

The broad-scale distribution of five jellyfish species across a temperate coastal environment

Thomas K. Doyle · Jonathan D. R. Houghton ·
Sarah M. Buckley · Graeme C. Hays ·
John Davenport

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Abstract Jellyfish (medusae) are sometimes the most noticeable and abundant members of coastal planktonic communities, yet ironically, this high conspicuousness is not reflected in our overall understanding of their spatial distributions across large expanses of water. Here, we set out to elucidate the spatial (and temporal) patterns for five jellyfish species (Phylum Cnidaria, Orders Rhizostomeae and Semaestomeae) across the Irish & Celtic Seas, an extensive shelf-sea area at Europe's northwesterly margin encompassing several thousand square kilometers. Data were gathered using two independent methods: (1) surface-counts of jellyfish from ships of opportunity, and (2) regular shoreline surveys for

stranding events over three consecutive years. Jellyfish species displayed distinct species-specific distributions, with an apparent segregation of some species. Furthermore, a different species composition was noticeable between the northern and southern parts of the study area. Most importantly, our data suggests that jellyfish distributions broadly reflect the major hydrographic regimes (and associated physical discontinuities) of the study area, with mixed water masses possibly acting as a trophic barrier or non-favourable environment for the successful growth and reproduction of jellyfish species.

Keywords Irish Sea · Hydrographic regimes · Rhizostomeae · Semaestomeae

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T. K. Doyle (✉)
Environmental Research Institute,
University College Cork, Lee Road,
Cork, Ireland
e-mail: t.doyle@ucc.ie

J. D. R. Houghton · G. C. Hays
Institute of Environmental Sustainability,
School of the Environment and Society,
University of Wales Swansea, Singleton Park,
SA2 8PP Swansea, UK

S. M. Buckley · J. Davenport · T. K. Doyle
Department of Zoology, Ecology and Plant Sciences,
University College Cork, Distillery Fields,
North Mall Cork, Ireland

Introduction

The ecological role of jellyfish (more specifically medusae of the Phylum Cnidaria: Orders Rhizostomeae and Semaestomeae) within coastal marine systems has received much recent attention. This interest has been largely driven by the propensity of jellyfish to form extensive nuisance blooms and their associated socio-economic effects (CIESM, 2001). For example, during the 1980s blooms of *Pelagia noctiluca* occurred throughout the Mediterranean and caused widespread concern to both fishermen and tourists

(CIESM, 2001). Since then, many other examples of jellyfish blooms impacting negatively on economies have been reported worldwide (e.g. Graham et al., 2003; Kawahara et al., 2006). This was recently illustrated by the outbreak of *Sanderia malayensis* in the Yangtze Estuary for the first time in 2004 that resulted in fisheries being dominated by a 98% jellyfish by-catch (Xian et al., 2005).

There is also a concern that jellyfish might capitalise upon the niche left by the removal of top predators (e.g. planktivorous fish), with once abundant fish stocks being replaced by jellyfish-dominated communities (Brierley et al., 2005). Such regime shifts might be further exacerbated by increased eutrophication and climate change that are intrinsically linked to global human population trends (Cloern, 2001), suggesting that this issue may remain highly topical for the foreseeable future. However, our ability to respond to these globally important issues is often hampered by a lack of baseline data. Indeed, Mills (2001) remarked that research efforts should be redirected towards the study of the population dynamics of some of the common and abundant jellyfish species, about which we know next to nothing beyond their names.

An area where this problem has recently come to light is the Irish and Celtic Seas, an extensive shelf-sea area at Europe's northwesterly margin spanning several thousand square kilometers. Despite being one of the most intensively studied bodies of water in the world (Allen et al., 1998; Evans et al., 2003), our overall knowledge of jellyfish biogeography within the region remains largely dependent on the classic studies of Delap (1905) and Russell (1970). Although invaluable, the findings of these previous studies are generally limited to generic statements, with jellyfish described in such terms as northern or southern boreal species (Russell, 1970). To elucidate these patterns further, we collected data for five scyphozoan species over three consecutive years (2003–2005). Given the extensive spatial and temporal coverage of our study, data were gathered using two independent methods: (1) surface-counts of jellyfish from ships of opportunity, and (2) regular shoreline surveys for stranding events. From this, we provide an empirical account of how jellyfish may be distributed across a large,

temperate coastal environment, and comment upon the factors that may ultimately drive observed patterns.

Methods

Study area

The Irish & Celtic Seas form part of the northeast Atlantic shelf seas, represent a network of extensive shallows and have a long and complex coastline (Le Fèvre, 1986). The majority of this seaboard is within the 100 m-depth contour of the continental shelf. Jellyfish data were collected from the southern and central Irish Sea and the northern extreme of the Celtic Sea to the south (51.0° N to 53.5° N and –3.0° W to –11.0° W) (Fig. 1).

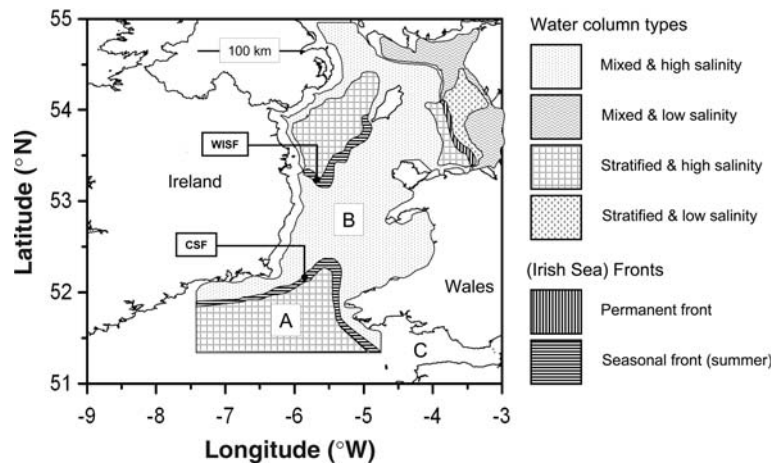
Shoreline surveys

Regular shoreline surveys were carried out across the study area during the period June 2003–September 2005, to record the presence or absence of stranded jellyfish. Surveys were timed to coincide with low tide and constituted an outward leg along the high water mark and a return leg along the waters edge. Jellyfish were identified to species level and tallied using the following categories to give an indication of relative abundance: 0, 1–10, 11–50, 51–100, 101–500, and >500 per length of coastline surveyed. Data were additionally converted to numbers of individuals per 100 m of coastline. Lastly, to derive an indirect measure of seasonality, (and provide baseline data for the Celtic and Irish Seas) shoreline surveys were conducted during each month with the presence of stranded jellyfish taken as evidence that individuals were also present within the water column at that time.

Visual counts from ships of opportunity

Visual counts of jellyfish were made from ships of opportunity (ShOps) traversing the Irish & Celtic Seas during the summer months (June–September)

Fig. 1 Hydrographic map of the main water bodies, and frontal systems within the Celtic and Irish Seas. In respective order, the labels (A), (B) and (C) correspond to the Celtic Sea, Irish Sea and Bristol Channel. CSF, Celtic Sea Front; WISF, Western Irish Sea Front. Figure reproduced from Golding et al. (2004)



of 2004 and 2005. Three independent ferry crossings were utilised that roughly followed the 51.5°, 52.0° and 53.5° N parallels (termed transects T1, T2, and T3). During the entire study period a total of 20 crossings were made (2004: $N = 5$; 2005: $N = 15$). All observations ($N = 4,265$ min) were made from an elevated position from the beam of the ShOps, during daylight hours (07:00–21:00 h) (Fig. 2). Jellyfish were identified to species level, and their numbers estimated per 5-min intervals using the following categories: 0, 1–10, 11–50, 51–100, 101–500, and >500 (Note: jellyfish abundance was on occasion so great that estimates beyond this resolution were impractical). Sample periods were 15 min long with 5-min breaks between successive samples. After three successive sample periods a 20 min break was taken, and after every 3–4 h a 1-h rest period was taken. Location (latitude and longitude), time, sea state (Beaufort Scale) and glare, were recorded every 15 min. Glare was determined using a system of arbitrary octares whereby the field of view is visually divided into eight equal sections, and the number of sections obscured by glare taken as an estimate (Houghton et al., 2006).

To determine the depth of the observational field (i.e. maximum and minimum distances perpendicular from the vessel beyond which estimates of jellyfish abundance were invalid) an independent trial was carried out. Under varying seas states (Beaufort Scale: Force 1–4), 278 random objects (flotsam and jetsam) were

identified from the ferry observation deck (Fig. 2). Angle of inclination (degrees from horizontal) for each object was measured using an inclinometer, and converted to horizontal distance from the vessel using simple trigonometry. Distance of objects from the vessel was plotted on frequency histograms and the spread of data tested for normality (Anderson–Darling normality test). This revealed an interesting pattern with sightings of objects at low sea states (i.e. calm weather $\leq$ force 3 on the Beaufort) being skewed and non-parametric (Anderson–Darling; $P > 0.05$); yet during elevated sea states ($\geq$ force 4 on the Beaufort scale), the distance of sighted objects was normally distributed (Anderson–Darling; $P > 0.05$). Where necessary, data were then normalised, and for all sea states mean distance of objects from vessel calculated (Fig. 2). By use of two standard deviations ($\pm$) as outer limits, the observational field (m) was calculated for each sea state (Fig. 2). Use of this value as width, and the distance travelled in 5-min (calculated from latitude and longitude) as length, jellyfish count data were converted to a density value (indiv./m²). To aid analysis, these values were further converted to indiv./1,000 m².

Sea surface temperature

Sea surface temperature data (independent point estimates for individual days during each month of the year: $N = 23,423$) for the study area were

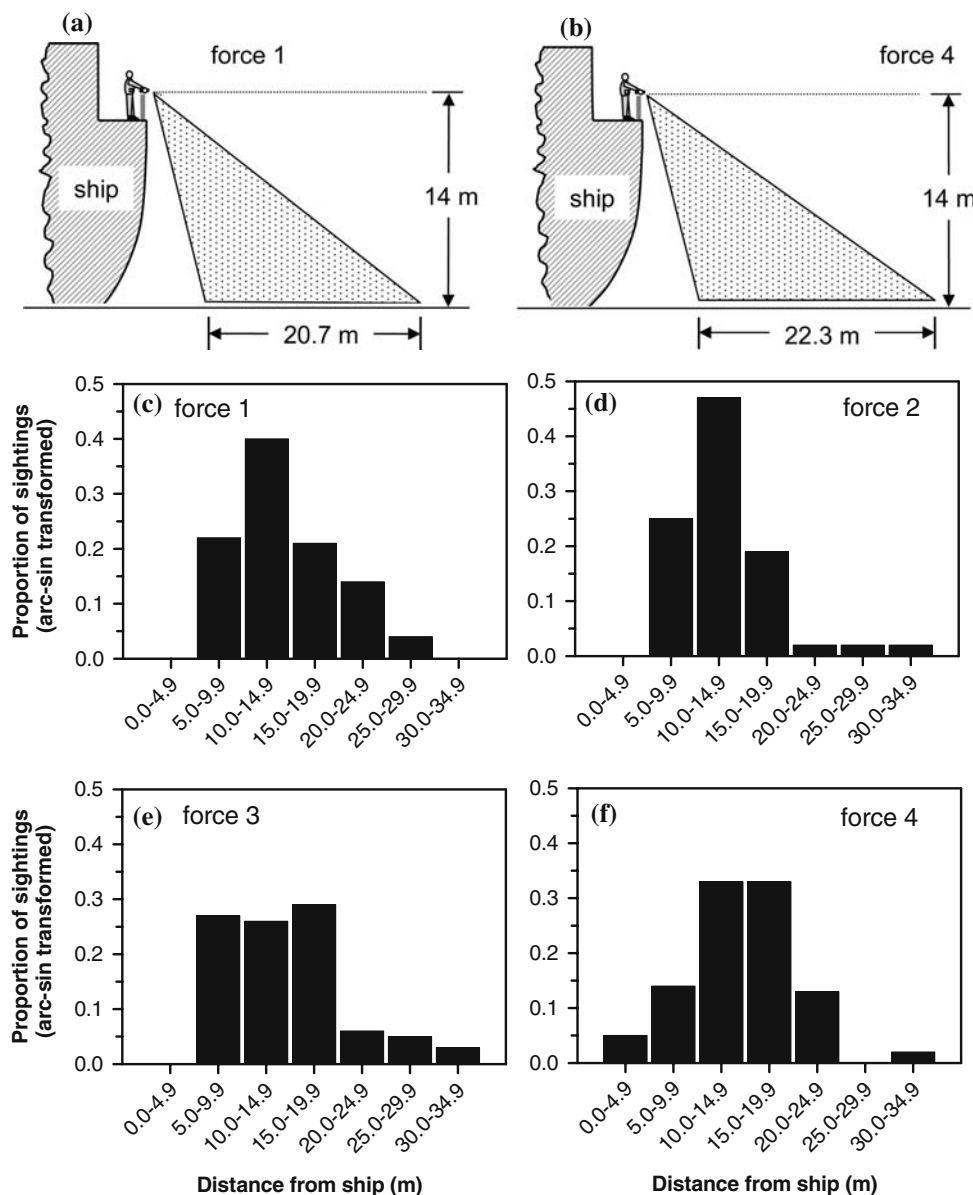


Fig. 2 Inclinator trials to assess detectability of objects under different sea states and the determination of observational fields. **(a)** and **(b)** Observational fields (i.e. the maximum and minimum distance from the observational platform that random object detection becomes unfeasible). The example shows how the observational field was when conditions were calm **(a)** (force 1; Beaufort

scale) narrower than at higher sea states **(b)** (force 4; Beaufort scale). **(c)–(f)** Frequency histograms for random objects sighted under varying sea states. Only at force 4 did the distance of sighted objects become randomly distributed. Sample sizes are as follows: Force 1 **(c)** $N = 106$; Force 2 **(d)** $N = 53$; Force 3 **(e)** $N = 63$; Force 4 **(f)** $N = 56$

obtained from the International Council for Exploration of the Seas (ICES; <http://www.ices.dk/ocean/>). We restricted our analysis to an area 51° N to 55° N and –3.0° W to –9.0° W and

to the years 1975–2004. Data were grouped into latitudinal bands of 1° width (i.e. 51–52° N), and annual mean temperatures and standard deviation determined for each.

Results

Shoreline surveys (1): spatial distribution of jellyfish stranding events

Over the three study years a total of 158 beaches were examined, with >1,200 individual beach surveys conducted (Fig. 3(a)). A total of 609 individual stranding events (defined as >10 individuals per length of coastline (between 0.1 km

and 2 km)) were recorded with >32,000 individual jellyfish examined (Fig. 3; Table 1).

Shoreline surveys (2): seasonality of stranding events

Three species (*Aurelia aurita* L., *Cyanea lamarckii* Péron & Lesueur, and *Chrysaora hysoscella* L.) washed ashore over similar timescales, with

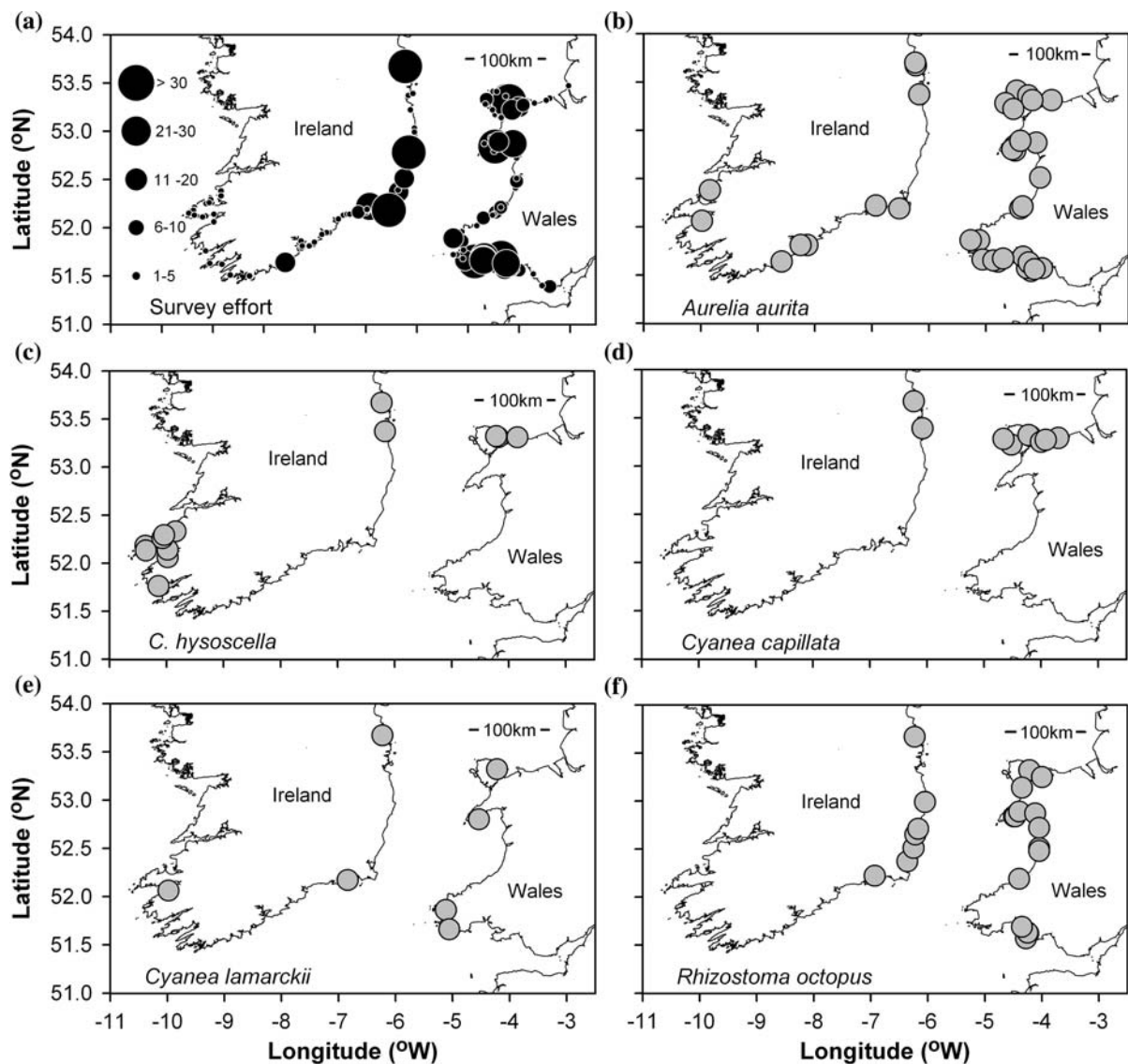


Fig. 3 (a) Survey effort (i.e. the number of times a particular beach was surveyed) during 2003–2005. Relative scale marked on the figure. (b)–(f) The location of jellyfish

stranding events for respective species where the number of individuals to strand was >10 per length of coastline (between 0.1 km and 2 km)

Table 1 Summary of jellyfish stranding data (Ireland and Wales) (2003–2005; $N = 158$ beaches)

	No. of sites recorded (as propn.)	Total no. of indiv. (N)	Total no. of stranding events (N)	Mean no. of stranded indiv. (SD)	Mean standing density (indiv. 100 m ⁻¹) (SD)	Max stranding density in (indiv. 100 m ⁻¹)
<i>A. aurita</i>	0.37	15,745	147	107.1 ± 169.2	15.4 ± 29.5	120
<i>C. hysoscella</i>	0.16	2,160	66	32.7 ± 78.7	3.2 ± 6.1	30
<i>C. capillata</i>	0.11	4,530	91	49.8 ± 94.8	7.3 ± 20.1	120
<i>C. lamarckii</i>	0.13	460	38	12.1 ± 14.7	1.4 ± 2.5	15
<i>R. octopus</i>	0.34	9,370	279	33.6 ± 83.1	4.6 ± 12.4	100

the majority of stranding events occurring between June and July (Fig. 4). However, initial stranding events (i.e. the first time a particular species was observed to strand in a particular year) were more variable between species with *A. aurita* evident in April, *C. lamarckii* in May and *C. hysoscella* in June. *Cyanea capillata* L. however, appeared temporally discrete from the three species already described, with stranded individuals not recorded prior to mid-July, although the overall duration of stranding events occurred over a similar timescale of several months. Lastly, and most notably, *Rhizostoma octopus* L. displayed a quite unique stranding pattern, with the temporal spread of events well in excess of all other species examined (Fig. 4) (c.f. Houghton et al., 2006).

Results from ShOps

Chrysaora hysoscella was frequently observed along T1, but was largely absent from the other two transects T2 & T3 (Figs. 5 and 6). *C. hysos-*

cella did not appear to form spatially discrete aggregations, but was observed for continuous and extensive periods of time at relatively constant densities (ca. 0.11 indiv. 1,000 m⁻²).

Like *C. hysoscella*, *C. lamarckii* was typically observed throughout the length of T1 in low densities (ca. 0.03 indiv. 1,000 m⁻²). The species was largely absent from the central transect (T2) that crossed the southern Irish Sea, although it was observed again in the most northerly transect (T3) near the Irish coast.

Cyanea capillata displayed a marked latitudinal distribution with the species only observed in the most northerly transect (T3). Although the species did not appear to form discrete aggregations (0.02 indiv. 1,000 m⁻²), it was only found in the western half of the crossing closest to the Irish coast.

One species that did form high density (0.33 indiv. 1,000 m⁻²) and spatially discrete aggregations was *A. aurita*. The majority of individuals were observed in two main areas: (1) coastal waters bordering south-west Wales (T1) or (2) close to the Irish coast along T3. In a similar fashion, *R. octopus* formed extensive aggregations close to shore, almost exclusively towards the westerly end of T2, although individuals were occasionally spotted in open water (0.09 indiv. 1,000 m⁻²).

Sea surface temperature

Mean sea surface temperature decreased with latitude in a northerly direction (Fig. 7) ($F_{1,3} = 40.89$, $r^2 = 0.91$, $P < 0.05$). The overall range of temperatures did not increase in a linear fashion ($P > 0.05$) but rather appeared to increase distinctly between 52° N and 54° N, with the minimum (1°C) and maximum temperatures

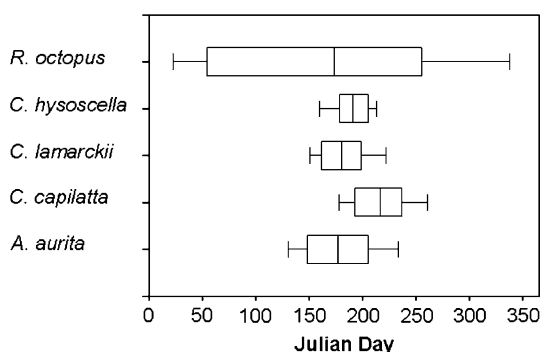


Fig. 4 Seasonality of jellyfish stranding events. The mid-line within each box represents the median stranding date for respective species. Boxes represent 1st and 3rd quartiles (i.e. encompassing 50% of all stranding events) with 90% of all stranding events bounded by the error bars

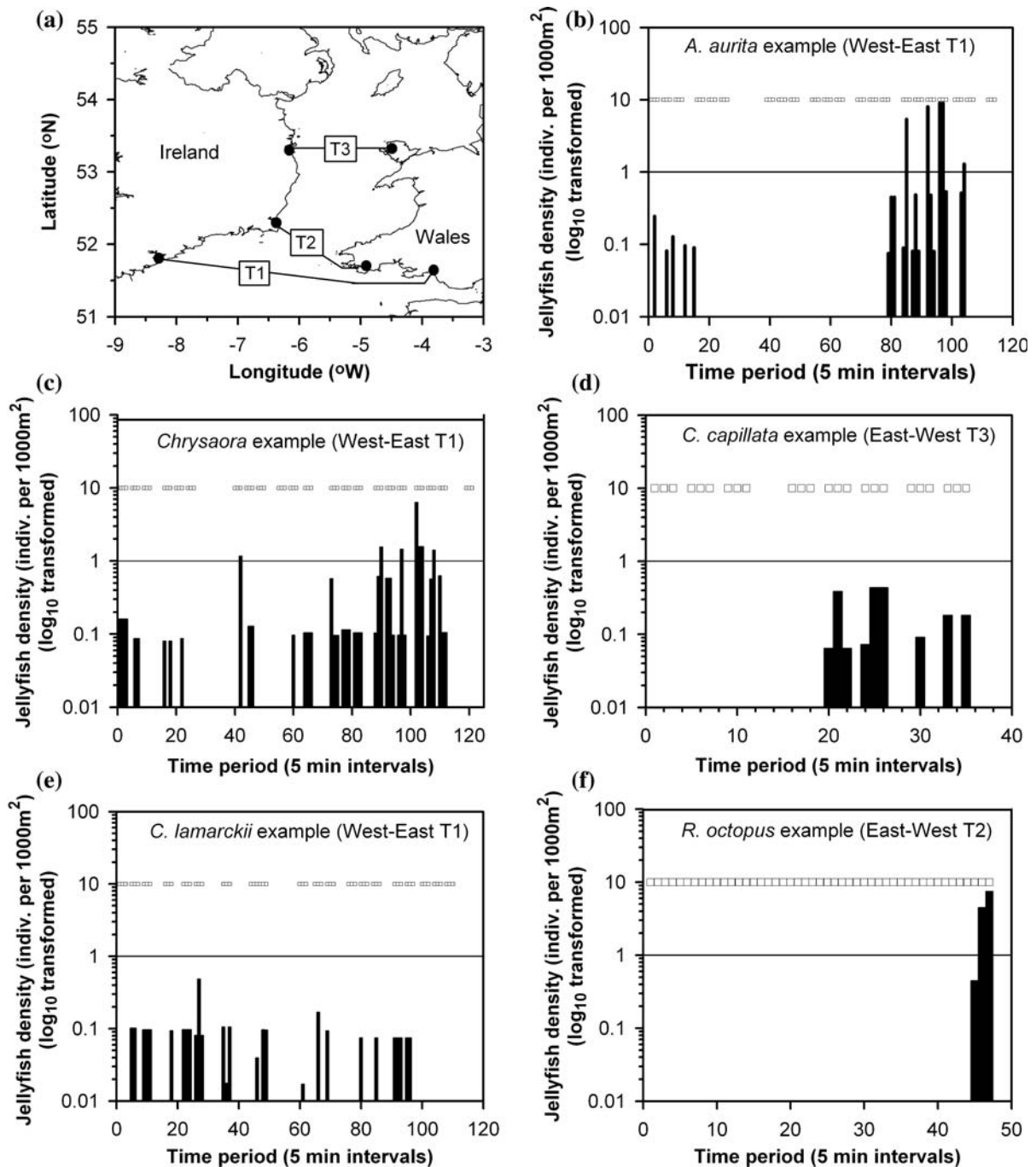


Fig. 5 (a) Three transects used for at-sea estimates of jellyfish abundance termed T1–T3, respectively. (b)–(f) Examples for each species showing the density of jellyfish recorded in each 5-min time period. The temporal patterns of sampling (i.e. periods when data were collected) are

shown by (□). Full coverage was not attempted as the integrity of the abundance estimates would have decreased through observer fatigue. Regular, short breaks were recorded in each 5-min time period. The temporal patterns were subsequently taken. Direction of travel (e.g. east–west) and transect identifier (T1–T3) are marked on each figure

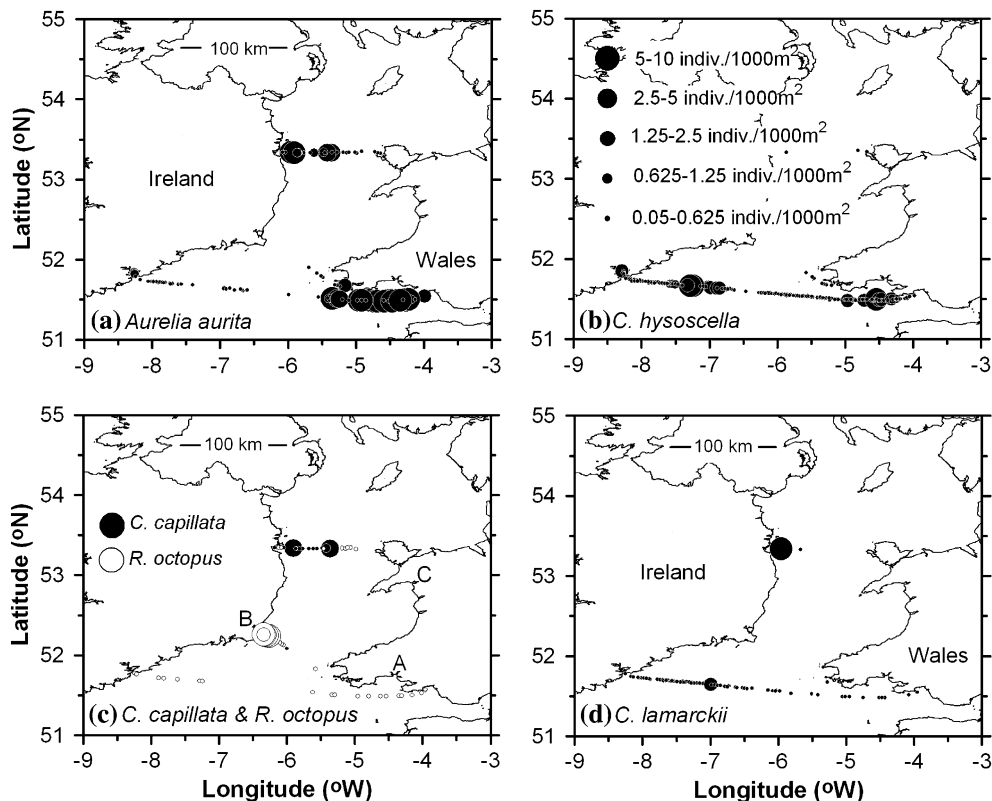


Fig. 6 At-sea distribution maps for the five jellyfish species examined. Relative scales and species are shown on the figures. For (c) the letters A, B, and C denote the three bays described by Houghton et al. (2006) as 'Rhizostoma hotspots', where extensive aggregation of the

jellyfish covered vast areas of the respective bays between 2003 and 2005. Clockwise from bottom the bays are entitled Carmarthen Bay (A), Rosslare Harbour (B) and Tremadoc Bay (C)

(21°C) recorded within a single latitudinal band (53–54° N).

Discussion

Scyphozoan jellyfish share many morphological, behavioural and life history characteristics that determine their successful survival and reproduction in coastal marine environments (Arai, 1997). However, their ecological importance within these environments is often grossly underestimated because of a paucity of information regarding their life history and general ecology (Mills, 2001). For example, when medusae are absent from the water column, jellyfish are still present in the benthos in the form of polyps, yet very few in-situ studies have been conducted on the population dynamics

of these propagules (Boero et al., 1996). This can be attributed their small size (< 2 mm) and operational difficulty in identifying polyps accurately to species level (Pitt, 2000). Conversely, the jellyfish (or medusa) phase represents one of the most conspicuous and abundant members of coastal planktonic communities at times. Ironically, this high visibility of jellyfish is not reflected in our overall understanding of their spatial distributions across large expanses of water, particularly in terms of whether they are randomly dispersed throughout, or show species-specific preferences for certain areas.

Consequently, our most salient finding is that jellyfish species across the Celtic and Irish Seas displayed distinct species-specific distributions. This inference that jellyfish may not be randomly distributed across entire seas has been alluded to

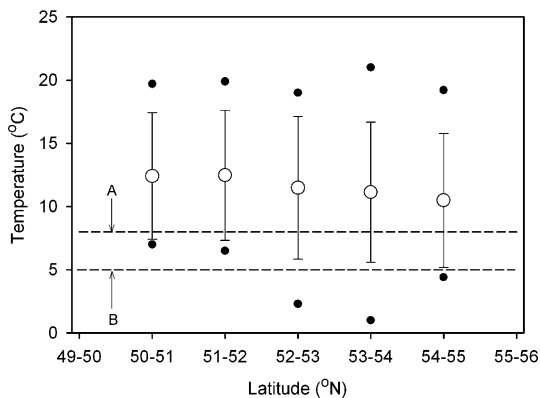


Fig. 7 Mean annual sea surface temperatures (± 2 SD) for each latitudinal band throughout the Celtic and Irish Seas from 1975 to 2004. Maximum and minimum recorded temperatures are shown by ($\bullet$). Calculations are based on the following sample sizes: 50–51° N ($N = 2,817$); 51–52° N ($N = 2,602$); 52–53° N ($N = 1,442$); 53–54° N ($N = 8,354$); 54–55° N ($N = 8,208$). Possible upper temperature limit for *C. capillata* strobilation: (A) described in Verwey (1942) and (B) Gröndahl (1988). These data are supported by (Hay et al., 1990) who described a similar pattern for the North Sea with an absence of *C. capillata* below 53° N

before (Hay et al., 1990). In this previous study, it was suggested that density driven current systems, frontal systems and turbulent mixing provided the dynamic structure that controlled the distribution of jellyfish within particular water masses of the North Sea. Such factors were not considered here, as further work is required on the ability of different species to maintain their position in particular areas i.e. it is feasible that large *R. octopus* medusae (up to 80 cm bell diameter) may display some nektonic behaviour whilst smaller species, such as *A. aurita*, may be more prone to passive transport. Nevertheless, general statements regarding species distribution can be made. For example, given that there is a net northerly flow of water into the Irish Sea from the Celtic Sea (Evans et al., 2003) it was interesting to note an abundance of *C. hysoscella* in the Celtic Sea (Figs. 5 and 6) that was not observed in the waters of the southern Irish Sea. The inference here is that if jellyfish distribution were merely a function of the predominant current regimes, then southerly species such as *C. hysoscella* would be widely distributed throughout the entire study area. As this was not the case, then either some physical boundary (e.g. the Celtic Sea Front) and/or some

behavioural mechanism helped maintain individuals in a particular area (Graham et al., 2001; Sparks et al., 2001).

Our data also yielded a more general pattern of jellyfish spatial segregation. For example, the warm southerly waters of the Celtic Sea were largely dominated by *C. hysoscella*, *C. lamarckii* and in coastal waters, *A. aurita*. In the far north a different species composition was seen, with substantial numbers of *C. capillata*, *A. aurita* and a distinct reduction in *C. hysoscella* and *C. lamarckii*. However, it is when we consider the central transect (T2; Fig. 5) that these apparent patterns become intriguing, as jellyfish as a whole appear largely absent from this section of the study area. Similar patterns have been reported by Houghton et al. (2006) following their recent aerial surveys of the Irish and Celtic Sea. Although low numbers of *C. hysoscella* and *C. capillata* were observed between 52.0° N and 53.0° N, the principal finding was that extensive jellyfish aggregations composed of *R. octopus* were predominately found at the mouths of three large estuarine bays (see Fig. 6(c)). In concordance with that finding, one of these bays (Ross-lare Harbour on the east coast of Ireland) was also identified in the present study as an area of high *R. octopus* abundance (Fig. 5(f)). Although the adaptive significance of this spatial distribution remains unclear, the predominance of *R. octopus* in such environments contributes to an emerging understanding of the gelatinous plankton ecology of the region as a whole. If the overall hydrography of the Celtic and Irish Seas is considered, it appears that jellyfish distributions broadly reflected the major hydrographic regimes (and associated physical discontinuities) with high jellyfish abundance in stratified waters, low abundance in the central mixed areas and high abundance again in the bordering estuaries.

Superimposed upon this general consideration of current regimes and water masses are a number of physical parameters that may play some role in species distribution. For example, it has been proposed that the distribution of *C. capillata* may in some way reflect thermal regimes experienced during the benthic stage with the majority of ephyrae released at cool temperatures in the range of 5–8°C (Verwey, 1942; Gröndahl, 1988).

The relevance here is not the exact temperature at which strobilation occurs, but rather the assertion that waters in the southern Irish and Celtic Seas (50.0°–52.0° N) may simply be too warm for successful strobilation of *C. capillata* (Fig. 7). Therefore, although this possible thermal restriction may not determine the eventual distribution of medusae, it may partially explain the presence or apparent absence of this species from particular areas.

Moving briefly to the methods themselves, accurately quantifying jellyfish distribution is notoriously difficult and rife with problems unique to their gelatinous composition, large size and sometimes localised concentrations (Hamner et al., 1975; Graham et al., 2003). Nets tend to clog quickly and provide little spatial coverage unless huge surveys are performed, as was the case by Hay et al. (1990) and Brodeur et al. (1999). Hence other methods for extensive surveys are required, with for example, acoustic methods being developed recently (Brierley et al., 2005) and aerial surveys for large jellyfish been used by Purcell et al. (2000) and Houghton et al. (2006). Here, we combined two approaches: beach surveys and surface counts from ships of opportunity (ShOps). These two approaches have both good and bad aspects. They provide good spatial coverage at low cost, but do not provide quantitative estimates of abundance for any species given difficulties in assessing diel vertical migration and potential concentration of animals in shallow near-shore environments. Beach surveys gave broadly similar results to the ferry transects, but it should be noted that *C. hysoscella* were poorly sampled by these beach surveys which may reflect the fact that they do not strand in accordance with their at-sea abundance (compare Fig. 3(c) with 6(b)). Hence, we recommend that beach survey data should only be used as one index of jellyfish abundance and distribution and should ideally be backed up by other sampling techniques.

In summary, the combination of surface jellyfish counts from ships of opportunity and shore-line surveys over three consecutive years provided new insights into the distribution, and assemblage of jellyfish communities across a large, temperate coastal environment. The overall

inference is that the complex physical structure of the Celtic and Irish Seas creates a mosaic of environments that provides suitable habitat for a wide range of jellyfish species. These findings support the previous assertion that jellyfish may display centres of preferred distribution (Sparks et al., 2001) and that their occurrence in particular areas is not as passive as once thought.

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