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Original Article

Balancing fishery and conservation: a case study of the barrel jellyfish *Rhizostoma octopus* in South Wales

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In Wales, the barrel jellyfish *Rhizostoma octopus* is commercially harvested to produce high-value medical grade collagen. Although the fishery is presently not regulated, there are concerns how it may affect the leatherback turtle (*Dermochelys coriacea*), which preys on *R. octopus* in local waters. We combined monitoring data and morphometric and weight measurements in models to estimate the potential impact of *R. octopus* fishery on foraging turtles. We found a significant quadratic relationship between bell diameter and wet weight of *R. octopus*, with bell diameter explaining 88% of the variability in wet weight. *R. octopus* biomass in the Carmarthen Bay varied inter-annually between 38.9 and 594.2 tonnes y^{-1}. The amount of *R. octopus* needed to satisfy a leatherback turtle's daily energetic requirements was estimated at 85.1–319.1 kg. Using leatherback turtle sighting data, our models show that during a jellyfish 'low year", the *R. octopus* population could be completely depleted by an average of two foraging turtles along with the current level of commercial harvesting (4.3 tonnes). During a jellyfish "high year", the current level of commercial harvesting is predicted to have relatively little impact on food supply for even the maximum number of foraging leatherback turtle reported in the area. However, uncertainties related to the jellyfish's life cycle in the local waters need to be resolved for proper management of this emerging fishery.

Keywords: Barrel jellyfish, Conservation, Fishery, Leatherback turtle, Rhizostomeae, *Rhizostoma octopus*

Introduction

The frequently reported but debatable increase of jellyfish worldwide (Brotz *et al.* 2012; Mills, 2001; Condon *et al.* 2013) is on the one hand threatening traditional fisheries and marine economy (Lynam *et al.* 2011; Quiñones *et al.* 2013; Gjelsvik Tiller *et al.* 2014; Palmieri *et al.* 2014), and on the other hand raising the prospect of harvesting jellyfish, especially those of the order Rhizostomae, for food and other commercial applications (Purcell *et al.* 2013; Gibbons *et al.* 2016) (Table 1). The barrel jellyfish *Rhizostoma octopus* is one of the largest jellyfish species in United Kingdom waters and can measure over 1 m in diameter and weigh up to 35 kg (Doyle *et al.* 2007a; Lilley *et al.* 2009). Aerial surveys over the Irish Sea consistently found *R. octopus* in dense patches in the coastal areas, especially in Carmarthen Bay, Tremadoc Bay, and Rosslare Harbour (Houghton *et al.* 2006a; Lilley *et al.* 2009). In Carmarthen Bay, commercial harvesting of *R. octopus* started in 2014 to produce high-value medical grade collagen. Although this new fishery is presently unregulated, there are concerns over its potential impacts on leatherback turtles foraging in the area. Mitigation procedures are in place to avoid sea turtle by-catch (Hobson, 2015), but the danger of depleting the food source for leatherback turtles remains.

The leatherback turtle was listed by the IUCN as "critically endangered" from 2000 to 2013, but its status has recently improved due to some success with the conservation efforts (IUCN, 2014). The Northwest Atlantic subpopulation is now considered "least

Table 1. Reported commercial harvesting of Rhizostomeae jellyfish (see Note 1) for food with the exception of *R. octopus* in Wales, UK, which is harvested to produce medical grade collagen. nd = no data.

Family	Species	Tonnes harvested (year)	Location	References
Cassiopeidae	*Cassiopea ndrosia*	nd	Philippines	Purcell *et al.* (2013)
Catostylidae	*Acromitus hardenbergi*	nd	Malaysia, Indonesia, Thailand	Kitamura and Omori (2010) Purcell *et al.* (2013)
Catostylidae	*C. mosaicus*	33 (1995–1996), 14 (1996–1997), 10 (1997–1998)	Australia	Kingsford *et al.* (2000), Omori and Nakano (2001), Purcell *et al.* (2013)
Catostylidae	*C. mastigophora*	32,115 (2013)	Indonesia	Kitamura and Omori (2010), Purcell *et al.* (2013), Asrial *et al.* (2015)
Catostylidae	*Crambionella annandalei*	nd	Myanmar	Kitamura and Omori (2010), Purcell *et al.* (2013)
Catostylidae	*Crambionella orsini*	Nd	Red Sea, Iranian Gulf, Bengal Bay	Omori and Nakano (2001)
Cepheidae	*Cephea cephea*	nd	nd	Purcell *et al.* (2013)
Lobonematidae	*Lobonemoides gracilus*	nd	Philippines, Vietnam, Thailand	Purcell *et al.* (2013)
Lobonematidae	*Lobonemoides robustus*	Nd	Philippines Vietnam, Thailand, Indonesia, Myanmar	Kitamura and Omori (2010)
Rhizostomatidae	*Nemopilema nomura*	nd	North western Pacific, China	Omori and Nakano (2001), Purcell *et al.* (2013)
Rhizostomatidae	*Rhizostoma octopus*	4.3 (2015)	Wales, UK	This paper
Rhizostomatidae	*Rhizostoma pulmo*	nd	Turkey	Omori and Nakano (2001), Purcell *et al.* (2013)
Rhizostomatidae	*Rhopilema hispidum, R. esculentum*	15 034 (2000–2005), 220 000 (2010)	Vietnam, China, Thailand, Indonesia, Myanmar, Japan, China, Vietnam, Malaysia	Hsieh *et al.* (2001), Nishikawa *et al.* (2008), Kitamura and Omori (2010) Purcell *et al.* (2013), Dong *et al.* (2014)
Rhizostomatidae	*Rhopilema spp.*	388 267 (2012)	China, Thailand, Indonesia, Bahrain, Malaysia, Myanmar, Iran, Nicaragua, Russia, Falklands, Philippines, UK	FAO (2014) (see note 2)
Stomolophidae	*Stomolophus meleagris*	14 220 (2011), 20 988 (2012)	Mexico, USA	López-Martínez and Álvarez-Tello (2013), Purcell *et al.* (2013), FAO (2014)

Note 1: The reported target species may not be accurate because of confusion about jellyfish taxonomy or incorrect identification by fishers (Brotz, 2016).
Note 2: Not all jellyfish harvested were reported to FAO and jellyfish tended to be reported as the genus Rhopilema or simply as "jellyfish" (Kingsford et al., 2000).

concern" but other subpopulations in East Pacific, West Pacific, Southwest Atlantic, and Southwest Indian Ocean remain critically endangered (IUCN, 2014). The leatherback turtle migrates long distance between its nesting grounds and foraging grounds (Houghton *et al.* 2006b; Dodge *et al.* 2014). It feeds on gelatinous zooplankton, of which it must consume at least 50% of its body weight per day (James and Herman 2001; López-mendilaharsu *et al.* 2009; Heaslip *et al.* 2012). It is known to visit UK waters and feed on *R. octopus* (Penrose, 2014). Of the 179 sightings of leatherback turtle in Wales in 1960–2013, 22% of them were associated with *R. octopus* hotspots (Houghton *et al.* 2006b). There have been three sightings confirming leatherback turtle predation on barrel jellyfish in Carmarthen Bay and Tremadoc Bay (Pierpoint, 2000).

Stock assessment of *R. octopus* is critical to managing the fishery, but direct biomass measurement can be difficult and time consuming. Many jellyfish species exhibit specific allometric relationships between their morphometric measurements and wet weights (Kingsford *et al.*, 2000; Houghton *et al.*, 2007). In this study, we conducted morphometric and weight measurements of *R. octopus*, and combined the results with monitoring data in models to estimate the potential impact of *R. octopus* fishery on leatherback turtles foraging in Carmarthen Bay.

Material and methods

R. octopus morphometric and weight measurements

Fresh specimens of *R. octopus* were collected on board of a commercial fishing boat in Carmarthen Bay in July–September 2014 and July–August 2015 (Figure 1). The jellyfish were caught by trawling a gill net (mesh size: 5 × 5 cm). Upon net retrieval, the majority of the caught *R. octopus* was immediately processed by commercial fishers; opportunistic samples of intact specimens were removed for measuring the bell diameter (maximum distance between the marginal velar lappets). Individual wet weights were measured in 2015 using a digital scale. Oral arm lengths were not measured due to time constraints of the commercial operation.

In addition to fresh specimens, we also used *R. octopus* stranded on beaches. As stranding of *R. octopus* frequently occurs in south Wales, measurements of stranded specimens may provide an alternative way to monitoring and stock assessment when live specimens are not available. Stranded specimens were collected at Tenby North beach and Freshwater East beach (Figure 1) on 11th and 17th of July 2015, respectively. Specimens with visible signs of damage or decomposition were not used. Bell diameters and weights were measured as described before. In addition, two oral arms of each specimen were measured from the

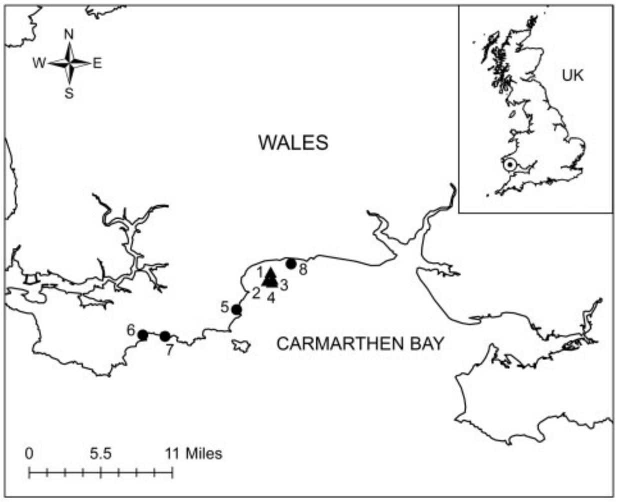

Figure 1. Locations of sampling sites for *Rhizostoma octopus* in 2014 (1–4; ▲) and 2015 (5–8; ●). Beach stranded specimens were collected at (5) Tenby North beach and (6) Freshwater East beach. Inlay map: Black circle indicates the sampling area.

central point of the arms to the end of the terminal club, and the mean oral arm lengths were calculated.

The measurements were grouped as fresh vs. stranded specimens. All data were tested for normality (Shapiro-Wilks test) and equal variances (Levene test); non-parametric tests were used when normality was not satisfied. Mann-Whitney U test was used to compare the median bell diameters and unpaired Student's t-test was used to compare the wet weights between the two specimen groups. Upon showing no significant differences between the two groups, data were pooled for non-linear quadratic regression analysis of allometric relationship between bell diameter and wet weight. Non-linear quadratic regression was preferred because it was the best fit for the data and it allowed for comparison with the previously published equation (Doyle *et al.*, 2007b; Houghton *et al.*, 2007). Bell diameter measurements made on four dates in 2014 were compared by one-way ANOVA.

R. octopus abundance

Between 2003 and 2011, aerial survey of *R. octopus* in Carmarthen Bay was conducted 16 times according to Houghton *et al.* (2006a). The surveys were conducted as part of two projects (funded by the Interreg European Regional Development Fund between 2003–2006 and 2008–2012) whenever the weather conditions were suitable (i.e. low winds, no/high cloud cover and when there was no military activity on the Carmarthen Bay firing range; see Houghton *et al.* 2006a for details). In brief, estimates of jellyfish species were made from ca. 150 m above water over a 5-min period by an observer on either side of the plane. Jellyfish numbers were estimated in groups (0, 1–10, 10–50, 50–100, 100–500, 500+); once assimilated with the locational data of the flight and corrected for glare (Houghton *et al.* 2006a) an estimate of jellyfish number in Carmarthen Bay could be made. The aerial survey data were corrected for surface visibility (detectability) by multiplying the surface estimates by the mean amount of time that *R. octopus* spent at the surface (10%; Hays *et al.*, 2012; Hobson, 2015). This value was determined using data from 72 CEFAS data-storage tags deployed in September 2008 and 2009 on *R. octopus* in Carmarthen Bay, Wales. 25 tags were recovered (containing dive data for between 2 and 28 days) before the death of the jellyfish (Hays *et al*, 2012). The mean annual abundance data were then multiplied by the mean weight (11.0 kg; see "Results" section) to get the biomass (tonnes).

Leatherback turtle abundance and foraging time

The TURTLE database, compiled by Marine Environmental Monitoring, lists all marine turtle sighting and stranding reports around the UK and Ireland dating back to 1748. Here we used 2001–2015 sighting data to estimate the number of leatherback turtle and the amount of time each spent foraging in Carmarthen Bay.

Model 1: leatherback turtle dietary requirement

To calculate the amount of *R. octopus* required to sustain the population of leatherback turtles foraging in Carmarthen Bay (assuming *R. octopus* as the sole food source), we used the following equation:

$$Y = K \times T \times N \tag{1}$$

where Y is the biomass required (tonnes); K is the biomass required to meet a leatherback turtle's daily energy requirement (tonnes d^{-1}); T is the time (days) spent by a leatherback turtle foraging in Carmarthen Bay each year; N is the number of leatherback turtle foraging in Carmarthen Bay each year.

Using the gross energy content of *R. octopus* (0.11 kJ g^{-1} wet weight; Doyle *et al.*, 2007b) and an assimilation efficiency of 80%, Fossette *et al.* (2012) estimated a 300 kg leatherback turtle (I_{300}) consumes 68.6 kg d^{-1} of jellyfish to meet its minimum energy requirements, and 257 kg d^{-1} to meet its maximum energy requirements. The average weight of an adult leatherback turtle is ca. 400 kg (Davenport, 1998; Georges and Fossette, 2006); using the metabolic theory (Brown *et al.*, 2004), we estimate its jellyfish consumption (I_{400}) as $1.24 \times I_{300}$ which equals 85.1 and 318.9 kg d^{-1} to satisfy minimum and maximum energy requirements, respectively. These numbers were used in the models to calculate the *R. octopus* biomass needed to sustain leatherback turtles (assumed average weight = 400 kg) in Carmarthen Bay.

Model 2: Potential impact of *R. Octopus* fishery

To calculate the residual *R. octopus* biomass in Carmarthen Bay after consumption by leatherback turtles and commercial harvesting, we used the following equation:

$$B' = B - (Y + J) \tag{2}$$

where B' is the residual biomass (tonnes); B is the initial biomass (tonnes); Y is the biomass required to sustain leatherback turtle population (tonnes); J is the biomass harvested commercially (tonnes).

To calculate the theoretical recovery time required by the residual medusae population to return to the original biomass level, we used published maximum and minimum growth rates of *R. octopus* medusae: The maximum growth rate was taken from Kruger (1968), who monitored the increase in *R. octopus* bell diameter in Helgoland, Germany from June to September (same season as for commercial harvesting in Carmarthen Bay). By converting the bell diameters to wet weights we obtained a growth rate of 0.2 d^{-1}. The minimum growth rate was based on another Rhizostomeae jellyfish *Nemopilema nomurai* in the Sea of Japan, which grows at a rate of 0.02 d^{-1} in terms of wet weight between August and December (Kawahara *et al.*, 2006). The recovery time is then calculated as:

$$B = B' \times e^{rt} \qquad (3)$$

Where r is the growth rate of *R. octopus* (d^{-1}); t is the time required for *R. octopus* to recover to initial population biomass (d).

Equations (1)–(3) were used to examine the different scenarios by varying the number of leatherback turtles visiting Carmarthen Bay, the amount of time each turtle spends foraging, the turtle's energy requirement, and the initial *R. octopus* biomass.

Results

Morphometric and weight measurements

Morphometric and weight measurements were made on four occasions in 2015 (Supplementary Table S1). Between fresh specimens and stranded specimens, there were no significant differences in their median bell diameters (fresh = 68.5 cm; stranded = 61.9 cm; Mann-Whitney test $W = 425.5$, $p = 0.09$) or mean wet weights (fresh = 10.9 ± 4.7 kg; stranded = 11.0 ± 4.1 kg; t-test $t_{24} = -0.098$, $p = 0.92$) (Supplementary Figure S1). The two data sets were subsequently combined in further analysis.

The mean bell diameter was 65.9 cm (±11.7 *SD*) and the mean oral arm length was 41.1 cm (±12.4). There was a significant linear relationship between bell diameter and oral arm length (Supplementary Figure S2). The measured mean wet weight was 11.0 kg (±4.3). The total catch on 23 July 2015 was 57 individuals for a total weight of 632 kg, giving an average weight of 11.1 kg per individual, which is almost identical to the measured mean weight. There was a significant quadratic relationship between bell diameter and wet weight (Figure 2) ($F_{23} = 83.22$, $r^2 = 0.88$, $p < 0.0001$).

Temporal variation in *R. octopus* size and biomass

Bell diameters showed significant temporal variation in 2014 (ANOVA: $F_{3,109} = 8.71$, $p < 0.0001$) (Supplementary Figure S3), and the mean diameter decreased significantly between August and September. Although weight measurements were not made in 2014, we used the quadratic regression from Figure 2 to estimate wet weights from bell diameters. For comparison, we included a previously published quadratic equation (Doyle *et al.*, 2007b; Houghton *et al.*, 2007). The two equations predict very different weights, particularly for the large specimens (Figure 3).

Using the aerial survey data from 2003 to 2011 and applying the mean weight (11.0 kg) measured in this study, we estimated the population biomass of *R. octopus* in Carmarthen Bay (Supplementary Figure S4). Except for 2005 when no *R. octopus* was observed, and 2006–2007 when no data were collected, *R. octopus* biomass varied between 38.9 and 594.2 tonnes, and an annual mean of 260 tonnes was used in the models.

Leatherback turtle abundance and foraging time

Between 2001 and 2015, 16.9% leatherback turtle sightings in the United Kingdom occurred in Wales, and within Wales, 27.3% of them occurred in Carmarthen Bay (Supplementary Table S2). The maximum recorded number of live leatherback turtles was five for Carmarthen Bay; hence, we used one to five and an average of two turtles in our models. The majority of sightings (92%) occurred between July and September (Supplementary Figure S5); therefore, we set the maximum foraging time to 90 days in the models.

Model outputs

Commercial harvesting of *R. octopus* in Carmarthen Bay was at 4.3 tonnes based on 2015 record. Assuming an initial *R. octopus* biomass of 260 tonnes, Models 1 and 2 were used to calculate the residual biomass after commercial harvesting and predation by leatherback turtles, as a function of the number of leatherback turtle foraging for a maximum of 3 months. With one turtle, the residual biomass was between 248.0 tonnes (95.4% for minimum energy requirement) and 227.0 tonnes (87.3% for maximum energy requirement). With 5 turtles, the residual biomass was 112.1–217.4 tonnes (43.1–83.6%) (Figure 4).

Based on the average food requirement by individual leatherback turtle, and by varying its foraging time between 10 and 90 days, the model predicts that with one turtle the residual *R. octopus*

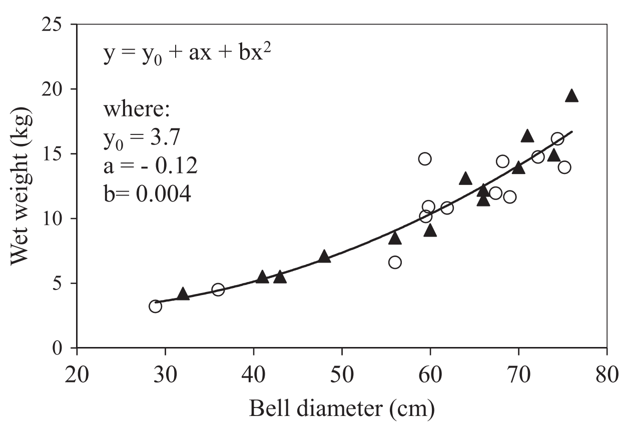

Figure 2. Quadratic regression of wet weights vs. bell diameters of *R. octopus*. Data were compiled from fresh specimens (▲) and stranded specimens (○) from 2015; $r_2 = 0.88$, $p < 0.0001$.

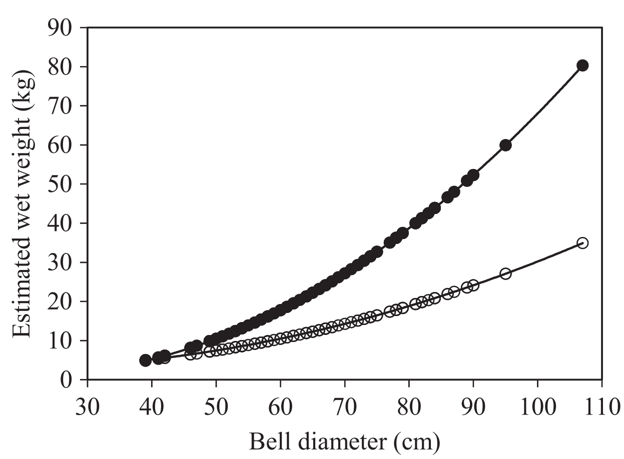

Figure 3. Wet weights estimated from bell diameters for the 2014 samples based on a previously published quadratic equation (●) (Houghton *et al.*, 2009;2007; Doyle *et al.*, 2009;2007b) and the quadratic equation from this study (○).

biomass was 237.5–253.7 tonnes (91.4–97.6%), and with five turtles it was 164.8–245.6 tonnes (63.4–94.5%) (Supplementary Figure S6).

We estimated the time required for the residual *R. octopus* medusae to recover to the initial population biomass level as a function of growth rate (Supplementary Figure S7). With an initial biomass of 260 tonnes and 1–5 leatherback turtles foraging at mean energy requirement for 90 days, the residual population would take 4.4–22.7 days to recover at the minimum growth rate, and 0.5–2.3 days at the maximum growth rate.

The aerial survey data showed that *R. octopus* abundance in Carmarthen Bay could vary by 15-fold. We used the models to examine how likely the jellyfish population will be depleted by commercial harvesting (4.3 tonnes) and foraging by leatherback turtle (3 months at mean energy requirement). At the low initial *R. octopus* biomass (38.9 tonnes), only two leatherback turtles would deplete the entire *R. octopus* population (Figure 5). In contrast, at the high initial biomass (594.2 tonnes), even with five leatherback turtles the residual biomass would remain high (84.0%).

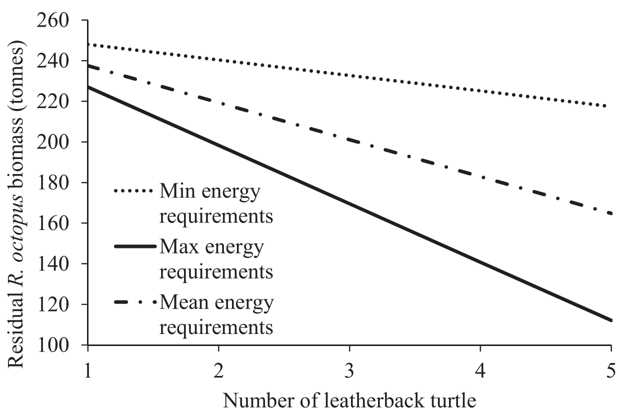

Figure 4. Residual *Rhizostoma octopus* medusae biomass in Carmarthen Bay as a function of number of foraging leatherback turtle and their energy requirement. Commercial harvesting of *R. octopus* was set at 4.3 tonnes; initial population biomass was set at 260 tonnes; leatherback turtle foraging time was set at 90 days y^{-1} in the area.

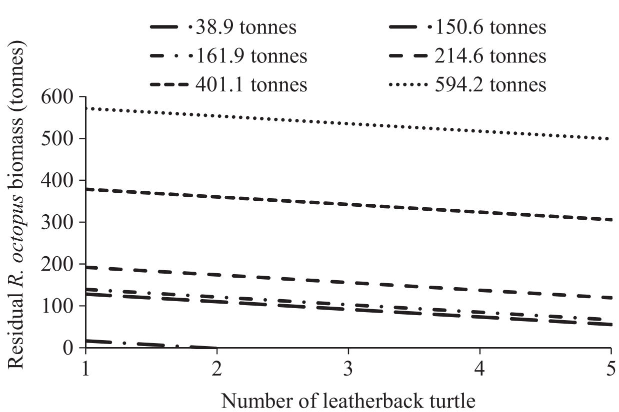

Figure 5. Residual *Rhizostoma octopus* medusae biomass in Carmarthen Bay as a function of number of leatherback turtle and initial *R. octopus* biomass. Commercial harvesting of *R. octopus* was set at 4.3 tonnes; mean dietary requirement of leatherback turtle was set at 202.1 kg d^{-1}; foraging time was set at 90 days.

Discussion

Morphometric and weight characteristics of *R. octopus*

Jellyfish population size can vary considerably in time and in space (Kingsford *et al.*, 2000; Pitt and Kingsford, 2003; Bastian *et al.*, 2014). To aid more effective monitoring of jellyfish population, simple morphometric measurements can be used to estimate individual biomass (Lucas, 2009; Bastian *et al.*, 2014). In this study, we established a quadratic equation where the bell diameter explains 88% of the variability in wet weight of *R. octopus*. A similar relationship was also reported for the *R. octopus* population in Rosslare Harbour, Ireland (Doyle *et al.*, 2007b; Houghton *et al.*, 2007), but it tends to overestimate the wet weight, especially for the larger specimens. It is worth noting that the majority of the Rosslare Harbour samples had a bell diameter of <50 cm, whereas in Carmarthen Bay the majority were ≥ 50 cm; it is therefore questionable whether the earlier equation was valid for our samples. Nevertheless, others have reported different morphometric relationships for the same species in different locations. For example, Bastian *et al.* (2014) showed that the allometric relationship for three jellyfish species in the Irish Sea was different when compared to other studies; they also found significantly different average mass per individual between the western and the eastern regions of the Irish Sea, presumably due to the different food environments. Recent studies found that the different *R. octopus* populations around the United Kingdom and France were genetically distinct (Lee *et al.*, 2013; Glynn *et al.*, 2015). Glynn *et al.* (2015) presented further evidence that the populations in Carmarthen Bay, Celtic Sea, Tremadoc Bay and Solway Firth originated from a single population but are geographically separated after the last glacial maximum, which may explain the different allometric relationships between the populations. Further comparison of the allometric relationships among the different populations will prove useful, especially if the *R. octopus* fishery expands to the other areas.

In 2014, the mean bell diameter decreased from August to September. Houghton *et al.* (2007) observed a similar decline in *R. octopus* bell diameter in the month of September, and they attributed this to two possible reasons: (i) The larger individuals strand after becoming reproductively spent, thereby leaving the smaller medusa in the water column; (ii) Environmental variations lead to different growth rates and sizes between months. Medusae are known to shrink when food is scarce or after spawning (Lucas, 2001; Lilley *et al.*, 2014). When kept in captivity without food for 5 weeks, *R. octopus* decreased to 7–11.6% of its original weight (Russell, 1970). Commercial fishers reported that *R. octopus* harvested in September appeared to be more fragile, suggesting a change in its body integrity due to reproductive exhaustion or food limitation later in the season.

No significant difference in the allometric relationship was found between stranded specimens and fresh specimens. These results mean that aerial survey and boat-based survey of *R. octopus* can be augmented by beach survey for several important advantages: No costly equipment is required; surveys can be done without concerns over weather condition and passenger safety; stranded specimens are deceased so that the measurement is non-destructive; stranded specimens are easier to handle, as live *R. octopus* tends to produce abundant irritating mucous when stressed; citizen scientists can make and report measurements after some simple training. As the sight of *R. octopus* stranding on beaches often captures public's interest, the prospect of using citizen surveys would help the industry and regulatory agency to broaden data coverage.

Leatherback turtle dietary requirement

Although direct measurement of leatherback turtle predation on *R. octopus* in Carmarthen Bay is not available, we used Model 1 to determine that the amount of *R. octopus* required per day by an adult leatherback turtle was 85.1, 202.1, and 319.1 kg to meet minimum, mean and maximum energy requirements, respectively. Given a mean weight of 11.0 kg for *R. octopus*, these energy requirements are equivalent to ca. 7.7, 18.4, and 29.0 jellyfish per day, respectively. The mean estimate is almost identical to that of Davenport (1998), who observed that a 400 kg leatherback consumed ca. 200 kg of *R. octopus* per day. Heaslip *et al.* (2012), using animal-borne cameras to study daytime foraging of leatherback turtles around Cape Breton Island, Canada, estimated that the amount of prey consumed averaged 330 kg d^{-1}, or 73% of the turtle's body mass (455 kg). If we scale these results to a 400 kg leatherback turtle, the amount of prey required would be 299.6 kg d^{-1}, which is close to the maximum energy requirement estimated by our model. On the other hand, Jones *et al.* (2012) estimated a leatherback turtle (250–450 kg) needs to consume a minimum of 65 kg d^{-1} of jellyfish to meet daily energetic requirements, which is comparable to the minimum energy requirement calculated by our model.

Our models relied on turtle sighting data with several caveats: First, the same turtle could be sighted and reported multiple times. However, tagging study has shown that leatherback turtle tends to travel continuously and is unlikely to be sighted repeatedly within a relatively confined area such as Carmarthen Bay (Hays *et al.*, 2006). Conversely, the number of leatherback turtle could be underestimated if some sightings go unreported or some turtles are not seen while under water (Houghton *et al.*, 2006b). However, leatherback turtle makes shallower dives in colder waters to conserve energy and to exploit the shallower distribution of jellyfish (James *et al.*, 2006; Casey *et al.*, 2014; Burns *et al.*, 2015). Therefore, it is suggested that northern foraging areas are best for sighting leatherback turtle (James *et al.*, 2005). Several studies have shown that when eating large jellyfish, leatherback turtles bring the prey to the surface and take several minutes to consume it (James *et al.*, 2005; Myers and Hays, 2006). This behaviour would make them more noticeable in temperate waters.

Many studies have shown that leatherback turtles forage in the Northwest Atlantic for 3–5 months before returning to breed in tropical waters (Hays *et al.*, 2006; Houghton *et al.*, 2006b; Fossette *et al.*, 2010). This corresponds well with the TURTLE database, where most sightings occurred between July and September. Accordingly, our models estimated that over a 90-day period, a single leatherback turtle could consume 7.7–28.7 tonnes of *R. octopus*, which is up to six times the amount that is currently being commercially harvested. However, it is unlikely that a turtle would spend all 90 days in Carmarthen Bay; therefore, the models could have overestimated the amounts of *R. octopus* required.

Management considerations for *R. octopus* fishery

Presently commercial harvesting of *R. octopus* in Carmarthen Bay was limited to the summer months (July–September). Based on the estimated *R. octopus* growth rates, the residual medusae population would take less than a month to return to its original biomass level and therefore, theoretically, commercial harvesting would have relatively small impact on the overall medusae biomass. Nevertheless, aerial surveys showed that *R. octopus* abundance did fluctuate considerably between years in Carmarthen Bay. Indeed, our models predict the worst case scenario for a jellyfish "low year" (initial biomass 38.9 tonnes) when commercial harvesting would severely compromise the food supply for an average number (2) of leatherback turtle in Carmarthen Bay.

There are limitations to our analysis. First, our models assume that leatherback turtle eats only *R. octopus*, but it is known to consume other jellyfish species in UK waters. Conversely, the models do not consider other predators that prey on *R. octopus*. For example, fulmar (*Fulmaris glacialis*) has been seen eating *Rhizostoma spp.* off the Isle of Mann (Arai, 2005). There was also anecdotal evidence of Risso's dolphin (*Grampus griseus*) eating *R. octopus* in Cardigan Bay, Wales (C. Benson, pers. comm.). It is not known whether these predators consume *R. octopus* regularly or only opportunistically, and more research is needed to quantify the predation pressure on *R. octopus* from species other than leatherback turtle.

Harvesting jellyfish could also remove a potential food source for scavengers on the sea floor. For example, in the Norwegian deep-sea, baited camera recorded that jellyfish carcasses were quickly consumed by scavengers such as Atlantic hagfish, galatheid crab, and the lysianassid amphipod (Sweetman *et al.*, 2014). It is not known how much *R. octopus* contributes to the benthic food web in Carmarthen Bay, but it is an issue that should be addressed when managing jellyfish fishery in the area.

Commercial harvesting of jellyfish is increasing globally with an estimated catch of ca. 500 000 tonnes per year (López-Martínez and Álvarez-Tello, 2013). Unlike finfish and shellfish, regulation and management of jellyfish fisheries are not well developed (Richardson *et al.*, 2009). Some jellyfish species are already over-harvested requiring stock enhancement, such as the edible jellyfish *Rhopilema esculentum* in China (Dong *et al.*, 2010, 2014), or they are in danger of being over-exploited, such as *Crambione mastigophora* in Indonesia (Asrial *et al.*, 2015). The Australian government took a precautionary approach when licensing a *Catostylus mosaicus* jellyfish fishery by setting the allowable catch to 15% of the virgin biomass (estimated at 10 000 tonnes) in the first year (Department of Natural Resources and Environment, 2002); it also restricted the harvesting to hand-dip netting by five boats, required continual monitoring and set a minimum bell diameter catch limit.

Based on available information, we estimated that the present level of commercial harvesting of *R. octopus* has a relatively minor impact on the food supply for leatherback turtle in years with an average to high medusae biomass. However, if the fishery continues to grow, there is a risk of depriving the turtles of food, especially in years when medusae biomass is low. Repeated aerial survey augmented by boat-based sampling and beach survey would allow scientists to generate a more reliable continuous assessment of the *R. octopus* population to inform the fishery and turtle conservation. To support long-term sustainable management of *R. octopus* fishery, there is a need to fill the knowledge gap on the species' natural life history in South Wales. For example, it is not known whether the medusae population in Carmarthen Bay is recruited locally (i.e. from polyps in local water) or brought in by currents. Likewise, data on its *in situ* mortality and recruitment rates, or how it is affected by local/regional environmental conditions are also lacking. It is advisable that the industry and the government take a proactive approach to monitoring and studying the species in order to prevent unintended long-term consequences of this new fishery to the local ecosystem.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the article.

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