Vol. 459: 121–134, 2012
doi: 10.3354/meps09737

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 12

Basking sharks in the northeast Atlantic: spatio-temporal trends from sightings in UK waters

Matthew J. Witt[1,2,*], Tom Hardy[3], Louise Johnson[4], Catherine M. McClellan[2], Stephen K. Pikesley[2], Sue Ranger[2,5], Peter B. Richardson[5], Jean-Luc Solandt[5], Colin Speedie[4], Ruth Williams[3], Brendan J. Godley[2]

[1]Environment and Sustainability Institute, University of Exeter, Cornwall Campus, Penryn TR10 9EZ, UK
[2]Centre for Ecology and Conservation, University of Exeter, Cornwall Campus, Penryn TR 10 9EZ, UK
[3]Cornwall Wildlife Trust, Allet, Cornwall, UK
[4]Wave Action, 3 Beacon Cottages, Falmouth TR11 2LZ, UK
[5]Marine Conservation Society, Ross on Wye HR9 5NB, UK

ABSTRACT: Basking sharks *Cetorhinus maximus* have undergone widespread historic exploitation in the northeast Atlantic and are of conservation concern. A greater knowledge of their spatial and temporal habitat use is required to better inform subsequent monitoring and management strategies. Techniques such as light-based geolocation have provided great insights into individual movements, but currently available data do not permit extrapolation to the population level. Public recording schemes may, however, help to fill shortfalls in data gathering, especially when analysed in conjunction with data from these other techniques. We analysed 11 781 records (from 1988 to 2008) from 2 public recording databases operating in the UK. We describe 3 sightings hotspots: western Scotland, Isle of Man and southwest England, and highlight the marked seasonality of basking shark sightings, which were at their greatest during the northeast Atlantic summer (June to August). We further highlight a significant correlation between the duration of the sightings season in each year and the North Atlantic Oscillation, an atmosphere–ocean climate oscillation that has been linked to forcing of marine ecosystems. We augment patterns from public sightings records with effort-related data collected by boat-based transects at 2 regional sightings hotspots (western Scotland and southwest England). Analysis of reported body size data indicated that the annual proportion of small sharks (<4 m length) sighted by the public decreased, the proportion of medium-sized sharks sighted (4–6 m) increased, and the proportion of large sharks sighted (>6 m) remained constant. These patterns may be indicative of a population recovery following systematic harvesting in the 20th century.

KEY WORDS: Basking shark · *Cetorhinus maximus* · Public sightings · Citizen-science · Marine vertebrates · Conservation

INTRODUCTION

Gaining knowledge on the ecology of large marine vertebrates is complex due to the logistically challenging nature of gathering observations in the habitats they occupy. These species often spend only small amounts of time at or near the surface, decreasing the periods during which they can be observed and recorded using visual surveying methods. Evolving biotelemetry techniques (Wilson et al. 2008), where electronic tags gather information on an individual's location and sometimes behaviour, have advanced our knowledge of marine vertebrates, their physiology, behaviour and ecology (Cooke 2008). While the number and diversity of species instrumented with biotelemetry technology is increasing

*Email: m.j.witt@exeter.ac.uk

(see Hammerschlag et al. 2011 and Godley et al. 2008 for examples of taxon-specific reviews), the method can only provide information at the level of the individual, and scaling observed behaviours to infer population level insights is complex. However, with comprehensive coverage and large sample sizes (Hawkes et al. 2011), or by synthesizing data from multiple taxa (Burger & Shaffer 2008, Block et al. 2011), such insights can be gained.

More knowledge, but at a coarse scale (spatial and temporal), on the abundance, distribution and behaviour of large marine vertebrates can be obtained using dedicated *in situ* census techniques, such as distance surveying (Buckland et al. 2001), which can provide wide spatial scale 'snap-shots' of distribution and abundance and help highlight regions of relative importance, e.g. the SCANS II project for small cetaceans (Hammond 2006). These types of approaches can be expensive and, in general, monitoring programmes are of comparatively short durations when compared to the multi-decadal lifespans of long-lived vertebrates. Furthermore, these studies can be limited in their ability to allow inference of patterns through space and time, particularly with respect to environmental change that operates over decades and beyond, e.g. anthropogenic driven climate change (see Robinson et al. 2009 for review) or oscillations in climate such as the North Atlantic Oscillation (NAO; Hurrell 1995), which is of particular interest in northern Europe. The NAO is associated with westward wind stress blowing from the North Atlantic Ocean onto the European landmass (Hurrell 1995). These winds influence the level of nutrient mixing in the water column, the degree of thermal stratification and subsequent growth conditions for plankton (Fromentin & Planque 1996). As such, they exert a strong influence on marine ecosystems, including plankton (Fromentin & Planque 1996, Lynam et al. 2004), fish and top predators (Thompson & Ollason 2001) (reviewed by Ottersen et al. 2001).

Data collected by public sightings programmes may help in gathering useful information on marine vertebrates (López et al. 2002), producing substantial datasets that can be multi-annual in nature and can have wide spatial coverage. These features may allow some facets of ecology to be explored and offer population-level insights that may otherwise remain cryptic. Public sightings data must be analysed with considerable care, as they lack information on the degree of observer effort necessary to determine standardised rates of detection, which facilitates comparisons across space and time. Even when considering this important caveat, vast datasets on public sightings may hold information that is otherwise lacking for many large vertebrate species, demonstrating the utility of 'citizen-science' (Cohn 2008) monitoring programmes.

The long-lived basking shark *Cetorhinus maximus* is the world's second largest fish species (Compagno 2001), has a circumglobal distribution (Kenney et al. 1985, Valeiras et al. 2001, Francis & Duffy 2002, Wilson 2004, Sandoval-Castillo et al. 2008) and can undertake extensive trans-ocean basin migrations (Gore et al. 2008, Skomal et al. 2009), although the relative frequency and importance of these migrations are unknown. The species is an obligate ram-feeding zooplanktivore (Compagno 2001) with an apparent preference for calanoid copepod zooplankton, such as *Calanus helgolandicus* (Sims & Merrett 1997) and *C. finmarchicus*. The basking shark is slow to mature and has low fecundity (Matthews & Parker 1950), which makes the species slow to recover from exploitation (Kunzlik 1988). Seasonally abundant aggregations of basking sharks form in continental shelf habitats for feeding and presumed reproduction (Kenney et al. 1985, Darling & Keogh 1994, Southall et al. 2005). Basking shark size (body length) at first reproduction is thought to be between 5 and 7 m (Compagno 2001 and reviewed by Sims 2008), at approximately 12 and 16 yr of age, although individuals can attain maximum lengths of approximately 10 m (circa 50 yr of age; Compagno 2001, but see Natanson et al. 2008 for discussion on the complexities of inferring age from body size).

Basking sharks have been subject to historic exploitation throughout their range (Kunzlik 1988) and are protected under Appendix II (2002 onwards) of the Convention on International Trade of Endangered Species (CITES 2010), and Appendices I and II (2005 onwards) of the Convention on Migratory Species (CMS 2009). The International Union for Conservation of Nature (IUCN) Red List of Threatened Species assessed the global status of the basking shark as 'Vulnerable' (1996 onwards), with the north Pacific and northeast Atlantic stocks, which have been subject to targeted historic fisheries, assessed as 'Endangered' (Fowler 2005) from 2000. These assessments are based primarily on past records of rapidly declining local populations as a result of fisheries exploitation and slow population recovery rates (Fowler 2005). In the UK, the basking shark is protected under the Wildlife & Countryside Act (1981) (1998 onwards) and more recently in Scotland by the Nature Conservation Act (2004).

Population size estimates for the basking shark in the northeast Atlantic are lacking, and tracking efforts to date (Sims et al. 2003) demonstrate short-term (months) movements on the northeast Atlantic continental shelf but as yet have been unable to robustly describe the scale of movement exhibited by individuals on repeat annual cycles. The capacity exists, however, for extensive movement (to many thousands of kilometres; Gore et al. 2008). Limited genetic studies have been unable to confidently describe the structuring of the northeast Atlantic population (Noble et al. 2006), although genetic diversity is thought to be globally low for the species (Hoelzel et al. 2006).

With cumulative anthropogenic activity in the northeast Atlantic becoming increasingly well described (Halpern et al. 2008), including fisheries (Witt & Godley 2007, Lee et al. 2010), large vessel traffic and marine renewable energy installations (Witt et al. 2012), there is a growing need to better understand the spatial and temporal dynamics of basking shark distribution, abundance and behaviour to inform marine spatial planning activities. We therefore undertook a comprehensive assessment of basking shark surface sightings from 2 public recording programmes operating in the UK. We set out to: (1) describe spatio-temporal patterns of basking shark sightings (including seasonal and inter-annual trends) to expand upon existing knowledge (e.g. Cotton et al. 2005, Southall et al. 2005), (2) investigate the annual patterns of sightings with respect to environmental forcing, as represented by the NAO, and (3) investigate patterns in basking shark demography through analysis of reported basking shark body lengths to ascertain whether there are any signals of recovery post-exploitation. We further contextualise patterns of basking shark sightings from public records with information gathered from dedicated *in situ* boat-transect surveys. These surveys enable a formal quantification of basking shark sighting abundance in regions with relatively high levels of public sightings.

MATERIALS AND METHODS

Public sightings

Public records of surface sightings of basking sharks were obtained from 2 databases, viz. Basking Shark Watch (BSW; www.mcsuk.org/sightings/baskingshark.php) managed by the Marine Conservation Society (MCS; UK) and Seaquest Southwest (SSW; www.cornwallwildlifetrust.org.uk/conservation/living seas/send_us_your_marine_sighting) hosted by Cornwall Wildlife Trust.

Basking Shark Watch

The MCS basking shark sightings database (n = 12 872 records, 1988 to 2008) was initiated in 1987 to provide a general indication of the distribution and seasonality of basking shark surface sightings in UK coastal waters (R. Earll & J. Turner unpubl.). MCS has promoted public participation in BSW through media releases and the distribution of promotional materials at public forums. The degree of promotional effort undertaken each year was categorised using the ordinal scale (1 to 3), where 1 represented general operation of the scheme and 3 represented significant promotional effort. This metric of effort was used to contextualise the number of records received in each year. MCS encouraged the public to submit their sightings by telephone or post using dedicated sightings cards that assist detailed recording. An internet-based recording facility was introduced in 2001, and the recording cards were eventually discontinued in 2007.

Seaquest Southwest

The Cornwall and Devon Wildlife Trusts in conjunction with the Environmental Records Centre for Cornwall and the Isles of Scilly operate the SSW public sightings database. SSW was initiated in 1997 to gather records of all large marine vertebrates, including basking sharks, within the waters of the region (n = 3494 records of basking sharks, 1988 to 2008). Members of the public are encouraged to submit their sightings of basking sharks by the use of telephone and via the internet.

Database preparation

Each record of a basking shark sighting contained a varying degree of information, from approximate numbers of sharks sighted with date, time and nearest town (at its simplest form), to more detailed accounts that included geographic coordinates of location, shark sizes (body length) and site description (at its most detailed). We first interrogated data within each database (BSW and SSW) to remove obvious duplicate records. We then eliminated potential repeat sightings of basking sharks occurring across the 2 databases, particularly for southwest England where the 2 reporting schemes operated simultaneously. This was achieved by intersecting sightings records by their date; subsequently, any SSW record that occurred on the same date as a BSW record in southwest England was removed if its reported location was within 25 km from the BSW sighting record. Individual basking shark site fidelity is unknown, and to date tracking studies (Sims et al. 2003) have only utilised light-based geolocation, which has coarse spatial resolution (~50 km radius of real location). As such, little is known of the daily rates of movement, and we therefore arbitrarily chose the separation distance of 25 km. The 2 databases were then merged and subjected to further interrogation, which led to the removal of 4108 records. Records were removed for the following reasons: sighting not of a basking shark, sighting prior to 1998, sighting off the northeast Atlantic continental shelf, absence of location data and/or date of sighting, number of basking sharks sighted not reported, record collected using more formal survey methods and sighting of a dead individual (see Table S1 in the supplement at www. int-res.com/articles/suppl/m459p121_supp.pdf). We then determined the day of year of occurrence for each record. The cleansed dataset formed from the merging of BSW and SSW data (years 1988 to 2008) represented 11 781 records of basking shark surface sightings (BSW: n = 9161 records; SSW: n = 2620).

Spatial patterns of occurrence

We constructed a hexagonal grid that encompassed the UK marine region (coastline to 200 nautical miles [n miles] offshore). Using this grid, we ascertained on a 10 d interval for each year, e.g. Days 1 to 10, Days 11 to 20, whether grid cells (~500 km^2, pixel height 25 km or 13.5 n miles) contained one or more records of basking shark surface sightings. Since the temporal and spatial scales of individual basking shark site fidelity are unknown, we arbitrarily chose 10 d intervals and a 500 km^2 area over which to summarise the public sightings data. We then determined the mean annual number of 10 d periods in which each hexagonal grid cell received one or more sighting records. Data were temporally partitioned in this manner to limit the opportunity for repeat sightings of basking sharks that may show fidelity to quasi-persistent oceanographic features, such as tidal mixing fronts that may occur over short periods of time. The procedure highlighted 3 regions of high relative basking shark surface sightings, which we term aggregations or 'hotspots' that informed further regional-based analysis; these regions were western Scotland, Isle of Man and southwest England.

To ascertain the spatial distribution of public sighting records occurring within each regional aggregation (hotspot), we calculated relative estimates of density using a kernel smoothing approach (Worton 1989; see Laver & Kelly 2008 for review). This method statistically estimates the probability of occurrence of a spatial phenomenon, e.g. observations of basking sharks, over a grid using a definable smoothing parameter. This results in an utilisation distribution (UD) that describes the likelihood of the density of observations across the grid. From the UD, areas of constant density can be extracted and displayed as polygons or lines. For each region, we compiled all sightings data by the hexagonal grid cell in which they occurred. We then took the first record to occur in each grid cell in successive 10 d periods (irrespective of the year of occurrence) and aggregated these data to a single dataset, from which we then derived a spatial estimate of relative density. Kernelling enabled spatial patterns to be determined without concern for the varying number of records among regions. To limit the influence of large aggregations of basking sharks, particularly given the difficulties in adequately enumerating group size, the kernelling procedure only used records of sightings and not the number of sharks associated with each record. Two parameters were used in the kernel density estimation procedure: grid resolution and a smoothing parameter. The grid resolution was set at 1 km; this parameter value was used to achieve a balance between the computationally demanding kernelling process and the minimum realistic spatial resolution and positional accuracy of the sightings data. Sightings records were smoothed using a parameter of 30 km for western Scotland, 5 km for Isle of Man and 10 km for southwest England. Selection of the kernel smoothing parameter was predominantly driven by the spatial scale of each region and the complexity of coastline morphology, e.g. embayments, peninsulas and deep intrusions into land (sea lochs), which ultimately physically constrains the spatial pattern of basking shark distribution.

Effort-corrected boat-based surveying

To contextualise public sighting records, we used previously published data collected by *in situ* boat-based line transect surveys conducted as part of

The Wildlife Trusts' Basking Shark Survey (sailing boat; 11.7 m length) in western Scotland (Speedie et al. 2009) and southwest England (Speedie & Johnson 2008). This method of surveying enabled abundance estimates to be obtained, which were expressed with respect to the number of hours surveyed (sharks h^{-1}) at a 25 km^2 resolution. Transect routes were weather dependent, and routes were structured to cover broad geographical regions reported as being productive for surface sightings of basking sharks (i.e. western Scotland and southwest England). Boat-based surveys were intended to cover each transect route at least twice during each survey season (Fig. S1 in the supplement). Body lengths (in m) of basking sharks encountered near to the survey route were assessed by careful comparison to the known length of the survey vessel (at distances of less than 10 m during calm conditions). Boat-based surveys in western Scotland occurred between 2002 and 2006, providing 146 ± 84 surveys yr^{-1} (range 65 to 288). Mean ± SD survey duration was 1.3 ± 1.0 h (range 0.13 to 5.9), and surveys were conducted predominantly in the months of July, August and September. Boat-based transect surveying in southwest England occurred between 2002 and 2005, providing 112 ± 29 surveys yr^{-1} (range 73 to 137). Mean survey duration was 1.3 ± 1.3 h (range 0.12 to 8.3), and surveys were conducted predominantly in the months of April, May and June. Data from these transect surveys were used to derive sightings per unit effort (sharks h^{-1}) only when sea states (World Meteorological Organisation scale) were 3 or less (Speedie et al. 2009).

Environmental context

We obtained data on the NAO winter-time index (from https://climatedataguide.ucar.edu/sites/default/files/cas_data_files/asphilli/nao_station_djfm.txt; accessed 26 March 2012) to examine the relationship between this large ocean basin scale climatic forcing event and the duration of the basking shark sightings season in each year (1998–2008). The NAO winter-time index represents the normalised mean atmospheric pressure difference between the persistent pressure systems localised to Iceland and the Azores, and is generally expressed as the average of monthly normalised pressure differentials for December to March. The duration of the sightings season, for each year, was taken to be the number of days between the first and last sighting in each year derived from a subset of data representing 90% of each year's sightings records centred upon the median sighting.

Body size from public sightings

We summarised records of basking shark sightings with estimates of body length (only using records with 5 or fewer sharks sighted; n = 5019 records) into 3 categories: <4 m, 4–6 m and >6 m. Given the difficulties of following individual sharks in large aggregations, we arbitrarily chose to limit the number of body length estimates from groups of sharks to 5 individuals. We felt this was appropriate given that coastal behaviour of sharks when in aggregations is commonly described as nose-to-tail following (Harvey-Clark et al. 1999, Sims et al. 2000a, Francis & Duffy 2002), which makes discriminating individuals and their body length more difficult for lay observers.

Size class categories arose as a best fit from the structure of the differing public recording schemes, i.e. BSW provided body size according to 5 categories, <2 m, 2–4 m, 4–6 m, 6–8 m and >8 m, whereas SSW provided uncategorised estimates of body length. We therefore re-categorised all data into 3 categories <4 m, 4–6 m and >6 m. These classes were chosen to best reflect small (proxy for young), medium-sized (proxy for juvenile) and large sharks (proxy for adult) based on available syntheses regarding size at first sexual maturity for male and female basking sharks (Sims 2008).

The proportion of surface-sighted sharks with body sizes in each of these categories was determined for each year (1988 to 2008), and patterns of change through time were investigated using linear modelling within the R statistical framework (R Development Core Team 2008) using the package lm with year as the independent term.

RESULTS

Spatio-temporal distribution patterns from public sightings

Public records of basking shark surface sightings within the BSW and SSW databases (Fig. 1; n = 11781; 1988 to 2008) occurred in waters of the UK (including Northern Ireland and Isle of Man; n = 11318), Channel Islands (n = 46), Republic of Ireland (n = 376) and France (n = 41). Of the total database, 11625 records (98.7% of all records) occurred within 12 n miles of land, highlighting the coastal nature of the dataset. Highest densities of public sightings records occurred along western facing shores (Fig. 1). Spatio-temporal filtering of sightings records, used to minimise the bias of re-

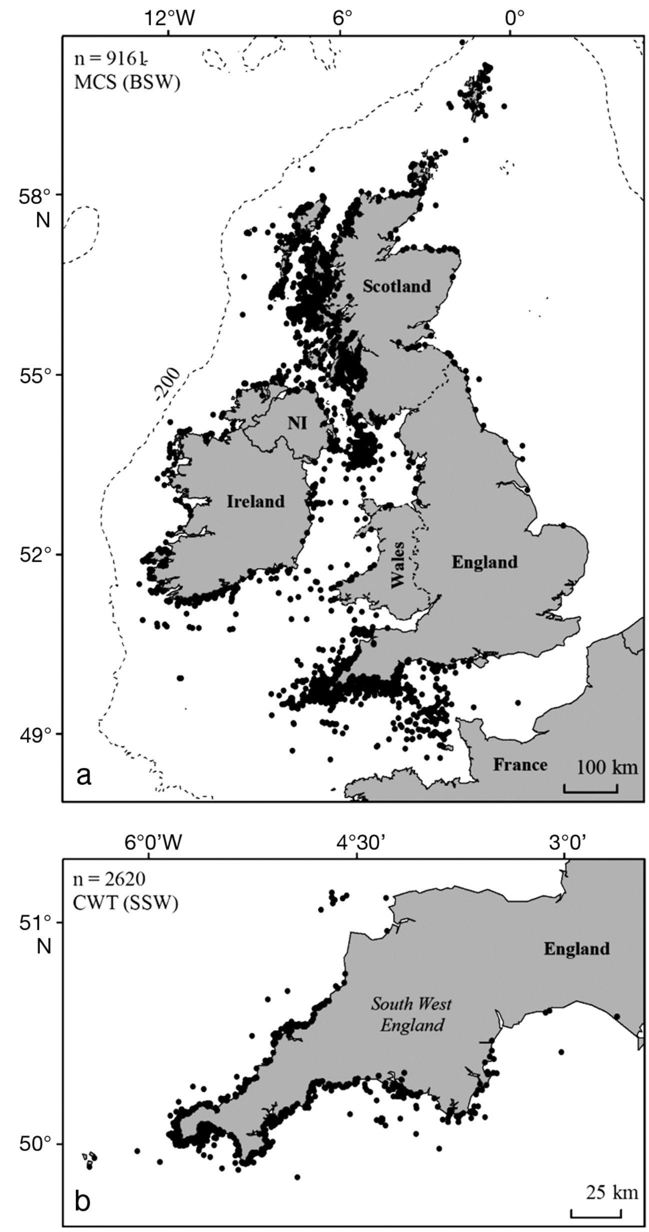

Fig. 1. *Cetorhinus maximus*. Spatial distribution of basking shark sighting records (1988 to 2008), showing the locations of all sightings records (●) in (a) the Basking Shark Watch (BSW) database operated by the Marine Conservation Society (MCS) and (b) the Seaquest Southwest database hosted by Cornwall Wildlife Trust. Broken line indicates 200 m isobath

sighting sharks, highlighted 3 regions where the density of basking shark surface sightings was highest in the dataset (Fig. 2a): western Scotland, Isle of Man and southwest England, which builds upon the knowledge from Southall et al. (2005). Once data were subject to kernelling (Fig. 2b–d; records occurring within 12 n miles of land), several coastal features appeared important for sightings: (1) straits between islands, e.g. in western Scotland, (2) headlands, e.g. in Isle of Man, and (3) near-shore regions with deep water access, e.g. in southwest England, with apparent consistency through time (see Fig. S2).

While the pattern over the 21 yr study period was generally of increasing public records of basking sharks (Fig. 3a; quadratic regression in R; $F_{2,18} = 18.9$, $R^2 = 0.68$; $p < 0.01$), some apparent peaks and troughs in the annual number of sightings occurred. In all 3 regions, comparatively smaller numbers of public-derived records were obtained during the late 1980s and early 1990s. Most noticeable was the generally greater number of public records since 2004 in western Scotland (Fig. 3b) and the Isle of Man (Fig. 3c), whereas the numbers of public records in southwest England appeared more variable (Fig. 3d). There was no significant relationship between the level of promotion effort in each year and the number of basking shark sightings reported to MCS (Spearman rank correlation; rho = 0.4, p = 0.07).

The annual sightings season for basking sharks appeared to start earliest in southwest England (April; Fig. 4c), followed by Isle of Man and western Scotland (May; Fig. 4a,b). The month of peak sightings progressed northwards, in general starting in southwest England (June; Fig. 4c), then Isle of Man (June–July; Fig. 4b) and finally Scotland (August; Fig. 4a).

The temporal distribution of the dates of sightings within each year was variable (Fig. 5a) with the median day of the sightings year slowly increasing during the late 1980s and early 1990s, followed by a gradual decrease and subsequent increase (although see Fig. S3 for regional variations). There was no significant linear relationship between year and the median day of the sightings season (Spearman rank correlation; rho = –0.19, p = 0.42). During the 2000s, the intra-annual temporal distribution of records became less synchronous at the regional level with the median day of the sightings season becoming progressively earlier for Scotland and Isle of Man and later in southwest England (Fig. S3).

Spatial distribution patterns from boat-based transects

Estimates of basking shark relative density derived by boat-based transect surveys (sharks h^{-1} $cell^{-1}$ on a 0.25 km^2 grid; mean ± SD), for regions spatially coin-

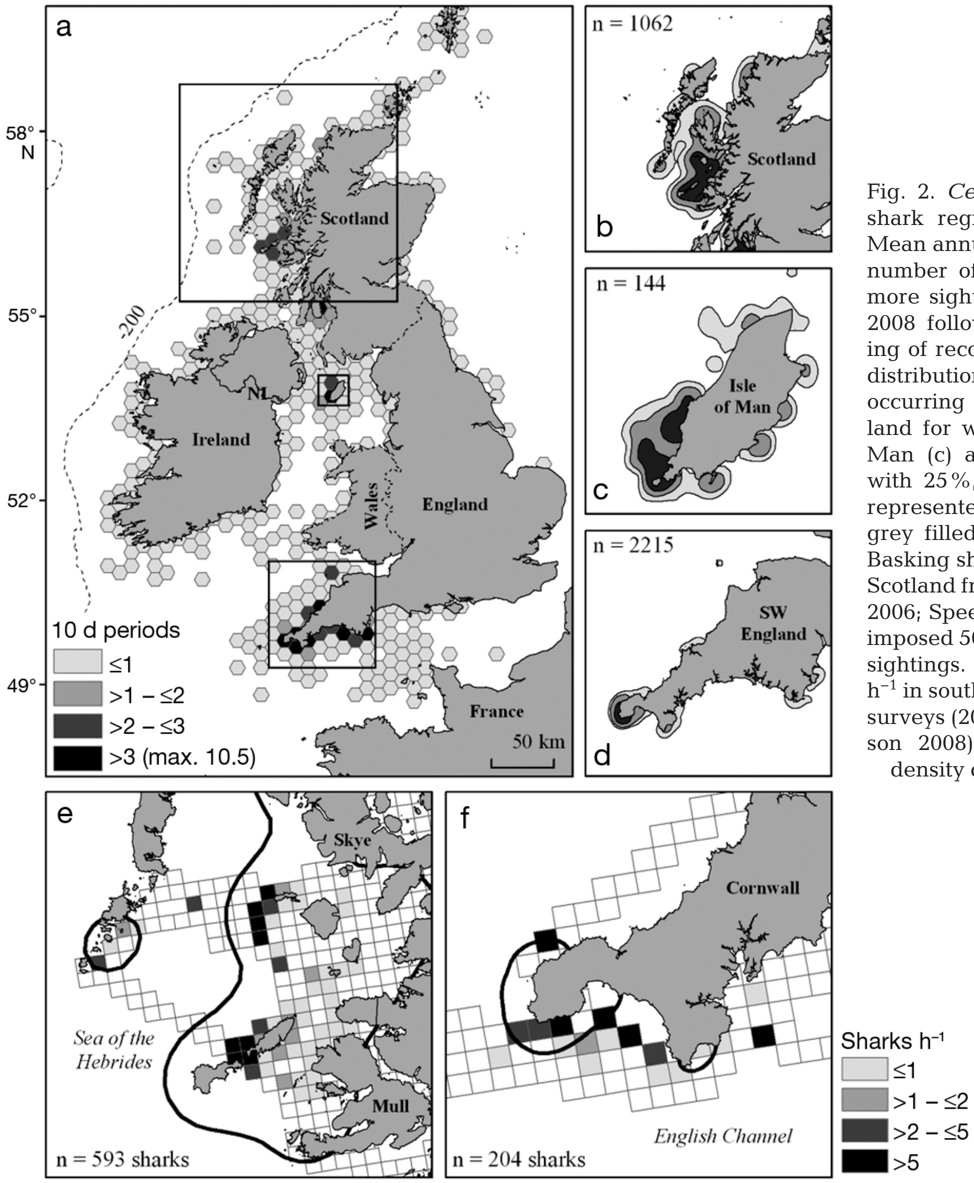

Fig. 2. *Cetorhinus maximus*. Basking shark regional sighting hotspots. (a) Mean annual sighting density as mean number of 10 d periods with one or more sightings for the period 1988 to 2008 following spatio-temporal filtering of records. (b–d) Kernel smoothed distribution of basking shark sightings occurring within 12 nautical miles of land for western Scotland (b), Isle of Man (c) and southwest England (d), with 25%, 50% and 75% of records represented by black, dark and light grey filled polygons, respectively. (e) Basking shark sightings h^{-1} in western Scotland from transect surveys (2002 to 2006; Speedie et al. 2009), with superimposed 50% density contour of public sightings. (f) Basking sharks sightings h^{-1} in southwest England from transect surveys (2002 to 2005; Speedie & Johnson 2008), with superimposed 50% density contour of public sightings

cident to areas containing 50% or more of all public sightings records (as identified by kernelling), were 3.1 ± 8.5 sharks h^{-1} for western Scotland (Fig. 2e; range 0.1 to 50 sharks h^{-1}; 2002 to 2006) and 3.1 ± 3.0 sharks h^{-1} for southwest England (Fig. 2f; range 0.1 to 8.3 sharks h^{-1}; 2002 to 2005; see Fig. S1 for survey effort).

Environmental context

There was a statistically significant positive correlation between the duration of the sightings season (days) and the NAO winter-time index (Fig. 5b; Spearman's rank correlation; rho = 0.45; p = 0.03). This pattern was evident following the censoring of 2 outlier data points; first in 1991, when the total number of records for the year was low (n = 254) and basking shark sightings during December in the Isle of Man extended the duration of the sightings season; and a second in 1996, a year in which the NAO is known to have undergone a large single year reversal in phase and intensity, and the NAO index was –3.78 (see Greene & Pershing 2003 for a discussion on these anomalous events). Without censoring of these data points there was no significant correlation (Spearman's rank correlation; rho = 0.264; p = 0.25).

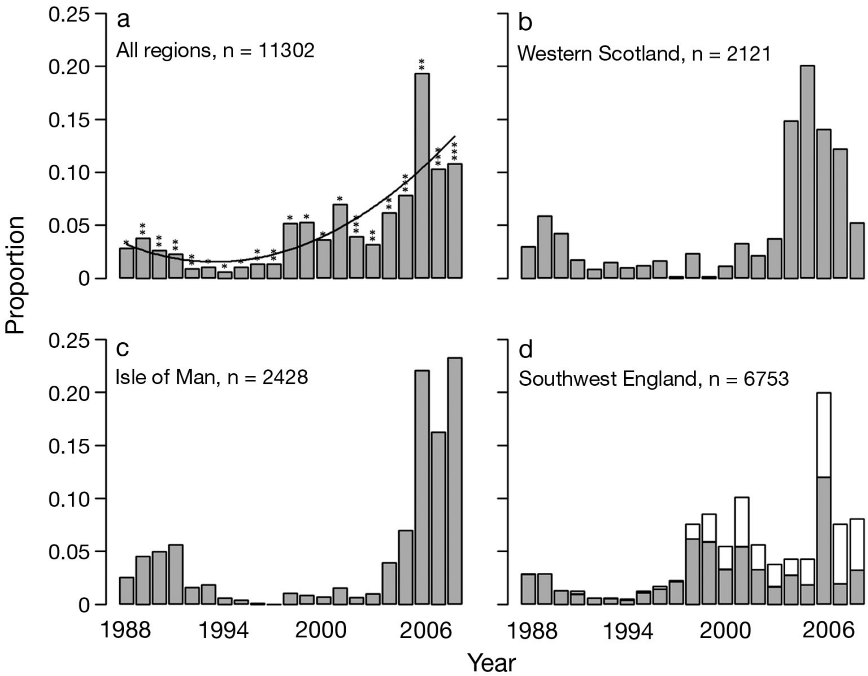

Fig. 3. *Cetorhinus maximus.* Annual time series (1988 to 2008) of basking shark surface sighting records occurring within 12 nautical miles of land for (a) all regions (with quadratic regression: solid line, $F_{2,18}$ = 18.9, R^2 = 0.68; p < 0.01; asterisks indicate a qualitative assessment of the degree of Marine Conservation Society Basking Shark Watch [BSW] scheme promotion to the public, where 1 represents little promotion and 3 represents significant promotion), (b) western Scotland, (c) Isle of Man and (d) southwest England (grey bar shows proportion from BSW and open bar from Seaquest Southwest)

Body size from public sightings

The annealed (BSW and SSW) basking shark public sightings database contained 5019 records with estimated basking shark body lengths (n = 7959 sharks in total). The proportion of sharks reported in each of 3 body size classes was 0.32 for sharks <4 m (n = 2518 sharks), 0.61 for sharks 4–6 m (n = 4856) and 0.07 for sharks >6 m (n = 585).

We investigated possible changes in the annual proportions of basking shark sightings reported in each of these body length size classes. Two statistically significant patterns were identified: the annual proportion of basking sharks <4 m in length declined through time (Fig. 6a; linear regression, $F_{1,19}$ = 11.39, R^2 = 0.37, p < 0.01), whereas the annual proportion of basking sharks 4–6 m increased through time (Fig. 6b; linear regression, $F_{1,19}$ = 10.94; R^2 = 0.37; p < 0.01). There was no relationship between year and the proportion of large sharks sighted (Fig. 6c; linear regression, $F = 0.658_{1,19}$, R^2 = 0.03, p = 0.42). However, patterns of body size through time occurring in each of the regions were, for the majority, non-linear as highlighted by local order polynomial regressions (Cleveland 1979) (Fig. S4).

Body size from boat-based transects

Information on basking shark body lengths was also collected during dedicated *in situ* boat-based transects in western Scotland (2002 to 2006, n = 332 sharks) and southwest England (2002 to 2005, n = 78 sharks). These data were summarised to the same size classes as used for the public sightings data. The proportion of sharks observed in each of 3 body size classes was 0.14 for sharks <4 m (n = 63 sharks), 0.22 for sharks 4–6 m (n = 95) and 0.64 for sharks >6 m (n = 252 sharks). We did not analyse these body length data for trends through time, as the respective time series for western Scotland and southwest England were of a limited duration (5 and 4 yr, respectively). It is clear, however, that in general the size distribution is markedly further skewed to large size classes than the public sightings data.

DISCUSSION

Data from public sightings programmes, once adequately quality controlled, can provide insights into large marine vertebrate ecology (particularly for species that use coastal habitats), including phenology of seasonal appearance in coastal waters and potential habitat preference and thus the putative risks faced. Despite basking sharks being an important species of conservation concern, and in the absence of ongoing dedicated effort-corrected surveys, the available data are all that exist from which to generate insights to direct conservation activities at large spatial and temporal scales. We discuss the utility of this dataset in the context of 3 overarching questions.

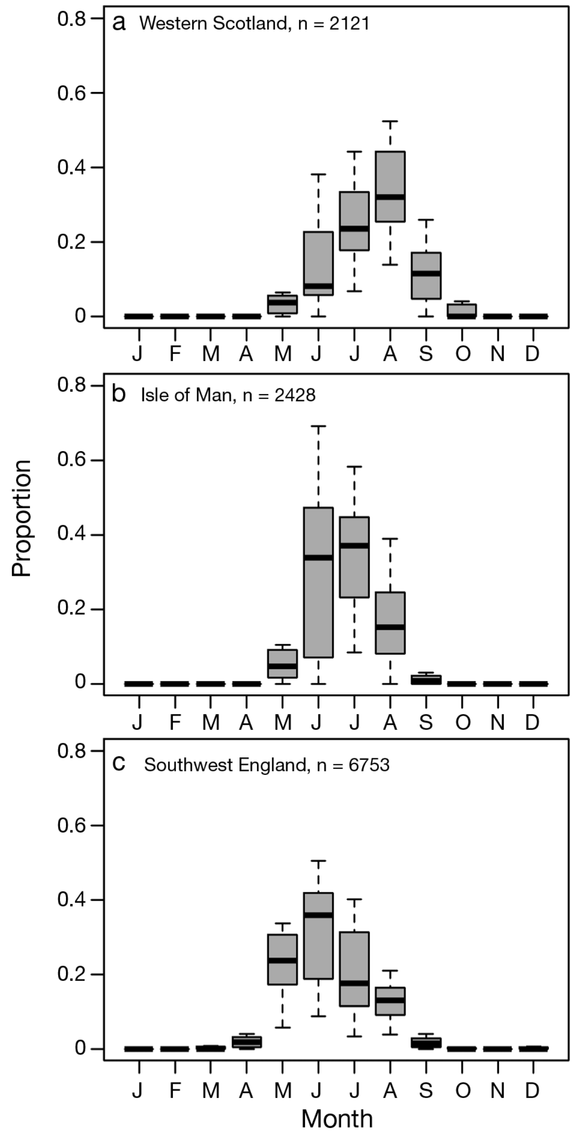

Fig. 4. *Cetorhinus maximus.* Monthly patterns of basking shark surface sightings, showing 25th, 50th (bold horizontal line; median) and 75th percentiles of the proportion of records occurring in each month between 1988 and 2008 for regional hotspots, for (a) western Scotland, (b) Isle of Man and (c) southwest England

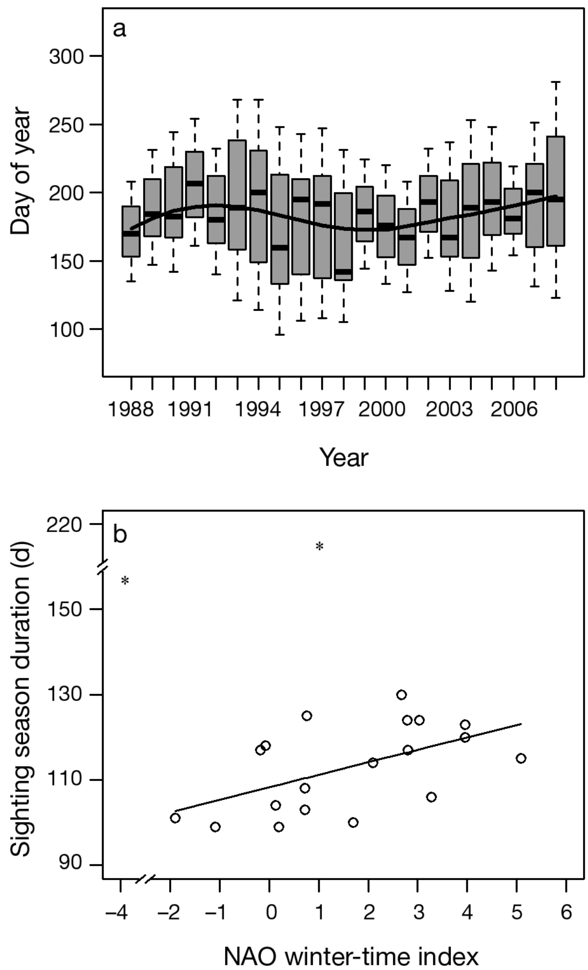

Fig. 5. *Cetorhinus maximus*. Long-term annual distribution of surface sighting seasonality and relationship between sightings season duration and the North Atlantic Oscillation (NAO). (a) Statistical distribution of sighting days by year for main sightings regions. Bold horizontal line in each box is median day of sighting in each year, upper and lower box limits indicate 25th and 75th percentiles of days of sightings in each year. Solid line: smoothed estimate of median day of sighting through time (lowess in R, Cleveland 1979) where span is 0.6. (b) Annual sighting season duration and the NAO winter-time index. Note truncated *x*- and *y*-axes and outliers (stars). Least squares fit line through data (solid line)

1. Spatio-temporal patterns of public sightings: Are basking shark hotspots consistent through space and time?

Spatial analysis of basking shark surface sightings from the general public (1988 to 2010) highlighted 3 regional hotspots: western Scotland, Isle of Man and southwest England, areas which had been previously identified by Southall et al. (2005) but using a shorter time series of records from the BSW database (1987 to 2004) alone. A defined seasonality in basking shark sightings (occurring late spring to early autumn across UK waters, with regional variation) was evident, which similarly supports existing knowledge.

Corroboration of the seasonal patterns observed in the sightings data, for at least southwest England, is provided by monthly aerial surveying for large marine vertebrates in coastal waters (coastline to 6 n miles offshore) of Cornwall (Leeney et al. 2012).

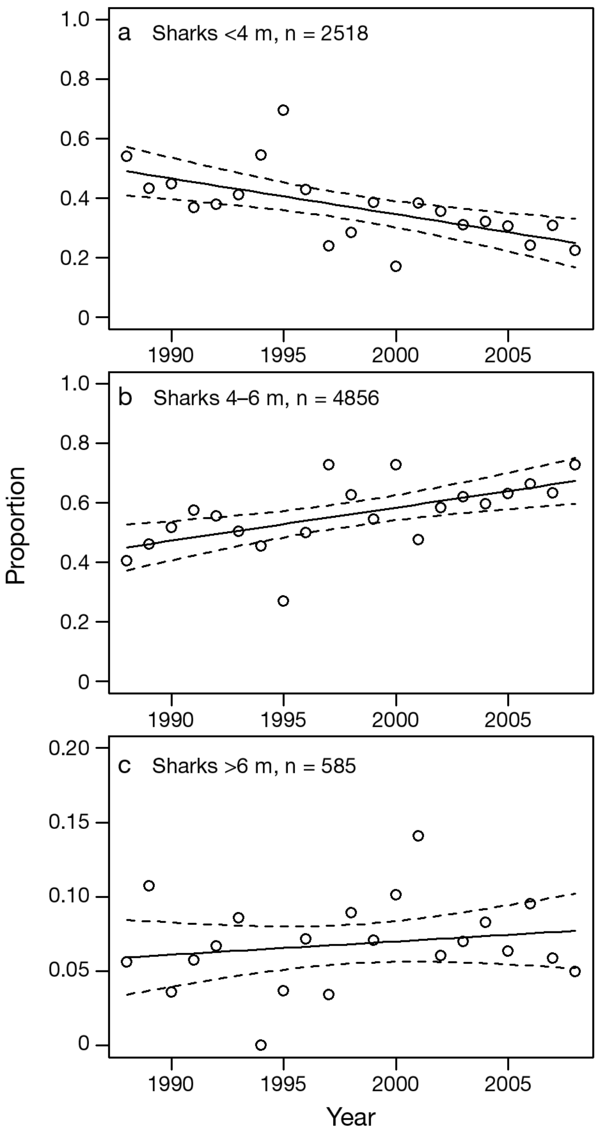

Fig. 6. *Cetorhinus maximus*. Body size of sighted sharks. Annual proportion of sharks sighted (a) <4 m, (b) 4–6 m and (c) >6 m in length. Regression from linear modelling (solid line) and associated confidence intervals (broken lines)

These surveys suggest that basking sharks are either not present during winter months or are at depth (Shepard et al. 2006) and hence not amenable to sighting, perhaps influenced by the distribution of zooplankton prey, which are typically deeper and more offshore during winter months (Colebrook 1985, Greene & Pershing 2000, Beaugrand et al. 2001). Furthermore, basking shark depth utilisation data extending into autumn and winter (n = 2; November to January), collected by Sims et al. (2003), show that little time spent is spent by these planktivores near the surface during this period.

The pattern of basking shark sightings records occurring within each year showed a marked seasonality, peaking earlier in southwest England and later in the Isle of Man and western Scotland. This observed pattern could be due to northward movement or seasonal expansion of a putative northeast Atlantic population of basking sharks to higher latitudes to feed as the 'bloom' of copepod prey extends northwards with the season (Sims et al. 2006). Light-based geolocation tracking of basking sharks (Sims et al. 2003) has shown that some individuals move between the hotspot regions identified in this study. Sightings data cannot, however, provide further insights into the extent of this movement at the individual level, and the possibility remains that different individuals may be sighted later in the year in Scotland than those observed earlier in the year in southwest England.

2. What impact does environment have on basking shark sightings?

Concordance of the seasonal patterns of basking shark surface sightings with sea surface temperature and copepod prey has undergone prior analysis (for southwest England using MCS BSW data, 1988 to 2001; Cotton et al. 2005), including an investigation into the potential relationship of the abundance of basking sharks sighted with climatic phenomena, such as the NAO. These authors identified a significant association between sea surface temperature and shark sighting abundance for southwest England, where warmer mean annual temperatures were associated with greater abundance of sharks. Similar to Cotton et al. (2005), but using an updated time series, we detected a significant correlation between the length (duration in days) of the sightings season in any one year and the state of the NAO. We used sightings season duration, in place of shark abundance, given the lack of robust effort correction (bias reduction) that could be applied to the public sightings data. The effects of NAO are thought to differ somewhat on the dominant prey types for basking sharks; for example, during the NAO positive phase, *Calanus finmarchicus* abundance increases, while *C. helgolandicus* decreases and vice versa during the NAO negative phase (Fromentin & Planque 1996). Whether the correlation between westward wind stress (described by the NAO index) and the duration of the basking shark sighting season is due to temperature or prey, an interaction of both or sightings probability due to weather conditions, has yet to be determined. Elucidating the potential influencing mechanisms of NAO would, however, require considerable effort using formal abundance survey methods over many seasons on a large spatial scale. These requirements are important given the challenges faced in ecological studies where large-scale phenomena that have the potential to influence patterns are rarely matched in the datasets used to investigate their potential influence, ultimately complicating or potentially invalidating predictions (Levin 1992). Importantly, our finding highlights that population estimates based on visual detection techniques should potentially be undertaken in years when a larger proportion of the putative northeast Atlantic population is available for enumeration, i.e. when the NAO is positive.

3. Are basking sharks recovering from past exploitation?

Basking sharks under exploitation are likely to be particularly prone to rapid population declines since fecundity is low, growth is generally slow, and sexual maturity comes late; these life history characteristics may also result in populations taking many years to recover from exploitation. The northeast Atlantic saw historic targeted hunting of this species principally in Norway, Ireland and Scotland, where at least 81 639 basking sharks were killed between 1952 and 2004 (ICES 2006); the recovery status of the species is currently unknown (Sims 2008). Significant exploitation ended in the UK in 1953 and in Ireland in 1975 (Kunzlik 1988), although a largely opportunistic fishery operated from the Firth of Clyde, Scotland, from 1982 to 1994. Harvesting continued in Norway until the turn of the millennium (CITES 2005). Incidental mortality in fisheries continues to be reported within the public sighting databases (for the UK), although the numbers are comparatively small (130 individuals over 21 yr; Table S1). There have been many more sightings of basking sharks in recent years. However, it is difficult to separate changes in abundance of records (and potentially sharks) from increases in awareness and the influence of environment.

When public sightings data are examined more closely for reported body size, there is evidence of changing patterns through time, with a decreasing trend in the proportion of small sharks (<4 m) and an increasing trend for medium-sized sharks (4–6 m). Given that our data may carry effort-related bias, interpretation of trends should be made cautiously; however, this may signify a population that is slowly recovering with the maturation of the younger sharks that remained following the period of exploitation in the later part of the 20th century. There is some lack of agreement in the size structure of sharks reported in the 2 datasets, i.e. the public sightings database and the boat-based transects database, with the boat-based surveys identifying a considerably greater proportion of large sharks (>6 m). This lack of concordance could exist for several reasons, including that boat-based transects might be accessing regions that support larger individuals (potentially engaged in courtship and reproduction) that are not accessible to lay observers in coastal areas, limiting the opportunity to be sighted by the public. Further, the number of sharks observed during boat-based surveys represents only 7% of those reported by public sightings. Whatever the underlying reason for this difference, its existence highlights the need for cautious interpretation of both datasets—one which lacks effort correction (public sightings) and the other which was focused on regions previously identified as supporting considerable numbers of sharks.

What future monitoring efforts are required?

Data from basking shark public sighting schemes provide a spatio-temporal overview of the whereabouts of basking sharks in UK waters, and can provide a key focus for efforts seeking to estimate population size. For example, these data may help to focus aerial surveying or boat-based survey activities. Public-derived data also complement studies investigating the geo-political extents of basking shark distribution, particularly for those individuals that move large distances (Southall et al. 2006). Further efforts towards genetics studies (Hoelzel et al. 2006), photo-identification (Sims et al. 2000b), effort-related surveying (Speedie et al. 2009), understanding depth utilisation (Shepard et al. 2006), particularly for coastal waters, and tracking (Sims et al. 2003, Gore et al. 2008) will further help to elucidate the ecology of basking sharks and will lend additional support to the interpretation of public sightings data. Photo-identification work (Sims et al. 2000b) and high-resolution GPS-based satellite-tracking (see Sims et al. 2009, Witt et al. 2010) would provide essential information on the degree of site residency shown by basking sharks, thereby building an understanding of the likelihood of re-sighting. When combined, data from these diverse survey methods will help yield a greater understanding of how this species might be better conserved and protected in UK waters and provide necessary insights into the population status of this species in the northeast Atlantic. This is exemplified by the relationship gained from the public sightings data on the association between sightings season duration and the intensity and phase of NAO, which provides context for more optimal timing of monitoring efforts and population estimates.

CONCLUSION

Given our increasing anthropogenic footprint in marine ecosystems (Halpern et al. 2008) and the challenges of conducting large-scale long-term wildlife monitoring programmes (financial and logistical), all available data on species of conservation concern need to be analysed in a concerted way so that future conservation activities might be appropriately directed. Here we show how sightings data gathered from across large spatial and temporal scales can provide key information on the whereabouts of a large marine vertebrate recovering from past exploitation into an ever changing marine environment with newly emerging risks. Public sightings data, when amalgamated with other information, such as focused aerial surveying efforts (Leeney et al. 2012) at key sightings hotspots and beyond, can ultimately aid efforts for spatial planning seeking to ensure the long-term recovery of the species.

Acknowledgements. M.J.W. was supported by a PRIMaRE Post-doctoral Research Fellowship, MERiFIC and by the Darwin Initiative. C.M.M. is supported by the European Union through the Interreg IVa Channel Habitat Atlas for Resource Management (CHARM) programme. B.J.G. receives additional funding from the Darwin Initiative and NERC. C.S. is supported by the Shark Foundation (Hai-Stiftung). We thank L.A. Hawkes and S.A. Maxwell for critical comments during the preparation of this work. The manuscript was improved by the comments of the editor and 3 anonymous reviewers.

LITERATURE CITED

Beaugrand G, Ibañez F, Lindley JA (2001) Geographical distribution and seasonal and diel changes in the diversity of calanoid copepods in the North Atlantic and North Sea. Mar Ecol Prog Ser 219:189–203

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ and others (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford

Burger AE, Shaffer SA (2008) Application of tracking and data-logging technology in research and conservation of seabirds. Auk 125:253–264

CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) (2005) Consideration of proposals for amendment of Appendices I and II: inclusion of the basking shark (*Cetorhinus maximus*) on Appendix II of CITES. Available at www.cites.org/eng/cop/12/prop/E12-P36.pdf (accessed on 26 January 2011)

CITES (2010) Appendices I, II and III. Available at www.cites.org/eng/app/appendices.php (accessed on 26 January 2011)

Cleveland WS (1979) Robust locally weighted regression and smoothing scatterplots. J Am Stat Assoc 74:829–836

CMS (Convention on the Conservation of Migratory Species of Wild Animals) (2009) Appendices I and II. Available at www.cms.int/documents/appendix/appendices_e.pdf (accessed on 26 January 2011)

Cohn JP (2008) Citizen science: Can volunteers do real research? Bioscience 58:192–197

Colebrook JM (1985) Continuous plankton records — overwintering and annual fluctuations in the abundance of zooplankton. Mar Biol 84:261–265

Compagno L (2001) FAO Species catalogue for fisheries purposes. Sharks of the world — an annotated and illustrated catalogue of shark species known to date. Food and Agriculture Organization of the United Nations, Rome

Cooke SJ (2008) Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. Endang Species Res 4:165–185

Cotton PA, Sims DW, Fanshawe SAM, Chadwick M (2005) The effects of climate variability on zooplankton and basking shark (*Cetorhinus maximus*) relative abundance off southwest Britain. Fish Oceanogr 14:151–155

Darling JD, Keogh KE (1994) Observations of basking sharks, *Cetorhinus maximus*, in Clayquot Sound, British Columbia. Can Field Nat 108:199–210

Fowler SL (2005) *Cetorhinus maximus*. In: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4. Available at www.iucnredlist.org (accessed on 14 July 2010)

Francis M, Duffy C (2002) Distribution, seasonal abundance and bycatch of basking sharks (*Cetorhinus maximus*) in New Zealand, with observations on their winter habitat. Mar Biol 140:831–842

Fromentin JM, Planque B (1996) *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus.* Mar Ecol Prog Ser 134:111–118

Godley BJ, Blumenthal J, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ (2008) Satellite tracking of sea turtles: Where have we been and where do we go next? Endang Species Res 4:3–22

Gore MA, Rowat D, Hall J, Gell FR, Ormond RF (2008) Transatlantic migration and deep mid-ocean diving by basking shark. Biol Lett 4:395–398

Greene CH, Pershing AJ (2000) The response of *Calanus finmarchicus* populations to climate variability in the Northwest Atlantic: basin-scale forcing associated with the North Atlantic Oscillation. ICES J Mar Sci 57: 1536–1544

Greene CH, Pershing AJ (2003) The flip-side of the North Atlantic Oscillation and modal shifts in slope-water circulation patterns. Limnol Oceanogr 48:319–322

Halpern BS, Walbridge S, Selkoe KA, Kappel CV and others

(2008) A global map of human impact on marine ecosystems. Science 319:948–952

Hammerschlag N, Gallagher AJ, Lazarre DM (2011) A review of shark satellite tagging studies. J Exp Mar Biol Ecol 398:1–8

Hammond PS (2006) Small cetaceans in the European Atlantic and North Sea (SCANS-II). Final report. Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, UK

Harvey-Clark CJ, Stobo WT, Helle E, Mattson M (1999) Putative mating behavior in basking sharks off the Nova Scotia coast. Copeia 1999:780–782

Hawkes LA, Witt MJ, Broderick AC, Coker JW and others (2011) Home on the range: spatial ecology of loggerhead turtles in Atlantic waters of the USA. Divers Distrib 17: 624–640

Hoelzel AR, Shivji MS, Magnussen J, Francis MP (2006) Low worldwide genetic diversity in the basking shark (*Cetorhinus maximus*). Biol Lett 2:639–642

Hurrell JW (1995) Decadal trends in the North-Atlantic Oscillation — regional temperatures and precipitation. Science 269:676–679

ICES (International Council for the Exploration of the Sea) (2006) Report of the Working Group on Elasmobranch Fisheries (WGEF). ICES document CM 2006/ACFM 31. International Council for the Exploration of the Sea, Copenhagen

Kenney RD, Owen RE, Winn HE (1985) Shark distributions off the northeast United States from marine mammal surveys. Copeia 1985:220–223

Kunzlik P (1988) The basking shark. Department of Agriculture and Fisheries for Scotland, Aberdeen

Laver PN, Kelly MJ (2008) A critical review of home range studies. J Wildl Manag 72:290–298

Lee J, South AB, Jennings S (2010) Developing reliable, repeatable, and accessible methods to provide high-resolution estimates of fishing-effort distributions from vessel monitoring system (VMS) data. ICES J Mar Sci 67: 1260–1271

Leeney RH, Broderick AC, Witt MJ, Richardson PB, Jarvis DS, Buchanan J, Godley BJ (2012) Marine megavertebrates of Cornwall and the Isles of Scilly: relative abundance and distribution. J Mar Biol Assoc UK (in press). doi:10.1017/S002531541100155X

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

López A, Santos MB, Pierce GJ, Gonzalez AF, Valeiras X, Guerra A (2002) Trends in strandings and by-catch of marine mammals in north-west Spain during the 1990s. J Mar Biol Assoc UK 82:513–521

Lynam CP, Hay SJ, Brierley AS (2004) Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnol Oceanogr 49:637–643

Matthews LH, Parker HW (1950) Notes on the anatomy and biology of the basking shark (*Cetorhinus maximus* (Gunner)). Proc Zool Soc Lond 120:535–576

Natanson L, Wintner S, Johansson F, Piercy A and others (2008) Ontogenetic vertebral growth patterns in the basking shark *Cetorhinus maximus.* Mar Ecol Prog Ser 361:267–278

Noble LR, Jones CS, Sarginson J, Metcalfe JD, Sims DW, Pawson MG (2006) Conservation genetics of basking sharks. Final report for Defra Tender CR 0288. Dept Environment, Food and Rural Affairs, London

Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC (2001) Ecological effects of the North Atlantic Oscillation. Oecologia 128:1–14

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Robinson RA, Crick HQP, Learmonth JA, Maclean IMD and others (2009) Travelling through a warming world: climate change and migratory species. Endang Species Res 7:87–99

Sandoval-Castillo J, Ramirez-Gonzalez J, Villavicencio-Garayzar C (2008) First record of basking shark (*Cetorhinus maximus*) in Mexico? Mar Biodivers Rec 1:e19

Shepard ELC, Ahmed MZ, Southall EJ, Witt MJ, Metcalfe JD, Sims DW (2006) Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. Mar Ecol Prog Ser 328: 205–213

Sims DW (2008) Sieving a living: a review of the biology, ecology and conservation status of the plankton-feeding basking shark *Cetorhinus maximus*. Adv Mar Biol 54: 171–220

Sims DW, Merrett DA (1997) Determination of zooplankton characteristics in the presence of surface feeding basking sharks *Cetorhinus maximus.* Mar Ecol Prog Ser 158: 297–302

Sims DW, Southall EJ, Quayle VA, Fox AM (2000a) Annual social behaviour of basking sharks associated with coastal front areas. Proc R Soc Lond B Biol Sci 267: 1897–1904

Sims DW, Speedie CD, Fox AM (2000b) Movements and growth of a female basking shark re-sighted after a three year period. J Mar Biol Assoc UK 80:1141–1142

Sims DW, Southall EJ, Richardson AJ, Reid PC, Metcalfe JD (2003) Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. Mar Ecol Prog Ser 248:187–196

Sims DW, Witt MJ, Richardson AJ, Southall EJ, Metcalfe JD (2006) Encounter success of free-ranging marine predator movements across a dynamic prey landscape. Proc R Soc Lond B Biol Sci 273:1195–1201

Sims DW, Queiroz N, Humphries NE, Lima FP, Hays GC (2009) Long-term GPS tracking of ocean sunfish *Mola mola* offers a new direction in fish monitoring. PLoS ONE 4:e7351

Skomal GB, Zeeman SI, Chisholm JH, Summers EL, Walsh HJ, McMahon KW, Thorrold S (2009) Transequatorial migrations by basking sharks in the Western Atlantic Ocean. Curr Biol 19:1019–1022

Southall EJ, Sims DW, Metcalfe JD, Doyle JI and others (2005) Spatial distribution patterns of basking sharks on the European shelf: preliminary comparison of satellite-tag geolocation, survey and public sightings data. J Mar Biol Assoc UK 85:1083–1088

Southall EJ, Sims DW, Witt MJ, Metcalfe JD (2006) Seasonal space-use estimates of basking sharks in relation to protection and political-economic zones in the North-east Atlantic. Biol Conserv 132:33–39

Speedie CD, Johnson LA (2008) The basking shark (*Cetorhinus maximus*) in West Cornwall. Key sites, anthropogenic threats and their implications for conservation of the species. Research Report NERR 0018. Natural England, Sheffield

Speedie CD, Johnson LA, Witt MJ (2009) Basking shark hotspots on the west coast of Scotland: key sites, threats and implications for conservation of the species. Com-

missioned Report No. 339. Scottish Natural Heritage, Inverness
Thompson PM, Ollason JC (2001) Lagged effects of ocean climate change on fulmar population dynamics. Nature 413:417–420
Valeiras J, López A, García M (2001) Geographical seasonal occurrence and incidental fishing captures of basking shark *Cetorhinus maximus* (Chondricthyes: Cetorhinidae). J Mar Biol Assoc UK 81:183–184
Wilson SG (2004) Basking sharks (*Cetorhinus maximus*) schooling in the southern Gulf of Maine. Fish Oceanogr 13:283–286
Wilson RP, Shepard ELC, Liebsch N (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. Endang Species Res 4:123–137
Witt MJ, Godley BJ (2007) A step towards seascape scale conservation: using vessel monitoring systems (VMS) to map fishing activity. PLoS ONE 2:e1111
Witt MJ, Åkesson S, Broderick AC, Coyne MS and others (2010) Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. Anim Behav 80: 571–581
Witt MJ, Sheehan EV, Bearhop S, Broderick AC and others (2012) Assessing wave energy effects on biodiversity: the Wave Hub experience. Philos Trans R Soc Lond A Math Phys Eng Sci 370:502–509
Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168

Editorial responsibility: Rory Wilson, Swansea, UK

Submitted: August 24, 2011; Accepted: March 28, 2012
Proofs received from author(s): June 28, 2012