# The ocean sunfish *Mola mola*: insights into distribution, abundance and behaviour in the Irish and Celtic Seas

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Here we provide baseline data on the distribution and abundance of *Mola mola* within the Irish and Celtic Seas, made during aerial surveys from June to October during 2003–2005. These data were considered in conjunction with concurrent observations of three potential jellyfish prey species found throughout the region: *Rhizostoma octopus*, *Chrysaora hysoscella* and *Cyanea capillata*. A total area of 7850 km² was surveyed over the three years with an observed abundance of 68 sunfish giving a density of 0.98 ind/100 km². Although modest, these findings highlight that the species is more common than once thought around Britain and Ireland and an order of magnitude greater than the other apex jellyfish predator found in the region, the leatherback turtle (*Dermochelys coriacea*). Furthermore, the distribution of sunfish sightings was inconsistent with the extensive aggregations of *Rhizostoma octopus* found throughout the study area. The modelled distributions of predator–prey co-occurrence (using data for all three jellyfish species) was less than the observed co-occurrence with the implication that neither jellyfish nor sunfish were randomly distributed but co-occurred more in the same areas than expected by chance. Finally, observed sunfish were typically small (∼1 m or less) and seen to either bask or actively swim at the surface.

## INTRODUCTION

For many pelagic marine predators, our understanding of range, distribution and seasonal movements is often limited. Paradoxically, it is often some of the most immediately recognizable and familiar species that pose the greatest questions to researchers trying to gather even the most basic of life history data. Such problems stem from a historical limitation in observing pelagic species away from the relative convenience of coastal waters. Even within these confines the issue of detectability comes to light with many species obscured from view by the ocean's surface for protracted periods of time. In recent years, however, major advances have been made in our understanding of pan-oceanic movements of marine megafauna through satellite telemetry and data logging such as the extraordinary oceanic movements of the white shark, *Carcharodon carcharius* (Boustany et al., 2002; Bonfil et al., 2005), bluefin tuna, *Thunnus thynnus* (Block et al., 2005) and the deep-water foraging of planktivorous whale sharks, *Rhincondon typus* (Eckert & Stewart, 2001). However, despite such advances we are sometimes left with behavioural questions that are unanswerable without direct observation. This issue was brought to light by Sims & Quayle (1998) during their study of the basking shark, *Cetorhinus maximus*, who argued that the natural foraging behaviour of these well documented animals remained poorly understood owing to the problem of tracking individuals and quantifying food abundance simultaneously.

Another immediately recognizable yet poorly understood group of fish are the Molidae; or ocean sunfishes (Class Osteichthyses: Order Tetraodontiformes: Family Molidae). These epipelagic migrants have been recorded in the temperate and tropical regions of the Mediterranean, Atlantic, Indian and Pacific Oceans (Wheeler, 1969; Sims & Southall, 2002) and contain the largest of all teleost fish, *Mola mola* that can reach 3.1 m (10 ft) from tip to 'tail' fin, 4.26 m (14 ft) from dorsal fin to anal fin tip and weigh up to 2235 kg (4927 lbs) (Carwardine, 1995). Yet despite their size and apparent ubiquity, little is known about the basic biology of the species owing to a scarcity of records and an invariably low encounter rate that has prevented the establishment of any sustained investigation (Sims & Southall, 2002; Streelman et al., 2003).

The resulting notion of sunfish as solitary, elusive ocean wanderers was radically challenged, however, with reports of extensive by-catch figures from Spanish drift gill-net fisheries within the Mediterranean revealing that ocean sunfish comprised between 70% and 93% of the total catch between 1992 and 1994 (Silvani et al., 1999). More recent reports from the Californian swordfish fisheries also suggested high numbers with sunfish representing 29% of the total catch, far outnumbering the target species (Cartamil & Lowe, 2004). Despite efforts to minimize the impact of such activity (i.e. sunfish are often brought on board and returned to the sea alive as their meat is not edible; Silvani et al., 1999), such high levels of by-catch must have undoubted ecological consequences. Indeed, as many researchers currently strive to reduce pelagic by-catch of such non-target species, a more detailed understanding of the behaviours and life history traits of sunfish is urgently required before we can assess the ecological impact of their removal from the marine ecosystem (Myers & Worm 2003; Cartamil & Lowe, 2004).
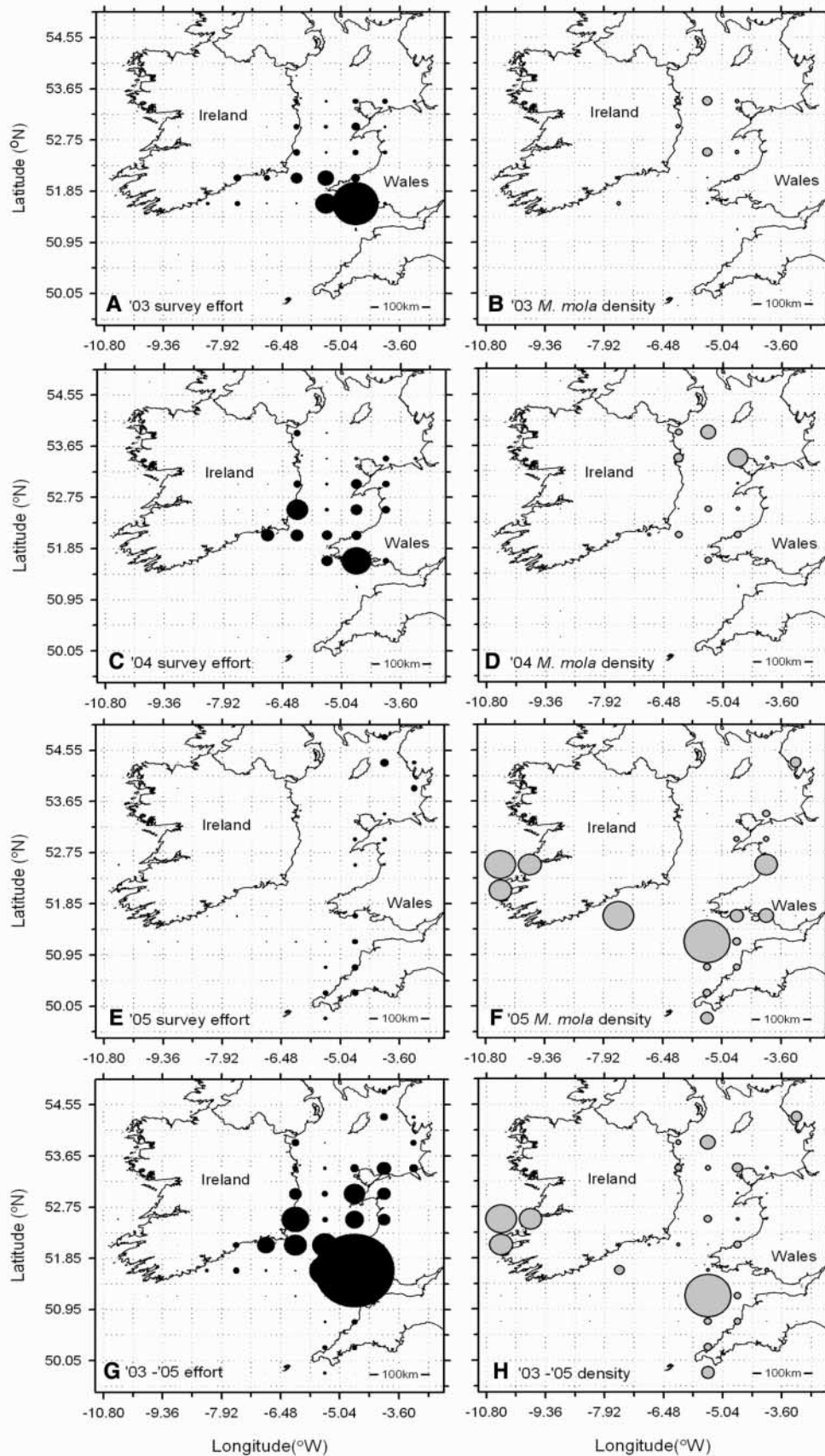
**Figure 1.** Aerial survey data 2003–2005. (A), (C) and (E) show survey effort data (i.e. area surveyed (km$^2$) within each grid square in each year) for 2003, 2004 and 2005 respectively. (G) Combined plot for all years (2003–2005). Plots are on a comparative scale with the greatest survey effort (i.e. the largest bubble) in each year as follows: 2003=740 km$^2$; 2004=463 km$^2$; 2003=123 km$^2$; 2003–2005 (combined)=1280 km$^2$. Sunfish sighting data for each year respectively are shown as density (ind/km$^2$) in (B), (D) and (F) with combined data (2003–2005) given in (H). The dimensions of plots are again comparable with the greatest density in each survey year as follows: 2003=0.026 ind/km$^2$; 2004=0.056 ind/km$^2$; 2005=0.130 ind/km$^2$.
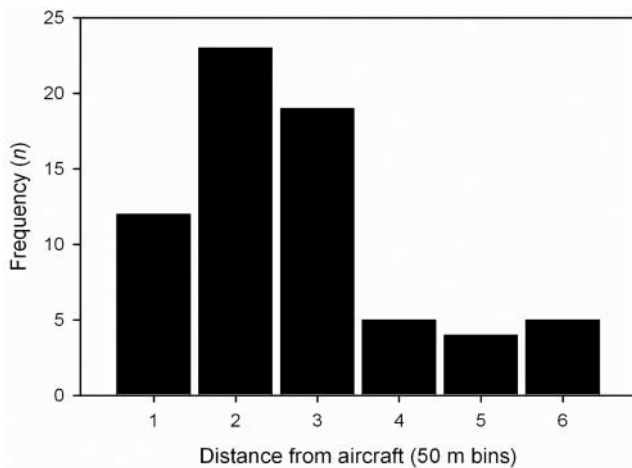
**Figure 2.** Frequency histogram showing the distance of observed sunfish from the survey aircraft. Data have been grouped into 50 m bins. g(0) (i.e. the point where all animals would be observed) is taken as 50 m to account for 'blind spot' directly beneath the aircraft (see Houghton et al., in press). The perpendicular truncation distance beyond which animals are not detected ('*w*' in density equation) was taken as 300 m from the aircraft beyond which observations were not made.

Around the coasts of Britain and Ireland *Mola mola* is the most frequently reported member of the Molidae with *Ranzania laevis* sighted only very rarely, and *Mastrurus lanceolatus* apparently absent from the region (Wheeler, 1969). The assumption, relatively speaking, is that *Mola mola* may be more thermally tolerant of such temperate waters, although individuals sighted at the surface are most commonly reported to be 'basking' or swimming on their sides, with the inference that they are weak or dying, again possibly chilled to insensibility by the cold water (Fraser-Bruner, 1951; McCann, 1961; Schwartz & Lindquist, 1987). Consequently, the perception of the species remains of an elusive and infrequent visitor to our shores, which finds itself in an environment not entirely

**Table 1.** *The encounter rate of sunfish in each survey year, under varying sea states. Data are rounded up to the nearest km².*

| Survey year | Sea state (Beaufort scale) | Area surveyed (km²) | Encounter rate (i.e. area surveyed to observe 1 ind/km²) |
|---|---|---|---|
| 2003 | 0 | 0 | 0 |
| 2003 | 1 | 1488 | 1488 |
| 2003 | 2 | 1665 | 104 |
| 2003 | 3 | 0 | 0 |
| 2003 | 4 | 0 | 0 |
| 2004 | 0 | 8 | 0 |
| 2004 | 1 | 1627 | 68 |
| 2004 | 2 | 786 | 786 |
| 2004 | 3 | 447 | 447 |
| 2004 | 4 | 85 | 85 |
| 2005 | 0 | 254 | 51 |
| 2005 | 1 | 524 | 31 |
| 2005 | 2 | 455 | 51 |
| 2005 | 3 | 347 | 0 |
| 2005 | 4 | 54 | 0 |

conducive to its survival. In an attempt to shed further light on this issue and provide more contemporary baseline data for *Mola mola*, we report findings on its distribution and abundance throughout the Irish and Celtic Seas during 2003–2005. Direct observations were made as part of a broader aerial survey programme focusing on seasonally occurring leatherback turtles, *Dermochelys coriacea* and surface aggregations of their jellyfish prey (Houghton et al., in press) and, as such, our data are broadly considered within this context.

## MATERIALS AND METHODS

Direct counts of *Mola mola* were made from June to September during 2003, 2004 and 2005 throughout the Irish and Celtic Seas (50.0–55.0°N −3.0–11.0°W). Data were gathered from an altitude of ∼150 m (500 ft) at a constant speed of 100 knots (185 km h$^{-1}$) using standard distance sampling techniques (Buckland et al., 2001). The observational field was arbitrarily determined with an inclinometer to a 250 m wide swathe either side of the transect line (i.e. from 50 m perpendicular to the side of the aircraft to 300 m). Data were not collected directly beneath the aircraft to a distance of 50 m as the view from the observer's window did not permit it; nor beyond 300 m as the detectability of target species decreased dramatically after this point (see Houghton et al., 2006).

Concurrently, aerial surveys were used to map the aggregations of three large schyphozoan species known to occur in British and Irish waters throughout the summer months (Hays et al., 2003): the barrel jellyfish *Rhizostoma octopus*, the lion's mane jellyfish *Cyanea capillata*, and the compass jellyfish, *Chrysaora hysoscella*. All three species were readily identifiable from the aircraft (i.e. species could be accurately and consistently determined), although quantitative estimates of abundance were only made for *Rhizostoma octopus* which aggregate near the surface when the sea is calm. Data for *Chrysaora* and *Cyanea* were recorded as presence or absence as these species are more prone to dispersal throughout the water column, rendering quantitative estimates of abundance unrealistic (Sparks et al., 2001; Brodeur et al., 2002). Detailed methods and validation exercises are discussed in Houghton et al. (2006).

## RESULTS

A total of 11,951 km of aerial surveying was conducted in 2003 and 2004 (2003: 33 h, 6068 km; 2004: 32 h, 5883 km), encompassing the length and breadth of the southern Irish Sea and constituted a total area of 5976 km² (10% of the total possible survey area in the southern Irish Sea: 2003=3030 km²; 2004=2946 km²). In 2005, survey locations were changed to investigate the north-western Irish Sea, the Celtic Sea and south-western Ireland. This represented a further 19 h survey time (3777 km) with a total survey area of 1874 km² (Figure 1).

In total, 68 sunfish were spotted for all three years combined (2003 N=16; 2004 N=23; 2005 N=31) (Figure 1C,D). This corresponded to an overall encounter rate of one sunfish every 178.24 km² in 2003, 105.18 km² during 2004 and 51.08 km² in 2005. Anderson−Darling normality tests revealed that the distance at which sunfish
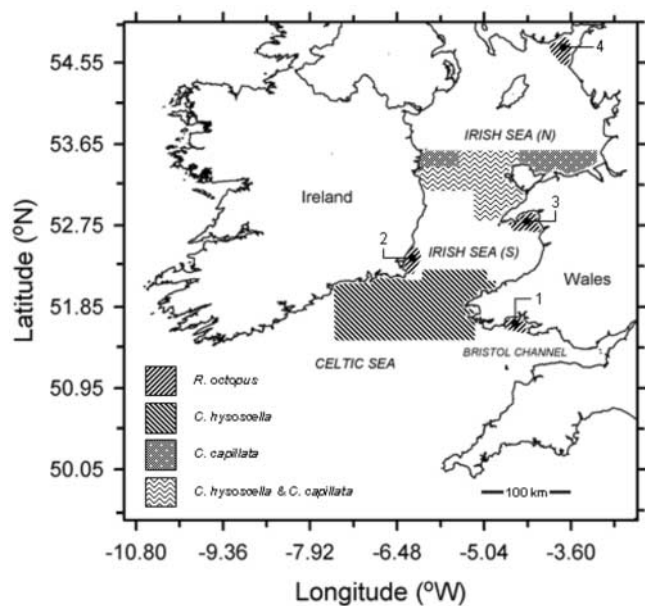
**Figure 3.** Schematic of the Irish and Celtic Seas showing the location of *Rhizostoma octopus* 'hotspots' previously reported in Houghton et al. (in press & 2006). The four locations are as follows: (1) Carmarthen Bay; (2) Rosslare harbour; (3) Tremadoc Bay (from Houghton et al., in press); and (4) Solway Firth (from Houghton et al., 2006). Generalized presence and absence data for *Chryosaora hysoscella* and *Cyanea capillata* are shown in schematic form based on data for 2004 published in Houghton et al. (in press).

were sighted from the aircraft were not normally distributed ($P < 0.05$) (Figure 2). The median distance was 152 m (minimum 55 m; maximum 395 m). The interquartile range of sightings ranged from 106 to 181 m.

Count data were converted into densities using the following equation (Buckland et al., 2001):

$$D = \frac{N}{2wLP_a} \qquad (1)$$

where: D=density; N=number of animals detected; w=perpendicular truncation distance beyond which animals are not detected (km); L=length of survey track (km); $P_a$=probability that an object at distance $x$ is detected (see Buckland et al., 2001). This revealed an overall density of sunfish for the three years combined as 0.98 sunfish per 100 km$^2$ (2003: 0.60 ind 100 km$^{-2}$; 2004: 0.89 ind 100 km$^{-2}$; 2005: 1.87 ind 100 km$^{-2}$).

Returning to the raw count data, Table 1 shows how encounter rate (i.e. area surveyed to encounter 1 sunfish) varied between years and under varying sea states. Given the low number of observations and reduced survey effort during rougher sea states (force 3–4 on the Beaufort scale) it was not possible to assess how this factor may have influenced our ability to detect sunfish from the air. Consequently, it was not possible to correct our estimates of abundance for this variable; although the reduced detectability of megafauna with increasing sea states is well documented (see Buckland et al., 2001).

Regarding the size of sighted animals, although it was not possible to directly measure this variable from the air, estimates were made by comparison with proximate
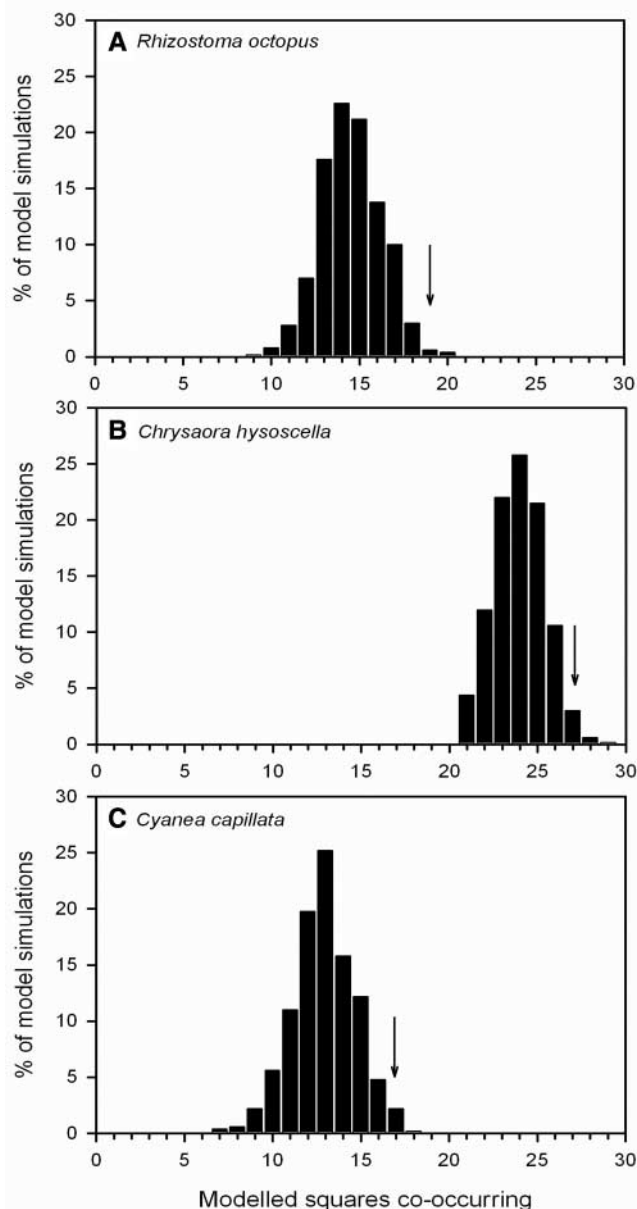


**Figure 4.** The modelled co-occurrence of sunfish with three species of jellyfish. Solid arrows show observed co-occurrence.

seabirds that individuals were typically in the size-range of 1 m or under, with no extraordinarily large specimens sighted. In terms of behaviour, sunfish were typically seen actively swimming both in coastal and open sea areas, although individuals were intermittently seen to characteristically 'bask' on their side at the surface.

Lastly, to test for the co-occurrence of predator with potential prey, we simulated the likely association between sunfish and jellyfish assuming that the distribution of both groups was random across the study area. A generalized schematic showing the broad distribution of the three target species (based on data presented in Houghton et al., 2006) is shown in Figure 3. The study area from ~51°N–55°N to ~−3°W–11°W was divided into grid squares of 50 km×50 km. This gave a total of 143 grid squares of which 53 were actually sampled during serial surveys (Figure 1). We then ran a simulation in which species occurrence in these grid squares was

random. For example, sunfish were seen in 31 squares, so in each model run we randomly selected 31 grid squares for simulated sunfish occurrence. Similarly *Rhizostoma* were seen in 25 squares and so again in each model run we randomly selected 25 grid squares for simulated *Rhizostoma* occurrence. For each model run the number of grid squares within which sunfish and *Rhizostoma* co-occurred was determined. This procedure was repeated for simulated co-occurrence of sunfish with both compass jellyfish and lion's mane jellyfish. For each species pair, we ran 500 model simulations.

The frequency distributions of modelled co-occurrence therefore represent the probability density function for likely rates of co-occurrence assuming that both species were randomly distributed. These modelled frequency histograms were then compared to the observed results from the aerial surveys.

In all three cases, the observed co-occurrence of sunfish and jellyfish was much greater than the centre point of modelled simulations (Figure 4). The probabilities of these high levels of co-occurrence happening by chance assuming all species were randomly distributed were 1.0% for *Rhizostoma*-sunfish, 3.8% for *Chrysaora*-sunfish and 2.4% for *Cyanea*-sunfish. Therefore, none of the species associations were consistent with the random distribution model.

## DISCUSSION

The ability of some large pelagic predators to survive, migrate and reproduce on a diet that consists primarily of gelatinous zooplankton raises a number of interesting ecological questions. A classic example is provided by leatherback turtles in the northern Atlantic that migrate thousands of kilometres after a protracted reproductive period in the tropics, to forage upon seasonally abundant aggregations of jellyfish at high latitudes (Hays et al., 2004a,b; James et al., 2005). How individuals replenish post-reproductive and migratory energy deficits on a diet composed almost entirely of water remains unclear, nonetheless it must hold true that the increased gelatinous productivity of the temperate oceans renders the journey worthwhile (Hays et al., 2004a). For pelagic fish, there are so far only a few species for which gelatinous zooplankton are the only known prey, and there has been a recent call for studies to look at this very issue (Arai, 2005). However, even those with specialist diets may also indirectly consume commensal or parasitic organisms such as hyperiid arthropods present on the prey (Arai, 2005). As such, there remains no sharp division between specialists and generalists (e.g. spiny dogfish *Squalus acanthias*, Linnaeus 1756) that periodically prey upon gelatinous organisms (Ates, 1988; Harbison, 1993; Arai, 2005). Most commonly, *Mola mola* are taken as jellyfish specialists which poses a particular energetic challenge given that they are not only the largest extant teleost, but carry more eggs per individual than any other vertebrate (Nelson, 1994; Carwardine, 1995). In itself, this provides compelling evidence that the assumption of gelatinous organisms (with their high water and salt content relative to organic content) as 'poor food' may be short-sighted (Arai, 2005). Indeed, it has been argued that given the high rates of digestion (and presumably of assimilation)

such organisms may provide sources of energy comparable to better recognized prey such as arthropods (Arai, 2005). Nonetheless, there may be a requirement for *Mola mola* to periodically supplement their gelatinous diet with prey such as squid, sponges, crinoids, eel grass, crustaceans, small fish and deep water eel larvae, all of which have been removed from the gut of individuals, indicative of foraging at the sea-floor and into deep water (Norman & Fraser, 1949; Clemens & Wilby, 1961; Hart, 1973).

When we compare the numbers reported here with the previous data presented by Silvani et al. (1999) and Cartamil & Lowe (2004), the density of sunfish reported here appears modest. Nonetheless, our findings do suggest that they may not be as uncommon as previously thought (Wheeler, 1969) and provide empirical data on a species that is poorly understood in British and Irish waters. Interestingly, the observed abundance of sunfish (N=68) was also an order of magnitude greater than the other large jellyfish specialist, the leatherback turtle (N=4; Houghton et al., in press). As efforts increase to understand the importance of jellyfish as prey items (Arai, 2005), such simple data, in time, may prove useful. Nevertheless, without a thorough insight into the vertical distribution and surface behaviour of sunfish within the region we are unable to account for any individuals that may have evaded observation, and as such the numbers reported here cannot be taken as absolute abundance. Indeed, recent studies have shown *Mola mola* to be a more accomplished diver than once thought, venturing to depths of ~600 m up to 20 times a day (Thys, 2002). Although the shallow bathymetry of the Irish and Celtic Seas (typically <100 m) prevents such elaborate behaviour, this previous study does highlight that sunfish are not always lethargic at the surface where they can be identified by aerial survey. However, for the purpose of discussion, there exists compelling evidence of a distinct diel diving pattern for *Mola mola* off southern California; reported daytime periods were characterized by brief, repeated dives below the thermocline (Cartamil & Lowe, 2004). In this study, sunfish spent only between 20 and 30% of their time in the top 5 m of the water column, which if taken as broadly consistent with the present study (an assumption we have no empirical data to support), this would translate to an approximate 1 in 4 chance of observing any particular animal from the air, with the implication that any numerical data presented here are indeed an underestimation of absolute abundance.

In relating the pattern of sunfish to their gelatinous prey, at least three scenarios are possible in the comparison of modelled and observed co-occurrence of sunfish with the various jellyfish species. First, the centre of the distribution for the modelled co-occurrence could be very similar to the observed co-occurrence. This outcome could be interpreted as sunfish and jellyfish species both being randomly distributed. Second, the observed co-occurrence could be much higher than the centre of the modelled distribution. This outcome could be interpreted as sunfish and jellyfish species both being clumped in the same areas and so co-occurring more often than expected by chance. Third, the observed co-occurrence could be much less than the centre of the modelled distribution. This third outcome would suggest that species were not both randomly distributed and also that their clumping occurred in different areas.

Of these three potential outcomes, we found that for all three species associations, the modelled co-occurrence was less than the observed co-occurrence. The implication is that neither jellyfish nor sunfish are randomly distributed but co-occur more in the same areas than expected by chance. This conclusion fits with the intuitive interpretation of our results with *Rhizostoma octopus* being found in certain coastal hotspots, *Chrysaora hysoscella* more frequently sighted in the southern sections of the study area, *Cyanea capillata* having a more northerly distribution and sunfish being found in all the areas where jellyfish were most abundant (Figures 3&4). Potentially there might be some trophic interaction with sunfish feeding more in the jellyfish hotspots. Further examination of these species associations may be able to test this hypothesis.

Relating this broad distribution to our previous knowledge of *Mola mola*, what is reasonably established is a preference for schyphozoan jellyfish and in particular the moon jellyfish *Aurelia aurita* (Thys, 1994). It has been argued that this association reflects physical constraints on prey ingestion imposed by the small rigid mouths of sunfish whereby jellyfish are sucked in through the beak, shredded and then spat out; the process being repeated until the item is small enough to be swallowed (Thys, 1994). This may explain why sunfish do not appear to aggregate in the extensive aggregations of *Rhizostoma octopus* (unlike leatherback turtles in the Irish Sea; Houghton et al. (in press)), as the manipulation of such large and robust prey (up to 80 cm across; Russell, 1970) may be highly demanding. Therefore, if we consider that *Aurelia aurita* might provide a suitable prey species for sunfish within the Irish and Celtic Seas (albeit tentatively), then the typically cosmopolitan distribution of this jellyfish species with temperate coastal marine systems (Russell, 1970) may possibly reflect the broad and apparently random distribution of their potential predators. However, as *Aurelia aurita* were not recorded from the air (as a result of its small size, and an inability to observe the species at all in anything other than perfectly calm sea states), any such suggestion remains purely speculative.

Regarding more direct insights, observations of sunfish actively swimming throughout the study area support the suggestion that sunfish are active in coastal, temperate seas during the summer months (Sims & Southall, 2002). Moreover, in this previous study, all *Mola mola* observed were in the size-range of 0.5–0.7 m total length, which were broadly consistent with our estimations of sunfish size made from the air. We do not imply, however, that larger sunfish are entirely absent from British and Irish waters with numerous anecdotal records such as the individual weighing 363 kg washed ashore on Tayside, Scotland, in 1960 (source: British Marine Life Study Society). Nevertheless, given the consistent observation of smaller sunfish in the present study and the extensive area covered, it seems most probable that such specimens are far less common. It has been suggested that the increased presence of smaller, young sunfish in coastal waters may be owing to local current regimes carrying them further inshore than adults (Sims & Southall, 2002) or alternatively, represent an ontogenetic or seasonal migration with individuals moving inshore from deep water overwintering sites to capitalize upon the seasonal abundance

of gelatinous prey (Norman & Fraser, 1949; Fraser-Brunner, 1951; Hart, 1973; Lee, 1986). Such questions cannot be answered in the context of our study, and require further more bespoke investigation. Nevertheless, the notion of sunfish migration is not completely unfounded with Myers & Wales (1930) and Reiger (1983) suggesting broad scale movements to remain within a preferred temperature range. In light of such recent evidence, the notion of sunfish as merely passive opportunists (McCann, 1961; Holt, 1965; Lee, 1986) is becoming less likely with time. Undeniably, there is a largely inactive component to their behaviour but recent tracking studies off southern California suggest sunfish movements may in fact be highly directional with even some evidence of some magneto-receptive capabilities (Cartamil & Lowe, 2004).

To summarize, our findings provide a broad scale assessment of sunfish density within the Irish and Celtic Seas. The observed abundance, albeit modest, highlights that the species is more abundant in the region than once thought, and an order of magnitude greater than the other apex jellyfish predator: the leatherback turtle. Individuals sighted were typically small and observed to either bask or actively swim at the surface, consistent with previous studies. Lastly, regarding predator–prey relationships, we found that for all three species associations, the modelled co-occurrence was less than the observed co-occurrence. The implication is that neither jellyfish nor sunfish are randomly distributed but co-occur more in the same areas than expected by chance. Although simple, we hope these data provide further baseline information on a poorly understood species within British and Irish waters and offer some limited insights to the species as a whole.

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