

# Cnidaria in UK coastal waters: description of spatio-temporal patterns and inter-annual variability

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*Concern has been expressed over future biogeographical expansion and habitat capitalization by species of the phylum Cnidaria, as this may have negative implications on human activities and ecosystems. There is, however, a paucity of knowledge and understanding of jellyfish ecology, in particular species distribution and seasonality. Recent studies in the UK have principally focused on the Celtic, Irish and North Seas, but all in isolation. In this study we analyse data from a publicly-driven sightings scheme across UK coastal waters (2003–2011; 9 years), with the aim of increasing knowledge on spatial and temporal patterns and trends. We describe inter-annual variability, seasonality and patterns of spatial distribution, and compare these with existing historic literature. Although incidentally-collected data lack quantification of effort, we suggest that with appropriate data management and interpretation, publicly-driven, citizen-science-based, recording schemes can provide for large-scale (spatial and temporal) coverage that would otherwise be logistically and financially unattainable. These schemes may also contribute to baseline data from which future changes in patterns or trends might be identified. We further suggest that findings from such schemes may be strengthened by the inclusion of some element of effort-corrected data collection.*

**Keywords:** citizen science, jellyfish, life cycle, public sightings, Scyphozoa, Hydrozoa

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## INTRODUCTION

The past decade has seen concerns expressed over blooms, future biogeographical expansion and habitat capitalization by pelagic species of the phylum Cnidaria (Mills, 2001; Brodeur *et al.*, 2002; Lynam *et al.*, 2006; Attrill *et al.*, 2007; Purcell *et al.*, 2007; Richardson *et al.*, 2009). Gelatinous plankton (subsequently referred to as jellyfish) blooms in coastal waters can have negative implications for human activities (Purcell *et al.*, 2007; Purcell, 2009), with both social and economic repercussions (Doyle *et al.*, 2007), as well as potential impacts on other species competing for the same habitat (Lynam *et al.*, 2005a).

Fluctuations in jellyfish abundance have potentially been linked with climate indices such as the North Atlantic Oscillation (NAO) and the North Pacific Decadal Oscillation (NPDO) (e.g. Lynam *et al.*, 2004, 2005b; Purcell, 2005) as well as variation in sea surface temperature (SST) (e.g. Lynam *et al.*, 2011), pH (Attrill *et al.*, 2007), salinity (Bastian *et al.*, 2011a), eutrophication (Purcell *et al.*, 2007) and habitat modification (Richardson *et al.*, 2009). Future climate change may modify oceanographic dynamics, thereby further influencing

(positively or negatively) abundance and distribution of marine planktonic communities (Hays *et al.*, 2005). These factors may also be related to increases in abundance associated with opportunistic expansion, following decreased predatory pressure as a result of declining fish abundance due to commercial fisheries (Pauly *et al.*, 1998; Mills, 2001; Lynam *et al.*, 2006).

Large-scale spatial knowledge and understanding of jellyfish ecology is data deficient (Doyle *et al.*, 2007; Purcell, 2009), although local scale insight has improved. For coastal waters of the UK, an extensive review of historic literature (~100 years) (Russell, 1970) exists, and more recently, jellyfish medusae studies have focused on the waters of the Celtic, Irish, and North Seas as well as the Solent estuarine system on the south coast of the UK. These studies have used a variety of methods to obtain data, including: ships of opportunity (Doyle *et al.*, 2007; Bastian *et al.*, 2011a); trawl surveys (primarily as by-catch; Lynam *et al.*, 2005b, 2011; Bastian *et al.*, 2011b); aerial surveys (Houghton *et al.*, 2006a, b; Lilley *et al.*, 2009); electronic tagging (Hays *et al.*, 2011); shoreline surveys (Doyle *et al.*, 2007); and analysis of historical records (Lilley *et al.*, 2009).

Analyses of incidentally-collected sightings/strandings data, from public recording schemes for other marine species, have identified significant spatial and temporal patterns and trends and provided insight into regional and large-scale national distributions (Witt *et al.*, 2007, 2012; Leeney *et al.*, 2008; Pikesley *et al.*, 2012). In the UK, a

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public sightings scheme (<http://www.mcsuk.org/sightings/jellyfish.php>) managed by the Marine Conservation Society (MCS), UK, allows members of the public and other interested parties to report sightings and strandings data for eight species of Cnidaria. These include six species of the class Scyphozoa: *Aurelia aurita* (Linnaeus, 1758) (moon); *Cyanea capillata* (Linnaeus, 1758) (lion's mane); *Chrysaora hysoscella* (Linnaeus, 1766) (compass); *Cyanea lamarckii* (Péron & Lesueur, 1810) (blue); *Pelagia noctiluca* (Forsskål, 1775) (mauve stinger) and *Rhizostoma octopus* (Macri, 1778) (root mouth or barrel); and two species of the class Hydrozoa: *Physalia physalis* (Linnaeus, 1758) (Portuguese man-of-war); and *Verella verella* (Linnaeus, 1758) (by-the-wind-sailor). The last two species are not true 'jellyfish' but are included in the MCS 'Jellyfish' Survey data for completeness, as they are occasionally found in coastal waters and on beaches of the UK. As far as we are aware, this database has the largest spatial and temporal coverage for jellyfish sightings in UK coastal waters.

Here we describe spatial and temporal patterns (including seasonal and annual trends) for these eight species of the phylum Cnidaria, across the coastal waters of the UK, between 2003 and 2011 (9 years), as recorded by the MCS UK national 'Jellyfish' Survey database.

## MATERIALS AND METHODS

### Data preparation

The MCS 'Jellyfish' Survey was initiated in 2003 to enhance the understanding of the spatial and temporal patterns of jellyfish occurrence in UK coastal waters, through the recording of sightings and strandings of the adult medusae. The MCS promotes public awareness of this scheme annually, typically at the end of July, through national and regional media releases (newspaper, radio and television). Awareness of the scheme is also furthered by marketing via the MCS website and by distribution of promotional materials, including electronic and hard copy ID cards (Supplementary Figure S1). Members of the public were required to submit their written records of sightings and strandings by post, using a standardized form, but this was superseded in 2007 by an on-line submission form.

The MCS UK database held 7229 records (2003–2011). A Geographical Information System (GIS) (ArcMap 10: ESRI, Redlands, US, <http://www.esri.com>) basemap was used for the UK and Ireland using coordinates conforming to the British National Grid (BNG) projection (metres). The locations of all sightings/strandings, hereafter referred to as sightings, were converted from Ordnance Survey grid references to decimal degree coordinates (longitude, latitude: WGS84); the year and month of occurrence for all sightings were also determined. These location data were added to the basemap, applying a transformation from WGS84 to BNG. These data were then validated as follows. Records without location data and/or date ( $N = 110$ , 1.5% of records), without species identification ( $N = 444$ , 6.1% of records) were removed. Absence records (no sightings recorded) ( $N = 673$ , 9.3% of records) were removed as there was no record of effort associated with these data and therefore they could not provide a meaningful contribution to the analysis. One individual recorder was identified within the dataset who had contributed data

between 2004 and 2009 ( $N = 951$ , 13.2% of records) from a single location, Harlech Bay, North Wales, (~5.5 km of coastline). As these data, in part, conformed to a pseudo-standardized survey method they were removed to minimize bias and analysed separately. In total, 5051 records were retained for eight species of Cnidaria. Each of these remaining records represented single or multiple sightings, beached or at sea.

### Statistical analysis

To investigate any relationship between sightings by year and preceding winter NAO (December, January, February and March) climate indices data were sourced (UCAR, 2013). To contextualize the number of yearly records received in relation to public awareness of the sightings scheme, a measure of yearly promotional effort (number of press hits that publicised the scheme) for printed media (2003 to 2010) was categorized using an ordinal scale of 1 (minimum) to 3 (maximum).

Spearman's rank correlations were calculated to investigate any relationship within our data between sightings by year as a proportion of all sightings and (a) preceding winter NAO and (b) promotional effort of the database. Generalized linear modelling (GLM) was used to investigate species-specific sightings as proportion of all sightings by year. Statistical analysis was undertaken with the program R (R Development Core Team, 2008).

To calculate the density of sightings we used a polygon sampling grid, divided by UK regional areas, to sum the coincident length of coastline and sightings locations for each polygon. This enabled us to calculate sightings  $\text{km}^{-1}$  for each region. To ascertain a spatial pattern of species richness we used a polygon sampling grid of  $50 \times 50$  km squares to sum individual species occurring in each grid square. To investigate the potential for spatial patterns in cnidarian aggregations we used the same polygon sampling grid to sum individual species-specific sightings of 100 Cnidaria or more.

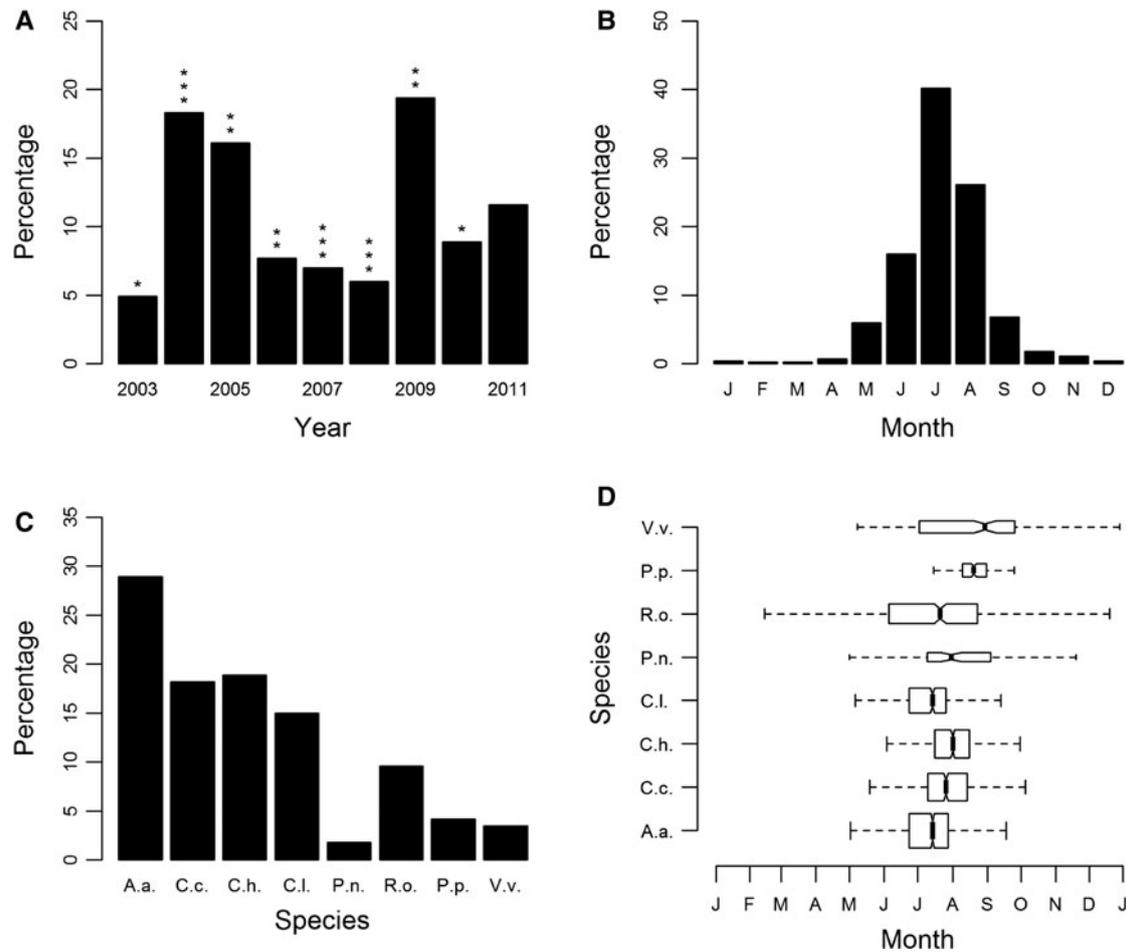
## RESULTS

### Temporal variation and species composition

#### MAIN DATABASE

Sightings of jellyfish fluctuated annually, with peak years being 2004, 2005 and 2009 (Figure 1A; Supplementary Figure S2). There was no statistically significant correlation between yearly sightings and promotional effort of the scheme or between yearly sightings and winter NAO. Seasonality was clearly evident, with the number of records peaking in the months of June, July and August (Figure 1B).

The most commonly sighted species was *Aurelia aurita* ( $N = 1460$ , 28.9% (of validated records)), there were also regular sightings for *Cyanea capillata* ( $N = 920$ , 18.2%), *Chrysaora hysoscella* ( $N = 955$ , 18.9%), *Cyanea lamarckii* ( $N = 756$ , 15%) and *Rhizostoma octopus* ( $N = 483$ , 9.6%) (Figure 1C). Of these, *R. octopus* was the only species with year-round presence (Figure 1D). The only other scyphozoan or 'true' jellyfish, *Pelagia noctiluca* was only recorded occasionally ( $N = 91$ , 1.8%), with infrequent sightings (Supplementary Figure S3E). *Chrysaora hysoscella* sightings significantly decreased during this study (GLM:  $F_{1,7} = 12.39$ ,



**Fig. 1.** Sightings for all cnidarian species expressed as a percentage of sightings from 2003 to 2011 (main database): (A) by year; (B) by month; (C) species-specific sightings expressed as a percentage of all sightings from 2003 to 2011; (D) species-specific sightings by month. Box shows median and inter-quartile ranges. Box widths are proportional to the square-roots of the number of observations in the box, outliers are not drawn. In (A) asterisks indicate an assessment of the yearly promotional effort of the jellyfish sightings scheme categorized using an ordinal scale of 1 (minimum) to 3 (maximum) promotional effort. In (C) and (D) species are identified as follows: A.a., *Aurelia aurita*; C.c., *Cyanea capillata*; C.h., *Chrysaora hysoscella*; C.l., *Cyanea lamarckii*; P.n., *Pelagia noctiluca*; R.o., *Rhizostoma octopus*; P.p., *Physalia physalis*; V.v., *Verella verella*.

$P < 0.01$ ); this was the only species for which there was a statistically significant trend. The Hydrozoa, *Physalia physalis* ( $N = 211$ , 4.2%) and *Verella verella* ( $N = 175$ , 3.5%) were also recorded infrequently with *P. physalis* having a very short sightings season (Figure 1D), with the vast majority of sightings occurring in 2008 and 2009; 93% of all *P. physalis* records were attributable to these years (Supplementary Figure S3G).

#### HARLECH BAY DATABASE

Peak years for sightings of jellyfish from Harlech Bay (location map: inset Figure 2C) were 2004, 2005 and 2006; records of sightings were lower for 2007, 2008 and 2009. There were no sightings data available for 2003, 2010 or 2011 (Figure 2A). Seasonality was clearly evident with the number of records peaking in the months of June and July (Figure 2B).

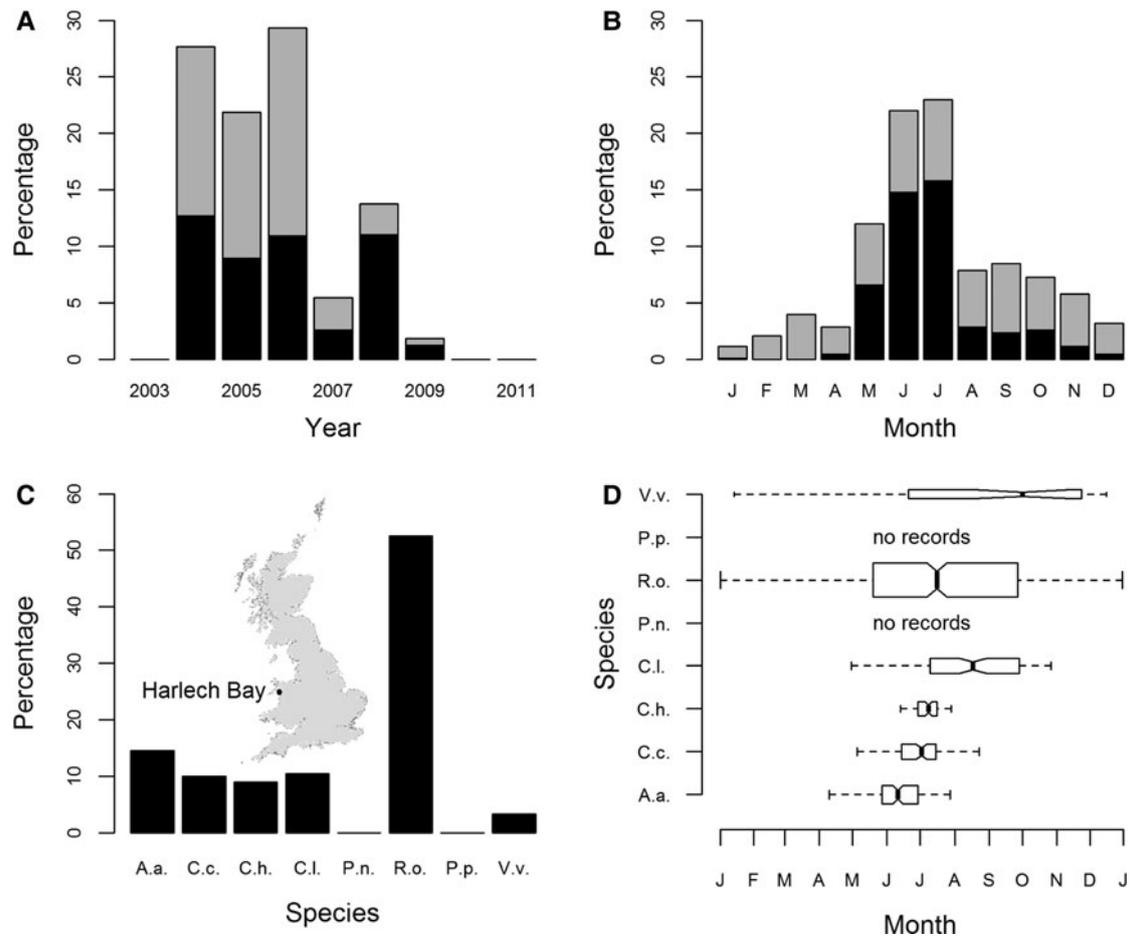
The most commonly sighted species was *R. octopus* ( $N = 499$ , 52.5% (of validated records)) (Figure 2C). Five other species were regularly sighted: *A. aurita* ( $N = 139$ , 14.6%); *C. capillata* ( $N = 95$ , 10%); *C. hysoscella* ( $N = 86$ , 9%); *C. lamarckii* ( $N = 100$ , 10.5%); and *V. verella* ( $N = 32$ , 3.4%). Of these, *R. octopus* and *V. verella* were sighted throughout

the year (Figure 2D). There was a marked decrease in the proportion of *R. octopus* sightings in 2008 and 2009, 20% and 33% of annual sightings, respectively, compared with the peak year for *R. octopus* sightings 2006, 63% of annual sightings (Supplementary Figure S4E). There were no recorded sightings for *P. noctiluca* or *P. physalis* (Figure 2D).

#### Spatial distribution

Within the main database for UK coastal waters (excluding the Republic of Ireland) the greatest number of sightings were from western shores (Figure 3A; Table 1). The south-west had the highest density of sightings (0.64 sightings  $\text{km}^{-1}$ ), higher than the north-east (0.22 sightings  $\text{km}^{-1}$ ), the north-west (including Northern Ireland) (0.15 sightings  $\text{km}^{-1}$ ) and the south-east, which presented the lowest (0.13 sightings  $\text{km}^{-1}$ ); species richness was also greatest in the south-west (Figure 4A). The Bristol Channel had the highest incidence of species-specific cnidarian aggregations (Figure 4B).

Of the most commonly sighted species, *A. aurita* were ubiquitously distributed (Figure 3B), *C. capillata* and *C. hysoscella* had a clear north/south divide in their distributions (Figure 3C, D) and *C. lamarckii* had a greater number of sightings



**Fig. 2.** Sightings for all cnidarian species expressed as a percentage of sightings from 2004 to 2009 (Harlech Bay database); (A) by year; (B) by month; (C) species-specific sightings expressed as a percentage of all sightings from 2004 to 2009; (D) species-specific sightings by month. Box widths are proportional to the square-roots of the number of observations in the box, outliers are not drawn. In (A) and (B) *R. octopus* sightings are shown as mid-grey, all other species as black. In (C) and (D) species are identified as in Figure 1. The inset in part (C) shows the location of Harlech Bay in relation to the UK.

to the south-west and north-east (Figure 3E). The key areas for sightings of *R. octopus* were the coastal waters of Wales and western Scotland (Figure 3G). *Pelagia noctiluca*, *P. physalis* and *V. veleva* were predominantly sighted to the south and west of the UK (Figure 3F, H, I).

## DISCUSSION

Six species of scyphomedusae are indigenous to UK coastal waters (Russell, 1970). A typical scyphozoan life cycle results in adult medusae being present in the water column during the summer months (Figure 5). The presence of adult medusae then characteristically decreases through the autumn once eggs or planulae have been released. With the exception of the holopelagic *Pelagia noctiluca*, a suitable shallow, shaded, benthic substrata is required for attachment of these planulae and further development of the scyphistoma (Russell, 1970). Both the main sightings database and the Harlech Bay subset reflected this life cycle, with seasonality of sightings of adult medusae clearly evident. The majority of Scyphozoa sightings occurred in the months of June, July and August; *Aurelia aurita* and *Cyanea lamarckii* appeared earlier in the season than *Cyanea capillata* and *Chrysaora hysoscella*, similar patterns have been previously recorded

(e.g. Doyle *et al.*, 2007; Bastian *et al.*, 2011a). *Rhizostoma octopus* had the longest sighting season of all Scyphozoa, which may be attributable to this species surviving into winter at greater depths (Russell, 1970). The seasonality of *R. octopus* sightings also reflected previous studies (Doyle *et al.*, 2007).

Seasonality of Hydrozoa sightings varied considerably. Within the main database *Veleva veleva* were sighted March to January whereas *Physalia physalis* were predominantly sighted in late August, this was driven by mass sightings events in 2008 and 2009. Within the Harlech Bay data, sightings of *V. veleva* were recorded throughout the year; no sightings were recorded for *P. physalis*. This lack of sightings for *P. physalis* seems contradictory, as both *V. veleva* and *P. physalis* are oceanic, surface free-floating species, and therefore their distribution has the potential to be driven by prevailing wind conditions. *Veleva veleva* and *P. physalis* had similar spatial distribution patterns, with the majority of sightings from south-west shores. However, closer inspection revealed that *P. physalis* tended to be concentrated to the south of this region and *V. veleva* to the north. This fine-scale nuance in distribution may be an artefact of *P. physalis* sightings being associated with the mass sightings events of 2008 and 2009.

There was no clear temporal trend in annual cnidarian sightings within the main database or the Harlech Bay

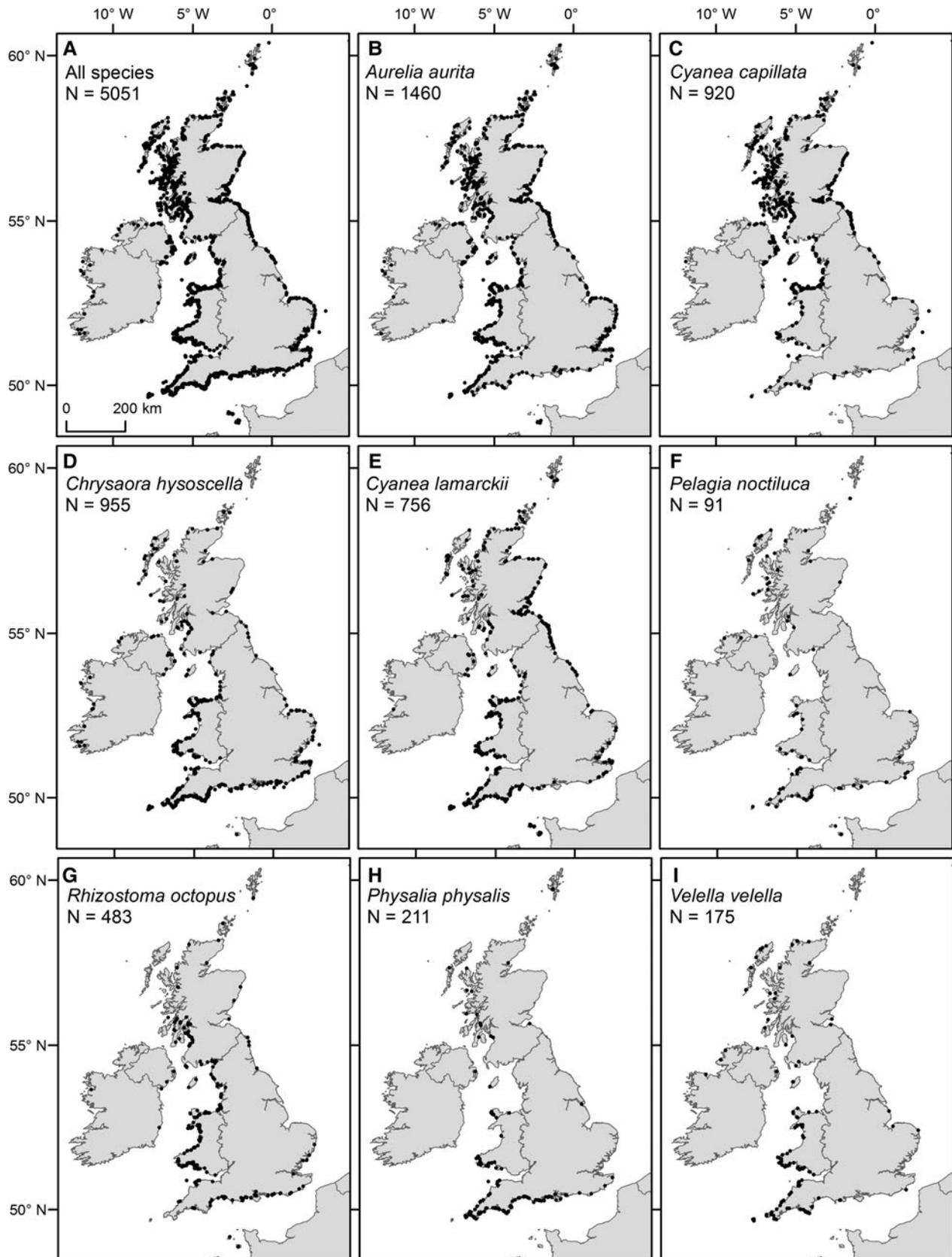
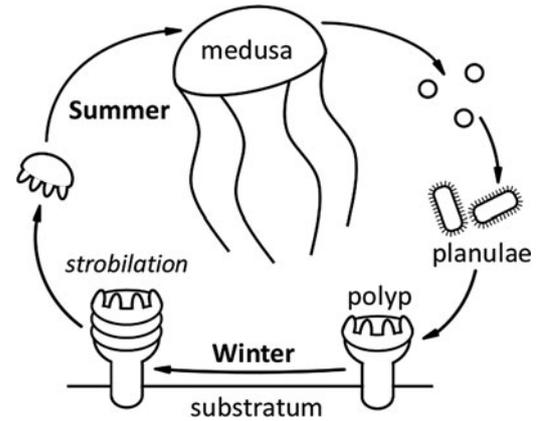


Fig. 3. Spatial distribution of sightings from 2003 to 2011 (main database), for (A) all species and (B–I) specified species, as detailed in figure parts.

**Table 1.** Cnidaria sightings for UK coastal regions as defined in Figure 4B.

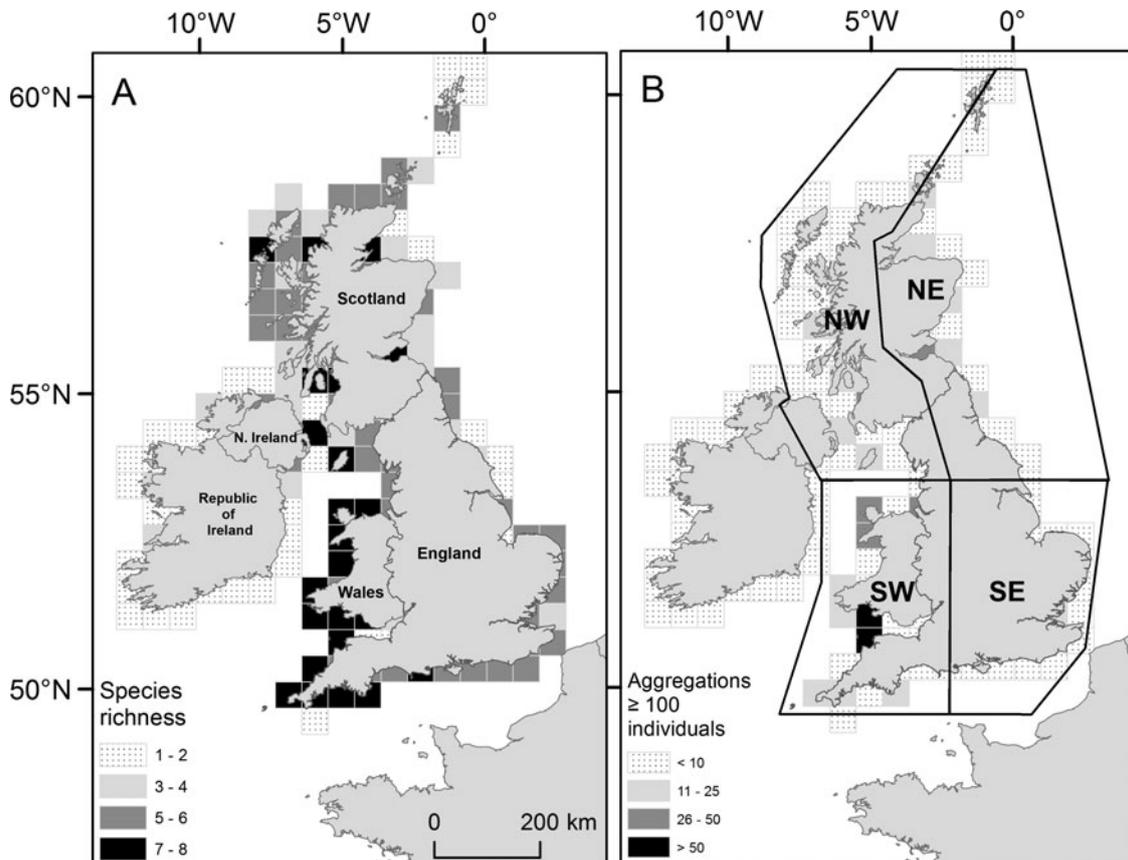
UK region	Total sightings	Coastal length (km)	Sightings ( $\text{km}^{-1}$ )
North-east	763	3480	0.22
North-west (including Northern Ireland)	1387	9381	0.15
South-east	453	3391	0.13
South-west	2376	3709	0.64

subset; however, sightings from Harlech Bay decreased between 2007 and 2009. This decrease may be attributable to a diminished survey effort, although preceding years represented near continuous survey effort (MCS, personal communication). The main database showed inter-annual variability with notable peaks and troughs. There was no correlation between these and promotional effort of the sightings scheme or NAO. Timing and periodicity of recruitment of planulae to the seabed depends on a number of biotic and abiotic factors, such as sexual maturation and reproductive strategy of the medusa, water temperature and turbulence, and physical characteristics of the substratum (Lucas, 2001). Subsequent development of the scyphistoma (budding/strobilation), has been linked with factors such as temperature, salinity, light intensity and photoperiod (e.g. Purcell,



**Fig. 5.** A typical Scyphozoa life cycle. A suitable shallow, shaded, benthic substrata is required for attachment of planulae and further development of the scyphistoma. Note: *Pelagia noctiluca* is an oceanic species with direct development and has no benthic stage; *C. hysoscella* is a hermaphrodite (Russell, 1970).

2007), dissolved oxygen concentrations (Condon *et al.*, 2001) and prey availability (Han & Uye, 2010). Inter-annual variability may also be driven by hydroclimatic forcing such as wind stress, temperature or currents (Lynam *et al.*, 2004) or through transition in climate regimes (Brodeur *et al.*, 2008). There is also evidence for contrasting relationships



**Fig. 4.** (A) Species richness for Cnidaria sighted from 2003 to 2011 (main database) in UK coastal waters. Total number of individual species present summed by a  $50 \times 50$  km sampling grid; (B) Cnidaria aggregations for UK coastal waters from 2003 to 2011 (main database). Species-specific sightings of 100 Cnidaria or more were summed using the same sampling grid as in (A). (A) and (B) are displayed in accordance with their respective monochrome shaded legend. UK regional areas are drawn in part (B): north-west (NW); north-east (NE); south-east (SE); and south-west (SW).

between climate indices and Scyphozoa abundance that may also be related to locally variable oceanographic parameters (Lynam *et al.*, 2005b, 2011; Attrill *et al.*, 2007). As this study holds records for multiple species over a wide spatial extent, it is unlikely that one environmental or biological parameter can explain variability in temporal trends. The observed patterns are likely manifest from environmental forcing resulting in a combination of environmental and biological drivers influencing species biology.

Species-specific inter-annual variability was also evident, and the records of no one cnidarian species displayed a uniform temporal pattern. There was a significant decreasing trend for *C. hysoscella*. However, our data spans a short time-frame (9 years) and this trend may not be representative of long-term trends. Indeed, evidence exists for worldwide oscillations in jellyfish populations of approximate 20 year periodicity (Condon *et al.*, 2013). However, robust detection of trends in jellyfish populations are hampered by a lack of a defined baseline; more specifically there is a paucity of long-term data sets, >20 years (Condon *et al.*, 2012).

The south-west region had the highest number of sightings (and greatest coastline densities), greatest species richness, and also had the highest incidence of cnidarian aggregations. *Aurelia aurita* were universally distributed throughout the regions with highest abundance of all species, this is recognized as a cosmopolitan species (Russell, 1970; Lucas, 2001). However, there were clear geographical demarcations between some species; *C. hysoscella* were nearly always observed in southerly waters, whereas *C. capillata* were sighted in northerly waters. This spatial delineation probably reflects the availability of suitable thermal niches for these species (Holst, 2012). *Rhizostoma octopus* were principally sighted in coastal waters of western Scotland and Wales. The Harlech Bay database identified this area as a hotspot for *R. octopus*, with this species accounting for 57% of all sightings between 2004 and 2007, although there was a marked decrease of sightings during 2008/2009, the reason for which is unclear. *Pelagia noctiluca* were primarily sighted in south-west and north-west waters. There were no sightings from Harlech Bay. This is an oceanic species with direct development (no benthic life cycle stage), and is previously described as occurring off western shores in association with oceanic waters (Russell, 1970). The distribution patterns for *V. velilla* and *P. physalis* were comparable to each other, with the majority of sightings from south-west shores. As south-westerly winds prevail for winter, summer and autumn across the UK (Lapworth & McGregor, 2008) these spatial patterns potentially reflect the wind conditions at the time, driving the distribution of these free-floating surface species.

Without quantification of sightings effort, analysis of incidentally collected data should be made cautiously. However, data collected through citizen-science schemes can provide a valuable resource (Silvertown, 2009), and with appropriate care, these data can provide an insight into species' regional and national patterns and trends (Pikesley *et al.*, 2012; Witt *et al.*, 2012). In this study, incidentally-collected data for cnidarian species have been seen to reflect previously-documented temporal and spatial patterns. In addition, data collected from a single location over a significant timescale have revealed location-specific trends.

Although studies of this nature may not be able to isolate the drivers behind observed patterns, they can provide for

large-scale (spatial and temporal) coverage that would otherwise be logistically and financially unfeasible. We also suggest that they have the potential to contribute significantly to baselines, providing both seasonality and distribution data (particularly when data are derived from survey schemes that are ongoing), from which future changes in patterns or trends may be identified. The likelihood of important insights being more robustly elaborated would be greatly increased by the incorporation of focused, effort-corrected surveys at locations along the UK coastline, including all nil returns, in at least some locations across the geographical footprint of the project.

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## Supplementary materials and methods

The supplementary material referred to in this paper can be found online at [journals.cambridge.org/mbi](http://journals.cambridge.org/mbi).

## REFERENCES

- Attrill M.J., Wright J. and Edwards M. (2007) Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnology and Oceanography* 52, 480–485.
- Bastian T., Haberlin D., Purcell J.E., Hays G.C., Davenport J., McAllen R. and Doyle T.K. (2011a) Large-scale sampling reveals the spatio-temporal distributions of the jellyfish *Aurelia aurita* and *Cyanea capillata* in the Irish Sea. *Marine Biology* 158, 2639–2652.
- Bastian T., Stokes D., Kelleher J.E., Hays G.C., Davenport J. and Doyle T.K. (2011b) Fisheries bycatch data provide insights into the distribution of the mauve stinger (*Pelagia noctiluca*) around Ireland. *ICES Journal of Marine Science* 68, 436–443.
- Brodeur R.D., Decker M.B., Ciannelli L., Purcell J.E., Bond N.A., Stabeno P.J., Acuna E. and Hunt Jr G.L. (2008) Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. *Progress in Oceanography* 77, 103–111.
- Brodeur R.D., Sugisaki H. and Hunt Jr G.L. (2002) Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Marine Ecology Progress Series* 233, 89–103.
- Condon R.H., Decker M.B. and Purcell J.E. (2001) Effects of low dissolved oxygen on survival and asexual reproduction of scyphozoan polyps (*Chrysaora quinquecirrha*). *Hydrobiologia* 451, 89–95.
- Condon R.H., Duarte C.M., Pitt K.A., Robinson K.L., Lucas C.H., Sutherland K.R., Mianzan H.W., Bogeberg M., Purcell J.E., Decker M.B., Uye S., Madin L.P., Brodeur R.D., Haddock S.H.D.,

- Malej A., Parry G.D., Eriksen E., Quiñones J., Acha M., Harvey M., Arthur J.M. and Graham W.M. (2013) Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences of the United States of America* 110, 1000–1005.
- Condon R.H., Graham W.M., Duarte C.M., Pitt K.A., Lucas C.H., Haddock S.H.D., Sutherland K.R., Robinson K.L., Dawson M.N., Decker M.B., Mills C.E., Purcell J.E., Malej A., Mianzan H., Uye S., Gelcich S. and Madin L.P. (2012) Questioning the rise of gelatinous zooplankton in the world's oceans. *BioScience* 62, 160–169.
- Doyle T.K., Houghton J.D., Buckley S.M., Hays G.C. and Davenport J. (2007) The broad-scale distribution of five jellyfish species across a temperate coastal environment. *Hydrobiologia* 579, 29–39.
- Han C.-H. and Uye S. (2010) Combined effects of food supply and temperature on asexual reproduction and somatic growth of polyps of the common jellyfish *Aurelia aurita* s.l. *Plankton and Benthos Research* 5, 98–105.
- Hays G.C., Bastian T., Doyle T.K., Fossette S., Gleiss A.C., Gravenor M.B., Hobson V.J., Humphries N.E., Lilley M.K., Pade N.G. and Sims D.W. (2011) High activity and Lévy searches: jellyfish can search the water column like fish. *Proceedings of the Royal Society, B* 279, 465–473.
- Hays G.C., Richardson A.J. and Robinson C. (2005) Climate change and marine plankton. *Trends in Ecology and Evolution* 20, 337–344.
- Holst S. (2012) Effects of climate warming on strobilation and ephyra production of North Sea scyphozoan jellyfish. *Hydrobiologia* 690, 1–14.
- Houghton J.D., Doyle T.K., Davenport J. and Hays G.C. (2006a) The ocean sunfish *Mola mola*: insights into distribution, abundance and behaviour in the Irish and Celtic Seas. *Journal of the Marine Biological Association of the United Kingdom* 86, 1237–1243.
- Houghton J.D., Doyle T.K., Wilson M.W., Davenport J. and Hays G.C. (2006b) Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. *Ecology* 87, 1967–1972.
- Lapworth A. and McGregor J. (2008) Seasonal variation of the prevailing wind direction in Britain. *Weather* 63, 365–368.
- Leeney R.H., Amies R., Broderick A.C., Witt M.J., Loveridge J., Doyle J. and Godley B.J. (2008) Spatio-temporal analysis of cetacean strandings and bycatch in a UK fisheries hotspot. *Biodiversity and Conservation* 17, 2323–2338.
- Lilley M.K.S., Houghton J.D.R. and Hays G.C. (2009) Distribution, extent of inter-annual variability and diet of the bloom-forming jellyfish *Rhizostoma* in European waters. *Journal of the Marine Biological Association of the United Kingdom* 89, 39–48.
- Lucas C.H. (2001) Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia* 451, 229–246.
- Lynam C.P., Gibbons M.J., Axelsen B.E., Sparks C.A., Coetzee J., Heywood B.G. and Brierley A.S. (2006) Jellyfish overtake fish in a heavily fished ecosystem. *Current Biology* 16, 492.
- Lynam C.P., Hay S.J. and Brierley A.S. (2004) Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnology and Oceanography* 49, 637–643.
- Lynam C.P., Hay S.J. and Brierley A.S. (2005b) Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. *Journal of the Marine Biological Association of the United Kingdom* 85, 435–450.
- Lynam C.P., Heath M.R., Hay S.J. and Brierley A.S. (2005a) Evidence for impacts by jellyfish on North Sea herring recruitment. *Marine Ecology Progress Series* 298, 157–167.
- Lynam C.P., Lilley M.K.S., Bastian T., Doyle T.K., Beggs S.E. and Hays G.C. (2011) Have jellyfish in the Irish Sea benefited from climate change and overfishing? *Global Change Biology* 17, 767–782.
- Mills C.E. (2001) Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* 451, 55–68.
- Pauly D., Christensen V., Dalsgaard J., Froese R. and Torres Jr F. (1998) Fishing down marine food webs. *Science* 279, 860–863.
- Pikesley S.K., Witt M.J., Hardy T., Loveridge J., Loveridge J., Williams R. and Godley B.J. (2012) Cetacean sightings and strandings: evidence for spatial and temporal trends? *Journal of the Marine Biological Association of the United Kingdom* 92, 1809–1820.
- Purcell J.E. (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. *Journal of the Marine Biological Association of the United Kingdom* 85, 461–476.
- Purcell J.E. (2007) Environmental effects on asexual reproduction rates of the scyphozoan *Aurelia labiata*. *Marine Ecology Progress Series* 348, 183–196.
- Purcell J.E. (2009) Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. *Hydrobiologia* 616, 23–50.
- Purcell J.E., Uye S.-I. and Lo W.-T. (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series* 350, 153–174.
- R Development Core Team (2008) *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at: <http://www.Rproject.org> (accessed 8 May 2014).
- Richardson A.J., Bakun A., Hays G.C. and Gibbons M.J. (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology and Evolution* 24, 312–322.
- Russell F.S. (1970) *The medusae of the British Isles II. Pelagic Scyphozoa with a supplement to the first volume on hydromedusae*. Cambridge: Cambridge University Press.
- Silvertown J. (2009) A new dawn for citizen science. *Trends in Ecology and Evolution* 24, 467–471.
- UCAR (2013) Hurrell PC-Based North Atlantic Oscillation Index (Monthly). <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based> (accessed 4 March 2013).
- Witt M.J., Broderick A.C., Johns D.J., Martin C., Penrose R., Hoogmoed M.S. and Godley B.J. (2007) Prey landscapes help identify potential foraging habitats for leatherback turtles in the NE Atlantic. *Marine Ecology Progress Series* 337, 231–243.
- and
- Witt M.J., Hardy T., Johnson L., McClellan C.M., Pikesley S.K., Ranger S., Richardson P.B., Solandt J.-L., Speedie C. and Williams R. (2012) Basking sharks in the northeast Atlantic: spatio-temporal trends from sightings in UK waters. *Marine Ecology Progress Series* 459, 121–134.

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