

JELLYFISH AGGREGATIONS AND LEATHERBACK TURTLE FORAGING PATTERNS IN A TEMPERATE COASTAL ENVIRONMENT

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Abstract. Leatherback turtles (*Dermodochelys coriacea*) are obligate predators of gelatinous zooplankton. However, the spatial relationship between predator and prey remains poorly understood beyond sporadic and localized reports. To examine how jellyfish (Phylum Cnidaria: Orders Semaestomeae and Rhizostomeae) might drive the broad-scale distribution of this wide ranging species, we employed aerial surveys to map jellyfish throughout a temperate coastal shelf area bordering the northeast Atlantic. Previously unknown, consistent aggregations of *Rhizostoma octopus* extending over tens of square kilometers were identified in distinct coastal “hotspots” during consecutive years (2003–2005). Examination of retrospective sightings data (>50 yr) suggested that 22.5% of leatherback distribution could be explained by these hotspots, with the inference that these coastal features may be sufficiently consistent in space and time to drive long-term foraging associations.

Key words: aerial survey; *Dermodochelys coriacea*; foraging ecology; gelatinous zooplankton; jellyfish; leatherback turtles; planktivore; predator–prey relationship; *Rhizostoma octopus*.

INTRODUCTION

Understanding the distribution of species is central to many ecological studies, yet this parameter is sometimes difficult to measure even for species that may be abundant and play important trophic roles. In some cases it is the environment itself that makes surveys difficult, such as in remote rainforests or the deep sea, while in other cases it is aspects of the animals own biology that impedes studies. For example, within plankton research there are a range of nets and autonomous recorders that have been used routinely for many decades to assess the distributions of species (Harris et al. 2000). Yet many gelatinous zooplankton such as jellyfish (Phylum Cnidaria: Orders Semaestomeae and Rhizostomeae) remain poorly studied because they either (a) break up in nets and/or (b) are so patchily distributed that they are difficult to study using traditional techniques (Mills 2001). Despite this, the group is highly topical within marine systems with much recent attention directed towards their influence as predators (e.g., Arai 1988). Comparatively, their role as prey remains largely understudied with many species depicted incorrectly as a trophic dead end as their low nutritional value makes them an unlikely food item for vertebrates (Arai 2005). However, there is a growing body of evidence to suggest the contrary with an emerging list of potential predators ranging from larval fish (Arai 2005) through to large oceanic sea birds (Catry et al. 2004). However, perhaps the best known jellyfish predator

remains the leatherback turtle *Dermodochelys coriacea* that ranges widely throughout temperate waters during summer and autumn months (e.g., Brongersma 1972). The reliance of such a large animal (up to 916 kg; Davenport 1998) on an energetically improbable diet remains intriguing, as the demands of growth and metabolism have to be met in the context of reproductive periods lasting several months with foraging and breeding grounds often separated by thousands of kilometers (Hays et al. 2004a, b, Arai 2005). In the Atlantic, this constitutes large-scale migration from tropical breeding sites to more temperate foraging grounds. For example, leatherbacks nesting within the wider Caribbean basin are known to migrate to the cool, temperate waters around the Canadian seaboard, Western Europe, and beyond (Ferraro 2004, Hays et al. 2004a, b). At these distant foraging grounds leatherbacks have been observed to consume great quantities of jellyfish (up to 200kg/d; Duron-Dufrenne 1987) with turtles regularly seen in areas where jellyfish are abundant at the surface (James and Herman 2001).

Despite such tantalizing insights, it remains unknown as to how or whether temperate jellyfish aggregations drive the broad-scale distribution and foraging behavior of leatherback turtles. This long-standing question has implications for ecologists and conservationists alike following recent reports that implicate fisheries by-catch as a proximate cause for the regional declines in leatherback turtles (Spotila et al. 2000, Lewison et al. 2004). Therefore, with the clear goal of better understanding the association of predator and prey, we conducted low-level aerial surveys over three years to identify and map jellyfish aggregations throughout the Irish Sea, an area

Manuscript received 7 June 2005; revised 23 February 2006; accepted 20 March 2006. Corresponding Editor: E. Sala.

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spanning several thousand square kilometers that is regularly visited by migratory leatherbacks. By examining jellyfish assemblages on such a spatial and temporal scale, we were able to make an initial assessment of how historical sightings of leatherbacks might reflect the distribution of their gelatinous prey.

METHODS

Mapping the prey: aerial surveys

Estimates of jellyfish abundance were made during aerial surveys from an altitude of 152 m (500 ft) at a constant speed of 185 km/h (100 knots). Numbers of jellyfish observed within a 250-m observation strip each side of the aircraft were tallied every five minutes by each observer and combined to give an estimate of abundance (detailed methods are described in Houghton et al. 2006). Aggregations were mapped (51.2–55.0° N, 3.0–8.5° W) from June to October over consecutive years (2003–2005) for three scyphozoan species: the barrel jellyfish, *Rhizostoma octopus*; the lion's mane, *Cyanea capillata*; and the compass, *Chrysaora hysoscella*. Random transects were carried out periodically throughout the three years to ensure that the aggregations had remained spatially consistent on an intra- and interseasonal scale (Fig. 1). To validate aerial observations, jellyfish stranding events were also recorded through regular beach surveys at low tide. Data were collected for all U.K./Irish scyphozoan species although only the three species observed from the air were considered for the present study. For *Rhizostoma octopus* bell diameter was also recorded. Lastly, from the air, the location and abundance of leatherback turtles were noted using standard distance sampling techniques (Buckland et al. 2001).

Mapping the predator: historical databases—leatherback turtles

We examined an existing data set for anecdotal sighting and stranding data for leatherback turtles around the United Kingdom and Ireland. The database (entitled "TURTLE"; available online)⁴ was compiled by Marine Environmental Monitoring (MEM), a member of the DEFRA "Collaborative U.K. Cetacean and Marine Turtle Strandings Project." This database is a public access resource compiling U.K. and Irish records of sightings and strandings dating back to 1748. We restricted our analysis to the area consistent with our aerial survey program (51.2–55.0° N, 3.0–8.5° W).

Sightings data for leatherbacks revealed a strong coastal bias (distance from shore = 7.4 ± 0.6 km (mean \pm SE); minimum 0.0 km, maximum 35.8 km; $n = 143$). To account for this, a 15-km buffer was created around the entire coastline (ArcView 3.2; ESRI 1999) with sightings beyond this removed from the analysis (see Appendix). The resulting area was divided into 61 separate coastal

"zones" (20 \times 15 km), accounting for $\sim 72\%$ of all turtle records ($n = 103$) and a spatial coverage of $\sim 25\%$ of the entire area.

To control for area, we converted the number of live sightings to a density value (i.e., individuals/100 km²). From this, leatherback distribution did not appear to be random. Therefore, we redistributed the 103 observations between the coastal zones, with the chances of a turtle occurring in each zone proportional to the relative sea area of that zone. This procedure was iterated 1000 times. Lastly, to produce an index of *Rhizostoma* abundance, the total number of jellyfish observed in each section over the three survey years was corrected for effort to give the mean number of jellyfish observed within a given 5-min survey period (7710 m²).

Data analysis: removing potential biases

We examined International Council for the Exploration of the Seas data (available online)⁵ to derive effort for a range of fishing activities within U.K. waters: demersal, pelagic, shrimp and *Nephrops*, and other shellfish (excluding *Nephrops* and shrimp). Such diverse activities cannot be described by a simple common metric and, as such, the overall value of different species by area (financial yield per ICES unit) is taken as a proxy for fishing effort. Data were available as arbitrary yet directly comparable categories, from the highest yield (denoted by a score of 5 in our analysis) to no yield at all (scored 0). Next, we estimated the number of recreational moorings in each zone, making the broad assumption that pleasure craft would remain active within their respective zones, with coastal demographics (present population) the final factor included in our analysis. These combined factors could not explain the distribution of leatherback sightings (Kendall's Tau_b; $P > 0.05$), implying they had not rendered the data unusable for assessing potential links between predator and prey.

RESULTS

Mapping jellyfish aggregations from the air

During 2003–2005 (June–October), we surveyed a combined total of 7700 km² (2003, 3034 km²; 2004, 2941 km²; 2005, 1725 km²; Fig. 1a, c, and e). During 2003 and 2004 we encountered three areas where *Rhizostoma* were repeatedly observed in high densities (i.e., >800 individuals/5 min): Carmarthen Bay in South Wales, Tremadoc Bay in North Wales, and Rosslare on the southeast coast of Ireland (Fig. 1). Survey coverage was revised in 2005, with the Solway Firth identified as a fourth area where *Rhizostoma* occurred in significant numbers (≤ 600 individuals/5 min; Fig. 1f).

Rhizostoma aggregations sometimes extended over several tens of kilometers. Although we do not know the density of *Rhizostoma* beneath the surface, on occasion jellyfish were so abundant that we could only conclude

⁴ (<http://www.strandings.com>)

⁵ (<http://www.marlab.ac.uk>)

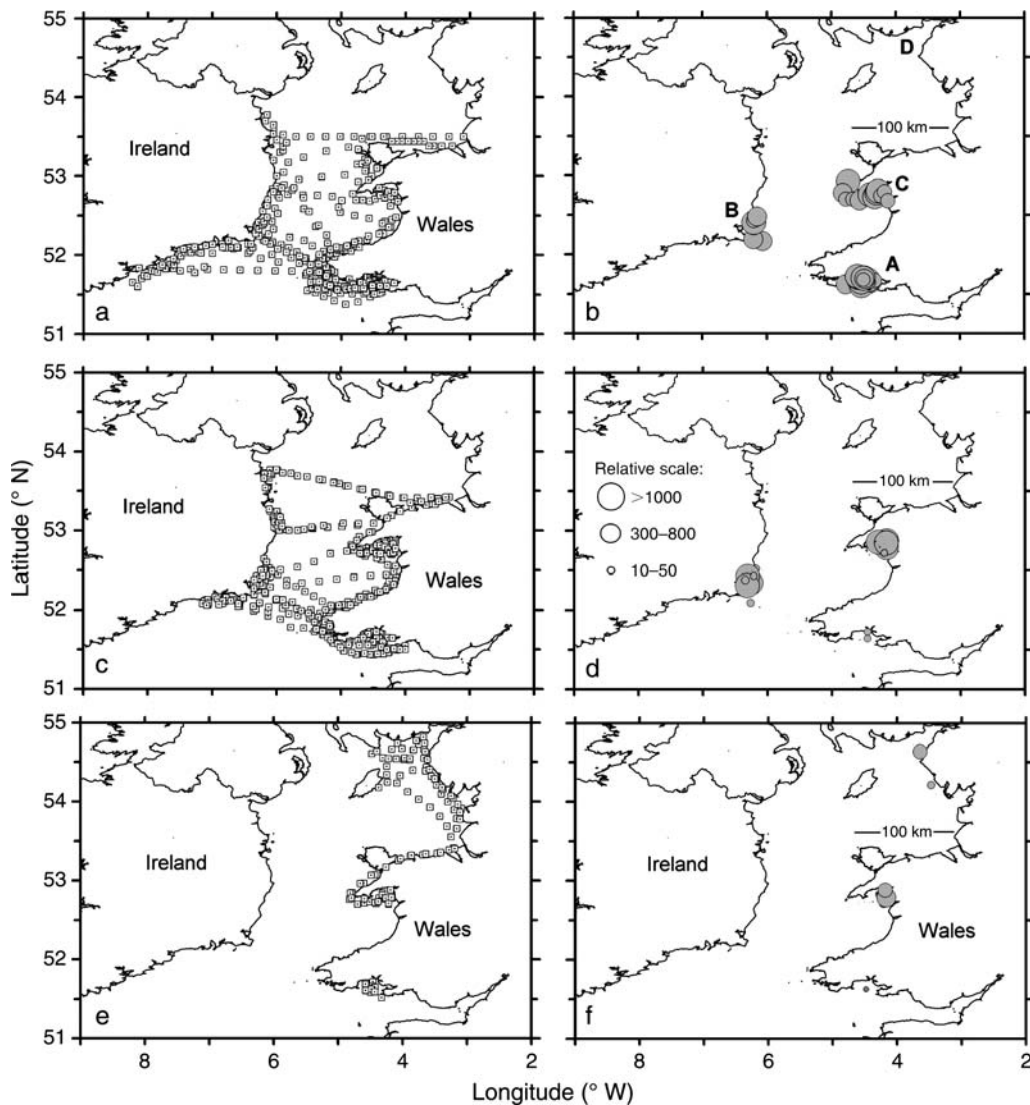


FIG. 1. Areas covered during aerial surveys are shown for (a) 2003, (c) 2004, and (e) 2005. Each square represents the midpoint of a 5-min survey unit (7710 m²). Distribution of *Rhizostoma* aggregations are also shown for (b) 2003, (d) 2004, and (f) 2005. Data are total abundances for the period between July and September (leatherback peak season) in each year. Each circle represents a measure of abundance during a single 5-min observation period. Relative scale of aggregations is shown in panel (d) ranging from >1000 to 10–50 jellyfish/5 min. Locations of hotspots are shown in panel (b): A, Carmarthen Bay; B, Rosslare harbor; C, Tremadoc Bay. A fourth possible hotspot (D, Solway Firth) is also shown although this site was only surveyed once under good conditions, thus preventing a full assessment of its temporal and spatial constancy.

there were >1000 individuals seen in five minutes of flying (i.e., a density of at least 0.13 individuals/m² at the surface). Assessing how the aggregations extended below the surface was unfortunately beyond the scope of the present study. This is an undeniable limitation to our estimates of abundance and will hopefully form the basis of future fine-scale studies at sea level. Nonetheless, even if we restrict our interpretation of our data to two dimensions we are still left with the conclusion that these “hotspots” extend over tens of square kilometers and contain many millions of jellyfish (Fig. 1). Apart from *Rhizostoma*, other species were never seen in huge

aggregations, implying that they did not occur predominantly at the surface, did not form aggregations, or (in the case of *Aurelia aurita*) were not readily visible from the air. These species were excluded from the further analysis given the more qualitative nature of these data.

Regarding shoreline data, 135 beaches were surveyed to validate aerial observations. 1226 individual surveys were conducted, amounting to 1112 km surveyed over the three years. *Rhizostoma octopus* was found to strand on a year round basis, with both small and large individuals present at each time of the year (see Appendix).

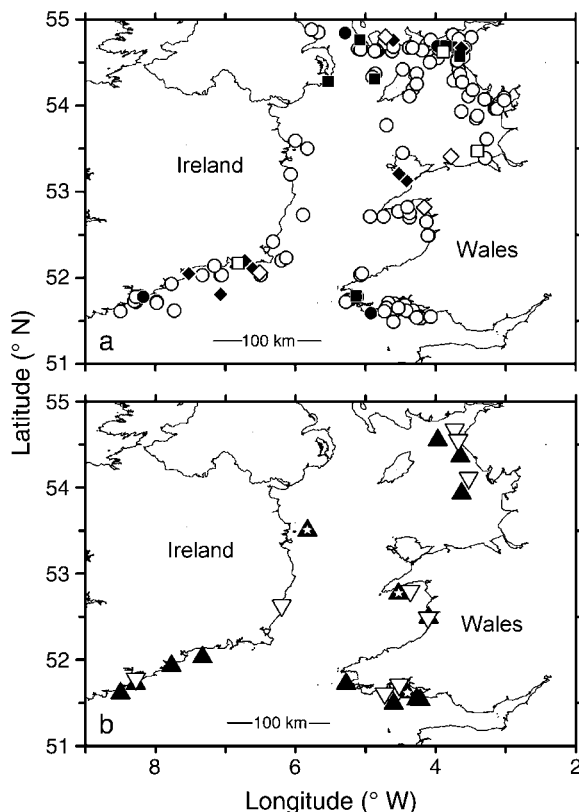


FIG. 2. (a) All leatherback sightings (for a given section of the Irish Sea) from 1950 to 2005 ($n = 143$). Data are plotted according to decade: 2000–2005 (open circles); 1990s (solid circles); 1980s (open squares); 1970s (solid squares); 1960s (open diamonds); and 1950s (solid diamonds). (b) Sightings where turtles were associated with jellyfish (solid triangles) and when foraging activity was confirmed (open triangles). The three live turtles sighted during 2003 and 2004 aerial surveys are marked with stars. The three sightings confirming predation on *Rhizostoma octopus* were in Carmarthen Bay (51.65° N, 4.53° W and 51.61° N, 4.73° W) and Tremadoc Bay (52.80° N, 4.36° W). Predation of *Chrysaora hysoscella* was observed on a single occasion in Tremadoc Bay (54.67° N, 3.73° W).

Historical analysis of leatherback database

From the TURTLE database 147 live leatherbacks were sighted in the Irish Sea between 1908 and 2005 (Fig. 2). However, only four turtles were reported prior to 1950 (1908, 1938, 1948, and 1949), leaving analysis prior to this date impractical. Beyond this, the number of sightings increased from one during 1951–1955 to 71 from 2001 to 2005 (Fig. 3a). However, this apparent increase most likely reflects the centralization of records on a national scale, improvements to the reporting mechanism itself, and increased awareness of leatherback turtles in British and Irish waters.

Regarding seasonality, leatherbacks were most frequently sighted between July and September ($n = 125$; 87.67%; Fig. 3b). Arguably, this may reflect an increase in boat traffic during summer months although the absence of unit effort prevented a more detailed analysis.

Nevertheless, to assess whether sightings occurred in the same places over time, or whether different hotspots emerged at different times (e.g., Solway Firth at one particular point in time and Carmarthen Bay at another point) data were grouped by decade from 1950 onwards (Fig. 2a). This revealed no distinct pattern other than to confirm that turtles had been sighted widely throughout the Irish Sea in each decade examined.

Comparison of the 1000 randomized leatherback distributions with the observed distribution revealed the number of leatherbacks in a single zone ($n = 16$) and the number of zones with no leatherbacks observed ($n = 24$) were larger than would be expected by random chance ($P < 0.001$ for both). This nonrandom grouping was further confirmed using a chi-square test ($\chi^2 = 253.70$, $df = 61$, $P < 0.01$).

Linking predator with prey

During 2003 and 2004 three live and one dead leatherback turtle were observed from the air with two of the live animals found within 1 km of *Rhizostoma* aggregations (Fig. 2). There are 25 previous reports from

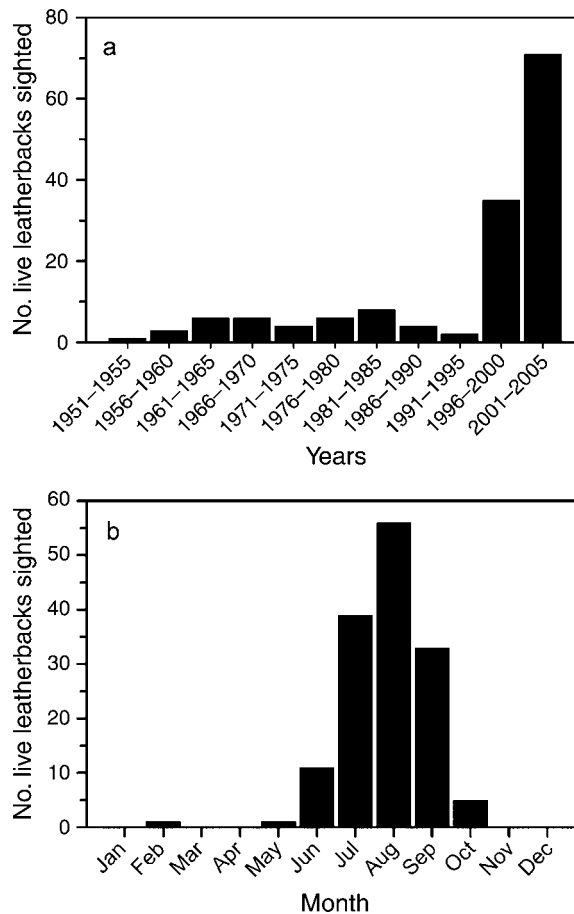


FIG. 3. (a) Live leatherback turtle sightings since 1950 (from TURTLE database). (b) Seasonality of live leatherback turtles sightings (total $n = 143$; 1950–2005).

the region (TURTLE database) that state leatherbacks were “feeding/swimming amongst/or associated with jellyfish.” A further 10 records specifically state individuals feeding on jellyfish. Only four records accurately identified the prey species, and of these, three were *Rhizostoma* and the other was *Chrysaora* (Fig. 2b).

A more empirical association was found when leatherback density was correlated against the *Rhizostoma* index in each of the coastal zones. A Kendall's Tau_b nonparametric test revealed 22.5% of the variation in leatherback distribution could be explained by the distribution of *Rhizostoma* ($P < 0.05$). Additionally, zones of high leatherback abundance were characterized by higher rates of incidental mortality (Kendall's nonparametric test; $r^2 = 0.42$, $P < 0.05$).

DISCUSSION

Foraging decisions are made over a wide range of spatial and temporal scales, based on differences between prey patches, factors within individual patches, and the motivational state of a forager (Baum and Grant 2001). Although the exact response of a particular predator to changes in the spatial distribution of its prey is often poorly understood, temporal variations in the distribution of the predator itself can sometimes provide an insight into highly dynamic prey that may be difficult to track in other ways (Boyd 1996). This has particular relevance within the marine environment where it is often difficult to measure simple variables and life history traits by direct observation (Boyd 1996). The scale of this problem is proportional to the spatial scale within which the predator and prey operate (e.g., Sims and Quayle 1998), which over recent years has driven a number of technological advances that allow empirical data to be gathered from previously intractable environments. However, as our real time capabilities increase, we should be careful not to devalue historical data, as often they can provide insights beyond the scope of contemporary findings alone (Jackson et al. 2001, Pandolfi et al. 2003). The long-standing conundrum of jellyfish–leatherback turtle foraging associations presents one such scenario given a wealth of recent studies into their migratory habits (e.g., Ferraroli et al. 2004, Hays et al. 2004b, James et al. 2005) that overlies an almost nonexistent knowledge of how such behaviors are determined by the distribution and seasonality of their prey. This can largely be explained by the sheer scale of leatherback movements rendering direct observations impractical, but also by the fact that postnesting migrations are dispersed (Ferraroli 2004, Hays et al. 2004b) and do not appear to center on spatially restricted foraging grounds. In this context, the co-occurrence of leatherbacks and *Rhizostoma* becomes important as it suggests that migratory movements may reflect the distribution of particular prey items. Nonetheless, in terms of absolute abundance we cannot claim that the numbers of turtles sighted are representative of the actual numbers present, given no prior knowledge of

the vertical distribution and surface behavior of the species within the Irish Sea. However, our objectives were not merely to report numbers, but to consider the overall distribution of sighted individuals in terms of prey aggregations. Consequently, we feel that this limitation in our analysis does not compromise this key element of the study.

More importantly, given that jellyfish are widespread throughout temperate coastal waters (Russell 1970), we must also emphasize that *Rhizostoma* is simply one species that they feed upon. Indeed in recent years, leatherbacks off Nova Scotia have also been observed to feed on *Cyanea capillata* (James and Herman 2001) and off North Carolina, USA, on *Stomolophus meleagris* (Grant and Ferrell 1993). It should also be noted that significant numbers of *Cyanea capillata* have been previously shown to strand around the north coast of Wales (>50 individuals/100 m; Houghton et al. 2006), which must in some way contribute to relatively high numbers of leatherbacks sighted in that area. Moreover, *Rhizostoma* itself can sometimes occur in extraordinary abundance outside of the hotspots, as in 1978 when the species was reported all around the coast of Ireland (O'Connor and McGrath 1978). So while the hotspots are certainly not the sole factor determining the distribution of leatherbacks in U.K. and Irish waters, they appear sufficiently consistent in space and time to drive an increased occurrence of turtles in these specific areas over the past 50 years.

This relationship between *Rhizostoma* spp. and leatherback turtles has been briefly alluded to before within European waters. Along the Atlantic coast of France, leatherbacks have been observed to feed extensively on *Rhizostoma* spp. while also consuming *Chrysaora hysoscella*, *Aurelia aurita*, and more rarely, *Cyanea lamarckii* (Duguy 1982, Duron-Dufrenne 1987). Given the geographical proximity of France to the Irish Sea, such findings tentatively suggest that the association of leatherbacks and *Rhizostoma* may extend further into the wider region of Europe's Atlantic fringe. Furthermore, given the persistent stranding of *Rhizostoma* throughout the year, the temporal inference is that the species may provide a food source for leatherbacks beyond the scope of other scyphozoans that are largely absent from the water column during the autumn and winter months (Russell 1970).

This leads us to a more general discussion of how leatherbacks might interact with prey assemblages over consecutive seasons. For example, long-term telemetry of leatherback turtles tagged in their foraging grounds off Nova Scotia has shown that after migrating south at the end of the summer and overwintering at low latitudes, individuals turtles then return to high latitudes the following summer and seem to maintain fidelity at least to the approximate area they frequented the previous year (James et al. 2005). However, these tracking results show no evidence for fidelity to specific foraging bays or such localized areas. Consequently, it is

unlikely that leatherbacks maintain knowledge of the *Rhizostoma* hotspots in the Irish Sea and travel directly to these bays each year. It is more likely that some individual turtles maintain fidelity to the northeast Atlantic and that they occasionally stumble into a number of hotspots, whereupon they can feed until cooling waters drive their southerly migration.

In summary, the distribution of *Rhizostoma octopus* explained almost a quarter of the variance in sighted leatherbacks over a period of >50 years, on a scale spanning several thousand square kilometers. We do not imply that leatherback distribution is entirely driven by this single species, and we fully acknowledge that other jellyfish species play an important role. However, we believe our results represent a solid foundation for further studies into leatherback foraging behavior that also highlights the broader issue of how jellyfish as prey may form integral links within temperate coastal marine systems.

ACKNOWLEDGMENTS

Funding was provided by INTERREG IIIA (European Regional Development Fund), the Countryside Council for Wales Species Challenge Fund, and the Marine Conservation Society. Special thanks to David Jones, Vincent, Sean, and Christina Rooney, Jim and Rose Hurley, Kevin McCormack, Eithne Lee, Maria Doyle, Kate Williamson, Irena Kruszona and colleagues, Vernon Jones, and Tom Stringell; and to Rod Penrose and Chris Pierpoint of Marine Environmental Monitoring for compiling the TURTLE database.

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APPENDIX

A description of the construction of coastal zones, a figure showing construction of the coastal zones, and a figure showing stranded specimens of *Rhizostoma octopus* (*Ecological Archives* E087-123-A1).