fish, squid, seabirds,

17   pinnipeds and cetaceans (Hill et al. 2006, Trathan & Hill 2016). The Antarctic Peninsula and

18   Scotia Arc region has been identified as the area with the highest concentration of krill within

19   the Southern Ocean (Atkinson et al. 2008), supporting high levels of predator biomass and

20   other biodiversity, particularly in the northern Scotia Arc (e.g. Hogg et al. 2011). Southern

21   Ocean fishery management is required to be sufficiently dynamic to be able to adapt quickly

22   to changes in both prey and predator ecology, to spatially and temporally regulate harvesting

23   at sustainable levels in order to minimise any negative impacts on the Antarctic ecosystem

24   from such direct anthropogenic activities (Trathan et al. 2021). Within the Scotia Arc

1   spatiotemporal overlap with the summer feeding season of baleen whales has been limited

2   to the South Orkney stratum, because the krill fishery has been restricted to winter months

3   in the South Georgia stratum and there has been no krill fishing effort in the South Sandwich

4   Islands stratum (CCAMLR 2021). However, both whales and the fishery exploit the same krill

5   populations (Trathan et al. 2021). Catch limits need to be set with reference to updated

6   estimates of both krill and predator biomass (Constable 2001 & 2011, Constable et al. 2000,

7   Kawaguchi & Nicol 2020, Krafft et al. 2021). While krill are regularly monitored at a small

8   number of locations in the Southern Ocean (e.g. Fielding et al. 2014, Reiss et al. 2008, Krafft

9   et al. 2018), regular monitoring of predator biomass is also crucial for sustainable fishery

10 management, particularly in areas targeted by krill fisheries. This is particularly important for

11 baleen whales, as they are significant krill consumers and many species are increasing in

12 abundance following their protection from commercial whaling (e.g. Branch et al. 2004,

13 Leaper & Miller 2011, Bortolotto et al 2016, Calderan et al. 2020).

14 Since commercial whaling ended, very few large-scale surveys designed to assess whale

15 recovery in the polar South Atlantic (Scotia Arc) region have been conducted. Three

16 circumpolar surveys of the Southern Ocean were carried out between 1978/79 and 2003/04

17 (International Whaling Commission's IDCR/SOWER), yielding circumpolar and regional

18 abundance estimates for blue and humpback whales (Branch 2007 & 2011). However, these

19 surveys were designed primarily to measure minke whale abundance (Matsuoka et al. 2003).

20 Minke whale occurrence is typically concentrated at the ice edge (Kasamatsu et al. 1998; Herr

21 et al. 2019), so in the South Atlantic surveys were conducted in the southern Scotia Arc, while

22 South Georgia in the northern Scotia Arc is the location where the majority of historical

23 whaling effort took place. Modern whaling catches of >176,000 whales were made at South

24 Georgia (Allison 2016), indicating that the northern Scotia Arc was a key feeding ground for

1   many baleen whale species. The Commission for the Conservation of Antarctic Marine Living

2   Resources (CCAMLR) 2000 synoptic krill survey surveyed both whales and krill across the

3   Scotia Arc, providing information on both whale abundance (Hedley et al. 2001) and krill

4   consumption by whales (Reilly et al. 2004). However surveys of South Georgia waters were

5   limited by poor weather conditions, and abundance estimates from this historically important

6   region were very small ($\tilde{N}$ = 116 baleen whales, Hedley et al. 2001; no uncertainty estimates

7   provided).

8   In 2019, this synoptic krill survey was (in large part) repeated (Krafft et al. 2021), and included

9   cetacean observers collecting line-transect data over an area similar to the 2000 survey. For

10   the first time, the remote South Sandwich Islands were also surveyed, an area known from

11   satellite tracking to be an important feeding site for humpback whales (Zerbini et al. 2006 &

12   2011, Horton et al. 2020) but never corroborated by direct surveys. Here we report for the

13   first time estimates of total baleen whale abundance and krill consumption in the South

14   Georgia and South Sandwich Islands (northern and eastern Scotia Arc) and provide a new

15   feeding ground estimate of abundance for humpback whales in the Scotia Arc, spanning the

16   known feeding range of the southwest Atlantic breeding stock. These are essential data to

17   contribute to the CCAMLR krill risk assessment framework (CCAMLR 2019, paragraph 5.17),

18   which combines localised estimates of krill consumption needs of various predators with

19   estimates of krill biomass at the same spatio-temporal scale, to test the likely impacts of a

20   range of different krill fishing scenarios.

21

22   **2.   METHODS**

23   **2.1. Cetacean survey field methods**

1   Three of the vessels that participated in the 2019 CCAMLR synoptic krill survey, the *RRS*

2   *Discovery* (DIS), *FV Cabo de Hornos* (CDH) and *RV Kronprins Haakon* (KPH) contributed data to

3   this study, although in the case of CDH and KPH only humpback whale data were contributed.

4   Within the Scotia Arc, these surveys covered three main areas, defined by the Food and

5   Agriculture Organisation of the United Nations (FAO) as Subarea 48.2 South Orkney Islands

6   and Scotia Sea (SO), Subarea 48.3 South Georgia (SG) and Subarea 48.4 South Sandwich

7   Islands (SS) (Figure 1). As in the 2000 survey, all vessels surveyed parallel transects across

8   these strata, with DIS surveying the South Georgia and South Sandwich regions, CPH surveying

9   South Georgia and the South Orkney Islands/Scotia Sea, and KPH surveying transects in all

10   three strata.

11   Line transect survey protocols were standardized as far as possible prior to survey, but

12   differed in practice, as numbers of observers differed across vessels. Observation watches

13   were carried out through daylight hours during periods with visibility at least 1 km in Beaufort

14   sea state <6; data collected outside these limits were removed from these analyses. Line

15   transect effort was suspended whenever the vessel stopped for scientific sampling on station

16   (trawl and net hauls, oceanographic sampling, etc.). On transect data were collected on vessel

17   position, speed and heading, wind speed and direction, sea state, weather conditions and

18   visibility every 15 minutes, or whenever environmental conditions changed. On DIS, a team

19   of four observers maintained effort between 05:30 and 20:00 (local time). Two observers

20   were on watch at any one time, with a third acting as data recorder; the observers rotated

21   every hour, such that the same pair of observers always watched together. The observation

22   platform located above the bridge was approximately 19 m above sea level (ASL) and had an

23   unobstructed view of 180° forward. Distances were estimated using reticle binoculars and

24   angles from the vessel's heading were measured with an angle board. On CDH, observations

1   were carried out by a single observer during daylight hours from a platform 10.5 m ASL;

2   observations were only made from the starboard side, since visibility there was significantly

3   better than on the port side. The primary search area was from 350° - 45° relative to the ship's

4   heading, with a secondary search area from 45° to 90°. Distances to whales were estimated

5   by eye, and random checks on accuracy were made by using a stopwatch and comparing the

6   distances using the ship's speed and assuming no animal movement. Observations were

7   carried out mainly from inside the bridge or outside in front of the bridge when weather

8   conditions allowed. On KPH, observer effort was carried out by two dedicated observers. The

9   observation platform was approximately 25 m ASL and, due to an obstructed view to

10 starboard, dedicated observations were usually made within the forward port quarter (270°

11 - 360°, relative to the ship's heading). However, observers also scanned outside of this sector,

12 and occasionally recorded observations within that part of the forward starboard quarter that

13 was not obstructed.

14

15 **2.2. Estimation of abundance**

16 Line transect cetacean survey data collected by all three survey vessels were used to estimate

17 the abundance of humpback whales across the Scotia Arc, which is thought to represent the

18 summer feeding ground range of southwest Atlantic humpback whales (Zerbini et al. 2019).

19 The abundance of all baleen whales was also estimated for the two CCAMLR Statistical

20 subareas 48.3 (South Georgia; SG) and 48.4 (South Sandwich; SS), using survey data from DIS

21 alone, to provide total whale biomass estimates for these areas.

22 The CCAMLR 2019 survey was designed primarily to estimate krill biomass and to investigate

23 krill ecology and not as a line transect survey for cetaceans. A design-based approach to

24 abundance estimation, for which there should be an equal probability of coverage throughout

1   the study area (Buckland et al. 2001, Hiby & Hammond 1989), was therefore not considered

2   appropriate and a model-based method (Hedley et al. 1999, Hedley & Buckland 2004) was

3   adopted. A two-stage process was followed in which detection functions were first fitted to

4   perpendicular distance estimates and generalised additive models (GAM) were then applied,

5   using an offset derived from the detection function to account for effective search area (Miller

6   et al. 2013). Abundance was estimated by summing the product of predicted density and cell

7   area over a grid of resolution 0.14° latitude and longitude (median cell area 140 km^2).

8   Detection functions were fitted with the *R* package *Distance* (Miller et al. 2019). A multiple

9   covariate distance sampling (MCDS) framework was implemented with group size, sea state,

10   visibility and observer team as potential covariates, applied to count data from individual

11   vessels and to data pooled across all three vessels. For the two vessels KPH and CDH, sightings

12   made outside their respective 90° primary fields of view were excluded. Fitting detection

13   functions to data pooled across the three vessels proved challenging due to small sample sizes

14   within the study area for CDH and KPH. We therefore included sightings from transect lines

15   in areas adjacent to the Scotia Sea study area in the detection function, which increased

16   sample sizes and allowed good fits to be obtained. Half-normal and hazard-rate key functions

17   with no adjustment terms were tested and the best fitting models were selected by

18   minimising the Akaike Information Criterion (AIC).

19   Density surface models and associated variances were fitted to count data using the *R*

20   package *dsm*, which also allowed for uncertainty in the detection function to be propagated

21   through to the abundance estimates (Miller et al. 2013, Bravington et al. 2021). Data were

22   partitioned into segments with mean length 10.6 km (range 0.9 – 35 km); the maximum length

23   of segments was constrained by regular changes in observer teams. Coordinates were

24   projected to UTM zone 21S so that *x* and *y* coordinates represented similar spatial scales. The

1   covariates included in the models are listed in Table 1, although only those found to be

2   contributing significantly to model fit were retained. Environmental covariates were checked

3   for correlation by constructing a Pearson correlation matrix and, of the variables retained in

4   models, the maximum Pearson correlation value was 0.23. Negative binomial and Tweedie

5   (Dunn & Smyth 2008) distributions were tested, all variables were included and by setting

6   *Select = True*, covariates not contributing to model fit were automatically penalised out

7   (Marra & Wood 2011). Plots of smooth functions were examined and, where the distribution

8   of data points was markedly skewed, explanatory variables were log transformed to achieve

9   a more even distribution. Model residuals were investigated using *rqgam.check.* The best

10   fitting models were selected on the basis of maximising deviance explained and minimising

11   the coefficient of variation attributed to the GAM, and the resulting predictions were checked

12   by comparison with plots of effort and sightings made across the study area.

13   Spatial models were fitted to humpback whale density estimates pooled across all vessels for

14   the entire study area. The *dsm* package assumes observations are carried out on both sides

15   of the track-line, i.e. through 180° to generate an offset accounting for the effective area

16   searched that takes the general form:

17   $$Offset = 2 * ESW * l$$

18   where ESW is the effective strip width derived from the detection function and l is the line

19   segment length. Therefore, to account for effort having been applied through 90° on KPH and

20   CDH, segment lengths for those vessels were halved. Data from DIS only were used to model

21   the abundance of all baleen whales in SG and SS, including unidentified baleen whales, but

22   excluding sightings recorded as unidentified large whales, a category that could include sperm

23   whales.

24

1 **2.3. Krill consumption by whales**

2 Lunge feeding by baleen whales is energetically costly and therefore its efficiency in terms of

3 energy gained over cost is dependent on prey density (Goldbogen et al. 2011). However, given

4 sufficiently dense aggregations of prey it is an extremely efficient method of feeding

5 (Goldbogen et al. 2019, Potvin et al. 2021), permitting rapid weight gain. Lockyer (1981)

6 concluded from seasonal catch data that most humpback whales arrived in South Georgia

7 before the end of December with a body weight of around 15 t and weight increase appeared

8 to slacken off in February with an overall weight gain of 15 t, effectively doubling the animal's

9 weight in a period of only three months. Estimation of krill consumption by baleen whales is

10 based on whale abundance estimates, estimated daily prey consumption rates and either the

11 length of stay of whales in feeding areas or the proportion of their annual prey requirement

12 consumed there. Reviews of methods for estimating prey consumption rates (Reilly et al.

13 2004, Leaper & Lavigne 2007) point out some of the difficulties associated with the estimation

14 of this parameter for species in which there is marked seasonal asymmetry in feeding rates

15 and for which direct measurements of consumption are unavailable. Humpback whales

16 undertake long migrations: in the case of the southwest Atlantic population their winter

17 breeding habitat in the coastal waters of Brazil is located over 4,000 km from feeding habitats

18 around the South Sandwich Islands and South Georgia (Clapham & Mead 1999, Zerbini et al.

19 2011a). While humpback whales may feed opportunistically during migration (Danilewicz et

20 al. 2009, Owen et al. 2017) the bulk of their annual energy requirements must be supplied by

21 prey consumption during the period they forage within southern feeding grounds. There are

22 essentially two approaches to the estimation of consumption rates, a supply approach,

23 historically based on feeding rates derived from weights of the stomach contents of whales

24 killed commercially or for research purposes, and a demand approach based on studies of

1   energy budgets. Recent work on energy budgets has focussed on the costs of anthropogenic

2   disturbance (e.g. Pirotta et al. 2021, Braithewaite et al. 2015) for which relative measures are

3   meaningful, but in order to estimate absolute biomass of prey consumed, a series of

4   parameters have to be estimated and assumptions made, leading Reilly et al. (2004) to

5   conclude the more direct supply approach to be more reliable. However, assumptions

6   regarding digestion rates, the length of time ingested food remains in the stomach and the

7   frequency with which the stomach is filled introduce unquantifiable uncertainty in that

8   approach (Leaper & Lavigne, 2007). Few quantitative data are available on the weights of

9   mysticete stomach contents. Kawamura (1980) reviewed qualitative data available from

10   commercial whaling on the prey species of whales and provided data on the weights of fin

11   whale stomach contents from catches in the Bering Sea. Tamura et al. (1997) estimated daily

12   consumption rates from minke whales lethally sampled in Antarctic regions and Reilly et al.

13   (2004) extrapolated from these estimates to larger species using an allometric model

14   approximated by an exponential function. Allometric scaling from the smallest baleen whale

15   species does not take into account differences in feeding rates between species arising from

16   niche separation (Friedlaender et al. 2006). Given the uncertainties in both approaches, we

17   opted for the energetic demand method.

18   Population demography also needs to be taken into account in consumption rate estimation

19   as energetic demands and therefore prey consumption rates vary according to age, sex and

20   reproductive status; recent insights into this intraspecific variation have been gained by

21   quantitative assessment of total body lipid from historic whaling data (Irvine et al. 2017). The

22   population demography of humpback whales using the Scotia Arc (i.e. sex-specific

23   proportions of adults and juveniles) is not directly known, so was inferred from the available

24   literature. In their review of humpback whale life history parameters, Zerbini et al. (2010)

1   considered the range of parameters compatible with maximum rates of population growth.

2   A population rate of increase (*r*) in the range 7% - 11% (Zerbini et al. 2010) resulted in the

3   proportion of breeding age females being in the range 34% - 44%. However Zerbini et al.

4   (2010) aimed to measure maximum possible growth rates in a population that was far from

5   recovery, and the southwest Atlantic population is thought now to be close to recovery, with

6   median predicted population growth between 2015 and 2019 at *r* = 2.94% (Zerbini et al.

7   2019). In the western North Atlantic, lower population growth rates (*r* ~ 3%, Stevick et al.

8   2003) are associated with proportions of breeding females at the lower end of this range

9   (averaged annual proportion of mature animals in the Gulf of Maine feeding ground is 68.7%,

10   Robbins 2007). Therefore, for the purposes of this study we took a conservative approach and

11   assumed the Scotia Arc humpback population is likely similar to the lower range value from

12   Zerbini et al. (2019) of 34% breeding age females and a sex ratio of 1:1 (i.e. 68% total mature

13   animals, similar to the mature proportion estimated for the Gulf of Maine feeding ground).

14   Mean body mass of humpback whales is based on Trites & Pauly (1998). For other baleen

15   whale species we have used body mass estimates compiled by Reilly et al. (2004) which

16   assume a mean body mass for each species; we did not adjust for population demography as

17   the proportion of adult and juvenile components are not known for these species in the South

18   Atlantic.

19   The basal metabolic rate (BMR) is the energy required by an organism to maintain

20   homeostasis. Kleiber (1975) identified an allometric relationship between BMR and body

21   mass in animals, calculated as BMR = $70M^{0.75}$ where BMR is measured in kilocalories per day

22   and M is body mass in kilograms. All whales require additional energy for activities that

23   include locomotion and prey capture, in females of reproductive age for foetal growth in

24   pregnancy and for subsequent lactation, mature males may incur additional energetic costs

1   associated with reproduction and calves require energy for growth. Further energetic costs

2   may arise from stressors such as anthropogenic disturbance, attacks by predators or changes

3   in the distribution of prey.

4   When BMR is expressed in kiloJoules per day, Kleiber's equation becomes BMR = $293.1M^{0.75}$

5   and a multiplication factor >1 may then be applied to estimate the average daily metabolic

6   rate, usually referred to as the field metabolic rate (FMR) of the form FMR = $\beta(293.1M^{0.75})$

7   (Leaper & Lavigne 2007), where β may be expected to vary according to age, sex and

8   reproductive status. In their review of methods for the estimation of prey consumption by

9   whales, Leaper & Lavigne (2007) found most researchers had assumed β to be in the range 2-

10   5 but cautioned that such values were not necessarily derived from actual data and found no

11   evidence for an upper bound of $\beta > 4$. A direct approach to the measurement of FMR has been

12   applied to a wide range of terrestrial mammals, some pinniped and odontocete species using

13   a doubly labelled water (DLW) method (Lifson & McClintock 1966, Nagy 1983, Speakman

14   1997, Nagy et al. 1999). However, the DLW method requires intervention in the form of taking

15   blood samples and injecting labelled water that, in the case of cetaceans, has restricted its

16   application to captive animals. Nagy (2005) reviewed the relationship between FMR and body

17   mass using data derived from DLW experiments and developed the following formula for

18   terrestrial mammals:

19 $$FMR = 4.82M^{0.734}$$

20   Evolutionary adaptation to life in low temperature aquatic environments may, however,

21   result in elevated metabolic rates compared with terrestrial mammals (e.g. Costa & Williams

22   2000). When applied to pinnipeds and bottlenose dolphins (*Tursiops truncatus*) the FMR

23   values estimated by the DLW method were up to six times higher than those estimated by

24   Nagy's equation for terrestrial mammals (Costa & Williams 2000). In a study of harbour

1   porpoise (*Phocoena phocoena*) energetics, FMR estimates obtained by the DLW method were

2   correlated with respiration rates in captive animals, which were then compared with

3   respiration rates of free-ranging porpoises to obtain FMR estimates up to two times those

4   predicted by Nagy's equation (Rojano-Donãte et al. 2018). However, differences between

5   small odontocetes and baleen whales in body size, behavioural activity and feeding strategies

6   suggests caution in extrapolation of the high FMR values estimated for the smaller species.

7   Simple allometric scaling does not take into account that much of the body mass of large

8   whales consists of blubber, which has a lower metabolic rate than other tissues, such as

9   muscle (Costa & Williams 2000) which may therefore tend to lower BMR and therefore FMR.

10 On the other hand, the energetic implications associated with conversion of ingested food to

11 blubber and the reverse process in fasting periods to mobilise stored energy may tend to raise

12 metabolic rates, as for example the efficiency in converting stored energy to milk energy in

13 lactating mammals has been estimated at 84% (Oftedal 2000). Using a state-dependent

14 foraging model, Wiedenmann et al. (2011) estimated blue whales expend between 2.07 and

15 3.1 times the daily estimate of BMR (with a mean value of 2.29).

16 Comparing Nagy's equation for FMR with Kleiber's BMR equation in humpback whales gives

17 a β value of 2.25. We therefore take a conservative approach and assume that in males and

18 non-breeding females β is in the range 2-2.5. Given a birth rate in the range 0.36 − 0.42

19 (Zerbini et al. 2010) we assume breeding age females are either pregnant or lactating in two

20 out of every three years. Pregnancy requires additional energy to grow and support the foetus

21 and placenta, and lactation is one of the most energetically expensive physiological processes

22 in mammals (Hanwell & Peaker 1977). In a study of grey whale (*Eschrichtius robustus*)

23 energetics, the estimated cost of pregnancy was an additional 18% and of lactation 28% of

24 annual energy requirements (Villegas-Amtmann et al. 2015). Analysis of historical whaling

1   records from Western Australia (Irvine et al. 2017) found pregnant female humpback whales

2   had energy stores 26.2% higher than non-pregnant females. Using the data given above for

3   the increased energy store of pregnant humpback whales and the proportional increase of

4   lactation over pregnancy in grey whales, we estimate the mean β for females over a three

5   year period to be in the range 2.8-3.5. Immature animals need additional energy for growth

6   and in the period from weaning at one year of age to reaching sexual maturity at the age of

7   five, their average annual gain in body mass is approximately 7% (Chittleborough 1965,

8   Clapham 2000). Innes et al. (1987) using allometric functions of body mass found feeding rates

9   of growing juvenile marine mammals to be approximately double that of adults, although this

10   was largely based on pinnipeds with baleen whales represented by a single study of captive

11   grey whale calves (Wahrenbrock et al. 1974). We therefore assumed β to be in the range 3-4

12   for juvenile humpback whales.

13   The energetic content of krill varies with age, sex and reproductive status (Färber-Lorda et al.

14   2009). Schaafsma et al. (2018) reviewed the energetic value of zooplankton species in the

15   Southern Ocean, quoting values of 5.45 kJg^{-1} wet weight for female and 3.83 kJg^{-1} for male

16   *Euphausia superba Dana* sampled in South Georgia (Clarke 1984). Assuming a 1:1 sex ratio of

17   krill we use a mean value of 4.64 kJg^{-1} and divide the estimated annual energy requirement

18   of whales by this value to obtain the weight of krill needed to be assimilated to meet the

19   energy demand. The assimilation efficiency of prey by baleen whales was estimated to be

20   80% (Lockyer 1981, Kenny et al. 1997) resulting in a multiplication factor of 1.25 for the

21   quantity of prey needed to be consumed. A further assumption needs to be made of the

22   proportion of overall annual consumption of prey by humpback whales during the summer

23   period spent in high latitude habitats, for which we took the value of 85% suggested by

24   Lockyer (1981).

1

2   **3.   RESULTS**

3   Effort tracks and humpback whale sightings from all three vessels in the study area are shown

4   in Figure 2, revealing concentrations of humpback whale sightings in two main areas, one to

5   the east and northeast of the South Sandwich Islands, the other to the north and northwest

6   of South Georgia. For each vessel and each survey region, effort expressed as total line length

7   is summarised in Table 2, and the number of humpback whale sighting events and counts are

8   summarised in Table 3, which excludes sightings truncated at perpendicular distances >2.5

9   km and outside the 90° primary fields of view for CDH and KPH. Sightings of all mysticete

10 species recorded by DIS are summarised in Table 4. These sightings and effort data are

11 available from the British Antarctic Survey Polar Data Centre (DOI: XXX).

12

13 **3.1. Abundance of humpback whales in the Scotia Arc**

14 The detection function selected was a hazard rate function with truncation at 2.5 km

15 incorporating sea state and observer team as covariates (Figure 3); a Tweedie distribution

16 (Dunn & Smyth 2008) was selected for the GAM, based on goodness of fit. The variables

17 retained were tabulated in the model output summary with smooths plotted in Figure 4, and

18 explained 41.4% of the total deviance (Table 5). Phytoplankton density emerged as a highly

19 significant explanatory variable, both as chl-*a* values concurrent with the survey and those for

20 the previous year. These two variables were not significantly correlated, although the values

21 for April 2018 were correlated with adjacent months (data not shown), so the variable

22 CHL_Apr2018 was interpreted as representing a generic value for phytoplankton density in

23 the previous autumn. The predicted abundance of humpback whales across the Scotia Sea

24 was 24,543 (CV = 0.26, 95% CI 14,863 – 40,528) (Table 6). The resulting density surface model

1 (Figure 5) showed two main areas of high density, one to the north-west of South Georgia

2 and the other mainly to the north and north-east of the South Sandwich Islands.

3

4 **3.2. Abundance of baleen whales in South Georgia and the South Sandwich Islands**

5 For combined baleen whales, the best fitting detection function also included observer team

6 and sea state as covariates (Figure 6). The GAM retained fewer variables compared with the

7 humpback whale model (Table 7, Figure 7) and deviance explained was lower than for

8 humpback whales at 21%. The point estimate of baleen whale abundance (Table 8) was

9 43,824 (CV = 0.15, 95% CI 33,509 – 59,077); the density surface model is shown in Figure 8.

10

11 **3.3. Estimation of krill consumption**

12 *3.3.1. Humpback whales*

13 Table 9 lists the FMR for individual whales and annual energy requirements (AER) for each

14 age and sex class of the humpback whale population. For the estimated humpback whale

15 population (n = 24,543) this results in an annual consumption of 3.5-4.5 million tonnes (Mt)

16 of krill. Assuming 85% is consumed in high latitude feeding grounds, the total wet weight of

17 krill consumed in the study area would be 3-3.8 Mt.

18

19 *3.3.2. All baleen whales*

20 Estimating the consumption by all baleen whales was challenging because 27% of the total

21 count of whales input to the abundance model were not identified to species level. We

22 assume that the species composition of unidentified sightings and the resulting abundance

23 estimates were in proportion to that of the identified sightings, although there may be bias

24 in the unidentified category associated with differences between species in size, behaviour or

1   prominence of diagnostic identification features. Table 10 lists the FMR for individual whales

2   of mean body mass and the AER for the estimated abundance of each baleen whale species.

3   Assuming β to be in the range 2-3, 85% of annual consumption would amount to 4.8-7.2 Mt

4   of krill consumed.

5

6   **4.   DISCUSSION**

7   Here we provide the first estimates of whale abundance and krill consumption for the waters

8   surrounding South Georgia and the South Sandwich Islands (north and east Scotia Sea),

9   regions that were historically whaled and that currently support a regulated commercial krill

10   fishery (Trathan et al. 2021). Total abundance of baleen whales across this region is estimated

11   to be 43,824 (CV = 0.15) and based on the large proportion of humpbacks identified during

12   the surveys (83%, Table 3), the majority of these whales are likely to be that species. South

13   Georgia was an epicentre of commercial whaling in the early 20th century (Hart 2001), and

14   over 173,000 whales were killed within a day's sailing of its shores (Allison 2016). The fishery

15   closed in the 1960s, and whales were rarely seen for the next three decades. Humpback and

16   southern right whales re-appeared at South Georgia in the 1990s (Moore et al. 1999) but their

17   occurrence was patchy. For example, the SOWER survey of South Georgia waters in 2000

18   provided a regional estimate of only 116 baleen whales (Hedley et al. 2001; no estimate of

19   uncertainty provided). Reports from visitors to South Georgia showed an increase in sightings

20   up to the 2001 - 2005 period, but reduced sightings in the latter half of that decade

21   (Richardson et al. 2012). Since 2013, sightings of humpback whales in the summer months of

22   January and February have increased rapidly however (Jackson et al. 2020). Our 2019

23   estimate of baleen whale abundance in South Georgia waters is 31,676 (CV=0.16), suggesting

1 a dramatic increase in whales returning to this historically important habitat over the last 20

2 years.

3

4 **4.1. Humpback whale recovery in the Scotia Arc**

5 The large estimate of humpback whale abundance in the Scotia Arc presented here confirms

6 the strong recovery of the southwest Atlantic population reported from their winter breeding

7 habitats in Brazil (Zerbini et al. 2019). The feeding ground range of the southwest Atlantic

8 humpback population is estimated to span 20-50°W and south from 40°S to the ice edge in

9 the east, and between 50-70°W from 40°S to the Falkland Islands (Zerbini et al. 2011b).

10 Humpbacks are now rarely seen in the latter location, although they were occasionally caught

11 there (Frans & Augé 2016). Modelled recovery of the southwest Atlantic population predicts

12 breeding ground abundance to be over 24,000 in 2019 (median N = 24,925, probability

13 intervals 22,369 – 27,007, Zerbini et al. 2019). This estimate is closely concordant with our

14 abundance estimate of 24,543 (CV = 0.26%) humpback whales present across the Scotia Arc

15 in the same year. The CV of 26% compares favourably with earlier design- and model-based

16 abundance estimates in the southwest Atlantic region (Branch 2011, Hedley et al. 2001),

17 especially given the circumstances of differences between vessels, constraints imposed by

18 team size, the very large area covered, frequent poor viewing conditions and a survey not

19 primarily designed as a cetacean line transect survey. Larger team sizes would have been

20 ideal, such that a dual platform approach could be used to estimate the probability of

21 detection on the track-line (Buckland et al. 2004). Here, we do not have data to correct for

22 the proportion of animals potentially missed on the track-line (i.e. we assumed $g(0) = 1$), so

23 our estimates may be negatively biased and therefore represent conservative estimates of

24 abundance. Humpback whale abundance in the Scotia Sea was previously estimated at 2,493

1   (CV=0.55) in 2001 (Hedley et al. 2001, Reilly et al. 2004); our new surveys indicate an order of

2   magnitude increase in the abundance of this species in the last two decades, and given the

3   survey constraints we consider this a conservative estimate.

4

5   **4.2. Baleen whale abundance**

6   The CV of the abundance estimate for all baleen whales (15%) was lower than that for

7   humpback whales alone, probably due to the larger sample size. When apportioned to species

8   in the same proportions as for counts of identified species, the point estimate of humpback

9   whale abundance derived from the all baleen whale category (36,444) was higher than the

10   estimate obtained from identified humpback whale sightings (24,543), although it fell within

11   the 95% CI of 14,863 − 40,528. Such an increase is to be expected given the assumed

12   predominance of humpback whales in the unidentified category and suggests that the point

13   estimate for humpback whales is conservative. Pooling data from all baleen whale species

14   into a single category potentially raises problems for modelling if there are differences in

15   detectability and habitat partitioning, leading to variation in the influence of environmental

16   parameters or variation in prey species. In this case, species identity could not be used as a

17   covariate because 27% of all baleen whale sightings were unidentified to species level.

18   Since the global moratorium on commercial whaling came into effect in 1986, populations of

19   all baleen whale species (Allison 2016) have not been hunted, and are showing evidence of

20   recovery in the southwest Atlantic (Calderan et al. 2020, Weir et al. in press, Crespo et al.

21   2019, Zerbini et al. 2019, Viquerat & Herr, 2017). Here, we estimate that over 45,000 baleen

22   whales used South Georgia and South Sandwich Islands waters in summer 2019, a signal that

23   whales are again becoming a significant component of the ecosystems of these waters. The

24   majority of the whales sighted in both areas were humpback whales. Humpback whales were

1 the first species to be exploited during the modern whaling period (Zerbini et al. 2011b), and

2 therefore have had more time to recover than later exploited species such as the blue, fin and

3 sei whales. Studies on wintering grounds show that humpback whales can have population

4 growth rates up to 12% (Wedekin et al. 2017, Noad et al. 2019), which are also higher than

5 those known for right whales (~7%, Cooke et al. 2001) or anticipated for fin and blue whales

6 (Vikingsson et al. 2009, Williams et al 2011). Satellite tracking of humpback whale movements

7 on their Southern Ocean feeding grounds in the east Antarctic shows association with the

8 marginal ice zone and with areas recently uncovered by retreating ice (Andrews-Goff et al.

9 2018, Riekkola et al. 2019), likely associated with elevated krill abundance. Similarly, in the

10 western Antarctic Peninsula region, tracked humpback whales showed a preference for

11 habitats proximal to sea ice, while avoiding bays in which elevated levels of sea ice persisted

12 in summer (Friedlaender et al. 2021). In the Scotia Arc, the main feeding ground of humpback

13 whales is closer to the polar front than the ice edge (Zerbini et al. 2006, Horton et al. 2020).

14 This is likely a function of the density and abundance of krill present in the northern Scotia

15 Arc, advected to South Georgia (Murphy et al. 2007).

16 Baleen whale abundance at South Georgia (~31,000 whales) was roughly double that seen at

17 the South Sandwich Islands, although the South Georgia stratum was less than 10% larger in

18 area than the South Sandwich Islands stratum. This abundance is likely due to the unique

19 oceanography of the South Georgia shelf (Young et al. 2014) which makes South Georgia a

20 high density area for krill, and therefore attracts krill predators (Trathan et al. 2007). South

21 Georgia lies between two major fronts, the Polar Front to the north, and the southern

22 Antarctic Circumpolar Current front to the south. The latter loops around three sides of the

23 island (Figure 1) and brings Antarctic krill into the shelf waters in large quantities. The South

24 Sandwich Islands are more remote and less well studied, but also support significant

1   populations of krill predators (e.g. Stryker et al. 2020) as they lie along the southern boundary

2   of the Antarctic Circumpolar Current and receive krill from the Antarctic Peninsula and

3   Weddell Sea. Whaling was limited at the South Sandwich Islands, with 1,134 whales estimated

4   to have been killed in local waters (Allison 2016). This was initially due to the remoteness of

5   the location and poor weather conditions, but the less restricted factory ships did not

6   subsequently hunt there either, suggesting that this area either was not a historical hotspot

7   for whales, or that they were so heavily exploited across the region that by the time factory

8   ship whaling began there were insufficient numbers to make hunting worthwhile at the South

9   Sandwich Islands (Hart, 2006).

10

11   **4.3. Krill consumption by baleen whales**

12   In this study, we assume that all baleen whales using the Scotia Arc region are feeding on

13   Antarctic krill. However, some baleen whale species in the Scotia Arc may also feed on other

14   prey species. While all species feed predominantly on Antarctic krill south of 60°S, fin whales

15   may also feed on *Thysanoessa macrura* (Herr et al. 2016) and right whales may feed on

16   copepods (Valenzuela et al. 2019, Jackson et al. 2020), although south of 50°S they are

17   anticipated to feed predominantly on krill (Tormosov et al. 1998). Feeding on other species

18   was therefore expected to be negligible. A further assumption made in order to estimate krill

19   consumption is that 85% of the annual consumption by whales takes place within their high

20   latitude feeding habitats. The proportion of annual energy requirements ingested during the

21   summer season at high latitudes is unknown and this is a topic that deserves further research

22   in order to better understand the annual energy budgets of migratory baleen whales (Owen

23   et al. 2017). Migration is not synchronous, as whales leave their winter breeding habitat over

24   a period of two months and this may have ecological consequences as numbers in the feeding

1   grounds gradually increase and subsequently gradually decrease across the feeding seasons.

2   The sex ratio of humpback whales is biased towards males in breeding habitats (Barlow et al.,

3   2011), suggesting females may remain in feeding habitats during years in which they are not

4   breeding. Acoustic monitoring has confirmed that some humpback whales remain in high

5   latitude habitats year round (Van Opzeeland et al. 2013, Schall et al. 2020) as do some blue

6   whales (Širović et al. 2009) and similarly, humpback, blue, fin and minke whales have been

7   acoustically detected in high latitude Arctic habitats year round (e.g. Moore et al. 2012). This

8   suggests the simple paradigm of migration between summer feeding habitats at high latitudes

9   and winter breeding habitats at low latitudes does not apply to all individuals of a population

10   in each year, and that for some individuals a higher proportion of their annual energy needs

11   may be met in high latitude habitats. We might also expect the abundance of whales in high

12   latitude feeding habitats to be greater than in lower latitude breeding areas. This variation in

13   migratory behaviour raises issues for management and calls for further research to better

14   understand demographic aspects of migration phenology and the winter ecology of baleen

15   whales at high latitudes.

16   The estimate of 4.8 - 7.2 million tons of krill consumed by all baleen whales in South Georgia

17   and the South Sandwich Islands represents 7 - 10% of the total available krill biomass

18   estimated during the 2019 season in the CCAMLR 2000 survey area, extending from the

19   Antarctic Peninsula to the South Sandwich Islands (Krafft et al. 2021). In the 2019/2020 fishing

20   season, the commercial krill fishery took 115,319 tonnes of krill from South Georgia and no

21   krill from the South Sandwich Islands (CCAMLR 2021). Spatiotemporal overlap between the

22   krill fishery and the summer feeding season of baleen whales has been limited to the South

23   Orkney (48.2) stratum, in areas where we predict relatively low densities of humpback

24   whales. In the South Georgia (48.3) stratum, fishing has been restricted to the winter months

1   of June to September and there has been no fishing effort in the South Sandwich (48.4)

2   stratum (Table 11). Although a range of krill consumption values based on the 95% CI of

3   abundance estimates could be provided, that would not be equivalent to a 95% CI in

4   consumption rates due to the unknown variance of energy budget estimates, which were not

5   statistically based. Such an approach was therefore considered potentially misleading and

6   instead, a range of consumption estimates were calculated for both humpback and all baleen

7   whales, based on point estimates of whale abundance and likely energy requirement rates

8   relative to body weight. There is clearly room for improvement in better understanding

9   energy budgets of migratory whales and further research into this field should be a high

10   priority in order to improve the precision of prey consumption rates. Here, we have aimed at

11   providing a range of estimates, recognising the uncertainty inherent in methods of calculating

12   consumption rates.

13   Climate change is driving changes in the ecology of a wide range of marine organisms

14   (Poloczanska et al. 2016) including the distribution of Antarctic krill, which may be contracting

15   southwards (Atkinson et al. 2019). Ecological relationships between sympatric krill predators,

16   such as humpback and minke whales are likely to be affected by rapid warming in the

17   Antarctic region (Friedlaender et al. 2021). Southern right whales have shifted their feeding

18   distribution in the southeast Atlantic in recent decades which may be a response to changes

19   in the distribution of prey (van den Berg et al. 2020) and it is expected that other whale species

20   may similarly respond to changes in the distribution of prey. The increase in abundance of

21   recovering whale populations may in itself drive ecological changes, on the one hand through

22   increased competition for food resources that could lead to niche specialisation and on the

23   other hand through increased primary productivity driven by faecal fertilisation of the ocean

24   (Lavery et al. 2014, Roman & McCarthy 2010). Models of the impacts of climate change on

1 Southern Ocean ecosystems predict future declines in whale populations as a consequence

2 of expected future reduced prey availability and increased interspecific competition (Tulloch

3 et al. 2019), although the complexity of ecological relationships in the oceanic food web

4 causes inevitable uncertainty. Current changes in whale and krill ecology highlights the need

5 for further research into the processes involved in this predator-prey relationship, especially

6 in developing a more robust, statistically based understanding of feeding rates and

7 requirements, and the need for regular monitoring of abundance and distribution of these

8 key species.

9

1 "Krill". Also, officers, crew, and scientific personnel onboard these vessels are thanked for

2 carrying out the surveying.

3

4 **REFERENCES**

5 Allison C (2016) IWC individual and summary catch databases. Available from the

6   International Whaling Commission, Impington, Cambridge

7 Andrews-Goff V, Bestley S, Gales NJ, Laverick SM, Paton D, Polanowski AM, Schmitt NT,

8   Double MC (2018) Humpback whale migrations to Antarctic summer foraging grounds

9   through the southwest Pacific Ocean. Sci Rep 8(1):12333

10 Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and

11   increase in salps within the Southern Ocean. Nature 432:100-103

12 Atkinson A, Siegel V, Pakhomov EA, Rothery P, Loeb V, Ross RM, Quetin LB, Schmidt K, Fretwell

13   P, Murphy EJ, Tarlin GA, Fleming AH (2008) Oceanic circumpolar habitats of Antarctic

14   krill. Mar Ecol Prog Ser 362:1-23

15 Atkinson A, Hill SL, Pakhomov EA, Siegel V, Reiss CS, Loeb VJ, Steinberg DK, Schmidt K, Tarling

16   GA, Gerrish L, Sailley SF (2019) (2019) Krill (*Euphausia superba*) distribution contracts

17   southward during rapid regional warming. Nat Clim Change 9(2):142-147

18 Barlow J, Calambokidis J, Falcone EA, Baker CS, Burdin AM, Clapham P J, Ford JKB, Gabriele

19   CM, LeDuc R, Mattila DK, Quinn II TJ, Rojas-Bracho L, Straley JM, Taylor BL, Urbán R J,

20   Wade P, Weller D, Witteveen BH, Yamaguchi M (2011) Humpback whale abundance in

21   the North Pacific estimated by photographic capture-recapture with bias correction

22   from simulation studies. Mar Mamm Sci, 27(4):793-818

23 Belkin IM, O'Reilly JE (2009) An algorithm for oceanic front detection in chlorophyll and SST

24   satellite imagery. J Mar Syst 78:319-326

Best P, Brandao A and Butterworth D (2001) Demographic parameters of southern right whales off South Africa. J Cetacean Res and Manag (Special Issue) 2:161-169

Bortolotto GA, Danilewicz D, Andriolo A, Secchi E and Zerbini AN (2016) Whale, whale, everywhere: Increasing abundance of western South Atlantic humpback whales (Megaptera novaeangliae) in their wintering grounds. PLOS ONE, 11(10), pp. 1–17.

Braithwaite JE, Meeuwig JJ, Hipsey MR (2015) Optimal migration energetics of humpback whales and the implications of disturbance. Conserv Physiol 3:cov001

Branch TA, Matsuoka K and Miyashita T (2004), Evidence for increases in Antarctic blue whales based on Bayesian modelling. Mar Mamm Sci, 20: 726-754.

Branch TA (2007) Abundance of Antarctic blue whales south of 60°S from three complete circumpolar sets of surveys. J Cetacean Res Manag 9:253-262

Branch TA (2011) Humpback abundance south of 60°S from three complete circumpolar sets of surveys. J Cetacean Res Manag (Special Issue) 3:53-70

Bravington MV, Miller DL, Hedley SL (2021). Variance Propagation for Density Surface Models. J Agric Biol Environ Stat 26: 306-323.

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, UK

Buckland S, Anderson D, Burnham K, Laake J, Borchers D, Thomas L (2004) Advanced Distance Sampling. Oxford University Press, Oxford, UK

Calderan SV, Black A, Branch TA, Collins MA, Kelly N, Leaper R, Lurcock S, Miller BS, Moore M, Olson PA, Širović A, Wood AG, Jackson JA (2020) South Georgia blue whales five decades after the end of whaling. Endang Species Res 43:359-373

1   CCAMLR (2019) Report of the thirty-eighth meeting of the Commission. CCAMLR. Hobart,

2   Australia

3   CCAMLR (2021) Fishery Report 2020: Euphausia superba in Area 48, CCAMLR Secretariat.

4   Available from https://fishdocs.ccamlr.org/FishRep_48_KRI_2020.pdf

5   Chittleborough RG (1965) Dynamics of two populations of the humpback whale, *Megaptera*

6   *novaeangliae* (Borowski). Mar Freshw Res 16: 33-128

7   Clapham PJ, Mead JG (1999) *Megaptera novaeangliae*. Mamm Species, (604):1

8   Clapham PJ (2000) The Humpback Whale. Seasonal Feeding and Breeding in a Baleen Whale.

9   In: Mann J, Connor RC, Tyack PL & Whitehead H, Eds., Cetacean Societies, Field Studies

10   of Dolphins and Whales, The University of Chicago, Chicago, p 173-196

11   Clarke A (1984) Lipid Content and Composition of Antarctic Krill, *Euphausia superba* Dana. J

12   Crustac Biol 4.5 (1 October 1984):285-294

13   Constable AJ, de la Mare WK, Agnew DJ, Everson I, Miller D (2000) Managing fisheries to

14   conserve the Antarctic marine ecosystem: practical implementation of the Convention

15   on the Conservation of Antarctic Marine Living Resources (CCAMLR). ICES J Mar Sci

16   57:778-91

17   Constable AJ (2001) The ecosystem approach to managing fisheries: achieving conservation

18   objectives for predators of fished species. CCAMLR Sci 8:37-64

19   Constable AJ (2011) Lessons from CCAMLR on the implementation of the ecosystem approach

20   to managing fisheries. Fish Fish 12:138-151

21   Cooke J, Rowntree V, Payne R (2001). Estimates of demographic parameters for southern

22   right whales (*Eubalaena australis*) observed off Peninsula Valdes, Argentina. J

23   Ceteacean Res Manag (Special Issue) 2:125-132

1   Costa DP, Williams TM (2000) Marine mammal energetics. In The biology of marine mammals

2   (J. Reynolds & J. Twiss eds), Smithsonian Institution Press, Washington DC, USA, p 176-

3   217

4   Cox MJ, Candy S, de la Mare WK, Nicol S, Kawaguchi S, Gales N (2018) No evidence for a

5   decline in the density of Antarctic krill *Euphausia superba* Dana, 1850, in the Southwest

6   Atlantic sector between 1976 and 2016. J Crustac Biol 38.6:656-661

7   Cox MJ, Candy S, De la Mare WK, Nicol S, Kawaguchi S, Gales N (2019) Clarifying trends in the

8   density of Antarctic krill *Euphausia superba* Dana, 1850 in the South Atlantic. A response

9   to Hill et al. J Crustac Biol 39:323-327

10   Crespo EA, Pedraza SN, Dans SL, Svendsen GM, Degrati M, Coscarella MA (2019) The

11   southwest Atlantic southern right whale, *Eubalaena australis* population is growing but

12   at a decelerated rate. Mar Mamm Sci 35(1):93-107

13   Danilewicz D, Tavares M, Moreno IB, Ott PH, Trigo CC (2009) Evidence of feeding by the

14   humpback whale (*Megaptera novaeangliae*) in mid-latitude waters of the western

15   South Atlantic. Mar Biodivers Rec, 2 (May 2014):10-13

16   Dunn PK, Smyth GK (2008) Evaluation of Tweedie exponential dispersion model densities by

17   Fourier inversion. Stat Comput, *18*(1):73-86

18   Färber-Lorda J, Gaudy R, Mayzaud P (2009) Elemental composition, biochemical composition

19   and caloric value of Antarctic krill. Implications in Energetics and carbon balances. J Mar

20   Syst, 78(4):518-524

21   Fielding S, Watkins JL, Trathan PN, Enderlein P, Waluda CM, Stowasser G, Tarling GA, Murphy

22   EJ (2014) Interannual variability in Antarctic krill (*Euphausia superba*) density at South

23   Georgia, Southern Ocean: 1997-2013. ICES J Mar Sci 71(9):2578-2588

Frans VF, Augé AA (2016) Use of local ecological knowledge to investigate endangered baleen whale recovery in the Falkland Islands. Biol Conserv 202:127-137

Friedlaender A, Lawson G, Halpin P (2006) Evidence of resource partitioning and niche separation between humpback and minke whales in Antarctica: implications for interspecific competition. Rep Int Whaling Comm SC/58/E32, (February):1-37

Friedlaender AS, Joyce T, Johnston DW, Read AJ, Nowacek DP, Goldbogen JA, Gales N, Durban JW (2021) Sympatry and resource partitioning between the largest krill consumers around the Antarctic Peninsula, Mar Ecol Prog Sers, 669, 1–16

Goldbogen JA, Calambokidis J, Oleson E, Potvin J, Pyenson ND, Schorr G, Shadwick RE (2011) Mechanics, hydrodynamics and energetics of blue whale lunge feeding: efficiency dependence on krill density. J Exp Biol, 214(1), 131-146

Goldbogen JA, Cade DE, Wisniewska DM, Potvin J, Segre PS, Savoca MS, Hazen EL, Czapanskiy MF, Kahane-Rapport SR, DeRuiter SL, Gero S (2019) Why whales are big but not bigger: Physiological drivers and ecological limits in the age of ocean giants. Science, 366(6471), 1367-1372

Groch KR, Palazzo Jr JT, Flores PC, Adler FR, Fabian ME (2005) Recent rapid increases in the right whale (*Eubalaena australis*) population off southern Brazil. Lat Am J Aquat Mamm 4:41-47

Hanwell A, Peaker M (1977) Physiological effects of lactation on the mother. Symp Zool Soc Lond 41:297-311

Hart IB (2001) PESCA: A history of the pioneer modern whaling company in the Antarctic. Aidan Ellis Publishing. Salcombe, Devon

Hart IB (2006) Whaling in the Falkland Island Dependencies 1904-1931: Pequena.

Hedley S, Buckland S, Borchers D (1999). Spatial modelling from line transect data. J Cet Res Manag, 1(3):255-264

Hedley S, Reilly S, Borberg J, Holland R, Hewitt R, Watkins J, Naganobu M, Sushin V (2001) Modelling whale distribution: a preliminary analysis of data collected on the CCAMLR-IWC Krill Synoptic Survey, 2000. Sci Comm Int Whaling Comm:1-38

Hedley SL & Buckland ST (2004) Spatial models for line transect sampling. J Agric Biol Environ Stat 9(2): 181-199.

Herr H, Viquerat S, Siegel V, Kock K-H, Dorschel B, Huneke WGC, Bracher A, Schröder M, Gutt, J (2016) Horizontal niche partitioning of humpback and fin whales around the West Antarctic Peninsula: evidence from a concurrent whale and krill survey. Polar Biol 39:799-818

Herr H, Kelly N, Dorschel B, Huntemann M, Kock K-H, Lehnert LS, Siebert U, Viquerat S, Williams R & Scheidat M (2019) Aerial surveys for Antarctic minke whales (Balaenoptera bonaerensis) reveal sea ice dependent distribution patterns. Ecol Evol 9(10): 5664-5682.

Hiby AR, Hammond PS (1989) Survey techniques for estimating abundance of cetaceans. Rep Int Whaling Comm (special issue) 11:47-80

Hill SL, Murphy EJ, Reid K, Trathan PN, Constable AJ (2006) Modelling Southern Ocean ecosystems: krill, the food-web, and the impacts of harvesting. Biol Rev Camb Philos Soc 81:581-608

Hogg OT, Barnes DK, Griffiths HJ (2011) Highly diverse, poorly studied and uniquely threatened by climate change: an assessment of marine biodiversity on South Georgia's continental shelf. PLOS ONE 6(5):e19795

1   Horton TW, Zerbini AN, Andriolo A, Danilewicz D, Sucunza F (2020) Multi-decadal humpback

2   whale migratory route fidelity despite oceanographic and geomagnetic change. Front

3   Mar Sci 7:414

4   Innes S, Lavigne D, Earle W, Kovacs K (1987) Feeding Rates of Seals and Whales. J Anim Ecol,

5   56(1):115-130

6   IWC (1998) Report of the Scientific Committee. Annex G. Report of the Sub-Committee on

7   Comprehensive Assessment of Southern Hemisphere humpback whales. Rep Int

8   Whaling Comm 48:170-182

9   IWC (2001) Report of the Workshop on the Comprehensive Assessment of Right Whales: A

10   worldwide comparison. J Cetacean Res Manage (special issue) 2:1-60

11   Irvine LG, Thums M, Hanson CE, McMahon CR, Hindell MA (2017) Quantifying the energy

12   stores of capital breeding humpback whales and income breeding sperm whales using

13   historical whaling records. R Soc Open Sci 4:160290

14   Jackson JA, Kennedy A, Moore M, Andriolo A, Bamford C, Calderan S, Cheeseman T, Gittins G,

15   Groch K, Kelly N, Leaper R, Leslie MS, Lurcock S, Miller BS, Richardson J, Rowntree V,

16   Smith P, Stepien E, Stowasser G, Trathan P, Vermeulen E, Zerbini AN, Carroll E (2020)

17   Have whales returned to a historical hotspot of industrial whaling? The pattern of

18   southern right whale *Eubalaena australis* recovery at South Georgia. Endang Species

19   Res 43:323-339

20   Kasamatsu F, Ensor P & Joyce GG (1998) Clustering and aggregations of minke whales in the

21   Antarctic feeding grounds. Mar Ecol Prog Ser 168: 1-11.

22   Kawamura A (1980) A review of food of balaenopterid whales. Sci Rep Whales Res Inst, Tokyo,

23   32(32):155-197

1 Kawaguchi S, Nicol S (2020) Krill fishery. Pages 137-158 in Lovrich G, Thiel M eds. Fisheries

2   and Aquaculture. Oxford University Press, Oxford, UK

3 Kawamura A (1980). A review of food of balaenopterid whales. Sci Rep Whales Res Inst,

4   Tokyo, 32(32):155-197

5 Kenney RD, Scott GP, Thompson TJ, Winn HE (1997) Estimates of prey consumption and

6   trophic impacts of cetaceans in the USA northeast continental shelf ecosystem. J

7   Northwest Atl Fish Sci 22 (August 1995):155-171

8 Kleiber M (1975) The Fire of Life: an Introduction to Animal Energetics. Robert E Kreiger

9   Publishing Co., Huntington, NY

10 Krafft BA, Krag LA, Knutsen T, Skaret G, Jensen KHM, Krakstad JO, Larsen SH, Melle W, Iversen

11   SA, Godø (2018) Summer distribution and demography of Antarctic krill *Euphausia*

12   *superba* Dana, 1850 (Euphausiacea) at the South Orkney Islands, 2011–2015. J Crustac

13   Biol 38:682-688

14 Krafft BA, Macaulay G, Skaret G, Knutsen T, Bergstad OA, Lowther A, Huse G, Fielding S,

15   Trathan P, Murphy E, Choi S-G, Chung S, Han I, Lee K, Zhao X, Wang X, Ying Y, Yu X,

16   Demianenko K, Podhornyi V, Vishnyakova K, Pshenichnov L, Chuklin A, Shyshman H, Cox

17   MJ, Reid K, Watters GW, Reiss CS, Hinke JT, Arata J, Godø OR, Hoem N (2021) Standing

18   stock of Antarctic krill (*Euphausia superba* Dana 1850 (Euphausiacea)) in the southwest

19   Atlantic sector of the Southern Ocean, 2019. Submitted to the J Crustac Biol

20 Lavery TJ, Roudnew B, Seymour J, Mitchell JG, Smetacek V, Nicol S (2014) Whales sustain

21   fisheries: Blue whales stimulate primary production in the Southern Ocean. Mar Mam

22   Sci 30:888-904

23 Leaper R, Lavigne D (2007) How much do large whales eat? J Cetacean Res Manag 9(3):179-

24   188

Leaper R, Miller C (2011) Management of Antarctic baleen whales amid past exploitation, current threats and complex marine ecosystems. Ant Sci 23(6): 503-529.

Lehodey P, Conchon A, Senina I, Domokos R, Calmettes B, Jouanno J, Hernandez O, Kloser R (2015) Optimization of a micronekton model with acoustic data. ICES J Mar Sci 72:1399-1412

Lifson N, McClintock R (1966) Theory of use of the turnover rates of body water for measuring energy and material balance. J Theor Biol 12:46-74

Lockyer C (1981) Growth and energy budgets of large baleen whales from the Southern Hemisphere. Mammals in the Seas 3 (FAO Fisheries Series No. 5), (October):379-487

Loeb VJ, Santora JA (2015) Climate variability and spatiotemporal dynamics of five Southern Ocean krill species. Prog Oceanogr 134:93-122

Marra G, Wood SN (2011) Practical variable selection for generalized additive models. Comput Stat Data Anal 55(7):2372-2387

Matsuoka K, Ensor P, Hakamada T, Shimada H, Nishiwaki S, Kasamatsu F & Kato H (2003) Overview of minke whale sightings surveys conducted on IWC/IDCR and SOWER Antarctic cruises from 1987/79 to 2000/01. J Cetacean Res Manag 5(2): 173-201.

Miller DL, Burt ML, Rexstad EA, Thomas L, Gimenez O (2013) Spatial models for distance sampling data: recent developments and future directions. Methods Ecol Evol 4:1001-1010

Miller DL, Rexstad E, Thomas L, Laake JL, Marshall L (2019) Distance sampling in R. J Stat Softw 89(1):1-28

Moore MJ, Berrow SD, Jensen BA, Carr P, Sears R, Rowntree VJ, Payne R, Hamilton PK (1999) Relative abundance of large whales around South Georgia (1979-1998). Mar Mamm Sci 15(4):1287-1302

1   Moore SE, Stafford KM, Melling H, Berchok C, Wiig Ø, Kovacs KM, Lydersen C, Richter-Menge

2   J (2012) Comparing marine mammal acoustic habitats in Atlantic and Pacific sectors of

3   the High Arctic: year-long records from Fram Strait and the Chukchi Plateau. Polar Biol

4   35:475-480

5   Murphy EJ, Watkins JL, Trathan PN, Reid K, Meredith MP, Thorpe SE, Johnston NM, Clarke A,

6   Tarling GA, Collins MA, Forcada J, Shreeve RS, Atkinson A, Korb R, Whitehouse MJ, Ward

7   P, Rodhouse PG, Enerlein P, Hirst AG, Martin AR, Hill SL, Staniland IJ, Pond DW, Briggs

8   DR, Cunningham NJ, Fleming AH (2007) Spatial and temporal operation of the Scotia Sea

9   ecosystem: a review of large-scale links in a krill centred food web. Philos Trans R Soc

10   Lond, Ser. B: Biol Sci 362(1477):113-148

11   Nagy KA (1983) The Doubly Labeled Water (3HH18O) Method: A Guide to its Use. University

12   of California Publication 12-1417, USA, Los Angeles, University of California

13   Nagy KA, Girard IA, Brown TK (1999) Energetics of free-ranging mammals, reptiles, and birds.

14   Annu Rev Nutr 19(July):247-277

15   Nagy KA (2001) Food requirements of wild animals: predictive equations for free-living

16   mammals, reptiles, and birds. Nutr Abstr Rev Series B 71:21R-31R

17   Nagy KA (2005) Field metabolic rate and body size. J Exp Biol 208(9):1621-1625

18   Noad M, Kniest E, Dunlop RA (2019) Boom to bust? Implications for the continued rapid

19   growth of the eastern Australian humpback whale population despite recovery. Popul

20   Ecol 61(2):198-209

21   Oftedal O T (2000) Animal Nutrition and Metabolism Group Symposium on Regulation of

22   maternal reserves and effects on lactation and the nutrition of young animals: Use of

23   maternal reserves as a lactation strategy in large mammals, P Nutr Soc, 59, 99–106.

1   Owen K, Kavanagh AS, Warren JD, Noad MJ, Donnelly D, Goldizen AW, Dunlop RA (2017)

2   Potential energy gain by whales outside of the Antarctic: prey preferences and

3   consumption rates of migrating humpback whales (*Megaptera novaeangliae*). Polar Biol

4   40:277-289

5   Pirotta E, Booth CG, Cade DE, Calambokidis J, Costa DP, Fahlbusch JA, Friedlaender AS,

6   Goldbogen JA, Harwood J, Hazen EL, New L, Southall BL (2021) Context-dependent

7   variability in the predicted daily energetic costs of disturbance for blue whales. Conserv

8   Physiol 9:coaa137

9   Poloczanska ES, Burrows MT, Brown CJ, García Molinos J, Halpern BS, Hoegh-Guldberg O,

10   Kappel CV, Moore PJ, Richardson AJ, Schoeman DS, Sydeman WJ (2016) Responses of

11   Marine Organisms to Climate Change across Oceans. Front Mar Sci 3:62

12   Potvin J, Cade DE, Werth AJ, Shadwick RE, Goldbogen JA (2021) Rorqual Lunge-Feeding

13   Energetics Near and Away from the Kinematic Threshold of Optimal Efficiency. Integr

14   Org Biol, 3(1)

15   Reilly S, Hedley S, Borberg J, Hewitt R, Thiele D, Watkins J, Naganobu M (2004) Biomass and

16   energy transfer to baleen whales in the South Atlantic sector of the Southern Ocean.

17   Deep Sea Res Part II 51(12-13 SPEC.ISS.):1397-1409

18   Reiss CS, Cossio AM, Loeb V, Demer DA (2008) Variations in the biomass of Antarctic krill

19   (*Euphausia superba*) around the South Shetland Islands, 1996–2006, ICES J Mar Sci

20   65:497-508

21   Richardson J, Wood AG, Neil A, Nowacek DP, Moore M (2012) Changes in distribution, relative

22   abundance and species composition of large whales around South Georgia from

23   opportunistic sightings: 1992 to 2011. Endang Species Res 19:149-156

1   Riekkola L, Andrews-Goff V, Friedlaender A, Constantine R, Zerbini AN (2019) Environmental

2   drivers of humpback whale foraging behavior in the remote Southern Ocean. J Exp Mar

3   Biol Ecol 517(January):1-12

4   Robbins J (2007) Structure and Dynamics of the Gulf Of Maine Humpback Whale Popuation.

5   PhD thesis, University of St Andrews, Scotland

6   Rocha Jr RC, Clapham PJ, Ivashchenko YV (2014) Emptying the oceans: a summary of industrial

7   whaling catches in the 20th century. Mar Fish Rev 76:37-48

8   Rojano-Donãte L, McDonald BI, Wisniewska DM, Johnson M, Teilmann J, Wahlberg M, Højer-

9   Kristensen J, Madsen PT (2018) High field metabolic rates of wild harbour porpoises. J

10   Exp Biol 221(23)

11   Roman J, McCarthy JJ (2010) The whale pump: marine mammals enhance primary

12   productivity in a coastal basin. PLOS One 5:e13255

13   Schaafsma FL, Cherel Y, Flores H, van Franeker JA, Lea MA, Raymond B, van de Putte AP (2018)

14   Review: the energetic value of zooplankton and nekton species of the Southern Ocean.

15   Mar Biol 165:129

16   Schall E, Thomisch K, Boebel O, Gerlach G, Spiesecke S, Van Opzeeland I (2020) Large-scale

17   spatial variabilities in the humpback whale acoustic presence in the Atlantic sector of

18   the Southern Ocean. R Soc Open Sci 7:201347

19   Širović A, Hildebrand JA, Wiggins SM, Thiele D (2009) Blue and fin whale acoustic presence

20   around Antarctica during 2003 and 2004. Mar Mamm Sci 25:125-136

21   Speakman JR (1997) Doubly Labelled Water: Theory and Practice. UK, London, Chapman and

22   Hall

23   Stevick PT, Allen, J, Clapham, PJ, Friday, N, Katona, SK, Larsen, Lien, FJ, Mattila, DK, Palsbøll

24   PJ, J. Sigurjónsson, Smith, TD, Øien, N, Hammond PS (2003) North Atlantic humpback

whale abundance and rate of increase four decades after protection from whaling. Mar Ecol Prog Ser 258:263-273

Strycker N, Wethington M, Borowicz A, Forrest S, Witharana C, Hart T, Lynch HJ (2020) A global population assessment of the Chinstrap penguin (*Pygoscelis antarctica*). Sci Rep 10(1):19474

Tamura T, Ichii T, Fujise Y (1997) Consumption of krill by minke whales in Areas IV and V of the Antarctic. IWC Sci Comm Working Paper SC/ M, 17:1-9

Tormosov DD, Mikhaliev YA, Best PB, Zemsky VA, Sekiguchi K, Brownell RL (1998) Soviet catches of southern right whales *Eubalaena australis*, 1951–1971. Biological data and conservation implications. Biol Conserv 86:185-197

Trathan PN, Forcada J, Murphy EJ (2007) Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. Philos Trans R Soc Lond, Ser. B: Biol Sci 362(1488):2351-2365

Trathan P.N., Ratcliffe N., Masden E.A. (2012). Ecological drivers of change at South Georgia: the krill surplus, or climate variability. Ecography 35:983-993

Trathan PN, Hill SL (2016) The importance of krill predation in the Southern Ocean. In: Siegel V (ed) Biology and Ecology of Antarctic krill. Springer, Berlin, Germany

Trathan PN, Fielding S, Hollyman PR, Murphy EJ, Warwick-Evans V, Collins MA (2021) Enhancing the ecosystem approach for the fishery for Antarctic krill within the complex, variable and changing ecosystem at South Georgia. ICES J Mar Sci

Trites AW, Pauly D (1998) Estimating mean body masses of marine mammals from maximum body lengths. Can J Zool 76:886-896

Tulloch VJD, Richardson AJ, Matear R, Brown C (2019) Future recovery of baleen whales is imperiled by climate change. Glob Change Biol (November 2018):1-19

Valenzuela LO, Sironi M, Rowntree VJ, Seger J (2009) Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). Mol Ecol 18(5):782-791

van den Berg GL, Vermeulen E, Valenzuela LO, Bérubé M, Ganswindt A, Gröcke DR, Hall G, Hulva P, Neveceralova P, Palsbøll PJ, Caroll EL (2020) Decadal shift in foraging strategy of a migratory southern ocean predator. Glob Change Biol 2021; 27:1052-1067

Van Opzeeland I, Van Parijs S, Kindermann L, Burkhardt E, Boebel O (2013) Calling in the cold: pervasive acoustic presence of humpback whales (*Megaptera novaeangliae*) in Antarctic coastal waters. PLOS One 8:e73007

Víkingsson GA, Pike DG, Desportes G, Øien N, Gunnlaugsson Th, and Bloch D (2009) Distribution and abundance of fin whales (Balaenoptera physalus) in the Northeast and Central Atlantic as inferred from the North Atlantic Sightings Surveys 1987-2001. NAMMCO Sci. Publ. 7:49-72

Villegas-Amtmann S, Schwarz LK, Sumich JL, Costa DP, Peters DPC (2015) A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. Ecosphere, 6(10)

Viquerat S, Herr H (2017) Mid-summer abundance estimates of fin whales *Balaenoptera physalus* around the South Orkney Islands and Elephant Island. Endang Species Res32:515-524

Wahrenbrock EA, Maruschak GF, Eisner R, Kenney DW (1974) Respiration and metabolism in two baleen whale calves. Mar Fish Rev 36:3-9

Ward E, Zerbini AN, Kinas PG, Engel MH, Andriolo A (2011) Estimates of population growth rates of humpback whales (*Megaptera novaeangliae*) in the wintering grounds off the coast of Brazil (Breeding Stock A). J Cetacean Res Manag (Special Issue) 3:145-149

1 Wedekin LL, Engel MH, Andriolo A, Prado PI, Zerbini AN, Marcondes MMC, Kinas PG, Simões-

2   Lopes PC (2017) Running fast in the slow lane: rapid population growth of humpback

3   whales after exploitation. Mar Ecol Prog Ser 575:195-206

4 Wiedenmann J, Cresswell KA, Goldbogen J, Potvin J, Mangel M (2011) Exploring the effects of

5   reductions in krill biomass in the Southern Ocean on blue whales using a state-

6   dependent foraging model. Ecol Modell, 222(18), 3366-3379

7 Williams R, Hedley SL, Branch TA, Bravington, Mark B, Zerbini AN, Findlay KP (2011) Chilean

8   Blue Whales as a Case Study to Illustrate Methods to Estimate Abundance and Evaluate

9   Conservation Status of Rare Species. Cons Biol, 25(3) 526-535

10 Young EF, Thorpe SE, Banglawala N, Murphy EJ (2014) Variability in transport pathways on

11   and around the South Georgia shelf, Southern Ocean: Implications for recruitment and

12   retention. J Geophysi Res, Oceans 119:241-252

13 Zerbini AN, Andriolo A, Heide-Jorgensen MP, Pizzorno JL, Maia YG, VanBlaricom GR, DeMaster

14   DP, Simoes-Lopes PC, Moreira S, Bethlem C (2006) Satellite-monitored movements of

15   humpback whales *Megaptera novaeangliae* in the southwest Atlantic Ocean. Mar Ecol

16   Prog Ser 313:295-304

17 Zerbini AN, Clapham PJ, Wade PR (2010) Assessing plausible rates of population growth in

18   humpback whales from life-history data. Mar Biol 157:1225-1236

19 Zerbini AN, Andriolo A, Heide-Jorgensen MP, Moreira SC, Pizzorno JL, Maia YG, Vanblaricom

20   GR, DeMaster DP (2011a) Migration and summer destinations of humpback whales

21   (*Megaptera novaeangliae*) in the western South Atlantic Ocean. J Cetacean Res and

22   Manag (SPEC. ISS. 3):113-118

1   Zerbini AN, Ward EJ, Kinas PG, Engel MH, Andriolo A (2011b) A Bayesian Assessment of the

2   Conservation Status of Humpback Whales (*Megaptera novaeangliae*) in the Western

3   South Atlantic. J Cetacean Res Manag (Special Issue) 3:131-144

4   Zerbini AN, Adams G, Best J, Clapham PJ, Jackson JA, & Punt, AE (2019) Assessing the recovery

5   of an Antarctic predator from historical exploitation. R Soc Open Sci 6(10)

6

7   **TABLES**

8   Table 1 – Covariates included in the generalised additive models (GAMs).

Variable name	Description
(x,y)	Lon & lat coordinates transformed to UTM zone 21S
depth	Depth extracted from GEBCO 2019
sdDepth	Standard deviation of depth in 20km grid cells
SST	Monthly sea surface temperature extracted from NOAA Ocean Color
sstFronts	SST fronts extracted using package *grec*, Belkin & O'Reilly (2009)
CHL	Monthly chl-*a* extracted from NOAA Ocean Color
chlFronts	CHL fronts extracted using package *grec*, Belkin & O'Reilly (2009)
CHL_mmmyyyy	Monthly chl-*a* extracted from NOAA Ocean Color for 12 preceding months
SSS	Sea surface salinity
zooc	Reprocessed zooplankton concentration as carbon in sea water, Lehody et al (2015)
iceDist	Distance to sea ice at its maximum extent in September 2018
curl	FNMOC Wind and Ekman Transport Data. Curl of Surface Wind Stress

9

10   Table 2 - Realised effort (Km) for each vessel in each region (as defined by CCAMLR

11   Statistical Areas, Figure 1)

Vessel	South Georgia	South Orkneys	South Sandwich	All
DIS	2123	0	3031	5154
CDH	560	415	0	975
KPH	1276	1672	206	3154
All	3042	1043	3134	7219

12

13   Table 3 - Summary of humpback whale sightings by each vessel in each region. Note that for

14   CDH and KPH only sightings within their primary 90° field of view are included and for DIS

15   sightings were truncated at a perpendicular distance of 2.5 km.

41

Vessel	South Georgia		South Orkneys		South Sandwich		All	
	Sightings	Count	Sightings	Count	Sightings	Count	Sightings	Count
DIS	94	169			77	145	171	314
CDH	12	19	8	21			20	40
KPH	12	20	22	29	13	15	47	64
All	118	208	30	50	90	160	238	418

1

2 Table 4 - Numbers of mysticete sightings recorded by DIS, data truncated at a perpendicular

3 distance of 2.5 km.

Species	South Georgia (SG)		South Sandwich (SS)		SG & SS	
	Sightings	Count	Sightings	Count	Sightings	Count
Antarctic blue whale	5	8			5	8
Fin whale	12	15	22	34	34	49
Sei whale			1	1	1	1
Antarctic minke whale			2	2	2	2
Humpback whale	94	169	77	145	171	314
Southern right whale	1	1	2	3	3	4
Unidentified baleen whale	49	69	31	40	80	109
All baleen whales	161	262	135	225	296	487

4

5 Table 5 – Approximate significance of smooth terms in the humpback whale model, where

6 edf is the estimated degrees of freedom, Ref.df constrains the maximum number of knots in

7 the smooth function and p-value is an approximate indication of significance.

Variable term	edf	Ref.df	p-value
s(x,y)	6.97	29	<0.001
s(log(CHL))	2.07	9	<0.01
s(log(CHL_Apr2018))	2.44	9	<0.001
s(sstFronts)	0.32	9	0.15
s(iceDist)	0.13	9	0.066

8

9 Table 6 – Abundance estimates for humpback whales across the Scotia Sea

Region (CCAMLR area)	Stratum area (km^2)	Point estimate	95% CI	CV
South Georgia (48.3)	1,033,249	12,103	7,145 – 20,499	0.27
South Sandwich (48.4)	944,953	11,656	5,865 – 23,164	0.36
South Orkney (48.2)	856,650	785	208 – 2,960	0.76
Scotia Sea total	2,834,852	24,543	14,863 – 40,528	0.26

10

11 Table 7 – Approximate significance of smooth terms in the model for all baleen whales in

1   South Georgia and the South Sandwich Islands. Column identifiers as given in Table 5.

Variable term	edf	Ref.df	p-value
s(x,y)	12.16	16	<0.001
s(log(CHL))	2.48	9	0.08
s(sstFronts)	1	9	0.11

2

3   Table 8 – Abundance estimates for all baleen whales in South Georgia and the South

4   Sandwich Islands

Region (CCAMLR area)	Stratum area (km²)	Point estimate	95% CI	CV
South Georgia (48.3)	1,033,249	30,905	22,361 – 42,713	0.17
South Sandwich (48.4)	944,953	12,919	7,796 – 21,409	0.26
Total	1,978,202	43,824	33,509 – 59,077	0.15

5

6   Table 9 - Field metabolic rate (FMR) for individual whales and annual energy requirements

7   (AER) for each age and sex sector of the humpback whale population.

Sex	Age	Body weight (kg)	FMR (kJ/day)	% Population	Population AER (MJ * 10⁶)
Male	Immature	12,314	3507 - 4676	16%	1,473 – 1,964
	Mature	28,323	4367 - 5458	34%	3,897 – 4,871
Female	Immature	15,645	4197 - 5596	16%	1,762 – 2,350
	Mature	32,493	6534 - 7986	34%	6,047 – 7,559
Total					13,179 – 16,743

8

9   Table 10 - Field metabolic rate (FMR) for individual whales and annual energy requirements

10   (AER) for the estimated abundance of baleen whale species.

Identified species	Proportion of identified species	Ñ	Mean body weight (kg)	Biomass (tons)	FMR (MJ/day)	AER (MJ * 10⁶)
Humpback whale	83.16%	36,444	25,151	958,014	1,171 – 1,756	15,573 – 23,360
Antarctic blue whale	2.11%	925	84,328	81,319	2,901 – 4,351	979 - 1,469
Fin whale	12.89%	5,649	48,768	288,045	1,924 – 2,886	3,966 – 5,950
Sei whale	0.26%	114	17,780	2,143	903 – 1,354	37.5 – 56

Minke whale	0.53%	232	6,565	1,583	428 - 641	36 - 54
Right whale	1.05%	460	55,880	26,943	2,130 – 3,196	358 - 537

1

2

3   Table 11. Monthly catch history of *Euphausia superba* (tonnes) in 2019 and 2020 for the strata SO,
4   SG and SS (CCAMLR 2021).

5

	2019			2020		
Stratum	SO (48.2)	SG (48.3)	SS (48.4)	SO (48.2)	SG (48.3)	SS (48.4)
December	21010	0	0	5460	0	0
January	37422	0	0	63065	0	0
February	45770	0	0	59169	0	0
March	56556	0	0	31376	0	0
April	1816	0	0	15125	0	0
May	0	0	0	10	0	0
June	0	751	0	229	18152	0
July	0	16693	0	0	35536	0
August	0	37317	0	0	43500	0
September	0	17037	0	0	18131	0

6

7

8

1 **FIGURES**
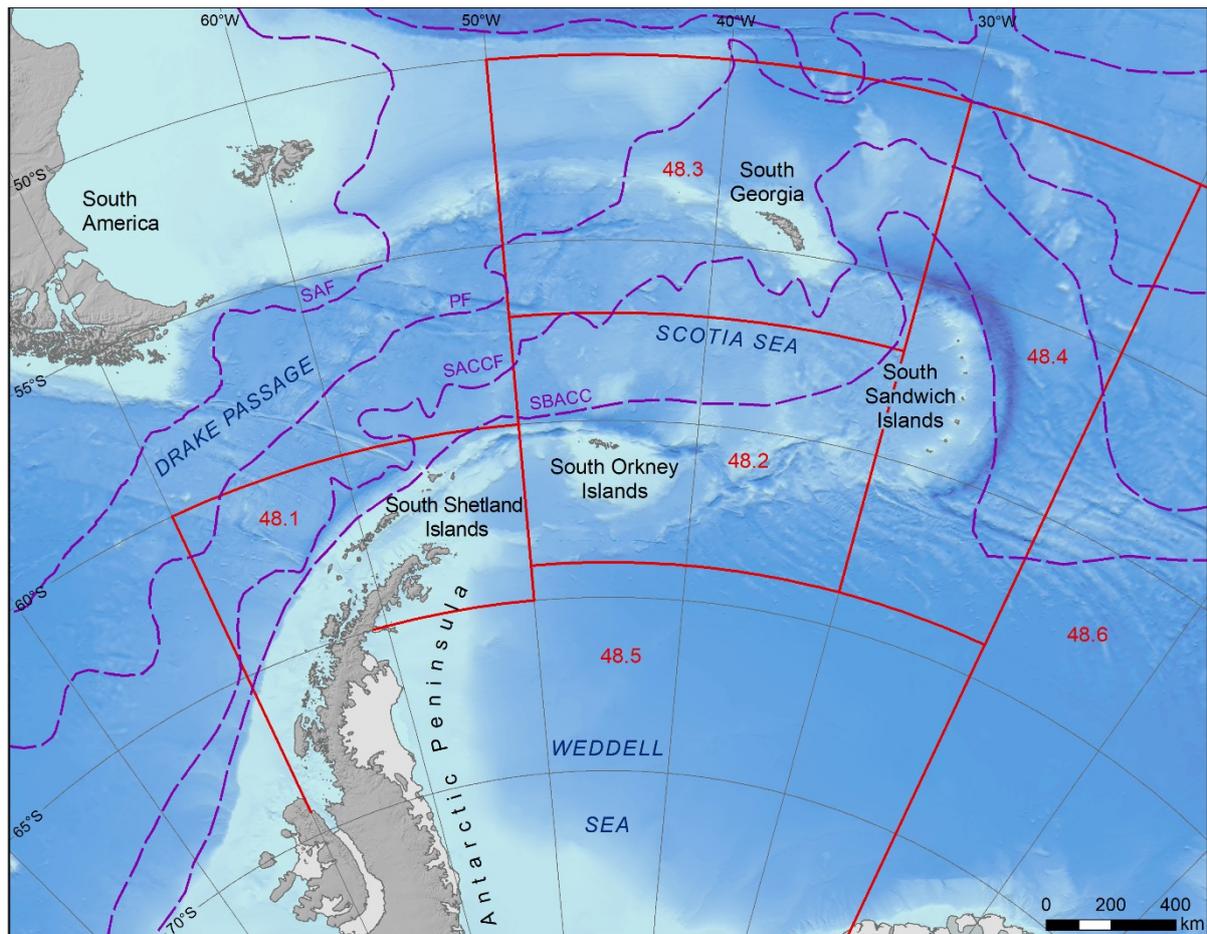
2

3 Figure 1. The study area showing the location of the three CCAMLR Statistical Areas strata

4 48.2 (South Orkney Islands), 48.3 (South Georgia) and 48.4 (South Sandwich Islands). The

5 Polar Front (PF), the Southern Antarctic Circumpolar Current Front (SACCF) and the

6 Southern Boundary of the Antarctic Circumpolar Current (SBACC) are marked by dashed

7 lines.
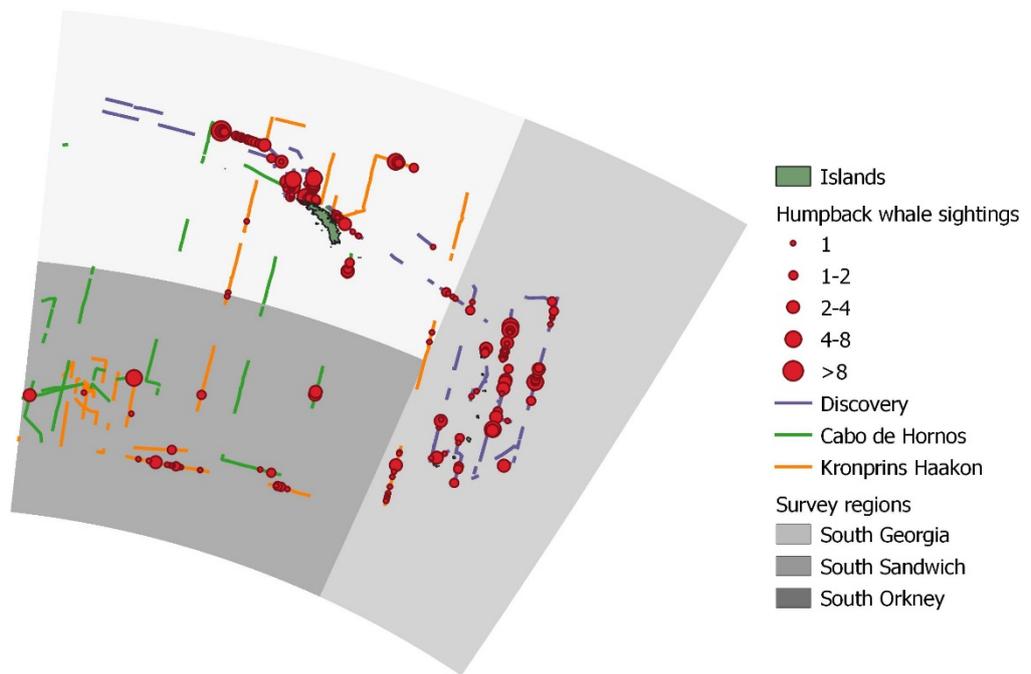
1

2   Figure 2. Transect lines and humpback whale sightings overlaid on survey region boundaries.

3   For orientation see Figure 1.

4
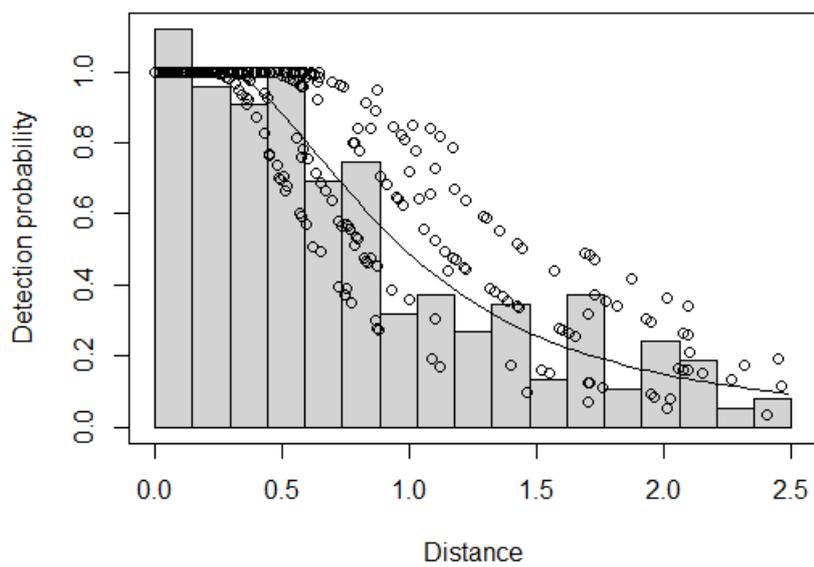
1   Figure 3. Perpendicular distances and fitted detection function for humpback whales, with

2   observer team and sea state as covariates.

3

4   Figure 4. Plots of smooth functions for the humpback whale GAM.

5

6

7

8

9
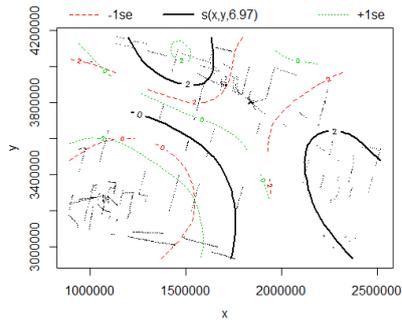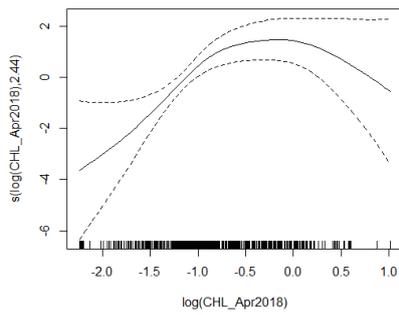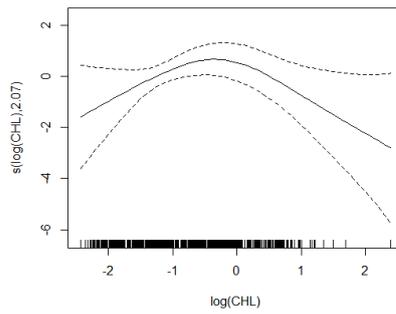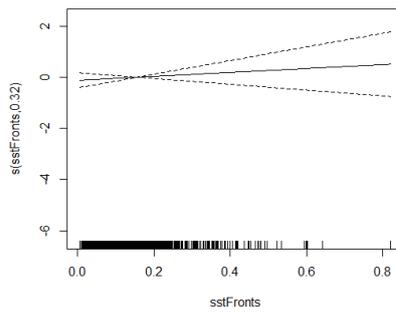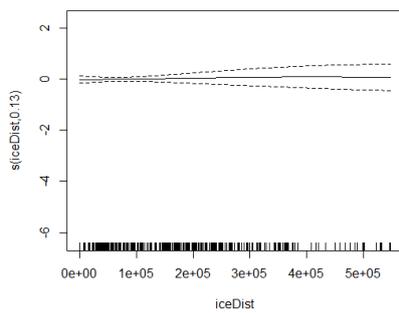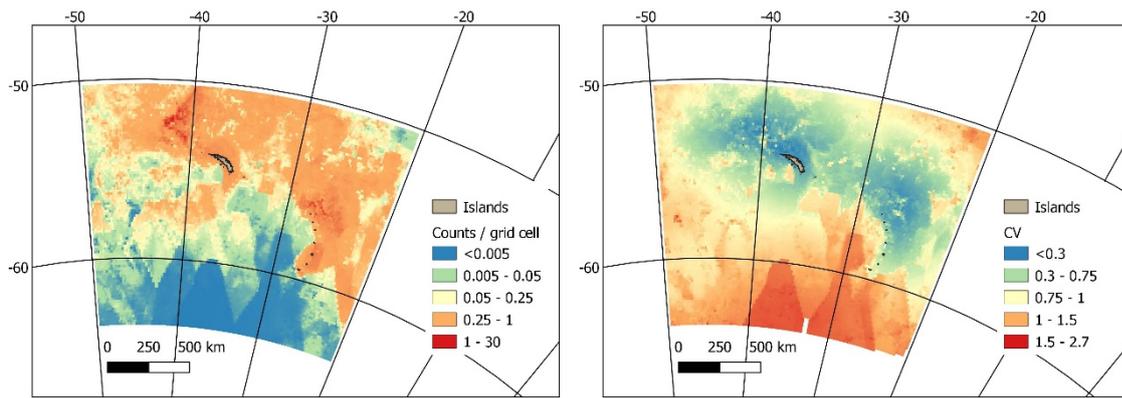
1

2   Figure5. Predicted humpback whale density expressed as counts per grid cell (left) and CV of

3   estimates (right). Latitude and longitude grid lines at 10° intervals.

4
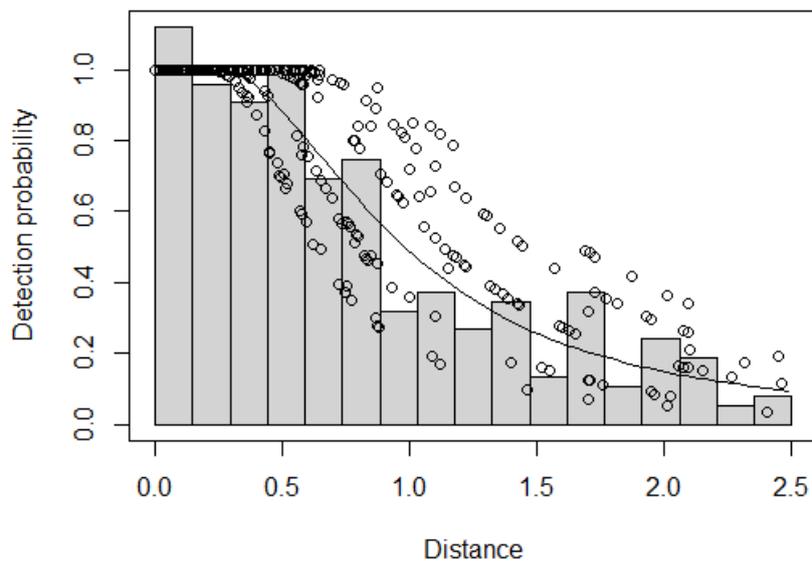
5

6   Figure 6. Perpendicular distances and fitted detection function for baleen whales, with

7   observer team and sea state as covariates.

8
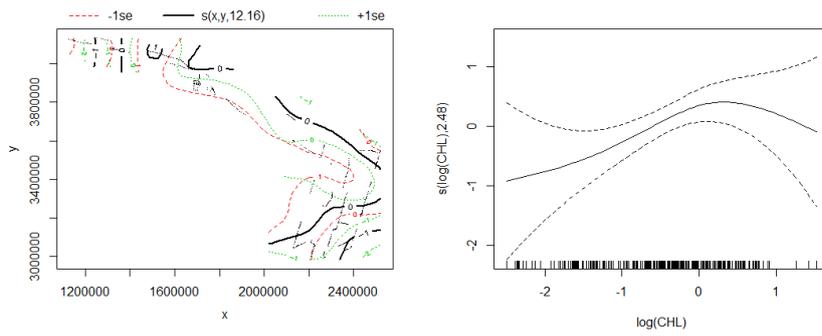
1
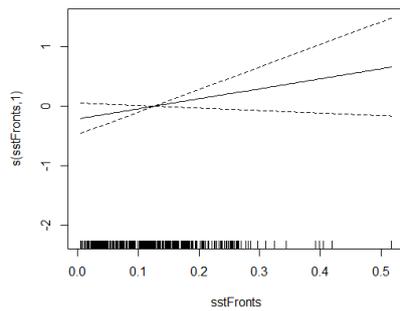
2

3 Figure 7. Plots of smooth functions for the baleen whale GAM.
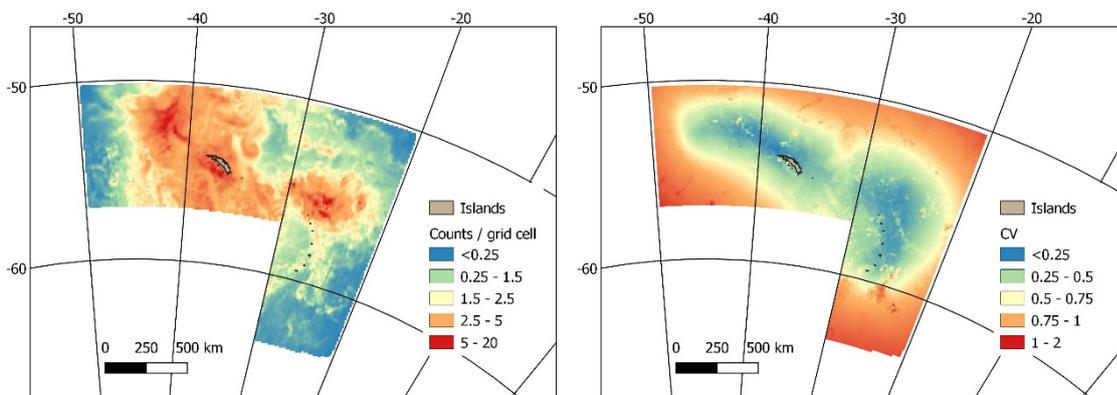
4

5 Figure 8. Predicted baleen whale density expressed as counts per grid cell (left) and CV of

6 estimates (right). Latitude and longitude grid lines at 10° intervals.