Upwellings, canyons and whales: An important winter habitat for balaenopterid whales off Mauritania, northwest Africa

MICK E. BAINES AND MAREN REICHELT

Wildscope, 4, Tremola Avenue, Saltdean, Brighton, BN2 8AT, UK

Contact e-mail: mick.baines@wildscope.com

ABSTRACT

The aim of this study was to identify critical habitats for baleen whales in the Mauritanian upwelling zone using data collected from a platform of opportunity: a 60 day geophysical survey approximately 100km southwest of Cap Blanc, Mauritania in winter (2012/13). The bathymetry of the 5,500km^2 study area was complex, including parts of the Cap Timiris Canyon system. Large whales, including sei and blue whales, accounted for 70% of the 238 cetacean sightings. Species identification was often problematic, especially in the case of balaenopterid whales, so data for all whales of this genus were pooled for the estimation of abundance and distribution. Spatial modelling was applied to estimate abundance and to plot a predicted density map of balaenopterid whales. Depth and the chlorophyll-*a* concentration when at its peak (in the previous September) were significant predictors of whale density. Point abundance in the study area was estimated at 272 whales (95% CI 265–279) and density was highest in the depth range 500–2,250m near to the canyon system (6.18 whales/100km^2, 95% CI 6.03–6.51). Steep seabed topography created by canyons running off the shelf edge, together with the strong upwelling system, probably create optimal habitats for the euphausiid prey of sei and blue whales. Sei whales were observed skim-feeding at dawn or dusk on seven occasions; in one sighting an aggregation of 18 skim-feeding sei whales were observed. The high density of these baleen whale species in such a highly productive area and direct observation of feeding behaviour in sei whales, provides evidence of feeding during the winter breeding season, when they have previously been presumed to feed less. This study demonstrates the potential value of collecting further data on seismic survey vessels and would improve understanding of cetacean ecology in remote and under-explored regions.

KEYWORDS: HABITAT; OCEANOGRAPHY; FEEDING GROUNDS; MODELLING; ATLANTIC OCEAN; ABUNDANCE ESTIMATE; SEISMIC SURVEY; SEI WHALE; BLUE WHALE

INTRODUCTION

Upwellings of cold, nutrient-rich ocean water drive high levels of primary productivity, in which zones of high zooplankton density form and provide rich feeding habitats for fish, seabirds and cetaceans (Butler *et al.*, 2002; Croll *et al.*, 2005; Joiris, 2011; Tynan *et al.*, 2005). Off the coast of northwest Africa, the Mauritanian upwelling zone near Cap Blanc is considered exceptionally productive (Hernández-Léon *et al.*, 2007; Peña-Izquierdo *et al.*, 2012; Voituriez and Chuchla, 1978) and of great importance as a feeding ground for both resident and wintering seabirds (Camphuysen and van der Meer, 2005; Wynn and Knefelkamp, 2004; Wynn and Krastel, 2012). Although cetaceans have been recorded during surveys that primarily targeted offshore seabird communities in this region (Camphuysen, 2000; Camphuysen *et al.*, 2012), no dedicated systematic surveys of offshore cetaceans from which density estimates could be obtained have been carried out here to date (Kaschner *et al.*, 2012). The aim of this study is to identify critical habitats for baleen whales off Mauritania using data collected from a platform of opportunity.

The winter distributions of baleen whale species in the northeast Atlantic are poorly understood (Clapham *et al.*, 1999; Prieto *et al.*, 2012a; Reeves *et al.*, 2004; Reilly *et al.*, 2008), largely due to the relatively low levels of offshore survey effort at lower latitudes in the Atlantic. Recent insights have been gained from acoustic monitoring using the SOSUS hydrophone arrays (Charif and Clark, 2009) but logistical difficulties and funding restraints have resulted in limited visual survey effort in offshore waters during the winter months. This paper presents data on cetaceans viewed during a 60 day geophysical survey from November 2012 to January 2013 in a study area of approximately 5,500km^2 straddling the continental shelf edge southwest of Cap Blanc, Mauritania (Fig. 1).

Seismic survey vessels provide a platform of opportunity offering a number of key advantages. Vessels are typically large, with comfortable, high observation platforms. Surveys may last many weeks or months, allowing sustained periods at sea in all seasons of the year, often in remote and relatively unexplored regions of the world that would otherwise be prohibitively expensive to achieve in a vessel dedicated to a cetacean survey. In addition, the systematic survey design, albeit not targeting wildlife, results in the collection of detailed oceanographic data that can potentially provide useful insights into cetacean habitats. However, offshore geophysical surveys use air-guns to produce pulses of low frequency sound, and these have the potential to modify the distribution of cetaceans at the time of the survey and therefore cause bias in the results (Castellote *et al.*, 2012). Issues arising from survey design affect the choice of methods used to analyse the resulting sightings data. Line transect surveys should ideally incorporate some form of random probability sampling, in which transect lines are replicated so that each point within the study area has an equal probability of being sampled (Buckland *et al.*, 2001; Thomas *et al.*, 2007). The systematic design of seismic surveys (see Methods below), which progressively extend coverage across the survey area, give rise to spatio-temporal correlation and can violate the principles of random sampling which are fundamental to conventional analytic methods such as DISTANCE sampling (Buckland *et al.*, 2001).

Spatial modelling provides a statistically robust alternative to conventional line transect analyses and is applicable to

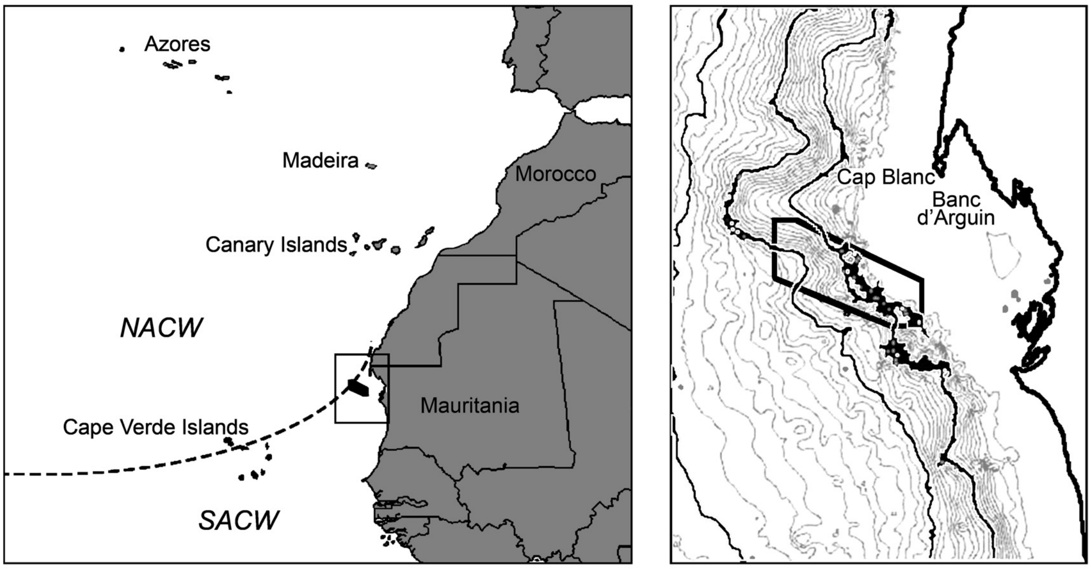

Fig. 1. Map showing the location of the study area off northwest Africa (Fig.1a, left); the dotted line shows the approximate boundary between North Atlantic Central Water (NACW) and South Atlantic Central Water (SACW). The rectangular area off the coast of Mauritania is expanded (Fig.1b, right) to show the location of the polygonal study area in relation to coastal bathymetry. Isobaths are at 100m intervals, with those at 1,000m intervals in bold.

data from platforms of opportunity (Cañadas and Hammond, 2006; Hedley *et al.*, 1999). Model-based abundance estimates have been shown to produce results very similar to those obtained from conventional, design-based line transect data, but with higher precision (Gómez de Segura *et al.*, 2007). There is no requirement to place transect lines randomly, providing coverage is representative of habitats within the region of interest, which is achieved by the comprehensive coverage of a geophysical survey. Spatial models were therefore applied to estimate the abundance and distribution of whales in relation to the undersea topography and oceanography of this highly productive area, and demonstrate that this area supports high densities of baleen whales.

METHODS

Survey design

The survey was designed as a 3D seismic survey, in which closely spaced parallel transect lines were surveyed in a systematic, progressive pattern through the study area (IAGC, 2011), with seismic operations carried out continuously. The survey vessel towed a set of 12 evenly-spaced parallel streamers of 7km in length. The need to maintain the geometry of this configuration required a wide radius when turning. The most efficient survey plan follows a so-called racetrack, in which the survey is conducted in swathes, as illustrated in Fig. 2. However, this survey design results in spatio-temporal correlation as effort moves slowly across the study area. Seismic source activity is confined largely to the straight lines and is turned off through the first part of the turns, with a gradual ramp-up of energy and a so-called soft start being initiated in the final section of each turn, so source activity is spatially correlated. There may also be uneven coverage during daylight hours, depending on the phase relationship between the racetrack and diel cycles; in the survey reported on here, each pair of survey lines took approximately 24 hours to complete, so some contiguous sections of lines were transited at night. The distribution of effort in the turns was also uneven as they were concentrated towards the centre of the swathe at the outer parts of the turns (Fig. 2). Vessel speed averaged approximately four knots, which was slow compared with typical dedicated cetacean surveys, e.g. 10 knots for SCANS surveys (Hammond *et al.*, 2002).

Data collection

Two teams, each of two experienced marine mammal observers (MMOs), took part in the survey changing over approximately at the half-way point. In the first team, Richard Woodcock had 12 years of experience and Peter Tuffy 5 years of experience as MMOs on seismic surveys, and in the second team (the authors) both had 11 years of experience. All four observers had previous experience either as fisheries observers or of cetacean research. Observations were carried out continuously through daylight hours, from a platform with an eye height of 21.5m. Protocols developed by the UK's Joint Nature Conservation Committee (JNCC) specifically for data collection by MMOs on seismic surveys (JNCC, 2010) were followed for data collection and recording. JNCC protocols require a set of environmental variables including sea state, wind force and direction, swell height, glare, visibility and depth to be recorded whenever one of the variables changes, or at least every hour during effort periods. Species identity and group size were recorded for each sighting event, together with an estimate of the bearing and range of the sighting. The closest distances between the animals and the seismic source (whether active or not) and their behaviour during sighting events were also recorded.

Whales were encountered as single individuals, pairs or small coherent groups, or as loose aggregations. When whales were seen in close proximity to one another (the separation criterion was not strictly defined but was approximately <1km), they were considered a single sighting event and the count of whales present in that sighting was estimated by tracking the location and pattern of blows and

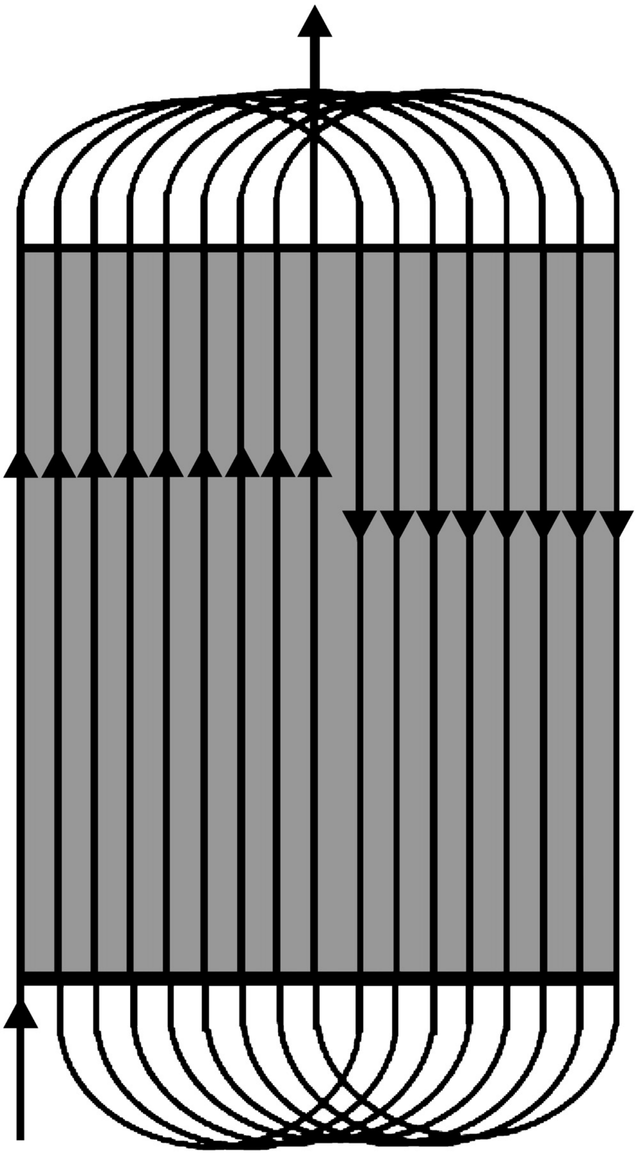

Fig. 2. Diagram showing an idealised racetrack design for a seismic survey. A single swathe is shown, although larger surveys are typically acquired in multiple swathes. Note that as observer effort is maintained through the turns, the area covered by the sighting survey is greater than the geophysical survey area (shaded).

surfacing cues. When higher densities of whales were encountered and it became difficult to track individuals or small groups, counts of all animals in view at one time were recorded as a single sighting.

Without the option to approach a sighting, species identification was often problematic, particularly in the case of balaenopterid whales, when only blows and/or dorsal fins were seen. In order to maximise the data set available for modelling, data for all balaenopterid whales were pooled.

Bathymetry data

A geographical information system (GIS) bathymetry raster layer was developed using the open source software package System for Automated Geoscientific Analyses (SAGA, 2013). Echo-sounder data collected at 25m intervals along survey lines spaced 500m apart were combined with depths recorded by the MMOs during line turns and effort outside the core geophysical survey area. The combined data set was interpolated into a raster grid with cell size of 0.02° latitude and longitude (approximately 2.1 × 2.2km). Inverse distance weighting was used for interpolation because the set of input points was dense enough to capture the extent of variation, and both maximum and minimum values would be retained in a continuous layer, with a smoothed gradation between input points. Approximate positions for sightings were calculated using the range and bearing from the observer's position, depths for sighting positions were then extracted from the bathymetry raster layer and these were used to calculate mean depths for each species or species group.

Analysis of baleen whale data

The initial analysis of the sightings data was carried out using DISTANCE Version 6 (Thomas *et al.*, 2009). Detection probabilities for balaenopterid whales were modelled as smoothed functions of perpendicular distance using both conventional distance sampling (CDS) and multiple covariate distance sampling (MCDS) methods, with sea state, swell height and visibility as potential covariates in the case of MCDS. The Akaike information criterion (AIC) (Akaike, 1973) and coefficient of variation were used to select the best fitting models (Buckland *et al.*, 2001) and to determine which covariates to include. It was assumed that all whales on the trackline were detected, i.e. the probability of detection at 0 distance from the trackline, $g(0) = 1$ (Buckland *et al.*, 2001) and, given the high platform height and slow speed of the vessel, together with the prominent characteristics of whales blows, any change to this assumption was likely to have been minimal. Although the best fitting models were obtained by truncating the data, truncation was not considered desirable in order to maximise the data set available for spatial modelling. Detection functions from half-normal models without truncation were extracted for each of the two observer teams for incorporation in models; a separate detection function was generated for each of the two observer teams in order to account for any potential differences between the two. A table of model selection parameters is provided in the supplementary data file.

Abundance and distribution were estimated using generalised additive models (GAMs) (Hastie and Tibshirani, 1990; Wood, 2006). A single data set was compiled comprising effort and associated sightings. The mean length of each effort record made in the field was 3.7km (SD = 1.3), a length found to perform well in studies using similar methods (Williams *et al.*, 2006). No further partitioning of the data was therefore necessary and the field records were used as the effort segments for input to the modelling process. In the case of effort segments when the vessel was turning, segment length was calculated from the duration of the segment and vessel speed, and not from the straight-line distance between start and end points.

The response variable associated with each effort segment was the count of balaenopterid whales first seen in that segment (Baleen count) rather than the count of groups, in order to account for the different way in which groups were defined in high and low density situations. Modelling counts as the response variable has been found to be highly robust to variation in segment length (Hedley, 2000); unequal segment length was accounted for by including segment length in model offset terms. A set of potential explanatory variables was generated for each segment, comprising the latitude (*Lat*) and longitude (*Lon*) of the mid-point, sea state (*Sea*), wind speed (*Wind*), swell height (*Swell*) and visibility (*Viz*). The mean depths (*Depth*) for each segment were extracted from the GIS bathymetry layer. The depth range within each cell (*Range*) was calculated by creating raster layers for maximum and minimum depth and subtracting one from the other. Seismic source activity (*SSA*) was converted to a Boolean variable (on or off). Observer or observer team identity was considered as a potential variable, but its incorporation in models was rejected due to spatio-temporal correlation; potential differences between the two teams were addressed by incorporating separate detection functions in the model offset term. Sea state and wind speed are strongly correlated, so only one of these terms was used. Sea state was recorded as one of four categories in the JNCC protocol (glassy, slight, choppy, and rough) and assignment to a category was often a matter of subjective judgement, while wind speed was measured on the ship's instruments, so sea state was dropped in favour of wind speed.

Sea surface temperature (SST) and chlorophyll-*a* concentration (mg/m^3) (CHL) were obtained from the NOAA Ocean Color website (NOAA, 2014) as monthly composite data at a resolution of 4km. Chlorophyll-*a* provides a measure of primary productivity, but as balaenopterid whales feed on zooplankton or small schooling fish, a time lag might be expected between the time of peak primary production and the peak time of prey availability for whales. Chlorophyll-*a* concentrations within the study area were therefore summed for each month in the six month period August 2012 to January 2013 using the formula:

$$CHL_{total} = \sum_{n} \left(\frac{CHL_n \mathrm{A}_n}{10^9} \right)$$

Where CHL_{total} is the total estimated weight of chlorophyll-*a* in metric tons, CHL_n is the chlorophyll-*a* concentration in the nth cell and A_n is the area of the cell in m^2. The results were plotted (Fig. 3) to determine the month of peak primary production, and values from that month (September) were extracted as a potential explanatory variable (CHL_{peak}) in addition to the chlorophyll-*a* values for the concurrent month (*CHL*).

Animal density can be expressed as counts per unit area, so counts can be modelled, providing that an offset term representing the area effectively searched is included, and the fitted model may then be used to predict density (Hedley *et al.*, 1999). The offset term representing the estimated area surveyed in each effort segment was calculated as:

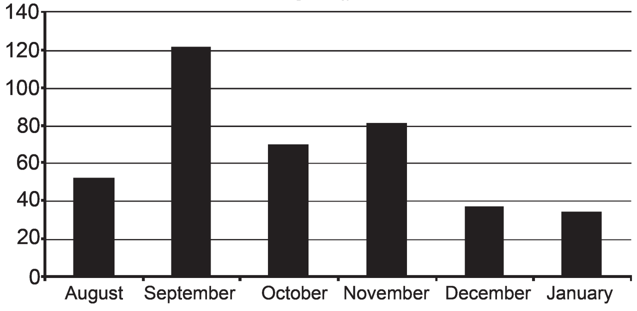

Fig. 3. Estimated monthly quantities (metric tons) of chlorophyll-*a* in the study area from August 2012 to January 2013.

$$Offset = \log\left(\frac{2l_i}{f(0)} \right)$$

Where l_i is the length of the segment and $f(0)$ is the estimated probability density function evaluated at zero perpendicular distance. The general structure of the model incorporating the offset term was:

$$\widehat{N}_i = \exp\left[\log\left(\frac{2l_i}{f(0)} \right) + \theta_0 + \sum_k f_k(z_{ik}) \right]$$

where θ_0 is the intercept, f_k represents smoothed functions of explanatory covariates, and z_{ik} is the k^{th} covariate in i^{th} the effort segment.

Whale sightings tended to be clustered rather than randomly distributed, so a Poisson error distribution was inappropriate due to over-dispersion, and a quasi-likelihood error distribution was assumed, in which variance is proportional to the mean. A GAM was developed using the mgcv package in program R (Wood, 2006), with a 'quasipoisson' family and log link. The model fitting process was guided by minimising the GCV score, maximising the deviance explained, examination of residual plots, and comparison of predicted density with plots of actual sighting positions.

Explanatory variables in a GAM can be multi-dimensional, and models with Lat and Lon as one-dimensional variables were compared with models in which these were combined as a two-dimensional variable [Lat, Lon]. The flexibility of a smooth term in the GAM is determined by the number of knots in the thin-plate regression spline, which for a one-dimensional variable is set by default to 10. If the degrees of freedom of a variable approached nine, the number of knots for that variable were increased. Non-significant terms were dropped unless it increased the GCV score. The argument *gamma = 1.4* was passed to the model as an *ad hoc* method of avoiding overfitting (Wood, 2006).

A data frame was then constructed based on a raster grid with a cell size of 0.02 minutes latitude and longitude, and the mgcv *predict.gam* function applied to estimate the predicted count of whales per cell. The values for each cell were summed to obtain an overall abundance estimate and the values plotted as a GIS raster layer of predicted whale density.

Variance was estimated using a jackknife method, which has been shown to perform well with spatially modelled estimates (Hedley, 2000). Survey day was used as the resampling unit. The data from three randomly selected days were removed and an abundance estimate generated from the GAM. This was repeated using a function written in *R* to produce a set of 300 estimates. The distribution of abundance estimates cannot include negative values and is positively skewed, so a log-normal distribution was assumed for the calculation of 95% confidence intervals using a modified version of the Cox method (Zhou and Gao, 1997).

RESULTS

Bathymetry

The bathymetry of the study area is illustrated in Fig. 4 as a three-dimensional image, as an aid to the interpretation of

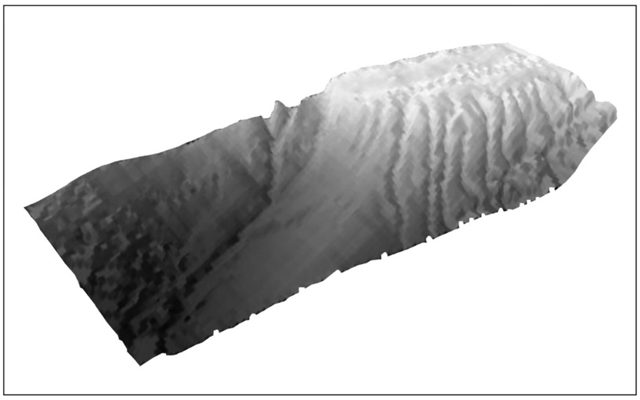

Fig. 4. Bathymetry of the study area displayed as a 3D shaded relief plot with a view-point from the southwest. A series of deeply incised channels run down the southwest face of the continental shelf and a canyon extends from approximately the mid-point of the north side to the southwest corner of the study area.

the two-dimensional plots. Sea bed topography was both varied and complex. The continental shelf extended into the northeast of the study area as a level plain with a depth of less than 100m. Along its southern and southwestern face, the shelf edge was dissected by a series of incised, dendritic channels. A canyon feature ran down the northwest face of the shelf edge, then turned westwards extending across to the south-western border of the study area at a depth of a little over 2,000m. In its upper reaches, the canyon was divided into three main tributary canyons, separated by ridges and terraces.

Upwellings and primary productivity

The extent of the northwest African upwelling system through an annual cycle from June 2012 to May 2013 is illustrated in a set of plots of monthly composite SST values provided in the supplementary data file. The upwellings appeared throughout the year as regions of cooler water extending from Mauritania through Western Sahara to the middle latitudes of Morocco. The area of upwelling reached its greatest extent in northern Mauritania and southern Western Sahara between December 2012 and February 2013, coinciding with the period of the survey. The supplementary file also includes higher resolution plots of SST values in the near vicinity of the study area for the three months of the survey, and chlorophyll-*a* concentrations for the six months (August 2012 to January 2013).

Survey effort

In some 680 hours of observation between 15 November 2012 and 14 January 2013, a total of 2,838km of effort was recorded, which is equivalent to an overall mean of 0.52km of transect effort for each km^2 of the study area. Note however, that observer effort was not evenly distributed through the study area (Fig. 5), in part because some sets of adjacent transect lines were surveyed at night. The division of the survey into two swathes is also apparent in this figure, with the change in observer teams coinciding with the swathe change.

Viewing conditions varied predominantly due to the prevailing northeasterly winds. Wind speeds were Beaufort force 4 or less for 56% of the total effort time and swells were classed as moderate (2–4m) for 61% of the time. There was no fog or precipitation, but wind-blown sand reduced visibility to moderate (1–5km) or poor (<1km) for 12% of effort time.

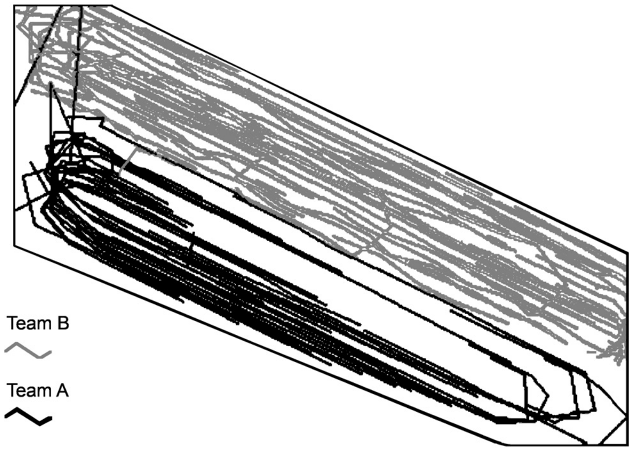

Fig. 5. Plot showing the distribution of realised effort lines within the study area. The gaps in coverage represent areas surveyed at night when no observations could be carried out. Note that effort during turns between transect lines are represented by straight lines connecting points at which an effort record was made, whereas in fact the vessel track followed smooth curves. Effort by the two teams is depicted in different line weights.

Sightings

A total of 236 cetacean sighting events were recorded and 15 species identified (see supplementary data file for a summary of all sightings). Large whales accounted for 70% of sightings, although short-beaked common dolphins (*Delphinus delphis*) were more abundant, being encountered in groups of up to an estimated 500 individuals. Sightings of balaenopterid whales are summarised in Table 1.

The identification to species level of whales of the genus Balaenoptera was frequently impossible, so a conservative approach was taken for species identification. When blows were the only feature seen and they could be distinguished from the blows of sperm whales (*Physeter macrocephalus*), sightings were recorded as unidentified baleen whales. When dorsal fins and the backs of surfacing whales could be seen, it was frequently only possible to assign sightings to a two-species category, Bryde's whale (*Balaenoptera edeni*) or sei whale (*B. borealis*). On seven occasions, all at dawn or dusk, medium-sized balaenopterids were observed and photographed skim-feeding, with their rostra held raised above the surface of the sea for extended periods; their smooth rostra which lacked lateral ridges and had distinctive down-curved tips, positively identified these animals as sei whales. The largest single aggregation of skim feeding sei whales encountered was a count of 18 at dusk on 4 January 2013, when whales appeared to converge on the survey vessel from both sides as darkness fell. Some of these animals came to within a few metres of the ship, despite the fact that the seismic source was active. On no occasion was the potentially sympatric Bryde's whale specifically identified. A z-test found no significant difference between the mean depths at which positively identified sei whales (1,233m), sei/Bryde's whales (1,373m, $p = 0.62$), and unidentified baleen whales (1,255m, $p = 0.94$) were recorded.

Table 1

Summary of balaenopterid sightings.

Species	Sightings (n)	Group size			Depth (m)		
		Mean	Min	Max	Mean	Min	Max
Blue whale	8	1.25	1	2	772	45	1,556
Fin whale	1	2	2	2	856	856	856
Sei whale	7	5.3	1	18	1,233	43	2,123
Sei/Bryde's whale	51	2.3	1	25	1,373	43	2,220
Unidentified balaenopterid	75	2.4	1	25	1,260	47	2,245

Blue whales (*B. musculus*) were identified on eight occasions, with a total count of ten animals. At least two of the unidentified baleen whale sightings had blow characteristics suggesting the likelihood that they were also of this species, but only those sightings in which the characteristic small dorsal fin and body colour could be distinguished were recorded as blue whales. Fin whales (*B. physalus*) were identified on one occasion, when two individuals were seen together.

The question of whether sightings of whales were affected by source activity was initially addressed by comparing sighting rates when the source was and was not active. There were 32 sightings of balaenopterids during 204 hours of observation while the source was inactive (0.16/hour), and 106 sightings in 436 hours when the source was active (0.24/hour). A chi^2 test with Yates' correction indicated that the higher sighting rate while the source was active was statistically significant (chi^2 = 18.35, $df = 1$, $P < 0.01$). However, this result reflects the spatial bias in source activity, as the region in which most balaenopterid sightings were made coincided with the area over which the source was always active. A second approach was therefore taken, by comparing the closest distance that animals came to the seismic source, with the null hypothesis being that if their distribution was not changed by an avoidance reaction when the source was active, there would be no significant difference in the closest range to an active or inactive source. In fact, the mean approach distance was closer when the source was active (1,931m) compared to when it was inactive (2,233m), although a t-test indicated that this difference was not significant ($t = 1.02$, $P = 0.31$).

Model predictions

The best fitting GAM, in which the deviance explained was 43%, took the form:

$$Baleen\_count \sim offset(Offset) + s(Lat, Lon) + s(Depth) + s(CHL_{peak}) + Month + Wind + Viz$$

In which Lat and Lon were combined as a two-dimensional variable, and Month, Wind and Viz were included as linear terms. The most significant environmental predictors of whale density were Lat, Lon ($p < 0.01$), CHL$_{peak}$ ($p < 0.01$) and Depth ($p = 0.02$).

Balaenopterid sightings were made throughout the study area (Fig. 6), but the largest aggregations were to the north of the canyon, and 93% of sightings were encountered at depths of between 500 and 2,250m. The density of baleen whales predicted by the GAM in the study area as a whole was 4.97 whales/100km^2 (95% CI 4.84–5.09), but the density in the depth band 500–2,250m was 6.18 whales/100km^2 (95% CI 6.03–6.51). The point estimate of balaenopterid abundance in the study area was 272 individuals (95% CI 265–279). The plot of predicted density for January 2013 (Fig. 7) shows the main concentration of whales located close to the north side of the main canyon's upper reaches and extending from there to the northwest.

Observations of dead whales

During the course of the survey, dead whales were observed floating on the surface on two occasions. These were both of mysticete whales, one of which could not be identified, the other being a medium-sized balaenopterid, probably a sei/Bryde's whale. The latter had suffered massive traumatic injuries consistent with the possibility of ship strike, although it could not be ascertained whether these had been inflicted pre or post mortem. Both whales were observed in deeper water in the vicinity of the main north–south shipping lane.

DISCUSSION

Factors affecting the reliability of estimates

The high density of effort in this survey resulted in a relatively high degree of precision in the model-based abundance estimate. However, the systematic design and slow progress of the survey resulted in spatial and temporal correlation of effort. The survey was divided into two swathes, with the swathe change coinciding with crew change. Count rates of whales were 3.6 times higher in the second, more northerly swathe ($n = 284$, rate = 0.18 whales/km) compared with the earlier surveyed southern section ($n = 65$, rate = 0.05 whales/km). Because there was no overlap in space or time, it was not possible to determine whether this difference in sighting rates was due to there being more suitable habitat in the area covered by the second swathe, or an influx of animals part way through the survey, or perhaps both these factors. There may also have been differences in observer efficiency between the two teams, although separate detection functions for the two teams were applied in an effort to account for this.

It is possible that some whales reacted to the survey by moving away before being visually detected. It should therefore be borne in mind that the estimates presented here represent the abundance and distribution of whales during the operation of a seismic survey, which may conceivably differ from results that might have been obtained had there not been such a survey in progress at the time. Behavioural responses, such as changes in direction, were observed on some occasions when animals came close (<1km) to the

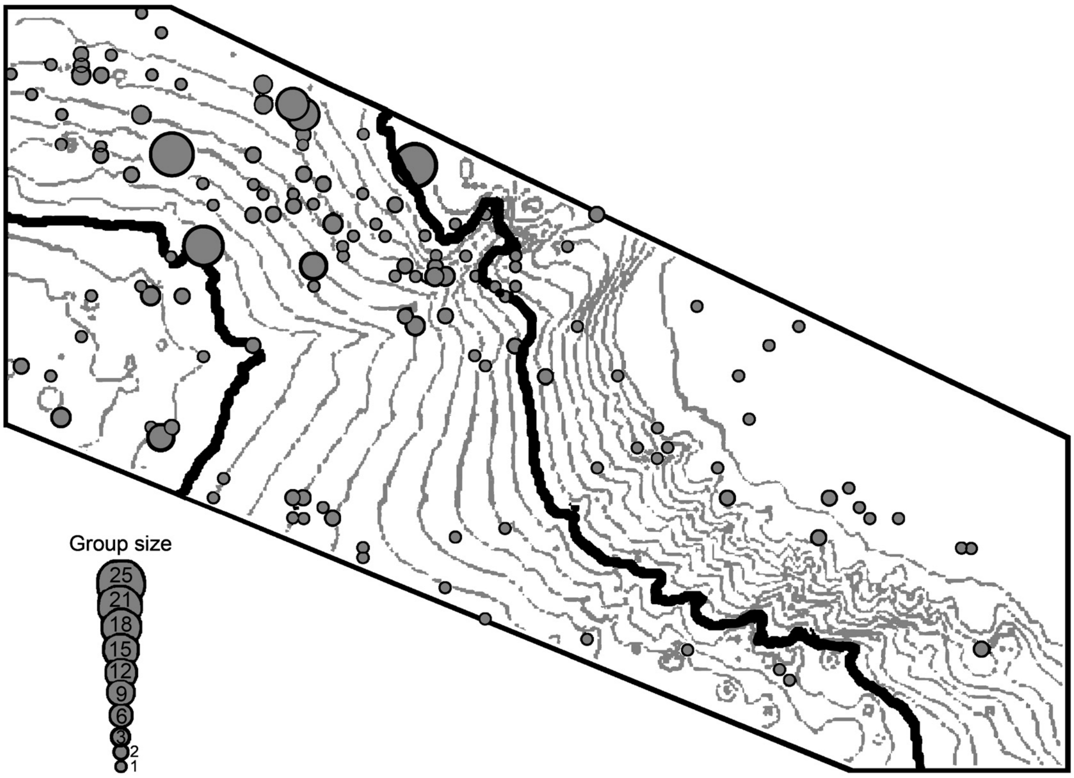

Fig. 6. Balaenopterid sighting positions. Isobaths are at 100m intervals, with those at 1,000m intervals in bold.

active source, but no evidence of avoidance reactions by whales was found within the data.

Potential errors in the estimation of group size were not addressed and this may have led to errors in density estimates that were not taken into account. Counts of small groups were probably less prone to error than counts when larger numbers of whales were in view at one time, although there were occasions when two animals swam together in such close proximity that the presence of a second animal was only discovered when photographs were later examined. There was greater scope for error when high densities of whales were encountered and it became difficult to track individual animals. However, a conservative approach to group size estimation was adopted, so any errors are likely to have resulted in an underestimate of abundance.

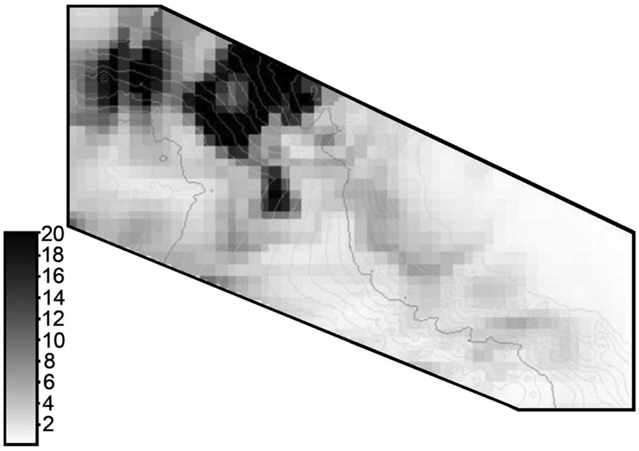

Fig. 7. Plot of the predicted density of balaenopterid whales (count/100km^2) for January 2013.

There was typically only one observer on watch at any one time during the survey, with a maximum of two for short periods of time, and this may have resulted in reduced observer efficiency. Each of the factors discussed above and the assumption that g(0) = 1, had the potential to bias abundance estimates downwards, so the results given here are probably conservative and should be regarded as minimum values.

Oceanographic characteristics of the study area

The Mauritanian upwellings occur where the southward flow of North Atlantic Central Water meets the northward flowing, less saline and nutrient-rich South Atlantic Central Water, over which strong northeasterly winds drive warmer surface waters (Peña-Izquierdo *et al.*, 2012). The upwellings off Cap Blanc are persistent throughout the year, but are strongest from November to February (Mittelstaedt, 1991) and show considerable inter-annual variability (Demarcq, 1998). In the period 1987–2006, the upwelling system off northwest Africa has intensified, and upwelled waters off Cap Blanc have increased their offshore spreading (Marcello *et al.*, 2011). The mixing of nutrient-rich cold water with the warmer surface water in the presence of strong sunlight creates optimal conditions for the primary production of phytoplankton and thence the secondary production of zooplankton. The cetacean data presented here were collected during the main upwelling season between November and January, which coincides with the time of year when northeast Atlantic populations of those balaenopterid species that feed predominantly on zooplankton, i.e. blue and sei whales, are thought to have migrated southwards. This is the whales' breeding season when they have been presumed to feed little, but their high density in this very productive area, and direct observation of feeding in the case of sei whales, suggests that they aggregate here in order to take advantage of a locally abundant food supply.

Submarine canyons worldwide have been shown to create attractive habitats for a range of cetacean species, in the case of baleen whales this is thought to be by a process of enrichment and concentration of prey (Moors-Murphy, 2014). The canyon feature running through the study area and the series of channels incised into the shelf edge appear to form part of the recently discovered Cap Timiris Canyon system (Krastel *et al.*, 2006). The canyon is thought to have been created originally by a major terrestrial river system during an era when glaciation had reduced sea levels (Antobreh and Krastel, 2006). The region is now extremely arid and there are no significant fluvial inputs from the Sahara Desert. Although sediment transport from rivers has now ceased, the predominantly northeasterly Harmattan winds carry large quantities of aeolian sand that precipitates into the sea. This was a prominent feature during the survey, as fine sand was continuously deposited on the open decks of the ship. The appearance of the canyon, which has a V-shaped cross-section and a sparse pattern of sedimentation, indicates that it remains active; this activity is thought to be caused by the erosive action of ocean currents carrying sediments through the canyon in the reverse direction to the original fluvial currents (Antobreh and Krastel, 2006; Krastel *et al.*, 2006). The complex bathymetry formed by the various canyon features of the Cap Timiris system creates a diversity of habitats and shapes local patterns of current flow and upwellings, contributing to the creation of hot-spots of primary productivity and biodiversity.

Sei whale

The winter distribution of sei whales in the northeast Atlantic is poorly understood. Few sightings have been reported from northwest Africa and there are no historic estimates of abundance that can be compared with those reported here. Until now, the best indication of the winter distribution of sei whales has come from records kept by whalers, although these data are bedevilled by confusion between sei and Bryde's whales (Horwood, 1987; Prieto *et al.*, 2012a). In the period 1976–79, the unregulated whaling boat *Sierra*, together with associated vessels, tended to hunt in the region 18–22°N, 20–25°W from November to May, targeting balaenopterids, including sei whales (Best, 1992).

Relatively high levels of survey effort have been carried out in the Canary Islands, but sei whales have only occasionally been reported, with small numbers seen between autumn and early spring, which is during their migration (Carrillo *et al.*, 2010). A survey conducted by the International Fund for Animal Welfare (IFAW) in April 2005 between the latitudes of 20°N and 37°N, found only one sei whale in off-shelf waters (Boisseau *et al.*, 2010), while a survey of coastal waters of southern Morocco in 1996 failed to find any live whales, although a newborn Bryde's whale was found stranded (Notarbartolo di Sciara *et al.*, 1998). A sighting of a single whale during a seabird and cetacean survey off Mauritania for an environmental impact assessment of the Chinguetti oilfield in March 2003 was recorded as a sei whale (Anon, 2003), although no details were given to positively distinguish the sighting from the sympatric Bryde's whale. In April 2001, at least two sei whales were sighted off Mauritania by a touristic expedition vessel, the species identification was confirmed by Prieto *et al.* (2012a). While balaenopterid whales have been recorded during seabird surveys off Mauritania (Camphuysen, 2000; Camphuysen *et al.*, 2012) sei whales have not been specifically identified. Sightings of sei whales further south in the Gulf of Guinea appear to be extremely rare (Weir, 2010).

A total of 33 sei whales were identified in seven sighting events during the survey reported on here. Based on their observed behaviour and blow characteristics, together with the localisation of sightings within a similar depth range, the opinion of the observers was that a high proportion of the medium sized rorquals encountered during this survey and not identified to species level, were probably also sei whales.

The paucity of sei whale sightings previously reported from the wider region highlights the significance of the results presented here for the identification of important areas for this species in winter. The main concentration of whales was found immediately north of the canyon feature, off the outer edge of the continental slope in waters of 500–2,250m depth. Similar habitats in terms of circulation patterns, upwellings and canyon features occur along the entire outer shelf edge of Mauritania (Krastel *et al.*, 2006; Peña-Izquierdo *et al.*, 2012), an area that has recently been found to be of prime importance for both resident and wintering seabirds (Camphuysen and van der Meer, 2005; Wynn and Knefelkamp, 2004; Wynn and Krastel, 2012). It is therefore possible that an area of importance for sei whales in winter may extend throughout the entire outer shelf region of Mauritania, and may perhaps include much of offshore Western Sahara into which the upwelling system extends.

Sei whales that summer in the northeast Atlantic off Scotland, Norway and Iceland are thought to move south to winter somewhere to the south of the Iberian peninsula or off northwest Africa. However, recent studies using satellite tags (Prieto *et al.*, 2012b) have shown that sei whales seen on migration off the Azores in spring, move to summer feeding grounds in the Labrador Sea, while a single animal tagged in autumn moved southeast from the Azores and was last recorded between Madeira and the Canary Islands. This raises the possibility that sei whales wintering off Mauritania may belong to either or both northwest and northeast Atlantic 'stocks'.

North Atlantic sei whales appear to be stenophagous, feeding exclusively on copepods and euphausiids, typically by skim-feeding at the surface (Brodie and Vikingsson, 2009; Prieto *et al.*, 2012a). The concentration of sei whales in such a productive area, together with direct observations of skim-feeding behaviour, provides evidence of feeding during the winter breeding season, when feeding was thought to be uncommon. The sensory systems used by balaenopterids to detect their prey are not well understood. There is no evidence to suggest they detect prey acoustically, in the manner of echo-locating odontocetes. Indeed, sei whale vocalisations show a diel pattern, with increased rates of vocalisation during the day, perhaps in a social context, and reduced rates during the night when they mainly feed (Baumgartner and Fratantoni, 2008). Right whales may use sensory hairs to detect zooplankton density (Kenney *et al.*, 2001), but it appears most likely that sei whales use available light to visually locate high-density patches of zooplankton. This could explain the circumstances of the sighting made at dusk on 4 January 2013 when an estimated 18 skim-feeding sei whales appeared to be attracted to the survey vessel, approaching to within a few metres of the ship from either side. The vessel was well lit at night, with floodlights illuminating the working areas on the back deck and spotlights directed at the towed equipment. It seems likely that either their prey was attracted by the vessel's lights, or the whales were attracted by the lights which assisted their location of zooplankton swarms, or both.

Bryde's whale

The taxonomy of Bryde's whales remains unresolved and there may be more than one species in the African Atlantic; in southern Africa a smaller inshore type found in neritic habitats has been distinguished from the 'ordinary' type found further offshore (Best, 1977; Best, 2001). Little is known about the Bryde's whales of the northeast Atlantic, and we assume that any occurring within the present study area belong to the offshore type, *Balaenoptera edeni*.

In contrast to the stenophagous behaviour of sei whales, Bryde's whales tend to be more catholic, targeting a range of prey species including small schooling fish, squid and euphasiids (Pauly *et al.*, 1998; Tershy *et al.*, 1993). Analysis of stomach contents recorded by whaling vessels off southern Africa showed a seasonal variation in prey type, with 'shrimps', presumed to be *euphausiids*, being unimportant in the (austral) autumn and winter, becoming increasingly important in spring and predominating in summer (Best, 2001). However, this may simply reflect seasonal changes in prey availability rather than any seasonal change in dietary preference.

A marked seasonal change in the distribution of the southern African offshore Bryde's whales has been reported on the basis of whaling records and a single marked individual, the whales moving north towards equatorial waters in winter, when they were absent from the southwest African whaling grounds (Best, 2001). A similar movement towards equatorial waters in winter has been reported for northwest Pacific Bryde's whales (Kishiro, 1996). By analogy, it might be expected that equivalent movements take place in the northeast Atlantic, in which case they would likely be absent from the more northern parts of their range in winter, when this survey was carried out. However, the distribution and seasonal movements of this species in the northeast Atlantic remain unclear. Whaling records cite catches of Bryde's whales off southern Spain in the 20th century (Sanpera and Aguilar, 1992), but the species identification was probably unreliable due to confusion between Bryde's and sei whales. A juvenile Bryde's whale was found stranded near Dakar, Senegal, in late March 1955 and sightings have been reported recently from the Azores in summer (Silva *et al.*, 2014; Steiner *et al.*, 2007). Mauritania therefore lies within the range of this species, but the seasonality of their occurrence here remains obscure.

The identification of Bryde's whales at sea depends on seeing the diagnostic lateral ridges on the rostrum, and this is problematic without a close approach in good viewing conditions (Gendron and Rosales, 1996). So although this species was not positively identified during the survey, its presence among those sightings recorded as Bryde's/Sei whales cannot be discounted.

Blue whale

Blue whales are stenophagous, feeding almost entirely on euphausiids, and populations that summer in higher latitudes are thought to migrate to lower latitudes in winter when their prey becomes unavailable (Clapham *et al.*, 1999). However, the population structure of blue whales is complex and it is possible that not all animals make seasonal migrations. There is evidence of year-round occurrence in some tropical waters, e.g. in the eastern tropical Pacific (Reilly and Thayer, 1990), and of some whales remaining at higher latitudes at least in the early part of winter (Charif and Clark, 2009). Migratory behaviour may also vary with sex and age class. Knowledge of blue whale ecology and status remains limited and the winter distribution of blue whales in the North Atlantic is poorly understood (Clapham *et al.*, 1999; Reeves *et al.*, 2004; Reilly *et al.*, 2008). Surveys at different times of year would be needed to establish the seasonality of blue whale presence in Mauritania, but from the geographic location alone, it would appear possible that these whales belong to the same population that migrates west of the British Isles and inhabits Icelandic and Norwegian waters in summer. Further evidence in support of this link comes from photo-identification studies: a blue whale encountered off Mauritania in March 2005 was matched with photographs of the same individual taken off Iceland in July of both 1997 and 1999 (Sears *et al.*, 2005).

Blue whales are the largest animal ever to have existed and their energetic demands and therefore prey requirements are correspondingly large (Rice, 1978). The conventional view that blue whales feed primarily in their high latitude summer habitats and that they fast in their low latitude calving areas has been modified in the light of subsequent studies (Reilly and Thayer, 1990). Blue whales have been found feeding in highly productive, lower latitude upwelling zones during the winter in several regions of the Pacific, e.g. in Chile (Hucke-Gaete *et al.*, 2004), Monterey Bay, California (Fiedler *et al.*, 1998), Australia (Gill, 2002) and New Zealand (Torres, 2013). In Monterey Bay, the distribution of blue whales has been found to be closely associated with the edges of a submarine canyon in an area of upwelling (Croll *et al.*, 2005; Schoenherr, 1991), a habitat with similar oceanographic characteristics to our study area in Mauritania. Euphausiids and copepods undertake a diel vertical migration to avoid visual predation by day (Lampert, 1993), feeding at night on phytoplankton in the upper water column. Optimal habitats for these zooplankton species are therefore found in upwelling zones with high primary productivity, over deep bathymetry that facilitates predator avoidance. Croll *et al.* (2005) suggest that topographic breaks created by the Monterey Submarine Canyon edge form just such optimal habitats for euphausiids by providing water depths of 1,000m or more, close to highly productive, recently upwelled, near-shore waters. A similar situation occurs in Mauritania, where canyon features close to the shelf edge are associated with a highly productive upwelling zone, and these topographic features may form an important contributory factor in creating optimal habitats for zooplankton, that in turn attract both blue and sei whales.

CONCLUSIONS

This study highlights the potential value of data collected by trained and experienced observers on seismic survey vessels in furthering our understanding of cetacean ecology in remote and under-explored regions. The importance of Mauritania's offshore habitats for wintering seabirds has become recognised in recent years; the findings presented here suggest the area is also important for balaenopterid whales, particularly sei and blue whales. The winter distribution of both sei and blue whales in the northeast Atlantic has so far been shrouded in mystery, and both species are classified as endangered in the IUCN Red List of Threatened Species (Reilly *et al.*, 2008). Relatively high densities of whales were recorded in the outer margins of the continental shelf edge, but the extent of this high density area and the regularity and seasonality of its use needs to be established by further research in order to inform management of potential impacts, particularly in the light of the nascent offshore hydrocarbon industry in the region.

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