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Seal carrion is a predictable resource for coastal ecosystems

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Abstract

The timing, magnitude, and spatial distribution of resource inputs can have large effects on dependent organisms. Few studies have examined the predictability of such resources and no standard ecological measure of predictability exists. We examined the potential predictability of carrion resources provided by one of the UK's largest grey seal (*Halichoerus grypus*) colonies, on the Isle of May, Scotland. We used aerial (11 years) and ground surveys (3 years) to quantify the variability in time, space, quantity (kg), and quality (MJ) of seal carrion during the seal pupping season. We then compared the potential predictability of seal carrion to other periodic changes in food availability in nature. An average of 6893 kg of carrion $\cdot yr^{-1}$ corresponding to 110.5×10^3 $MJ\cdot yr^{-1}$ was released for potential scavengers as placentae and dead animals. A fifth of the total biomass from dead seals was consumed by the end of the pupping season, mostly by avian scavengers. The spatial distribution of carcasses was similar across years, and 28% of the area containing >10 carcasses ha^{-1} was shared among all years. Relative standard errors (RSE) in space, time, quantity, and quality of carrion were all below 34%. This is similar to other allochthonous-dependent ecosystems, such as those affected by migratory salmon, and indicates high predictability of seal carrion as a resource. Our study illustrates how to quantify predictability in carrion, which is of general relevance to ecosystems that are dependent on this resource. We also highlight the importance of carrion to marine coastal ecosystems, where it sustains avian scavengers thus affecting ecosystem structure and function.

Keywords: Predictability, Resource Subsidy, Coastal, Carcass, Pinniped, Relative standard error, Scavenger.

1 Introduction

Many ecosystems are spatially linked by flows of nutrients and energy (e.g. Polis et al. 1997; Power and Rainey 2000; Anderson and Polis 1998; Reiners and Driese 2001). Such flows shape the structure and function of donor and receiving ecosystems by regulating nutrient availability and the dynamics of consumers that depend on them (Polis and Hurd 1996b).

Coastal regions are often affected by marine-derived inputs transferred from the ocean to the terrestrial ecosystem (Polis and Hurd 1996a, b; Polis et al. 1997; Rose and Polis 1998; Stapp and Polis 2003; Barton 2015). A noticeable example of this is the stranding of plant detritus and carrion on the shore (Polis et al. 1996). Animals also play a key role in the transport of marine nutrients when they move from one system to another. Salmon (Cederholm et al. 1999), sea turtles (Bouchard and Bjorndal 2000) and penguins (Erskine et al. 1998) play a fundamental role in this process by congregating at similar times of the year and in defined areas. The periodic availability of carrion and other nutrients released at such animal aggregations attract terrestrial foragers to the coast (e.g. Polis and Hurd 1995), locally increase the number of invertebrate consumers (e.g. Sánchez-Piñero and Polis 2000; Janetski et al. 2009; Spiller et al. 2010), and nourish soil and plants (Fariña et al. 2003). Despite the known effects of such inputs on both consumers and plants, few studies have examined the variation and predictability of these resources in coastal ecosystems. Whether a periodic resource pulse is predictable or not has important implications for how they are used by consumers and how they affect ecosystem function.

A challenge to understanding resource predictability is its definition and measurement. If similar food resources occur in similar places and at similar times each year we might consider this to be “predictable”, but how should “predictability” be quantified? Colwell (1974) was one of the first to define the predictability of periodic phenomena, by using their constancy (temporal uniformity) and contingency (consistency of timing between years). However, this method uses data categorised into classes and not continuous measures of true totals. Alternatively, a pulsed resource can be described as having low frequency, large magnitude and short duration (Yang et al. 2008), but these attributes can characterise both unpredictable and predictable resource pulses. Other attributes of predictability can be relevant from a consumer perspective. This can include whether resource availability is related to day length or the lunar cycle (Horning and Trillmich 1999), or whether it is stable in space and time (Cama et al. 2012), thus permitting consumers to find it (Weimerskirch 2007) and adapt their foraging behaviour to its availability (Overington and Lefebvre 2011). Although there are many examples of animal responses to the predictability of resource subsidies at both ecosystem and individual levels (e.g. Davenport 1995; Graham et al. 2006; Furness et al. 2007; Hoogenboom et al. 2013; Reid et al. 2012; Monsarrat et al. 2013; Oro et al. 2013), a clear definition of predictability is often not given. This means that measures of predictability are typically study-specific, and cannot be compared across ecosystems or resources.

When a subsidy is temporally and spatially constrained, consumers can predict where and when it will occur using prior knowledge and learning (Stephens and Krebs 1986), or programmed and evolved responses to signals (Berthold 1996). Female savanna elephants (*Loxodonta africana*), for instance, use past experience to adjust their timing of reproduction according to seasonal pulses in vegetation productivity (Wittemyer et al. 2007). Seabirds arrive to certain areas at times of high food availability, even if this means beginning to move before the food itself is detectable (Weimerskirch 2007). In these cases, both elephants and seabirds can predict resource availability, and respond to the location and timing of a resource, as well as its quantity and quality. While it is clear that some animals predict timing, spatial distribution, quantity, and quality of a resource, no study to our knowledge has examined all these aspects of predictability at once. A method to quantify the different aspects of predictability in common units will greatly help to understand how the characteristics of resources affect the response of populations dependent upon them and their success.

In this study, we examined resource predictability in a coastal island ecosystem that experiences seal carrion pulses. Like many other animal aggregations, the inputs of nutrients released by pinnipeds when forming breeding colonies are likely to be substantial for the coastal systems. In sea lion colonies, for instance, onshore mortality together with defecation are major sources of nutrients (Fariña et al. 2003). Seal colonies represent an important system for studying the predictability of a resource as there is an annual pulse of carrion which is used either directly by above ground secondary consumers, or indirectly as a source of nutrients to primary producers (Anderson and Polis 1998).

Here we asked the question: Is seal carrion a predictable resource for scavengers on seal colonies? We investigated the seal carrion (placentae and dead seals) produced during the pupping season in one of the largest grey seal (*Halichoerus grypus*) colonies in the UK (Isle of May, Scotland). We evaluated variability in the timing, spatial distribution, biomass, and energy content of this carrion by calculating their relative standard errors (RSE). This provides a common metric to evaluate variability across different measurement units. We hypothesised that the RSEs of seal carrion production would be similar to those of resources that animal consumers are known to predict (e.g. salmon runs). The flux of carrion to the local avian scavenging community was estimated as the biomass consumed at the end of the seal pupping season. Finally, we discuss the potential importance of seal carrion for the ecosystem as a whole.

2 Methods

2.1 Study area

This study was undertaken on the Isle of May (56°11’19”N, 2°33’27”W), situated at the entrance to the Firth of Forth on the east coast of Scotland. The island (1.8 x 0.5 km), covers an area of 45 ha, with the long axis extending in a northwest-southeast direction (Fig. 1). The Isle of May is a designated Special Area of Conservation (SAC) because it hosts a breeding colony of grey seals. This colony contributed ca. 4.3% to the annual UK pup production in 2010 (2153 pups born) and appears to be increasing since then (SCOS 2016).

The main scavenger occurring on the island is the great black-backed gull (*Larus marinus*): 40 pairs were counted nesting on the Isle of May during summer 2012 (SNH 2012). Between October and March the Scottish resident gull population receives immigrants from Scandinavia and Russia (Forrester et al. 2007).

2.2 Data collection

We used a combination of aerial surveys and ground visual censuses of pups and carcasses to quantify the characteristics of the carrion resource (placentae and dead seals) available at the seal colony.

Aerial survey data

The Sea Mammal Research Unit (SMRU, University of St. Andrews) has carried out annual aerial surveys of the Isle of May (and all other major Scottish grey seal breeding colonies) since the early 1990s, in order to estimate seal pup production (number of pups born per year) and the mean pupping date. Surveys were carried out annually up until 2010, when the frequency was reduced to every two years. The number of white coated pups and moulted pups are counted from a series of 3-6 aerial photo surveys carried out at approximately 10-12 day intervals throughout the breeding season. The pup counts are used together with estimates of 'time to moult' and 'time to leave' (Wyile, 1988) to model the birth curve and obtain estimates of total pup production (with 95% confidence limits) and mean pupping date. Dead pups were also counted for each survey, but pup mortality was not estimated. For further details of the methods see SCOS (1996).

The number of dead pups counted in aerial surveys was used here to approximate the number of carcasses released into the ecosystem every year for the decade 2000-2010 and the year 2012. The highest number of dead pups counted each year (among all the aerial surveys) was considered to be the most accurate, even though it is still likely to be an underestimation. To minimise this underestimation, data from ground visual census of carcasses conducted in 2008 and 2012 were used (223 and 226 carcasses, respectively; see below). Both censuses showed a greater number of dead pups than the highest count obtained by aerial surveys performed in both years. Therefore an error of underestimation was calculated from the percentage of dead pups missing in the temporally closest aerial survey count when the ground visual census was completed in 2008 and 2012 (35.0% and 42.0% of extra carcasses were found in the two years, respectively). As the underestimation was reasonably consistent between the two years, the mean error (38.5%, SD = 5.0%) was then used to adjust counts for all other years.

Ground visual census data

Ground visual census of carcasses was carried out at the end of the breeding season (late November to early December) in 2008, 2012 and 2013. Carcasses were detected by a team (3-6 people) systematically searching the seal breeding areas of the island. Sex and developmental stage (from 1 to 5, according to Kovacs and Lavigne, 1986) were determined for each carcass. However, those that appeared starved, scavenged, or in late state of decay could not be scored for sex and/or developmental stage (coded N/A). Starvelings (pups starved to death whose carcass lacked the natural layer of blubber) and dead adults were also recorded. GPS fixes (Garmin eTrex Summit; accuracy: <15m RMS) or marks on aerial photographs (in 2012), were made for all dead animals.

Carcasses recorded during the ground visual census of 2012 were scored for consumption state as follow: A = intact, B = lacked both eyes and/or showed one opening on the body, C = showed multiple openings, D = body looked flat and lacked some internal organs, head and/or some bones, E = remains (only bones, fur and skin). To assign an estimated mass loss to each consumption state, during the 2013 pupping season 11 experimental carcasses were deployed and weighed at regular time intervals to monitor changes in mass due to scavenging activity. The mean cumulative mass loss (in %) for consecutive consumption states was then calculated.

2.3 Data analysis

We calculated several attributes of the carrion resources on the Isle of May from aerial and ground surveys. These included the timing, quantity, quality, spatial distribution, and consumption of carrion.

Timing of pupping

Mean pupping dates for the decade 2000-2010 and 2012 were compared and the inter-annual variability in timing calculated.

Quantity of seal carrion

Seal carrion was divided into two sources: placentae and dead seals. The annual total estimated pup production was used to calculate the mean annual biomass of placentae produced during the period 2000 – 2010 and 2012. For this purpose average biomass of placentae was acquired by analysing placenta samples collected in the field during the pupping season 2013: six whole placentae (including amnion) were collected, weighed (± 10g) and sampled in fresh condition. Biomass (kg) of placentae available to the ecosystem for each year was then estimated by multiplying the pup production by the average wet mass of a grey seal placenta.

Because pup carcasses were not weighed during the ground visual census, the discrepancy between the mass of alive and dead pups estimated by using raw data collected by Baily (2014) was then used to adjust mass values according to

Kovacs and Lavigne (1986). Differences in mass of alive (n = 80) and dead (n = 37) pups belonging to the 2nd-3rd-4th developmental stages were analysed. The 1st and 5th stages were excluded from this analysis because of low sample size. For this reason, mass (kg) of pup carcasses was first calculated by using the equations provided by Kovacs and Lavigne (1986) and the resulting values were finally adjusted by subtracting the difference in mass found between alive and dead pups. Biomass of pups was estimated considering sex and developmental stage of carcasses; mass of pups of non-identifiable sex was approximated by averaging the mass of male and female pups for the different developmental stages. Mass of dead female pups belonging to the first developmental stage was given as a conservative value for starvelings and pups where developmental stage was not known. The mean maternal mass at weaning according to Pomeroy and Fedak (1999) was given for female adult carcasses (117 ± 18kg). A value of 234 kg was assigned to dead male adults, as breeding adult males are typically twice the mass of females when animals mate (Pomeroy and Fedak 1999). Mass of dead juvenile seals (called yearlings) was assumed as 56.4 ±6.3 kg (Addison and Stobo 1993).

Quality of seal carrion

Energy content of placenta produced each year during the period 2000 – 2010 and 2012 was estimated by analysing the gross energy density (MJ kg^{-1}) of placenta samples collected in 2013 by bomb calorimetry (Sciantec Analytical Service, UK). The energy content (MJ) of the total biomass of placentae was estimated by multiplying the total biomass with the energy density of grey seal placenta.

The body composition of pup carcasses was calculated according to Lang et al. (2011), in which percentages of water, protein and fat of grey seal pups at day 3 and 12 post-partum and at weaning are given. Percentages belonging to pups nursed by primiparous grey seal mothers, instead of multiparous, were used as a conservative approximation. Day 3 post-partum percentage of each body component was given to first and second stage carcasses, but also to starvelings and pups where developmental stage was not known. Day 12 post-partum percentages were assigned to third stage carcasses, whereas fourth and the fifth stage carcasses were assigned percentages calculated at weaning (Table 1). Body composition of female adult carcasses was also estimated from Lang et al. (2011), considering percentages of body components for primiparous grey seal mothers at day 12 post-partum.

Values provided by Lidgard et al. (2005) were used for male adult and juvenile carcasses. Percentages of each body component were then transformed in terms of biomass (kg) before estimating their energy content (MJ). Similar to body mass, body composition might also differ between dead pups and healthy living pups. Reduction or lack of blubber is evident in starvelings (Trites and Jonker 2000; Baily 2014). However, there is no documentation comparing alive and dead starveling pups. The energy content of protein and fat was quantified based on values of energy densities of 39.33 kJ g^{-1} and 17.99 kJ g^{-1} for fat and protein, respectively (Schmidt-Nielsen 1997). Zero energy was attributed to the water component. Results from this analysis represent an approximation of biomass and energy released into the ecosystem at the moment when carcasses become immediately available to the ecosystem. This analysis does not take into account possible variation in biomass and energy content of carrion over time caused by decomposition.

Spatial distribution of seal carrion

To identify the areas of the island impacted by carcasses, the locations of dead seals recorded during ground visual censuses in 2008, 2012 and 2013 were used to produce maps showing the kernel smoothed intensity of the point pattern created by the carcasses. From here onwards, the term *intensity* is used only when referring to kernel smoothed intensity of the point process for carcasses, while the term *density* is used in the strict sense in all other cases. Both measurements have the same units (n carcasses or placentae m^{-2}). Kernel estimation is a tool used in spatial ecology for detection of hotspots within the landscape (areas of high abundance or biomass) (Nelson and Boots 2008). Here, the spatial pattern of dead seals was analysed in order to produce maps showing the kernel smoothed intensity of the point pattern created by the carcasses. Boundaries of the island and locations of dead pups were projected onto a map using the British National Grid Reference System based on the OSGB36 datum (Ordnance Survey Great Britain 1936). The intensity of carcasses was calculated for the area of the island within the mean low water boundary (697102 m^2). Likelihood cross-validation was used to select the proper smoothing bandwidth for each year as it assumes an inhomogeneous Poisson process. The edge effect was set as ‘false’ as carcasses were not observed outside the window represented by the island (20 x 20 m pixels were used). Polygons of areas delimited by a minimum intensity of 0.001 carcasses m^{-2} were used as spatial thresholds of presence of carcasses and identified for each year. The union and the intersection of these polygons was plotted to highlight areas of persistent availability of carrion from year to year. Simple biomass density (kg m^{-2}) was also calculated for the whole island and for the total area formed by the above-mentioned polygons. Mean density (n placentae m^{-2}) and biomass (kg m^{-2}) of placentae for the decade were also estimated considering the area of the island at mean low water (697102 m^2).

Carcass consumption by scavengers

The consumption of carrion by gulls was calculated for the 2012 pupping season. To do so, the estimated percentage of scavenged mass, calculated according to the given consumption state (from A to E), was removed from each carcass mass. The scavenged portion of the total biomass available was then calculated as: starting mass – consumption state mass = scavenged mass.

Statistical analysis

We calculated means, standard errors, and relative standard errors (RSE = standard error / mean *100) expressed as a percentage, as measures of inter-annual variability of the different characteristics of the seal carrion resource (mean pupping date, biomass, energy and density of both placentae and carcasses).

We used two-way analysis of variance (ANOVA) to test for the effect of pup status (dead/alive), developmental stage (1-5), and their interaction on carcass mass.

We used Ripley’s function (Ripley 1977) to analyse inter-annual variation in the spatial pattern and distribution of carcasses. This method is used in epidemiology, but also in forensic science and plant ecology (Lancaster and Downes 2004), and provides a visual comparison of the spatial distribution of points belonging to different patterns, as well as the identification of clustering. Considering a circle of radius *r* and the number of points inside the circle, the Ripley’s K function represents the expected number of points within a distance *r* from an arbitrary point, divided by the intensity of points occurring in the study area. The linearised $\hat{L}$ function is the corresponding transformation of the Ripley’s K function and here it is used to facilitate the visualisation (Santos and Schiavetti 2014). As the point patterns of this study varied from location to location, the inhomogeneous *Linhom (r)* function was used as proposed by Baddeley (2008). The three functions for 2008, 2012 and 2013 were estimated using the Ripley's isotropic correction for a polygonal window, as an edge correction is needed to reduce bias (Ripley 1988, Baddeley 1998). They were then tested for Complete Spatial Randomness (CSR) by running Monte Carlo permutations (n = 99) for statistical tests (Lancaster and Downes 2004) providing a level of significance of clustering. The latter functions were finally compared by computing a bootstrap 95% confidence band for each function and plotted together in order to evaluate whether the pattern of the functions was repeated in years showing overlaps. We interpreted the observed spatial patterning of carcasses against the null hypothesis of a random distribution of carcasses. This null model was indicated by a horizontal line of null x values between the x and y axes corresponding respectively to the radius *r* (in metres) and the $\hat{L}$ function values. The function *Linhom (r)* is located above the horizontal line when the spatial pattern of points is aggregated and below it when it is uniform. Spatial analyses were run using R 3.1.1 and the following packages: Spatstat, Maptools, Rgdal, Rgeos, Ggplot2 and Splancs (Baddeley and Turner 2005, Wickham 2009, Bivand and Lewin-Koh 2014, Bivand and Rundel 2014, Bivand et al. 2014).

2.4 Comparison with salmon runs

To complement our empirical analyses, we investigated if carrion provided by the Isle of May seal colony was a predictable food supply relative to other published studies. We focused on salmon runs during the spawning season as a predictable resource for a wide range of consumers, in particular predatory bears which predict salmon availability (Luque and Stokes 1976; Fortin et al. 2007). The papers reviewed were Reimchen (2000), Gende et al. (2001), Dickerson et al. (2002), Quinn and Adams (1996), and Hocking and Reimchen (2009) which included data on annual variability of salmon runs.

3 Results

3.1 Timing of mean pupping dates

The annual mean pupping date observed during 2000-2010 and 2012 was 30 October (SE = 0.58; n = 12; RSE = 1.97%) (Fig. 2a).

3.2 Quantity of seal carrion

Aerial survey data showed that the mean pup production was 1988 (SE = 47.72; n = 12; RSE = 2.40%) pups per year. Therefore, the same mean number of placentae was released yearly. The mean mass of a placenta was 1.6 kg (SD =

0.24) (Table 2) and the resulting total biomass for the period 2000-2010 and 2012 was estimated to be 3124.3 kg·yr^{-1} (SE = 74.99; n = 12; RSE = 2.40%). The mean number of dead pups estimated by aerial surveys was 262 (SE = 16.32; n = 12; RSE = 6.23%), representing a mean annual mortality of 13.3 % (SE = 0.91) (Fig. 2b).

Ground visual censuses performed in 2008 and 2012 recorded similar numbers of dead seals (adult and pups), with 229 and 233 respectively, whereas in 2013 a total of 165 carcasses were observed. The mean number of seal carcasses counted for the three years was 209 (SE = 22.03; n = 3; RSE = 10.54%). On average, more than half the carcasses (55.63%; SE = 4.15) were second stage pups (Fig. 3), aged between 1.7 and 7.9 days. Starvelings formed 8.66% (SE = 3.94) of the total number of carcasses. Dead adults were found every year (2.12% of the total number of carcasses; SE = 0.70), and 12 out of 14 individuals were female.

There was a significant difference in mass between dead and live pups (ANOVA, $F_{1,115}$ = 34.84, P < 0.001), and between pup stages (ANOVA, $F_{2,114}$ = 46.49, P < 0.001), but there was no significant interaction (ANOVA, $F_{2,114}$ = 0.11, P = 0.9). Therefore, the average difference in mass of 8.02 kg measured between alive and dead pups for the three developmental stages was used to calculate the biomass contributed by dead pups (Table 3). The mean annual biomass of dead seals (adults and pups) was estimated to be 3768.2 kg (SE = 713.73; n = 3; RSE = 18.94%). The second developmental stage contributed the greatest proportion and represented 42.1% (SE = 5.16) while the mass of adult carcasses represented 14.6% (SE = 5.04) of the total biomass released.

3.3 Quality of seal carrion

Mean gross energy density of placentae was estimated to be 21.8 MJ·kg^{-1} (SD = 1.15). From this the estimated average annual energy delivered as placentae on the Isle of May was 68.1 x 10^{3} MJ (SE = 1.64; n = 12; RSE = 2.41%).

The biomass of dead seals was primarily composed of water (58.6%; SE = 1.46). Fat (18.9%, SE = 2.15) and protein (19.9%; SE = 0.62) inputs combined reached 1481.7 kg·yr^{-1} (SE = 329.43; n = 3; RSE = 22.23%) and were estimated to release 42.4 x 10^{3} MJ·yr^{-1} (SE = 10.42; n = 3; RSE = 24.58%) of energy to the ecosystem. Fat was the largest contributor to the total energy released (67.2%; SE = 3.12).

3.4 Spatial distribution of seal carrion

The mean annual placental density on the island was 0.003 placentae m^{-2}, (SE = 0.00007; n = 12; RSE = 2.33%) while the mean annual placental biomass per area unit was 0.004 kg m^{-2} (SE = 0.0001; n = 12; RSE = 2.50%).

Carcasses found on the Isle of May were distributed according to the main breeding sites, mainly in the north and south of the island. The three years showed similar patterns with most dead pups located above the mean high water line. However, 13.1% (SE = 3.85) of carcasses occurred in the area between mean high water and mean low water (166902 m^2). The mean kernel smoothed intensity was estimated to be 0.0003 carcasses m^{-2} (SE = 0.00003; n = 3; RSE = 10.00%) on the whole island for the three years, whereas the mean density of carcasses in the polygons was 0.005 carcasses m^{-2} (SE = 0.001). The highest intensity each year was observed in the area between Rona and North Ness, particularly in 2012 when the maximum intensity was 0.03 carcasses m^{-2} (Fig. 4). The union of polygons characterised by an intensity equal or higher than 0.001 covered 11% of the total area of the island at mean low water. Two thirds of this area was located in the north. The intersection of polygons (areas shared across years) corresponded to 3% of the total area of the island and 28% of the union of polygons (Fig. 5). The biomass per unit area was 0.006 kg m^{-2} (SE = 0.001; n = 3; RSE = 16.67%) for the whole island and 0.09 kg m^{-2} (SE = 0.03, n = 3; RSE = 33.33%) for the area covered by the polygons.

Initially the spatial pattern of carcasses was highly aggregated, but as the value of the inhomogeneous *Linhom (r)* function increased, it became uniform. The overlap of the three curves demonstrated that areas with carcasses were repeated and had a similar distance across years, both in the north and in the south of the island. The 2008 curve, however, showed a faster decrease towards uniformity (Supplementary material Appendix 1 Fig. A1).

3.5 Carcass consumption by scavengers

The mean cumulative mass loss (% of starting mass) for consecutive consumption states (A-E) observed on experimental carcasses deployed in 2013 was calculated (Table 4). In 2012, the total biomass scavenged was 1032.0 kg representing 21.4% of the total mass available. The energy intake by scavengers was 12.8 x 10^3 MJ.

3.6 Comparison with salmon runs

Our results showed that the annual variability in the timing, quantity (expressed as number and mass of carcasses) and quality (expressed as energy) of dead seals and placentae ranged between 1.97% and 24.50% of relative standard errors (RSE). The spatial intensity of biomass for dead seals had the highest value among all (33.33%; Fig. 6). The analysis of published data indicates that variability in the timing of salmon spawning, quantity and biomass per unit of salmon across years ranges between 1.67 and 25% (RSE). Both seal carrion and salmon runs showed the lowest RSE in their timing relative to quantity and density (Fig. 6; Supplementary material Appendix 1 Table A1).

4 Discussion

Predictability of the carrion resource

Although predictability is a widely used concept in ecology, there has not been a standard definition of resource predictability. In this study, we used relative standard errors (RSE) to standardise different kinds of data (timing, abundance, biomass, energy, density of two separate carrion sources) to compare different studies. We showed that seal carrion had a similar range of RSE as spawning salmon runs. Salmon runs clearly are predictable because brown bears (*Ursus arctos*, in undisturbed conditions) move towards rivers an average of two weeks before the arrival of salmon (Fortin et al. 2007) to prey on the spawning fish to accumulate fat for hibernation (Hilderbrand et al. 1999). We suggest this range of RSE values could be used as a benchmark for comparing predictability in future studies dealing with other resources and ecosystems.

The timing, quantity, quality and spatial distribution of seal carrion were selected as key attributes of the resource that can be expected to have a major influence on the ecological response of its consumers. Quantity and nutrient content of the food were chosen as they correlate with survival, health, reproductive success of animals, but also population and ecosystem dynamics (White 2008; Marcarelli et al. 2011). Moreover, when a resource is predictable in time and space, animals can learn how to predict its future occurrence (e.g. Reimchen 2000; Wittemyer et al. 2007; Schindler et al. 2013). The animal learning process involves the temporal awareness (when food occurs), which can be promoted by environmental cues

(Frederiksen et al. 2004), but also spatial perception (where food occurs) (Sherry et al. 1992). Individual bears, for instance, return to the same river to fish for salmon year after year (Luque and Stokes 1976). Timing and location were therefore the other crucial features used to describe the predictability of a resource. Furthermore, predictability of salmon runs in riparian systems leads to synchronisation between feeding strategy and food input in black bears (*Ursus americanus*), wolves (*Canis lupus*) and riverine and coastal mink (*Neovison vison*) (Ben-David et al. 1997; Reimchen 2000; Darimont et al. 2003). Recently, it has been demonstrated that brown bears (*U. arctos*) and glaucous-winged gulls (*Larus glaucescens*) shift their spatial distribution from early to late sockeye salmon (*Oncorhynchus nerka*) spawning areas according to the precise timing of spawning of different populations (Schindler et al. 2013).

The relative influence of the timing, spatial distribution, quantity, and quality of a food resource on the behaviour and learning of its consumers, seems largely unknown. Our comparison between seal carrion and salmon runs showed that timing had lower RSEs than quantity and density. Does this mean that low variability in timing is the most important factor determining resource predictability for scavenging gulls and bears? Or simply, are foragers less responsive to interannual variation in food quantity rather than timing? In Sigler et al. 2004, pre-spawning aggregation of eulachon (*Thaleichthys pacificus*), a small ocean fish, had seasonal impacts on the abundance of Steller sea lions (*Eumetopias jubatus*) attending the area for feeding despite the peak in quantity of this resource greatly varies between years (RSE = 65%). Also in this case, the timing was more consistent (RSE = 33.33%; values derived from Sigler et al. 2004). There are very few studies giving details on the inter-annual variation of pulsed resources, and none considering all four components of predictability considered here. Thus, it is difficult to understand how animals assess the individual and combined variations of timing, spatial distribution, quantity, and quality before responding to predictable pulses.

Considering absolute values given in studies on other apparently predictable resources, it appeared that sea turtle eggs provide an amount of energy to plants, decomposers and detritivores similar to seal carrion at pupping (91.1 x 10^3 MJ on 21 km stretch of beach; Bouchard and Bjorndal 2000). Seabird chick mortality on nesting islands in the Gulf of California, instead, provides up to 10-fold higher mass of carrion per area unit than seals on the Isle of May (Polis and Hurd 1996a, Sánchez-Piñero and Polis 2000). Moreover, a much higher biomass of marine plankton deposits on the shore of upwelling areas (ca. 4 kg m^{-2}; Davenport 1995).

Carrion consumption

At the end of the breeding season 21.4% of the dead seal biomass available on the Isle of May was scavenged resulting in an estimated energy intake of 12.8 x 10^3 MJ. Because of low air temperatures, decomposition rate in winter at high latitude is slow (Beasley et al. 2012), and scavenging is likely the main determinant of mass loss by carcasses. Considering that the daily energy required by a great black-backed gull is 2.6 MJ (Camphuysen et al. 1993; Walter and Becker 1997), the total amount of energy released as dead seals and placentae (110.5 x 10^3 MJ) would be equivalent to 42500 daily rations for these birds, which would be enough to feed more than a thousand gulls per day during the duration of the seal pupping season. This is likely an underestimate as the scavenging activity may continue once the seal pupping season has concluded. Incomplete depletion of the carcasses may have occurred because of their high abundance (Reimchen 2000; Wilmers et al. 2003), and/or low abundance of scavengers and availability of alternative food sources (e.g., fishery discards). In fact, it may take six weeks for a single seal pup carcass to be entirely scavenged by the local gull population (Quaggiotto et al. 2016). Placentae are likely to be immediately and fully consumed by gulls because they are easier to handle and 1.6 times more nutritious than seal carcasses. Energy density of placenta has rarely been measured. In this study grey seal placenta contained three times more energy than harp seal *Pagophilus groenlandicus* placenta (4.73 MJ kg^{-1}; Lavigne and Stewart 1979), but similar amounts to that of west Atlantic grey seals (23 MJ kg^{-1}; Yunker et al. 2005).

We cannot ascertain here whether gulls predict carrion resource pulses. However, gulls are known to respond to other predictable food sources, such as fishery discards (Bartumeus et al. 2010; Cama et al. 2012). Gulls at the open sea distribute according to fishery vessel density during fish discarding time, with apparent optimal foraging strategies (Cama et al. 2012). Seal carrion on the Isle of May might be crucially important for scavenging gulls as a predictable food resource, in particular, in preparation for winter. This is similar to salmon for many predatory and scavenging animals during autumn (Cederholm et al. 1999). Changes in seal carrion consumption by gulls may occur in the near future as a result of the fishery discards ban. Their reliance on carcasses, in fact, could increase after discards availability drops. It may also lead to the specialisation of the great black-backed gull in exploiting carrion, as this species is seen regularly scavenging at the grey seal colony on Sable Island (Canada) (Ronconi et al. 2014) and also on North Rona (N. Scotland) (Twiss et al. 2003).

We found that a proportion of dead seals (13%) occurred between mean high and low water. This means that carrion is exposed not only to gulls, but also to marine scavengers (Quaggiotto et al. 2016). However, these carcasses may represent only a proportion of carrion available to the marine system, as other dead seals are likely to have been already transported by tides and waves before the surveys were undertaken. To our knowledge, the effects of predictable carrion from seabird and pinniped (and therefore from the wider ocean) to small areas of the coastal marine environment have been little explored so far (Watts et al. 2011).

Broader ecosystem effects

Repeated and predictable events lead to long term impacts on ecosystems, and can promote lasting changes in the soil, microbial, and plant communities. Stable isotope $\delta^{15}N$ signatures of salmon found in plants and invertebrates (Hocking and Reimchen 2009), for instance, persist for decades after the salmon population disappeared (Koyama et al. 2005). Similar effects are also likely to occur at our study site. Moreover, a higher nitrogen enrichment is also expected in plants and soil than at other animal colonies because of the high position that pinnipeds have in the trophic chain (Erskine et al 1998). Since the distribution of seal carcasses was similar across years, hotspots of soil and vegetation enrichment by marine-derived nutrients might be identified from the maps produced here. The relationship between seal carrion distribution and nutrient hotspots at different spatial scales is an interesting avenue for future research.

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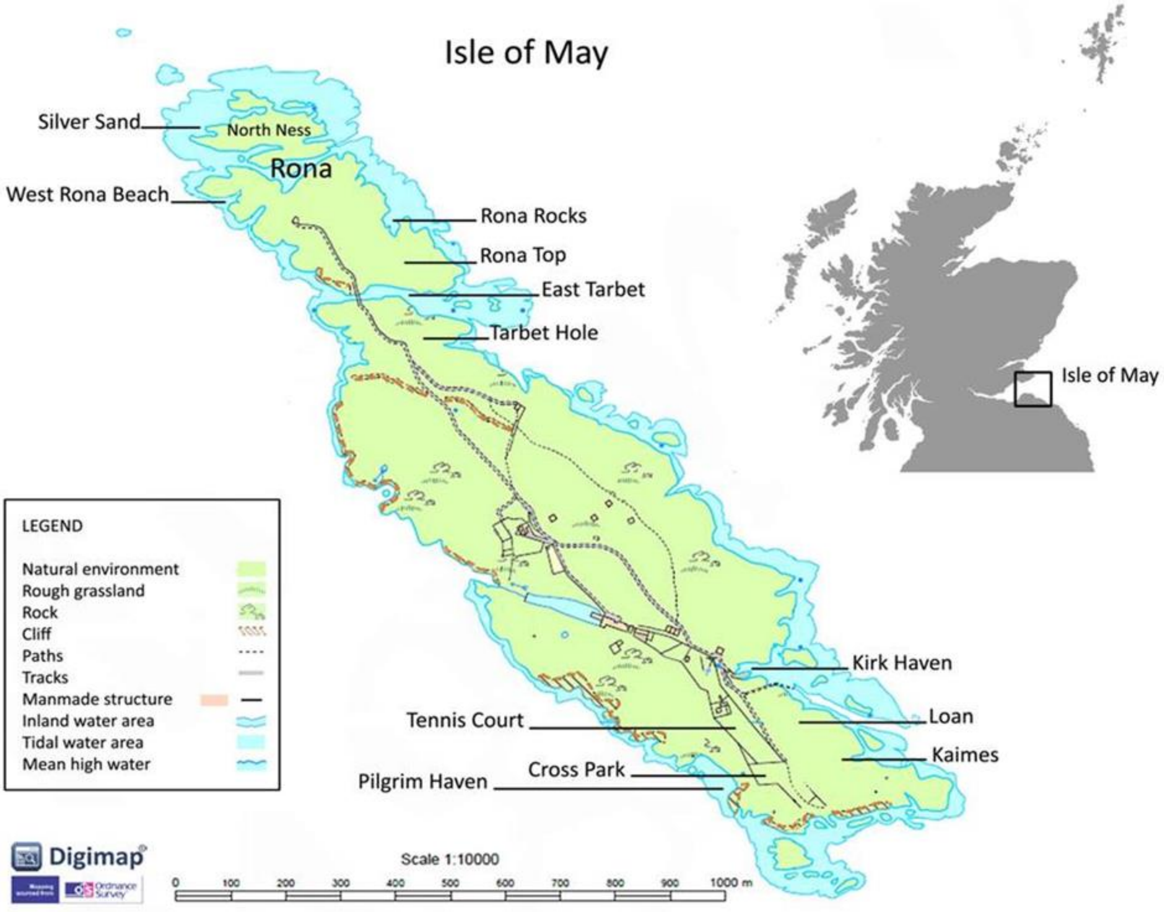


Figure 1. Map of the Isle of May. Maps provided by EDINA Digimap Service, http://digimap.edina.ac.uk/roam/os.

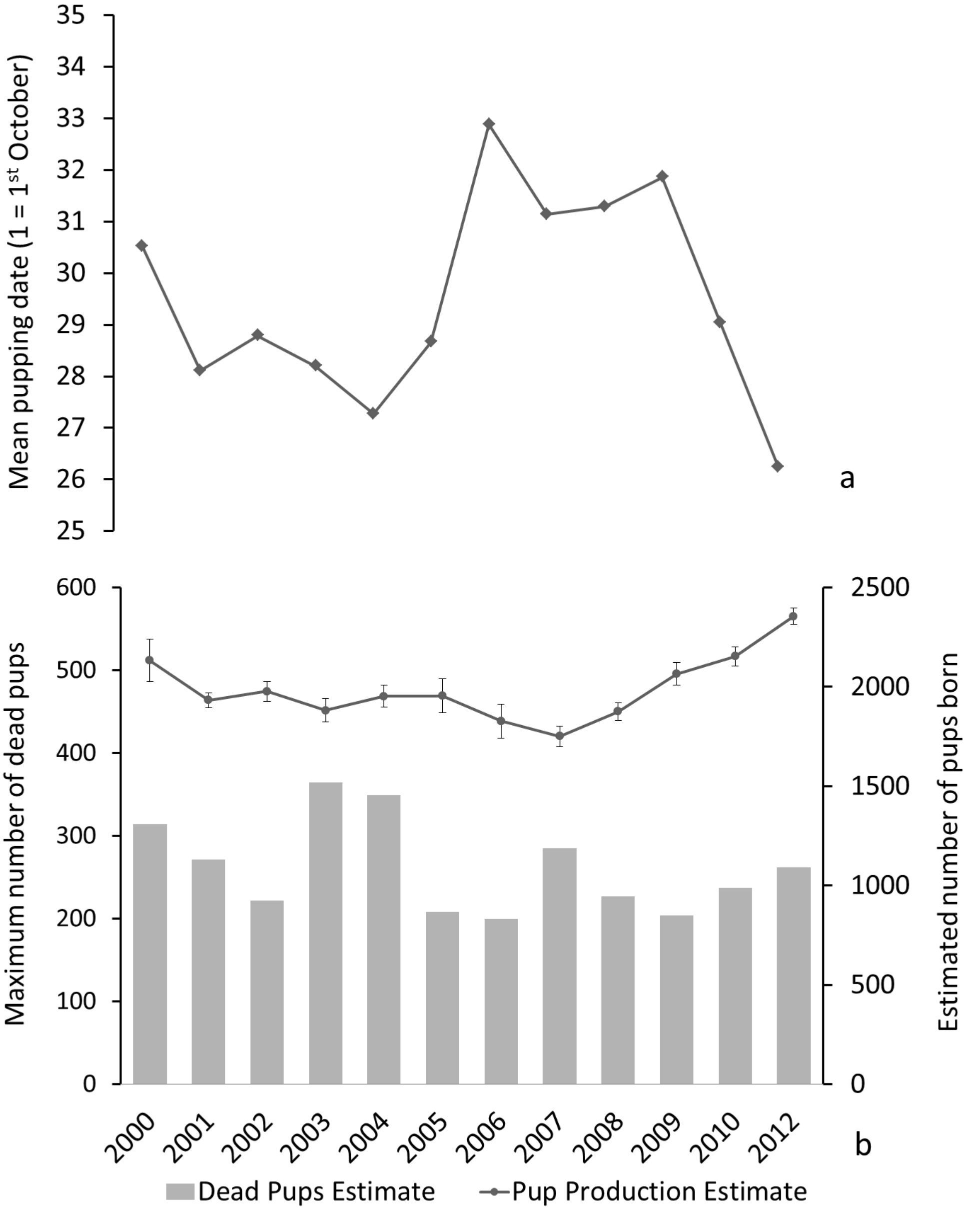


Figure 2. a) Mean pupping date for the decade 2000-2010 and 2012 from aerial survey data (1 = 1st Oct); b) Estimated maximum number of dead pups and total pup production for the years 2000 – 2010 and 2012. Number of dead pups re-estimated from aerial survey data is represented by columns and scaled to the y-axis on the left side. Pup productivity is represented by line with CV (%, ranged between 0.02 and 0.05) and scaled to the y-axis on the right side.

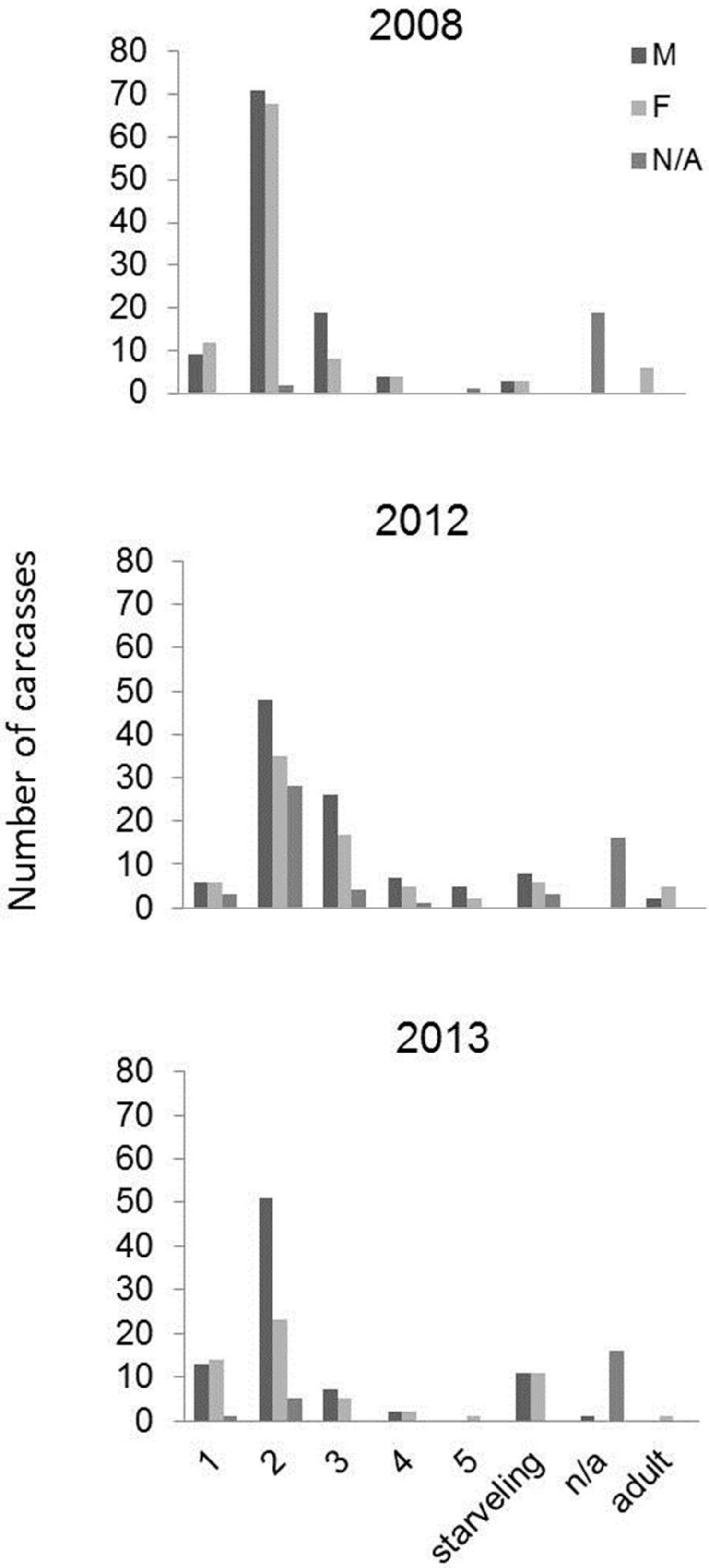

2008
80
70
60
50
40
30
20
10
0
M
F
N/A
2012
Number of carcasses
80
70
60
50
40
30
20
10
0
2013
80
70
60
50
40
30
20
10
0
1
2
3
4
5
starveling
n/a
adult

Figure 3. Number of dead pups per year belonging to different sex and developmental stages from the ground visual census performed in 2008, 2012 and 2013: M = male, F = female and N/A = not identified sex; 1 = first, 2 = second, 3 = third, 4 = fourth, 5 = fifth developmental stage, starveling = pups who died of starvation, n/a = not identified developmental stage and adult.

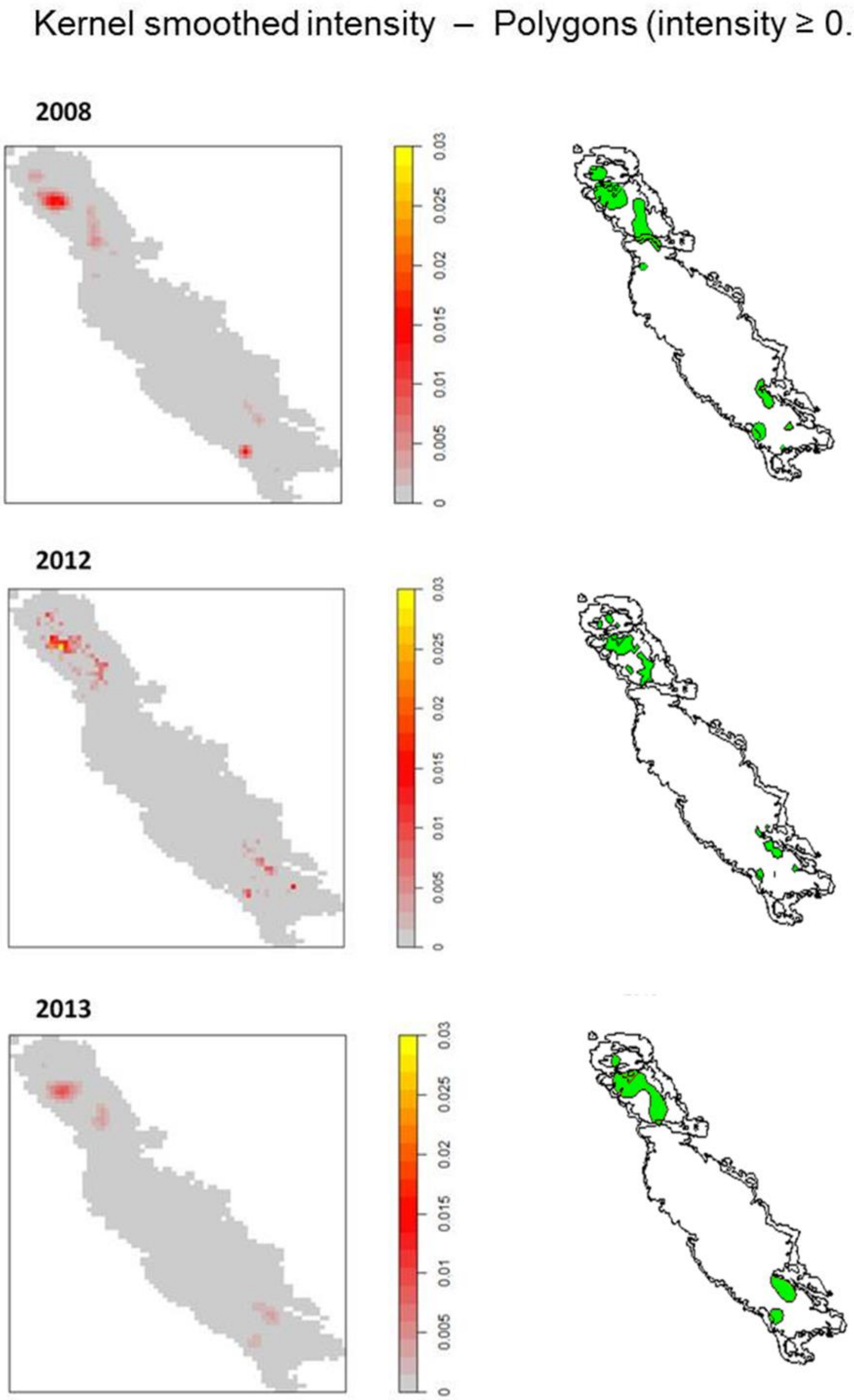


Figure 4. Kernel smoothed intensity of carcasses and polygons of density ≥ 0.001.

Left: maps of kernel smoothed intensity (n carcasses m^{-2}; range= 0 – 0.03) for carcasses counted during the ground visual censuses performed in 2008, 2012 and 2013. The smoothing bandwidth was selected by likelihood cross-validation. Pixel size: 20 x 20 m. Right: maps showing polygons (in green) characterised by intensity equal or higher than 0.001 carcasses m^{-2} in 2008, 2012 and 2013.

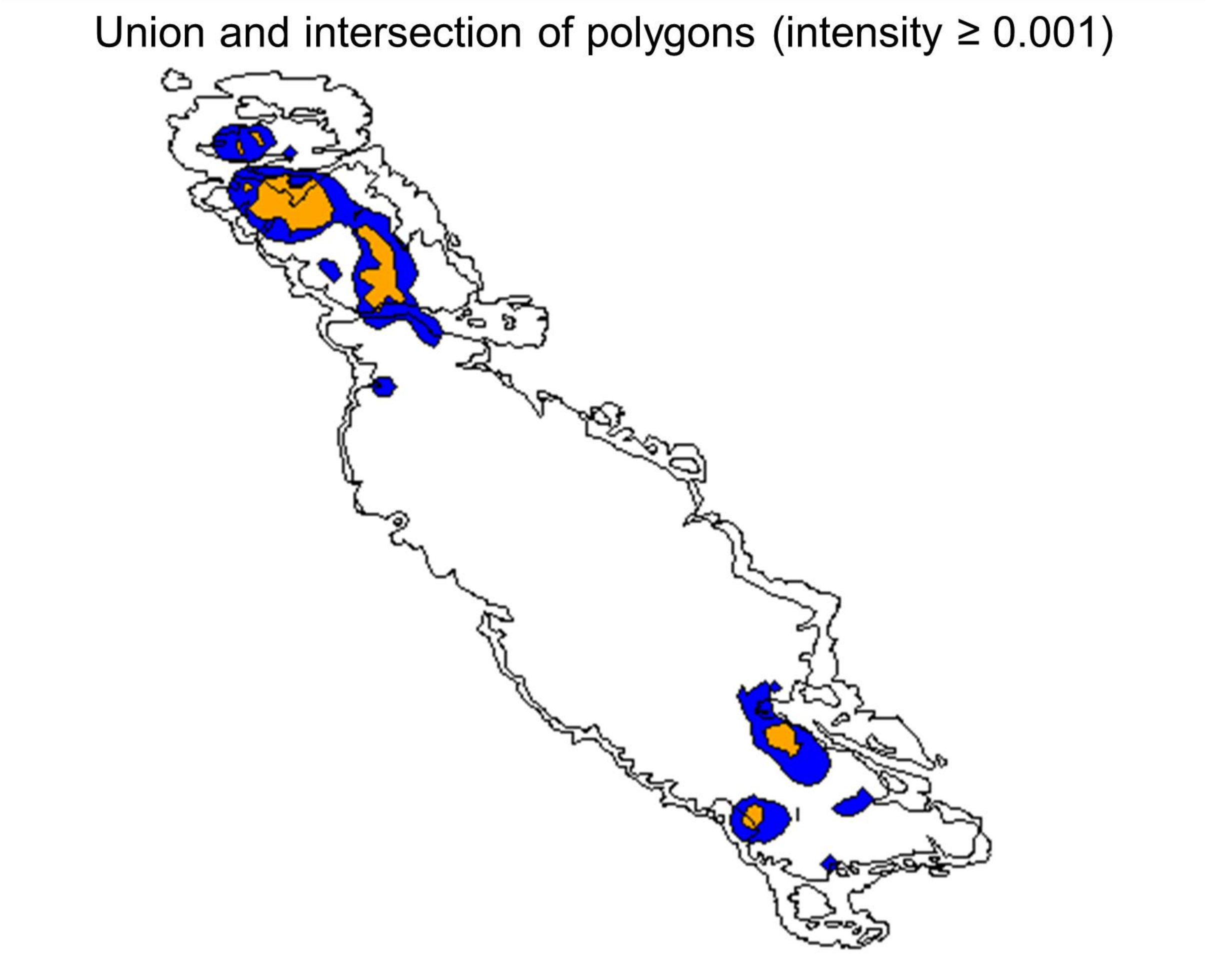


Figure 5. Union (sum) and intersection (overlap) of polygons of intensity ≥ 0.001. Union of polygons characterised by intensity equal or higher than 0.001 carcasses m^{-2} for any of the three years (2008, 2012 and 2013) (blue), and polygons of areas used in all three years (yellow).

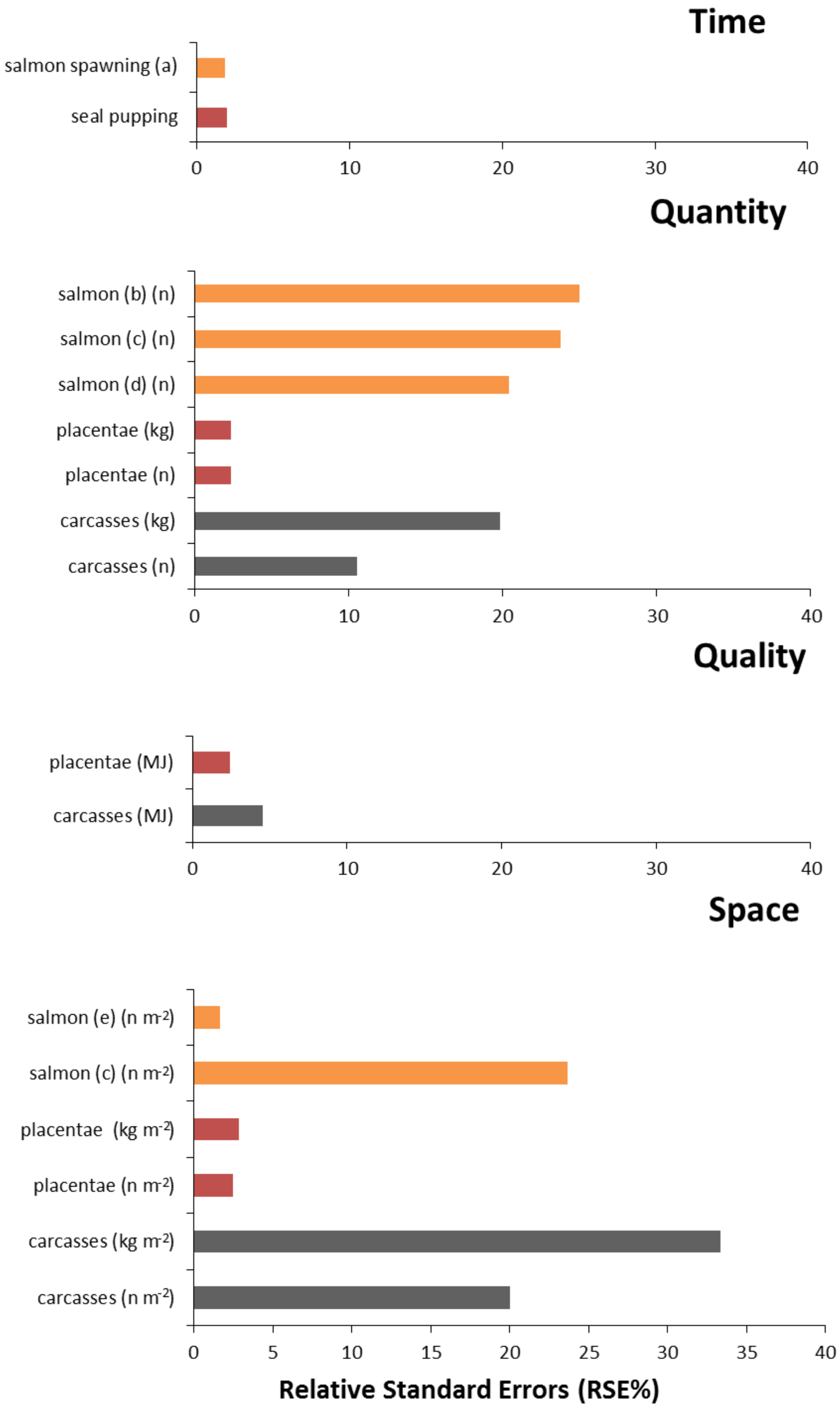

Time
salmon spawning (a)
seal pupping
0
10
20
30
40
Quantity
salmon (b) (n)
salmon (c) (n)
salmon (d) (n)
placentae (kg)
placentae (n)
carcasses (kg)
carcasses (n)
0
10
20
30
40
Quality
placentae (MJ)
carcasses (MJ)
0
10
20
30
40
Space
salmon (e) (n m-2)
salmon (c) (n m-2)
placentae (kg m-2)
placentae (n m-2)
carcasses (kg m-2)
carcasses (n m-2)
0
5
10
15
20
25
30
35
40
Relative Standard Errors (RSE%)

Figure 6. Comparison between RSE of resource availability resulting from the Isle of May seal carrion and spawning salmon. Inter-annual variability, measured as RSE, of carcasses (black) and placentae (red) occurring on the Isle of May during seal pupping seasons 2008, 2012 and 2013 and spawning salmon (orange) according to time (mean date for seal pupping and salmon spawning), quantity (abundance as n and total mass available as kg), quality (energy released as MJ) and space (density as n m^{-2} and kg m^{-2}). Reviewed papers: (a) Quinn and Adams 1996, (b) Reimchen (2000), (c) Gende et al. 2001, (d) Dickerson et al. 2002 and (e) Hocking and Reimchen (2009).

Table 1. Energy content for developmental stages of grey seal pups, adult female, and adult and juvenile male individuals according to energy density calculated per body component (%).

Stage	Body component	Component content (%) (Lang et al. 2011; Lidgard et al. 2005)	Energy density (MJ kg^{-1})	Energy content (MJ kg^{-1})
1 and 2	water	65.1	0	7.9
	fat	9.4	3.8	
	protein	22.6	4.1	
3	water	47.3	0	16.8
	fat	35.5	14.0	
	protein	15.1	2.8	
4 and 5	water	45.7	0	17.6
	fat	38.1	15.0	
	protein	14.4	2.6	
Adult female	water	55.2	0	12.7
	fat	23.9	9.4	
	protein	18.4	3.3	
Adult or juvenile male	water	52.8	0	13.8
	fat	27.3	10.7	
	protein	17.4	3.1	

Table 2. Grey seal placentae (n = 6) collected showing date, pup sex, total, amnion and placenta mass (kg).

Date of collection	**Pup Sex**	**Total Wet Mass (kg)**	**Amnion Mass (kg)**	**Placenta Mass (kg)**	**Wet Sample Mass (kg)**	**Dry Matter (%)**	**Energy Density (MJ kg^{-1})**
29-Oct	F	1.42	0.76	0.66	0.03	15.66	22.165
30-Oct	n/a	1.91	0.46	1.45	0.03	16.96	22.474
31-Oct	n/a	1.46	0.34	1.12	0.03	15.44	22.099
31-Oct	F	1.19	0.64	0.55	0.05	14.88	20.297
01-Nov	M	1.81	0.33	1.48	0.04	17.23	20.328
05-Nov	n/a	1.63	0.36	1.27	0.03	17.20	23.490

Table 3. Re-estimated mass of dead grey seal pups belonging to different developmental stages. Each developmental stage is associated with the re-estimated body mass (kg) for male and female pups calculated according to the equations of Kovacs and Lavigne (1986) and adjusted by the average difference in mass measured between alive and dead pups. When sex of pup was unavailable, the body mass was calculated using the mean body mass of both sexes.

Developmental Stage	**Mean mass (kg)**		
	Female	**Male**	**Sex not determined**
1	9.6	11.7	10.6
2	12.6	15.0	13.8
3	21.7	25.1	23.4
4	32.6	36.1	34.3
5	28.8	33.2	31.0

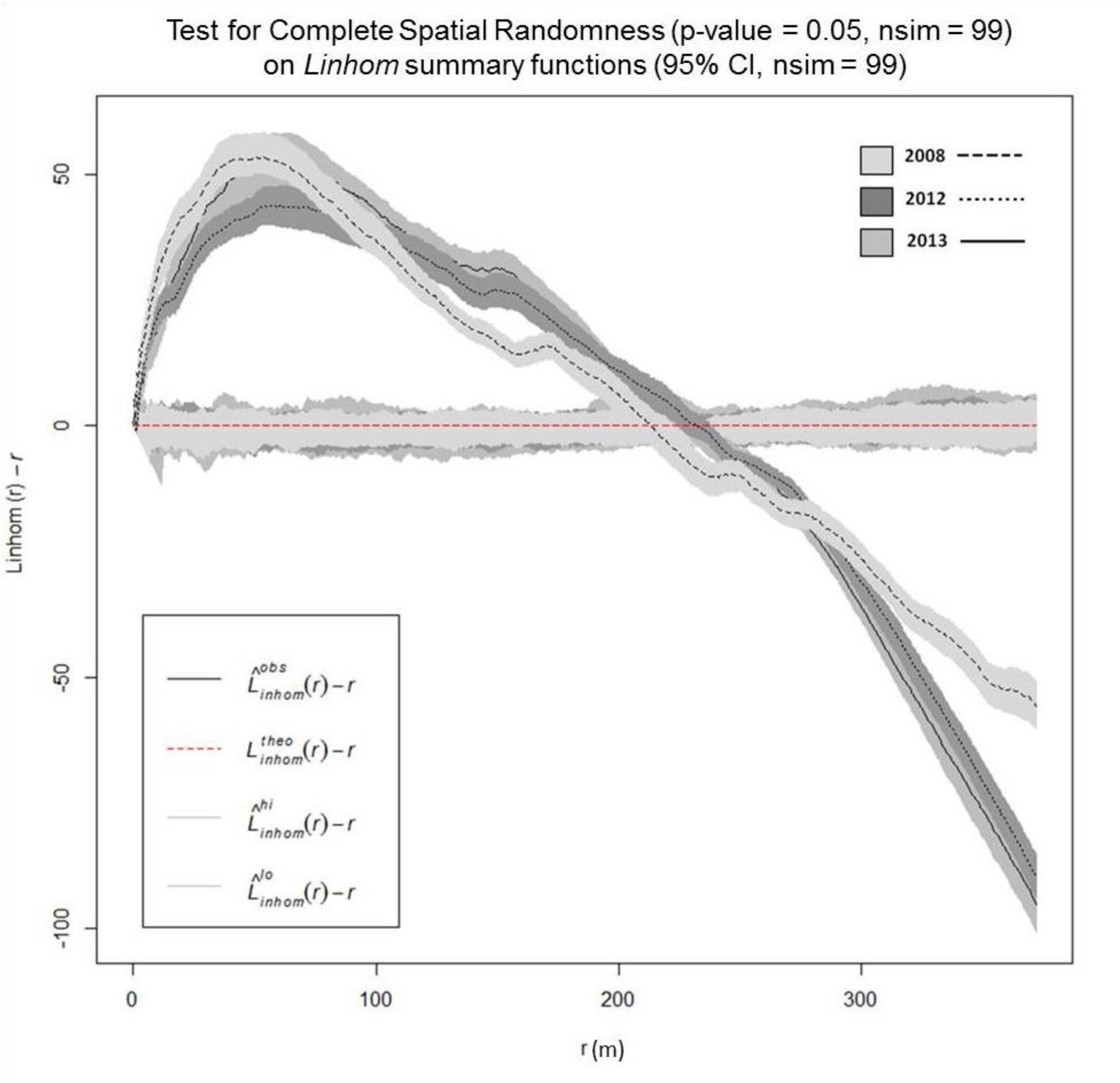
Table 4. States of consumption of scavenged carcasses (n = 11) with associated description and cumulative percentage mass loss.

State of consumption	Description	Mean % mass loss (SE)	n sample
A	intact	0.4 % (0.49)	15
B	lack of both eyes and occurrence of one opening on the body	10.2 % (2.23)	30
C	additional openings	31.3 % (4.89)	8
D	body appears flat and lacking internal organs; loss of the head; missing bones	41.2 % (2.43)	7
E	remains (only bones and skin)	65.2 % (3.00)	4

Supplementary material - Appendix 1.

Appendix 1 Figure A1. Test for Complete Spatial Randomness on *Linhom* summary functions.

Comparison among *Linhom* summary functions illustrating spatial point patterns of carcasses found in 2008 (light grey, dashed line), 2012 (dark grey, midline ellipsis) and 2013 (medium grey, continuous line) during the ground visual census. Bands of 95% confidence interval were obtained by bootstrap simulations (n = 99). The three functions were tested for Complete Spatial Randomness (CSR, dashed red line) by running Monte Carlo permutations (n = 99) for statistical tests, bands borders represent the p-value 0.05.



Two peaks in the aggregation pattern were observed in each year: one around 40-70 m and the other around 150-180 m, showing that the area of carcasses were repeated and had a similar distance across years, both in the north and in the south of the island. Around 215-230 m, the pattern became uniform and the function curves fell under the line illustrating complete spatial randomness (CSR). As the maximum r displayed does not exceed 400 m, aggregations further than this distance are not shown. There was no statistical significance for the test of CSR, as the observed patterns were outside of the simulation envelopes representing the p-value 0.05. This indicated that well defined areas of carrion availability occurred. Moreover the bootstrap 95% confidence bands of the functions overlapped demonstrating that the spatial pattern of carcasses is consistent across years.

Appendix 1 Table A1. Comparison between the Isle of May seal carrion availability and apparently predictable pulses in resource availability according to time (a), quantity (b), quality (c) and space (d).

Time (a)

Reference	Resource	Mean	SE	RSE	Effect
Present study	Seal pupping	30th Oct	0.58	1.97	Scavenging great black-backed gulls
Quinn and Adams 1996	Salmon spawning	2nd July	0.58	1.83	n/a

Quantity (b)

Reference	Resource	Mean	SE	RSE	Effect
Present study	Dead seals (ground visual census)	n = 209.0 3777.7 kg	22.03 720.87	10.54% 19.08%	Scavenging great black-backed gulls
	Placentae (aerial survey)	n = 1988.1 3124.3 kg	47.72 74.99	2.40% 2.40%	
Reimchen 2000	Salmon spawning run	n = 4,000	1011.60	25.00%	Black bears predation
Gende et al. 2001	Salmon spawning run (Hansen Creek)	n = 13791.3	3281.44	23.80%	Brown and black bears predation
Dickerson et al. 2002	Salmon spawning run	MaxN = 587.3	119.78	20.40%	Brown bears predation

Quality (c)

Reference	Resource	Mean	SE	RSE	Effect
Present study	Dead seals (ground visual census)	42.4 10^3 MJ	10.42	4.58%	Scavenging great black-backed gulls
	Placentae (aerial survey)	68.1 10^3 MJ	1.64	2.41%	

Space (d)

Reference	Resource	Mean	SE	RSE	Effect
Present study	Dead seals (ground visual census)	0.005 carc $m^{-2\ A}$ 0.09 kg $m^{-2\ A}$	0.001 0.03	20.00% 33.33%	Scavenging great black-backed gulls
	Placentae (aerial survey)	0.04 plac $m^{-2\ B}$ 0.07 kg $m^{-2\ B}$	0.001 0.002	2.50% 2.86%	

Gende et al. 2001	Salmon spawning run	1.73 salm m^{-2} [C]	0.40	23.68%	Brown and black bears predation
Hocking and Reimchen 2009	Salmon spawning run	16.3 kg m^{-1}	5.00	1.67%	Marine enrichment in riparian food webs

Summary table showing results obtained by the present study and other published sources. The table is divided horizontally according to the factors explaining predictability (time, quantity, quality and space) and by columns according to the type of predictable resource, values considered and effect observed in the ecosystem. Values in kg are of wet mass.

[A] calculated considering polygons of intensity higher than 0.001 (2008 = 55976 m^2, 2012 = 32746 m^2, 2013 = 50803 m^2);

[B] calculated considering polygons of intensity higher than 0.001 (mean of the three years, mean = 46508 m^2);

[C] calculated using data for Hansen Creek (8000 m^2).