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

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INTRODUCTION

The past decade has seen concerns expressed over blooms, future bio-geographical 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, 2009; Richardson et al., 2009). Gelatinous plankton (subsequently referred to as jellyfish) blooms in coastal waters can have negative implications for 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 (2003–2012; 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 lacks 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

Submitted 18 September 2013; accepted 20 January 2014

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Concern has been expressed over future bio-geographical 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 (2003–2012; 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 lacks 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.

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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 United Kingdom, an extensive review of historic literature (ca 100 years) (Russell, 1970) exists, and more recently, jellyfish medusa studies have focused on the waters of the Celtic, Irish, North Seas and 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 bycatch; 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; Leeney et al., 2008; Pikeyley et al., 2012; Witt et al., 2012). In the UK, a 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 and Lesueur, 1810) (blue), Pelagia noctiluca (Forsskål, 1775) (mauve stinger) and Rhizostoma octopus (Macrì, 1778) (root mouth or barrel) and two species of the Class Hydrozoa; Physalia physalis (Linnaeus, 1758) (Portuguese man-of-war) and Velella velella (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.

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 medusa. 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 7239 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 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 km⁻¹ for each region. To ascertain a spatial pattern of species richness we used a polygon sampling grid of 50 x 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). C. hysoscella sightings significantly decreased during this study (GLM: F₁,7 = 12.39, 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 Velella velella (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. velella (N = 32, 3.4%). Of these, R. octopus and V. velella 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 km<sup>-1</sup>), higher than the north-east (0.22 sightings km<sup>-1</sup>), the north-west (including Northern Ireland) (0.15 sightings km<sup>-1</sup>) and the south-east, which presented the lowest (0.13 sightings km<sup>-1</sup>); 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 (Figures 3C, D) and C. lamarckii had a greater number of sightings to the south-west and north-east (Figure 3E). The key area...
for sightings of *R. octopus* were the coastal waters of Wales and western Scotland (Figure 3G). *P. noctiluca*, *P. physalis* and *V. velella* were predominantly sighted to the south and west of the UK (Figures 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 holoplagic *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 *Velella velella* were sighted March to January whereas *Physalia physalis* were predominantly sighted in winter at greater depths (Russell, 1970). The seasonality of *R. octopus* sightings also reflected previous studies (Doyle et al., 2007).

There was no clear temporal trend in annual cnidarian sightings within the main database or the Harlech Bay subset; however, sightings from Harlech Bay decreased
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.
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, 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 between climate indices and Scyphozoa abundance that may also be

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

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<td>South-west</td>
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Fig. 4. A typical Scyphozoa life cycle. Sexes are distinct except in C. hysoscella, which is hermaphrodite. A suitable shallow, shaded, benthic substrata is required for attachment of planulae and further development of the scyphistoma. Note: P. noctiluca is an oceanic species with direct development and has no benthic stages.
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. *A. aurita* were universally distributed throughout the regions with highest abundance of all species, and are recognized as a cosmopolitan species (Russell, 1970; Lucas, 2001). However, there were clear geographic demarcation 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). *R. 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. *P. 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. velella* 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 baseline data, 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 geographic footprint of the project.

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The authors thank all participants in the Marine Conservation Society (MCS) jellyfish survey who generously contributed their data. The authors acknowledge the constructive input from two anonymous referees and the Associate Editor.

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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.

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blooms are a consequence of global oscillations. Proceedings of the National Academy of Sciences 110, 1100–1105.


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