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Distribution and abundance of sei whales off the west coast of the Falkland Islands

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ABSTRACT

Little information exists on the current status of Southern Hemisphere sei whales (*Balaenoptera borealis*). We assessed their distribution and abundance along the west coast of the Falkland Islands (southwest Atlantic) during February and March 2018, using line transect and nonsystematic surveys. Abundance estimates were generated for a single survey stratum using design- and model-based approaches. Sightings of sei whales and unidentified baleen whales (most, if not all, likely to be sei whales) occurred from the coast to the 100 m depth isobath that marked the offshore boundary of the stratum. The modelled distribution predicted highest whale densities in King George Bay and in the waters between Weddell Island and the Passage Islands. Sei whale abundance was estimated as 716 animals (*CV*=0.22; 95% *CI*=448–1,144; density=0.20 whales/km^2) using the design-based approach, and 707 animals (*CV*=0.11; 95% *CI*=566–877; density=0.20 whales/km^2) using the model-based approach. For sei whales and unidentified baleen whales combined, the equivalent estimates were 916 animals (*CV*=0.19; 95% *CI*=606–1,384; density=0.26 whales/km^2) and 895 animals (*CV*=0.074; 95% *CI*=777–1,032; density=0.25 whales/km^2). The data indicate that the Falkland Islands inner shelf region may support globally important seasonal feeding aggregations of sei whales, and potentially qualify as a Key Biodiversity Area.

KEYWORDS: *Balaenoptera borealis*, feeding ground, density, Atlantic Ocean, Southern Hemisphere, management, Key Biodiversity Area, coastal

The sei whale (*Balaenoptera borealis*) is distributed widely across both hemispheres (Horwood, 1987). It is classified as a globally endangered species as a direct result of past exploitation (Cooke, 2018). The total catches reported during modern whaling operations (primarily during the 20th century) included more than 17,000 sei whales in the North Atlantic, 70,000 in the North Pacific, and more than 200,000 in the Southern Hemisphere (Cooke, 2018). Although the extensive historical exploitation of some large whale species has resulted in significant conservation and management effort in recent decades to assess the status and recovery of stocks (Thomas, Reeves, & Brownell, 2016), the distribution, abundance, ecology, and status of sei whales has received relatively little focus worldwide. This is particularly the case in the Southern Hemisphere, where a recent review by the International Whaling Commission (IWC) found that there were no current estimates of sei whale abundance or trends in abundance (IWC, 2017). Similarly, a review of six Antarctic baleen whale species indicated that the sei whale was the only species for which no robust information was available on population abundance, trends, or stock boundaries, on either the feeding or the breeding grounds (Leaper & Miller, 2011).

The lack of assessment of sei whales is partly a result of their inhabiting oceanic, offshore environments and having unpredictable temporal occurrence in many geographic regions (Horwood, 1987; Prieto, Janiger, Silva, Waring, & Gonçalves, 2012), making the species logistically challenging to study. However, there have been increasing reports of sei whales inhabiting neritic waters around southern South America, including in the Penas and Tres Montes gulfs in Chile (Español-Jiménez, Bahamonde, Chiang, & Häussermann, 2019), the Magellan Strait (Acevedo et al., 2017), the Beagle Channel (Goodall, Boy, & Schiavini, 2007; Reyes Reyes et al., 2014), the Falkland Islands (White, Gillon, Black, & Reid, 2002; Frans & Augé, 2016), and the Golfo San Jorge in Argentina (Belgrano et al., 2007; Iñíguez et al., 2010). While many of those reports were opportunistic or anecdotal in origin (and may also reflect expanding observation effort), in combination they suggest that sei whales may be increasing in occurrence in the coastal waters around southern South America, perhaps as the result of a recovery in populations or a change in ecological habits, or both.

In the Falkland Islands, opportunistic sightings and interviews with residents suggest that baleen whales have been seen more regularly in coastal waters since the 1990s (Frans & Augé, 2016). Such information must be interpreted carefully because of spatial biases towards the areas around human settlements, lower observer presence during winter, and uncertainties regarding reported species identifications (particularly the potential confusion between sei and fin whales, *Balaenoptera physalus*). Nevertheless, that information formed the basis on which six apparent hotspots of whale occurrence were identified as potential Key Biodiversity Areas (KBAs) for whales in the Falkland Islands, and highlighted as priorities for research (Taylor, Pelembe, & Brickle, 2016). KBAs are sites that contribute significantly to the global persistence of biodiversity, and are identified via a set of global criteria with quantitative thresholds (KBA Standards and Appeals Committee, 2019). While KBAs have delineated boundaries and are potentially manageable as a unit, the process of KBA designation does not include requirements for management or specific conservation action, such as protected area designation (KBA Standards and Appeals Committee, 2019).

This study investigated the coastal distribution and abundance of baleen whales on the west coast of the Falkland Islands, particularly in relation to two of the potential KBA sites suggested by Taylor et al. (2016): King George Bay, which had been identified as supporting high densities of sei whales, and Queen Charlotte Bay, which had been identified as supporting high densities of both sei and fin whales (Figure 1). We applied a conventional design-based approach using line transect survey data to estimate the abundance of sei whales in the area, and modelled both transect and nonsystematic survey data using generalized additive models (GAMs) to predict distribution and generate a model-based abundance estimate. We also conducted a review of published summer (i.e., corresponding with expected occurrence on feeding grounds) density and abundance estimates for sei whales worldwide, and assessed our Falklands' estimates in that global context.

MATERIALS AND METHODS

The Falkland Islands are a South Atlantic archipelago located on the Patagonian continental shelf approximately 500 km east of the southern tip of South America (Figure 1). The study area was located on the west coast of the Falklands, with a focus on the shallow (<60 m depth) waters of King George Bay and Queen Charlotte Bay (Figure 1). Surveys were carried out between February 25 and April 1, 2018, using a 19.5 m yacht (under motor) with an average survey speed of approximately 7 knots (13 km h^{-1}) and an eye height of 5.1 m from the bridge roof vantage point.

Line Transect Survey

A line transect survey (LTS) was carried out with the aim of generating a design-based abundance estimate of baleen whales in the region. A single survey stratum of 3,599 km^2 was defined (Figure 1). The northern (West Point island: 51.3°S) and southern (Cape Percival: 51.8°S) limits of the stratum comprised topographic features that marked the natural limits to the large coastal expanse containing King George and Queen Charlotte Bays. The westerly border of the survey strata ran along the 100 m depth isobath (based on bathymetric data obtained from the General Bathymetric Chart of the Oceans 2014). Transects were generated from a systematic random sampling design in the software Distance 6.2 (Thomas et al., 2010). The lines were equally spaced at 10 km intervals, and in a northwest to southeast orientation (Figure 2). Although the study area included semi-enclosed bays with variable bathymetry, this orientation was selected so that the transects ran as perpendicularly as possible to the overall depth gradient from the coastline to the 100 m depth isobath. Seven transects were generated, with a total trackline of 353.5 km.

The LTS was conducted in passing mode. Two observers searched continuously and independently for cetaceans across a separate 90° quarter (port or starboard) from their beam to the bow, primarily using the naked eye but supplemented with binoculars to check species identifications and group sizes. Standardized environmental data were recorded at the start of each watch and whenever they changed thereafter, including sea conditions measured on the Beaufort scale (hereafter “Beaufort”), swell height, and visibility. The LTS was only carried out in Beaufort ≤ 4, swell height ≤ 2.5 m, and visibility >10 km.

When cetaceans were detected, information was recorded on the time and position, vessel heading, angle relative to the trackline (measured using an angle board), estimated radial distance to the sighting, species, and group size. Whale sightings that could not be reliably identified to species (predominantly comprising tall columnar blows observed at distance where the body was not clearly visible) were recorded as unidentified large baleen whales. Due to the coastal locality and complex topography of the study area (land horizons predominated), it was not viable to use reticle binoculars or a range-stick to estimate distance to animals. Consequently, distance estimation was by eye. Observers practiced distance estimation over several days while transiting to the study site. Additionally, some distance estimation was practiced during the survey by estimating distances to rocky outcrops and a dinghy, and comparing with radar readings.

Nonsystematic Survey

A nonsystematic survey (NSS) was carried out within the wider study area (Figure 1), with the aim of acquiring additional data on the distribution and occurrence of whales. The route was determined daily by prevailing weather conditions and logistical constraints. The NSS followed the same standardized visual survey methods as described for the LTS. However, on some days a closing mode was adopted to approach whale sightings for photo-identification following their initial detection. In those circumstances the active search effort was terminated, and the survey instead switched to "encounter mode" and ceased searching for new animals.

Design-based Abundance Estimation

Separate analyses were carried out using data sets containing sei whales only, and sei whales and unidentified large baleen whales combined (sei+ulbw). All unidentified baleen whales that were approached for identification during the survey were subsequently verified to be sei whales, and no other whale species were identified during the survey period (Weir, 2018). Consequently, it is likely that most, if not all, of the unidentified baleen whale sightings were also sei whales.

The abundance of sei whales and of sei+ulbw was estimated using standard distance sampling methods (Buckland *et al.* 2001) in Distance software version 7.1 (Thomas et al., 2010). The perpendicular distance x of each sighting from the trackline was calculated as: $x = r \sin(\theta)$, where θ is the angle between the sighting and the trackline and r is the radial distance to each sighting. To determine whether there was an effect of group size on detection, ln(*group size*) was regressed against the estimated detection probability. The regression was not significant for either data set, and consequently the observed mean group size was used.

For modelling detection probability, different key functions and adjustment terms were explored, and also whether the covariates Beaufort, swell height, observer, and group size improved model fit. A 5% right truncation of perpendicular distance was assessed for both data sets to determine whether model fit was improved. The final detection function was selected based on minimum Akaike's Information Criterion (AIC), the results of Kolmogorov-Smirnov and Cramer-von Mises goodness-of-fit tests, and visual inspection of model diagnostic plots (Buckland et al., 2001).

Estimation of Availability Bias

Availability bias, which occurs when animals on the trackline are missed because they are submerged, was calculated using equation 4 from Laake, Calambokidis, Osmek, and Rugh (1997) to estimate the probability of a single whale being available on the transect line, *â(0)*:

$$\hat{a}(0) = \frac{E[sf] + E[d]\left(1 - exp\left(\frac{-w(0)}{E[d]}\right)\right)}{E[sf] + E[d]}$$

where *E[sf]* is the average length of a surfacing, *E[d]* is the average length of a dive, and *w(0)* is the amount of time the ocean is in the observer's view on the transect line.

Information on sei whale dive behavior was acquired from focal follows carried out in the West Falkland study area (Weir, Taylor, Jelbes, & Stanworth, 2018). *E[sf]* was calculated as the average time that a whale's body, or associated cues such as its bow-wave or blow, was visible for detection while surfacing, with a value of 8.0 s (*n* = 14, SD = 1.8). Two estimates of *E[d]* from two different data sets were assessed (Weir et al., 2018). Data set 1 comprised cue rates, with a mean number of cues (surfacings) per whale per hour of 30.6 (*n* = 17, SD = 3.1), resulting in an *E(d)* of 109.6 s. Data set 2 comprised the mean interbreath intervals (IBIs) recorded during focal follows incorporating the complete dive cycles of individual whales, producing a mean *E[d]* of 129.6 s (*n* = 161, SD = 104.6). *w(0)* was calculated as the distance ahead of the vessel that whales could be detected divided by the average survey speed of 3.7 m/s (7.2 knots). Based on the radial distances of sightings close to the transect line, a distance of 1,000 m was selected as a minimum distance ahead that whales would be available for detection. Availability probability was also calculated using distances ahead of 2,000 m and 3,000 m.

Based on the estimated availability of an individual whale, the availability of a group of whales was estimated as:

$$\hat{a}(G,0) = 1 - (1 - \hat{a}(0))^G$$

where G is the number of animals in the group. This represents the probability that at least one whale in a group was at the surface, assuming asynchronous surfacing among individuals (Paxton, Scott-Hayward, Mackenzie, Rexstad, & Thomas, 2016), and serves as an upper bound for availability of groups larger than one. If whales in a group always surface synchronously, the Laake et al. (1997) estimate for a single whale represents a lower bound.

Distribution Modelling and Model-based Abundance Estimation

Prior to modelling, several quality-control measures were applied to the data collected during the NSS. Firstly, three days of NSS were removed from the data set because they were focused predominantly on photo-identification. Secondly, any tracks that doubled-back and covered the same area on the same date were removed, to leave only directional tracks. Finally, any effort legs of <30 min duration were removed. All cetacean sightings associated with the removed effort data were also omitted from the analysis.

Following editing of the NSS data, the active search effort collected across the wider study area in conditions considered favorable for detecting large whales (defined here as Beaufort ≤4, swell height ≤2.5 m, and visibility >5 km), and associated on-effort sightings from the LTS and NSS, were combined. Water depth (data source: BMT Argoss, 2014) and distance from shore were extracted in Quantum Geographic Information System (QGIS: https://qgis.org) for the midpoint of each 60 s effort segment. Effort data time-stamped every 60 s were combined into segments of 3 km target length in software R (R Core Team, 2018).

Generalized additive models (GAMs) were fitted using the R package `mgcv` version 1.8-26 (Wood, 2017). The number of whales detected in each effort segment was modelled as a negative binomial distribution to account for over-dispersion in the data, with logarithmic link function, and including an offset of ln(effective search area) to account for variation in segment length. Effective search area was calculated as segment length x twice the effective search half-width estimated from the fitted detection function (see above). Models were fitted using restricted maximum likelihood (REML: Marra & Wood, 2011).

Candidate covariates considered in the models to explain variation in density were northing and easting (as a 2-dimensional isotropic smooth function), depth, and distance from shore. Including northing and easting provides a base model of spatial variation in density, which may be further improved by additional covariates. Depth and distance from shore were correlated (Pearson correlation coefficient = 0.68), so were not considered in the same model. Model selection was based on minimum AIC. Adequacy of model fit was assessed by visual inspection of the QQ and residual plots. A variogram was computed using package `gstat` in R to check for evidence of spatial autocorrelation in model residuals.

A 3 x 3 km prediction grid was developed using the vector grid function in QGIS and a WGS 84 / UTM zone 21S projection. The size of the prediction grid cells was selected to match approximately the length of effort segments and effective strip widths in the modelled data. Only grid cells that overlapped completely or partially with the original 3,599 km^2 LTS stratum were retained in the prediction grid. However, grid cells for which the sea area comprised <30% of the total cell area were removed, resulting in a slightly reduced stratum surface area of 3,579 km^2 for the model-based abundance estimate. The water depth and distance from shore were calculated for the midpoint of each cell using QGIS. Due to the complexity of the coastline, the midpoints of a small number of cells (17 out of 465) occurred on land and were manually replotted in the adjacent sea area.

The best fitting models were used to predict the density (individuals/km^2) in each grid cell. The predicted number of animals in each grid cell was calculated as density multiplied by the area of the grid cell that lay within the survey stratum, calculated in QGIS. Maps of predicted density distribution were created in QGIS.

Model-based estimates of abundance and their uncertainty were calculated based on posterior simulation. 1,000 vectors of the model coefficients were simulated using `mvrnorm` from the `MASS` library in R (Venables & Ripley, 2002), from which 1,000 predictions of abundance were made. Mean abundance, its CV and percentile-based 95% confidence limits were calculated from the 1,000 predictions.

RESULTS

A total of 1,561.5 km of active search effort was achieved in favorable conditions between February 25 and April 1, 2018, comprising 346.1 km of LTS effort (completed February 26 to March 13) and 1,215.4 km of NSS quality-controlled effort (completed February 25 to April 1). There were 843 associated cetacean sightings (1,617 individuals), of at least four species (Table 1). The sei whale was the most numerous species recorded (460 animals: Table 1), and the only confirmed baleen whale species.

Design-based Abundance

The 346.1 km of realized LTS effort resulted in 241 cetacean sightings (Table 1; Figure 2). Most were baleen whales (*n* = 176, 73%) and the remainder were delphinids. Due to the passing mode implemented during the LTS, many baleen whale sightings remained unidentified to species level. The sei whales and unidentified large baleen whales recorded during the LTS had mean group sizes of 1.7 (*n* = 70, SD = 0.86, median = 1, range = 1–5) and 1.2 (*n* = 106, SD = 0.48, median = 1, range = 1–3) animals, respectively.

A hazard-rate model (no adjustments) was the best fitting detection function for both the sei whale data set and the sei+ulbw data set (Figure 3). Right truncation of the data did not improve model fit, as indicated by the results of Kolmogorov-Smirnov and Cramer-von Mises goodness-of-fit tests. Models including covariates had less support from the data as indicated by delta-AIC values greater than 2 compared to models without covariates (Burnham & Anderson, 2002). The effective strip half-width estimated for sei whales (*esw* = 857 m) was considerably narrower than that for sei+ulbw (*esw* = 1,408 m: Table 2). The resulting abundance estimates were 716 sei whales (*CV* = 0.22; 95% *CI* = 448–1,144), and 916 sei+ulbw (*CV* = 0.19; 95% *CI* = 606–1,384: Table 2). Density was 0.20 whales/km^2 for sei whales, and 0.26 whales/km^2 for sei+ulbw.

Availability Bias

Using the most conservative assumptions of single animals and a detection range extending only 1 km ahead of the vessel, a minimum value of $\hat{a}(0)$ was calculated as 0.92 and 0.88, respectively, for the two dive data sets (Table 3). $\hat{a}(0)$ increased to 0.99 for single whales at detection ranges of 2 km and 3 km, respectively. For groups comprising 2 or more animals surfacing independently, $\hat{a}(0)$ was at, or close to 1.0, at all three detection distances in both data sets (Table 3). The combined results thus indicate a range of availability probability of around 0.9 - 1.0. Incidental observations of sei whales in the Falkland Islands indicate that surfacings of animals in groups are often asynchronous, so we expect true availability to be greater than the minimum. Overall, we conclude that availability of sei whales in the study area was close to 1, and consequently no correction for availability bias was applied to the abundance estimates.

Model-based Distribution and Abundance

The 1,561.5 km of combined NSS and LTS search effort resulted in 270 associated sei whale sightings and 644 sei+ulbw sightings (Table 1).

The best fitting model fit of sei whale density retained smooth terms for geographic position (northing and easting) and water depth (Figure 4), explaining 15.5% of the deviance. The computed variogram showed no evidence for spatial autocorrelation of model residuals. The fitted relationship between sei whale density and depth showed that water depths between 20 and 80 m had a positive influence on density (Figure 4). The predicted density of sei whales was highest in King George Bay, and to the southwest of the Passage Islands located between King George Bay and Queen Charlotte Bay (Figure 5A). Predicted density was lower towards the western seaward limit of the study area. Model-based abundance was estimated as 707 animals (CV = 0.11; 95% CI = 566–877), with a mean density of 0.20 animals/km^2.

The best fitting model for the sei+ulbw data set also retained smooth terms for geographic position (northing and easting) and water depth (Figure 4), explaining 24.8% of the deviance. The computed variogram showed no evidence for spatial autocorrelation of model residuals. Water depth had a positive influence on density over a range similar to that for sei whales (Figure 4). The model produced a mean density of 0.25 animals/km^2, and an abundance of 895 animals (CV = 0.074; 95% CI = 777–

1,032). The distribution of predicted density was similar to that for sei whales but was less widespread in King George Bay and density was relatively higher between the Passage Islands and Weddell Island in the outermost region of Queen Charlotte Bay (Figure 5B).

Global abundance and density estimates

A review of published summer (i.e., corresponding with expected occurrence on feeding grounds) density and abundance estimates for sei whales worldwide is provided in Appendix S1. Most estimates originate from survey areas that are several orders of magnitude larger than the west coast of the Falklands, for example >2,000,000 km^2 in the North Atlantic and western Pacific Oceans (Hakamada & Matsuoka, 2016; Pike et al., 2019), and almost 7,000,000 km^2 in the eastern North Pacific (Hakamada, Matsuoka, Murasi, & Kitakado, 2017). The only estimate available for Southern Hemisphere sei whales appears to be 9,718 animals calculated for the waters south of 30ºS during 1978/79–1987/88 (Butterworth & Geromont, 1995; Appendix S1). Acknowledging the limitations arising from differing methods, study areas, and timeframes, available summer abundance estimates of sei whales amount to ~12,000 animals in the North Atlantic, ~35,000 animals in the North Pacific, and ~10,000 animals in the Southern Hemisphere (Appendix S1; Table S1). Global density estimates for individual survey strata/years ranged from 0.0000512 to 0.0224 whales/km^2, with most (96.7%) having values of less than 0.01 whales/km^2 (Appendix S1; Table S2).

DISCUSSION

Abundance and Density Estimation

Using design- and model-based methods, our abundance estimates for the west coast of the Falkland Islands comprised ~700 sei whales, and ~900 combined sei+ulbw. The estimates produced by the two approaches were very similar, noting that the surface area of the stratum used for the model-based approach was only 0.5% smaller than that used for the density-based approach. The density estimates were thus also very similar for both approaches (0.20 whales/km^2 for sei whales, and 0.25/0.26 whales/km^2 for sei+ulbw). Since most, if not all, of the unidentified baleen whales observed during the survey were likely to have been sei whales (Weir, 2018), the estimates for combined sei+ulbw are considered the most accurate representation of sei whale abundance. The model-based estimate is more precise, and consequently the total of 895 ($CV = 0.074$; 95% $CI = 777–1,032$) animals is proposed here as the best available estimate of sei whale abundance in the study area.

Our abundance estimates are the first published for sei whales in Southern Hemisphere waters in recent decades. Although comparison with the ~10,000 animals estimated across the entire Southern Hemisphere region during the 1970s/1980s (Butterworth & Geromont, 1995) is inappropriate due to differences in methods and analysis, it is nevertheless suggestive that the relatively small area around the Falkland Islands likely supports an abundance of sei whales that may be significant in a Southern Hemisphere context. The estimate for the small Falklands study area also exceeds many of the total estimates generated from much larger-scale surveys worldwide. It may be expected that Southern Hemisphere sei whales have increased in number since the end of large-scale commercial whaling, as has been demonstrated for some other southwest Atlantic whale populations such as humpback whales *Megaptera novaeangliae* (Bortolotto et al., 2017; Zerbini et al., 2019). Additionally, model projections indicate that the global population of mature sei whales could have recovered to approximately 30% of the preexploitation level by 2018 (Cooke, 2018).

Estimates of abundance are a function of survey area size, and a comparison of estimated densities thus provides a more robust method of evaluating the importance of Falklands' waters for sei whales in a global context. The density estimated on the west coast of the Falkland Islands (>0.2 whales/km^2) far exceeded those recorded during large-scale summer surveys in other regions, the next highest being 0.004 whales/km^2 estimated both in a 1989 survey of Icelandic and Greenland waters (Cattanach *et al.* 1993) and in the eastern North Pacific during 2010–2012 (Hakamada *et al.* 2017). The density of sei whales estimated in the Falklands' stratum was also an order of magnitude higher than estimated in any single survey stratum in Iceland during 1989 and 2007 (Cattanach, Sigurjónsson, Buckland, & Gunnlaugsson, 1993; Pike et al., 2019), and at least two orders of magnitude higher than all remaining strata in any geographic region or year. The Falklands study area therefore appears to support a globally significant aggregation of sei whales.

The underlying driver of sei whale occurrence in the Falkland Islands is predominantly feeding, as determined from observations of surface feeding behavior and numerous defecation events (Weir et al., 2019). Like many other baleen whale species, sei whales migrate seasonally between subtropical wintering grounds and higher latitude feeding areas. Within the southwest Atlantic, the Falklands represent a feeding destination at one end of that migration (Weir, Oms, Baracho-Neto, Wedekin, & Daura-Jorge, 2020). Consequently, the occurrence of sei whales in neritic waters around the Falklands is highly seasonal. The timing of the 2018 abundance survey corresponded with the documented seasonal peak in sei whale relative abundance around the Falklands during February and March (Weir et al., 2019), and it may be expected that abundance surveys carried out during other months might encounter lower densities.

While the abundance estimates described here followed standardized methods, some limitations are acknowledged. Firstly, although we explored availability bias, we could not account for perception bias (i.e. animals available on the trackline that were missed by the observers) due to logistical constraints that prevented the use of a double observer platform and because the analysis method used only perpendicular distances. The resulting estimates may therefore be slightly negatively biased. Other sei whale abundance surveys have assumed a g(0) of 1 (e.g., Hakamada et al., 2017), or have been unable to incorporate a correction for perception bias even when a double platform was used (e.g., Pike et al., 2019).

Secondly, the complex nature of the coastal study site with semi-enclosed areas and small islands meant that it was not possible to use standard distance estimation tools such as reticle binoculars or range-finding sticks, because the horizons were predominantly land rather than sea. As a result, distance estimation was carried out by eye, which may introduce some error. Thirdly, the survey stratum was relatively small in size, and sei whales are highly mobile animals. Spatial shifts in whale foraging aggregations around the Falklands may be expected over time, in response to dynamic prey fluctuations, leading to variation in the number of animals present in the survey area over time. However, the potential impacts of such shifts on the survey were minimized by limiting the NSS to five weeks and conducting the LTS over a relatively short, two-week period.

Conservation and Management Implications

The abundance estimates generated here for a localized region of the southwest Atlantic, highlight the need for more extensive abundance surveys for sei whales across the mid-latitudinal waters of the Southern Hemisphere. Currently, the absence of robust, contemporary data sets from other regions of the Southern Hemisphere precludes evaluating the status of the species in this important part of the global range (Leaper & Miller, 2011; IWC, 2017). There is also a need for information on stock structure in the Southern Hemisphere to better facilitate interpretation of future regional abundance estimates, since it is apparent that the existing defined IWC Management Areas in the southwest Atlantic do not reflect the movements of sei whales and require revision (Weir et al., 2020).

Globally, sei whales are usually documented in deep, oceanic habitats over or seaward of the shelf edge (Hakamada et al., 2017; Houghton et al., 2020), with only scarce occurrences over the shelf (Horwood, 1987; Prieto et al., 2012). In contrast, sei whales around the Falkland Islands routinely inhabit neritic, and often coastal, environments, presumably in response to the distributions of their favored prey species. Whalers reported large numbers of sei whales around the Falkland Islands during the early 20th century (Andrews, 1916), and the species comprised almost 65% of the catches during whaling operations at New Island on the west coast of the Falklands between 1905 and 1915 (Allison, 2016). In combination with recent surveys (Weir et al., 2019), those data indicate that neritic habitats around the Falkland Islands have supported feeding sei whale aggregations over at least the last century. Given the evidence for long-term use of the region, the globally significant densities recorded during the 2018 survey, and the lack of other documented areas of high abundance and persistent use for sei whales worldwide, Falklands' waters may qualify as a global KBA.

Two small areas in Queen Charlotte Bay (295 km^2) and King George Bay (55 km^2) on the west coast of the Falklands were highlighted as potential future KBAs in need of targeted research by Taylor et al. (2016). This study collected a systematic effort-related data set to address those data gaps. Although the site in Queen Charlotte Bay had been identified, based on local anecdotal sightings, as a potential KBA for both sei whales and fin whales, we did not observe any fin whales. Therefore, our consideration of potential KBAs in the Falklands relates solely to sei whales. The targeted surveys in

2018 demonstrated that high densities of sei whales were distributed over a much wider spatial area than suggested by the anecdotal data set of Frans & Augé (2016). In particular, comparatively higher densities were documented in the western part of the study area further from the shore, and around the uninhabited Passage Islands. That is likely the result of differences in spatial coverage, with the anecdotal data set biased towards the nearshore areas visible from coastal settlements. The 2018 systematic data set did not support the two small areas identified as potential KBAs as having particularly higher whale relative abundance compared with the surrounding waters. Moreover, such small areas are unlikely to represent a meaningful management unit for large, mobile marine predators such as sei whales, with overnight linear spatial movements by individuals of tens of kilometers documented in the Falklands via photo-identification and tagging data[1]. We therefore recommend that any KBA designated for sei whales in the Falkland Islands should occur at a spatial scale relevant to a baleen whale feeding ground, allowing for dynamic spatio-temporal shifts in feeding aggregations, and accounting for the high mobility of sei whales by incorporating sufficient linkage habitat to facilitate movements and maintain connectivity.

The high density of sei whales in neritic habitat around the Falkland Islands, overlaps with, and may increase their vulnerability to, human activities including shipping, coastal construction projects, oil transshipments, and the development of aquaculture. Potential direct and indirect (i.e., via their prey) impacts on whales include vessel strikes, acoustic disturbance (masking their calls or causing displacement), and habitat degradation (e.g., via oil spillages, or eutrophication). KBA designation does not include specific management requirements. However, given the apparent global importance of Falklands' waters for sei whales, we recommend that a long-term management plan be developed for the species that aims to monitor population trends and maintain a favorable conservation status via the assessment and mitigation of potential threats.

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[1] Unpublished data, Falklands Conservation, Jubilee Villas, Ross Road, Stanley, Falkland Islands.

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TABLE 1. Summary of cetacean sightings (S) and individuals (I) recorded during 1,562 km of line transect survey (LTS) and nonsystematic survey (NSS) effort on the west coast of the Falkland Islands.

Species	**LTS**		**NSS**		**Combined**	
	S	**I**	**S**	**I**	**S**	**I**
Sei whale *Balaenoptera borealis*	70	118	200	342	270	460
Unidentified large baleen whale	106	130	268	345	374	475
Killer whale *Orcinus orca*	1	1	1	8	2	9
Peale's dolphin *Lagenorhynchus australis*	39	132	72	247	111	379
Commerson's dolphin *Cephalorhynchus commersonii*	25	58	61	236	86	294
Total	241	439	602	1,178	843	1,617

TABLE 2. Summary statistics for design-based abundance estimates of sei whales, and combined sei whales and unidentified large baleen whales (sei+ulbw), during the West Falkland line transect survey in 2018.

Species	***L* (km)**	***n***	**No. of animals**	***n/L***	***esw***	***E(s)***	***D***	***CV***	***N***	**Lower 95% *CL***	**Upper 95% *CL***
Sei	346.1	70	118	0.202	857.1	1.69	0.199	0.22	716	448	1,144
sei+ulbw	346.1	106	130	0.508	1,407.5	1.41	0.255	0.19	916	606	1,384

L, realized effort; *n*, number of sightings; *n/L,* encounter rate (sightings per kilometer); *esw*, estimated effective strip half-width (m); *E(s)*, mean group size; *D*, density (whales/km^2); *N*, abundance; *CV*, coefficient of variation of density and abundance.

TABLE 3. Availability probability on the transect line, $\hat{a}(G, 0)$, of individual and groups (G) of up to five sei whales (the maximum group size encountered), at three assumed detection distances ahead of the vessel. See text for definition of data sets 1 and 2.

Group size	**Detection range (m)**		
	1000	**2000**	**3000**
Dive data set 1			
1	0.921	0.993	0.999
2	0.994	1.000	1.000
3	0.999	1.000	1.000
4	1.000	1.000	1.000
5	1.000	1.000	1.000
Dive data set 2			
1	0.883	0.985	0.998
2	0.986	1.000	1.000
3	0.998	1.000	1.000
4	1.000	1.000	1.000
5	1.000	1.000	1.000

FIGURE LEGENDS

FIGURE 1 Location of the study area off the west coast of the Falklands, including the survey stratum and the outlines of the potential whale Key Biodiversity Areas identified by Taylor et al. (2016) in King George Bay (KGB) and Queen Charlotte Bay (QCB).

FIGURE 2 Location of transects and cetacean sightings during the line transect survey. The positions of cetacean sightings were re-calculated based on their estimated distance from the vessel.

FIGURE 3 Detection functions for: (a) sei whales (n = 70); and (b) sei and unidentified large baleen whales (n = 106). Note the different scales of the perpendicular distance axes.

FIGURE 4 Modelled relationship between whale density and water depth (m) for: (a) sei whales; and (b) combined sei and unidentified large baleen whales. Shaded band represents the 95% confidence interval. Tick marks on the horizontal axis represent data points. The estimated degrees of freedom of the fitted smooth functions are provided in brackets.

FIGURE 5 Smoothed (Gaussian smooth) surface maps of predicted density (individuals/km^2) across the survey stratum of: (a) sei whales; and (b) combined sei and unidentified large baleen whales. Coefficients of variation of average predictions: (c) sei whales; and (d) combined sei and unidentified large baleen whales.

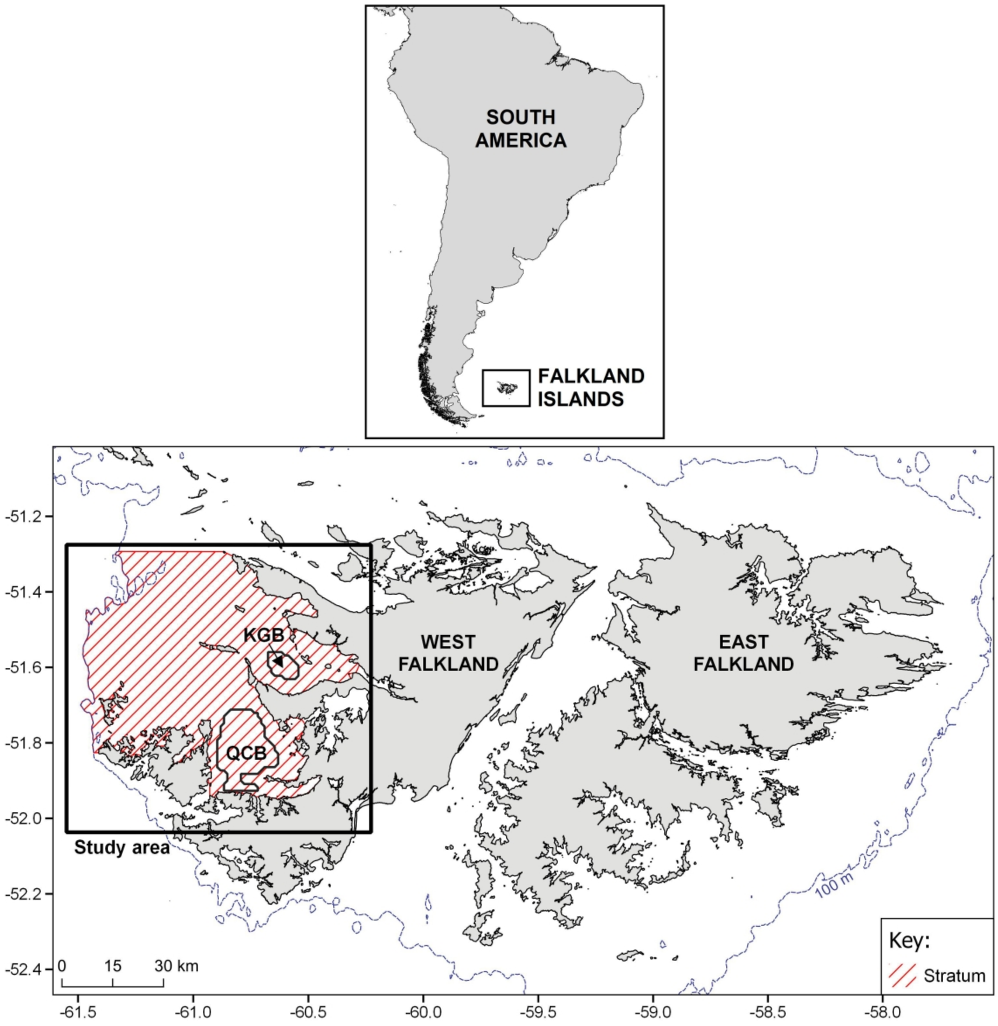

FIGURE 1 Location of the study area off the west coast of the Falklands, including the survey stratum and the outlines of the potential whale Key Biodiversity Areas identified by Taylor et al. (2016) in King George Bay (KGB) and Queen Charlotte Bay (QCB).

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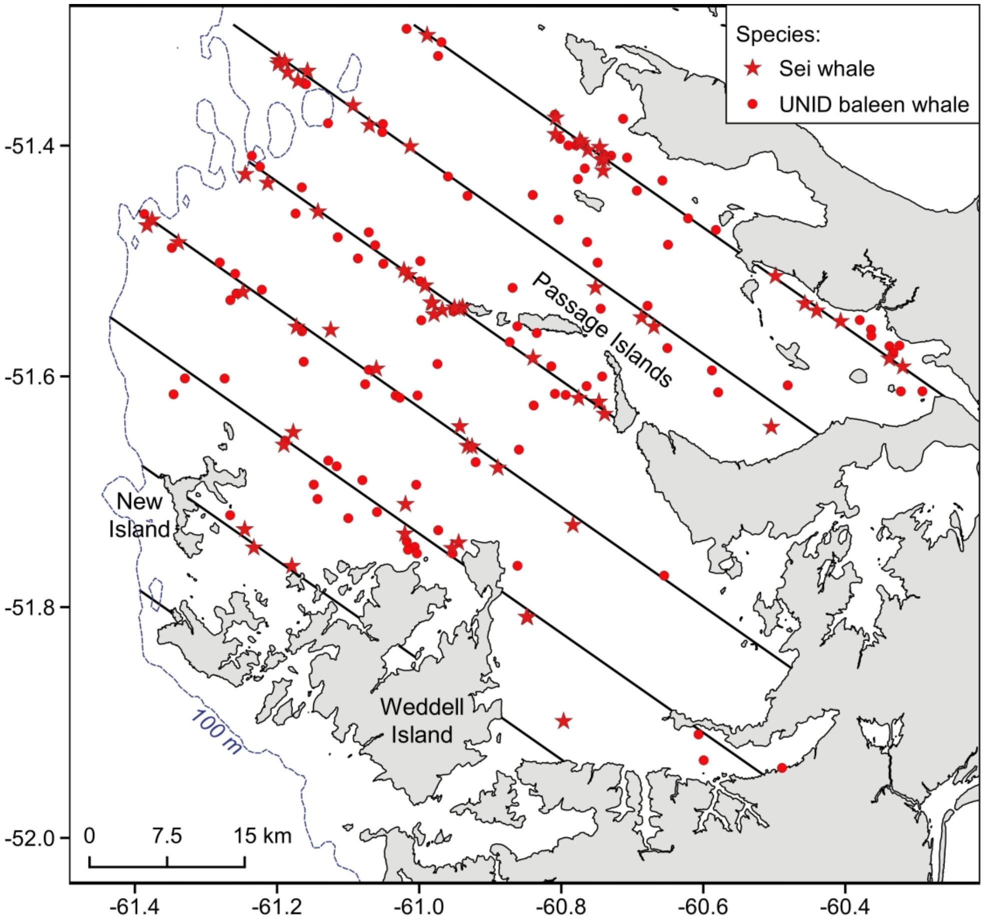

FIGURE 2 Location of transects and cetacean sightings during the line transect survey. The positions of cetacean sightings were re-calculated based on their estimated distance from the vessel.

208x190mm (600 x 600 DPI)

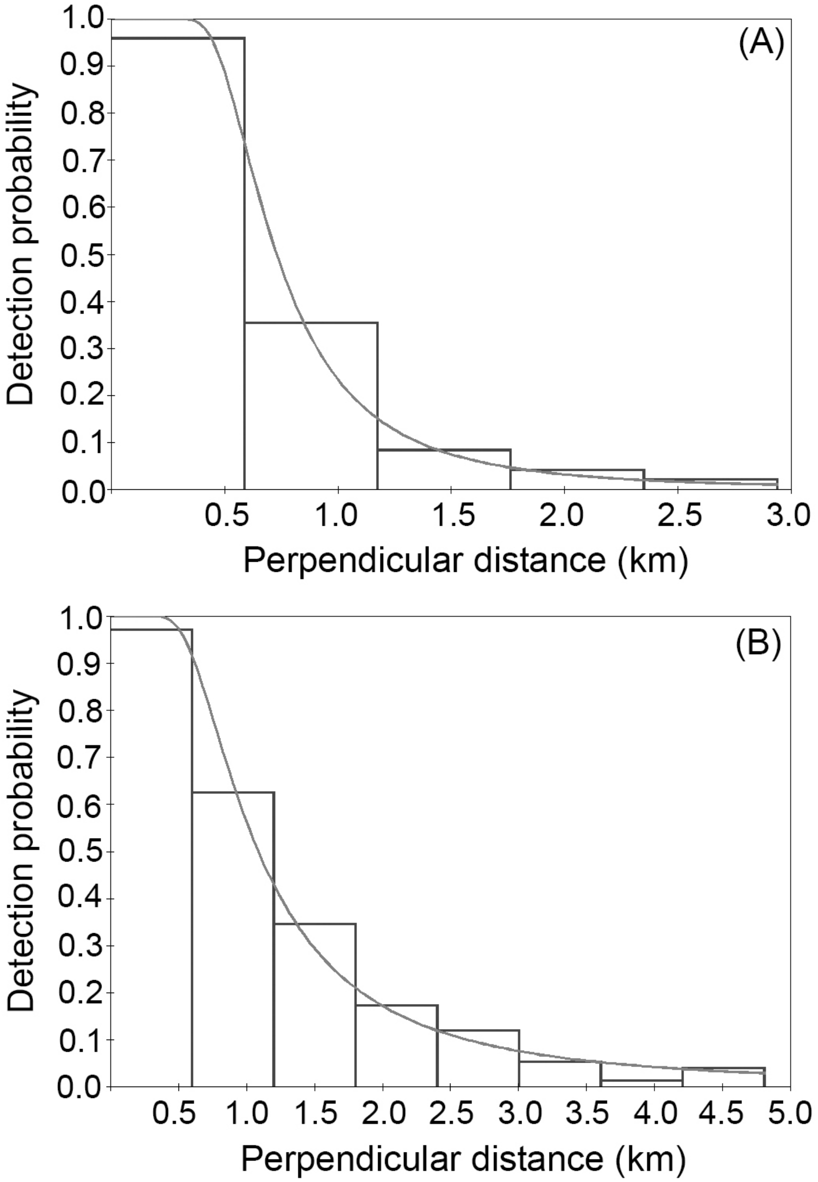

FIGURE 3 Detection functions for: (a) sei whales (n = 70); and (b) sei and unidentified large baleen whales (n = 106). Note the different scales of the perpendicular distance axes.

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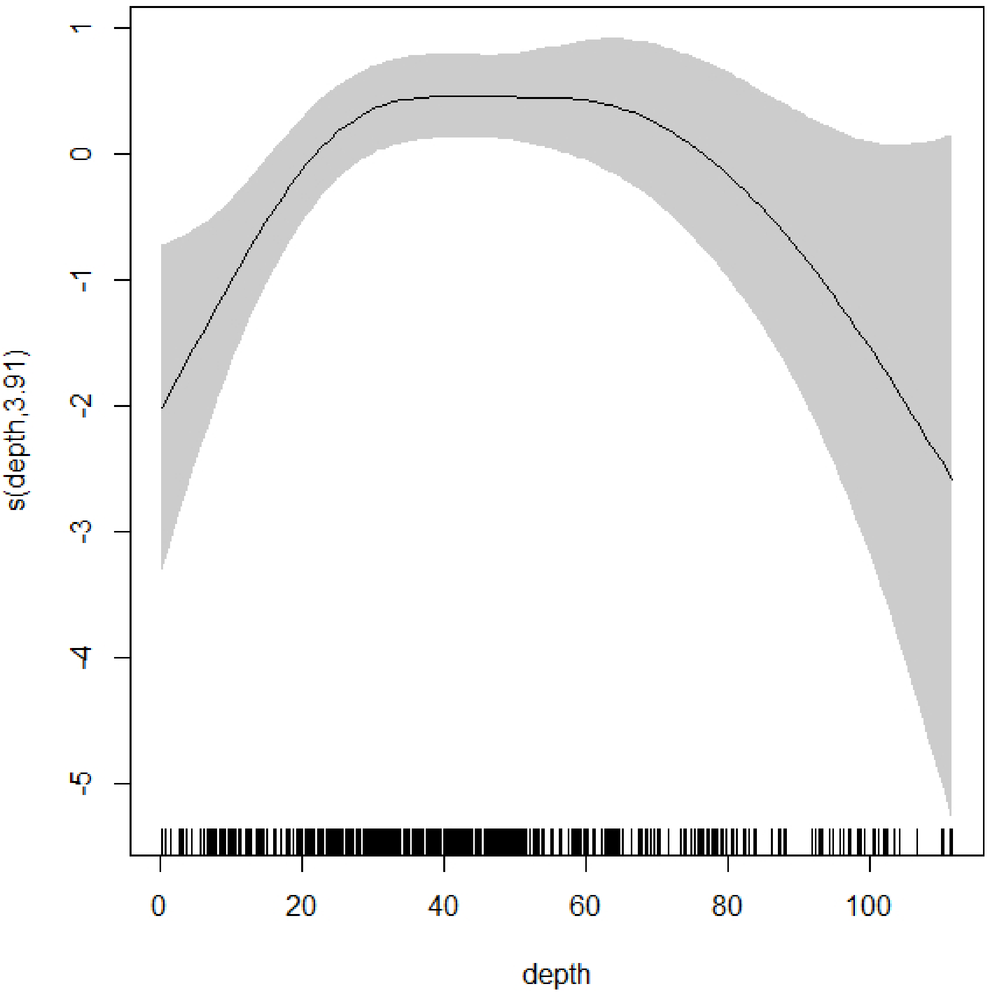

FIGURE 4 Modelled relationship between whale density and water depth (m) for: (a) sei whales; and (b) combined sei and unidentified large baleen whales. Shaded band represents the 95% confidence interval. Tick marks on the horizontal axis represent data points. The estimated degrees of freedom of the fitted smooth functions are provided in brackets.

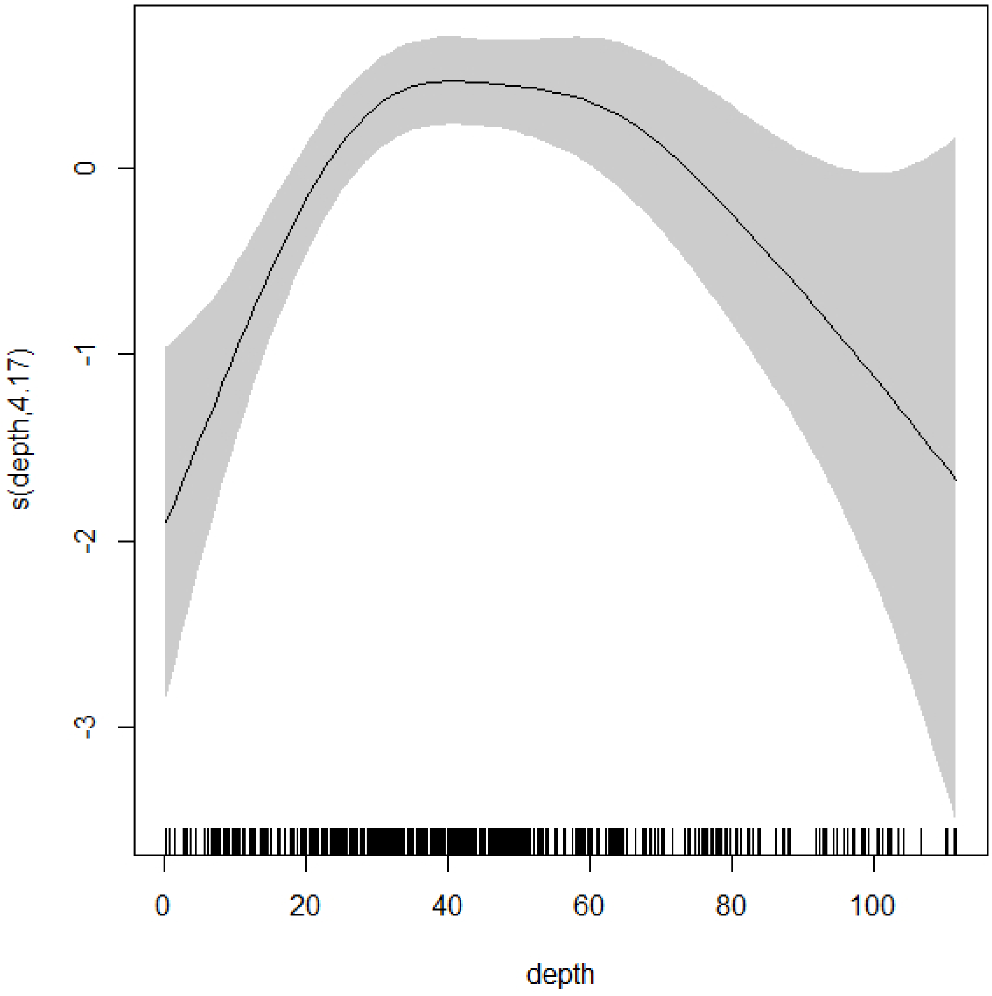

FIGURE 4 Modelled relationship between whale density and water depth (m) for: (a) sei whales; and (b) combined sei and unidentified large baleen whales. Shaded band represents the 95% confidence interval. Tick marks on the horizontal axis represent data points. The estimated degrees of freedom of the fitted smooth functions are provided in brackets.

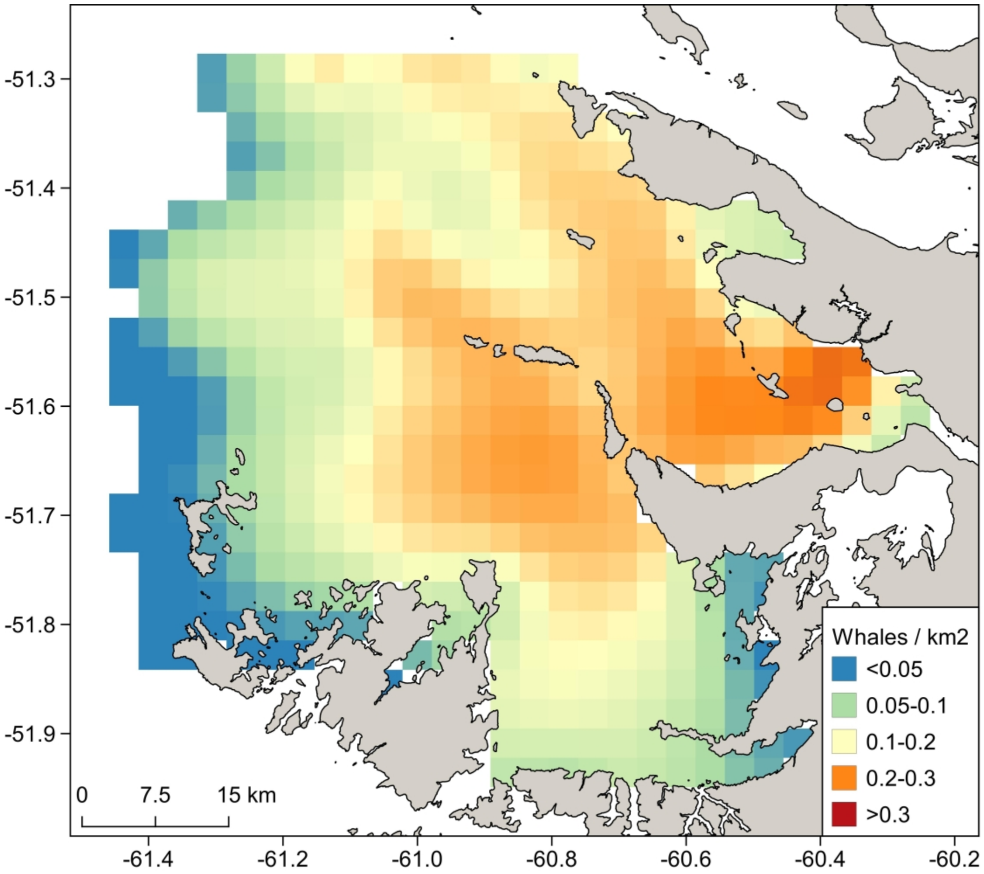

FIGURE 5A Smoothed (Gaussian smooth) surface maps of predicted density (individuals/km2) across the survey stratum of: (a) sei whales; and (b) combined sei and unidentified large baleen whales. Coefficients of variation of average predictions: (c) sei whales; and (d) combined sei and unidentified large baleen whales.

206x178mm (600 x 600 DPI)

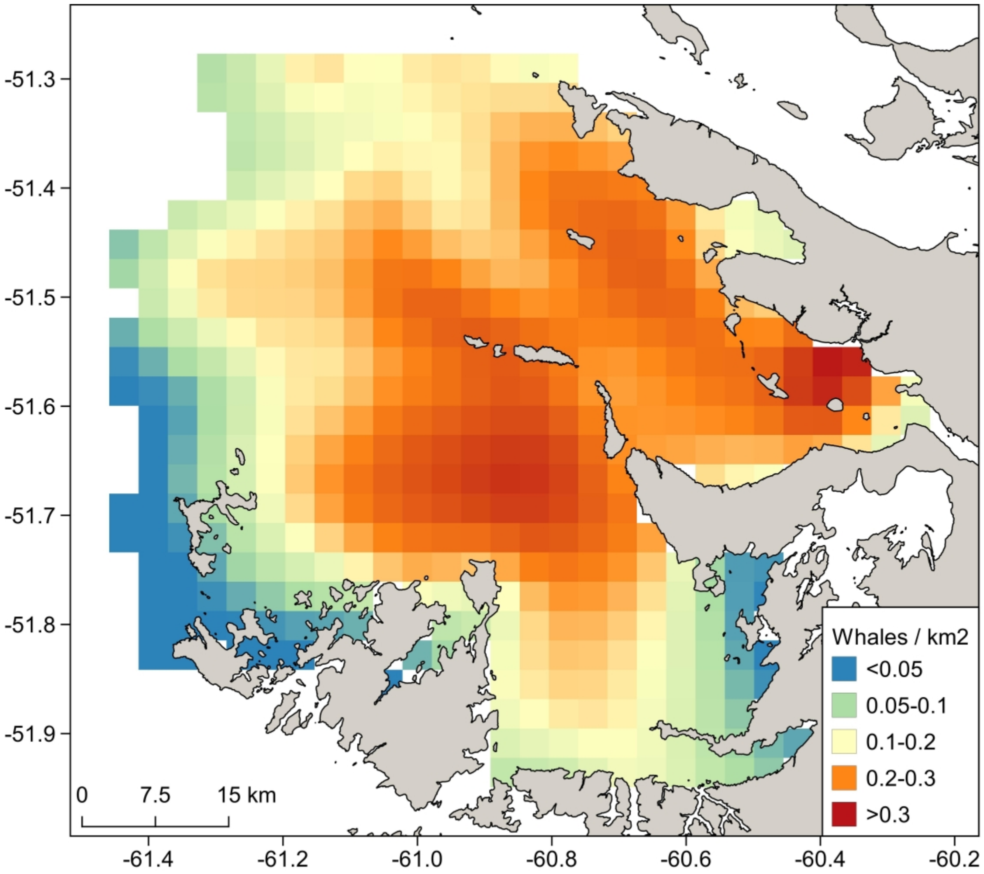

FIGURE 5B Smoothed (Gaussian smooth) surface maps of predicted density (individuals/km2) across the survey stratum of: (a) sei whales; and (b) combined sei and unidentified large baleen whales. Coefficients of variation of average predictions: (c) sei whales; and (d) combined sei and unidentified large baleen whales.

206x178mm (600 x 600 DPI)

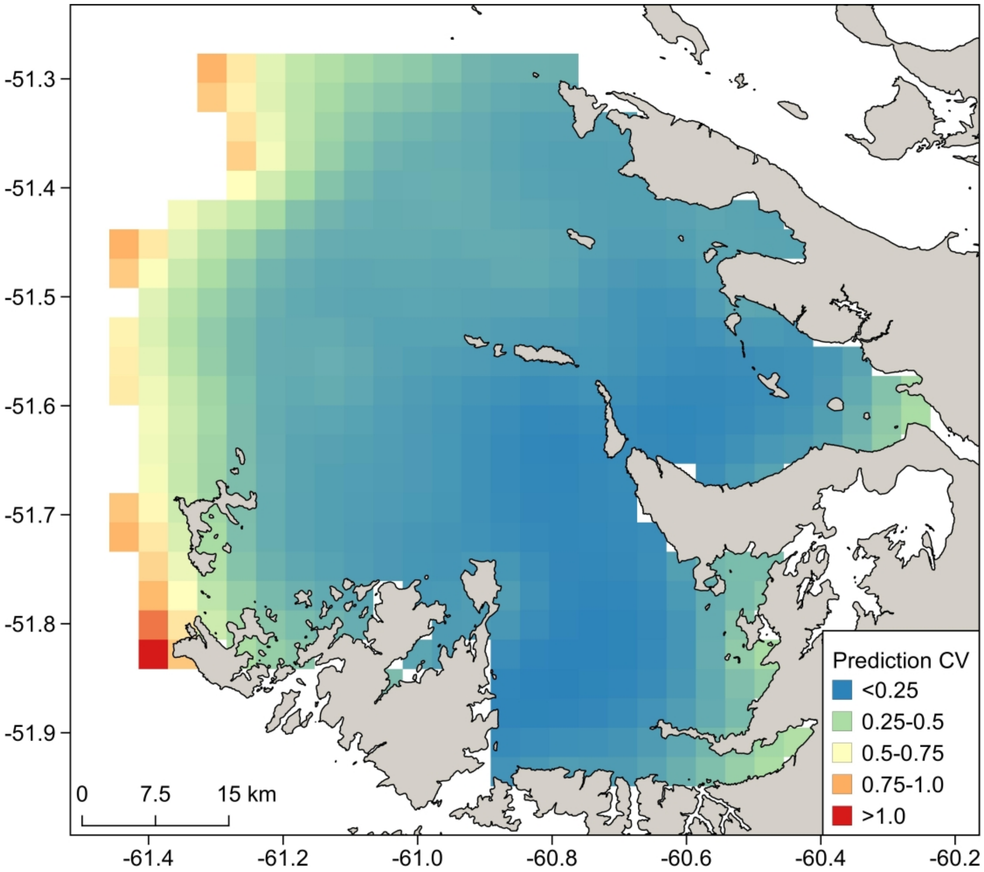

FIGURE 5C Smoothed (Gaussian smooth) surface maps of predicted density (individuals/km2) across the survey stratum of: (a) sei whales; and (b) combined sei and unidentified large baleen whales. Coefficients of variation of average predictions: (c) sei whales; and (d) combined sei and unidentified large baleen whales.

206x178mm (600 x 600 DPI)

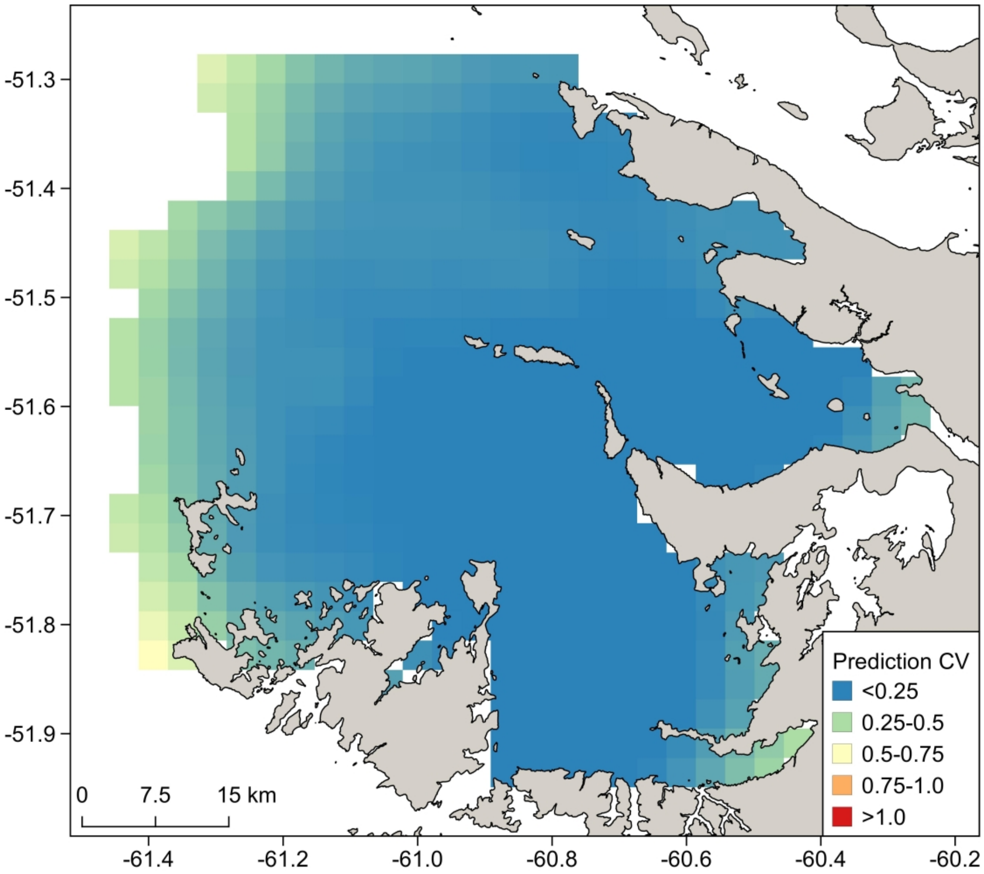

FIGURE 5D Smoothed (Gaussian smooth) surface maps of predicted density (individuals/km2) across the survey stratum of: (a) sei whales; and (b) combined sei and unidentified large baleen whales. Coefficients of variation of average predictions: (c) sei whales; and (d) combined sei and unidentified large baleen whales.

206x178mm (600 x 600 DPI)

Supporting Information

Appendix S1. Review of regional and global sei whale abundance estimates

We reviewed available published summer abundance estimates of sei whales (*Balaenoptera borealis*) by geographic region. Table S1 provides a summary of the abundance estimates, Table S2 provides a summary of density estimates by individual stratum, and Figure S1 shows the localities of the areas surveyed. Large-scale sighting surveys have been conducted in many additional potential range areas without recording sufficient sei whale sightings to generate an abundance estimate, for example Greenland (Hansen et al., 2019), European shelf waters (Hammond et al., 2013), the Gulf of Alaska (Rone ,Zerbini, Douglas, Weller, & Clapham, 2017), the Gulf of Mexico (Mullin & Fulling, 2004), and the eastern tropical Pacific (Wade & Gerrodette, 1993). Regional summaries are provided below, followed by a global summary.

NORTH ATLANTIC

North-west Atlantic

Several abundance estimates are available for US and Canadian waters from Florida north to the Labrador Sea (Table S1; Figure S1). However, the estimates span several decades and use differing methods, such that their comparability is questionable. For example, Mitchell and Chapman (1977) used strip census methods, which cannot be readily compared to more rigorous line transect methods. The area covered by Roberts et al. (2016) overlaps with the Mitchell and Chapman (1977) 'Nova Scotia stock.' However, those two estimates cannot be directly compared due to the different methods, and because Roberts et al. (2016) provided a mean density estimate for a 23-year period (1992–2014) which averages out any inter-annual variation in sei whale occurrence. Additionally, the seasonal timing of the surveys may have affected the abundance estimates recorded. For example, Palka (2006) attributed the higher abundance estimate of sei whales off the north-east US coast during 2004 to the timing of the survey several weeks earlier in the summer than in other years, corresponding with a higher occurrence of sei whales in that area during the spring time. Palka et al. (2017) recorded a much higher abundance of sei whales along the eastern US during spring (N = 6,292, CV = 1.02) than summer (N = 1,872, CV = 0.42). To maintain comparability with other regions of the North Atlantic where surveys have occurred during summer, the abundance estimates provided for the north-west Atlantic in Table S1 are limited to the summer period. Similar estimates of 1,519 and 1,872 sei whales have been generated for the waters between Florida and Nova Scotia during summer in the most recently published studies (Roberts et al., 2016; Palka et al., 2017; Figure S1). Additionally, a number of sei whales inhabit the waters from Labrador to west Greenland during the summer. Mitchell and Chapman (1977) reported 965 animals in that area in 1966–1969 using strip census methods. However, the paucity of information on stock structure and movements of sei whales within the North Atlantic make it difficult to evaluate whether some of those animals may also be included in the estimates for the central North Atlantic or the eastern US region. In conclusion, the summer estimate of 1,872 animals (Palka et al., 2017) is adopted for the north-west Atlantic region, but acknowledging that not all parts of the range were included.

Central North Atlantic

A series of large-scale North Atlantic sighting surveys (NASS) were conducted in the central North Atlantic during 1987, 1989, 1995, 2001, 2007 and 2015, primarily to form a scientific basis for managing anthropogenic takes (Pike, Gunnlaugsson, Mikkelsen, Halldórsson, and Víkingsson, 2019a). The methods used (both during the surveys and subsequent analyses), spatial areas covered, and timing of the surveys has varied between years and many resulting estimates have relatively wide confidence limits. In particular, Pike et al. (2019a) noted that most NASS surveys were conducted in late June and July when sei whales were generally still at low abundance in the northernmost parts of their range. However, most of the NASS publications report that when variation in geographic coverage and timing is accounted for between the surveys, then the resulting estimates are broadly comparable between years (Borchers & Burt, 1997; Cattanach, Sigurjónsson, Buckland, and Gunnlaugsson, 1993; Pike et al., 2019a). The 1989 NASS survey may be considered exceptional in extending further south and occurring later in the year than other NASS surveys, and may therefore have been optimal for assessing sei whale abundance in the central North Atlantic (Pike, Gunnlaugsson, Víkingsson, and Mikkelsen, 2011). The only other survey covering such a wide expanse of the central North Atlantic and extending south towards the latitudes favoured by sei whales earlier in the summer was the 2007 T-NASS which included extension areas towards Norway and Canada (Figure S1: Pike et al., 2019b). The abundance estimates from the 1989 and 2007 surveys were 10,300 (Cattanach et al., 1993) and 9,700 (Pike et al., 2019b) animals respectively, and thus approximately 10,000 animals are likely to inhabit the central North Atlantic region during summer.

North-east Atlantic

In European Atlantic (Norway to Portugal) shelf waters, a single sei whale observed during the SCANS-II survey in July 2005 resulted in an abundance estimate of 29 animals (*CV* = 1.0; Hammond et al., 2011). During the July 2007 CODA survey of deep waters from Scotland to north-west Spain, estimates of 366 and 590 animals respectively were generated from two different analyses (Macleod et al., 2009;

Hammond et al., 2011; Table S1). All sei whale sightings during that survey occurred in block 3 off north-west Spain, with none seen further north off the Atlantic seaboards of Ireland or Scotland.

North Atlantic: Conclusions

Using published summer abundance estimates of ~1,900 animals for the north-west Atlantic (Palka et al., 2017), ~10,000 animals in the central Atlantic in 2007 (Pike at al., 2019b) and ~500 animals in the eastern Atlantic in 2007 (Macleod et al., 2009; Hammond et al., 2011), the best available sei whale abundance estimate for the North Atlantic region is approximately 12,400 animals.

NORTH PACIFIC

In the North Pacific (north of 35ºN), summer abundance estimates of 5,086 and 29,362 sei whales have been generated for the areas west and east of 170º respectively (Figure S1: Hakamada & Matsuoka, 2016; Hakamada et al., 2017). Additionally, the averaged abundance estimated from the two most recent surveys (2008 and 2014) of the California Current system along the western US coast was 519 animals (Barlow, 2016). Consequently, the combined available estimates generated during summer over the years 2008–2014 in the North Pacific region indicate approximately 35,000 sei whales.

SOUTHERN HEMISPHERE

Little information on abundance is available for Southern Hemisphere sei whales. In the region south of 30ºS (Figure S1), estimates of 11,237 and 9,718 animals were generated as extrapolated point estimates from Japanese scouting vessel (JSV) data during 1965/66–1977/78 and 1978/79–1987/88 respectively (Butterworth & Geromont, 1995). However, the JSV surveys focussed on the higher-latitude Antarctic regions favoured by more commercially-valuable whale species, rather than the mid-latitude areas favoured by sei whales, and data were extrapolated to the latter regions. The International Whaling Commission (IWC) has not accepted those estimates, and states that current estimates of abundance or of trends in abundance of sei whales in the Southern Hemisphere are not available because their primary distribution occurs north of 60ºS, whereas the waters south of 60ºS were the focus of the IWC's International Decade for Cetacean Research (IDCR) and Southern Ocean Whale Ecosystem Research (SOWER) cruises (IWC, 2017).

GLOBAL ABUNDANCE

The comparability of the published sei whale abundance estimates within and between the regions is limited by the different methods used, low sample sizes (sometimes resulting in high uncertainty), unknown stock structure and spatio-temporal distribution patterns, the wide timeframe (spanning several decades) of the studies, overlapping and inconsistent survey areas, known inter-annual variability in sei whale occurrence, and differing methods for dealing with unidentified whales. However, the best available global summer abundance estimates of sei whales comprise ~12,000 animals in the North Atlantic over a similar period in 2007–2013, ~35,000 animals in the North Pacific over the period 2008–2014, and approximately 10,000 animals in the Southern Hemisphere in 1978/79–1987/88. While the North Atlantic and North Pacific estimates cover similar, relatively short, timeframes and could reasonably be compared, the estimate for the Southern Hemisphere is two decades older and considerably less robust. Additionally, a simple summing of regions to produce a global estimate is almost certainly inappropriate given the lack of information on sei whale stock structure and movements. Nevertheless, those regional estimates currently represent the best available data for sei whales.

Based on similar data and also specifically highlighting the lack of robustness of the datasets given the limitations described above, modelled population trajectories in the IUCN Red List assessment indicate that by 2020 the global population of sei whales may include ~40,000 mature animals and an aged 1+ population of ~80,000 animals (Cooke, 2018; Justin Cooke, pers. comm.).

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TABLE S1. Summary of published global abundance estimates for sei whales. *n*, number of sightings used in the abundance estimate; *N*, abundance; *CV*, coefficient of variation. Survey codes: CODA: Cetacean Offshore Distribution and Abundance in the European Atlantic; NASS=North Atlantic Sightings Survey; SCANS=small cetacean abundance in North Sea and European Atlantic continental shelf waters; T-NASS=Trans-North Atlantic Sightings Survey. Method: SC=shipboard strip census data (minimum counts); LT=line transect (distance sampling); DSM=habitat-based density modelling using distance sampling methodology; JSV=Extrapolated point estimates from Japanese Scouting Vessel data. Only summer estimates are tabulated, in order to maximise comparability between regions. Densities not directly reported in the papers were calculated from the given total survey area and abundance, and converted into standardised units.

Area	**Years**	**Season**	**Method**	***n***	***N***	**Range**	***CV***	**Density (whales/km^2)**	**Source**	**Information**
North-west Atlantic										
Nova Scotia stock (Florida to Nova Scotia)	1966–1969	Summer	SC	25	870	–	–	–	Mitchell and Chapman (1977)	Includes regions 2, 10, 11 and 12 in their Table 4.
Labrador Sea / West Greenland stock	1966–1969	Summer	SC	8	965	–	–	–	Mitchell and Chapman (1977)	Includes regions 5 and 8 in their Table 4.
US east coast (Florida to Nova Scotia)	1992–2014	Jul	DSM	585	1,519	–	0.30	–	Roberts et al. (2016)	
North-east US coast (Gulf of Mexico to Nova Scotia)	1998	Jul–Aug	LT	–	104	–	–	0.0004	Palka (2006)	Information in Table 7.
	2002	Jul–Aug	LT	–	57	–	–	0.0002		
	2004	Jun–Aug	LT	–	301	–	–	0.0011		
US east coast (Florida to Nova Scotia)	2010–2013	Summer	LT/DSM	–	1,872	849–4,129	0.42	–	Palka et al. (2017)	Cooke (2018) reported an abundance of 849 animals from this study, but that was the 2.5% CI.

Area	Years	Season	Method	*n*	*N*	Range	*CV*	Density (whales/km^2)	Source	Information
Central North Atlantic										
Norway, Iceland, Faroes, SE Greenland (NASS-87)	1987	Jun–Jul	LT	22	1,293	434–3,853	0.60	0.0010	Cattanach et al. (1993)	Values from Table 5. Timing and survey coverage in 1987 included only part of the known total stock.
Iceland and SE Greenland (NASS-89)	1989	Jul–Aug	LT	106	10,207	6,048–17,227	0.27	0.0044	Cattanach et al. (1993)	Values from Table 6.
Faroes (NASS-89)	1989	Jul–Aug	LT	1	132	39–443	0.69	0.0002		
Iceland, Faroes, Norway, SE Greenland (NASS-95)	1995	Jul–Aug	LT	–	9,249	3,700–23,116	–	–	Borchers and Burt (1997)	
Iceland, Faroes, SE Greenland (NASS-01)	2001	Jun–Jul	LT	26	1,494	843–2,245	0.24	0.0005	Pike et al. (2011)	Inclusion of lower certainty sei whales increases the estimate to 2,092 animals (CV=0.22).
Iceland, Faroes, SE Greenland to 52°S (core T-NASS 07)	2007	Jun–Aug	LT	40	5,159	1,983–13,423	0.47	0.0021	Pike at al. (2019b)	Extension areas included: (1) the eastern Barents Sea (west of 34°E), north to beyond Bear Island; and (2) a smaller south-west extension towards Canada to 42°S.
T-NASS 07 extension areas	2007	Jun–Aug	LT	14	4,578	1,381–15,172	0.60	0.0030		
Combined T-NASS 07 survey (core plus extension)	2007	Jun–Aug	LT	54	9,737	4,189–19,665	0.38	0.0024		
Iceland, Faroes, SE Greenland (NASS-15)	2015	Jun–Jul	LT	34	3,767	1,156–12,270	0.54	0.0011	Pike et al. (2019a)	69% of the total abundance occurred in stratum IP at the far south-west of the survey area.

Area	Years	Season	Method	*n*	*N*	Range	*CV*	Density (whales/km^2)	Source	Information
North-east Atlantic										
North Sea and European Atlantic shelf from Norway to Portugal (SCANS II)	2005	Jul	LT	1	29	6–152	1.0	0.00002	Hammond et al. (2011)	One sighting in Block P of the SCANS II survey area.
Scotland to NW Spain (offshore: CODA)	2007	Jul	LT	–	366	176–762	0.33	0.0004	Macleod et al. (2009)	Sei whales were recorded only in Block 3 off north-west Spain. The density in just Block 3 was 0.002.
Scotland to NW Spain (offshore: CODA)	2007	Jul	LT	12	590	299–1,164	0.36	0.0006	Hammond et al. (2011)	Reanalysis of Macleod et al. (2009) dataset.
Eastern North Pacific										
Central and eastern Pacific (north of 40°N, south of the Aleutian Islands, and between 170°E and 135°W)	2010–2012	Jul–Aug	LT	162	29,632	18,576–47,267	0.24	0.0042	Hakamada et al. (2017)	IWC-POWER study area. Abundance is the average of two models.
US west coast	2008+2014 (combined)	Jul–Dec	LT	17	519	374–	0.40	0.0005	Barlow (2016)	The geometric mean of both years is provided for the 2008+2014 estimate (Table 11). The value for 2014 (Table 8) was considered unusually high, due to northerly shift of warm water current.
	2014	Aug–Dec	LT	14	864	–	0.40	0.0008		
Western North Pacific										

Area	Years	Season	Method	*n*	*N*	Range	*CV*	Density (whales/km^2)	Source	Information
East of Japanese coast, west of 170°E, north of 35°N, south of Russian and US EEZ	2008	Jul–Aug	LT	68	5,086	1,988–13,623	0.38	0.0018	Hakamada and Matsuoka (2016)	JARPNII survey area.
Southern Hemisphere										
Waters south of 30ºS	1965/66–1977/78	–	JSV	–	11,237	–	–	–	Butterworth and Geromont (1995)	Estimates not accepted by the IWC.
	1978/79–1987/88	–	JSV	–	9,718	–	–	–		

TABLE S2. Summary of published sei whale density estimates for individual survey strata within the large-scale surveys reported in Table S1. Densities not directly reported in the papers were calculated from the given total survey area and abundance, and converted into standardised units. Only density values >0 were tabulated. The data are presented in order of decreasing density.

Area	**Stratum**	**Stratum size (km^2)**	**Year**	**Density (indiv./km^2)**	**Source**
Iceland extension	Extension SW	197,923	2007	2.24E-02	Pike et al. (2019b)
Iceland	60	450,888	1989	1.65E-02	Cattanach et al. (1993)
North-west Atlantic	GOM N	9,862	1998/99	9.53E-03	Palka (2006)
North-west Atlantic	Gom S	24,504	2004	8.16E-03	Palka (2006)
Central and eastern Pacific	2012S	1,815,661	2012	7.68E-03	Hakamada et al. (2017)
Central and eastern Pacific	2010S	1,252,752	2010	4.86E-03	Hakamada et al. (2017)
Iceland	IP	477,607	2015	4.52E-03	Pike et al. (2019a)
Iceland	SC	708,982	2007	4.47E-03	Pike et al. (2019b)
Iceland	70	303,790	1989	3.95E-03	Cattanach et al. (1993)
Iceland	95	238,022	1987	3.69E-03	Cattanach et al. (1993)
Iceland	95	238,022	1989	3.65E-03	Cattanach et al. (1993)
NW Spain	3	162,020	2007	3.64E-03	Hammond et al. (2011)
Iceland	RN	425,243	2007	3.60E-03	Pike et al. (2019b)
North-west Atlantic	Scotian	17,135	2002	3.33E-03	Palka (2006)
Central and eastern Pacific	2011S	1,952,188	2011	3.30E-03	Hakamada et al. (2017)
Western Pacific	7E	48,208	2012	3.28E-03	Hakamada and Matsuoka (2016)
Western Pacific	9	362,113	2009	3.02E-03	Hakamada and Matsuoka (2016)
Iceland	94	158,093	1989	2.64E-03	Cattanach et al. (1993)
Western Pacific	9	499,235	2008	2.41E-03	Hakamada and Matsuoka (2016)
NW Spain	3	162,020	2007	2.26E-03	Macleod et al. (2009)
Western Pacific	9S	290,575	2011	2.18E-03	Hakamada and Matsuoka (2016)
Iceland	93	74,637	1989	1.88E-03	Cattanach et al. (1993)
Iceland	IW	130,011	2015	1.75E-03	Pike et al. (2019a)
North-west Atlantic	GOM C	53,651	2004	1.75E-03	Palka (2006)
Western Pacific	8	162,789	2008	1.63E-03	Hakamada and Matsuoka (2016)
Iceland	RS	314,100	2007	1.46E-03	Pike et al. (2019b)
West US coast	Washington/Oregon	322,237	2014	1.45E-03	Barlow (2016)
Iceland	94	158,093	1987	1.31E-03	Cattanach et al. (1993)
Iceland	IG	322,250	2015	1.13E-03	Pike et al. (2019a)

Area	**Stratum**	**Stratum size (km²)**	**Year**	**Density (indiv./km²)**	**Source**
Western Pacific	8	162,789	2009	1.10E-03	Hakamada and Matsuoka (2016)
Iceland	Faroes	560,316	2001	8.76E-04	Cattanach et al. (1993)
Iceland	36	151,507	1989	8.51E-04	Cattanach et al. (1993)
Iceland	SW	679,070	2001	8.25E-04	Cattanach et al. (1993)
Iceland	2	64,915	1987	8.16E-04	Cattanach et al. (1993)
Iceland	W	514,787	2001	7.47E-04	Cattanach et al. (1993)
Western Pacific	7	166,306	2009	6.38E-04	Hakamada and Matsuoka (2016)
Central and eastern Pacific	2010N	818,468	2010	6.26E-04	Hakamada et al. (2017)
Faroes	FW	606,767	2015	6.20E-04	Pike et al. (2019a)
West US coast	Washington/Oregon	322,237	2008	5.24E-04	Barlow (2016)
West US coast	California	819,570	2014	4.84E-04	Barlow (2016)
North-west Atlantic	Shelf E	21,471	1998/99	4.66E-04	Palka (2006)
Iceland	36	151,507	1987	4.29E-04	Cattanach et al. (1993)
Central and eastern Pacific	2012N	488,511	2012	3.99E-04	Hakamada et al. (2017)
Western Pacific	8	162,789	2011	3.85E-04	Hakamada and Matsuoka (2016)
Iceland	8	199,490	1987	3.66E-04	Cattanach et al. (1993)
North-west Atlantic	Shelf E	21,471	2004	3.26E-04	Palka (2006)
West US coast	Washington/Oregon	322,237	2005	2.95E-04	Barlow (2016)
Western Pacific	7WRS	66,117	2012	2.47E-04	Hakamada and Matsuoka (2016)
Iceland	93	74,637	1987	2.14E-04	Cattanach et al. (1993)
Faroes	10	670,752	1989	1.97E-04	Cattanach et al. (1993)
West US coast	California	819,570	1996	1.83E-04	Barlow (2016)
West US coast	California	819,570	2008	1.74E-04	Barlow (2016)
Iceland	88	205,273	1989	1.61E-04	Cattanach et al. (1993)
European shelf	P	197,400	2005	1.47E-04	Hammond et al. (2011)
Iceland	J	503,088	2001	1.16E-04	Cattanach et al. (1993)
Western Pacific	7	166,306	2008	1.05E-04	Hakamada and Matsuoka (2016)
Iceland extension	Extension NE	1,315,320	2007	1.03E-04	Pike et al. (2019b)
West US coast	California	819,570	1993	9.52E-05	Barlow (2016)
West US coast	California	819,570	2001	5.86E-05	Barlow (2016)
West US coast	California	819,570	2005	5.12E-05	Barlow (2016)

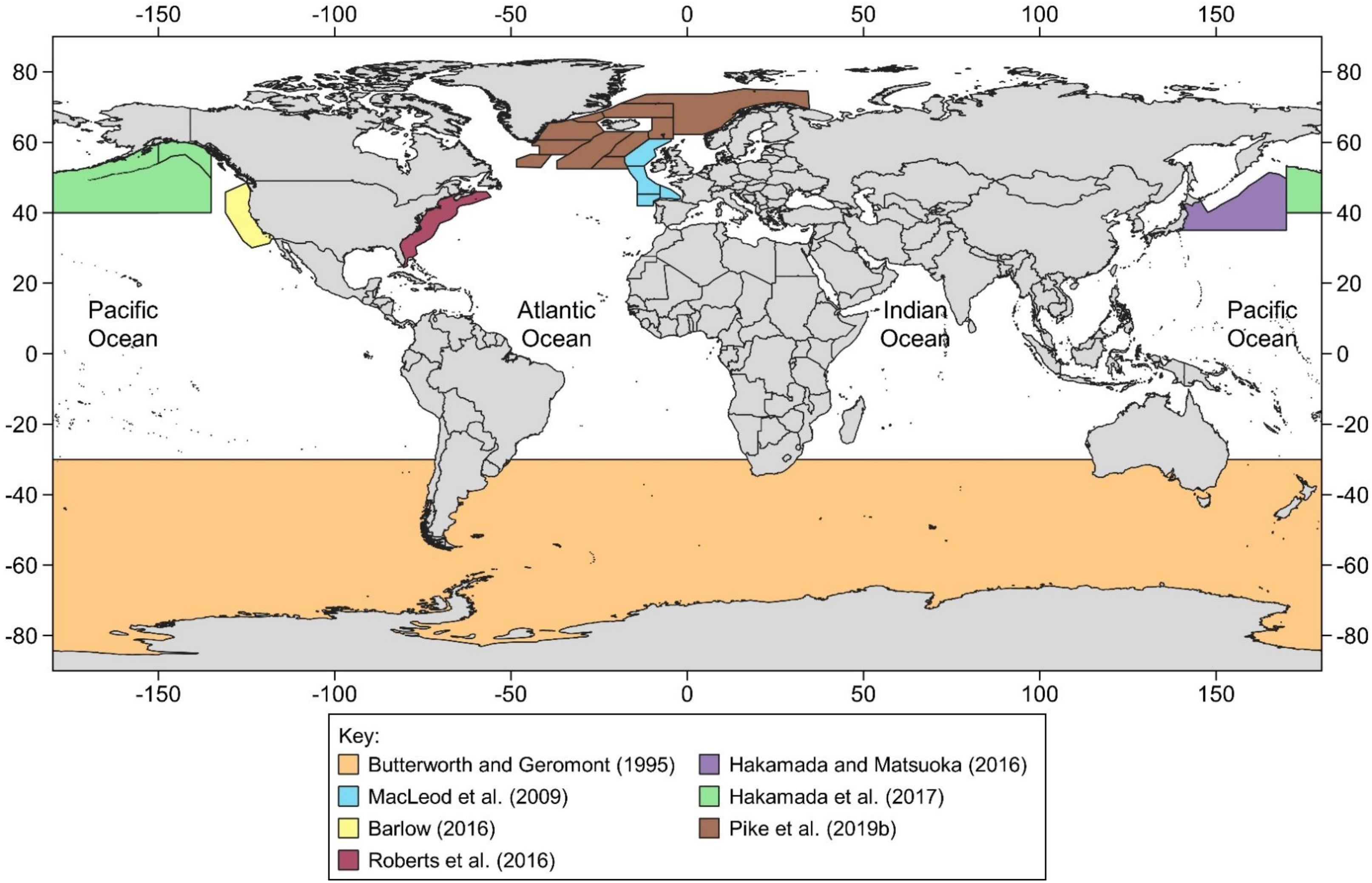

FIGURE S1. Survey areas relating to the global abundance estimates presented in Table S1. Similar areas of the north-west Atlantic were surveyed by Roberts et al. (2016), Palka (2006) and Palka et al. (2017). In the central North Atlantic, the 2007 survey area reported by Pike et al. (2019b) is shown as the most extensive recent estimate for that region.