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 ·yr^{-1} corresponding to 110.5×10^3 MJ 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.

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

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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 × 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.

2.2.1. 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.

2.2.2. 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