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The role of marine mammal carrion in the ecology of coastal systems

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To all I did not know and do not know yet.

Abstract

Carrion represents an important energy resource in the natural world, yet its ecological significance has often been overlooked. It also plays a crucial role facilitating energy transfer across trophic levels and between ecosystems. The aim of this thesis was to evaluate the role of marine mammal carrion in the ecology of coastal systems, investigating one of the most commonly occurring sources of marine mammal carrion in the UK, the grey seal (*Halichoerus grypus*).

This was addressed by providing first a detailed documentation of the fate of a grey seal pup carcass with insights on the scavenging ecology existing in both terrestrial and marine ecosystems. On the shore, great black-backed gulls (*Larus marinus*), juvenile gulls and ravens (*Corvus corax*) fed on the carcass showing a distinct temporal succession using the food resource. The underwater carcass was initially dominated by Echinodermata (starfish), whose abundance dropped lately, while Malacostraca (crabs) were present in similar number during the whole monitoring. Bacterial activity was evident in both experiments.

Predictability of seal carrion was then defined during the pupping season at one of the largest colonies in the UK, the Isle of May (Scotland). Data collected by aerial survey (11 years) and ground visual census (3 years) were used to estimate the inter-annual variability of carrion, from placentae and dead seals, according to its timing, biomass and energy released and spatial distribution on the island. For all measures considered, variability was below 34%, similarly to other resources, such as salmon runs, which appear to be predicted by consumers. Twenty one percent of the total biomass from dead seals was consumed at the end of the pupping season suggesting a clear response from the scavenging community to the presence of the resource carrion.

The predictable nature of seal carrion was then tested exploring the spatial and temporal distribution of scavenging gulls at three geographical scales (regional, local and patch scales). The great black-backed gull was affected by carrion availability occurring on the Isle of May, while the herring gull (*Larus argentatus*) was not. In particular, the number of adult and juvenile great black-backed gulls feeding was directly correlated with carrion abundance, while searching behaviour was greatest after the mean seal pupping date and at the peak in mortality.

The behavioural dynamics of scavengers were finally explored monitoring the feeding activity on pup carcasses and placentae of adult and juvenile great black-backed gulls. It was predicted that under conditions of predictable and abundant carrion an equal scavenging effort would be found for the two age classes when consuming carcasses. Hierarchical dominance was, instead, expected during scavenging activity on placenta as it represents a preferred energy-rich food item. Temporal trends of scavenging activity and time spent feeding on carcasses were in fact similar between the two, while young individuals spent more time feeding on placenta, highlighting the importance of this food source for juvenile gulls during winter. The house mouse was also found to scavenge on seal carrion, which until now has been undocumented.

This study demonstrates the importance of marine mammal carrion as a resource for multiple facultative scavenger species in both the marine and terrestrial environment.

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Author's Declaration

I declare that, except where explicit reference is made to the contribution of others, that this dissertation is the result of my own work and has not been submitted for any other degree at the University of Glasgow or any other institution.

Signature ______________________________

Printed name ______________________________

Abbreviations

AIC: Akaike's Information Criterion
CI: Confidence Intervals
GAM: Generalized Additive Model
GAMM: Generalized Additive Mixed Model
GBBG: Great black-backed gull
GLM: Generalized Linear Model
GLMM: Generalized Mixed Model
HG: Herring gull
JUV: Juvenile individuals
JNCC: Joint Nature Conservation Committee
LGGB: Lesser black-backed gull
LME: Linear Mixed-Effect model
MaxN: Maximum Number
NB: Negative Binomial
RSE%: Relative Standard Error
SAC: Special Areas of Conservation
SCOS: Special Committee on Seals
SE: Standard error
SMRU: Sea Mammal Research Unit
SRUC: Scotland's Rural College

Chapter 1: Introduction

Carrion (etymology: from Latin *caro*, “flesh”) is defined as the tissue of dead animals; ecology (Greek οἶκος, "house" and λόγος, "study") is the study of the interactions between organisms and their environment. The subject of the PhD thesis is the role of marine mammal carrion in the ecology of coastal systems as a food source for marine and terrestrial scavengers inhabiting these areas and the behavioural relationships established around this resource.

1.1 An overview on carrion ecology

Carrion is a common food resource and the importance for its consumers has often been undervalued (DeVault et al. 2003). In some food webs scavenging links have been underestimated 16-fold, so that the energy transferred through scavenging is likely to be greater than that transferred by predation (Wilson and Wolkovich 2011). Scavenging is a widespread life history strategy employed by many carnivorous animals (Selva and Fortuna 2007). The multiple impacts of carrion on the ecosystem are dependent on the environment where it occurs, the local scavenging community and behavioural dynamics established, the nature of carrion availability (predictable and unpredictable) and the combinations of these factors.

Fundamental differences exist between terrestrial and aquatic ecosystems that influence carrion ecology. The temperature characteristic of these environments, for example, affects the decomposition of carrion differently and consequently the scavenging activity to which it is exposed (Beasley et al. 2012). Higher temperatures cause greater microbial activity, which can prevent some vertebrate scavengers from consuming the carcass because of toxin production (DeVault et al. 2004; Burkepile et al. 2006). In water temperature fluctuations are minor and carrion can be preserved being available for longer to scavengers (Allison et al. 1991). Moreover, because of the three-dimensional space characterising the aquatic systems, the transfer of carrion between habitats is facilitated under the action of currents and waves (Britton and Morton 1994; Beasley et al. 2012).

However, land and ocean are connected by coastal areas where both marine and terrestrial carrion inputs are transferred between the two ecosystems. In particular, marine inputs strongly affect the population of a diverse range of animals living in this ecosystem of interface (Polis and Hurd 1996a; Polis et al. 1996; Polis et al. 1997; Rose and Polis 1998; Anderson and Polis 1998; Sánchez-Piñero and Polis 2000; Stapp and Polis 2003). In fact marine energy inputs can often exceed energy derived from plant primary production in small islands (Polis and Hurd 1996b).

Considering the multiple biomes and geographical areas in the world, birds, mammals and invertebrates are the most common scavengers found on vertebrate carcasses (Moleón and Sánchez-Zapata 2015). Among them vultures are considered the only obligate scavengers (Ruxton and Houston 2004a) together with abyssal fish (Ruxton and Bailey 2005) and some invertebrates. However, several other species behave opportunistically, adding facultative scavenging to their already existing predatory behaviour when carrion is available.

The trophic links established by facultative scavengers are important as they enhance the stability of the ecosystem (Selva and Fortuna 2007). The social structure of a scavenging community may be determined by hierarchical dominance. Inter- and intraspecific competition, in fact, drives subordinate species or individuals to adopt some behavioural strategies such as temporal and spatial segregation to optimise access to carrion and reduce aggressive events (Blázquez et al. 2009; Kendall 2014). Nestedness is also common in scavenging assemblages: a nested pattern is evident when the assemblage characteristic of a smaller or less visited carcass is a subset of the aggregation occurring at larger or more visited resources. Several studies highlight therefore that scavenging communities are structured and not random (Selva and Fortuna 2007; Moleón et al. 2015; Sebastián-González et al. 2016). The predictability of the food resource is one of the crucial determinants shaping the structure of a community, ultimately inducing some response by consumers at a population level (Polis and Hurd 1996a) such as changes in behaviour, ecology and adaptation (Overington and Lefebvre 2011). Wilmers et al. (2003b) found that animals with large foraging radii, such as bald eagles (*Haliaeetus leucocephalus*) and ravens (*Corvus corax*), monopolise the highly aggregate in space and time wolf (*Canis lupus*) and hunter (*Homo sapiens sapiens*) kills, while local dominant species (coyotes, *Canis latrans*) localise and access over-dispersed resources. However, at the feeding stations for vultures, where resources are more predictable than natural conditions, the most dominant species was the one monopolising the carrion and consuming it at a higher extent (Cortés-Avizanda et al. 2012). Predictability can also influence the diversity of scavenger aggregations, where unpredictable food resources allow for higher scavenger diversity by reducing dominance effects (Cortés-Avizanda et al. 2012). Adaptation by consumers to predictability has been demonstrated for both natural and artificial (or man induced) sources of food. Chum salmon runs (*Oncorhynchus keta*) in riparian systems, for instance, induced the eco-evolution between feeding strategy and food input in black bears (*Ursus americanus*) (such as the increase in number of bears when salmon spawn) (Reimchen 2000). In British Columbia number of bears increased also 2-3 weeks in advance of major increases in numbers of Pacific salmons (*Oncorhynchus* spp.). Organic refuse, such as food and butchery waste, has been found to influence animal food webs since medieval times: the urban domestic cat (*Felis catus*) population of Northern Europe in fact was sustained by preying on red kites (*Milvus milvus*), which in turn were the main scavengers of town refuses (O'Connor 2000). Temporal and spatial distribution of foragers can also change in response to food inputs, as demonstrated by Allen et al. (2014) who investigated seasonal movements of black tailed deer (*Odocoileus hemionus columbianu*) hunted by puma (*Puma concolor*) in Mendocino National Forest in California: an overlap in the distribution was found between predators and scavengers, such as the black bear (*U. americanus*) (Allen et al. 2014). In coastal systems, in particular, predictable marine inputs attract terrestrial consumers whose number increase in the areas closest to the sea (Stapp and Polis 2003), while at sea, fishery discards are another example of predictable carrion subsidy driving the distribution of gulls in the Mediterranean (Cama et al. 2012).

The indirect impact of carrion extends also to non-scavenging species, plants and soil. Passerine birds for instance were observed to take advantage of scavenging arthropods occurring on the carcass (Gende and Willson 2001; Moreno-Opo and Margalida 2013). Nutrients released during the decomposition process of carcasses were transferred to soil, enhancing its heterogeneity and shifting competitive relationships among regenerating herbaceous and tree species (Towne 2000; Bump et al. 2009).

Scavenging ecology has been largely neglected in the past for different reasons including the natural human aversion for rotten material and the challenges encountered during the data collection (DeVault et al. 2003).

However, over the last decades, interest in studying the ecological impact of carrion on the ecosystem has increased rapidly, so that today it is considered to be “the golden age for scavenging research” (Moleón and Sánchez-Zapata 2015). In particular, recent reviews demonstrated that carrion is widely used by predators and not only by obligate scavengers. Most carnivores adopt a flexible foraging strategy according to seasonal changes in prey and carrion availability (Pereira et al. 2014). For instance, at northern latitudes, ungulates die naturally during winter because of lack of food resources and consequential thermal stress thus providing carcasses (once defrosted) to predators such as the wolverine *Gulo gulo*. In the Serengeti (Africa), instead, the peak of dead wildebeests, which coincides with the end of the dry season, is exploited by the spotted hyena *Crocuta crocuta* and some species of vultures. These additional trophic links created by facultative scavenging activity increase the complexity of the food web stabilising it: in fact, once carrion is included in the food network, the number of connections between animals drastically increases (Wilson and Wolkovich, 2011). As a result, competitive and/or facilitative relationships between scavengers and predators due to variation in the availability of food for carnivores can influence the behaviour and population dynamics of both types of consumers (Moleón et al. 2014).

For these reasons it becomes crucial to assess the consequences that climate change and anthropogenic activity can have on carrion availability in order to predict potential changes in the scavenging dynamics forming around carrion. For instance, extreme weather conditions can provide more frequent pulses of carrion. Warmer winters, instead, can reduce the natural mortality of prey but increase the predation rate, as observed in the relationship between the re-introduced gray wolf (*Canis lupus*) and the elk (*Cervus elaphus*) in the Yellowstone National Park (USA) (Wilmers and Getz 2004). Human activity can also alter the natural provision of carrion and its predictability. Predictable anthropogenic food subsidies (PAFS), such as fishery discards at sea, human hunting and restaurants for endangered species, have in fact influenced the ecosystems modifying the natural biomass flow of the food web and affecting the behaviour of consumers. Opportunistic species may benefit more than others to the detriment of the overall community diversity (Oro et al. 2013).

In the light of the eminent importance of carrion as shaping force of the ecosystem, scientists require that greater attention is addressed to scavenging ecology. In particular, further investigations are needed on the relationships between obligate and facultative scavengers and the prey populations; the effects of carrion on trophic pathways within food webs and cascading effects on system stability (Wilson and Wolkovich 2011); the use of the Biomass Transformation Web theory (Getz 2011), based on flows among both live and dead biomass (Moleón et al. 2014); scavenging dynamics within the scenario of the global change and the role of food supply in a range of ecological and evolutionary processes at the ecosystem level (Oro et al. 2013). Moreover, there is a need to understand the contribution of different supplies of carrion to the total carrion resource pool and how the components of the scavenging community interact (microbes versus invertebrates versus vertebrates) (Barton et al. 2013b). Finally, recognising differences in carrion cycling belonging to different ecosystems (aquatic and terrestrial) and the ecology of their key scavengers would inform the mitigation of future effects of human activity on global ecosystem function (Beasley et al. 2012) and encourage the protection of crucial obligate and facultative scavenging species (Moleón and Sánchez-Zapata 2015).

1.2 The ecological role of marine mammals

All marine mammals possibly influence the ecosystems in which they live (Bowen 1997), due to their large body size and relative high abundance (Estes 1979; Ray 1981; Laws 1984). They affect the behaviour and life history traits of prey species and competitors, but also have important effects on nutrient storage and recycling (Katona and Whitehead 1988). However the role that they generally play in the ecological processes of coastal environments is not completely understood.

The movement of materials and nutrients between ecosystems is a common process in nature and it can be supported by fluxes of water, sediment, solutes, and gases or by biological transport when animals move from one system to another (e.g. Likens and Bormann 1975; Cederholm et al. 1999; Hedges et al. 1997; Bouchard and Bjorndal 2000; Bardgett et al. 2001; Nakano and Murakami 2001). Also marine mammals can take part in this process as biotic factors. In fact, many species periodically haul out onto dry land throughout the year and some species remain ashore continuously for several weeks during lactation

(Hindell 2009). At these particular times they are significant carriers of energy and nutrients across the marine/terrestrial interface and their influence extends further as their mobility increases (Moore 2002; Farina et al. 2003). Therefore marine vertebrates can exert important effects on the chemistry of soils through excreta and faeces (Mizutani and Wada 1988). In fact, the presence of marine bird and seal colonies is associated with increased concentrations of nitrogenous compounds such as ammonia and nitrite in soil (e.g. Iason et al. 1986; Erskine et al. 1998; Anderson and Polis 1999; Farina et al. 2003).

Breeding colonies also provide other sources of nutrients in the form of food remains and carrion which are either used directly by above ground secondary consumers, or indirectly by increasing the input of nutrients (Anderson and Polis 1999). For instance, in sea lion colonies transport of nutrients occurs primarily through defecation and secondarily via onshore mortality (Hutchinson 1950). Mortality and placentae deposition in seal breeding sites are a normal occurrence. Trampling and wounds due to interactions between adults and pups may lead to infections, which may result in death of the pups. This problem is more severe in crowded colonies where the likely number of interactions is higher (Hammill 2009). Such carcasses of neonate seals may attract scavenging birds and mammals that would transfer marine-derived energy inland (Moore 2002). Moreover, other organisms from many phyla and most marine ecosystems consume carrion, thus changes in benthic habitats and communities are expected.

1.3 The grey seal (*Halichoerus grypus*)

The grey seal is the only member of the genus *Halichoerus,* and a member of the family of the true seals or Phocidae. This species is a subarctic and temperate-water seal and it is distributed in both eastern and western sides of the North Atlantic.

Grey seals exhibit sexual dimorphism with the mature males weighing between 170 and 310 kg and adult females between 100 and 190 kg. They have a long lifespan where males may live for over 20 years and females often live over 30 years. Grey seals are highly successful predators in the North Atlantic. They feed on a variety of fish species and cephalopods (Hammond et al. 1994). However, a large proportion of their diet is sand eel (Ammodytidae), which can make up to over 70% of the diet at some locations and in some seasons. Other prey include whiting (*Merlangius merlangus*), cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius pollachius*), and flatfish such as plaice and flounder (Pleuronectoidei).

Seals mature at three to six years old. Females usually give birth, on land or on ice, to an individual white-coated pup, known as the *lanugo*, between September and March. In the north of the British Isles the breeding season is between October and November. Newborn pups weigh between 11 and 20 kg and by the end of the lactation period (18 days on average) can reach 40 kg. This is due to the fat-rich mother's milk, around 50–60% lipid (Fedak and Anderson 1982). From this milk, pups develop both lean body mass and a thick blubber layer depending on the level of maternal provision and pup metabolism (Fedak and Anderson 1982; Mellish et al. 1999). According to Mellish et al. (1999) pup growth rates increase significantly during lactation. They also found that fat deposition (up to 1.9 kg d^{-1}) accounted for the majority of pup mass gain, and this deposition was primarily determined by milk intake. Grey seal pups doubled and even tripled their birth mass by weaning (range 1.7–3.6 times). Overall, fat deposition accounted for 66% of mass, while protein deposition accounted for only 8% of mass. Therefore, variation in pup birth mass was primarily due to differences in protein stores, whereas variation in weaning mass was primarily due to differences in fat content (Mellish et al. 1999). After lactation, the pup enters a post-weaning fast for an average of 25 days (Bennett et al. 2007), losing approximately 0.5 kg of body mass per day. Although not fully understood, it is believed that physiological changes during this time are necessary for the development of diving ability. When the pup is weaned, females enter oestrus and mate with males. Gestation lasts 8 months, but the fertilised egg is not implanted until 4 months after conception to permit a 12-month breeding cycle (Hammond et al. 1994). Grey seals exhibit high site fidelity and often return to within metres of their previous pupping site in successive breeding years (Twiss et al. 1994).

Annual grey seal pup counts, by aerial survey, have been conducted since 1960 by the Natural Environment Research Council (NERC), acting through the Sea Mammal Research Unit (SMRU). The total population size is estimated taking into account pup survival to maturity, age at first pup production, adult longevity and adult female fecundity. Approximately 28% of the world's grey seals breed in the UK, of which 88% breed at colonies in Scotland (SCOS 2013). The main colonies are located in the Outer Hebrides and in Orkney, with others established between Shetland and the north and east coasts of mainland Britain (Figure 1.1). Small colonies are also present in the South West of England and in Wales. The grey seal population in the UK, whose growth is levelling off, was estimated in 2012 to have been 112,300 (SCOS 2013) (Figure 1.2).

The harbour seal (*Phoca vitulina*) UK population was instead estimated at 33,385 in the most recent counts (2007-2012). The harbour seal (IUCN category: least concern) has undergone dramatic decline during recent decades, particularly in Scotland (from 1990s, 50% in Shetland; 68% in Orkney; and 90%in the Firth of Tay), for unclear reasons (Lonergan et al. 2007).

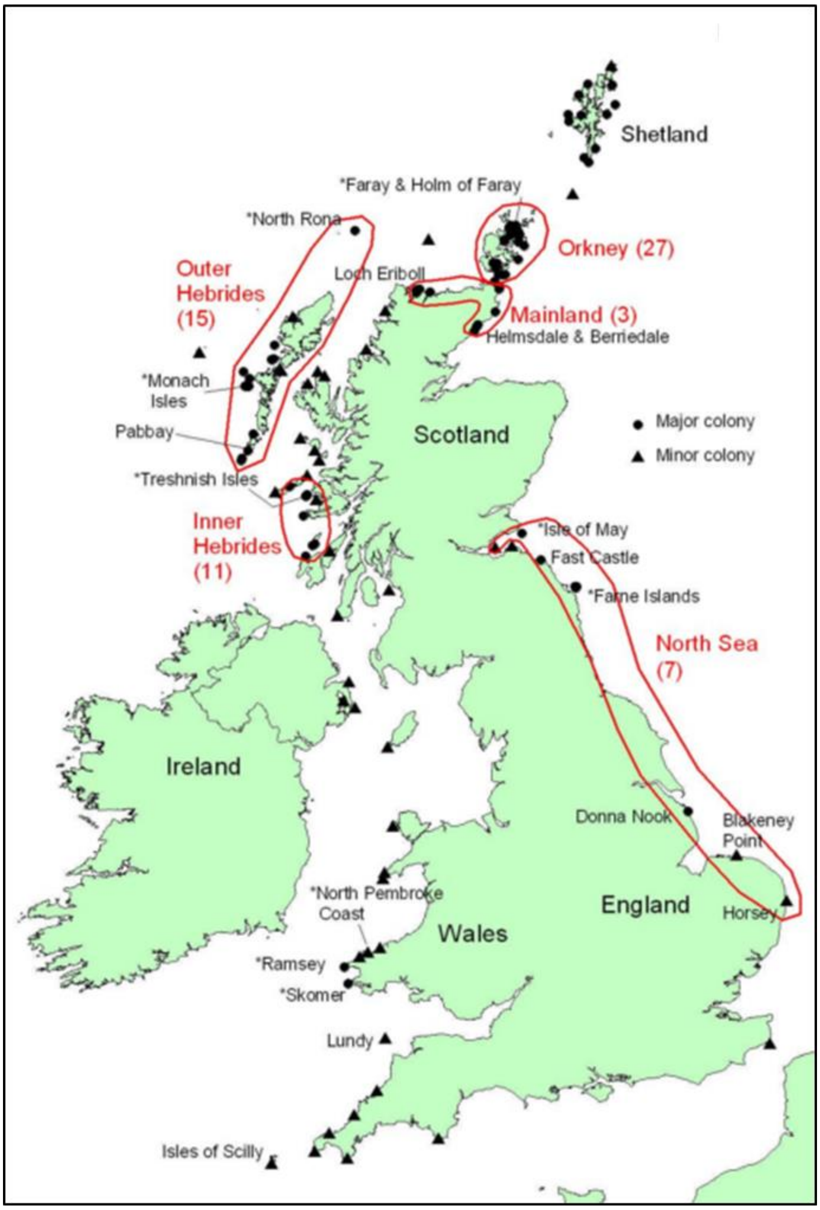

Figure 1.1 The main grey seal breeding colonies in the UK.
Colonies asterisked are potential Special Area of Conservation. Major colonies encircled are surveyed annually. Image provided by SCOS 2013.

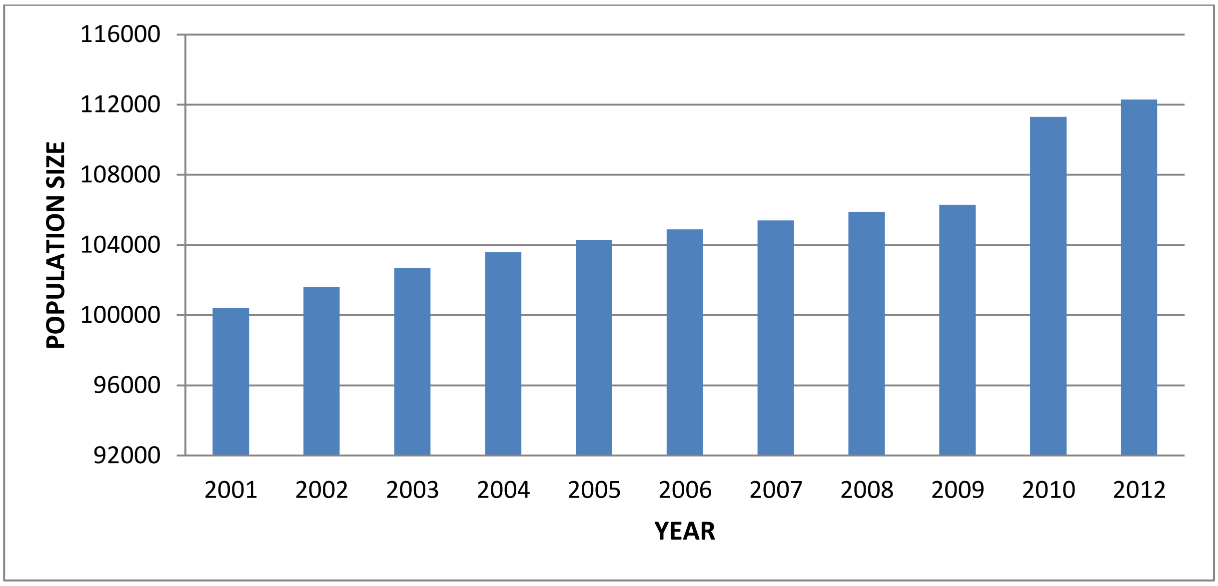

Figure 1.2 Population size estimates of grey seal in Scotland.

The total population size estimates from 2001 to 2012 (excluded 2011 when the survey was not carried out). Total population size estimates are made using the EDDSNM model of British seal population dynamics (numbers are posterior means of 95% credibility intervals). Data collected by SCOS (SCOS 2013).

1.4 Sources of grey seal carrion

1.4.1 Natural sources of grey seal carrion

Natural seal mortality is an important resource of carrion. For grey seals the highest mortality occurs between birth and weaning (Anderson et al. 1979; Baker 1984), with a mortality rate up to 30% in grey seal pups younger than one month (Twiss et al. 2003). In the grey seal, factors such as larger body mass, better condition at weaning, lower levels of post-weaning circulating immunoglobulins and habitat type have been shown to positively correlate with pre-weaning and first year survival (Hall et al. 2001; Twiss et al. 2003). Research in the 1960s and 1970s focused on causes of pup mortality in grey seals (Boyd et al. 1962; Coulson and Hickling 1964; Boyd and Campbell 1971; Bonner 1972; Anderson 1976; Anderson et al. 1979). Baker's study (1984) focused on pup mortality in North Rona, Monach Isles and Sound of Harris (Scotland, UK). Recently, the primary causes of pup mortality were detected in the seal colony of the Isle of May were starvation (30%), omphalitis-peritonitis (26%), septicaemia (22%), stillbirth (10%) and trauma (4%) (Baily 2014). Starvation is almost certainly due to the failure of formation, or the breakdown, of the bond between mother and offspring. The latter can happen on crowded breeding sites due to disturbance by adjacent adults, storms, high tides or humans, and also due to pups leaving their mothers and becoming lost. Another cause is the incidence of peritonitis associated with navel infections during parturition and skin infections caused by the abrasive action of sand. Among the secondary lesions, Baker and Baker (1988) observed several cases of jaundice and hepatic rupture leading to exsanguination and death.

In the UK, grey seals typically breed on remote uninhabited islands, coastal areas and in small numbers in caves. Preferred breeding locations allow mothers with young pups to move inland away from busy beaches and storm surges. However high mortality was found in gullies where pups were crushed by adults moving to and from the sea and also in deep, congested pools where they have drowned when they accompanied adults. Seals pupping on exposed beaches may experience higher levels of pup mortality as a result of limited opportunity to avoid storm surges (SCOS 2010). This happens when extreme weather conditions causes sudden changes in topography, as occurred in 1981 at Monach Isles beaches (Scotland). In conclusion, aggressive encounters with conspecifics (Baker and Baker, 1988), animal density and colony topography (e.g. Boyd et al. 1962; Summers et al. 1975) can all be responsible for pup mortality. However, Twiss et al. (2003) also highlighted the importance of maternal condition as an additional possible cause of pup death. First year survival of the grey seal population is estimated to be 50% in Britain, but thereafter it improves greatly (Hall et al. 2001) with natural adult mortality rate estimated to be around 5% (Thomas and Harwood 2005). However when survival rates estimates, along with fecundity estimates, for adult females breeding at North Rona and the Isle of May have been evaluated, results suggested that differences in vital rates among colonies may be widespread (SCOS 2010).

A second, but no less important, source of carrion is seal placenta. In the following half hour after the pup is born, seal mothers deliver the placenta. Unlike some other mammals, grey seals do not feed on their placenta. The amount of placenta available during the pupping season can therefore be easily estimated from pup productivity data.

1.4.2 Non-natural sources of grey seal carrion

In addition to natural mortality, human activities may be responsible of supplementary carrion inputs. Local conflicts between individual seals and fisheries or fish farms, is now managed and shooting is regulated under licence (Marine Scotland Act 2010). In 2014 in Scotland the number of culled grey seals was 163, less than 0.2% of the population, while the number of harbour seals (*P. vitulina*) culled was 42, 0.2% of the population (Scottish Governement 2015). Maritime traffic was thought to be another cause of seal deaths as in the last decade several damaged seal carcasses have been found on beaches in eastern Scotland and England and in Northern Ireland presenting the same type of injury. The characteristic wound consisted of a single smooth edged cut that starts at the head and spirals around the body, was thought to be caused by the contact with a ducted propeller, a system very common in a wide range of ships (Thompson et al. 2010). Recently, on the Isle of May, it was discovered that this lethal ‘corkscrew shaped’ wound could be caused by an attack from an adult male grey seal on weaned pups (Thompson et al. 2015).

1.4.3 Distribution of seal carrion

The spatial and temporal distribution of seal carrion depends on the site where the death of the animal occurs. For pinnipeds which spend lot of time in the water it may be difficult to quantify fatalities at sea and determine where and when they occur. However, by using information on stranding location and the currents moving the carcass before depositing it on the coast, it is possible to estimate the original site of death (Peltier et al. 2012). During the seal-breeding season, instead, carrion inputs are concentrated on the coastal area of the seal colony where it becomes easier to estimate their magnitude together with their spatial distribution due to their relative immobility. Nevertheless, tidal action, waves, weather conditions and coastal topography may facilitate the transfer of carrion also to the marine system. Extreme weather conditions, steep shore gradients and strong currents can in fact remove the carcasses from the coast, promoting their transport towards offshore areas in deeper waters. Movement of carcasses in the water are not only influenced by abiotic factors, the state of decomposition of the dead body when entering the marine system is in fact also crucial. Carcasses can in fact present two floating stages: the primary floating stage is caused by gases formed in the digestive tract while the secondary re-floating is due to bacterial growth within the body producing gas at sites other than the gastrointestinal tract (Teather 1994). Moreover, depth plays an important role in the re-floating process as well: at greater depths, in fact, the volume of gas produced is considerably less and highly soluble in water and in the surrounding tissues, impeding reflotation (Teather 1994).

In contrast to carcasses, placentae occur only at the seal colony during the pupping season. Spatial distribution of placentae is also likely to coincide with the location and temporal pattern of seal aggregations.

1.4.4 The marine mammal stranding data

The marine mammal species found in and around the British Isles include two native species of pinnipeds, the grey seal *H. grypus* and the harbour seal *P. vitulina*. The Arctic species ringed seal (*Phoca hispida*), harp seals (*Phoca groenlandica*), bearded seals (*Erignathus barbatus*) and hooded seals (*Cystophora crystata*) also occur occasionally in the UK (vagrants). Additionally, 23 cetacean species comprising whales, dolphins, porpoises (and vagrants) are also present.

The marine mammal stranding database, provided by the Scotland’s Rural College (SRUC), offers a partial picture of marine mammal mortality occurring at sea in Scotland. Grey seals represent the greatest source of carrion in comparison to other pinnipeds (72.2% of identified pinnipeds) and among all the marine mammals (21.2% of total marine mammals) occurring as strandings in Scotland (SRUC 2015, Table 1.1). This is in line with the fact that its population in the UK was estimated more than three times larger than that of the harbour seal (SCOS 2013). As the grey seal is likely to provide the highest number of carrion inputs to coastal ecosystems, it was chosen as the study species.

Table 1.1 Total marine mammal strandings (2001 - 2012) in Scotland collected by SRUC (SRUC 2015).

Species	**Strandings**
Pinnipeds	**2358**
Cystophora cristata	3
Erignathus barbatus	1
Halichoerus grypus	926
Phoca vitulina	352
Pinnipedia (indeterminate sp.)	1076
Cetaceans	**2004**
Balaenoptera acutorostrata	140
Balaenoptera borealis	1
Balaenoptera physalus	7
Cetacea (indeterminate sp.)	59
Delphinidae (indeterminate sp.)	102
Delphinus delphis	92
Delphinus delphis / Stenella coeruleoalba) (indeterminate sp.)	22
Globicephala melas	168
Grampus griseus	79
Hyperoodon ampullatus	20
Kogia breviceps	2
Lagenorhynchus acutus	117
Lagenorhynchus albirostris	100
Lagenorhynchus (indeterminate sp.)	10
Mesoplodon bidens	20
Mysticeti (indeterminate sp.)	6
Orcinus orca	6
Phocoena phocoena	877
Physeter microcephalus	47
Ziphiidae (indeterminate sp.)	1
Stenella coeruleoalba	48
Tursiops truncates	43
Ziphius cavirostris	31

Grey seal strandings occurring in Scotland showed a recent increase after the great mortality occurred in 2002 due to phocine distemper, a paramyxovirus of the genus Morbillivirus that is pathogenic for pinniped species, particularly seals (SRUC 2015; Figure 1.3). Some deaths derived from fishermen culls and corkscrew-shaped wounds are likely to be included in these figures.

The main areas of grey seal strandings in Scotland were located at the north-eastern coast. In particular, the highest number of reports came from Orkney (around 15% of the total strandings) (Figure 1.4). The monthly trend in grey seal strandings reported between 2010 and 2012, instead, showed a marked increase between November and January, coinciding with the pupping season (Figure 1.5). The following figures do not distinguish between natural and non-natural mortality.

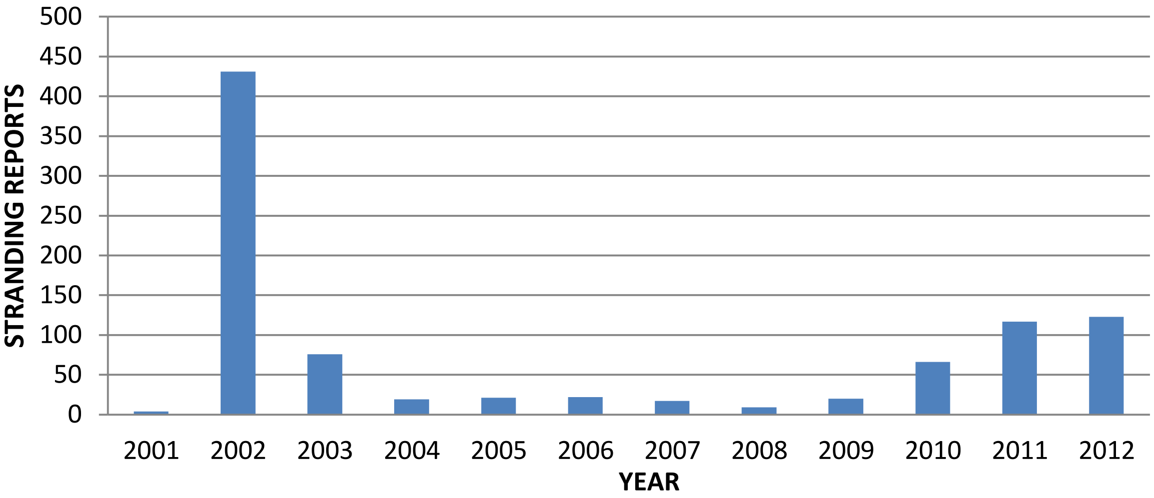

Figure 1.3 Total grey seals strandings (2001 - 2012) in Scotland collected by SRUC (SRUC 2015).

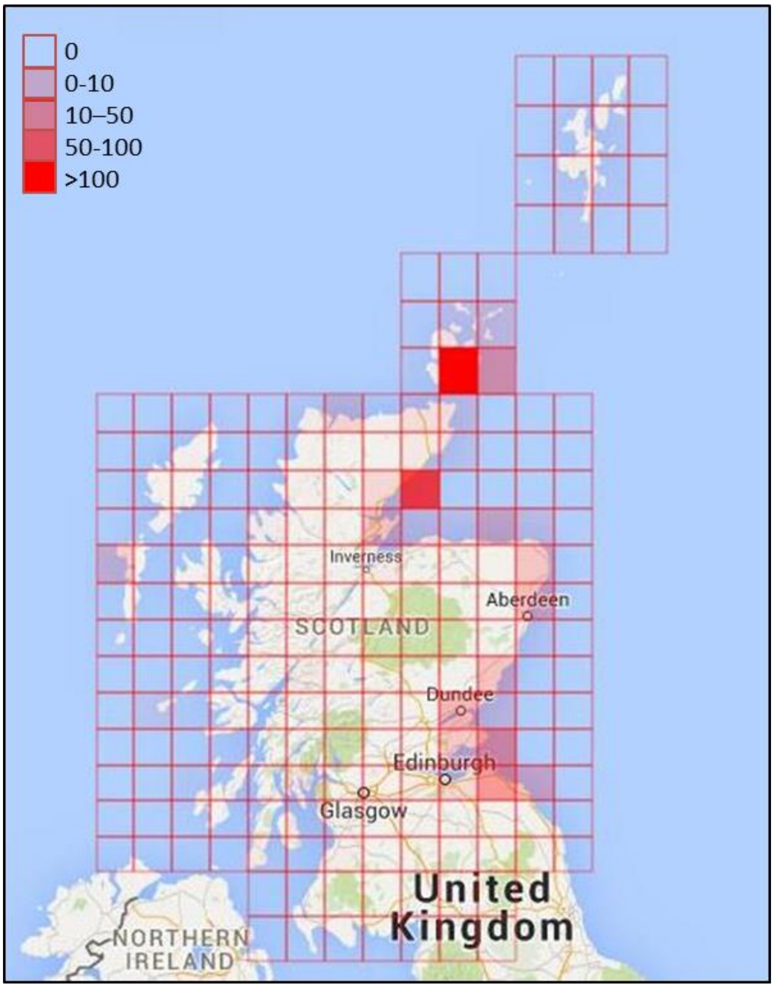

Figure 1.4 Map of grey seal strandings (2001 - 2012) in Scotland produced by SRUC (strandings.org).
Categories of strandings density in legend.

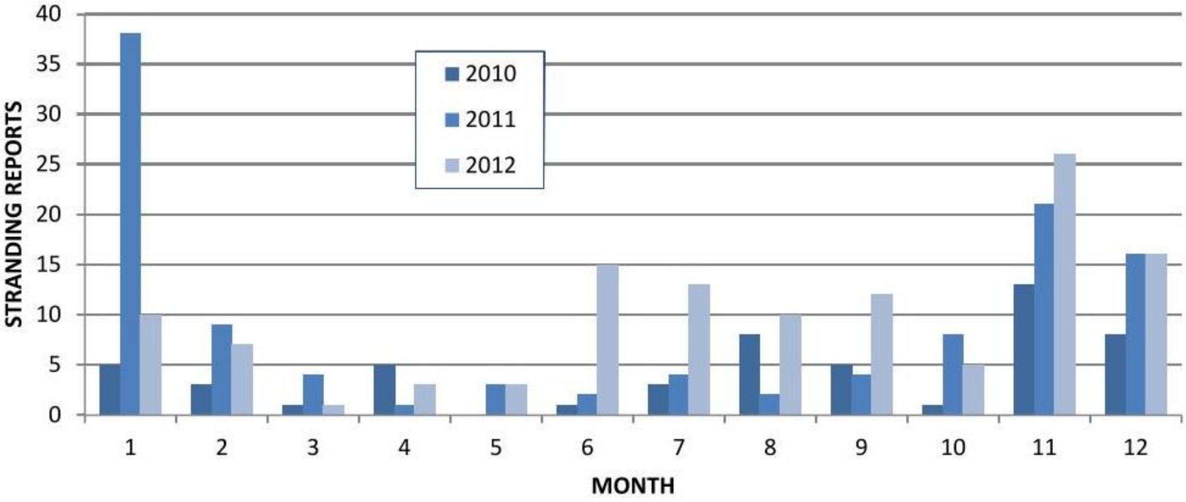

Figure 1.5 Monthly grey seal strandings reported in Scotland between 2010 and 2012 collected by SRUC. Image provided by SCOS 2013.

1.5 Scavengers

According to Getz (2011) scavengers are those animals which consume whole or specific parts of dead biomass (plants and animals) whose dimensions are typically smaller but sometimes larger than themselves (Getz 2011). Scavenging is a phylogenetically widespread foraging strategy of invertebrates and vertebrates, including such well-studied groups as ants, birds, crabs, fish and wolves (Wilson and Wolkovich 2011).

The most common scavengers in the terrestrial ecosystem are birds, mammals and invertebrates. An extensive literature has been dedicated to vultures, which represent an efficient ecosystem service with important implications for human welfare (Moleón et al. 2014). Among the foraging strategies adopted by vultures they have the ability to fly over long distances covering large areas and sharing social information on the location of a food item (Moleón et al. 2014). Mammalian scavengers such as hyenas, instead, are much less mobile (Houston 1979; Ruxton and Houston 2004b) and use mostly the sense of smell to detect carrion (Mills 1989). Many predatory birds, reptiles and mammals (Ruxton and Houston 2004b) behave as facultative scavengers utilising carrion when available (Jędrzejewski et al. 2002; DeVault et al. 2003).

Britton and Morton (1994) defined marine scavengers as organisms that are “able to detect carrion, usually by distance and touch chemoreception, deliberating to move toward it, and eventually consume either part or all of it”. Even if marine species that exhibit scavenging behaviour form an extensive group across phyla (Kaiser and Moore 1999), Britton and Morton (1994) have argued that almost all marine scavengers, apart perhaps from some nassariid gastropods and lysianassid amphipods, are facultative rather than obligate scavengers. Carcasses release chemical odours which can disperse across large distances (Ide et al. 2006) and this is an important factor which effects foraging. Chemical cues can also indicate the direction, quantity and quality of the food source. The quality is determined by detection of nitrogenous compounds such as amino acids, ATP, and sugars (Zimmer-Faust 1991), and when concentrations of the chemical reach a certain threshold, locomotory responses toward the carcass may be triggered (Britton and Morton, 1994). Carcasses provide a large amount of nutrients and increase the diversity of food sources and habitats available, thus increasing species richness in marine systems.

In many systems, the occurrence of carrion may be temporally unpredictable and it is only available for a limited time before it is eaten or decays (Houston 1979) and a scavenger cannot control the conversion of living animals to carcasses (Andrewartha and Birch 1984). Furthermore in many systems carrion is available episodically as a pulsed resource (Nowlin et al. 2008) and consequently scavengers experience times when food is abundant, alternating to episodes of shortage (Houston, 1979). In situations where food webs are subsidised consumer populations can sometimes become enhanced, although this may depend on the quantity and temporal variability of the subsidy and on the life history characteristics of the consumer species (Polis et al. 1996). Carrion availability varies across space, and thus could be a structuring force underlying the movement and the spatial distribution of scavengers (Wilmers et al. 2003b; Blázquez et al. 2009; Cortés-Avizanda et al. 2009). Moreover the composition of scavenger assemblages may vary with habitat type in which the remains occur, and hence the responses of different scavenger species to increasing inputs of carrion may vary between habitats. However, it might also be expected that the magnitude of the response of each scavenging species would be linked to the density of that species in the surrounding area (Ramsay et al. 1997b).

A large body of literature on scavenging ecology in the terrestrial environment has been developed during the last decade. Great attention has been devoted in the past to arthropod succession on carrion (e.g. Payne 1965; Putman 1983), with relevance to human forensics (Amendt et al. 2004). From an ecological perspective the state of carrion decomposition research has been previously overlooked (Carter et al. 2007). Moreover, the underestimated use of carrion by facultative scavengers (DeVault et al. 2003; Wilson and Wolkovich 2011), the formation of a defined structure in the scavenging assemblage (Selva and Fortuna 2007) and the possible alteration caused by human activities in the environment open new directions for future investigations.

Several studies have also been conducted on scavenging behaviour of marine organisms, but they are often confined to sublittoral or abyssal species (e.g. Bailey and Priede 2002; Kemp et al. 2006; King et al. 2007), often associated with fishing discards effects on seabirds and marine benthic scavenger populations (e.g. Camphuysen et al. 1995; Garthe et al. 1996; Ramsay et al. 1997b; Catchpole et al. 2006). Information on deep-sea scavengers occurring on whale-falls has been accumulated since the 1850s, and there is evidence that whale carcasses support a widespread, characteristic faunal community passing through at different successional stages (Smith and Baco 2003). Contrarily in shallow waters the influence of carrion availability on community structure is less well known (Ramsay et al. 1997b) and faunal colonization and decompositional changes on coastal carcasses seems to be understudied. The latter were investigated by forensic researchers to determine time of death for humans discovered in saltwater. In 2002, the Canadian Police Research Center evaluated aquatic scavenging organisms succession in a time interval of 140 days by using pig corpses as human models at two depths (7.6m and 15.2m). Five decompositional stages were identified (fresh, bloat, active, advanced and remains). Sediment type dictated the fauna present in the vicinity of the carcass: those bodies that rested on sand were scavenged much faster than those on rock, presumably due to the more abundant and greater diversity of animals which lived within the sand. Unlike the terrestrial environment, wounds and abraded skin on the carcass in marine conditions do not seem to attract scavengers (Anderson and Hobischak 2004).

1.5.1 Scavenging species in the coastal environment

Scavenging species inhabiting the coastal surface environment are vertebrates such as mammal and seabirds and invertebrates such as insects. Marine scavengers include molluscs, crustaceans, echinoderms and fish. In particular, scavengers known to feed on pinniped carrion include the southern and northern giant petrel (*Macronectes giganteus* and *Macronectes halli*) (Bruyn and Cooper 2005), black vulture (*Coragyps atratus)* (Pavés et al. 2008), kelp gull (*Larus dominicanus)* (Gallagher et al. 2015), great black-backed gull (*Larus marinus)* (Ronconi et al. 2014), red fox (*Vulpes vulpes)* (Culloch 2012) and arctic fox (*Alopex lagopus)* (Roth 2002), polar bear (*Ursus maritimus)* (Bentzen et al. 2007) and brown hyena (*Parahyaena brunnea)* (Kuhn et al. 2008).

In the marine system, the great white shark (*Carcharodon carcharias*) and the killer whale (*Orcinus orca*) adopt scavenging behaviour. Among the elasmobranchs, the Pacific sleeper shark (*Somniosus pacificus*) is thought to consume carcasses of Steller sea lions (Horning and Mellish 2014). Benthic gastropods Nassariidae and Buccinidae are opportunistic scavengers attracted from great distances by chemical stimuli emanating from suitable food (Morton

1990). Several studies have identified the hermit crab (*Pagurus bernhardus*) as one of the most important and abundant benthic scavengers that aggregate in areas of fishing activity (Morton and Yuen 2000). Together with starfishes, whelks, swimming crabs and fishes, hermit crabs feed upon fisheries discards which fall to the sea bed (Ramsay et al. 1997a; Ramsay et al. 1997b; Kaiser et al. 1998). In addition, *P. bernhardus* was shown to outcompete *Pagurus prideauxi* in areas of intense trawling activity (Ramsay et al. 1997a; Kaiser et al. 1998). Intraspecific competition for food among *P. bernhardus* also exists and the number of aggressive interactions and the intensity of competition increased with increasing numbers of individuals (Ramsay et al, 1997a). Field studies have shown that sublittoral fish, dabs (*Limanda limanda*) and whiting (*M. merlangus*) were attracted to bags baited with trawl discards in shallow water (Kaiser and Spencer 1996). The potential importance of smaller scavenger species, such as amphipods, in different habitats and their feeding behaviour have been understudied (Ramsay et al, 1997b).

1.6 Field sites

1.6.1 Isle of May

The Isle of May (56°11'N, 2°33'W), the main study site, is situated at the entrance to the Firth of Forth on the east coast of Scotland, lying approximately 8 km southeast of the coastal village of Anstruther and 17 km northeast of North Berwick. The island itself is 1.8 km long and less than half a kilometre wide with the long axis extending in a northwest-southeast direction. The island is effectively a single sill of olivine-dolerite ('greenstone') and is tilted in an easterly direction, with vertical cliffs up to 60 m in height on the western side, accompanied by numerous arches, stacks and caves. Several fault lines have given rise to intertidal channels which further divide the island into discrete islets, namely North Ness, Rona and the main island.

The Isle of May has been designated as a Special Area of Conservation (SAC) under the EC Habitats Directive (92/43/EEC), the entire site occupying 356.75 hectares. This designation is largely based on the Isle of May's role in supporting a large breeding colony of the grey seal, *H. grypus*, which is listed as an Annex II species under the Habitats Directive. Furthermore, the widely distributed rocky 'reefs' that fringe approximately 90% of the coastline of the island are an Annex I habitat and represent an additional qualifying feature for SAC designation (Moore, 2009).

The Isle of May represents an excellent site for field research being unique in its accessibility to seal colonies. Thanks to its remote location animals live in natural conditions with minimal anthropogenic disturbance (only researchers are allowed at the island during the seal pupping season).

Breeding colony and pupping site

The grey seal is believed to have bred on the Isle of May in the past (in fact in Gaelic "Rona" means "Sea Calf" as in seal), but there were no records of grey seal pups till the 1950s, when three pups were born (Baker and Baker, 1988). During the following decades, grey seals used the island to haul out, and numbers gradually increased until the Isle of May has become the biggest single island colony on the east coast of the UK (Hiby, 1996) and the fourth largest in the UK, contributing approximately 4.5% to the annual UK pup production (Moore, 2009). Much of the west and south-east coasts of the Isle of May are cliff-bound and unsuitable for breeding seals (Figure 1.6). Formerly, most pups (c. 90%) are born on the northern part of the island, which is mainly low rock, in an area of about 6 ha. This northern area is known collectively as Rona, but is composed of several discrete areas used for breeding with different access routes from the sea (Pomeroy et al. 2000). Baker and Baker (1988) describe the three breeding beaches characterized by the most important aggregations. Silver Sand is the only area of sandy beach on the islands (Figure 1.6). The tidal area, some 15 m long at low water and 6 m wide, is of clean sand, but most pups live on a much larger area of gently sloping stable sand behind the beach, which has a great deal of driftwood and other flotsam. By the end of the breeding season, this area is contaminated with matted, moulted seal hair, faeces and dead pups. West Rona Beach has access to the sea only by a narrow pebbly inlet about 5 m wide, with steep rocks up to 4 m high on either side. Most of the new-born pups are found at the edges of this gulley, protected by the rocks, but as they grow they tend to move, some to the level rocks above, but most to the level areas of mud and stagnant water inland. This area is fouled and completely cleared of vegetation by the middle of the breeding season. The latter two locations contain the overall highest observed density of seals (Pomeroy et al., 2000). Rona Rocks, on the north-east side of Rona, is an area of bare rock of about 100 m in depth and 200 m from end to end. The volcanic greenstone is largely fractured, with vertical faces of up to 3 m in height, and many deep faults and fissures. Most of the pools in the area are above normal high tide level, and are contaminated by the faeces and other debris of both seals and seabirds.

The number of areas used by seals for breeding expanded as the population increased (Pomeroy et al., 2000). Grey seals occupy two new locations in the southern part of the Isle of May. From 1990 the beach at Pilgrim's Haven on the south-west coast has been used by seals but there was no evidence of increased pup production there. It is a pebbly inlet ca 20m wide with rocky walls on both sides (personal observations). While areas around Kirk Haven were used increasingly in the 1990s, when up to 22% of the pups counted on Rona were then found at the minor southern sites. Kirk Haven breeding site is a narrow sandy beach presenting rocks on the each side (personal observations). The latter southern breeding sites on the Isle of May are also characterized by having pups born later in the season than the main northern sites: the mean pupping date occurs on the 5th November (+/- 10days) (Hiby et al. 1996).

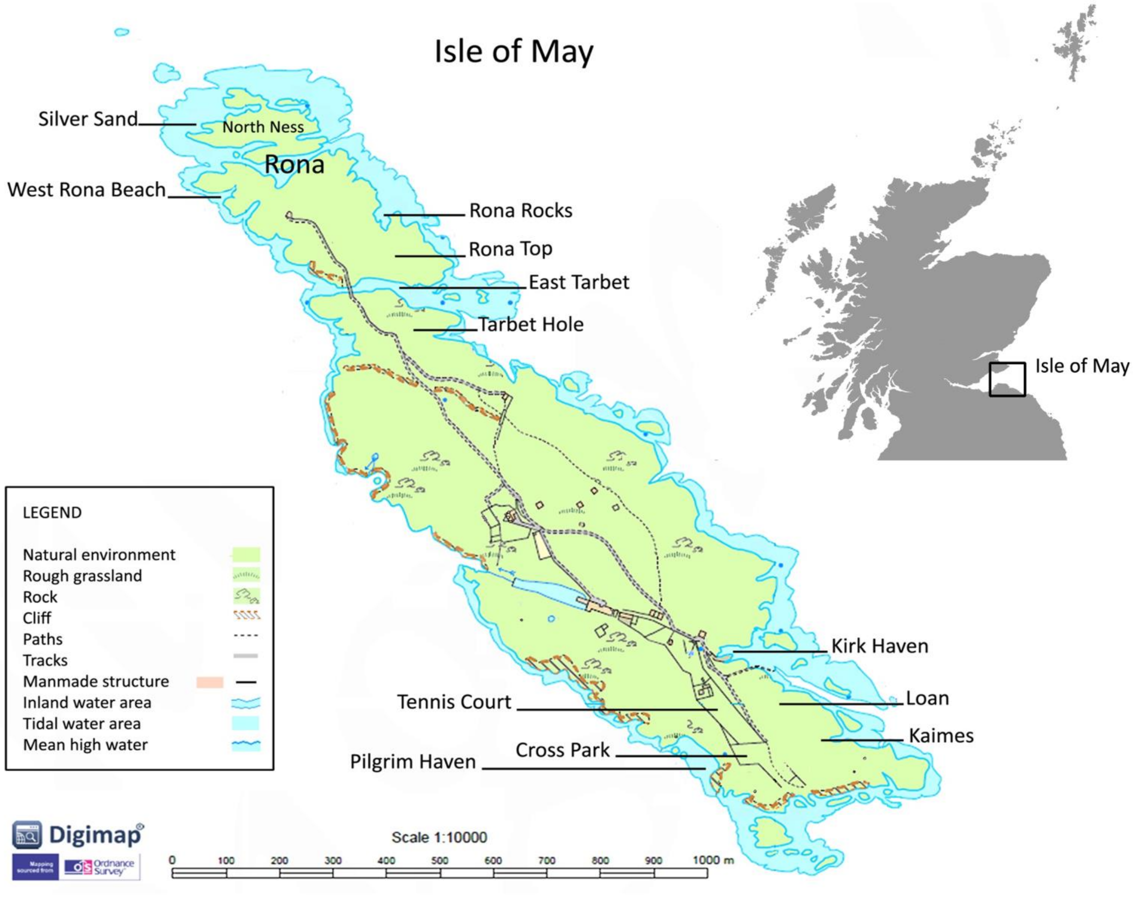

Figure 1.6 Map of the Isle of May.

Maps provided by EDINA Digimap Service, http://digimap.edina.ac.uk/roam/os.

1.6.2 Great and Little Cumbrae

Additional fieldwork was carried out on the islands of Great Cumbrae and Little Cumbrae which are located on the south-western coast of Scotland (see Figure 2.1 in Chapter 2). While Great Cumbrae is inhabited and represents a tourist attraction during summer, no people live in Little Cumbrae, with the exception of the island wardens. Despite the two islands being separated by less than a kilometre from each other, their morphology is different. In contrast to Great Cumbrae, which presents many fields dedicated to agriculture and farming, Little Cumbrae is characterised by many cliffs, rocky outcrops and wild vegetation. Some hauling-out sites for both grey and harbour seals occur on both islands.

1.6.3 Expected scavenging community

Several seabirds are scavengers, including the herring gull (*Larus argentatus*), the lesser black-backed gull (*Larus fuscus*) and the great black-backed gull (*Larus marinus*) (Camphuysen et al. 1995; Garthe et al. 1996). The great black-backed gull, in particular, is the largest species of gull and its distributed in both the western and eastern Atlantic coasts (Olsen and Larsson 2004) extending to the extreme northwest portion of Russia.

Gulls are opportunist carnivores, being both predator and scavenger, as their diets consist almost entirely of animal prey (Spaans 1971; Pierotti and Annett 1987; Annett and Pierotti 1989). They forage around ships in inshore areas, on shoaling fish, in the intertidal zone, in agricultural areas, on refuse tips and even in litterbins in busy streets. In coastal areas, gulls are proficient intertidal predators, foraging from the surface at low tides (Furness and Monaghan 1987), preying upon a wide range of animals such as crustaceans, molluscs and echinoderms. Small mammals, like rats and rabbits, or birds are part of their diet as well (Harris 1965).

Research on inter-specific interactions between the different gull species showed that the great black-backed gull out-competes the herring gull for food when the two species share the same breeding site (Rome and Ellis 2004), but also during scavenging activity on refuse tips (Greig et al. 1986) and fishery discards (Hudson and Furness 1988) during winter.

Large-scale studies in the North Sea have demonstrated that scavenging seabirds make extensive use of fishery waste, above all of offal and roundfish, but also to some extent of flatfish, cephalopods and benthic invertebrates (Camphuysen, 1995). Even if fishery discards are considered responsible for the growth in populations of several scavenging seabirds, these species have also been recorded feeding on grey seal carcasses. Baker (1984) stated that surveys for post-mortem medical inspections on pup carrion were difficult as scavenging birds eviscerated bodies within a short period after death, particularly if the animal died with the umbilicus exposed. Twiss et al. (2003) also observed predatory behaviour of great black-backed gull on weak or unprotected grey seal pups at the seal colony of Rona. The great black-backed gull and the herring gull are identified Amber and Red listed in Birds of Conservation Concern respectively (Eaton et al. 2015). Changes in food availability and disease might be the main threats for the herring gull (Monaghan 2007), while human persecution, botulism and viral infection, and predation by brown rats (*Rattus Norvegicus*) and American mink (*Neovison vison*) are the possible main threats that acted upon the great black-backed gull population (Zonfrillo 2007). The Isle of May gull populations were subjected to drastic culls between 1972 and 1986 when more than 45,500 gulls were killed to reduce the impact on other seabirds nesting on the island. The great black-backed gull population in particular was exterminated (SNH 2014). As the seal pupping season coincides with the food-scarce and cold winter months, these species could benefit heavily from eating carrion, possibly improving their current status. During the rest of the year, instead, a possible source of food for the gulls living in the island is the European rabbit (*Oryctolagus cuniculus*) that have been present here since at least the 13th century (Southern 1938). In particular, during summer a certain amount of carrion becomes available to the gulls in the shape of dead rabbits killed by the disease myxomatosis (personal observation).

The red fox (*Vulpes vulpes*), was spotted at the grey seal breeding colony of Donna Nook (England, UK) feeding on placenta or dead pups (Culloch et al. 2012), but this mammal is not present on the Isle of May. The house mouse (*Mus musculus*) is not excluded as potential scavenger on the island. Mice were probably introduced more than once during human occupation, as the island was already inhabited by monks before the 8th century. The population was estimated ranging from 450-3250 animals occurring across all the island including Rona and North Ness which are isolated at high tide (Triggs 1991). Predation on by gulls is probably low (Harris 1965).

The resident bird populations of Little Cumbrae were estimated to comprise 120 great black-backed gulls, 1200 lesser black-backed gulls and 2000 herring gulls (JNCC 2010). There are no data available on ravens (*Corvus corax*) nesting on the island, but it is likely that some individuals, if not resident, travel from the nearby island of Great Cumbrae (Zonfrillo personal comment). No rats live here.

1.6.4 Energy transfer pathways of seal carrion

Generally the relationship between carrion and scavenger has been neglected in food web models (Selva and Fortuna 2007). In particular, the role of seal carrion provided to coastal scavengers has been so far overlooked and little is known about the transfer of biomass and energy between trophic compartments and ecosystems. As seal carrion can occur in both the terrestrial and marine systems, it represents a source of food for different organisms, including carcasivores (or scavengers) and necrophages, but also bacteria during decomposition, before being available to detritivores and soil.

Seal breeding colonies have the potential to greatly influence the surrounding ecosystem with an influx of carrion in the shape of pup and adult carcasses and placentae. These resources may be exploited by terrestrial vertebrates such as gulls and mice, but also invertebrates (Figure 1.7). Some carcasses may be located in the intertidal area, where, being submerged by water and exposed to air according to the tidal action, they become available to both terrestrial and marine organisms. Under the influence of the tide and other environmental factors, such as weather conditions, wind and wave action, a certain amount of carcasses (and possibly also placentae) can be removed from the shore and be exposed to the marine system and its inhabitants such as scavenging starfish and crabs. The biomass resulting from seal carrion has therefore the potential of supporting terrestrial and marine communities of facultative and obligate scavengers. These scavengers will, in turn greatly influence the surrounding ecosystem by redistributing nutrients (Payne and Moore 2006). However, the part of dead biomass which is not transferred to scavengers is going back into the environmental constituents (nutrients and organic molecules) (Getz 2011). The present thesis will evaluate the biomass transfer between some of the ecoystem compartments mentioned above.

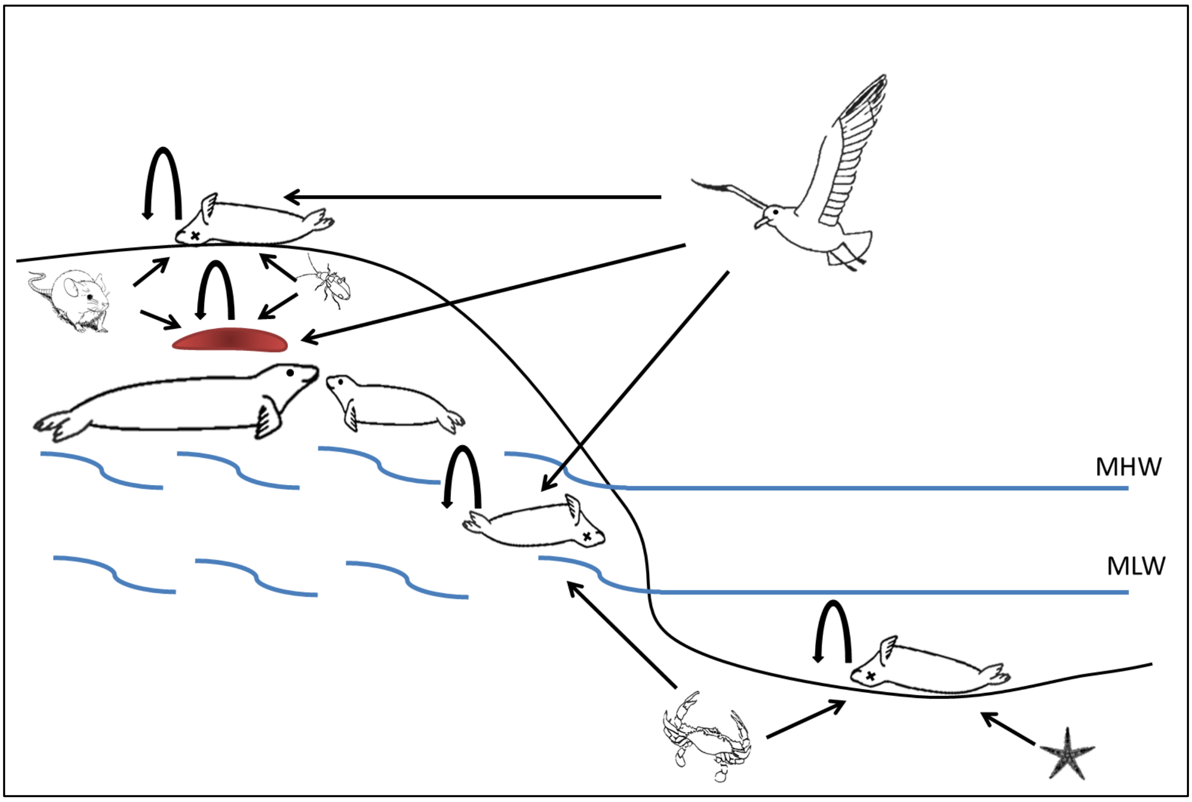

Figure 1.7 Energy transfer pathways of seal carrion in the terrestrial and marine ecosystems.
Biomass transfer through scavenging consumption or decomposition of a placenta located on land and a dead seal pup located on land, in the intertidal zone (between the mean high and low water levels) and underwater to vertebrate (gulls and mice), invertebrate scavengers (insects, crabs and starfish) and soil.

1.7 My PhD research

1.7.1 Knowledge gaps

Although much is known about marine mammals, their role in the coastal ecosystem is often considered of limited relevance and some ecological processes of intertidal environments in which marine mammals are involved are understudied. The grey seal, which periodically hauls out on land in the British Isles, represents a significant importer and exporter of energy and nutrients across the marine/terrestrial interface, both as alive individuals and potentially as carrion (Moore 2002).

Since the potential of coastal marine mammal populations as a source of carrion to local marine communities is not well known (Watts et al. 2011), an important step is determining whether scavenging on top predator carrion is

important and common. At the present time this information is lacking. Moreover, recent reviews highlighted the necessity of investigating:
1) differences between carrion cycling in marine and terrestrial ecosystems (Beasley 2012);
2) the importance of carrion as a distinct and underestimated resource in various ecosystems (Barton et al. 2013b), including the marine coastal system;
3) the influence of spatial and temporal pattern of occurrence of carrion on scavenging behaviour, with attention to facultative scavengers which adopt alternative strategies for energy acquisition (DeVault et al. 2003);
4) the scavenged component of carnivore diets (DeVault et al 2003) and its significance for key scavenging species in order to encourage their protection (Moleón et al 2015).

1.7.2 Aims

Understanding the connections between terrestrial and marine habitats is essential for the protection and management of both systems. Coastal systems have been and will be deeply altered throughout this century by a number of natural and anthropogenic effects, such as climate change. Therefore understanding the ecological interface between terrestrial and marine systems will provide a basis for the conservation and protection of coastal habitats and species. The management of marine mammal and seabird populations is expensive (and sometimes controversial), so a full understanding of the ecological role of those species is valuable in determining what efforts are appropriate.

This project took a multifaceted approach to determine the importance of seal carrion to scavengers and the coastal ecosystem. The aim was to answer the following questions:

1. How decomposition and scavenger consumption of seal carrion differ between marine and terrestrial ecosystems? (Chapter 2)

Simulating a dead pup stranding on a beach and a negatively buoyant carcass washed offshore, a detailed documentation of the decomposition of a grey seal pup carcass and its consumption by scavengers will be provided. It was predicted that the presence of the carcass on the beach alters the distribution of the local scavenging birds; thus more birds are expected to fly over the study area after the carcass deployment than the control area. Secondly, a temporal succession of scavengers caused by inter-specific competition and/or different levels of tolerance to decomposition was predicted to occur during consumption of the carcass in both the terrestrial and marine systems.

2. Is carrion provided by a seal colony, in the shape of placentae and carcasses, a predictable resource according to its timing, spatial distribution, biomass and energy released? (Chapter 3)

Predictability of seal carrion was examined by using data on aerial survey (11 years) and ground visual census (3 years) to evaluate the timing of the pupping season, quantifying the biomass and energy released by carrion and its spatial distribution. Inter-annual variability of these properties (expressed as percentage of relative standard errors, RSE%) was calculated and predicted to be similar to that one of other predictable resources such as salmons in spawning areas. The response of the local avian scavenging community to carrion in terms of biomass consumed at the end of the seal pupping season was finally estimated.

3. What is the influence of seal carrion on the spatial and temporal distribution, and behaviour of scavenging gulls? (Chapter 4)

This was first evaluated by analysing changes in the number of scavenging gulls occurring before and during the seal pupping season at regional scale (Scotland): an increase in the number of gulls counted on the Isle of May was predicted to appear between September and December, whereas a decreasing in abundance would have been observed in the surrounding region. BirdTrack data for South Scotland, WeBS counts for the Forth Estuary area and Daytime and Roost counts for the Isle of May were used for the comparison. At local scale (Isle of May), the relative abundances of gull species were predicted to change between day and night on the Isle of May. Assuming that gulls are mostly diurnal (Hailman 1964; Garthe and Hūppop 1996), the species dominating the Daytime counts would, therefore, represent the main exploiter of carrion. Differences in Daytime and Roost counts would also indicate the relative importance of the island as feeding and roosting site for the different species. At patch scale, a higher number of active gulls was predicted to be observed in areas where carrion occurs than in areas where it was not present. In particular, within the patch, it was predicted that foraging activity of scavenging gulls was positively related to carrion availability, so that the number of gulls flying over the patch was higher at the peak in availability of carrion (both carcasses and placentae), while the number of individuals feeding would be proportional to the amount of carrion.

4. Does seal carrion affect the behaviour among scavengers in conditions of abundant and predictable resources? (Chapter 5)

The feeding activity and intra-specific interactions among scavenging gulls was investigated during the seal pupping season on the Isle of May where conditions are characterised by predictable and abundant carrion availability. It was predicted that there would be no formation of hierarchical dominance showing either successive stages of monopolisation of the carcass or temporal segregation induced by adult great black-backed gulls. Therefore, it was expected that the feeding rates (cumulative time feeding per day per carcass) of adult and juvenile gulls were equal and would show similar trends with time. Placenta was considered as the preferred food due to its higher energy density and lower handling time compared to carcasses, and regardless of its abundance and predictability during the seal pupping season, dominant individuals would have more access to the resource. Therefore, it was predicted that feeding rate of adult gulls (cumulative time feeding per bird per placenta) would be greater than juveniles.

The final chapter (Chapter 6) presents an overall discussion of the implications arising from these scientific questions.

Chapter 2: First investigations of the consumption of seal carcasses by terrestrial and marine scavengers

2.1 Abstract

Marine mammal carrion contains a large amount of nutrients and energy of potential value to terrestrial and marine scavengers, but its impact on coastal habitats has not been studied. This study aimed to document in detail the fate of two grey seal (*Halichoerus grypus*) pup carcasses, one placed on the shore and one at a depth of 6 m, recording the changes in the carcasses and the succession of scavengers using these resources. The carcasses were monitored using time lapse and/or motion-activated cameras. On the shore, great black-backed gulls (*Larus marinus*), juvenile gulls and ravens (*Corvus corax*) fed on the carcass and there was a distinct shift in the relative proportions of bird groups feeding over the period observed. Herring gulls (*Larus argentatus*) spent significantly less of their time at the carcass feeding than other birds, while lesser black-backed gulls (*Larus fuscus*) were not observed scavenging despite being common on the island. Over the six week period of observation, more than 90% of the carcass was consumed. However, the deployment of the carcass did not influence the spatial and temporal distribution of the scavenging birds. The underwater carcass was monitored for two periods of two and one week duration. In the first period Echinodermata (dominated by *Asterias rubens*) had the highest maximum number of individuals at the carcass, followed by Actinopterigii (fish) and Malacostraca (crabs). Numbers of fish and starfish decreased in the second period, while crustaceans were present in similar numbers as previously. The daily mass loss of the carcasses was 0.56 and 0.07 kg day^{-1} in the terrestrial and marine ecosystem respectively. Both experiments showed evidence of bacterial activity. In the absence of any previous detailed study, the present work provides important insights into the role of seal carcasses in coastal systems, especially in an era when carrion from fisheries discards will become increasingly unavailable.

2.2 Introduction

Scavenging is a widespread and foraging strategy employed by many carnivorous animals (Selva and Fortuna, 2007). Although potentially valuable, carrion is often an unpredictable resource making scavenging a high risk-high reward strategy. This risk is reduced where animals can search large areas at low cost and can be accomplished by specialised birds (Ruxton and Houston, 2004a) and possibly by abyssal fish (Ruxton and Bailey, 2005). However, scavengers are often facultative rather than obligate: many large mammalian carnivores, for instance, switch from hunting to scavenging depending on prey availability (Pereira et al. 2014). In some food webs scavenging links have been underestimated 16-fold, so that the energy transferred through scavenging is likely to be greater than that transferred by predation (Wilson and Wolkovich 2011).

In UK coastal systems the families Laridae (gulls) and Corvidae (ravens) are opportunistic scavengers. In contrast to the Tubinares (petrels) which are seabirds highly dependent on carrion and use their excellent sense of smell to find it (Nevitt 2000), gulls and corvids employ sight, and probably olfactory information (Wikelski et al. 2015). This food-finding behaviour includes visual surveillance of the coast, recognition of the food item and attraction to the sight of other animals feeding (Frings et al. 1955). Although frequently observed, the role of marine mammal carrion on the scavenging activity of coastal birds is not clear as previous research on this subject has been opportunistic and qualitative (e.g. Bruyn and Cooper 2005; Reid and Forcada 2005; Van den Hoff and Newbery 2006).

Knowledge of marine scavengers, focused mainly on deep-sea whale-falls, has shown that whale carcasses can support a widespread and characteristic faunal community during different successional stages (Smith and Baco 2003). By contrast, the impact of carrion in shallow waters is less well known. As food falls occur together with other natural and anthropogenic perturbations, it is difficult to evaluate their impact on coastal scavengers, being mostly facultative and not exclusively dependent on carrion (Ramsay et al. 1997b). In shallow water the main scavengers are thought to be benthic invertebrates (principally crustaceans and molluscs). These species likely detect carrion from the dispersion of chemical cues indicating the location, quantity and quality of the food source

(Britton and Morton 1994). Faunal colonisation and decompositional changes from marine mammal carcasses in coastal systems also appear to be understudied and only studies took into account these phenomena (e.g. Dahlgren and Wiklund 2006; Glover et al. 2010).

The main factors driving the structure of the scavenging community include competitive and facilitative interactions, behavioural adaptations, carcass size and environment (Selva et al. 2005; Sebastián-González et al. 2013; Moleón et al. 2015; Sebastián-González et al. 2016). Intra and inter-specific interactions may lead to successional patterns in the scavenging community during the process of carrion consumption. Many forensic studies focused on post-mortem intervals and the associated fauna, but they examined mostly the succession of terrestrial arthropods (Amendt et al. 2004). Exceptionally, Anderson and Hobischak (2004) observed the sequence of marine invertebrates associated with submerged pig carcasses. Terrestrial vertebrates were rarely considered when exploring temporal occurrence of species linked to carrion (e.g. Cortés-Avizanda et al. 2012; Young et al. 2014).

The total UK populations of both harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) were estimated to be around 150,000 individuals in 2012 (SCOS 2013). Owing to their body size, high energy demand and sometimes high local abundance, seals can strongly influence marine ecosystems, as they are capable of transporting energy and nutrients over long distances and between habitats. Large aggregations of seals occur on mainland and island coasts and it is therefore likely that mortality allows the major transfer of energy and nutrients between trophic levels and habitats. Annual mortality rate of UK adult grey seal population is estimated to be around 5% (Thomas and Harwood 2005), whereas pup mortality can reach more than 30% in the first month of life in certain areas of the colony (Summers et al. 1975). As a result, large adult seal carcasses containing very large amounts of nutrients and energy are relatively rare (one was observed on Great Cumbrae while the terrestrial experiment was underway, personal observation), while the smaller pup carcasses are probably common following the seal breeding season. Both terrestrial and the marine food webs can be affected by seal carrion, but the recycling processes in which it is involved can be fundamentally different (Beasley et al. 2012). Beasley et al. (2012) identified the physical properties of air and water as main drivers of the fate of carrion in the two ecosystems. Other features of influence include the three-dimensional space of the aquatic system, which allows one more dimension for movements of carcasses. These properties can, then, lead to a diverse hierarchal structured assemblage of scavenging organisms (Beasley et al. 2012).

The aim of this study was to document the decomposition of a grey seal pup carcass and its consumption by scavengers in both a terrestrial and a marine environment. The terrestrial experiment was a simulation of a dead pup stranded on a beach, whereas the underwater experiment represents a negatively buoyant carcass washed offshore. Firstly, it was predicted that the presence of the carcass on the beach alters the distribution of the local scavenging birds; thus more birds are expected to fly over the study area after the carcass deployment than the control area. Secondly, a temporal succession of avian scavengers was predicted during consumption of the carcass, caused by dominance, inter-specific competition and/or different levels of tolerance to decomposition.

2.3 Methods

The grey seal pup carcasses were originally found dead due to natural mortality on the Isle of May (Firth of Forth, Scotland, UK) during the 2011 pupping season. The island is owned by SNH, and the collection of carcasses was approved under research licences issued by SNH. The Sea Mammal Research Unit (University of St Andrews) collected them when still in fresh condition (around 3 days after death) for the purpose of this project. Carcasses were frozen at -20^{o}C and stored at the University of Glasgow until the study commenced.

The terrestrial experiment required the approval of the manager of Little Cumbrae for operations on the littoral zone of the island. No Marine Licence was necessary for the underwater experiment, as the proposal was treated as a scientific experiment. The permission for the use of the seabed (to the south of Clashfarland Point) was granted by the Crown Estate and Marine Scotland Licensing Operations. Use of the shore for the placement of the recording equipment for the underwater camera was granted by the Bute Estate. Other authorities and institutes directly or indirectly involved in the experiment were informed, including the Local Authority's Environmental Health Department, the University Marine Biological Station Millport (UMBSM, now Field Studies Council

Millport), the local police, the Scottish Agriculture College (SAC now SRUC), the Scottish Environmental Protection Agency (SEPA), the Scottish Natural Heritage (SNH), the Sea Mammal Research Unit (SMRU) and the Scottish Society for the Prevention of Cruelty to Animals (SSPCA).

Terrestrial experiment

The terrestrial experiment was conducted on the island of Little Cumbrae, SW Scotland (55°43'50.46"N, 4°56'18.59"W) (Figure 2.1) between the end of July and September 2012. The resident bird populations of Little Cumbrae were estimated to comprise 120 great black-backed gulls (*Larus marinus*), 1200 lesser black-backed gulls (*Larus fuscus*) and 2000 herring gulls (*Larus argentatus*) (JNCC 2010). There are no data available on ravens (*Corvus corax*) nesting on the island, but it is likely that some individuals, if not resident, travel from the nearby Great Cumbrae (Zonfrillo personal comment). The study area (carcass present) and a control area (no carcass) were chosen at a distance of approximately 570 m from each other along the eastern coast of the island to avoid anthropogenic disturbance and were selected based on similar topographic features and ease of observation. Seabird surveys were undertaken at the study and control sites both before and after the deployment of a single grey seal pup carcass (study-before: N = 4; study-after: N = 13; control-before: N = 4; control-after: N = 11) at intervals of 2-6 days for the total duration of the experiment (from 18/07 to 5/09/2012) (Appendix A.1). Counts were performed to evaluate the traffic of birds in the areas before and after the deployment of the carcass as an indication of changes in behaviour and spatial use after the carcass became available in the study area. This methodology was previously used also to assess the impact of wind turbines on birds present in the area of installation (e.g. Barrios and Rodríguez, 2004; Everaert and Stienen, 2006). Continuous sampling (Martin and Bateson 1993) of flying birds was used to obtain the number of passages during a period of 2 hours at each site (2 hours per survey). Counts were undertaken at different times of the day, at low and high tide at both sites. As suggested by Gregory et al. (2004), the vantage points for counts were raised and/or concealed positioned and were chosen at a sufficient distance (30 m) from the areas to minimise disturbance. Areas of observations had an approximate size of 150 x 40 m covering both land and sea and only birds flying over this area were counted. The bird counts included herring gulls, lesser black-backed gulls, great black-backed gulls and ravens. Immature individuals belonging to the family Laridae, but of different species, were not distinguished and were grouped together. Avian scavengers were identified by researchers who were previously trained in bird identification and according to Grant (1982) and Holden et al. (2009). Prior to deployment, the seal carcass was intact, with the exception of a missing left eye. Its body length (nose to tail) was 110 cm and mass was 25.0 kg. The carcass was allowed to defrost and was deployed in the upper-littoral zone (at 3.49 m height and 38.8 m distance to the lower limit of the infralittoral zone) of the study area on the 26 July 2012. Appearance of the carcass was documented with photographs in order to define the decompositional stages. Mass loss was recorded by weighing the carcass on a plastic sheet using a digital scale (min = 10g, max = 40kg, accuracy = ± 10g) at approximately weekly intervals. The carcass was monitored by infrared motion-triggered and time-lapse cameras (n = 3; Bushnell Trophy Cam models 119436 and 119435) for the duration of the experiment. Cameras were located at a maximum distance of 3 m from the carcass. Two cameras were set on motion-triggered time lapse mode (two 8 MB resolution photographs every five minutes and every two minutes if movement-triggered) (Hamel et al 2013); the third camera was set on motion-triggered 10s video mode (640 X 480 pixels resolution when movement-triggered). The entire photo/video collection was used in the analysis including times (max 30 minutes) when the researchers were present in the study area. For the periods 8/13, 16/19-08 and 2/5-09 only videos were available due to malfunction of the other cameras. Birds occurring in the field of view of the cameras were identified from images and the times spent actively scavenging on the carcass (feeding) and present but not scavenging (not feeding) were recorded. Time spent both actively and inactively by gulls on the carcass was estimated from the number of minutes included between consecutive images till the gull disappeared. When the body of the carcass was found opened, the rectangular area containing the internal organs was measured. Daily maximum number of individuals (mean MaxN day^{-1}) feeding at one time at the carcass was calculated for each group of birds. Specimens of invertebrate scavengers were collected in the study area (on 02/08), preserved in ethanol 70% and identified in the laboratory using Smith (1989). At the end of the study, the remains of the carcass were disposed off at sea. Data on daylight hours and air temperatures were obtained from timeanddate.com and metoffice.gov.uk, respectively.

Underwater experiment

A second grey seal pup carcass was deployed on the seabed south of Clashfarland Point on Great Cumbrae, SW Scotland (55°45'44.40"N, 4°53'41.82"W) (Figure 2.1), on the 1st August and recovered on 17th October 2013. The carcass was secured to the wire mesh base of a purpose-built steel frame (120 x 60 x 93 cm, LxWxH). The monitoring system consisted of an underwater 24/7 CCTV wired camera (1/4 inch Sharp Color CCD, 24 white LEDs) attached to the frame and connected by 80 m cable to a SD-DVR, a memory card-digital video recorder onshore (Appendix A.2). The cable was protected from abrasion by being placed inside a length of garden hose. The unit was powered by two 12V-55Ah batteries (Camdenboss Electronics and Enclosures VRLA Lead Acid AGM). Batteries were charged and SD micro-card changed approximately every four days to keep the system working continuously. The carcass was intact, was 100 cm in length and had a mass of 19.7 kg. It was attached (still frozen to facilitate the deployment) to the base of the frame and then deployed at 6 m depth by the vessel Actinia (UMBSM). The frame's position on the seabed was adjusted by two SCUBA divers, who then ran the camera cable back up the shore, attaching it to the seabed at intervals using lengths of chain. The frame was located in the circalittoral zone, close to the border with the infralittoral zone. The seabed was characterized by gravel and sand substrate with extensive beds of kelp (*Laminaria* spp.) within 3-5 m of the frame at the start of the experiment. The carcass was monitored continuously for two periods (2-15/08 and 17-25/09). The interval between periods was caused by technical problems due to fouling by barnacles and ultimately leaks into the underwater camera, which had to be replaced. At the end of the experiment the carcass was removed from the frame by divers and placed within a waterproof dry-bag before being brought back to the shore. Excess water was drained from the dry-bag and then the carcass was frozen to -20°C while still in the bag and weighed. After carcass removal the camera frame equipment was recovered using the vessel winch and A-frame. Seawater temperatures were provided by the Field Studies Council Millport and data on daylight hours were obtained from timeanddate.com. Videos were analysed using iDRV Player (version V3.5 2011/1/5) and times when bad visibility occurred due to turbulence or bad light conditions or algae interference were excluded (Appendix A.3). Where possible, organisms were identified to the species level, but for the purpose of analysis the following taxonomic classes of marine organisms were considered: Gastropoda, Bivalvia, Asteroidea (starfish), Malacostraca (crabs) and Actynopterigii (fish). Different sources were used to identify organisms and their feeding guilds, including Naylor (2005) and the marine species databases marlin.ac.uk and marinespecies.org. Individuals occurring on the carcass were counted at 10 min time intervals. The daily maximum number of individuals (MaxN) was calculated for the five groups. The proportions of visits of crustaceans were calculated for day and night in the two periods. Agonistic events were recorded when observed.

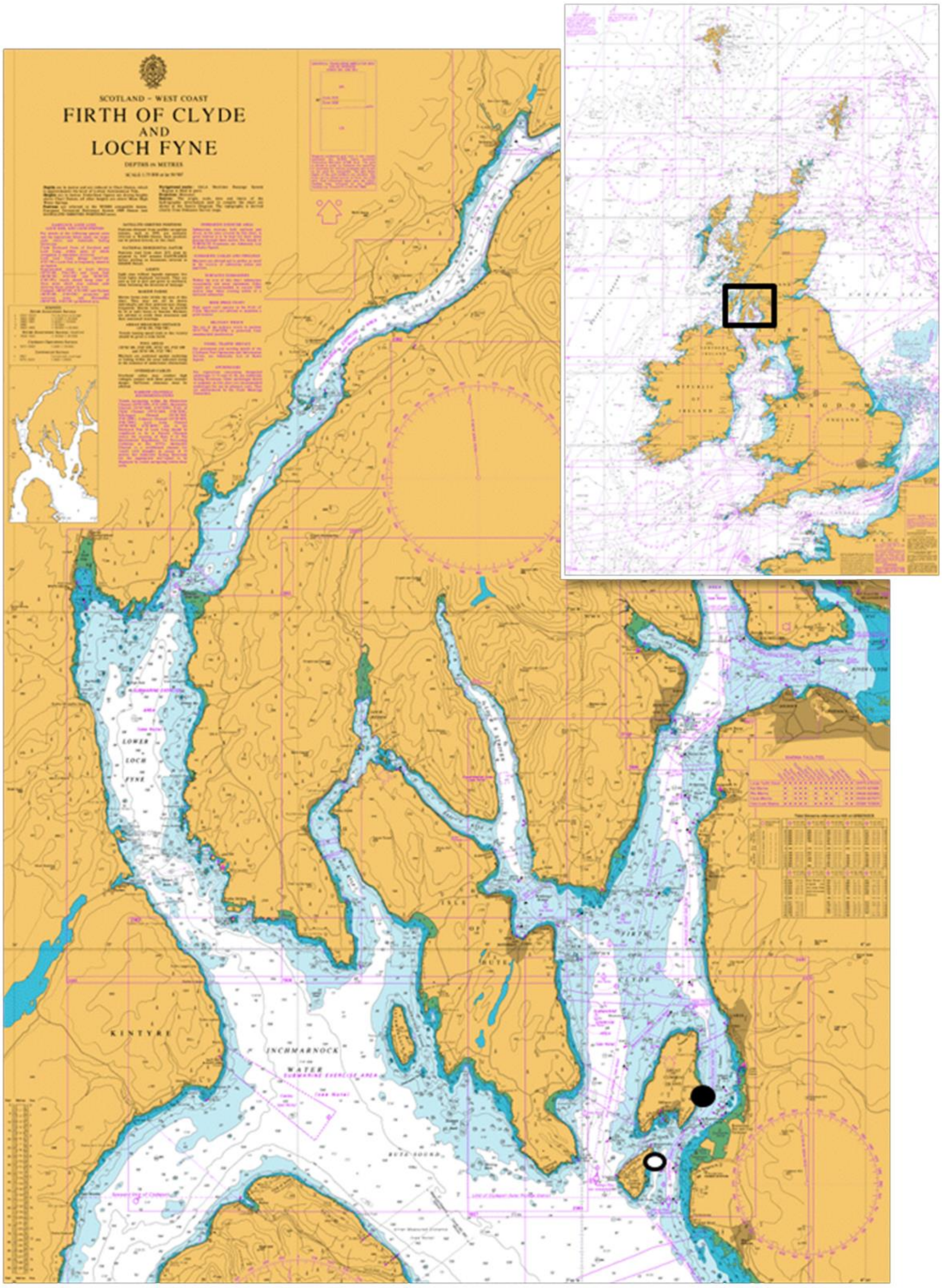

Figure 2.1 Map of locations of the experimental areas.

The terrestrial experiment was run in Little Cumbrae (o) and the underwater experiment in Great Cumbrae (•), West of Scotland, UK. Maps provided by EDINA Marine Digimap Service, http://edina.ac.uk/digimap.Crown Copyright / SeaZone Solutions Ltd [2008]. All Rights Reserved. Not to be used for Navigation.

2.3.2 Statistical analysis

Terrestrial experiment

Generalised linear models were carried out to evaluate whether the deployment of the seal carcass at the study area altered the distribution of the scavenging birds. The response variable was the number of passages of each group of birds counted in two hour survey (N passages 2hours^{-1}), while the explanatory variables were the Area (categorical: study and control), the Period (categorical: before and after the carcass deployment), the Tide (categorical: high and low) and the Time of the day (categorical: morning and afternoon). The primary aim was to test for a significant interaction effect between Area and Period as a significant interaction would imply that bird abundance changed differently in the study and control sites after the carcass was deployed. After exploring data according to Zuur et al. (2010), the model was run including all the explanatory variables and the only interaction of interest and the minimum adequate model was identified by step-wise removal of non-significant terms choosing the model with the lowest AIC. Dealing with counts, data were modelled with both Poisson and negative binomial distributions. The likelihood ratio test score was calculated in order to compare the null and final model. P values of significant terms came from an analysis-of-variance (anova function in R). Ravens were excluded from this analysis because of insufficient data.

A generalised linear model followed by a Tukey post-hoc multiple contrasts test were run to to investigate differences among the absolute feeding times (mins day^{-1}; response variable) among the groups birds (explanatory categorical variables). Again, dealing with count data were modelled with both Poisson and negative binomial distributions and the model with the lowest AIC was chosen. The analyses were performed in R 3.0.3 (R Development Core Team, 2012), using the packages ‘MASS’ for the model (glm.nb()) (Venables and Ripley 2002), ‘epicalc’ for the likelihood ratio tests (Chongsuvivatwong 2012) and ‘multcomp’ for the Tukey contrast test (Torsten et al. 2008).

A purely temporal scanning statistic was used to detect the predicted temporal succession of scavengers occurring during consumption of the carcass:

clusters of feeding activity (mins day^{-1}) of the same group of birds at particular times at the carcass during the experiment were therefore identified. The temporal scan statistic uses a window, defined as an interval time of variable size, which scans the temporal data to be analysed. The number of observed and expected observations inside the window is noted and the window with the maximum likelihood is the most likely cluster. This analysis was performed in the program SaTScan (Kulldorff et al. 2005): the purely temporal analysis was implemented by selecting a discrete Poisson probability model and a temporal cluster size between 2 days and 50% of the study period. A total of 9999 Monte Carlo simulations were made to calculate p-values for detected clusters.
Once checked for non-normal distribution running a Shapiro–Wilk test, the nonparametric pairwise Wilcox Mann-Whitney test with the adjustment method Holm, giving a strong control of the family-wise error rate, was used to compare the proportions of time spent actively feeding among groups of birds. Lesser black-backed gulls were excluded in the previously described three analyses because they were not observed feeding on the carcass.

Underwater experiment

A Poisson generalised linear model was used to evaluate differences in the composition of the scavengers' assemblage between the two periods of the carcass monitoring. The maximum number of individuals (MaxN; response variable) was explained by the following variables: taxonomic Class of animals (excluding gastropods and bivalves because of insufficient data), Period of monitoring (categorical: period1 and period2) and the Time of the day (categorical: day and night). The minimum adequate model was identified by step-wise removal of non-significant terms choosing the model with the lowest AIC as final model; score of the likelihood ratio test between null and chosen model was reported.

The proportions of visits made by malacostracans at day and night for the two periods were compared by using the nonparametric pairwise Wilcox Mann-Whitney test with the adjustment method Holm, after checking the non-normality nature of the data by using a Shapiro–Wilk test. Analyses were performed in R 3.0.3 (R Development Core Team, 2012) using the same packages mentioned previously.

2.4 Results

2.4.1 Terrestrial experiment

Temperature and daylight hours

The maximum and minimum air temperatures recorded in July were 18.1°C and 11.2°C, 19.7° and 11.8° in August and 15.3°C and 8.9°C in September. The daylight hours ranged from 16.83 to 16.10 hours in July, from 16.02 to 13.88 hours in August and from 13.80 to 13.50 hours in September.

Consumption and decomposition of the carcass

Within 24 h of placing the carcass, abrasions and wounds were evident. The first areas to be fed upon were the umbilicus and the eye region. From the camera footage, at day 2, a great black-backed gull was seen pulling out the intestines from the carcass which were then found spread over 18m^2. From day 3 initial wounds were further opened and fly larvae and adults (*Calliphora vicina, Lucilia sericata*, *Lucilia* sp.) together with the burying beetle (*Nicrophorous humator*) were present in the mouth, nostrils and underneath the body. Occasionally crabs were observed visiting the carcass during the night.

As the holes in the head and abdomen grew, wounds also began to appear on the flippers (day 8). At day 20 the spine and internal viscera were exposed and the head was disarticulated. The front flippers were consumed quickly. The rear flippers were only superficially damaged and appeared desiccated by the end of the experiment.

The carcass showed successive stages of decay over the course of the study. In the initial stage arthropods quickly colonised the carcass (day 3). The next stage was characterized by bloating (day 9) and liquefaction, in which the carcass appeared much flatter and the tissues within the openings started to decay. A strong putrid smell was noted, apparently caused by liquids leaking from the carcass (day 11). The collapse stage was observed when a large quantity of the tissue was consumed and the head broke down (day 21). Approximately nine days later, the carcass appeared to be in the putrefaction stage (day 30). The carcass was disposed of at day 42, when only remains (bones and mummified hide) were present.

Movement of scavengers

The presence of the carcass led to an increase of the mean number of great black-backed gulls, juvenile gulls, ravens and lesser black-backed gulls flying over the study area after the start of the experiment (Figure 2.2). In the control area the great black-backed and juvenile gulls together with ravens also increased their visits after the carcass became available, but there was a decrease in the presence of lesser black-backed and herring gulls.

No best fitting model carried out for each group of birds showed a statistically significant interaction between Area and Period (Appendix A.4). In particular, the distribution of great black-backed gulls was explained by the variables Tide ($P = 0.0296$), Area ($P < 0.0001$) and Period ($P = 0.0003$), whereas the number of herring gulls varied according to the Tide ($P = 0.0001$). The fitted models for the other groups of birds did not have significant terms (Appendix A.4).

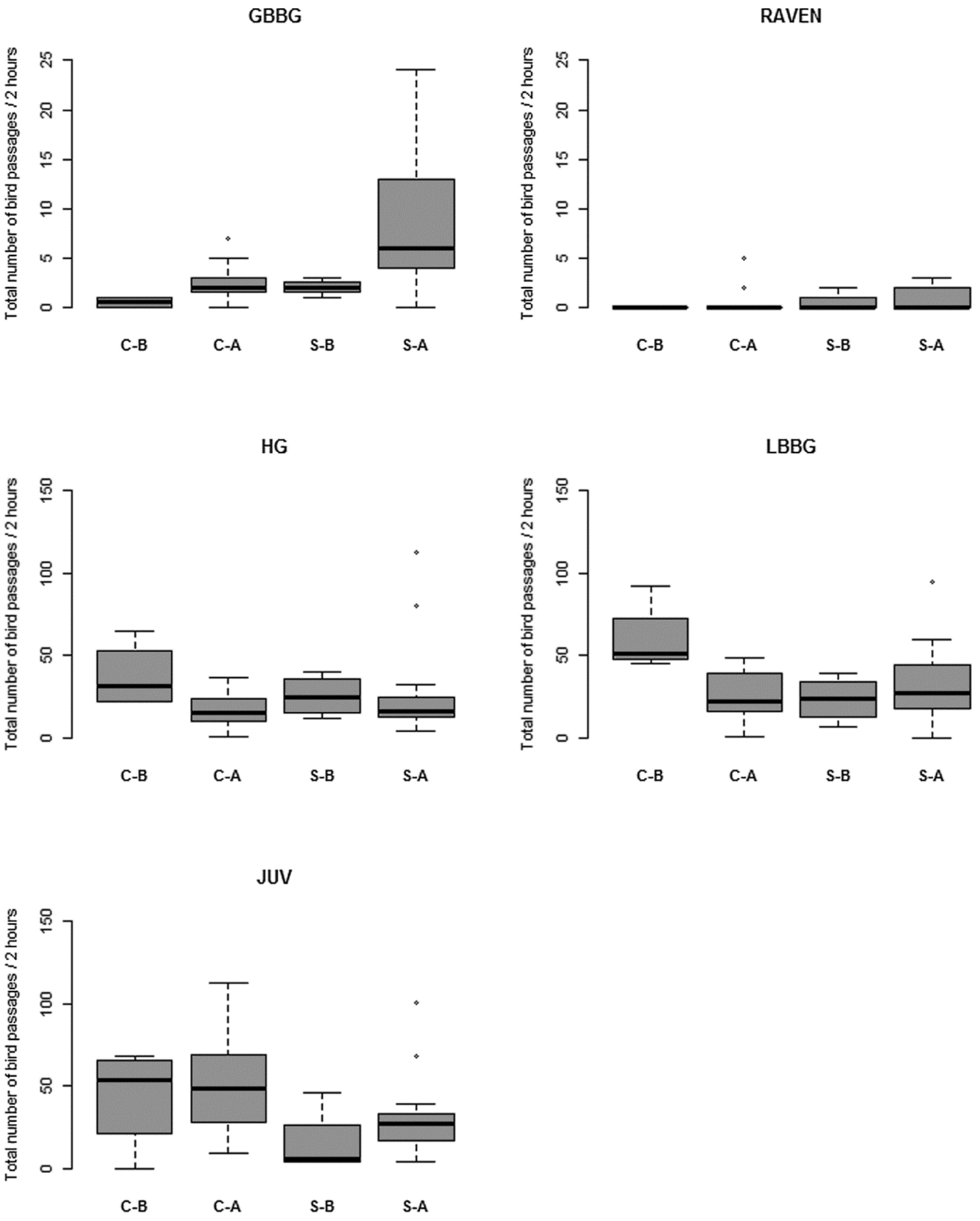

Figure 2.2 Total number of bird passages per 2 hour count.

Great black backed-gulls (GBBG), ravens (RAVEN) , herring gulls (HG), lesser black-backed gulls (LBBG) and juvenile gulls (JUV) in the control (C) and study (S) areas before (B) and after (A) the deployment of the carcass in the study site. On each box, the central mark is the median, the edges of the box are the lower hinge (25th percentile) and the upper hinge (75th percentile), the whiskers extend to the maximum and minimum data points, outliers are plotted individually.

Scavenging activity

Great black-backed gulls, herring gulls, juvenile gulls and ravens, but not adult lesser black-backed gulls, all scavenged the seal carcass (Figure 2.3). Juveniles spent more time at the carcass in comparison to the other group of birds for a total of 237.63 hours, both feeding (51.1%) and non-feeding (mins day^{-1}; Table 2.1). The second most frequent visitors were great black-backed gulls which spent a total of 41.02 hours on the carcass and actively scavenged for 81.4% of this time. Ravens made infrequent visits, spending 11.43 hours around the carcass and were feeding for 66.5% of the time. Herring gulls were rarely seen scavenging on the dead seal (20.8% of a total of 2.88 hours), spending most of the time attending the scene without participating. Adult lesser black-backed gulls did not scavenge the carcass and their presence occurred for a total of only 15 minutes. They were excluded from the subsequent analyses. The highest mean maximum number of individuals observed at the carcass at one time was observed in the juveniles. The latter were also the most frequent visitors of the experimental area, followed by great black-backed gulls, ravens and finally herring gulls (Table 2.1; images of scavenging birds in Figure 2.3). The absolute feeding times were compared between groups of birds and the great black-backed gulls scavenged more than the ravens (Tukey contrasts test, $P = 0.0116$), but less than the juvenile gulls ($P = 0.0383$). All the other comparisons between groups of birds were highly significant ($P < 0.001$).

Table 2.1 Daily means of feeding time, non-feeding time, number of visits and MaxN for groups of birds.

Means and standard errors (SE) are presented in minutes. GBBG = great black-backed gulls, HG = herring gulls, LBBG = lesser black-backed gulls, juvenile gulls and ravens.

	Adult gulls			Juvenile gulls	Ravens
	GBBG	**HG**	**LBBG**		
Feeding time day^{-1} (mins)	47.95	0.85	0	173.52	10.85
(SE)	(11.58)	(0.43)	(0)	(23.4)	(3.25)
Non-feeding time day^{-1} (mins)	10.93	3.27	0.37	165.98	5.48
(SE)	(2.45)	(1.25)	(0.25)	(33.47)	(0.25)
Visits (n day^{-1})	3.17	0.50	0.12	11.29	1.69
(SE)	(0.54)	(0.16)	(0.08)	(1.58)	(0.42)
Mean MaxN day^{-1}	0.86	0.33	0.07	1.83	0.67
(SE)	(0.009)	(0.07)	(0.04)	(0.18)	(0.12)

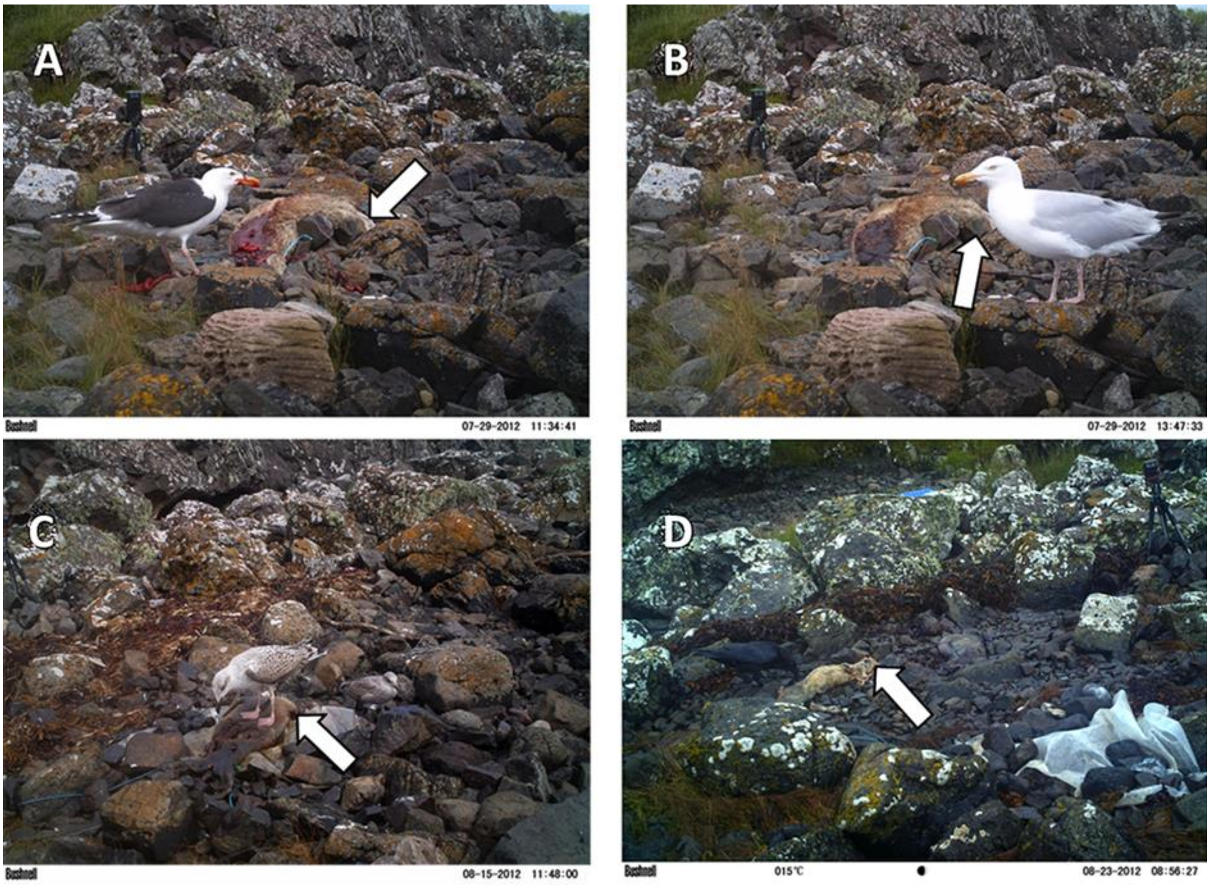

Figure 2.3 Avian scavengers occurring in the terrestrial experiment.

A white arrow indicates the seal’s head. A) Great black-backed gull pulling out the internal organs of the carcass (day 3); B) Herring gull visiting the study area (day 3); C) Two juvenile gulls (day 21); D) Raven feeding on the carcass at a late stage of consumption and decomposition (day 29).

Temporal pattern in the feeding activity of different groups of birds was observed during the experiment (Figure 2.4) and temporal clusters were detected at different times for different groups: the great black-backed gulls opened the carcass the day following its deployment (27/07) and contributed to the dismantling of the carcass for a temporal cluster of 11 days (interval time 27/07 – 06/08; P = 0.0001). Juveniles were the most common for a long period after the decrease in visits by great black-backed gulls (interval time 13-27/08; P = 0.0001). Ravens were active mostly in the final stage of consumption (interval time 23-31/08; P = 0.0001). Herring gulls visited the carcass forming the shortest time cluster (interval time 9-16/08; P = 0.0001) between great black-backed gulls and juveniles. The mass of the carcass decreased from 25.00 to 1.83 kg, resulting in an estimated daily mass loss of 0.56 kg.

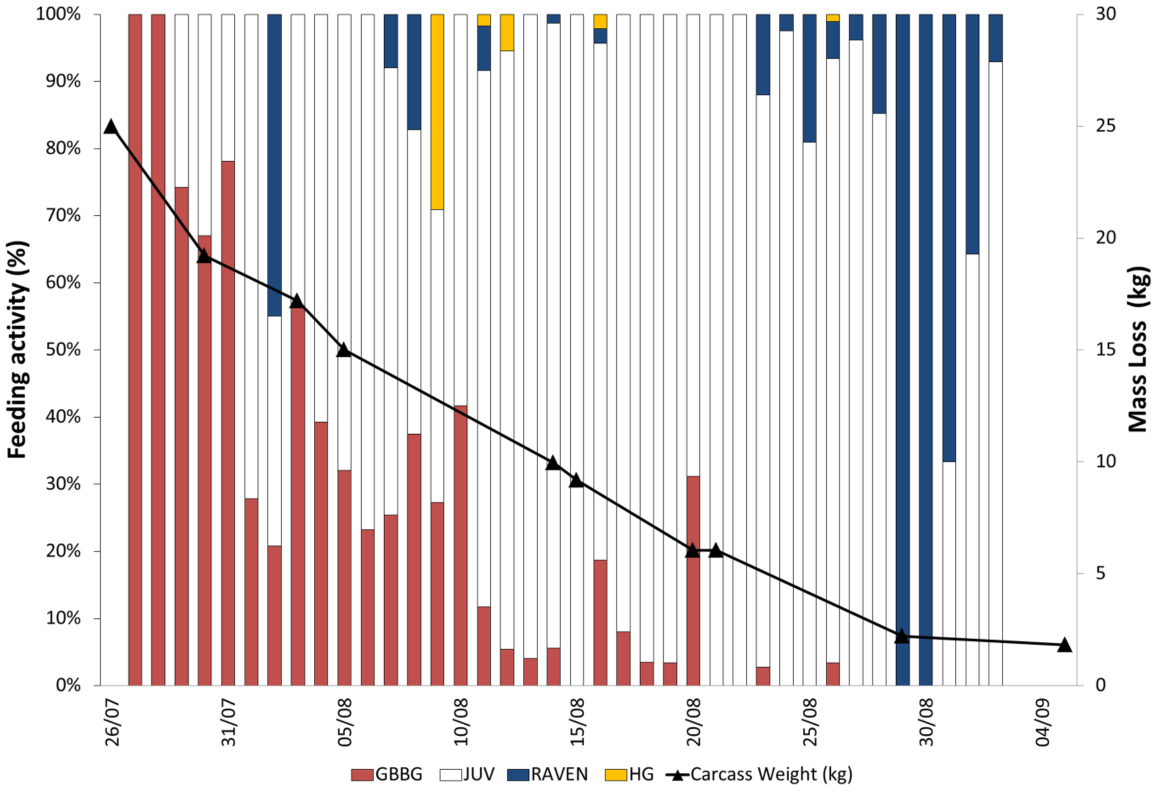

Figure 2.4 Daily feeding activity (percentage) of groups of birds.

Great black-backed gulls (GBBG, red), juvenile gulls (JUV, white), ravens (blue) and herring gulls (HG, yellow). Mass loss of the carcass (black ▲).

Great black-backed gulls (pairwise Wilcox Mann-Whitney test, P = 0.0017), juvenile gulls (P = 0.0005) and ravens (P = 0.0028) showed significantly higher proportion of feeding time than herring gulls.

2.4.2 Underwater experiment

Temperature and daylight hours

The daily seawater temperature ranged from 14.8°C to 17.0°C during the first survey period in August and 12.0°C to 13.0°C during the second period in September. The mean daily seawater temperature for the month of August was 15.3°C (SD = 0.81) and for September was 13.2°C (SD = 0.87). The daylight hours ranged from 16.03 to 13.90 hours in August and from 13.82 to 11.62 hours in September.

Consumption and decomposition of the carcass

Within five days from the start of the experiment the eye of the carcass was scavenged (Figure 2.5A). A large wound appeared on the front left flipper at day 10 (Figure 2.5B) and another one of smaller size on the top of the shoulder at the day 13. After three days (day 15) the nose was bitten, the mouth opened, showing the teeth and the abrasion around the eye enlarged. Several whitish patches also developed on the fur which broadens in the following days to cover all visible areas of the body surface. Furthermore, the seal’s head appeared to have risen a few centimetres from the base of the structure suggesting that the carcass was positively buoyant (Figure 2.5C). At the beginning of the second period of monitoring the carcass was still in this floating state showing a more advanced stage of decomposition (at day 48 of submersion). The body appeared white and covered by new greyish patches; the head was damaged exposing the facial bones, and the jaws were still attached (Figure 2.5D). At day 54 (end of the camera recording) several sections of epidermis with fur had detached denuding small areas of exposed dermis. When recovered (day 78), the carcass was barely recognisable: it was still positive buoyant, even if flattened, and presented exposed bones of the neck and pelvic. The whole body was covered by a thick grey layer of bacteria. The mass of the carcass at the end of the experiment was 14.45 kg, resulting in a total reduction of 5.25 kg and an estimated daily mass loss of 0.07 kg.

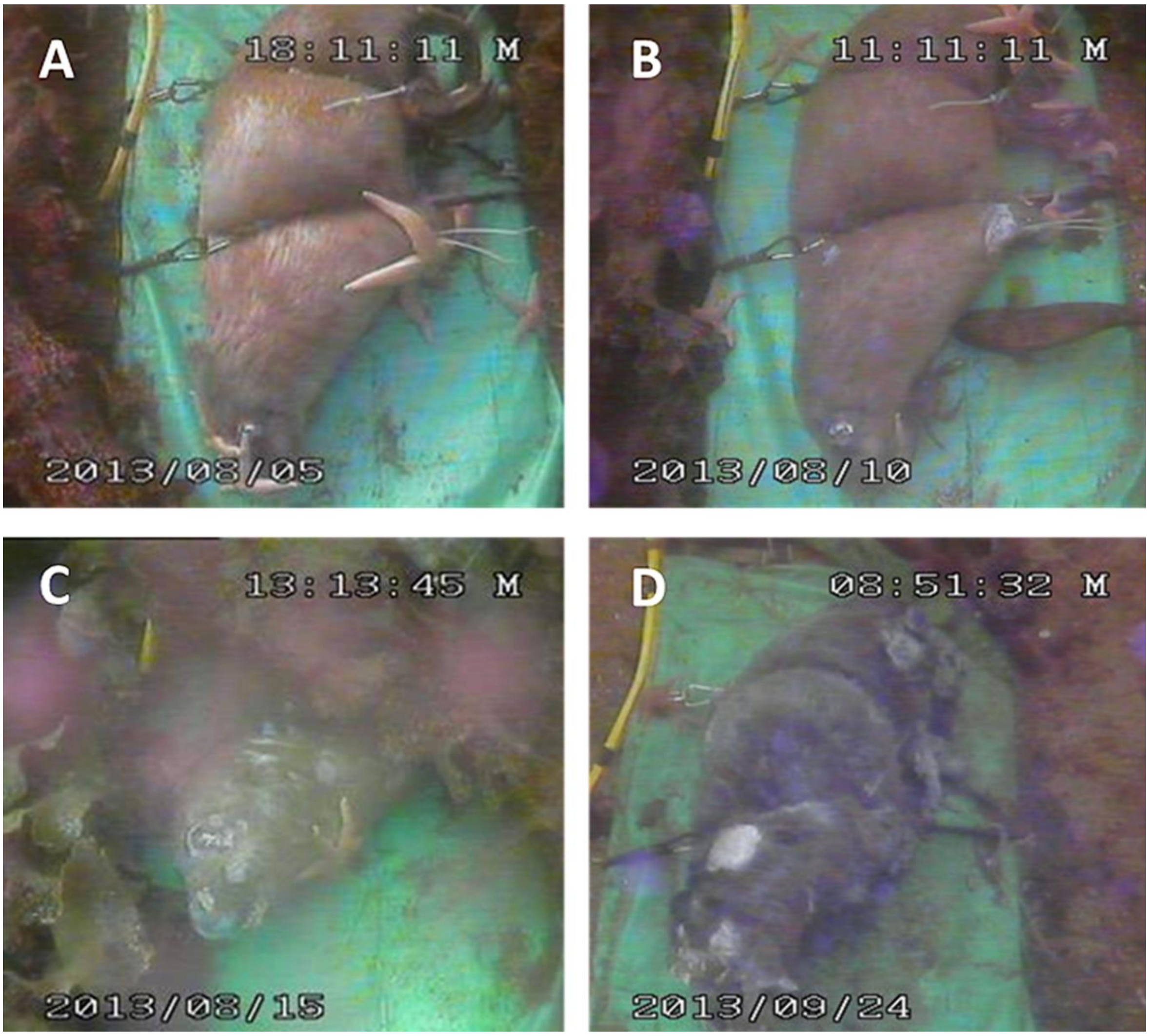

Figure 2.5 Underwater experiment at different stages of consumption and decomposition of the carcass.

A) The carcass shows a scavenged eye; starfish are feeding on it (day 5); B) A large wound appears on the front left flipper; a labrid, a crab and few starfish are present (day 10); C) The carcass shows positive buoyancy and several whitish patches; kelp is partially covering the dead seal (day 15); D) The carcass is at a late stage of decomposition and epidermis with fur detaches, bones are exposed on the area of the face (day 48).

Scavenging activity

Generally the carcass was visited by members of the phyla Mollusca, Arthropoda, Echinodermata and the subphylum Vertebrata. In total 4 phyla, 5 classes, 9 orders, 14 families and 16 species were identified (Table 2.2).

Table 2.2 Systematic classification of marine organisms occurring on the carcass.

For each species feeding guilds has been assigned: C = carnivore, D = detritivores, O = omnivore, Op = opportunistic, P = predator, S = scavenger, SF = suspension feeder.

Phylum	Class	Order	Family	Species	Feeding guild
Mollusca	Gastropoda	Neogastropoda	Muricidae	*Nucella lapillus*	O-P-S
	Bivalvia	Pectinoidea	Pectinidae	*Pecten maximus*	SF
Arthropoda	Malacostraca	Decapoda	Paguridae	*Pagurus bernhardus*	P-S
			Cancridae	*Cancer pagurus*	O-P-S
			Portunidae	*Carcinus maenas*	O-P-S
			Polybiidae	*Necora puber*	O- P
				Liocarcinus depurator	C-P
Echinodermata	Asteroidea	Forcipulatida	Asteriidae	*Asterias rubens*	C-S
				Marthasterias glacialis	P-S
Chordata	Actinopterygii	Gadiformes	Gadidae	*Pollachius virens*	P
				Pollachius pollachius	P
		Perciformes	Labridae	*Symphodus melops*	O -P
				Labrus mixtus	P
			Blenniidae		D - Op
			Gobidae		O
			Pholidae	*Pholis gunnellus*	P
		Pleuronectiformes	Pleuronectidae	*Limanda sp.*	P
		Syngnathiformes	Syngnathidae	*Syngnathus acus*	P
Tot **4**	**5**	**9**	**14**	**16**	

In the first period *Asterias rubens* belonging to the class Asteroidea (starfish) was the most common scavenger (mean MaxN = 11.03, SE = 0.72) followed by the classes Actinopterygii (fish; mean MaxN = 9.14, se = 1.16) and Malacostraca (crabs; mean MaxN=1.53, SE = 0.14) (Figure 2.6-1). The dog whelk *Nucella lapillus* was rarely observed and never more than one individual per time. The Atlantic scallop *Pecten maximus* was also observed in the video, however, its visits were probably coincidental. Starfish exhibited feeding preference on the head and on the areas of the joints. Some individuals were seen disappearing under the carcass and during the second period of monitoring a specimen was partly hidden in the eye cavity. Crabs scavenged in the same areas of starfish when accessible. Individual fish or schools were recorded, but particular behaviours were also noted: an adult of the family Labridae was seen interacting with the carcass by spitting its food on it, while the saithe *Pollachius virens* and the pollack *P. pollachius* were observed scraping their bodies on the surface of the carcass. During the night, a few individuals of *Pholis gunnellus* were seen around the carcass and sometimes attached to it pushing their heads on it. Agonistic interactions were only observed during the first period and involved intra- and inter-class events between two crabs (N = 4), a crab and starfish (N = 4), two starfishes (N = 2) and a crab and fish (N = 1). *C. pagurus* successfully forced several starfish to abandon the carcass by moving them with its claws. Only once was a starfish seen to force a crab to move away. In the second period the maximum number of asteroids reduced drastically (mean MaxN = 1.13, SE = 0.22) together with fish (mean MaxN = 2.8, SE = 0.81), while the relative abundance of crustaceans showed no obvious change (mean MaxN = 1.26, SE = 0.15) (Figure 2.6-2).

The best model describing the maximum number (MaxN) of organisms occurring on the carcass explained 22.84% of the deviance from the null model (likelihood ratio test: X^2 (df = 8) = 464.89, P < 0.001). It included the variables Period (P < 0.0001), Time (P = 0.0002), Class (P < 0.0001) and the interactions between Period and Class (P < 0.0001) and Time and Class (P = 0.0012), and excluded the remaining interactions (Appendix A.5).

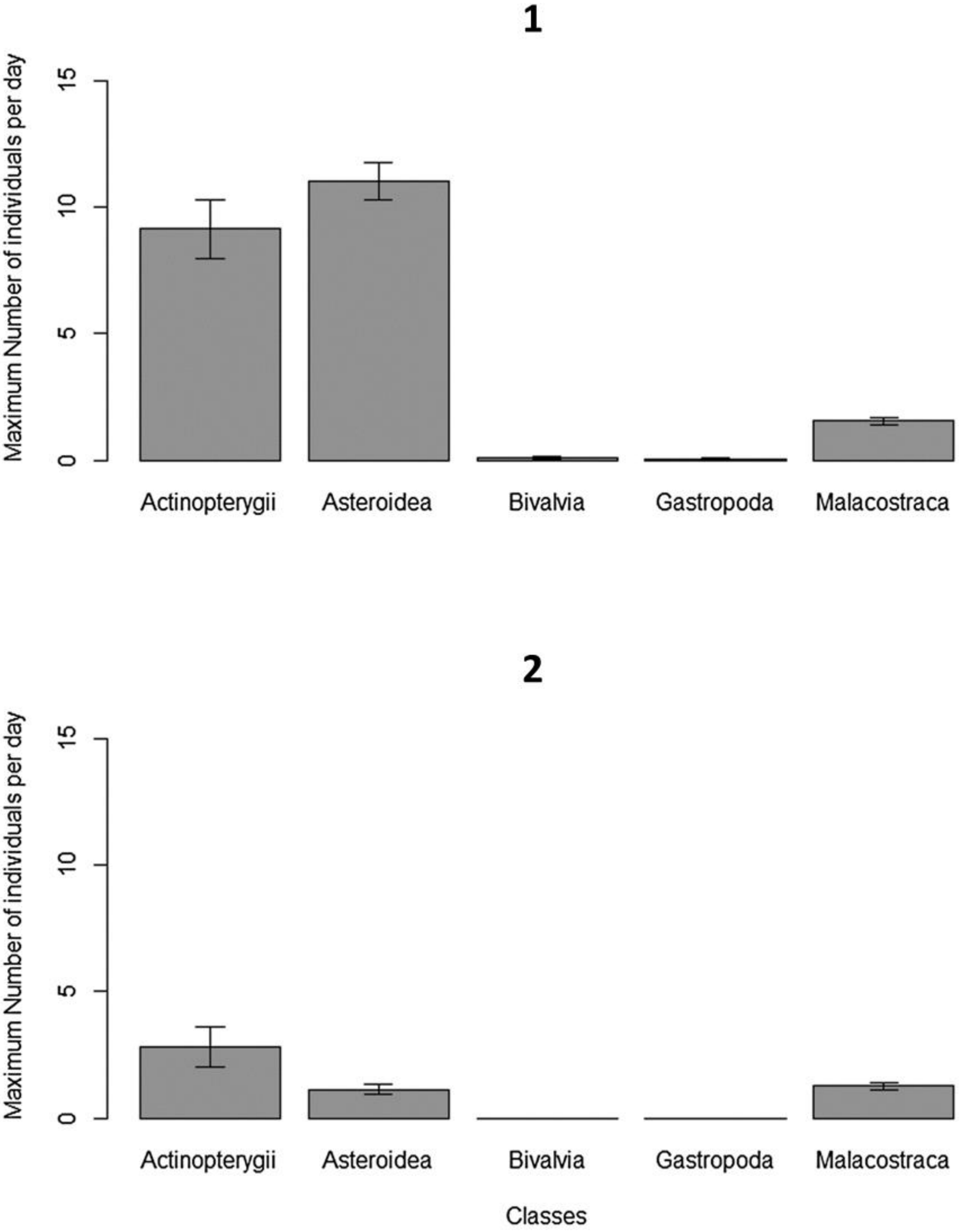

Figure 2.6 Maximum number of individuals (MaxN) for the observed classes in the two periods of monitoring (Period 1 and 2).

On each bar, the top of the bar is the mean of the MaxN day^{-1}, error bars are ± SE.

Crustaceans visited the carcass more often during the first stage of the experiment with 14.64 (SE = 2.45) and 8.33 (SE = 1.41) mean visits per day during the first and second periods, respectively. The proportion of visits of crabs in the first period of monitoring was significantly higher during night than during day (pairwise Wilcox Mann-Whitney test, P = 0.0001), while in the second period there was no difference (P = 0.61) (Figure 2.7).

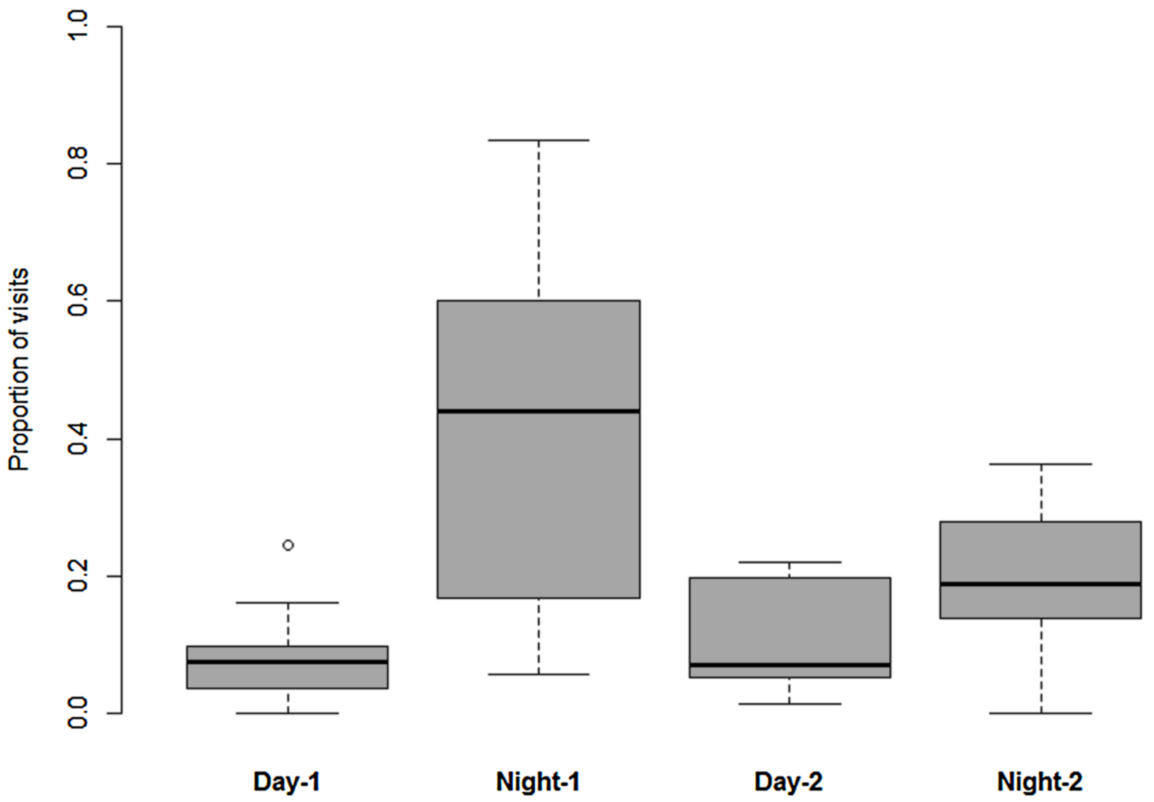

Figure 2.7 Proportions of presence of malacostracans during day and night in the two periods of monitoring.

On each box, the central mark is the median, the edges of the box are the lower hinge (25th percentile) and the upper hinge (75th percentile), the whiskers extend to the maximum and minimum data points, outliers are plotted individually.

2.5 Discussion

The present study represents the first detailed observations on scavengers feeding on pinniped carrion in both the terrestrial and marine systems: so far no study explored differences in carrion consumption between the two ecosystems

(Beasley et al. 2012). Existing literature concerning scavenging on seals consists mainly of singular opportunistic observations, as in the case of the red fox (*Vulpes vulpes*) and the southern giant petrel (*Macronectes giganteus*), seen feeding on dead seals around the colony (Culloch 2012) and in submerged conditions (Van den Hoff and Newbery 2006), respectively. Bruyn and Cooper (2005), instead, focused on inter- and intraspecific behaviour of southern and northern giant (*Macronectes halli*) petrels feeding on a southern elephant seal carcass, but for a limited time (150 and minutes). From stable isotope analyses seal carrion was found to be part of the diet of giant petrels (Forero et al. 2005) and without clear evidences also of Arctic foxes (*Vulpes lagopus*) (Roth 2002). Scat analyses combined with behavioural observations showed that seal carrion is also consumed by brown hyenas (*Hyaena brunnea*) on the Namibian coast (Kuhn et al. 2008). However, there are no studies investigating the patterns and processes involving these scavengers as part of a wider scavenging community and their interactions within it.

In Scotland, grey seal strandings represent the greatest source of carrion in comparison to other marine mammals (SRUC 2015, see Chapter 1). This species therefore is likely to represent a relevant source of carrion inputs for the coastal ecosystem and its scavengers.

2.5.1 Terrestrial experiment

This experiment described how scavenging seabirds dismantle a marine mammal carcass: eyes were the first body regions consumed and feeding at the umbilicus was the most accessible way for scavengers to open the carcass. Secondary openings appeared to arise as a result of longer pecking activity on the carcass. Pavés et al. (2008) have described how vultures first feed on the eyes of dead sea lion pups and adults, and then the naval, genitals and anus. However, as scavenging and decomposition occur simultaneously, it was not possible to separately measure each of the two processes. It is likely that the carcass was influenced by temperature and moisture levels, which strongly affect the decomposition rate (Barton et al. 2013b). The carcass was also consumed by invertebrate scavengers, where the colonization by fly larvae contributed to the liquefaction of the tissues (Putman 1983).

Results did not show a significant change in seabird passage in the study area compared to the control site after the deployment of the carcass. This can be related to the infrequency of this resource for the scavenging birds of Little Cumbrae, but also by the little interest showed by some species such as the lesser black-backed gull and the herring gull. An increase in the number of passages of the great black-backed gull after the deployment of the dead seal was, instead, observed, but in both areas. The effect of a predictable resource on seabird foraging has been suggested also in other studies: Cama et al. (2012) identified the high density of vessels providing fishing discards as the best explanatory variable for the distribution of gulls in the Western Mediterranean. Monsarrat et al. (2013), instead, observed that vultures also restricted their searching home range around artificially-maintained feeding stations when weather conditions were not optimal or food was scarce.

A defined temporal succession of scavenging birds feeding on the carcass was observed, in which segregation of different groups of birds was possibly related to competition owed to overlap in resource utilisation. The great black-backed gull was the first to approach the carcass and was able to break through the thick skin of the carcass. As described by Camphuysen et al. (1995), it is a “powerful scavenger”, which out-competes the herring gull for food when the two species share the same breeding site (Rome and Ellis 2004). In fact, despite being the most abundant species, the herring and lesser black-backed gulls seldom visited the carcass and rarely exploited it, even though they are both known to scavenge in other contexts (Camphuysen et al. 1995; Catchpole et al. 2006). During summer, Little Cumbrae is a breeding site for the three gull species with nesting occurring around mid- April and the first chicks hatching in May (Cramp et al. 1974). The numerous juveniles visiting the carcass may have been part of the new generation of gulls from the island. They were not observed early in the study during the dominance of the great black-backed gull on the carcass. Moreover, they spent a similar proportion between their active and inactive time at the carcass, possibly because of the lack of experience and the unfamiliarity with this food source. Seal carrion is a fairly uncommon resource outside of seal colonies (Culloch 2012) and juvenile gulls were unlikely to have previously encountered this food type. During the study period a natural seal carcass washed up on Great Cumbrae (personal observation), so such events clearly occur in this area. Despite being active carrion feeders (Heinrich 1988), ravens scavenged more consistently from day 30 onwards. It is likely that the ravens were unable to feed at the same time as the great black-backed gulls or juveniles, as found by Hewson (1995). In this study the mass loss of the carcass was approximately linear. Although the single sample prevents any meaningful statistical comparison, a carcass mass loss has previously been shown to follow a sigmoidal decrease with time, being initially untouched, but then being dismantled quickly (Putman, 1983; Carter et al., 2007). In the current experiment, instead, the carcass was detected almost immediately (on day 2 after the deployment) and consumed at a constant rate during time. On the final days the consumption rate decreased possibly due to the low availability of edible material left. The deterrent effect of decomposing matter and toxin production on the behaviour of terrestrial scavengers (DeVault et al. 2004; Selva et al. 2005; Parmenter and Macmahon 2009) was not observed, as the carcass was not abandoned prior to complete consumption.

2.5.2 Underwater experiment

The present experiment represents one of the few existing studies on the successional pattern of scavenging on carrion in the subtidal marine environment. Forensic science has paid attention to this subject before: Hobischak and Anderson (2002), for instance, examined the species and sequence of invertebrates associated with carrion, but in fresh water, whereas Anderson and Hobischak (2004) described which scavengers occur on experimental pig carcasses submerged in marine waters.

Results showed that abundance of scavengers attracted to the carcass changed during time. This suggests that temporal variation in the extent of exploitation of carrion by different scavengers exists. In the first period the scavenging community was dominated by asteroids which occurred in great number (up to 17 individuals) to colonize the carcass. *A. rubens* is one of the most abundant scavenging species found in fishery discards in the west of Scotland (Bergmann et al. 2002). Moreover, the experimental area was in the ideal habitat for this sublittoral species which prefers sandy, muddy substrates. The occurrence of adult and juvenile fish, obviously not observed feeding on the carcass, could be linked to shallow coastal waters which may offer protection from predation, in particular to new recruitment of juvenile gadoids during summer (Pihl 1982). Decapods exhibited nocturnal habits mostly in the first period, while they showed less preference for the dark during the second period, probably due to the reduction of daylight hours towards the autumn and in the number of starfish. Generally crabs are nocturnal predators with peaks of activity during high tide, like *C. pagurus* (Skajaa et al. 1998) and *C. maenas* (Naylor, 1958; Ropes, 1968), but they can also be diurnal (Novak 2004). In accordance with other studies focusing on scavenging aggregations on fishery discards in the Irish, Clyde and Adriatic Seas, *L. depurator* was the most abundant among all the other brachyuran scavengers (Ramsay et al. 1997a; Ramsay et al. 1998; Wieczorek et al. 1999). The infrequent visits of dogwhelks *N. lapillus* could be related to the fact that its seasonal peak in abundance occurs between April and June (Nickell and Moore 1992).

At the second stage of the experiment the carcass showed an increase of what appeared to be microbial mat covering its surface and even if the number of crabs stayed stable, a drastic drop in the number of asteroids together with the number of fish occurred. Also Burkepile et al (2006) found that crabs still scavenge on aged fish carrion. Bacteria use chemicals to compete against other microbes, but these chemicals can also act as a deterrent from carrion for animal scavengers (Burkepile et al. 2006). Scavenging marine organisms detect prey by olfactory foraging cues and different taxa have specific chemo-sensitivity according to the olfactory organ (e.g. Morton and Yuen, 2000; Tran et al., 2014). Therefore, the bacterial action is likely to be an important biotic factor influencing the post-mortem fate of a carcass in aquatic contexts. Burkepile et al. (2006) demonstrated that scavengers were 2.6 times more attracted by fresh carrion than microbe-laden carcasses. However, different species of crabs reacted differently, suggesting that species specific palatability exists. The present study focused on the scavenging mega-faunal succession on carrion, but it was evident that bacterial decomposers also benefited from it, taking part in the recycling of carrion. Dickson et al. (2011) described five different phases of bacterial colonisation on partial carrion proving that the rate at which successive stages appeared was temperature dependent with warmer waters allowing a faster decomposition. Therefore, seasonal changes in sea water temperature could underlie differences in the duration of successive decay stages dominated by either marine animals or bacteria.

The floating stage of carcass generally occurs when bacteria start to produce gas inside the body (Reisdorf et al. 2012). In the current study the appearance of microbes on the body’s surfaces coincided with the carcass becoming positively buoyant; a state which lasted until the end of the experiment. Carrion has two floating stages: the primary floatation is due to gas forming in the digestive tract, while the secondary floatation depends on bacterial activity within the corps (Teather 1994). Owing to the unknown post-mortem age of the experimental carcass and its frozen conditions before the deployment, it is very likely that secondary floatation would occur if the carcass had not been tethered. Putrefaction gases are likely to cause the surfacing of the carcass in shallow waters at temperature above 4°C (Moreno et al. 1992; Sorg et al. 1997; Petrik et al. 2004), whereas negative buoyancy is expected when carcass integrity is compromised (Anderson and Hobischak 2004). However, floating marine mammal carcasses may be exposed to scavenging birds when reaching the water surface and even mammals when stranded on the beach. For example, Hewson (1995) observed great black-backed gulls defending floating carrion and pulling it to shallow water for consumption. This process may cause the carcass to sink quickly back to the seabed making it available again to the marine community. The two periods of recording may then approximate the seabed phases in the cycle of floating and sinking that occurs with natural carcasses in the marine environment.

One other experiment carried out underwater observations and, similarly to the present study, the marine mammal carcasses were constrained to the seabed by using ropes during the period of monitoring (Glover et al. 2010). Thus, the floatation and natural drift of the carcasses were impeded. Glover et al. (2010), in fact, observed the first floating state of an experimental *Phocoena phocoena* for two days after implantation at 30m depth, but argued that negative buoyant carcasses are likely to occur at this depth. Pup carcasses are also likely to be found in shallow waters: during pupping season, for instance, a certain amount of dead pups may enter the marine system without reaching higher depths because trapped among rocks or sunk to the seabed. It is possible, in fact, that most of the carcasses provided during the grey seal pupping season are negative buoyant as the major cause of death is starvation (Baily 2014) which deprives the pups of blubber.

2.5.3 Comparison between terrestrial and marine experiments

Comparing the scavenging processes observed in the two experiments, it is clear that the daily mass loss of carrion was lower in the marine ecosystem than in the terrestrial one, with a ratio of 1:8. This could be in part due to the larger size of terrestrial scavengers and their endothermic nature in comparison to their marine counterparts which permitted a faster consumption rate of the carcass. Generally, at deeper depths (1200-1800), bathyal scavenger assemblages remove tissue from whale carcasses at rates of 40–60 kg day^{-1} (Smith and Baco 2003). However, the scavengers involved are not only invertebrates, as observed in the current study, but also large vertebrates such as sleeper sharks, hagfish and grenadiers which aggregate in large numbers to remove the soft tissue of the whale carcass. This process can last from months to years and involved mostly obligate scavengers. Together with the scavenger community, it was suggested that the size of the carcass is a factor determining the rate of its consumption. In fact, at the same depth, smaller cetacean carcasses were eaten at a lower rate (1.2 - 9.6 kg day^{-1}) than the whale falls (Jones et al. 1998; Smith and Baco 2003). Also on land larger carcasses (>100 kg) were found to be consumed 33 times faster than smaller ones (<10 kg) (Moleón et al. 2015). However, specialised scavengers may accelerate the process.

Changes in the scavenging community were detected over the duration of both experiments. On land, a hierarchical succession of dominant scavengers through competitive displacement of subordinates occurred during the exploitation of the carcass. Underwater, instead, a change in the numbers of scavengers between the two periods of monitoring might be caused by the deterrent effect of the microbial mat formed on the dead pup on starfish rather than crabs.

2.5.4 Future studies and implications

The terrestrial experiment provides a long term and continuous dataset from the initial to the final stage of seal carcass consumption on land. Several studies have continuously monitored carcasses in terrestrial ecosystems until the total consumption of the carcass (Blázquez et al. 2009; Sebastián-González et al. 2013; Huang et al. 2014; Moleón et al. 2015; Sebastián-González et al. 2016), but only few in the coastal system (e.g. Schlacher et al 2013). There is only one study of this type using marine mammal carrion in the terrestrial ecosystem that we are aware of (Pavés et al. 2008). The underwater experiment is one of the few existing studies on the succession of marine scavengers exploiting carrion in shallow waters (e.g. Anderson and Hobischak, 2004; Glover and Higgs, 2010). However, the long-term nature of the experiment and the technical constraints limited the collection of a continuous dataset. Similar complications have been encountered also in other studies (e.g. Anderson and Hobischak, 2004).

Further investigations are needed to assess the value of this food resource as energy and biomass inputs released to the ecosystem and its impact on the scavenging community. Coastal regions are, in fact, often affected by marine-derived inputs (Polis and Hurd 1996a; Polis and Hurd 1996b; Polis et al. 1997; Rose and Polis 1998) whose effects on the receiving ecosystem include alteration of trophic species dynamics (Polis et al. 1997, Briggs et al. 2012) and their distribution (Monsarrat et al. 2013). In particular, bird and marine mammal carrion is frequently deposited ashore because of large scale or seasonal weather perturbations, especially in areas where these animals live (Bodkin and Jameson, 1991). Despite the limited number of experimental carcasses used, this novel study brings new insights to our understanding of the ecological process involving the exploitation of pinniped carrion by coastal scavengers.

Marine mammal carrion could increasingly become an important part of the diet of European scavengers, partly because of the continual increase in grey seal pup production since the 1960s (SCOS 2013), but also because of regulations banning fish discards by pelagic and then demersal fishing operations (EU Regulation 1830/2013). Catchpole et al. (2006) estimated the partitioning of discards between marine and aerial scavengers based on the English *Nephrops norvegivcus* fisheries. The resulting bioenergetic model showed that 57% of discards was taken by seabirds with the remainder becoming available to marine fauna. The total amount of biomass and energy released were 4780 t and 19.7 x 10^9 kJ respectively (Catchpole et al. 2006). Considering the high usage of fishery discards by scavengers, it is uncertain what repercussions the reformed Common Fisheries Policies will have to the foraging behaviour of scavengers. The discard ban came into force on 1st January 2014 and will gradually require EU fishing vessels to land all of their catches (http://www.scotland.gov.uk). Accordingly, a recent publication by Heath et al. (2014) suggested that the discard ban may cause a bottom-up trophic cascade which will lead to a reduction in biomass of scavengers such as benthic invertebrates and birds. At this point other sources of carrion, such as pinniped carcasses, could represent an important alternative resource for scavengers and understanding their impact on the ecology of these species will become necessary.

Chapter 3: The role of a pinniped colony in the provision of carrion as a predictable resource for coastal systems

3.1 Abstract

Seal carrion is a pulsed resource of marine-derived nutrients provided by seal colonies to the coastal ecosystem in the shape of afterbirths and dead seals. When food is predictable, animals can respond to its temporal and spatial occurrence, but also its magnitude and energy value. This project aimed to define the resource of seal carrion occurring at the grey seal (*Halichoerus grypus*) colony on the Isle of May (Scotland, UK) in terms of predictability, evaluating its variability in time and space, as well as its quantity and quality. Data collected by aerial survey (11 years) and ground visual census (3 years) were used to evaluate the timing of the pupping season, quantifying the biomass and energy released by carrion and its spatial distribution. Each year an average of 6,893 kg corresponding to a 110.5 x 10^3 MJ was released for potential scavengers as placentae and dead seals, equivalent to 42,000 x gull daily rations. This study found that 32.5% of the total edible biomass from dead seals was consumed by the end of the pupping season mostlyby avian scavengers such as great black-backed gulls (*Larus marinus*). Distribution and clustering of carcasses were similar across different pupping seasons, and 28% of the total area presenting carcasses with a density higher than 0.001 carcasses m^{-2} was shared among all years. Seal carrion availability varied between pupping seasons and this was expressed as a percentage of relative standard errors (RSE%). For all measures of spatial and temporal variability the RSE% was below 34%, similarly to other resources, such as salmon runs, which appear to be predicted by consumers.

3.2 Introduction

Ecosystems are spatially connected by flows of nutrients and energy, which provide resource subsidies for consumers belonging to disparate trophic levels (Polis et al. 1997; Power and Rainey 2000; Reiners and Driese 2001). These resources can have an impact on the receiving habitat, both altering dynamics of consumers and regulating the flows of nutrients in the ecosystem (Marcarelli et al. 2011). Coastal regions are often affected by marine-derived inputs transferred from the ocean to the terrestrial ecosystem, and vice versa (Polis and Hurd 1996a; Polis and Hurd 1996b; Polis et al. 1997; Rose and Polis 1998), by abiotic factors such as marine currents, air circulation and weather conditions, which are responsible for the upwelling of nutrients (Field et al. 1980; Cury and Roy 1989) or strandings of plant detritus and carrion on the shore (Polis et al. 1996). Such marine resources can be responsible for aggregations of terrestrial animals to the coast (e.g. Polis and Hurd 1995; Rose and Polis 1998) and for local increases in the number of invertebrate consumers (e.g. Janetski et al. 2009; Spiller et al. 2010). However, before evaluating the impact of a resource on the ecosystem, it is essential to consider an appropriate scale, e.g. vultures and beetles, even if both scavengers, relate to the environment at different scales according to their mobility and activity (Wiens 1989).

In addition to the abiotic transfer of resources, animals can also transport marine nutrients and deliver them 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) have already been shown to play a fundamental role in this process affecting different components of the ecosystem. Salmon carrion for instance enriches soils and plants locally releasing nutrients (e.g. Quinn et al. 2009; Hocking and Reimchen 2009) and if the input is predictable the impact can be long term (e.g. Koyama et al. 2005) and the species composition of plants growing in that area change (Towne 2000; Barton et al. 2013a). Likewise, marine mammals affect coastal systems and their impact is substantial when they assemble in colonies for breeding. Empirical studies have demonstrated that high concentrations of ammonia and nitrate released by animal excreta are found in soil and plants growing in the vicinity of seabird and pinniped aggregations (Erskine et al. 1998; Farina et al. 2003). However, breeding colonies also provide other sources of nutrients in terms of food remains and carrion which are used either directly by above ground secondary consumers, or indirectly by increasing the input of nutrients (Anderson and Polis 1998). In sea lion colonies, for instance, onshore mortality is the second largest source of nutrients after defecation (Farina et al. 2003).

Carrion provided by salmon in spawning areas and seals at the breeding colonies are examples of seasonal pulses of biomass and energy released to the surrounding ecosystem and its local scavenging community. Being predictable, these subsidies are expect to influence the behaviour of their consumers (Overington and Lefebvre 2011). Predictability of resource subsidies is in fact an important concept applied to many ecological processes, but how is it explained? Colwell (1974) was one of the first to describe the *predictability* of an environment measuring environmental variation by using constancy and contingency of a phenomenon (temporally uniform and seasonal occurrence). More recently, instead, Yang et al. (2008) described the main features of a predictable resource as low frequency, large magnitude and short duration. Often the attribute ‘predictable’ is given to a particular food input when it induces some response by consumers at a population level (Polis et al. 1996) such as changes in behaviour, ecology and adaptation (Overington and Lefebvre 2011). There are, in fact, several examples in the literature focusing on the impact on the ecosystem caused by the predictability of a food subsidy (e.g. Davenport 1995; Graham et al. 2006; Furness et al. 2007; Monsarrat et al. 2013; Oro et al. 2013). However, its definition is often not given.

Before appraising the ecological consequences of a subsidy to the trophic web, it is important to evaluate its quantity and its proportional quality in terms of energy released (Marcarelli et al. 2011). Energy is a decisive factor in regulating animal population dynamics: the reproductive success of individuals and sudden growth of a population are often related to the quality of food available (see White 2008). According to foraging theory, in addition to quantity and quality, previous knowledge of the locations and temporal occurrence of food inputs are used by animals to predict their appearance (Stephens and Krebs 1986). For example, female Savanna elephants (*Loxodonta africana*) adjust their timing of reproduction according to future seasonal pulses in vegetation productivity using past experience and reproductive history (Wittemyer et al. 2007). This behaviour induces these animals to time birthing with the high quality primary production peak occurring 22 months in the future, aiding reproductive success and subsequent population growth. Quantity, quality, timing and spatial distribution of a food resource are therefore the main features to be considered for defining its predictability. Moreover, considering that the predictability of an ecosystem is inversely related to the variation in its properties at a temporal and spatial scale (McGrady-Steed et al. 1997), the lower the variation of a resource in time, space, quantity and quality, the more predictable it is.

In this study, the predictability of seal carrion subsidy (placentae and dead seals) provided by one of the largest grey seal (*Halichoerus grypus*, Fabricius, 1791) colonies in the UK, located on the Isle of May, Scotland, during the seal pupping season was investigated. The seal carrion resource was predicted to show annual variability (expressed as percentage of relative standard errors, RSE%) of its timing, spatial distribution, biomass and energy available similar to other apparently predictable resources, such as the salmon aggregating in the spawning areas. The response of the local avian scavenging community to carrion was estimated in terms of biomass consumed at the end of the seal pupping season. Finally, the potential importance of seal carrion for the wider ecosystem will be explained.

3.3 Methods

3.3.1 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 is 1.8 km long and less than half a km wide, covering an area of 45 ha, with the long axis extending in a northwest-southeast direction (Figure 3.1). The Isle of May is a Special Area for Conservation (SAC) due to the breeding colony of grey seals.

The grey seal is believed to have bred on this island in the remote past, but there were no systematic records of grey seal pups until the 1950s, when three pups were born (Baker and Baker 1988). Thirty pups were counted in 1977 (Eggeling 1985) and approximately 300 pups only two years later (Harwood and Wylie 1987); in 1994 the number increased to 1408 pups born (Pomeroy et al. 2000), while 1766 pups were counted in 1999 (SMRU unpublished data). The grey seal colony of the Isle of May appears now stable and contributes approximately 4.3% to the annual UK pup production (in 2010, SCOS 2013); pup mortality is around 12.5% in the first month of life (Baker and Baker 1988).

The northern parts of the island, known collectively as Rona, are characterised by several pupping areas. Most pups are born here, which is mainly flat rock, in an area of about 6 ha. Historically, the sandy Silver Sand and West Rona Beach and the rocky Rona Rocks were the first areas to be colonised (Pomeroy et al., 2000), but more recently seals started also occupying the southern parts of Rona such as Rona Top and the rocky and tidal East Tarbet. As the population increased, new locations in the southern part of the Isle of May have been used: from the 1990s seals started to occupy the pebbly Pilgrim Haven and sandy Kirk Haven which are respectively on the south-west and south-east coast (Pomeroy et al., 2000). The latter are also characterised by having pups born later in the season than the main northern sites (Hiby et al. 1996). More recently, new individuals gathered in the Loan, Kaimes, Tennis Court and Cross Park (Figure 3.1). These are grass flat areas in the south of the island, separated from the sea by a rocky area not used by the grey seals. Most of the west and south-east coasts of the Isle of May are cliff-bound and unsuitable for breeding seals.

The main scavenger occurring in the island is the great black-backed gull (*Larus marinus*). After a steady increase from 20 pairs counted in 2002, 40 pairs of great black-backed gulls (*L. marinus*) were counted nesting during summer 2012 (SNH 2012). After the breeding season most of the great black-backed gulls remain in Scotland (although some move south to England, Ireland or the European mainland), and between October and March the Scottish population increases owing to the arrival of other gulls from Scandinavia and Russia (Forrester et al. 2007).

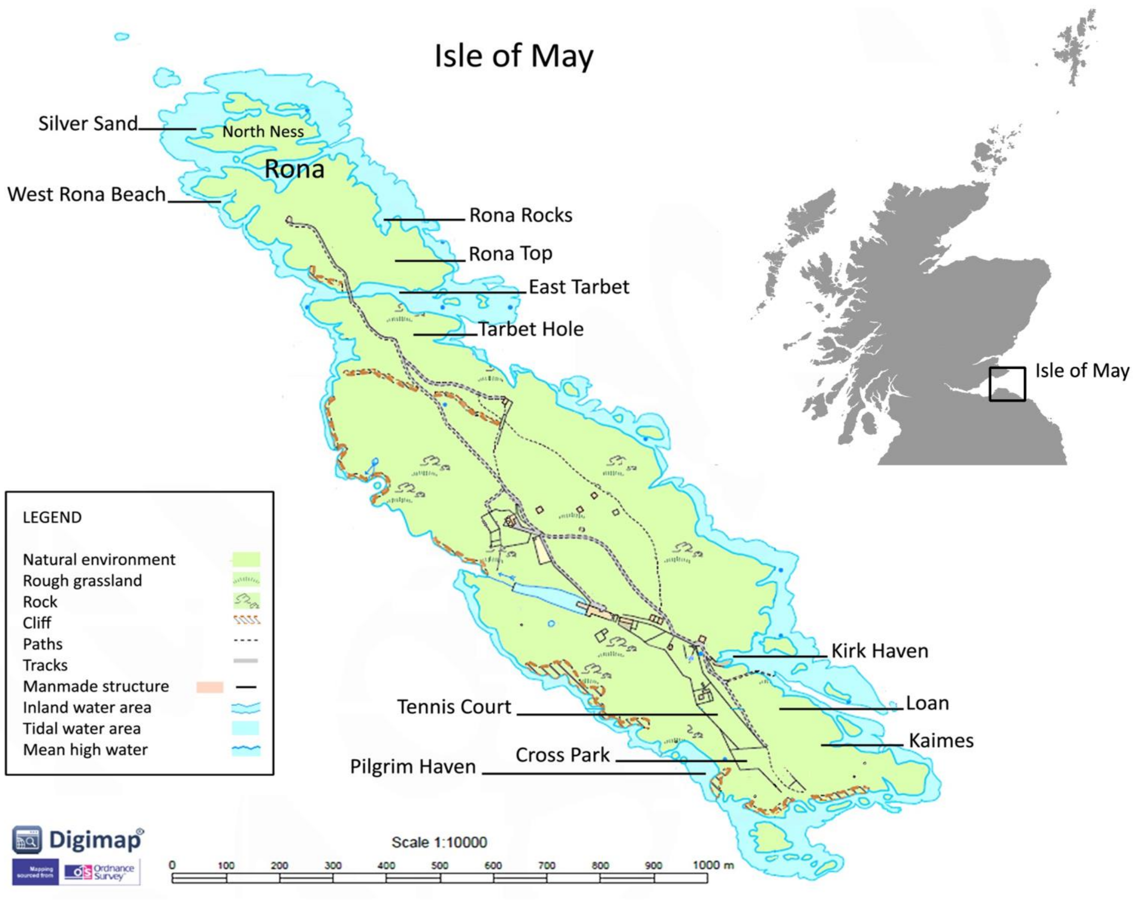

Figure 3.1 Map of the Isle of May

Maps provided by EDINA Digimap Service, http://digimap.edina.ac.uk/roam/os.

3.3.2 Data collection

In the present work the data collected by aerial surveys and ground visual censuses of pup carcasses were combined in order to investigate the predictability of seal carrion available at the seal colony.

Aerial survey data

The Sea Mammal Research Unit (SMRU) has performed aerial surveys since the early 1990s in order to estimate seal pup production (number of pups born per year) at major grey seal breeding colonies in Scotland. In the period 2000 – 2012 between 4 and 7 aerial surveys have been performed on the Isle of May every year from October to December. From 2012 surveys were made every two years. The survey aircraft conducted three transects along the island's long, northwest-southeast axis. The entire area of the island was photographed in this way at approximately 10 day intervals resulting in five surveys being conducted for each breeding season. Photos (Linhof AeroTechica film camera and a twin Hasselblad

H4D digital system in 2012) taken at a standard altitude of c370m over the island were processed counting white coats, moulted and dead pups. Pup production estimates (with 95% confidence limits) were obtained by modelling counts of living pups taking into account the birth process and the development of pups. The model considered also a misclassification parameter (permitting for the misclassification of moulted pups as white coats or vice-versa), whose variation may be function of the quality of the aerial photograph, or dependent on the observer, the light conditions and the body position of the pup when the photo was taken. Pup production data are presented with a coefficient of variation (CV). Dead pups were also counted for each survey, but no model was performed to estimate the pup mortality. Dead animals were distinguished from live pups because they appeared either to be bleeding, in bad condition or were attended or scavenged by gulls. As difficulties could arise in distinguishing fresh carcasses from live pups, it is possible that some dead individuals were not counted at first. However, they were likely to be recorded more easily in the successive aerial surveys, permitting, as result, a more precise total number of carcasses. For further details see SCOS (2009).

In the present study, the number of dead pups counted in the aerial surveys was used to approximate the number of carcasses released into the ecosystem. The highest number of dead pups counted each year (the highest among all the aerial surveys) was considered the closest number to reality, even if an underestimation. In order to minimise this underestimation, data obtained by ground visual census of carcasses (see below) made in 2008 and 2012 were used (229 and 233 carcasses, respectively). The latter, in fact, 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). 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 - early December) of the years 2008, 2012 and 2013. Carcasses were detected by a single individual in 2008 and by a team in 2012 and 2013 (3-6 people) systematically searching the seal breeding areas of the island.

The search team was spread out at approximately 5 m intervals in a line across the search axis. The areas covered were: the whole Rona, Tarbet Top, East Tarbet, Tarbet Hole in the north, the Loan, Pilgrim Haven, Kaimes, Cross Park and Tennis Court in the south and the south-eastern area. When possible, sex and development stage (according to Kovacs and Lavigne, 1986; see Table 3.1) were determined for each carcass. Sex and/or development stage could not be attributed to those carcasses in poor condition, scavenged, in late state of decay or starved. Starvelings (dead pups which appeared to have died because of starvation) and dead adult individuals were also recorded. A state of consumption (from A to E) was attributed to carcasses recorded during the ground visual census 2012. Each state corresponded to an estimated mass loss (expressed in percentage) which was calculated using true values of mass loss measurements (N = 64) of experimental carcasses combined with the observed state of consumption (for details see Table 5.2). GPS fixes (Garmin eTrex Summit; accuracy: <15metres RMS) or marks on aerial photographs (in 2012), were made for all dead animals.

Both aerial survey and ground visual census data did not consider the potential number of carcasses washed into the water during the season, but considered only the carcasses occurring on land.

Table 3.1 Development stages of grey seal pups.

Each development stage is associated with a description and age (days ± SD) according to Kovacs and Lavigne (1986).

Development Stage	Description	Ages days (± SD)
1	Yellow tint pelage, umbilicus present	2.4 (4.4)
2	Pelage white, should to hip region filled out	4.8 (3.1)
3	Pelage either to light grey, slight loss of lanugo in the facial region	12.1 (2.9)
4	Lanugo being shed	16.0 (2.9)
5	Moulted pup	>21

3.3.3 Data analysis

Timing

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

Biomass and energy content

The annual total estimated pup productivity was used to calculate the mean annual biomass and equivalent energy of placentae released during the period 2000 – 2010 and 2012. For this purpose average biomass and energy content values of placentae were acquired by analysing placenta samples collected in the field during the pupping season 2013. Six whole afterbirths (including amnion) were collected, weighed (± 10g) and sampled still in fresh condition. Samples were stored in individual plastic tubes and frozen for subsequent determination of water and energy content. When an afterbirth could be associated with a pup, its sex was also recorded. Analysis of the gross energy density (MJ kg^{-1}) of placenta samples was undertaken by bomb calorimetry (Sciantec Analytical Service, UK). Biomass (kg) of afterbirth available to the ecosystem for each year was then estimated by multiplying the pup production for each year by the average wet mass of a grey seal afterbirth. The energy content (MJ) of the total biomass of afterbirths was estimated by multiplying the total biomass with the energy density of grey seal afterbirth.

Before proceeding in calculating the biomass of dead pups resulting from the ground visual censuses, the discrepancy between the mass of alive and dead pups was estimated: differences in masses recorded during the seal breeding season 2011 between alive (N = 80) and dead (N = 37) pups belonging to the 2nd-3rd-4th development stages were analysed (Baily, 2014). The 1st and 5th were excluded because of the reduced sample size. Afterwards, mass (kg) of pup carcasses was calculated according to the equations provided by Kovacs and Lavigne (1986) and the resulting values were adjusted by subtracting the difference in mass found between alive and dead pups. Biomass of pups was estimated considering sex and development stage of carcasses; mass of unknown sex was approximated by averaging the mass of male and female pups for the different developmental stages. For starvelings and pups with an undetermined developmental stage the mass was estimated for dead female pups belonging to the first development stage as a conservative value. The mean maternal mass at weaning according to Pomeroy and Fedak (1999) was given for female adult carcasses (117 ± 18kg). A value equal to 234kg 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 56.4 ±6.3kg (Addison and Stobo 1993).

The body composition of 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. Values belonging to pups nursed by primiparous grey seal mothers, instead of multiparous, were used as a conservative approximation because they were lower. Similarly to body mass, also body composition might differ between dead pups and healthy alive pups. Reduction or lack of blubber is evident in starvelings for instance (Trites and Jonker 2000; Baily 2014). However, there is no documentation comparing alive and dead starveling pups. Day 3 postpartum values were given to the first and second stages carcasses, but also to starvelings and pups without a determined development stage. Day 12 postpartum values were assigned to third stage carcasses, whereas at weaning values to the fourth and the fifth stage carcasses (Table 3.2). Percentages of each component were then calculated in terms of biomass. Body composition of female adult carcasses was also estimated from

Lang et al. (2011), considering values of primiparous grey seal mothers at day 12 postpartum; whereas for male adult and juvenile carcasses, values provided by Lidgard et al. (2005) were used.

The energy content (MJ) of protein and fat was quantified based on values of energy densities provided by Schmidt-Nielsen (1997): 39.33 kJ g^{-1} and 17.99 kJ g^{-1} for fat and protein, respectively. 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 pup carcasses become immediately available to the ecosystem. The mean energy density for all the development stages of pup carcasses was 14.1 MJ kg^{-1} (SE = 3.11; Table 3.2). This analysis does not take into account the factors affecting the biomass and the energy of carrion over time, such as decomposition (see Chapter 5).

Table 3.2 Energy content for development stage of grey seal pups according to energy density calculated per body component (%).

Stage	Body component	Component content (%) (Lang et al. 2011)	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	

Spatial distribution

In order 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 map their distribution and intensity. From here onwards, the term *intensity* is used only when referring to kernel smoothed intensity of the point process for carcasses, while *density* in all other cases. Kernel estimation is a useful 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 the British National Grid using the WGS 1984 coordinate system. Defining the intensity function for a point process as the average number of points in a region, the intensity of carcasses was calculated for the island including the area to the mean low water boundary (697,102 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. Following the methods of Pomeroy et al. (2000), 20 x 20 m pixels were used. Polygons of areas delimited by a minimum intensity of 0.001 carcasses m^{-2}, used as spatial thresholds of presence of carcasses, were identified for each year. The union and the intersection of these polygons was plotted in order to highlight areas of persistent availability of carrion year to year. 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 (placentae m^{-2}) and the correspondent density of biomass (kg m^{-2}) of placentae for the decade were also estimated considering the area of the island at low mean water (697,102 m^2).

Carcass depletion by scavengers and remains

The depletion of biomass caused by gull scavenging activity was calculated for the pupping season 2012. The estimated percentage of scavenged mass, calculated according the given consumption state (from A to E), was removed from each carcass mass; afterwards the latter were summed to obtain the total scavenged biomass. Remains (skin and bones: 34.2% of dead pup mass) were considered as the inedible mass becoming available to invertebrate scavengers and the abiotic compartment of the soil.

Statistical analysis

Standard errors of the means and percentage of relative standard errors (RSE% = standard error/ mean *100) of results were used as measure of ecosystem variability expressing inter-annual variability of the different properties of the seal carrion resource (mean pupping date, biomass, energy and density of both placentae and carcasses).

A two way analysis of variance (ANOVA) was performed in order to evaluate whether mass varied between status of pups (dead/alive) and the development stage (1-5), including their interaction.

Pearson's Chi-square test was run in order to test the hypothesis that the number of carcasses belonging to different sex or development stage were independent of the year when they were counted.

Ripley's function (Ripley 1977) was used to analyse the spatial pattern and determine visually whether distribution of carcasses from different years were different. This method is used in epidemiology, but also in forensic science and plant ecology (Lancaster and Downes 2004) and permits visual comparison of the spatial distribution of points belonging to different patterns and to identify clustering. Considering a circle of *r* radius and the number of points inside the circle, the Ripley's K function represents the expected number of points within an *r* distance 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 did not have a homogeneous intensity of points, the inhomogeneous *Linhom (r)* function was used as proposed by Baddeley et al. (2000). 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); then they were 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. The null hypothesis was that the distribution of points is random and this was identifiable by a horizontal line of null x values between the x and y axes corresponding respectively to the radius (*r*) (here shown 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 under it when it is uniform.

Spatial analyses were run using R 3.1.1 and the following package: Spatstat, Maptools, Rgdal, Rgeos, Ggplot2 and Splancs (Baddeley and Turner

2005; Wickham 2009; Bivand et al. 2014; Bivand and Lewin-Koh 2014; Bivand and Rundel 2014).

3.3.4 Comparison with other studies

In order to investigate the extent to which seal carrion provided by the Isle of May was a predictable food supply, we compared our results with other published studies on predictable resources. The papers reviewed were: Davenport (1995), Polis and Hurd (1996b), Reimchen (2000), Bouchard and Bjorndal (2000) and Hocking and Reimchen (2009) whose study system was the coastal area. The key criterion for the inclusion of these published studies was that the papers showed there was a clear response in the behaviours of the users of the resource when it became available. These included, for instance, movements towards areas where the resources occur or higher density compared to other locations, resulting in important sources of sustainment for their consumers. In particular, movements or changes of behaviour which precede the actual availability of the carrion resource. When previous studies did not show values of variability between years, we compared our results to the original data given.

3.4 Results

3.4.1 Aerial survey data

The annual mean pupping date observed during the decade 2000-2010 and 2012 was the 30th October (SE = 0.58; RSE% = 1.97%) (Figure 3.2).

The mean pup production was 1988 (SE = 47.72; N = 12; RSE% = 2.40%) pups per year. The mean number of dead pups estimated was 262 (SE = 16.32; N = 12; RSE% = 6.23%), representing a mean annual mortality of 13.3 % (SE = 0.91; N = 12; RSE% = 6.84%) (Figure 3.3).

The number of placentae (corresponding to total pup production) was seven times more abundant than dead pups with a percentage of 88.4% (SE = 2.41; RSE% = 2.73%) of the total amount of carrion y number.

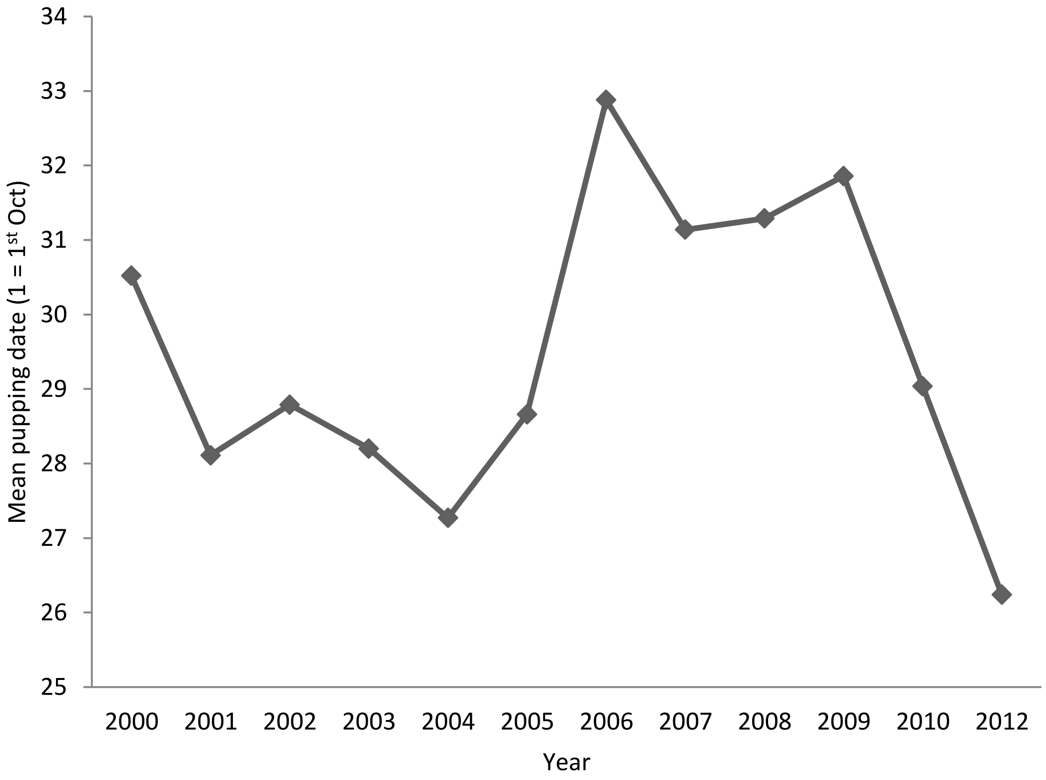

Figure 3.2 Mean pupping date (2000 – 2010 and 2012).

Mean pupping date for the decade 2000-2010 and 2012 from aerial survey data (1 = 1st Oct).

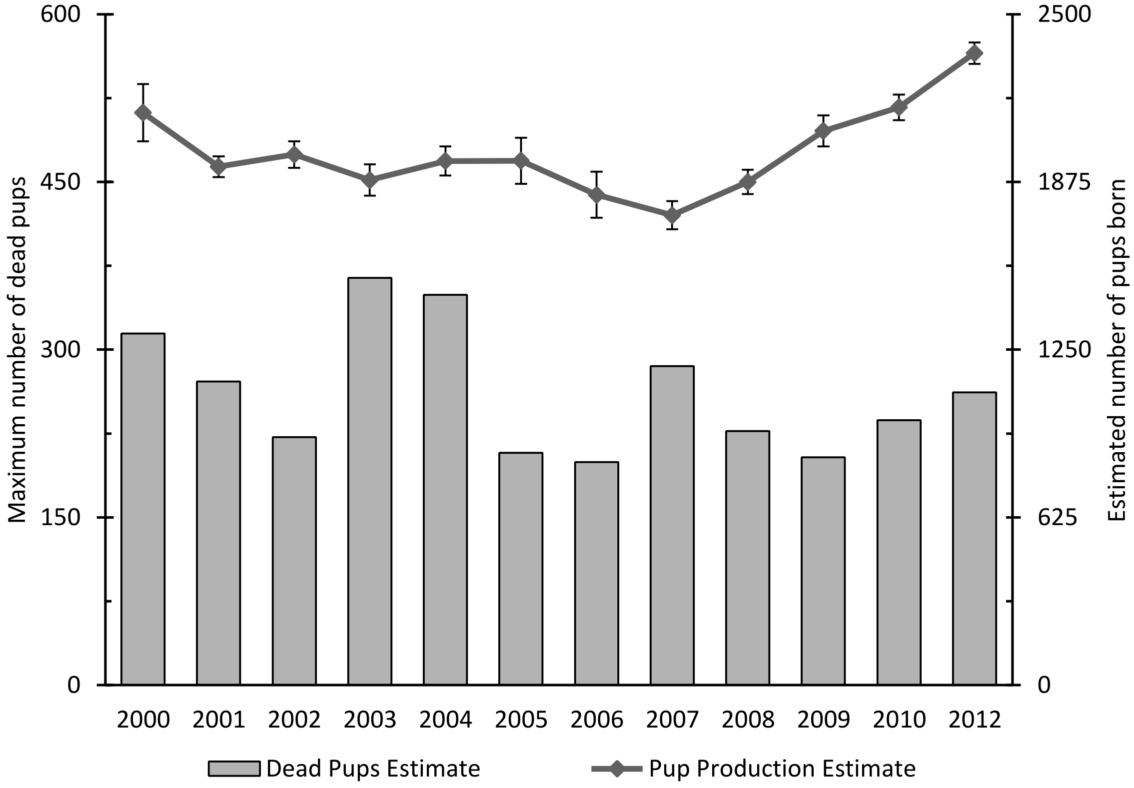

Figure 3.3 Estimated maximum number of dead pups and total pup production for the years 2000 – 2010 and 2012.

Number of dead pups re-estimated by aerial survey data is represented by columns and referred to the y-axis on the left side. Pup productivity is represented by line with CV (%, ranged between 0.02 and 0.05) and referred to the y-axis on the right side.

The mean mass of a placenta (including amnion) was 1.6 kg (SD = 0.24; N = 6) (Table 3.3) and the resulting total biomass for the period 2000-2010 and 2012 was estimated to be 3124.3 kg (SE = 74.99; N = 12; RSE% = 2.40%; range 2751.70 - 3700.88). The mean gross energy density was estimated as 21.8 MJ kg^{-1} (SD = 1.15; N = 6). From this the estimated average annual energy delivered as afterbirths on the Isle of May was 68.1 x 10^3 MJ (SE = 1.64; N = 12; RSE% = 2.41%).

Table 3.3 Information and measurements of grey seal afterbirths (N = 6).

For each afterbirth date of collection, sex of the pup, total, amnion and placenta mass were recorded. Samples were collected for further analyses of energy content.

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

For the study period 2000 – 2012 the mean placental density on the island was 0.003 afterbirths m^{-2}, (SE = 0.00007; N = 12; RSE% = 2.33%) while the mean placental biomass density was 0.004 kg m^{-2} (SE = 0.0001; N = 12; RSE% = 2.50%).

3.4.2 Ground visual census data

The ground visual censuses performed in 2008 and 2012 showed similar numbers of dead pups with 229 and 233, respectively whereas in 2013 a total of 165 carcasses were observed. The mean number of dead pups counted for the three years was 209 (SE = 22.03; N = 3; RSE% = 10.54%). Excluding carcasses with undetermined sex, a similar proportions of male (56.22%; N = 3; SE =2.64) and female (43.78%; N = 3; SE = 2.64) carcasses was found (X^2 = 3.02, df = 2, P = 0.22). For 9.61% of the carcasses it was not possible to detect the gender. On average around half of pups (53.63%; N = 3; SE = 4.15) were second stage pups (Figure 3.4), aged between 1.7 and 7.9 days (X^2 = 35.2285, df = 6, P < 0.0001). The following most abundant type of carcasses were those belonging to the third and first stages. The other stages were represented by mean percentages around five times lower. Starvelings formed 8.66% (N = 3; SE = 3.94) of the total number of carcasses. Dead adults were found every year (2.12% of the total number of carcasses; N = 3; SE = 0.70), and 12 out of 14 individuals were female. A single yearling was found dead in 2013.

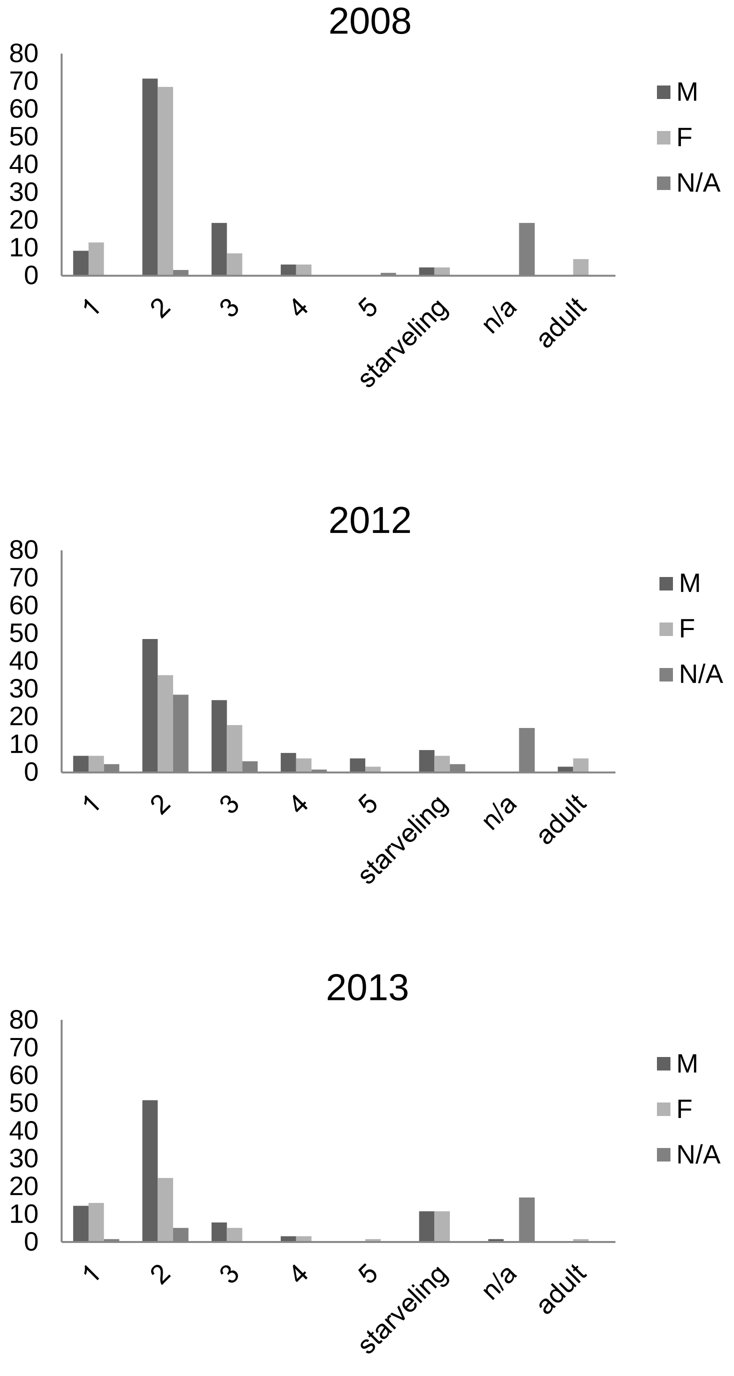

Figure 3.4 Ground visual census data according to sex and development stage.Number of dead pups per year belonging to different sex and development stages from the ground visual census performed in 2008, 2012 and 2013: M = male, F = female and n/a = non-available sex; 1 = first, 2 = second, 3 = third, 4 = fourth, 5 = fifth development stage, starveling = pups who died of starvation, n/a = non-available development stage and adult.

There was a significant difference in mass between dead and alive pups (ANOVA, status $F_{1,115} = 34.84$, $P < 0.001$), between pup stages (ANOVA, $F_{2,114} = 46.49$, $P < 0.001$) and there was no significant interaction (ANOVA, $F_{2,114} = 0.11$, $P = 0.9$). Therefore, the average difference in mass of 8.02 kg occurring between alive and dead pups for the three development stages was used to calculate the biomass from dead pups. Re- estimated masses of pups for each development stage are shown in Table 3.4.

Table 3.4 Re-estimated mass of dead grey seal pups belonging to different development stages.

Each development 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 on mass occurring between alive and dead pups. When sex of pup was unavailable, the body mass was calculated using the mean body mass of both sexes.

Development Stage	**Mean mass Kg (± SD)**		
	Female	**Male**	**Sex not determined**
1	9.6 (12.05)	11.7 (14.43)	10.6 (13.24)
2	12.6 (10.43)	15.0 (12.62)	13.8 (11.52)
3	21.7 (10.18)	25.1 (12.34)	23.4 (11.26)
4	32.6 (42.47)	36.1 (43.50)	34.3 (11.39)
5	28.8 (44.75)	33.2 (45.21)	31.0 (53.00)

The mean annual biomass of dead seals (adult and pups) was estimated to be 3768.2 kg (SE = 713.73; N = 3; RSE% = 18.94%; range 2411.7 – 4831.4kg). Male carcasses averaged 49.9% (N = 3; SE = 3.02) of the total biomass available, while the second development stage contributed the greatest proportion and represented 42.1% (N = 3; SE = 5.16) of the total biomass released.

A large percentage of the annual biomass of dead seals (adults and pups) was composed of water (58.6%; N = 3; SE = 1.46) in greater amount than fat (18.9%, SE = 2.15) and protein (19.9%; N = 3; SE = 0.62) combined (Figure 3.5). The latter two components, corresponding to an annual biomass equal to 1481.7 kg (SE = 329.43; N = 3; RSE% = 22.23%), were responsible for the release of 42.4 x 10^3 MJ (SE = 10.42; N = 3; RSE% = 24.58%; range: 23.8 – 59.8 x 10^3 MJ) of energy into the ecosystem. Fat contributed 67.2% (SE = 3.12) to the total energy, while protein to 32.8% (SE = 3.12).

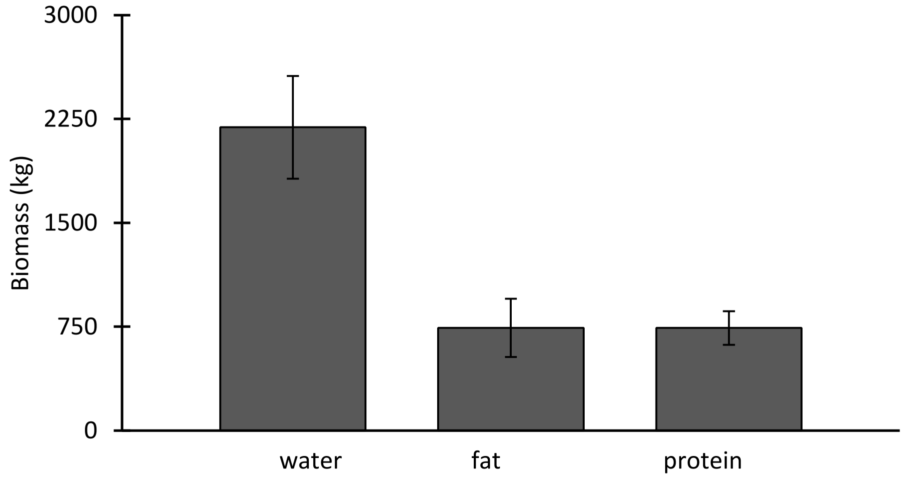

Figure 3.5 Biomass (kg, ± 1 SE) of dead pups according to proportion of water, fat and protein in the body and estimated from ground visual census in 2008, 2012 and 2013.

In 2012 the total biomass scavenged was 1032.0 kg representing 21.4% of the total mass available and 32.5% of the edible mass. Most of the carcasses were scavenged on the eyes or showed one or more openings on the body (consumption state B: 28.8%; consumption state C: 25.3%). Inedible (skin and bones) and not scavenged mass was 1681.3 kg (34.8%) and 2118.1 kg (43.8%), respectively. The energy intake by scavengers was 9.1 x 10^3 MJ, while 14.8 x 10^3 MJ and 18.6 x 10^3 MJ, respectively, were the energy of the uneaten and inedible mass left on the ground.

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 point patterns covering the following areas: North Ness, Rona and East Tarbet in the north and Pilgrim Haven, Kirk Haven and Loan in the south. Most of the dead pups found were located above the mean high water line, however on average 13.1% (SE = 3.85) of carcasses occurred in the area between the mean high and low water boundaries (166,902 m^2). The mean kernel smoothed intensity was estimated to be 0.0003 carcasses· m^{-2} (SE = 0.00003; 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; RSE% = 20.00%). The highest intensity each year was observed in the area between Rona and North Ness: in particular in 2012, the maximum intensity was 0.03 carcasses m^{-2} (Figure 3.6). The union of polygons characterised by an intensity higher than 0.001 covered 74,965 m^2 representing 11% of the total area of the island at mean low water and two thirds of it occurred in the north. The shared area among three years (or intersection), was 21,270 m^2 corresponding to 3% of the total area of the island and 28% of the union of polygons and occurred mostly in the north (83%) (Figure 3.7). The density of biomass was 0.006 kg m^{-2} (SE = 0.001; RSE% = 16.67%) for the whole island and 0.09 kg m^{-2} (SE = 0.03, RES% = 33.33%) for the area covered by the polygons.

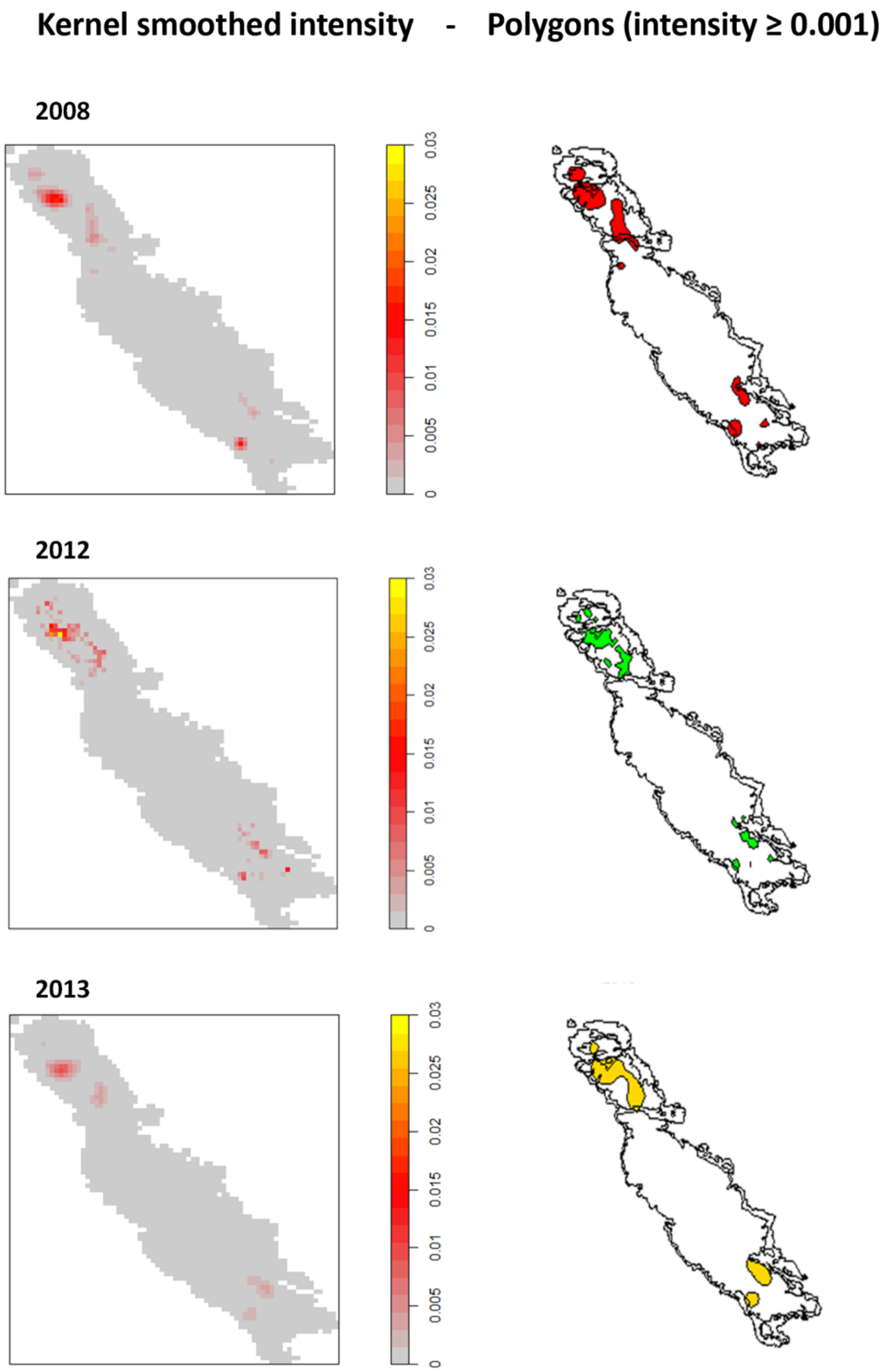

Figure 3.6 Kernel smoothed intensity of carcasses and polygons of density ≥ 0.001.

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 characterised by intensity equal or higher than 0.001 carcasses m^{-2} in 2008 (red), 2012 (green) and 2013 (yellow).

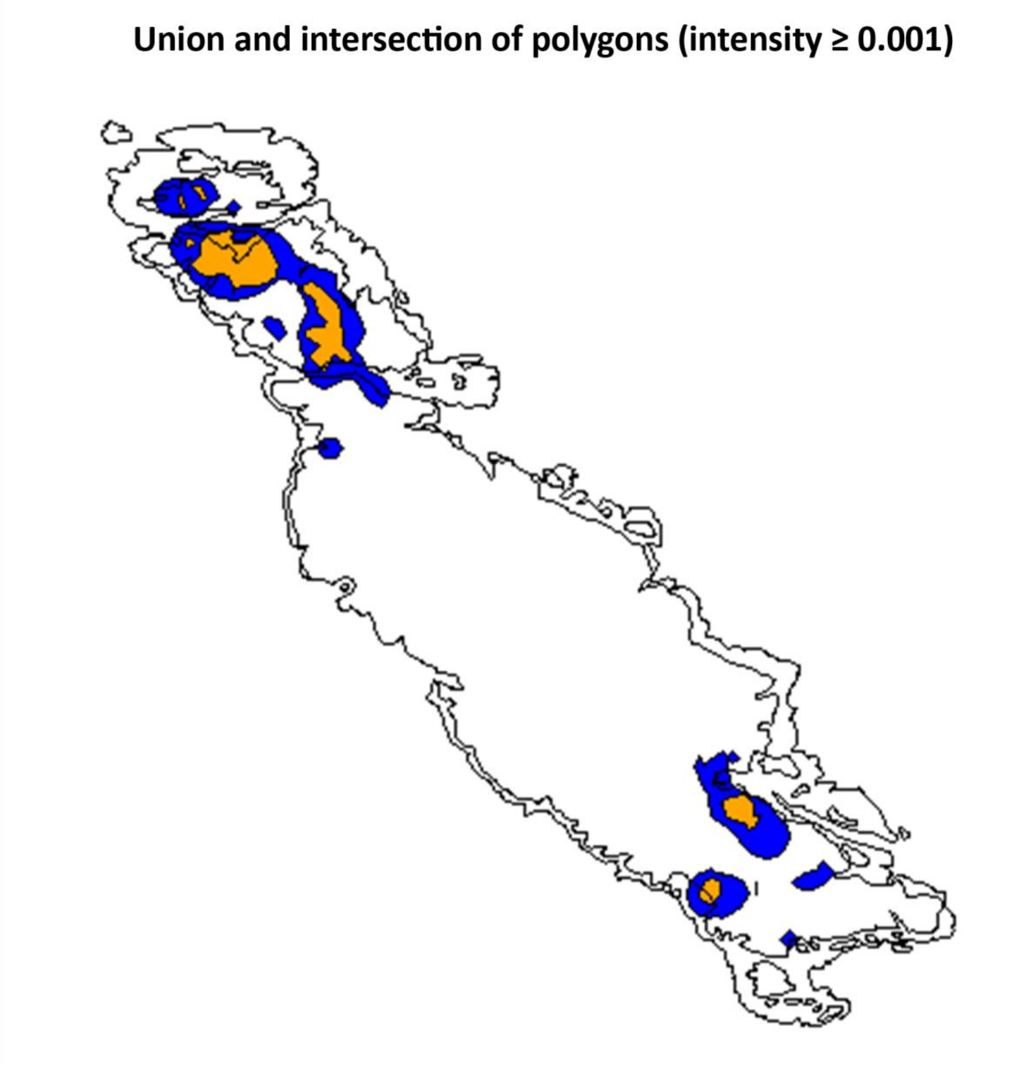

Figure 3.7 Union and intersection of polygons of intensity ≥ 0.001.

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).

Initially the pattern was highly aggregated, but as the value of the inhomogeneous *Linhom (r)* function increases, it became uniform. Two peaks in the aggregation pattern were observed in each year: one around 40-70m and the other around 150-180m, showing that the area of carcasses were repeated and had similar distance across years, both on the north and south of the island (Figure 3.8). Around 215-230m, 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 400m, 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. The 2008 curve, however, showed a faster decreasing towards uniformity.

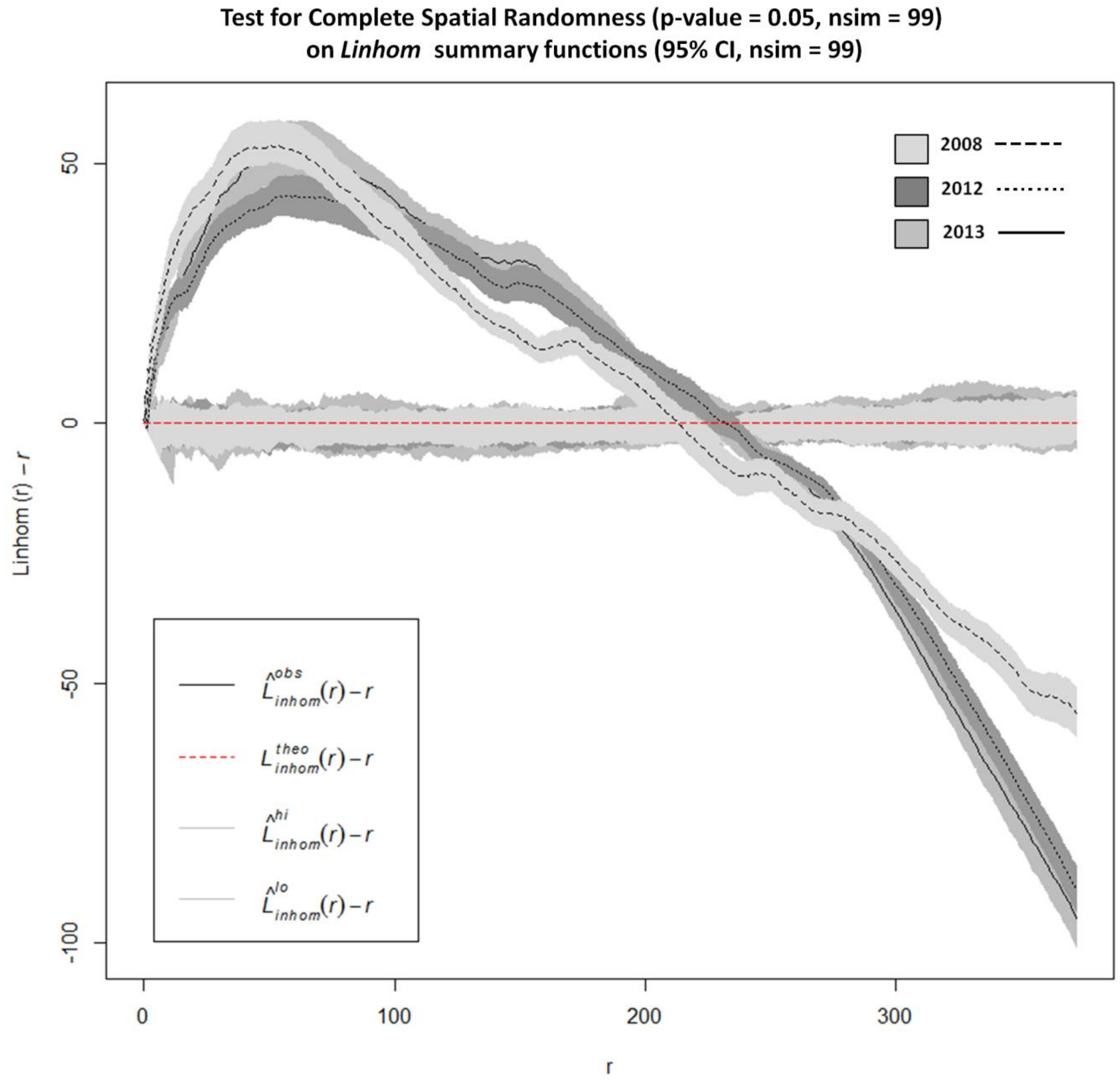

Figure 3.8 Test for Complete Spatial Randomness on Linhom summary functions.

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.

3.4.3 Comparison with other studies

Our results showed relative standard errors (RSE%) for the number of dead seals and placentae (between 1.97% and 24.50%) and 33.33% in the spatial intensity of biomass for dead seals (Figure 3.9). Reimchen (2000) and Hocking and Reimchen

(2009) showed variability in quantity and biomass density across years of between 1.67 and 25%. Several papers described the predictable resource according to its properties without presenting variability among events (Appendix B.1-2).

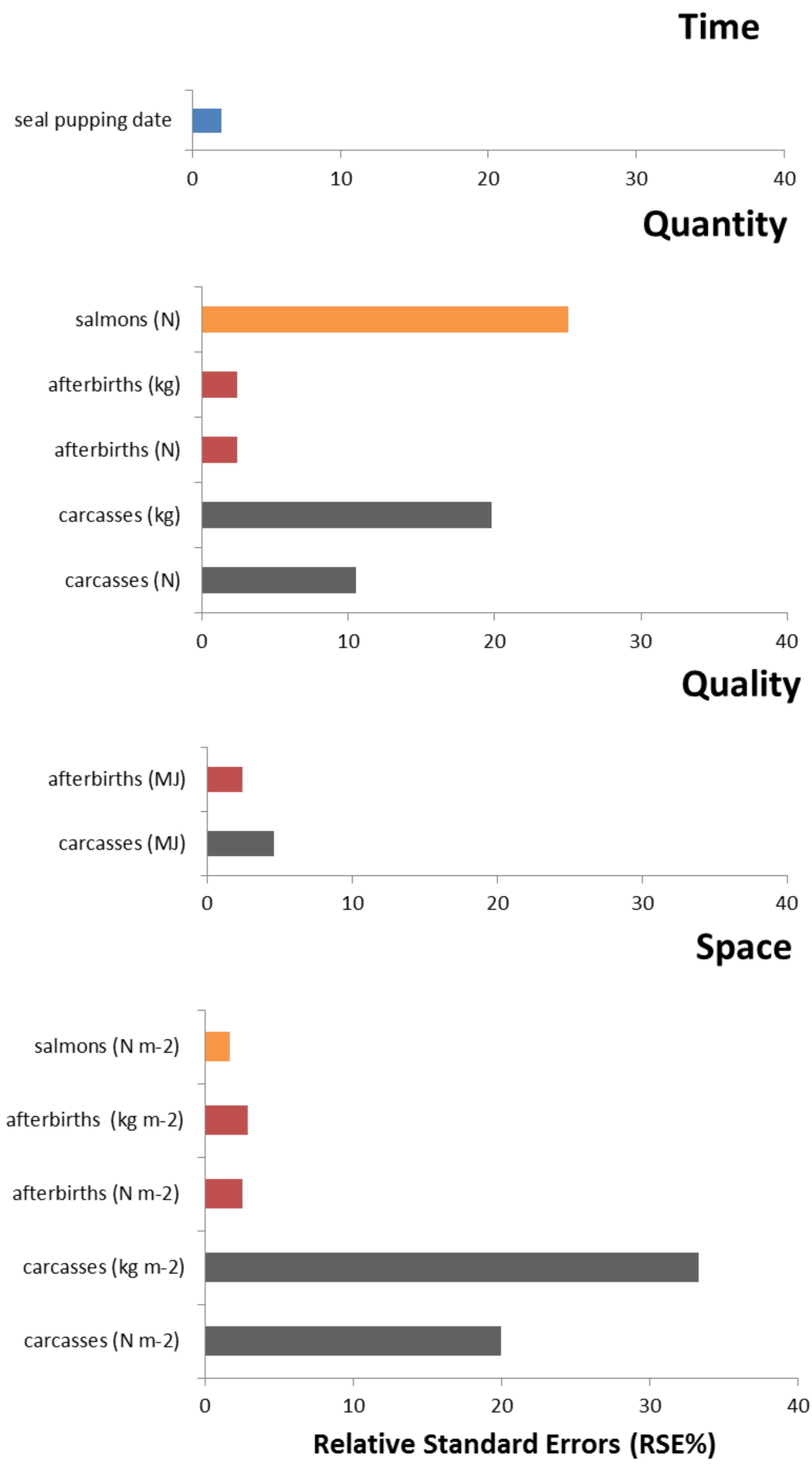

Figure 3.9 Comparison between RSE% of resource availability resulting from the Isle of May seal carrion and spawning salmons.

Inter-annual variability, measured as RSE%, of carcasses (black) and afterbirths (red) occurring on the Isle of May during seal pupping seasons 2008, 2012 and 2013 and spawning salmons (orange) according to Reimchen (2000) and Hocking and Reimchen (2009) according to time (date of occurrence), 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}).

3.5 Discussion

3.5.1 Isle of May carrion

Seal carrion on the Isle of May is an apparently stable resource occurring annually. Since the 1970s, when the grey seals appeared on the island for breeding, an increasing pulse of nutrients was released into the ecosystem from seal afterbirths and carcasses. During the last decade the mean pupping date occurred consistently at the end of October. However, the pupping season extends for up to 6 weeks (Harwood et al. 1991; Hiby et al. 1996) and during this prolonged period an average of 3124kg of afterbirths were discharged into the ecosystem. Although the population now appears stable (SCOS 2009), new areas have been occupied by pupping seals during the last decade: Pomeroy et al. (2000), describing the main areas used by seals in 2000, excluded a large part of the south of the island that are now colonised, such as the Loan, Tennis Court and Cross Park.

In order to estimate pup mortality we compared aerial survey with ground visual census data: this process was carried out to reduce as much as possible the underestimation of dead pups observed by the aerial survey. The mortality estimated was 13.3% in comparison to 12.5% given in Baker and Baker (1988). Representing the longest extent of time (circa 7 days) compared to other stages, the second stage of development was the most abundant among carcasses. Adult mortality on the island was rare, estimated adult survival on the Isle of May is high with low variance 0.950 (95% CI 0.933 - 0.965) (SCOS 2013). First year survival of grey seal pups depends on pup condition at weaning and differs between males (0.193, SE = 0·084) and females (0·617, SE = 0·155) (Hall et al. 2001). Pup mortality can also occur post-weaning, such as the lethal injuries called helical (corkscrew) wounds (Thompson et al. 2010). Interaction between ship propellers and seal was thought to be the most likely cause, but recently it was shown that these events can also be attributed to cannibalism by adults (Thompson et al. 2015).

Seal carrion biomass was calculated using true mass values of placentae and dead pups measured on the Isle of May, therefore estimates are accurate. Further investigations are, instead, necessary to improve the estimations of body composition and energy content of dead pups. Similar to mass, body composition of pups may vary between alive and dead pups, and this is certain in starvelings (Trites and Jonker 2000). As various causes of death can lead to different proportions of body components of the carcasses, in this study conservative estimates were used. Energy content of placenta has rarely been measured and in this study grey seal placenta was more than 3 times greater than for harp seals (*Pagophilus groenlandicus*) (4.73 MJ kg^{-1}; Lavigne and Stewart 1979), but it had a very similar value to the west Atlantic grey seal's one (23 MJ kg^{-1}; Yunker et al. 2005).

Distributions of carcasses were similar among years and certain areas were consistently influenced yearly by the occurrence of dead pups and placentae. However, the spatial pattern observed in 2008 (Figure 3.8) slightly differed from the other years, as smaller carrion patches were more distant from the main ones. This can be explained by the occupancy by seals of marginal areas in more recent years and their related mortality, so that carrion patches get closer. Grey seals are characterised by a high degree of site fidelity which bring them to the same area of the colony every year (Twiss et al. 1994) and mortality of pups can be related to specific topographical features (*sensu* Twiss et al. 2000). It was demonstrated that on the Isle of May females prefer to pup close to the sea or freshwater pools and mothers occupying further locations separate more often from their pup, reducing pup attendance. The latter together with increased aggressive behaviour among seals on the access routes to the water (Twiss et al. 2003) is likely to define areas of higher pup mortality, as observed in other pinnipeds (Doidge et al. 1984; Harcourt 1992; Baldi et al. 1996).

3.5.2 Impact on ecosystem compartments

Numerous marine-derived resources have been shown to influence the coastal ecosystem. In the Isle of May the great black-backed gull *L. marinus* is the main consumers of seal carrion and its behaviour was already reported by Twiss et al. (2003) at another grey seal colony in Scotland. Other scavengers such as the giant petrels *Macronectes halli* and *M. giganteus* in South Georgia are also important scavengers for different seal species (Hunter 1983). At the end of the breeding season 32.5% of the edible dead seals biomass available on the Isle of May was scavenged resulting in an energy intake estimate of 19.4 x 10^3 MJ. It is likely that the scavenging activity continues also after the seal pupping season has concluded and consumption increases. However, the lack of complete depletion of the carcasses may be related to the high abundance of these inputs (Wilmers et al. 2003b) and/or low abundance of scavengers. Generally, in the presence of a superabundant resource, greater than required by foragers (Rosenberg et al. 1982), the incomplete consumption of food items often occurs (e.g. Reimchen 2000) and a large proportion of it enters the detrital compartment (Yang et al. 2008). In our case, the incomplete consumption of carcasses can be related to the extended handling time and the necessity of effective skills to dismantle a dead seal. Placenta was seen to attract simultaneously a higher number of gulls than carcasses possibly due to it being the easier to obtain and utilise of the two different food items, often leading to its complete consumption (see Chapter 5). The energy resulting from placentae and dead seals utilizable by scavengers was respectively 68.1 x 10^3 MJ and 42.4 x 10^3 MJ. Considering that the daily energy requirement for 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 pups and placentae provides potentially more than 42 thousand daily rations for these birds. Coastal inputs can attract organisms from both the terrestrial and marine environments. Similarly to sea turtles eggs, between 26 and 31% of which are predated by raccoons (*Procyon lotor*) and ghost crabs (*Ocypode quadrata*) while still in the nest (Bouchard and Bjorndal 2000), seal carcasses might be exposed not only to gulls, but also to marine scavengers. A proportion of dead seals (13%) was in fact found between mean high and low water where scavenging crabs and amphipods live. However, the number of dead seals found in the intertidal area may represent only a proportion of carrion potentially available to the marine system. Some carcasses, in fact, may have been already transported by tides and waves into the water before the ground visual census was carried out.

Carrion is exploited when spatial variability of nutrient hotspots originated by seal carrion matches the scale of variability of foraging movements of scavengers. When exploring the effects of these nutrients on small scavengers, such as rodents or invertebrates, for instance, it becomes relevant to identify where they are released in a fine scale. The latter is valid also for other biotic and abiotic compartments of the ecosystem, such as plants and soil which can be influenced by carrion (and also defecation) at a small spatial scale as well. On the Isle of May the unused seal carrion, which counted for 78.6% of the total mass of dead seals, was still available at the end of the seal pupping season on the delimited areas of the island where seal aggregations occur. Smaller scavengers, such as rodents and invertebrates, may aggregate for consuming further biomass, while the soil can absorb marine nutrients through decomposition of uneaten seal skin and bones. Such processes related to the fate of carrion have been already demonstrated in previous studies. For instance, denser assemblages of arthropods were found on the supralittoral than inland where algal wrack and carrion occurred (Polis and Hurd 1996b); plants growing in the vicinity of seal and penguin colonies, but also riparian conifers on the bank side of salmon-bearing streams showed greater marine- derived nitrogen enrichment in comparison to more distant plants (Erskine et al. 1998; Koyama et al. 2005). Seal colonies, in particular, were responsible for the highest nitrogen enrichment reflecting the high position of the pinnipeds in the trophic chain (Erskine et al 1998).

3.5.3 Implications of predictability

Despite predictability being well recognised and widely used in ecology, a standard approach to define a resource predictable seems missing. Here, a useful metric, which considers the main properties of a food subsidy, is provided. Factors influencing predictability were decided according to their relevance on having a potential effect on ecological processes involving the interaction between a resource and its foragers. 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, animals can preempt its future occurrence (e.g. Reimchen 2000; Wittemyer et al. 2007). The animal learning process involves the temporal awareness (when food occurs), which can be promoted by environmental cues (Frederiksen et al. 2004a), but also by spatial perception (where food occurs) (Sherry et al. 1992). Timing and location were therefore the other crucial features used to describe the predictability of a resource. In fact, considering different spatial scales, when a subsidy occurs, the number of foragers increases (Polis and Hurd 1995a; Stapp and Polis 2003; Spiller et al. 2010), their distribution varies (Rose and Polis 1998), the home ranges of individuals change (Monsarrat et al. 2013) and the species trophic dynamics alter (Polis et al. 1997; Briggs et al. 2012). Unifying measures such as timing, spatial distribution, biomass and energy value of a resource are indispensable for interpreting the effects it has on the ecosystem and should represent the foundation of any investigation related to predictable resources.

Predictability is a measure of ecosystem stability explained by low variability in its properties both temporally and spatially. Standard errors and percentage of relative standard error (%RSE) were identified as tool for measuring the degree of predictability (McGrady-Steed et al. 1997). In particular, the %RSE was chosen in order to standardise data of different nature (date, abundance, biomass, energy, density of two separate carrion sources), taking into account the sample size and to compare different studies. Seal carrion and spawning salmon runs were demonstrated to be a predictable resource with %RSE between 1.67 and 33.33%. Predictability of salmon runs in riparian systems is responsible of co-evolution between feeding strategy and food input in black bears (*U. americanus*) and more recently in wolves (*Canis lupus*) (Reimchen 2000; Darimont et al. 2003). Depletion of seal carrion by gulls also suggested a clear response of consumers to this resource availability, but whether they developed any ecological adaptation to it has not been defined yet, even if it was demonstrated in the case of fishery discards (Bartumeus et al. 2010; Cama et al. 2012). Gulls at sea, in fact, were distributed according to fishery vessels density during fish discarding time, showing to optimise their foraging strategy (Cama et al. 2012). Repeatibility of predictable events can show also long term impacts on the ecosystem. Stable isotope δ^{15}N signatures of salmon have been found in plants and invertebrates (Hocking and Reimchen 2009) and persisted for decades after the salmon population disappeared (Koyama et al. 2005).

In the presence of a predictable superabundant resource, inter-events variation can be high, but not affecting the response of foragers: pre-spawning aggregation of eulachon (*Thaleichthys pacificus*), for instance, had seasonal impacts on the abundance of Steller sea lions (*Eumetopias jubatus*) attending the area for feeding (Sigler et al. 2004) despite the fact that food inputs greatly vary between years. A surplus of this subsidy was detected even when the quantity of this resource was at its minimum.

Comparing seal carrion to other apparently predictable resources, it appeared that sea turtle eggs released much greater energy (267.8 x 10^3 MJ), but this was calculated according to 21 km stretch of beach where turtles nest (Bouchard and Bjorndal 2000) (Appendix B.1-2). The energy enters different compartments: returning back into the marine system as hatchlings (26.8%), taken by predators (27.7%) or used by plants, decomposers and detritivores (34.0%). Seal carcasses, instead, were consumed by avian scavengers, and possibly mice, (32.5% of the edible mass), whereas the uneaten part became available to smaller scavengers and invertebrates or again to vertebrate scavengers for further consumption. Remains, considered as the inedible part of the carcasses (34.8% of the total biomass), were accessible to decomposers and soil. Also seabird colonies provide carrion as a pulsed food source: nesting islands in the Gulf of California, for instance, provide dead chicks in similar density of biomass to seal carrion, with a maximum of a tenfold difference (Polis and Hurd 1996b, Sánchez-Piñero and Polis 2000) (Appendix B.1-2). When comparing the absolute values describing different resources in its properties, difficulties arise as several different responses are expected according to the particular ecosystem. Its predictability, instead, drives some important ecological processes regardless of the ecosystem considered.

In conclusion, this study quantifies the value of seal carrion as a predictable food resource. Further investigation could reveal the importance and use of this resource by various scavenger groups, local vegetation as well as its effect on nutrient content of soils and sediments. In this way the often overlooked relevance of carrion in ecology will be rectified.

Chapter 4: The impact of marine mammal carrion on the spatial and temporal distribution of the scavenging community at different geographical scales

4.1 Abstract

Food resources drive the movement of animals: foragers migrate, change their home range, adopt different searching strategies and modify their behaviour to exploit food resources. When assessing the effect of food availability on the temporal and spatial distribution of a species, it is crucial to consider multiple geographical scales. Here, we evaluated the distribution and behaviour of scavenging gulls wintering on the seal colony of the Isle of May (Scotland, UK) in response to a pulsed and aggregated source of carrion during the pupping season. Three levels of resolution were considered: 1) at the regional scale (Scotland) temporal trends of herring gull (*Larus argentatus*) and great black-backed gull (*Larus marinus*) observed in South of Scotland, Forth Estuary and Isle of May were compared; 2) at the local scale (Isle of May), abundance of gull species recorded during the day and roosting at dusk were estimated to assess diel differences in their home range and relative species abundance on the island; and 3) at the patch level, temporal patterns of searching and feeding behaviour of gulls were measured in areas with and without available carrion. Results showed that great black-backed gull numbers increased during the seal pupping season on the Isle of May but not in the Forth Estuary and South Scotland suggesting a regional-scale effect of carrion availability. Herring gull trends, instead, were similar in all three areas considered. At the local scale, the great black-backed gull was the most dominant species during the day, whereas at dusk proportions changed in favour of the herring gull which roosted in higher numbers on the island. At the patch level gull activity was dominated by great black-backed gulls and juvenile gulls and was highest in carrion rich areas. The number of gulls feeding was directly correlated with carrion abundance, while searching behaviour was greatest after the mean seal pupping date and at the peak in mortality. Elucidating the relationship between

scavengers and carrion will not only aid our understanding of carrion ecology and inform studies investigating the current decline of scavenging gull species.

4.2 Introduction

Movements of animals are often driven by variation in the distribution of food resources occurring between the breeding sites and wintering areas (Rankin 1985; Dingle 1996). In this way animals enhance their survival, growth and reproductive success (Taylor and Taylor 1977). Movements, such as migration, occur when organisms' phenology and local environmental cues are synchronised and stimulate them to move to habitats characterised by higher food availability (Dingle and Drake 2007).

When prey species pursue seasonal movements searching for new resources, predators respond to prey availability by adjusting in turn, diet, habitat and behaviour. Similar to the relationship between prey and predator, scavengers are also linked to the availability and accessibility of food (Wilmers et al. 2003b; Blázquez et al. 2009). Sometimes a three way interaction among prey, predator and scavengers may also exist, as shown by seasonal black tailed deer (*Odocoileus hemionus columbianus*) killed by puma (*Puma concolor*) in northern California, the carcasses of which are later exploited by scavengers such as grey foxes, turkey vultures and ravens (Allen et al. 2014). Due to the ungulate migratory route, both kills and scavenging activity take place during summer and at similar altitude, suggesting that the three guilds share the same spatial and temporal distribution.

Carrion predictability is a key factor influencing scavenger behaviour (Pereira et al. 2014). Previous experience in successful foraging areas combined with recent pay-off from the same, in fact, influence the animal's future predictions (Harley 1981; Lefebvre 1983; Kamil and Yoerg 1985; Moody et al. 1996). Scavenging opportunities often occur in spatially limited and temporal pulses of carrion, making this source a predictable food supply for the local community (e.g.Deygout et al. 2010; Cama et al. 2012; Allen et al. 2014). Scavenging birds such as griffon vultures (*Gyps fulvus*), for instance, may rely on predictable resources. In particular, the introduction of feeding stations for conservation and management purposes were always preferred by these vultures over unpredictable natural carrion (Monsarrat et al. 2013). In some cases, this resulted in a narrowing of the birds’ home range around the feeding stations (in the absence of optimal flight conditions). Seasonal sources of carrion such as ungulate carcasses caused by starvation or natural mortality during the dry season are also selected by avian obligate scavengers (Kendall et al. 2014), which some of them are well adapted to using aggregated carrion (Cortés-Avizanda et al. 2012). The spatial and temporal distribution of a resource can therefore define the foraging areas of species. However, without considering multiple spatial scales related to the biology of the organism under study, results could be misinterpreted as some of the patterns could be overlooked (Wiens et al. 1993).

At a regional, large scale spatial overlap of species is expected, whereas the latter reduces at a smaller scale where spatial segregation (Pinaud and Weimerskirch 2007) can be explained by species prey preference or differences in foraging strategy (Cherel and Klages 1998; Weimerskirch et al. 2005). For instance, in several studies using tracking data seabirds may appear to be foraging in the same large geographical area, but, once the spatial scale is reduced, increasingly localised searching efforts of seabirds can be identified in narrower areas (e.g. area restricted search or ARS) (Pinaud and Weimerskirch 2007). Different levels of spatial and temporal overlap or separation can occur also between life stages of the same species. In particular, during winter juvenile birds can migrate along different routes, for longer distances than adults (Hake et al. 2003; Weimerskirch et al. 2006; Marques et al. 2009; Jorge et al. 2011) and rely on resources available in different locations. At the patch level, aggregations of conspecifics develop as searching foragers can be attracted by the feeding of other individuals (Pöysä 1992; Lima and Zollner 1996).This phenomenon, called local enhancement, is the result of social cues originated from individuals whose decision was made by copying conspecific behaviour (Simons 2004; Dall et al. 2005). In vultures, foraging success is related to social cues used for locating carrion (Jackson et al. 2008; Moreno-Opo et al. 2010). Finally, the finest scale over all is the food item (Gaillard et al. 2010) where other behavioural dynamics such as competitive events take place among consumers to gain access to the resource.

As has been shown previously (see Chapter 3), seal carrion appears to form one such predictable carrion pulse and therefore the distribution of scavenging gulls could be affected by the availability of seal carcasses and placentae occurring during the grey seal pupping season. Gulls are opportunist carnivores, being both predator and scavenger, as their diets consist almost entirely of animal prey (Spaans 1971; Pierotti and Annett 1987; Annett and Pierotti 1989). They forage around ships in inshore areas, on shoaling fish, in the intertidal zone, in agricultural areas, on refuse tips and even in litterbins in busy streets. In coastal areas, gulls are proficient intertidal predators, foraging from the surface at low tides (Furness and Monaghan 1987), preying upon a wide range of animals such as crustaceans, molluscs and echinoderms. Small mammals, like rats and rabbits, or birds are part of their diet as well (Harris 1965). In Scotland temporal and spatial changes in food supply and prey stocks, possibly linked to changes in fishing practices and higher resources available in urbanised areas, may be the cause of the observed decline of some seabird species in the North Sea (Frederiksen et al. 2004b). These changes possibly impact on the resident winter population of herring (*Larus argentatus*, Pontoppidan, 1763) and great black-backed gull (*Larus marinus,* Linnaeus, 1758) in particular, which would explain why the migratory lesser black-backed gull (*Larus fuscus,* Linnaeus, 1758) is not affected, as it is mainly a summer visitor to Scotland (Forrester et al. 2007). The gull species which overwinter on the Isle of May (Scotland, UK) are the herring gull and the great black-backed gull which are identified Red and Amber listed, respectively, in Birds of Conservation Concern (Eaton et al. 2015). Additional knowledge on the structure of the scavenging gull populations and its distribution can be used to enhance conservation management of important sites for wintering gulls such as the Isle of May.

In this study, we used a broad temporal and spatial approach to evaluate the influence of carrion on the distribution and behaviour of scavenging gulls before and during the grey seal season. Spatial scales were defined according to Johnson (1980): Scotland was the regional scale (distribution range or first order selection; 2 to 300 km), the Isle of May was the local scale (home range or second-order selection; 2 to 80 km) and the patch was the smallest scale considered (patch within home range or third-order selection; 100 to 2000 m). The scavenging species considered here were the great black-backed gull and the herring gull. The latter, differently from the great black-backed gull which consume seal carrion (Twiss et al. 2003), was rarely observed feeding on dead seals (see Chapter 2), despite its well-known scavenging habits (e.g. Monaghan et al. 1986; Hüppop and Wurm 2000). To avoid ambiguity in this study, carrion patch was intended as any area of the Isle of May containing carrion either dead seals or placentae.

The hypotheses tested were:

Regional scale

- carrion will have an effect at a regional scale: a positive temporal trend in the number of scavenging gulls counted on the Isle of May (Daytime and Roost counts) was predicted to occur before and during the seal pupping season (between September and December), whereas a fall in abundance would have been observed in the surrounding region during the same period of the year (BirdTrack data for South Scotland and WeBS counts for the Forth Estuary area at higher distance than 40 km from the Isle of May). A similar temporal trend to the one observed on the Isle of May was, instead, predicted to appear in the closest area surrounding the island (WeBS counts for the Forth Estuary area at lower distance than 40 km) as it would reflect the possible movements of gulls nearby the island.

Local scale

– carrion influenced the diel distribution of scavenging species at a local scale: assuming that gulls are mostly diurnal (Hailman 1964; Garthe and Hūppop 1996) and the great black-backed gull is the main species scavenging on dead seals, the relative abundances of gull species were predicted to change between day and night on the Isle of May, as the species dominating the Daytime counts would represent the main exploiter of carrion. Differences in Daytime and Roost counts would therefore indicate the relative importance of the island as feeding and roosting site for the different species.

Patch scale

Among patches

a – in areas where carrion occurred the number of gulls (moving, roosting, feeding and crossing over in flight) was higher than in areas where carrion was not present

Within patches

b – foraging activity of scavenging gulls was positively related to carrion availability: the number of gulls flying over the patches was higher at the peak of placenta and carcasses recorded during the seal pupping season, while feeding activity was directly proportional to the amount of carrion accessible (both placenta and carcasses).

4.3 Methods

4.3.1 Regional scale

Birdtrack data and WeBS counts

The British Trust for Ornithology (BTO) provided data on the seasonal pattern of gulls from the BirdTrack project and the Wetland Birds Survey (WeBS). The BirdTrack project collects daily birdwatching lists of bird species (seen and heard) at all times of the year from throughout Britain and Ireland and determines the proportion of lists with a given species. This would provide a good measure of frequency of occurrence of a determined species that can be used for population monitoring. The latter provides a standardised and effort-independent way of monitoring migration movements of birds across the whole UK (British Trust for Ornithology (BTO)). BirdTrack provided data on the relative percentage of complete birdwatching lists recording great black-backed gulls and herring gulls collected in South Scotland (Figure 4.1a) for the period 2005-2014, by week for each year.

WeBS monitors wetland birds around the UK, carrying out monthly Core Counts during the day at or near high tide on predetermined synchronised ‘priority dates’. Among the sites monitored, open coast and estuaries are also included. (For more details on the methods see: Bibby et al. 2000; Holmes and Stroud 1995; Rose and Scott 1997; Vinicombe et al. 1993). WeBS provided monthly counts of great black-backed gulls and herring gulls either roosting or feeding in the Forth Estuary (Figure 4.1b) for the period 1999-2013. The latter are monthly coordinated counts made principally during autumn and winter by volunteer ornithologists. The data here presented were originated by counts carried out in 50 sectors, which were grouped into three larger areas (Inner, North and South Forth) forming the Forth Estuary. The sectors of Ansthruther Bay and Elie Harbour on the north eastern coast were included in the larger area North Forth as not originally being part of the Forth Estuary. The counts included all gulls recorded within the sectors. As counts of gulls are optional in WeBS, sectors not showing data for gulls were excluded from the analyses. For the purpose of this project, the sectors were divided into two groups if they were located at a greater to or within a distance of 40 km from the Isle of May. This threshold was chosen as it is indicative of herring gull’s daily foraging trip distance (Spaans 1971; Sell and Vogt 1986; Kubetzki and Garthe 2003).

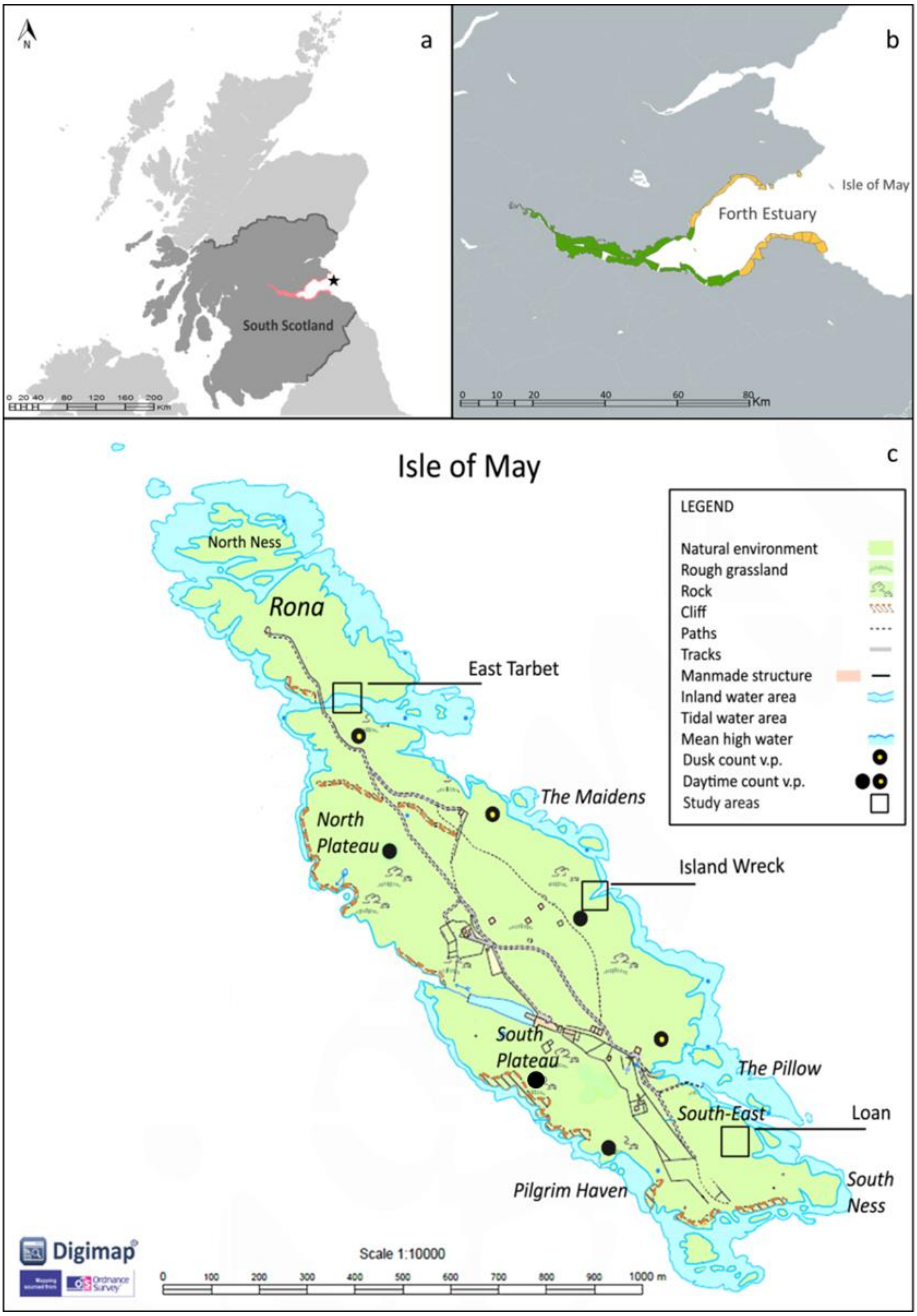

Figure 4.1 Multiple spatial scales used to study the influence of seal carrion on scavenging gulls.

a) South of Scotland (dark grey) where Bird Track data were collected (source: BTO), the highlighted area (pink) represents the Forth Estuary and the star symbol indicates the location of the Isle of May; b) the Forth Estuary where WeBS counts were performed (source: BTO): the two highlighted sub-areas of survey define higher (green) and lower (yellow) than 40 km distance from the Isle of May; c) the Isle of May where Roost, Daytime counts and among/within patches behavioural observations were made (see legend for details).

4.3.2 Local scale

The Isle of May

This study was undertaken on the Isle of May (56°11’ 19’’N, 2°33’ 27’’W; Figure 4.1c), situated at the entrance to the Firth of Forth on the east coast of Scotland. The island is 1.8 km long and less than 0.5 km wide, covering an area of 45 ha, with the long axis extending in a northwest-southeast direction. The Isle of May is owned by Scottish Natural Heritage (SNH) and it is a Special Area for Conservation (SAC) and also part of the Forth Islands Special Protection Area (SPA) due to the breeding colony of grey seals *H. grypus* and seabirds, such as terns, puffin, auks and gulls. SNH and Centre for Ecology and Hydrology (CEH) carried out biennial monitoring of gull populations nesting during spring on the Isle of May. Herring and lesser black-backed gull (*L. argentatus* and *L. fuscus*) populations increased since the 1990s and in 2011, 3,215 and 2,348 occupied nests were estimated, respectively. After a steady increase from 20 pairs counted in 2002, 40 pairs of great black-backed gulls (*L. marinus*) were counted nesting on the island during summer 2012 (SNH 2012). Within the Isle of May, most of the nests of great black-backed gulls were distributed on Rona, along the eastern side, but in fewer numbers on Tarbet, The Maidens and near the Island Wreck. For the three species (herring gull, lesser black-backed gull and great black-backed gull), first incubation occurs in the second half of April with the first chicks born in late May (Alampo and Lamont 2008; Alampo and Ash 2010). Common gulls were seen visiting the island, but not nesting (Squire and Pickett 2011). After the breeding season most of the herring and great black-backed gulls remain in Scotland (although some move south to England, Ireland or the European mainland), and between October and March the Scottish population increases owing to the arrival of other gulls from Scandinavia and Russia (Forrester et al. 2007). The lesser black-backed gulls, instead, leave the island in late September for wintering in southern areas.

The Isle of May grey seal colony contributes approximately 4.3% to the annual UK pup production (in 2010, SCOS 2013). During the decade 2000-2010 and 2012 the mean pup production was of 1988 (SE = 47.72) pups per year born around the 30th October (SE = 0.58), while the mean pup mortality at the seal colony during the same period was estimated to be 13.3 % (SE = 0.91) (see Chapter 3). When referring to the seal pupping season in this chapter, the period included between the mean pupping date (late October) and early December was considered. During this time interval of approximately 40 days, at least 50% of the pregnant females reach the seal colony, give birth and nurse their pups before they enter the post-weaning stage (Kovacs and Lavigne 1986).

Roost counts

Counts of birds at dusk are the most convenient tool to estimate winter gull population and seasonal movements (Burton et al. 2012). On the Isle of May point counts of roosting gulls (Roost counts) were performed at dusk during the grey seal pupping seasons from late October to the beginning of December in 2012 (N = 10) and from September to December in 2013 (N = 16). The interval times used were 17-18.00 GMT in September, 16-17.00 GMT in October and 15-16.00 GMT during November and December.

Point counts were carried out at the main roosting sites which were targeted after consulting with the SNH manager of the island (Figure 4.1c, yellow-spotted black dots): The Pillow-South Ness on the south-eastern side of the island, The Maidens on the east coast in front of the Low Light House and Rona located on the northern part of the island, representing the largest site among all (ca 10 times larger in area). The vantage points were respectively at the top of Kirk Haven hill, the Low Light House and Burnett's Leap. The latter was chosen because of the difficulties of using the North Horn located in Rona as a vantage point without disturbance to pupping seals. Roost counts were performed from south to north: in the smaller sites the Pillow-South Ness and The Maidens the number of gulls was recorded when light conditions were still good. As detectability declines rapidly during sunset and gulls reach the roosting sites at different times (Burton et al. 2012), in the largest roosting site of Rona five random sampled subsets of gulls with similar size were scanned in the stationary gull flocks when light conditions were good, while the total number of roosting gulls was recorded without discerning the species in darker light conditions. The average percentage occurrence of each species for the five random sampled subsets was calculated and used to finally determine the species relative abundance out of the total number of gulls counted (in principle similar to Banks et. al (2003) for wintering gulls in UK). When it was not possible to consider the random sampled subsets directly recorded in Rona, the average proportion observed in the other roosting sites were used. In order to make sure that counts were correct, a final total count was repeated until the same number of gulls was counted twice. During the Roost counts the following groups of birds were taken into consideration: great black-backed gull and herring gull. Juvenile gulls were recorded separately (Ralph et al. 1995) as a single category with all species pooled 2012, whereas in 2013 juvenile herring gulls were distinguished from juvenile great black-backed gulls. Time of day, site, high and low tide and weather conditions were also recorded whenever a gull count was made.

Daytime counts

Daytime counts were carried out to evaluate the number of gulls active on the island during the day. They were made between 12-14.00 GMT during the grey seal pupping seasons (from late October to the beginning of December) in 2012 (N = 5) and from September to December 2013 (N = 18).

Point counts of selected species (herring and great black-backed gulls) were undertaken at seven systematically placed stations located at a minimum distance of 250 m from each other (Ralph et al. 1995) (Figure 4.1c, both yellow-spotted black dots and black dots). The systematic stations were chosen in order to cover the whole island from North to South, on both eastern and western sides of the island: Rona, The Maidens, the North Plateau, the Island Wreck, the South Plateau, the South-East, and the Pilgrim Haven - South (Figure 4.1c). Time spent at each station was around 5 minutes, as the walking time between counting stations was less than 15 minutes (Ralph et al. 1995). The same species considered during Roost counts were considered also during Daytime counts.

4.3.3 Among and within patches

Behavioural observations

During the grey seal pupping season (from late October to early December) in 2012 the daytime behaviour of gulls was recorded from three areas. East Tarbet and the Loan were colonised by seals whereas in the area called Island Wreck there were few seals present (Figure 4.1c, squares).

East Tarbet is a seawater inlet influenced by tidal action situated on the eastern side between the main island and Rona. Here, seals move between the upper muddy/grassy area and lower rocky areas through a steep rocky slope to avoid the tide when pupping or to have access to the sea. While most seals give birth on the upper area, during low tide some seals are also found pupping below the high tide level (Figures 4.2a and 4.2b). The Loan is a flat muddy/grassy area located in the south eastern part of the island characterised by small freshwater pools. The latter create aggregation points for seals which move from their pupping sites to the pools to thermoregulate (Twiss et al. 2003). A rocky zone separates the Loan from the sea, making the area colonised by seals not affected by tide (Figure 4.2c). The area called the Island Wreck was also selected on the eastern side of the Isle of May. Grassy on the top and gradually rocky reaching the sea, this area was characterised by only few seals pupping (two adult seals and two pups) (Figure 4.2d).

Each behavioural observation was comprised of one hour of continuous sampling (used in e.g. Barrios and Rodríguez 2004; Everaert and Stienen 2006) suspended every 15 minutes by a focal scan (Martin and Bateson 1993), for a total of four scans. Continuous sampling and focal scans were performed in order to record, respectively, the number of gulls flying over the area (number of gull passages hour^{-1}) and the number of individuals moving, roosting and feeding in the area (for each behaviour, total number of gulls counted during the four focal scans). Gulls actively walking in the area were counted as moving gulls; non active gulls observed perching in the area were recorded as roosting gulls; gulls feeding on placentae, carcasses, seal milk and regurgitation on the ground and intertidal invertebrates were considered as feeding gulls. Individual gulls were distinguished within each focal scan, but not between focal scans and during the continuous sampling.

A total of 28, 30 and 6 observations were taken respectively in the Loan, East Tarbet and in the Island Wreck area between the 27th October and the 4th December 2012. Observations started one day after the mean pupping date, which in 2012 occurred on 26th October. Counts were undertaken daily at different times of the day, at low and high tide in the three areas. The vantage points for counts were raised and/or concealed positions in a hide and were chosen at a sufficient distance (>30 m) from the areas to minimise disturbance (Gregory et al. 2004). Areas of observations had an approximate size of 70 x 70m and only birds flying approximately over this area were counted. The bird counts included in the observations were herring, great black-backed gulls and juvenile gulls (species not distinguished). The number of seal carcasses available and not submerged by tide in the areas was also recorded.

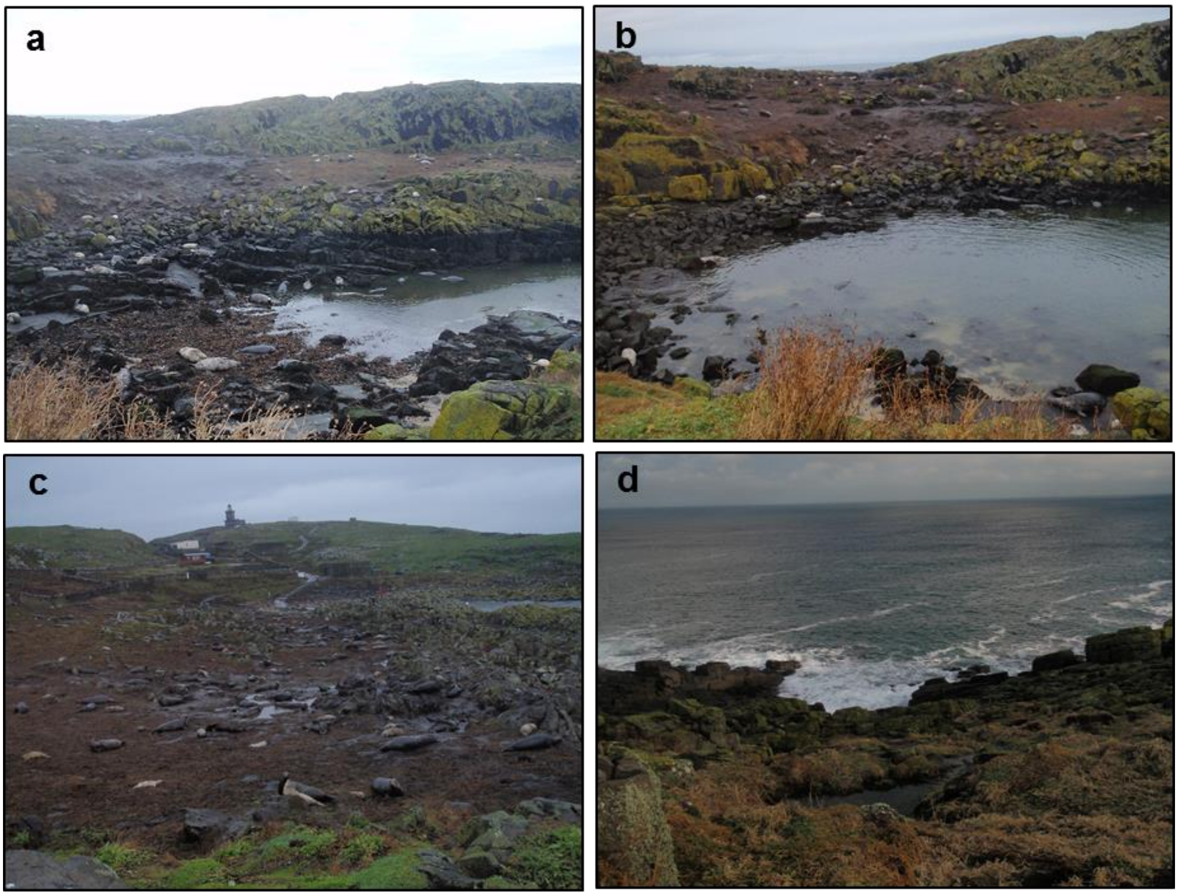

Figure 4.2 Areas used for behavioural observations.

a) East Tarbet at low tide; b) East Tarbet at high tide; c) the Loan; d) the Island Wreck.

4.3.4 Statistical analysis

Regional scale

In order to evaluate the potential influence of carrion on the distribution of gulls at a regional scale, the temporal trends of herring and great black-backed gulls between September and December (before and during the seal season) from the Birdtrack data, WeBS, Roost and Daytime counts were compared.

Birdtrack weekly percentages of complete birdwatching lists of herring and great black-backed gulls (N = 280) were re-scaled by considering as 100% the maximum percentage occurring in each year for both species. A linear mixed effect model (LME) was used to determine the relationship between the percentages of complete lists (response variable with normal distribution) and the fixed effect factors Species, Week and their interaction. The variable Year (from 2005 to 2014) was adopted as random effect factor selected *a priori* to explain the variation of percentages across years.

WeBS counts (non-normal distribution) (N = 2214) were modelled in a generalised linear mixed effect model (GLMM) having Species, Week and Distance from the Isle of May (< and > 40km distance) as fixed effect factors. The highest order of interaction among fixed effect factors was included in the model. The random structure was selected *a priori*: Area (North, South and Inner Forth Estuary), Sector and Year (from 1999 to 2013). An additional observation level random effect (OLRE) where each data point receives a unique level of a random effect was added to cope with over-dispersion in count data (Harrison 2014). If the model of best fit included the third way interaction this would show that the trend in the counts of gulls during time differed for each species at different distance from the Isle of May, suggesting that carrion availability at the seal colony influenced distribution of gulls at least in the closer area from the island (<40 km distance).

Daytime (N = 46) and Roost (N = 52) counts performed on the Isle of May were modelled in two distinct GLMs having Species, Week and their interaction as explanatory variables. Juvenile gulls counted in 2012 were here excluded as the species level was not recorded. The variable Year was considered as a fixed factor. Dealing with counts, Daytime and Roost data were modelled with both Poisson and negative binomial distributions.

For all the above described models, the range of the continuous explanatory variable Week considered was rescaled by using the range 0-14 instead of 35-49 to avoid inaccuracy of results due to lack of data between the 1st week (January) and the 35th (September). For all models carried out, the model of best fit was detected by backward model selection from the fully saturated model identifying the lowest Akaike's Information Criterion (AIC) and using likelihood ratio tests against the null model (Zuur et al. 2009; Bolker et al. 2009). When AIC values have a difference lower than 2, the simpler model was preferred. Visual checks of the residual plots were finally carried out to validate the model.

Local scale

Using Daytime and Roost counts during only the seal pupping season (late October to early December), the relative abundance of great black-backed gulls, herring gulls and juvenile gulls were used to evaluate changes between Daytime and Roost counts possibly suggesting the influence of carrion on the distribution of scavenging and non-scavenging species at the local scale. Assuming that gulls are mostly diurnal animals (Hailman 1964; Garthe and Hūppop 1996), the species dominating daytime counts would represent the main exploiter of carrion. At dusk, scavengers and non-scavengers would aggregate for roosting.

A general linear model (GLM) with a negative binomial error distribution, was carried out to explain the changes in number of gulls according to Species, Type of count (Roost and Daytime counts) and Year (2012 and 2013) as categorical explanatory variables. For this first model the number of juvenile gulls for the year 2013 (when the two species were counted separately) were calculated pooling the two species together. The full model was run including all the explanatory variables and the higher-order interactions, in order to identify the minimum adequate model by comparing the AIC scores of progressively simpler models. The model with the lowest AIC score was accepted as the fitted model. Significance-testing for the best fitted model was carried out by conducting a likelihood-ratio (Chi-square) test against the null model (Bolker et al. 2009). Model validation was performed through visual inspection of the residuals plots.

A second negative binomial GLM was performed to evaluate only the number of juveniles belonging to the species great black-backed gull and herring gulls counted in 2013. Again, the same process described above was used to select the best fitted model.

A Tukey contrasts test was carried out afterwards for both the GLMs to perform a multiple comparison of means among interacted categories (Type of count, Species and Year) for each factor included in the final model.

Patch scale

Among patches

Generalised linear models (GLMs) were carried out for each type of behaviour observed in 2012 to test differences in gull activity among the areas Loan and East Tarbet (where carrion occurred) and the Island Wreck (where carrion did not occur) for different species. The response variable was the total number of gulls observed, respectively, moving, roosting, feeding during the four focal scans and crossing over in flight during one hour of sampling for each day of observation. The explanatory variables were the area (East Tarbet, Loan and Island Wreck) and the species (great black-backed gull, herring gull and juvenile gull with the species pooled together). Dealing with count data, Poisson and negative binomial GLMs were performed and their AICs were compared in order to establish the best model. Categories (Activity vs. Species vs. Area) dominated by zero values were excluded from the models. A Tukey contrasts test was carried out afterwards to perform a multiple comparison of means among interacted categories for each factor.

Within patches

General additive models (GAMs) were used to describe the foraging activity of gulls, intended as feeding and searching efforts, in the Loan and East Tarbet. The response variables considered were the number of feeding and crossing over in flight gulls recorded, respectively, during the four focal scans and one hour count for each day of observation. Group of gulls (great black-backed gulls and juvenile gulls without distinction of species) and Area (Loan and East Tarbet) were the categorical explanatory variables. Carrion (sum of placentae and dead seals present), Sea level (in m, above Admiralty Chart Datum - ACD), Time (numeric) and Date (where 1 was equal to the first day of observation) were the explanatory continuous variables. Date was considered as it can give an indication of how gull activity can change during the seal season considering that placenta was likely to be available at the beginning of the period of observation, while the mortality peak happened close to the end of the season. If nonlinear patterns were found between the response and the continuous explanatory variables, the latter were tested as smoothers and the one presenting the lowest AIC was selected as definitive smoother (Zuur et al. 2010). If collinearity was detected between the proposed smoothers, the one having the highest AIC was declassed as the linear term in the model. Poisson and negative binomial GAMs were run in order to select the best model with lowest overdispersion and AIC values.

The latter analyses were performed in R 3.0.3 (R Development Core Team, 2012), using the packages ’nlme’ for the LME (Pinheiro et al. 2014), ‘lme4’ for the GLMER (Bates et al. 2014), ‘epicalc’ for the likelihood-ratio test (Chongsuvivatwong, 2012), ‘multcomp’ for the Tukey contrast test (Torsten et al. 2008), ‘MASS' for the negative binomial GLMs and GAMs (Venables and Ripley 2002) and ‘mgcv' for GAMs (Wood 2011).

4.4 Results

4.4.1 Regional scale

Model selection of percentage of completed lists of gulls in South Scotland supported the two way interaction between Week and Species suggesting that herring gull and great black-backed gull had different trends with time (Table 4.1). Great black-backed gulls were in fact decreasing faster from September towards December than herring gulls, which were recorded in a higher number of complete birdwatching lists (Figure 4.3a).

Table 4.1 Model selection for temporal trend of great black-backed gull and herring gull at regional scale using BirdTrack data.
Linear mixed effect model (LME); S = species, W = week, D = distance, Y = year

BirdTrack Data							
	df	**AIC**	**BIC**	**LogLik**	**Test**	**L. Ratio**	**p value**
1 ~ S*W (full)	**6**	**2255.876**	**2277.598**	**-1121.938**			
2 ~ S + W	5	2258.250	2276.370	-1124.125	1 vs 2	4.374121	0.0365
3 ~ S (null)	4	2269.747	2284.258	-1130.874	2 vs 3	13.497430	0.0002

The best model selected for estimating temporal trend of gulls in the Forth Estuary retained the three-way interaction between the terms Species, Week and Distance (Table 4.2). In fact, the log number of herring gulls decreased similarly from September to December regardless of the distance considered (Tukey Contrast, P = 0.4471), whereas distance influenced great black-backed gull numbers (Tukey Contrast, P < 0.001) (Figures 4.3b and 4.3c). Close to the Isle of May (<40km) great black-backed gulls were in higher abundance and showed a negative trend during time. At a further distance to the Isle of May, numbers of great black-backed gulls were very low and without any evident trend.

Table 4.2 Model selection for temporal trend of great black-backed gull and herring gull at regional scale using WeBS counts data.

Generalised mixed effect model (GLMM); S = species, W = week, D = distance, Y = year.

WeBS Counts

	df	AIC	BIC	LogLik	Test	Chisq df	Chisq	Pr (>Chisq)
1 ~ S*W*D (full)	**12**	**15388**	**15456**	**-7682.1**				
2 ~ S + W + D + S*W + S*D + W*D	11	15390	15452	-7683.9	1 vs 2	1	3.6882	0.054800
3 ~ S + W + D + S*W + S*D	10	15393	15450	-7686.6	2 vs 3	1	5.354	0.02067
4 ~ S + W + D + S*D	9	15403	15454	-7692.3	3 vs 4	1	11.4191	0.000727
5 ~ S + W + D	8	15456	15502	-7720.2	4 vs 5	1	55.7986	8.029e-14
6 ~ S + W	7	15460	15500	-7723.1	5 vs 6	1	5.8039	0.015990
7 ~ S	6	15489	15524	-7738.7	6 vs7	1	31.1286	2.415e-08
8 ~ 1(null)	5	16488	16516	-8238.7	7 vs 8	1	1000.188	< 2.2e-16

The best models selected for explaining the number of gulls counted at Daytime and Roost counts both dropped the factor Year but retained the two-way interaction between Species and Week showing that great black-backed gulls and herring gulls have different temporal trends on the Isle of May, but consistent across years (Figures 4.3d and 4.3e; Table 4.3 and 4.4). Herring gulls decreased towards the winter whereas the great black-backed gulls increased from September and during the seal season. At dusk, however, the number of gulls was generally higher than during the day for both species.

Table 4.3 Model selection for temporal trend of great black-backed gull and herring gull at regional scale using Daytime counts data.

Generalised linear model (GLM); S = species, W = week, D = distance, Y = year.

Daytime Counts

	df	AIC	BIC	Test	Chisq df	Chisq	p value
1 ~ S + W + S*W + Y (Poisson)	5	886.8152	895.9584				
2 ~ S + W + S*W + Y (NegBin full)	6	420.4126	431.3844				
3 ~ S + W + S*W	**5**	**418.4160**	**427.5592**	**2 vs 3**	**1**	**0.00340605**	**0.953461**
4 ~ 1 (null)	2	442.7998	446.4571	3 vs 4	**3**	30.38381	<0.001

Table 4.4 Model selection for temporal trend of great black-backed gull and herring gull at regional scale using Roost counts data.

Generalised linear model (GLM); S = species, W = week, D = distance, Y = year.

Roost Counts

	df	AIC	BIC	Test	Chisq df	Chisq	p value
1 ~ S + W + S*W + Y (Poisson)	5	2112.0444	2121.8006				
2 ~ S + W + S*W + Y (NegBin full)	6	629.3155	641.0229				
3 ~ S + W + S*W	**5**	**629.4460**	**639.2022**	**2 vs 3**	**1**	**2.130553**	**0.144389**
4 ~ 1 (null)	**2**	660.9782	664.8807	3 vs 4	3	37.5322	<0.001

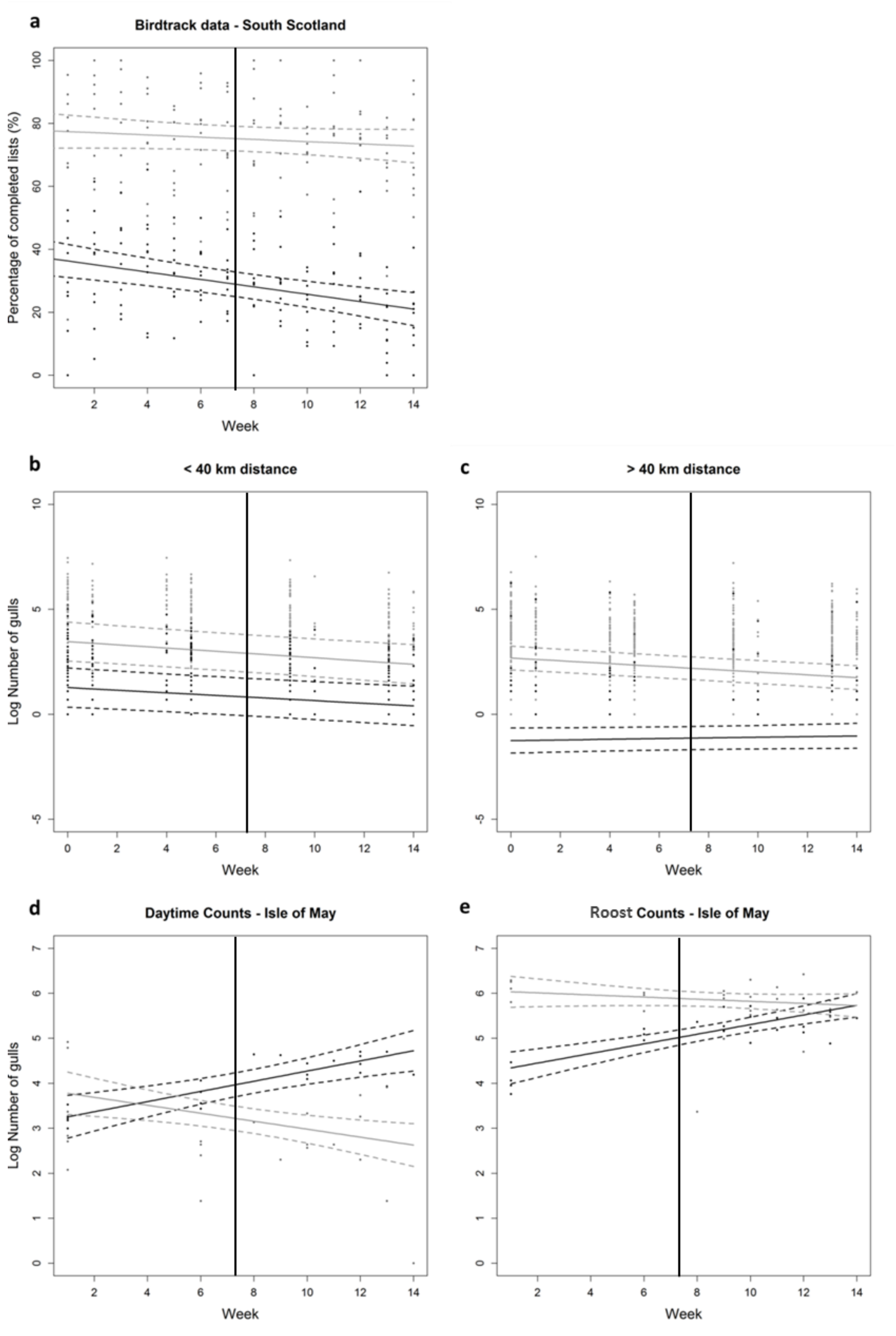

Figure 4.3 Fitted values for models explaining the distribution of gulls at regional scale.
Fitted values (solid line) taken from the model of best fit of the percentage of complete birdwatching lists collected in South Scotland (BirdTrack data) (a), the logarithm number of gulls counted at a lower (b) and higher (c) distance than 40 km from the Isle of May (WeBS counts), the logarithm number of gulls counted at daytime (Daytime counts) (d) and at dusk (Roost counts) (e) in the Isle of May versus week for herring gull (grey) and great black-backed gull (black) with 95% confidence intervals (dashed lines). The vertical line shows the timing of the mean pupping date; the seal pupping season expands from the line afterwards.

4.4.2 Local scale

Numbers of gulls counted in the Isle of May were best explained by a GLM with negative binomial distribution (likelihood ratio test: $X^2 = 166.15$, df = 8, $P < 0.0001$) that included the variables Type of count, Species, Year and the interactions between Type and Species and Species and Year (Table 4.5). No differences were found between counts performed in the two years, with the exception of juvenile gulls which were in lower abundance in 2013 (Table 4.6 and 4.7). Counts performed at dusk were different from those during the day (Table 4.7 Roost vs Daytime). Generally numbers of gulls were higher at night than during the day (Figure 4.4). The most common species during the day was the great black-backed gull, while at night the herring gull was in greater number.

Table 4.5 Model selection for number of gull per group counted at daytime and at dusk in 2012 and 2013.

Negative binomial generalised linear model (GLM): S = species or group of birds (great black-backed gull, herring gull, and juvenile gull), T = type of count (Daytime and Roost), Y = year (2012 and 2013).

	Number of gulls IOM					
	df	AIC	BIC	Test	Chisq df	LR stat
1 ~ S*T*Y	13	1001.3855	1034.722			
2 ~ S + T + Y + S*T + S*Y + T*Y	11	998.1234	1026.331	1 vs 2	2	0.737946
3 ~ S + T + Y + S*T + S*Y	**10**	**996.6670**	**1022.311**	**2 vs 3**	**1**	**0.5436266**
4 ~ S + T + Y + S*T	8	999.77	1020.287	3 vs 4	2	7.105541
5 ~ 1 (null)	2	1146.8174	1151.946	4 vs 5	6	159.0448

Table 4.6 Roost and Daytime counts performed on the Isle of May during the seal seasons 2012 and 2013.

Data are presented per year and per group of birds: GBBG = great black-backed gull, HG = herring gull and JUV = juvenile gull.

	Roost counts		**Daytime counts**	
	2012	**2013**	**2012**	**2013**
Mean (SE)	773.2 (68.02)	471.56 (42.36)	148.0 (24.74)	108.75 (9.28)
Range	444 – 1230	243 - 611	83 - 226	79 - 160
Date of peak	25th Nov	30th Nov	19th Nov	29th Nov

	Roost counts - 2012			**Daytime counts - 2012**		
	GBBG	HG	JUV	GBBG	HG	JUV
Mean (SE)	213.0 (22.7)	395.9 (42.61)	171.6 (22.53)	74.2 (10.45)	20.2 (7.75)	53.6 (12.40)

	Roost counts - 2013				**Daytime counts - 2013**			
	GBBG	HG	JUV GBBG	JUV HG	GBBG	HG	JUV GBBG	JUV HG
Mean (SE)	167.8 (14.48)	225.3 (33.28)	58.2 (7.16)	20.2 (4.79)	68.9 (4.39)	15.9 (4.48)	21.9 (2.50)	2.1 (0.51)

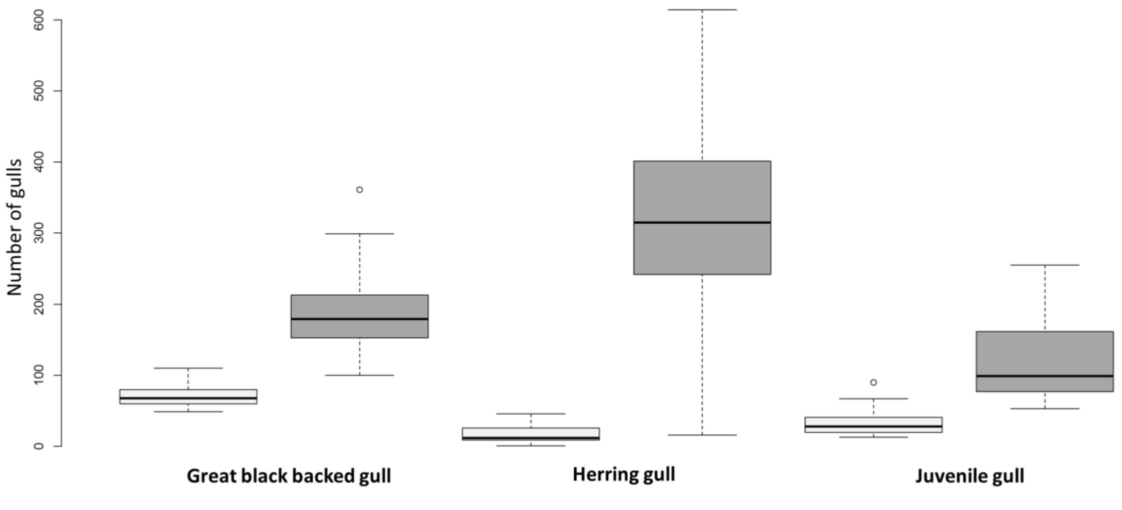

Figure 4.4 Mean number of great black-backed gulls, herring gulls and juvenile gulls (both species) from Daytime (white) and Roost (grey) counts performed on the Isle of May during the seal seasons 2012 and 2013.

On each box, the central mark is the median, the edges of the box are the lower hinge (25th percentile) and the upper hinge (75th percentile), the whiskers extend to the maximum and minimum data points, outliers are plotted individually.

Table 4.7 Tukey contrast tests performed between interacted categories of the explanatory variables Type (Daytime and Roost counts), Species (GBBG = great black-backed gull, HG = herring gull and JUV = juvenile gull – both species grouped together) and Year (2012 and 2013).

2012 vs 2013								
Type	**Roost**				**Daytime**			
	estimate	se	z value	Pr(>|z|)	estimate	se	z value	Pr(>|z|)
GBBGx2013 – GBBGx2012	-0.23865	0.18993	-1.257	0.9835	-0.07447	0.24146	-0.308	>0.99
HGx2013 – HGx2012	-0.56333	0.18891	-2.982	0.1105	-0.24094	0.26752	-0.901	0.9991
JUVx2013 – JUVx2012	-0.73789	0.19226	-3.838	0.0066	-0.80350	0.25046	-3.208	0.0577
Roost vs Daytime								
Year	**2012**				**2013**			
	estimate	se	z value	Pr(>|z|)	estimate	se	z value	Pr(>|z|)
GBBGxRoost –GBBGxDaytime	1.05453	0.22982	4.588	<0.001***	0.89035	0.2038	4.368	<0.001***
HGxRoost– HGxDaytime	2.97523	0.24456	12.166	<0.001***	2.65284	0.21782	12.179	<0.001***
JUVxRoost– JUVxDaytime	1.12014	0.23237	4.821	<0.001***	1.18575	0.21378	5.547	<0.001***
Between species at roost								
Year	**2012**				**2013**			
	estimate	se	z value	Pr(>|z|)	estimate	se	z value	Pr(>|z|)
HG - GBBG	0.61962	0.18391	3.369	0.0355*	0.29494	0.19477	1.514	0.9350
JUV - GBBG	-0.25960	0.18488	-1.404	0.9618	-0.75883	0.19712	-3.850	0.0065**
JUV - HG	-0.87922	0.18429	-4.771	<0.001***	-1.05377	0.19669	-5.357	<0.001***
Between species at daytime								
Year	**2012**				**2013**			
	estimate	se	z value	Pr(>|z|)	estimate	se	z value	Pr(>|z|)
HG - GBBG	-1.30108	0.28072	-4.635	<0.001***	-1.46755	0.22598	-6.494	<0.001***
JUV - GBBG	-0.32522	0.26950	-1.207	0.9881	-1.05424	0.22000	-4.792	<0.001***
JUV - HG	0.97587	0.28255	3.454	0.0264*	0.41331	0.23337	1.771	0.8294

The best model explaining the number of juvenile gulls counted in 2013 (GLM with negative binomial distribution, likelihood ratio test: $X^2 = 54.78$, df = 3, $P < 0.0001$) showed in general that there were higher numbers of juvenile gulls roosting than in the day (Table 4.8). In particular, juvenile great black-backed gull were the most abundant at both times of the day (Figure 4.5 and Table 4.9).

Table 4.8 Model selection for number of gull per species of juvenile gulls counted at daytime and at roost in 2013. Negative binomial generalised linear model (GLM): S = species (great black-backed gull, herring gull), T = type of count (Daytime and Roost).

Number of juvenile gulls IOM						
	AIC	BIC	Test	df	LR stat	p value
1 ~ S*T	**247.1255**	**254.7573**				
2 ~ S + T	254.9512	261.0566	1 vs 2	1	9.825686	0.001720915
3 ~ 1 (null)	295.9093	298.9620	2 vs 3	2	44.95813	< 0.001

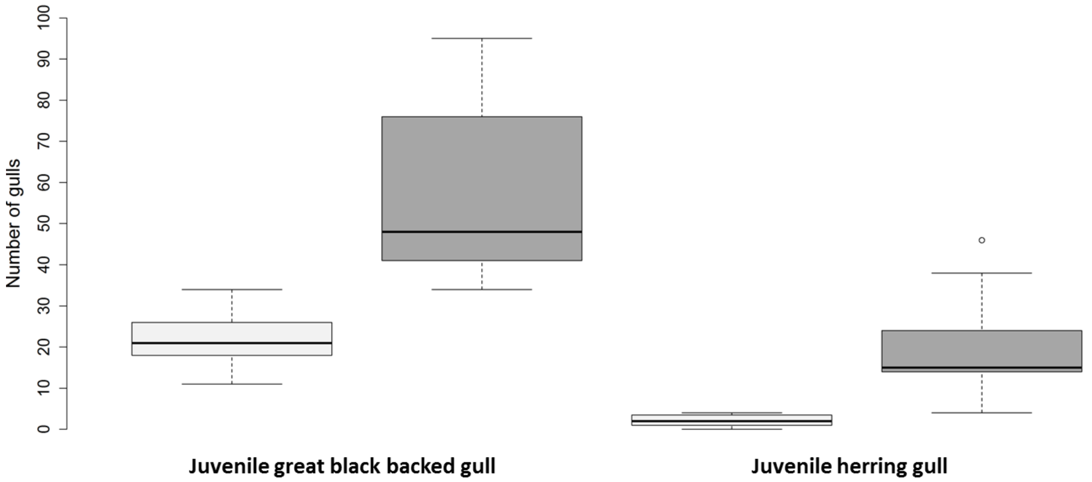

Figure 4.5 Mean number of juvenile great black-backed and juvenile herring gulls at Daytime (light grey) and Roost (dark grey) counts performed in the Isle of May during the seal season 2013.

On each box, the central mark is the median, the edges of the box are the lower hinge (25th percentile) and the upper hinge (75th percentile), the whiskers extend to the maximum and minimum data points, outliers are plotted individually.

Table 4.9 Tukey contrast test performed among interacted categories of the explanatory variables Type (Daytime and Roost counts), Species (JUV GBBG = juvenile great black-backed gull and JUV HG = juvenile herring gull).

<table>
<tr><th colspan="5">Between juveniles</th></tr>
<tr><th>Type</th><th colspan="4">Roost</th></tr>
<tr><td></td><td>estimate</td><td>se</td><td>z value</td><td>Pr(>|z|)</td></tr>
<tr><td>JUV HG – JUV GBBG</td><td>-37.889</td><td>6.527</td><td>-5.805</td><td><0.001***</td></tr>
<tr><th>Type</th><th colspan="4">Daytime</th></tr>
<tr><td></td><td>estimate</td><td>se</td><td>z value</td><td>Pr(>|z|)</td></tr>
<tr><td>JUV HG – JUV GBBG</td><td>-19.750</td><td>6.923</td><td>-2.853</td><td>0.0225*</td></tr>
<tr><th>Type</th><th colspan="4">Roost vs Daytime</th></tr>
<tr><td></td><td>estimate</td><td>se</td><td>z value</td><td>Pr(>|z|)</td></tr>
<tr><td>JUV GBBGxRoost – JUVGBBGxDaytime</td><td>36.347</td><td>6.728</td><td>5.402</td><td><0.001***</td></tr>
<tr><td>JUV HGxRoost – JUV HGxDaytime</td><td>18.208</td><td>6.728</td><td>2.706</td><td>0.0343 *</td></tr>
</table>

4.4.3 Patch scale

During the period of observation (1 – 39 days) in 2012 carrion was not available in the island Wreck area, while in the Loan and East Tarbet both placentae and seal carcasses occurred. Four and eight placentae were respectively recorded in the Loan and East Tarbet (between day 1 and 12), while day zero was the mean pupping date for 2012 (Figure 4.6). Seal carcasses, instead, were present during the whole period of observation and on day 30 the maximum number of 15 carcasses was reached in both areas. Due to bad weather the number of carcasses decreased drastically at day 31 in East Tarbet, where the dead seals were washed away from the original position and no longer recorded.

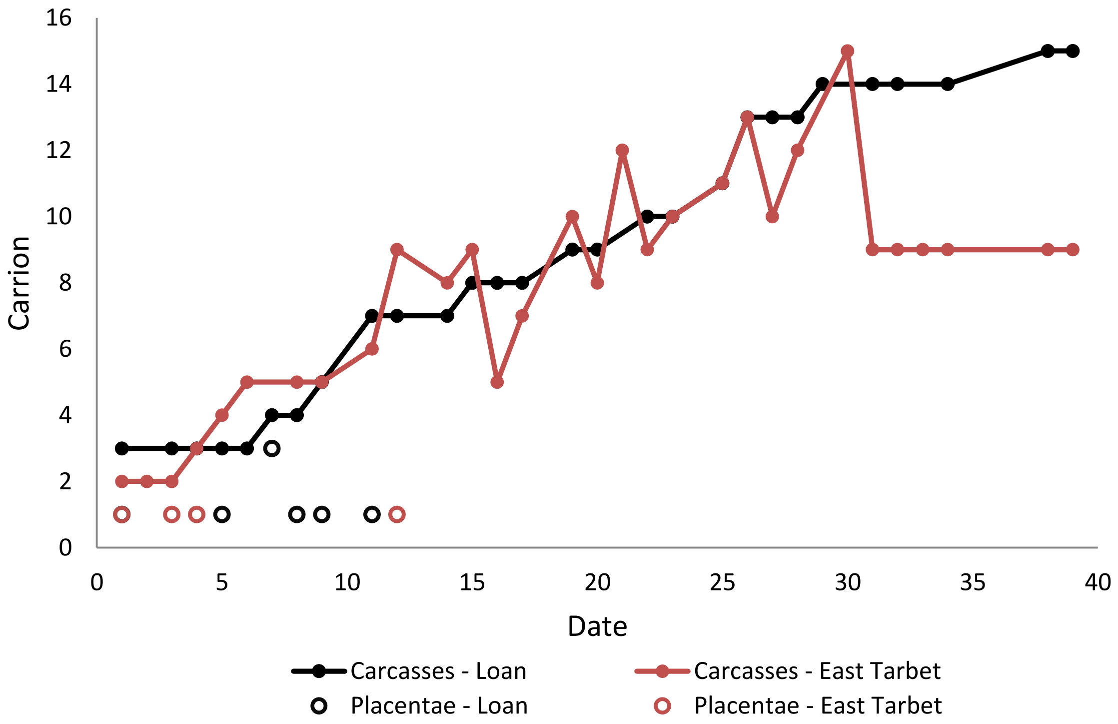

Figure 4.6 Number of seal carcasses and placentae occurring for each observation in the Loan (black) and in east Tarbet (red) during the seal season (Date, 1 = 27th Oct 2012).

Activity of gulls was generally higher in the Loan and East Tarbet compared to the Island Wreck area. In fact, only one great black-backed gull, one juvenile gull and no gulls were observed moving, roosting and feeding in this control area, respectively. Herring gulls were rarely seen active: a total of five, two and two individuals were counted in the three areas moving, roosting and feeding, respectively for the entire observation period. As the categories ‘Island Wreck’ and ‘Herring gull’ were dominated by or contained only zeros, they were removed from the models of the activities moving, roosting and feeding (Figure 4.7 and 4.8). Negative binomial GLMs were selected as best models for the four activities.

Counts of gulls showed that similar numbers of great black-backed gulls were observed moving within the two areas (Tukey, $P = 0.7176$), whereas juveniles were more often counted moving in the Loan than East Tarbet ($P < 0.0001$) (Figure 4.7). Few animals were seen roosting: the great black-backed gulls showed preference for roosting in East Tarbet ($P < 0.001$), whereas no significant difference was found between the areas for the juvenile gulls ($P = 0.0545$). Feeding activity of great black-backed gulls was similar in the two areas

(P = 0.5495); juvenile gulls, instead, were observed feeding in greater numbers in the Loan than in East Tarbet (P = 0.0080). No gulls were seen foraging in the control area. Flying over (crossing) observation areas was, instead, a common activity for all the groups of gulls, even if in the Island Wreck herring gulls were observed more often than great black-backed gulls and juveniles. The latter crossed equally both East Tarbet and the Loan (GBBG: P = 0.2506, JUV: P = >0.99). Comparing the two areas with the Island Wreck no significant differences were found between the number of flying gulls, with the exception of the number of great black-backed gull that was greater in East Tarbet compared to the Island Wreck area (P = 0.0031) (Figure 4.8). The number of herring gulls was lower than the other two groups of gulls in both East Tarbet (GBBG P < 0.001; JUV P < 0.001) and the Loan (GBBG: P < 0.001; JUV: P < 0.001). The number of herring gulls crossing East Tarbet and the control area was greater than in the Loan (P = 0.0111).

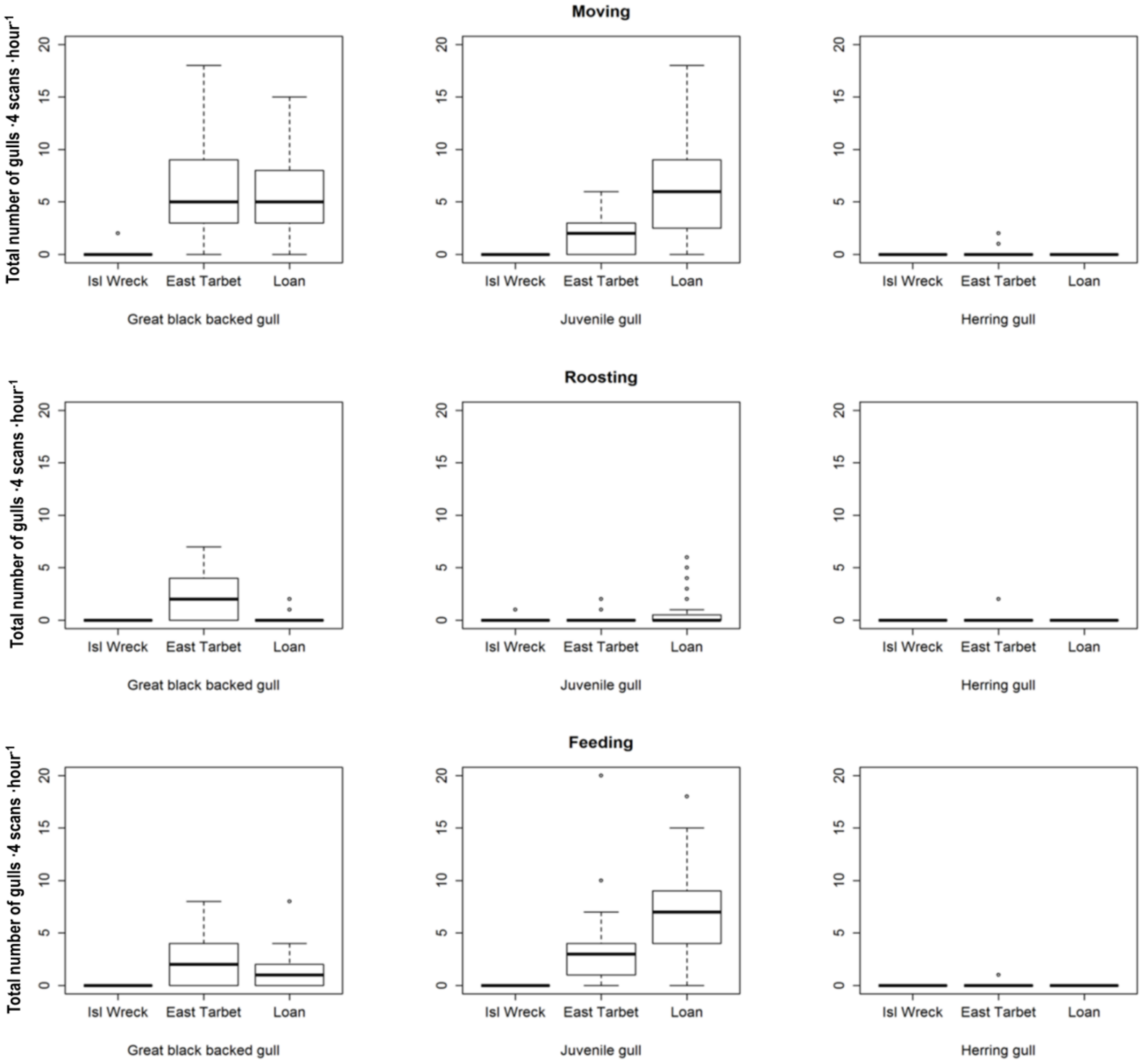

Figure 4.7 Total number of great black-backed, herring and juvenile gulls counted respectively moving, roosting and feeding during the four focal scans for each day of observation within the study areas (Island Wreck, East Tarbet and Loan).

On each box, the central mark is the median, the edges of the box are the lower hinge (25th percentile) and the upper hinge (75th percentile), the whiskers extend to the maximum and minimum data points, outliers are plotted individually.

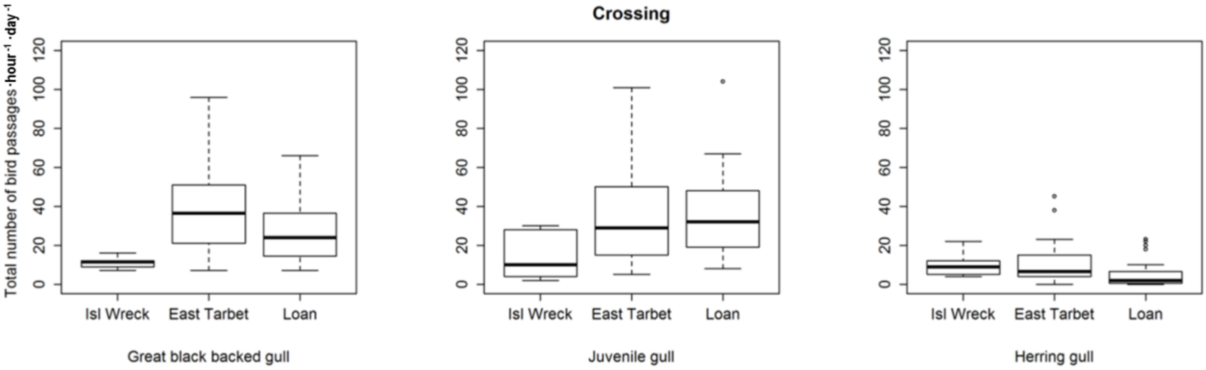

Figure 4.8 Total number of great black-backed, herring and juvenile gull passages recorded in one hour sampling for each day of observation flying over the study areas (Island Wreck, East Tarbet and Loan).

On each box, the central mark is the median, the edges of the box are the lower hinge (25th percentile) and the upper hinge (75th percentile), the whiskers extend to the maximum and minimum data points, outliers are plotted individually.

The feeding activity of gulls (total number of gulls during four focal scans day^{-1}) was best explained by a negative binomial GAM presenting Carrion as smoother, one for each Group of gulls (great black-backed gull, $P < 0.0001$ and juvenile gulls, $P = 0.0003$). Date ($P = 0.0025$) and Time ($P = 0.0066$) were included as linear terms, whereas the variable Area (Loan and East Tarbet) was dropped in the model selection as not significant (Appendix C.1). The number of gulls feeding on carrion increased according to the increasing number of placentae and seal carcasses available. The feeding pattern for the juvenile gulls showed a rise when the value of carrion is around seven, before increasing again (Figure 4.9a).

A second negative binomial GAM was selected for describing the crossing activity of gulls (total number of gulls hour^{-1} day^{-1}) over the carrion patches by using Date as smoother ($P < 0.0001$), the linear terms Sea level ($P = 0.0004$) and Carrion ($P = 0.009785$) and the categorical variable Area ($P = 0.0048$). Group of birds (great black-backed gull and juvenile gull) instead was dropped as not significant (Appendix C.2). The number of passages was at its greatest at the start of the observational study. Two peaks were detected around day 10 and day 32, separated by a fall in the number of crossing gulls around day 20, then after day 32 the number decreased again (Figure 4.9b).

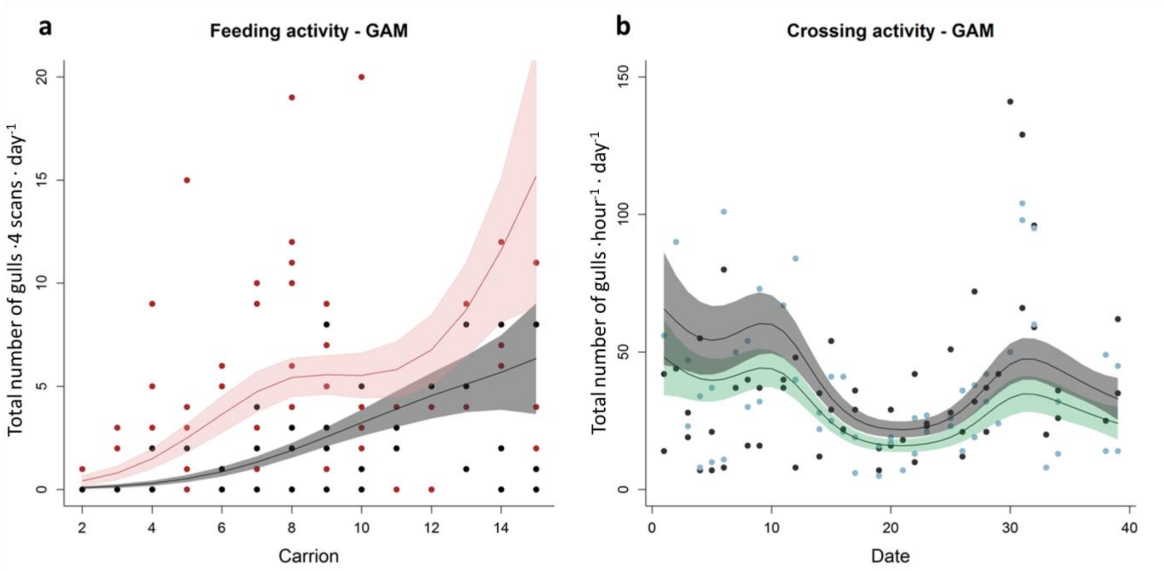

Figure 4.9 Trends in feeding and crossing activity of gulls at patch scale.

a) Trends in feeding activity of gulls (total number of gulls during four focal scans day^{-1}) according to carrion availability for great black-backed gulls (black dots and smoother) and juvenile gulls (brown dots and smoother); b) Trends in crossing activity of gulls (total number of gulls hour^{-1} day^{-1}) during time in the Loan (blue dots and smoother) and in East Tarbet (black dots and smoother). Shaded area on smoother line represents the 95% CIs.

4.5 Discussion

The objective of the present study was to assess the effect of seal carrion on the spatial and temporal distribution of scavenging gulls. Herring gulls and great black-backed gulls were the species considered in this work as the main component of the gull population wintering on the Isle of May. The latter are listed as species of conservation concern in the UK (Eaton et al. 2015) and the role of seal carrion as predictable food subsidy for these animals during winter is a topic so far overlooked.

The significance of carrion to gulls was demonstrated in this study in three ways. The species which fed on carrion (great black-backed gull) increased in abundance at the Isle of May at a time when they were falling in the surrounding region. Numbers in the species which did not feed on the seal carrion (herring gull) declined in the same way as abundance in the surrounding region. Both species showed a negative temporal trend also in the area closer to the Isle of May (less than 40 km distant) suggesting that seal carrion is not affecting the distribution of gulls on the coastal area. Herring gulls were more likely to leave the island to feed during the day than great black-backed gulls, rather than staying close to the carrion. Great black-backed gull numbers at areas with carrion were higher than in areas without carrion, while no such difference was seen for herring gull. Therefore for the seal carrion feeding species, great black-backed gull, the presence of carrion affected their abundance and behaviour at scales from the region to the patch. This relationship was investigated by using different types of data, such as counts and behavioural observations on gulls directly carried out on the Isle of May together with long-term database provided by JNCC. The latter represented a sensible alternative of more expensive methods such as telemetry, which would have been prohibitive if applied at a population level.

Little is known about the spatial ecology of these species especially during winter, as gulls disperse from the breeding sites and monitoring can be challenging. However, decadal surveys (Winter Gull Roost Survey or WinGS, BTO) and extensive work by Mitchell et al. (2004) revealed that the herring gull is resident in the UK between summer and winter, migrating during autumn, with Scotland holding 37% of the total UK wintering population. The great black-backed gull is also largely sedentary in the UK and its movements from the breeding colony appear to be relatively localised and mostly driven by feeding opportunities. Nevertheless southward movements, together with a substantial influx of non-breeders from Russia and Norway peaking in midwinter, are expected to explain the disparity in percentages between the wintering population estimates of England (70%) and Scotland (24%) (Wernham et al. 2002) as 85% of the nests are in Scotland (Mitchell et al. 2004). A ringed great black-backed gull juvenile was observed feeding on carrion on the Isle of May during the seal season 2013: it was a migrant from its natal site in Aberdeenshire in July 2013. On the Isle of May from 40 pairs of great black-backed gulls nesting during summer (SNH 2012), a maximum of 361 and 259 adults were counted at dusk in 2012 and 2013, respectively. The Isle of May therefore may not only be an important source of carrion but represents a winter roost site for gulls. However, the lower number recorded during the day suggested that not all the individuals observed at dusk stayed on the island during daytime, implying that a proportion of gulls of both species come back at dusk for roosting in the island and leave the following morning. As the number of great black-backed gulls counted on the coastal area of the Firth of Forth did not show any increase during the seal pupping season, it is possible that during the day these gulls use feeding sites which are not in the estuary or they forage at sea. In this study point counts were carried out, for both Daytime and Roost counts, as they represent the best compromise between accuracy and collection efforts (Ralph et al. 1995). However, difficulties can arise because of the uncertainty of recording the same bird twice (Gregory et al. 2004). This issue has been minimised counting gulls on the ground and not those birds observed flying over land or at sea and at a determined time of the day. Finally, as gull roosting sites were located in the same area where seal aggregated, it is likely that also gulls feeding on carrion at the time of the count have been recorded, maximising the accuracy.

At the local scale, a reversed relationship was found between proportions of species at dusk and at daytime. The great black-backed gull was the predominant species during the day and the herring gull was more common on the roosting sites. Our results showed that despite the abundant food resources on the Isle of May, the herring gull, together with a proportion of great black-backed gulls, appeared to forage somewhere else during the day. Therefore, a larger home range than the great black-backed gull could be attributed to the herring gull which potentially has alternative feeding habits than carrion, shared with first-winter conspecifics (Harris 1965). The competitive advantage of the great black-backed gull over the herring gull was the cause of diet partitioning during the breeding season (Rome and Ellis 2004; Steenweg et al. 2011) and during scavenging activity on fishery discards (Hudson and Furness 1988) and refuse tips (Greig et al. 1986) during winter. However, on the Isle of May only a few herring gulls stayed during daytime and competitive events between the two species were not seen (MMQ, personal observation). In fact, the few times that herring gulls were recorded feeding on the island they were pecking on milk regurgitation and not carrion. During the day the two species were therefore spatially and partially temporally segregated, however during night they shared the same roosting site. Generally, birds roost together for different reasons such as enhancement of thermoregulation (Watt et al. 2013; Brenner 1965; du Plessis and Williams 1994), avoidance of predators (Lack 1968), collective information sharing (Giraldeau et al. 2002) or family relationships when young individuals still depend on their parents (Lack 1968). In particular, herring gulls are known to be gregarious outside of the breeding season (Olsen and Larsson 2004).

The patch is the spatial level lower than the local and changes in the foraging behaviour are expected at this resolution. Results showed that activity of gulls was low in the area without carrion and no gulls were observed feeding in the same area, despite the possibility of exploiting intertidal resources such macro-invertebrates. Despite the low number of observations made on the Island Wreck, they are likely to provide a picture comprehensive enough as most of the counts were zero, and the error bars of boxplots presenting the data on gulls flying over the area were small (see Figure 4.7 and 4.8). The two more abundant groups of gulls, the juveniles and the great black-backed gulls, also flew across the Island Wreck area, suggesting that gulls were also flying between patches, possibly passing over other areas. Foragers should increase their searching efforts on patches where resources are abundant and predictable (Pinaud and Weimerskirch 2007) adopting a behaviour called Area- Restricted Search (ARS) to increase the food encounter rate and consequently food intake (Kareiva and Odell 1987). Social cues and consequent attraction towards conspecifics is another strategy acquired by social foragers for detecting patches (Beauchamp 1998) and it is used by a variety of animals(e.g. Kruuk 1967; Krebs 1974; Waite 1981; Pitcher and House 1987; Kirk and Houston 1995). This social behaviour could have affected the spatial distribution of the foragers on the Isle of May through local enhancement (Pöysä 1992), but also the habit of switching between patches (Houston et al. 1995; Frischknecht 1996) following the example of other individuals. Moreover, a learning component from present foraging success and past experience may have influenced the animal’s choice of returning to the patch (Bell and Baum 2002).

The finest spatial scale is the food item (Gaillard et al. 2010) that is exploited by the foragers in the patch. During the seal breeding season there were two main food sources available to scavengers: seal carcasses and placentae. The crossing behaviour displayed by both juvenile gulls and the great black-backed adults showed two distinct peaks during the seal season. The first peak was after the mean seal pupping date suggesting that gulls were searching longer for afterbirths, because they previously experienced a high density of this resource (Smith and Dawkins 1971). This is likely to be true, as data showed that during the days before the recorded peak in pupping, gull crossing rate was also higher. The second greatest point of the searching activity curve instead may be related to the time when seal carcasses were at the greatest abundance, which occurred on day 30, and the density of alive seals diminished revealing more detectable feeding opportunities to be selected. However, on day 31 the amount of carrion fell considerably in East Tarbet due to wave action, making our interpretation uncertain. Feeding behaviour in response to carrion availability demonstrated that the number of feeding gulls was related to the amount of carrion, as previously found in cinereous (*A. monachus*) and griffon vultures (*G. fulvus*) (Bosè and Sarrazin 2007; Moreno-Opo et al. 2010). Therefore, the behaviour of gulls adaptively changed according to the temporal variation in carrion opportunities during the pupping season.

Juvenile gulls were active scavengers on seal carrion on the Isle of May suggesting that it may be an important energy resource during winter, opportunistically exploited because of inexperience in foraging. Also young vultures feed on predictable carrion during the post-fledging stage in winter showing segregation from the adults which use predictable carrion preferably during summer when energy requirements are higher (Moreno-Opo et al. 2010).

Elucidating the relationship between scavengers and carrion will aid our understanding of carrion ecology and inform studies investigating the current decline of scavenging gull species. This study provided further insights in the cumulative impacts of food utilisation by gull species, which may help guide the future direction of gull conservation through effective management of areas characterised by abundant and predictable food resources for gulls, as already developed for other scavenging species such as vultures (Deygout et al. 2009; Deygout et al. 2010; Cortés-Avizanda et al. 2014). Due to the wide range of gull diet, seal carrion is an alternative resource. However, it can be still relevant to those populations overwintering on areas where seal colonies and predictable food occur. Buckley (1990) suggested that the return of the great black-backed gull after risking extinction around the beginning of the nineteen century was due to a reduction of both persecution and an increase of food supplies such as fish offal and refuse tips (Buckley 1990). Presently, new legislation reducing fishery discards in Europe (EU Regulation 1830/2013) could hasten the current decline of gulls by reducing foraging opportunities. In the future seal carrion may acquire increased significance for scavenging gulls.

Chapter 5: The impact of marine mammal carrion on the spatial and temporal distribution of the scavenging community at different geographical scales

5.1 Abstract

At seal colonies carrion is a common resource for scavengers whose influence on the behavioural dynamics of scavengers has not been fully defined. On the Isle of May, one of the largest grey seal (*Halichoerus grypus*) colonies in the UK, the feeding behaviour of juvenile and adult great black-backed gulls (*Larus marinus*) exploiting carrion was evaluated by monitoring 11 pup carcasses and 16 birth events (natural and experimental) using time lapse photography and video. No hierarchical succession of dominant scavengers through competitive displacement of subordinate individuals was predicted to occur under conditions of predictable and abundant carrion during the seal pupping season, leading to an equal scavenging effort by the two age classes. Hierarchical dominance was, instead, expected during scavenging activity on placenta as it represents a preferred energy-rich food item. Results indicate that temporal trend of scavenging activity and time spent feeding on carcasses were similar between adult and juvenile gulls and a nocturnal preference for feeding was evident. The house mouse was also found scavenging on carcasses during the night and it is likely this is the first study documenting this small rodent feeding on dead pinnipeds. Birth events attracted a higher number of competitors than carcasses, but no difference was found in the number of juvenile and adult gulls attending these births. However, adults spent less time than young con-specifics feeding on placenta, but were competitively superior during aggressive encounters with juvenile gulls both at carcasses and placenta. The present study gives an insight into the scavenging behaviour of different life stages of the main scavengers on grey seals and in particular highlights the importance of this food source for juvenile gulls during winter.

5.2 Introduction

Competition is ubiquitous in the lives of animals and the dominance of some species or individuals over others is often displayed through aggressive behaviour (Huntingford and Turner 1987). Dominant individuals out-compete subordinates during feeding, ultimately obtaining access to the food resource (Kruuk 1967; Houston 1975). Dominance is generally linked to larger body size and better fighting abilities than competitors (French and Smith 2005; Broom et al. 2009; Thornton et al. 2015). Moreover, age and sex are also crucial determinants of success during competitive events: young animals are usually subordinate to adults and lose more frequently when fighting, while sometimes males dominate females of the same age (Wallace and Temple 1987; Sheppard et al. 2013). Among scavengers, inter and intra-specific interactions drive most of the scavenging processes where the most dominant animals monopolise the carrion (see Chapter 2). This is evident among a wide range of obligate scavengers such as vultures and condors (Wallace and Temple 1987; Mundy et al. 1992; Donázar et al. 1999; Cortés-Avizanda et al. 2012). To overcome aggressive encounters and to reduce competition, subordinate individuals adopt some strategic behaviours, such as resource partitioning and spatial and temporal segregation (Blázquez et al. 2009). Less dominant individuals, therefore, may use different parts of the food item or adjust their arrival to the carcass to avoid competitors and increase foraging efficiency (Kruuk 1967; Houston 1975).

Social interactions are linked to resource availability and determine which individuals consume food when limited through competition (White 2008). In environmental conditions of food saturation, instead, a reduction of aggressive behaviour is expected (Wilmers et al. 2003b; Houle et al. 2006). In the absence of competition the consumption of the resource is predicted to be similarly partitioned among different consumers, either belonging to different species, age or sex. Additional factors influencing animal interactions are the distribution of resources and animal food preferences. Clumped resources, being defendable, promote a clear dominance hierarchy among consumers through competition (Houle et al. 2006). Moreover, according to optimal diet theory, the best diet is the one which maximises both the rate of energy and mass intake (Pyke et al. 1977), meaning that food with higher energy content and less handling time is preferred. During the consumption of a preferred resource, higher levels of competition are found and social dominance is encouraged (e.g. Rose 1994; Daily and Ehrlich 1994), eventually resulting in a change in food choice of subordinates when the density of dominant individuals increases (Pimm et al. 1985).

Carrion is common within pinniped colonies, and is likely to be extremely important to animals living nearby (Colombini and Chelazzi 2003). However, the potential of coastal marine mammal populations as a source of carrion to local marine communities is not well known (Watts et al. 2011). Grey seals (*Halichoerus grypus*) gather in late autumn in colonies for the pupping season. During this period carrion represents a predictable, abundant and nutrient-rich source of food in the form of placentae and dead pups for facultative avian scavengers such as great black-backed gulls (*Larus marinus*) (Ronconi et al. 2014 and Chapter 4). For many birds, scarcity of food corresponds to the wintering months, rather than during the breeding season, when food availability is super-abundant (Martin 1987). Thus, the energy acquired in wintering areas can be crucial for survival, especially for younger stages (Sanz-Aguilar et al. 2015) which have less experience in foraging and fewer skills in competing for food (Greig et al. 1983). Moreover, the two types of food item available at seal colonies greatly differ from each other, potentially establishing different relationships among consumers. Both seal carcasses and placentae are ephemeral resources; however, at the same temporal scale, the availability of a single placenta is shorter than a carcass as its smaller size and lower handling time permit a faster consumption. The energy density is also different, being higher for placentae (carcass: 14.1 MJ kg^{-1}, Table 3.2; placenta: 21.8 MJ kg^{-1}, Table 3.3). These differences could lead to a preference for placenta by scavenging gulls, which would potentially increase competition and enhance the establishment of the dominance hierarchy, while the abundant and longer lasting carcasses would relax the antagonistic interactions among consumers allowing a more egalitarian partition of the food resource.

Recognising and understanding the behavioural dynamics established among consumers would permit an estimation of the relative significance of carrion as source of food for its users. However, it is also crucial to consider the nature of feeding opportunities as different levels of food availability could change the relationship among foragers.

Here, the feeding activity and intra-specific interactions among scavenging gulls was investigated during the seal pupping season on the Isle of May where conditions are characterised by predictable and abundant carrion availability. It was predicted that there would be no formation of hierarchical dominance showing either successive stages of monopolisation of the carcass or temporal segregation induced by adult great black-backed gulls. Therefore, it was expected that the feeding rates (cumulative time feeding per day per carcass) of adult and juvenile gulls were equal and would show similar trends with time. Placenta was considered as the preferred food due to its higher energy density and lower handling time compared to carcasses, and regardless of its abundance and predictability during the seal pupping season, dominant individuals would have more access to the resource. Therefore, it was predicted that feeding rate of adult gulls (cumulative time feeding per bird per placenta) would be greater than juveniles. This study will provide not only greater insight into the ecology of seal carrion in an ecosystem context, but reveal new information on the feeding behaviour of one of the prominent avian scavenging species in the UK. Owing to an evident decline of several species of seabirds, more studies are needed if we are to implement management measures which take into account the needs of all life history stages of the species (Finkelstein et al. 2010).

5.3 Methods

5.3.1 Study area

Scavenging activity on seal carrion (carcasses and placenta) was monitored during the grey seal pupping season in 2013 on the Isle of May (56°11’ 19’’N, 2°33’ 27’’W) (Figure 5.1). This island is 1.8 km long and less than half a km wide, covering an area of 45 ha, with the long axis extending in a northwest-southeast direction. The Isle of May is a Special Area for Conservation (SAC) due to the breeding colony of grey seals *H. grypus*, one of the largest breeding colony of the UK contributing 4.5% to the annual UK pup production (in 2010, SCOS 2013). In 2013, the total number of seal pups found dead was 165. No pup production estimate was available for the 2013 seal season. However, the mean annual pup production for the decade 2000-10 and 2012 averaged 1988 (SE = 47.72), with a mean pupping date of 30 October (SE = 0.58).

The most visible scavengers occurring on the island are members of the family Laridae, the great black-backed gull (*Larus marinus*) and the herring gull (*Larus argentatus*). They both nest during summer and roost during winter on the island. Numbers of gulls per species counted on the island during the seal pupping season in 2013 are provided in Chapter 4. Carrion crows (*Corvus corone*) are also present on the island, but in low numbers. A previous study found only one crow nesting on the island (Alampo and Ash 2010).

5.3.2 Data collection and analysis

Carcasses

Fourteen grey seal pup carcasses were collected during the seal pupping season of 2013 (October and November) on the Isle of May (8.5% of total dead pups). Collection date, location, sex, developmental stage (1-5) according to Kovacs and Lavigne (1986), mass (± 0.01 kg) girth (± 0.5cm), body (nose to tail) length (± 0.5cm) and blubber thickness (± 0.5mm) by incision on the neck (where thinner; Beck and Smith 1995) were recorded (Appendix D.1). The carcasses were either completely intact or lacking one or both eyes prior to deployment. Carcasses were then placed on labelled metallic meshes at the edges of the main seal aggregations for the duration of the experiment (Figure 5.1). Carcasses were monitored by infrared time-triggered cameras (Bushnell Trophy Cam model 119436) for duration of between 8 and 34 days from the 28 October to the 30 November, dependent on when carcasses were found and collected. Cameras were located at a maximum distance of 5 m from the carcass, set on a triggered time-lapse mode and two photographs (8 MB resolution) were taken every five minutes (and every two minutes if movement-triggered) (Hamel et al. 2013). At approximately five-day intervals, carcasses were visited to download data from the cameras, record condition and mass. At the end of the study, the remains of each carcass was left *in situ* and weighed again in January 2014, if re-sighted.

Three carcasses (control carcasses, 12, 13 and 14) were collected and put into cages constructed from anti-mouse metal mesh (5mm aperture, 60L x 100W x 18H cm, weight = 1.16kg) to detect changes in mass without any scavenging activity involved from both avian and terrestrial scavengers (Appendix D.1).

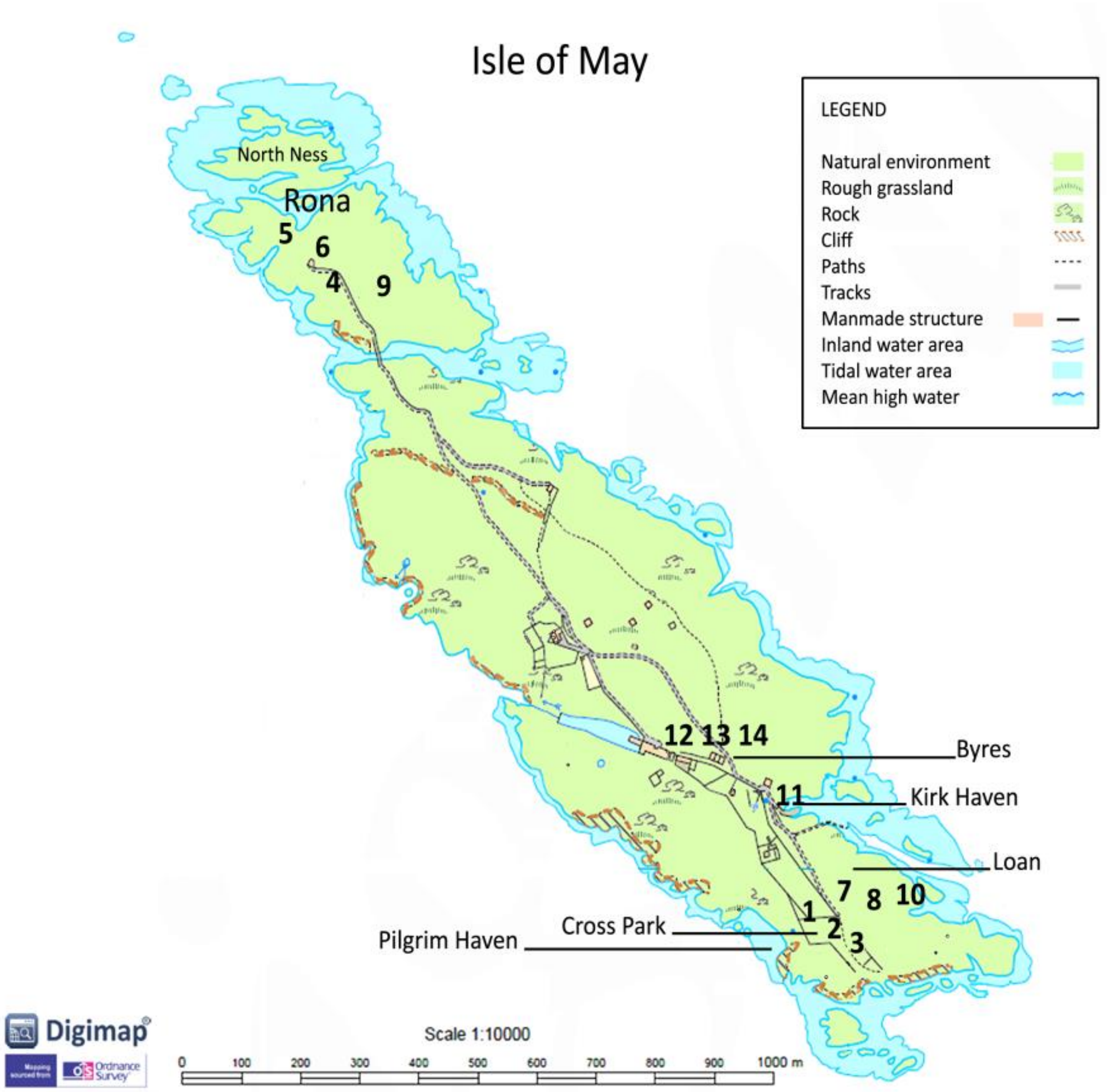

Figure 5.1 Map of the Isle of May.

Numbers indicate the location of experimental carcasses.Maps provided by EDINA Digimap Service, http://digimap.edina.ac.uk/roam/os.

Carcasses were scored for consumption state, where: A = carcass was intact, B = lack of both eyes and/or occurrence of one opening on the body, C = additional openings, D = body appeared flat and lacking internal organs and/or missing head and bones, E = remains (only bones and skin). For each consumption state the mean percentage mass loss was recorded from changes in mass (Figure 5.2).

Figure 5.2 Consumption states of carcasses (A - E).

The number of avian scavengers and non-scavenging passerine and non-passerine birds present around the carcass in an area of approximately 10 m radius was quantified and identified to the species level from photos. Juvenile gulls were distinguished from adults: individuals that exhibited at least some aspects of brown juvenile plumage or black beak, including birds belonging to their third winter, were classified as juveniles (Grant 1982). As individual recognition was not possible, only the maximum number (MaxN) of gulls appearing in the photo belonging to the two categories adults and juvenile gulls were considered. Time spent by gulls actively scavenging on the carcass was estimated from the number of minutes included between consecutive images till the gull disappeared. This is the maximum time that a bird could stay on the carcass. Birds observed roosting, walking or fighting were considered as not-feeding. When more than one bird was found scavenging simultaneously on the carcass, the resulting feeding time was adjusted according to the maximum number of active individuals.

Competitive events among individuals were also recorded and the successful bird identified. The bird showing aggressive behaviour and being able to displace its competitor from the area around the carcass was considered successful. Events were divided according to the following categories: competition between two adult gulls, two juvenile gulls and between one adult and one juvenile gull.

The scavenging activity of nocturnal mice was analysed separately as difficulties arose in determining the length of time in which they were feeding on the carcass, because of their small size and ability to hide underneath, behind and also inside the carcass. Time of arrival and maximum number of individuals (MaxN) for each experimental day was recorded. The proportion of photos in which mice were present out of the total number of photos taken by night (as they were only detected during the hours of darkness) was used as approximate estimate of mice attendance at the carcass per each experimental night.

Placenta

Scavenging activity on placenta was video-recorded (Nikon Coolpix P510). These experiments occurred in two ways. A previously-collected placenta was placed in an open area close to a hide from which observations were made (N = 6; observation 1-7), or if a natural seal birth occurred within range of an observer this was opportunistically recorded (N = 9; observations 8-16). Six whole afterbirths were collected in order to run the experimental events, they were weighed (± 10g), stored in individual plastic bags and frozen prior to the experiment. When an afterbirth could be associated with a pup, its sex was also recorded. Energy density for each experimental placenta was also estimated (Appendix D.2 and see Chapter 3). For both natural and experimental events, data collection (video and annotation when necessary) started once the placenta became available and ended either at its total consumption, when abandoned or when no longer visible because it had been moved by scavengers. For observations 1 and 2, the same experimental placenta was used, as it was ignored on its first deployment. The percentage of placenta consumed was estimated at the end of each event.

For both natural and experimental afterbirth events, species and life stage of scavenging birds occurring in the area of 10 m radius centered on the position of placenta were recorded. Juveniles were distinguished from adults as above. The maximum number of individuals present in the area (MaxN, feeding and not feeding grouped together), total feeding time and the number of ingestions, here called swallows, for each gull life stage were registered for each event. When more than one individual was in contact with the food item, the feeding time was calculated multiplying the number of gulls by the time spent feeding on placenta. Number of agonistic events was also recorded: adult against adult, juvenile against adult and juvenile against juvenile, including different species. The bird showing aggressive behaviour and being able to displace its competitor from the placenta was considered successful. Video analyses were performed using EventMeasure (SeaGIS Pty Ltd).

For experimental events the known mass of placenta was considered while for live births the mean mass was used (1.6 kg, SD = ±0.24; energy density: 21.8 MJ kg^{-1}; SD =± 1.15) (Appendix D.2). For one of the natural events (observation 13), it was not possible to quantify the gull's swallows as most of the placenta was consumed behind some rocks, preventing the observer from counting them precisely.

5.3.3 Statistical analysis

Carcasses

Only the feeding activity of adult and juvenile great black-backed gulls was used in the following statistical analyses. Herring gulls and carrion crows rarely visited the carcasses and so there was insufficient data for analysis.

Occasions when researchers were present in the area, cameras did not operate or were displaced by seals were not included. Carcasses 5 and 9 were excluded from the analysis as scavengers did not open them and scavenging activity observed was lower or equal to 1% of total monitoring time.

Mass loss of experimental carcasses was modelled using a linear mixed model (LME) where the mass change for a determined interval time between two mass measurements was explained by Feeding activity (total minutes per time interval) and the gull Stage (adult and juvenile), while the term Carcass was a random effect.

A general linear mixed effect model (GLMM) was performed to determine the effect of the fixed factors Stage (adult and juvenile), Experimental day (1/34 days, where 1 = first day of deployment of the carcass) and their interaction on the number of minutes of daily feeding activity of gulls (response variable with Poisson distribution). The variable Carcass (N = 9) was included as a random effect to explain the variation of scavenging activity across carcasses.

To explore variation in feeding activity among carcasses, a generalised linear models was also fitted for each carcass: Poisson and negative binomial GLM were performed using Stage, Experimental day and their interaction as before and finally the model with the lowest AIC was chosen, checking residual plots.

A general additive mixed model was carried out to detect differences in scavenging activity between gull stages (juvenile and adult) with time of day. In this model the proportion of time spent feeding for each hour of the day (response variable, binomial family) was modelled according to Stage (adult and juvenile) and Hour (1-24). Again, Carcass was used as the random effect. To take into account the temporal autocorrelation among hourly data the model was fitted using an AR(1) correlation structure (Zuur et al. 2009). The model of best fit was detected by the lowest Alkaike's Information Criterion (AIC) (Zuur et al. 2009).

A Chi-square goodness of fit test was carried out to test whether the observed frequencies of the number of competitions won by adult and juvenile gulls were as expected. Expected frequencies were set as equal number of aggressive events won by adult and juvenile individuals in order to understand which gull stage was competitively superior.

Finally two linear mixed model (LMEs) were performed to show mass loss of both experimental and control carcasses during time of deployment, to test the effect of scavenging activity on dead pups in comparison to carcasses located in cages and protected by scavengers.

Placenta

The non-parametric Mann-Whitney U-tests were performed to test for differences in the first arrival time of gulls between the two type of events (experimental and natural placentae), but also between maximum number (MaxN), feeding activity (minutes event^{-1}) and swallowing rate (N swallows min^{-1}) of the two gull stages. As for carcasses, the observed frequencies in the number of successful competitive performances of adult and juvenile gulls were tested with a Chi-square goodness of fit test against the expected frequencies, set as equal between the two gull stages.

The latter analyses were performed in R 3.0.3 (R Development Core Team, 2012).

5.4

5.5 Results

5.5.1 Carcasses

The collection of time-lapse photos analysed included 147,630 photos resulting in a total of 482,081 minutes of monitoring. Avian scavengers detected were the great black-backed gull, the herring gull and the carrion crow. The house mouse (*Mus musculus*) was also identified during nocturnal hours. Other species present but not feeding on the carcasses included oystercatcher (*Haematopus ostralegus*), redshank (*Tringa tetanus*), purple sandpiper (*Calidris maritima*), turnstone (*Arenaria interpres*), curlew (*Numenius arquata*), grey heron (*Ardea cinerea*), rock pipit (*Anthus petrosus*), starling (*Sturnus vulgaris*) and blackbird (*Turdus merula*).

Three carcasses were opened by adult great black-backed gulls after 7.25 days (carcasses 2, 4, 8; SE = 2.30), three by juveniles after 9 days (carcasses 3, 6, 7; SE = 7.02). One carcass was exclusively opened by mice after 4 days from its deployment (carcass 1), while one carcass started to be dismantled by the combined scavenging activity of both house mice and adult great black-backed gulls on its second day (carcass 10). For a carcass (carcass 11), instead, it was not possible to detect which scavenger got access first. At the end of the experiment two, out of a total of eleven deployed, carcasses were not opened by scavengers (carcasses 5 and 9) (Appendix D.3).

Excluding those ignored by consumers, the rest of experimental carcasses were monitored for a total of 460,899 minutes: adult and juvenile great black-backed gulls scavenged, respectively, for 3.0% and 3.4% of the whole time, while adult and young herring gulls and carrion crows for small portions of time (0.007%, 0.001% and 0.008%, respectively). The maximum number of scavengers foraging together was two, with the exception of the herring gull which always scavenged individually (Table 5.1). Scavenging activity of the mice was detected in 17.3% (SE = 1.48) of the photos taken by night and started on average at 16:52 (SE = 0. 28min); the maximum number of individuals detected was 10.

Table 5.1 Total feeding time (min) and maximum number (MaxN) of scavenging birds active on experimental carcasses.

	GBBG adult	GBBG juvenile	HG adult	HG juvenile	Carrion crow
Feeding time (min)	13847	15421	31	5	35
MaxN	2	2	1	1	2

The rate of mass loss of carcasses was positively related to feeding activity of great black-backed gulls, but no interaction between age class and total minutes spent feeding per interval was significant (Figure 5.3, Appendix D.4).

Feeding activity of gulls increased during time from the first day of carcass deployment. Best model (GLMM, Poisson distribution) retained the interaction between Stage and Experimental day (Appendix D.5) showing that feeding rate at carcasses increased similarly, but not equally, with time for adult and juvenile gulls (Figure 5.4). However, variation in the scavenging activity of the two stages was evident when looking at different carcasses individually (Figure 5.5). Best models showed that for five carcasses (2, 6, 7, 8 and 11) the interaction between stages was not significant, while for the rest it was (Figure 5.5). The first three carcasses to be deployed for the purpose of this experiment (1, 2 and 3) showed similar patterns characterised by null feeding activity during the early experimental days and a drastic increasing towards the late ones. Carcasses 6 and 8 were instead scavenged immediately once deployed causing a negative trend during time, whereas feeding activity gradually increased on carcasses 7 and 11. Different and opposite trends between stages were depicted when exploring scavenging activity on carcasses 4 and 10, where a decreasing in the feeding activity was observed, respectively, for adult and juvenile gulls, while the other stage’s trend stayed almost constant during time (Figure 5.5).

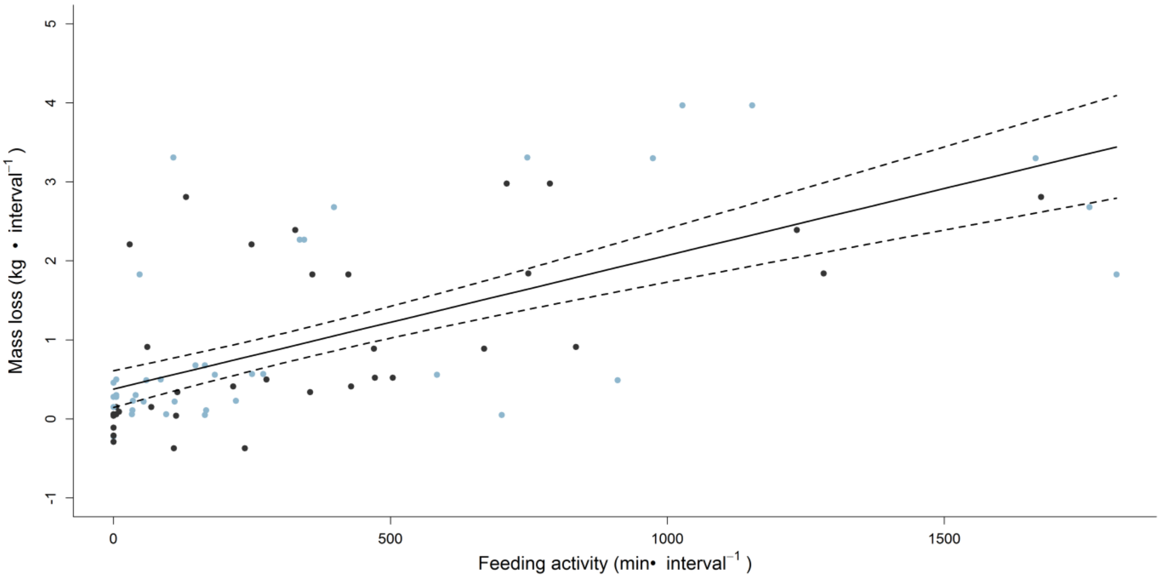

Figure 5.3 Plot of mass loss of experimental carcasses per monitored interval time versus feeding time of adult (black dots) and juvenile (blue dots) great black-backed gulls of the same interval.

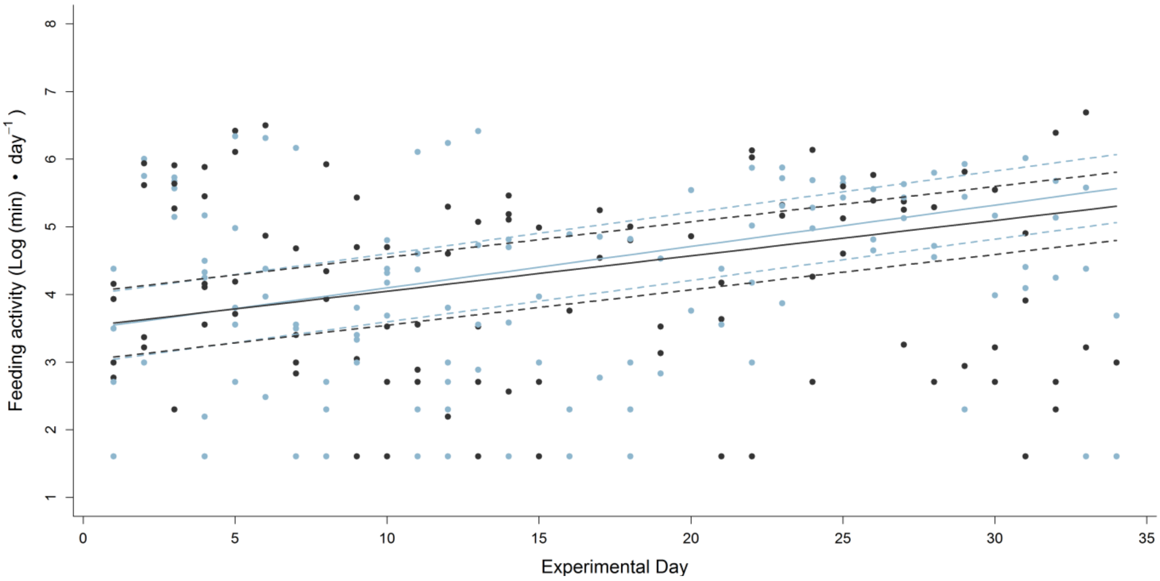

Figure 5.4 Fitted values (solid line) taken from the model of best fit (GLMM) of feeding activity (minutes day^{-1}) of adult (black) and juvenile (blue) great black-backed gulls versus Experimental day (where 1 is equal to the first day of deployment of the carcass) with 95% confidence intervals (dashed lines).

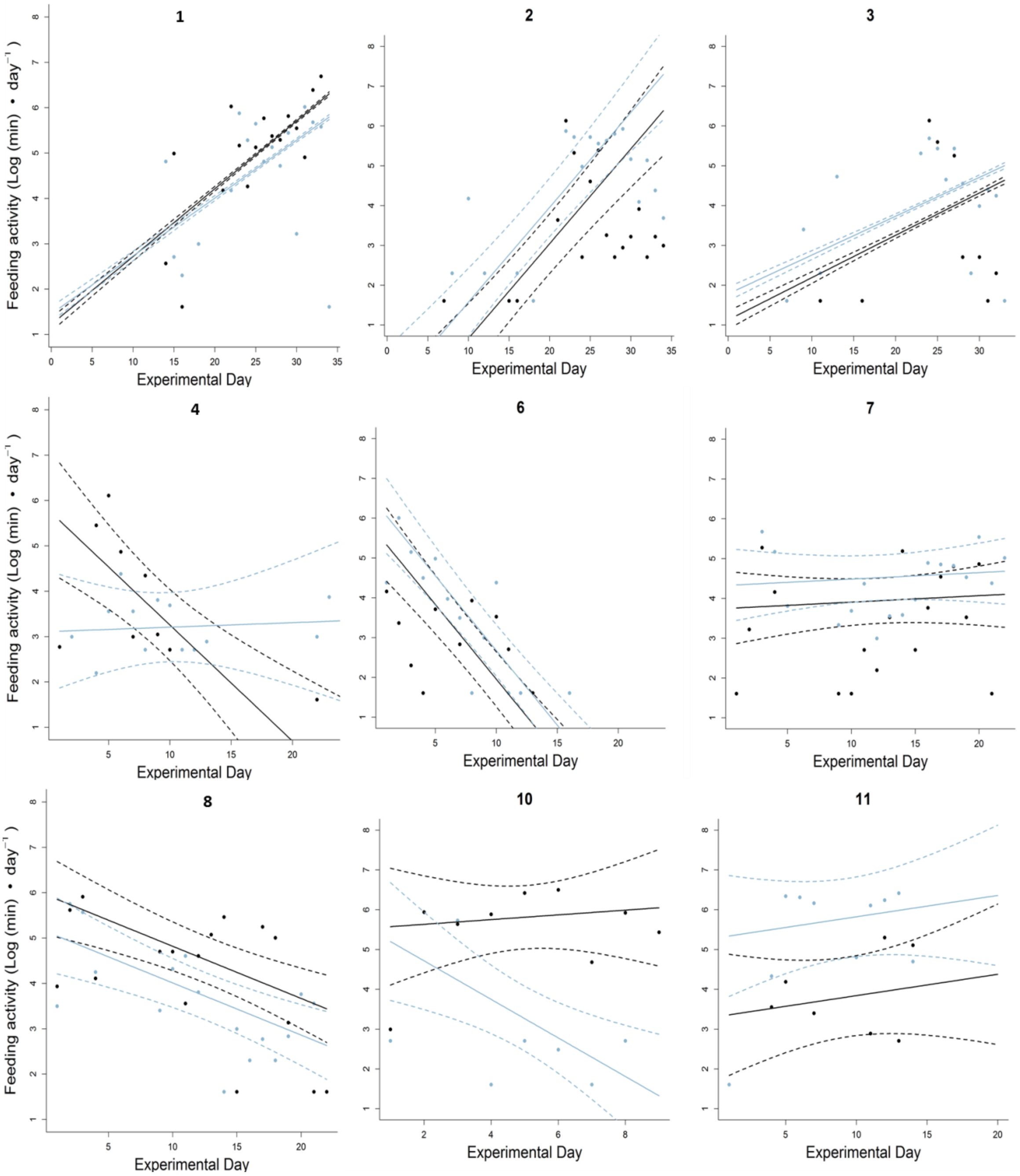

Figure 5.5 Fitted values (solid line) taken from the model of best fit (GLM) of feeding activity (minutes day^{-1}) of adult (black) and juvenile (blue) great black-backed gulls versus Experimental day (where 1 is equal to the first day of deployment of the carcass) with 95% confidence intervals (dashed lines) for individual carcasses (numbers on top of plots).

The proportion of feeding activity of gulls by hour (minutes hour^{-1}) was best explained by a binomial GAMM presenting Hour as unique smoother ($P < 0.001$) for both Stages of gulls ($P = 0.071$) (Figure 5.6 and Appendix D.6). The time spent feeding on carcasses increased during nocturnal hours and in the early hours after sunrise, but decreased during the day. Considering that the amount of hours with daylight in a day were 8.5 (SE = 0.14), while the hours of darkness were 15.5 (SE = 0.14), the mean feeding activity performed by the class of juvenile gulls during daylight and hours of darkness was, respectively, 4.8 (SE = 0.30) and 3.1 (SE = 0.20) minutes per hour. The adult stage scavenged, respectively, for a mean of 2.1 (SE = 0.21) and 3.9 (SE = 0.22) minutes per hour per carcass during the day and night.

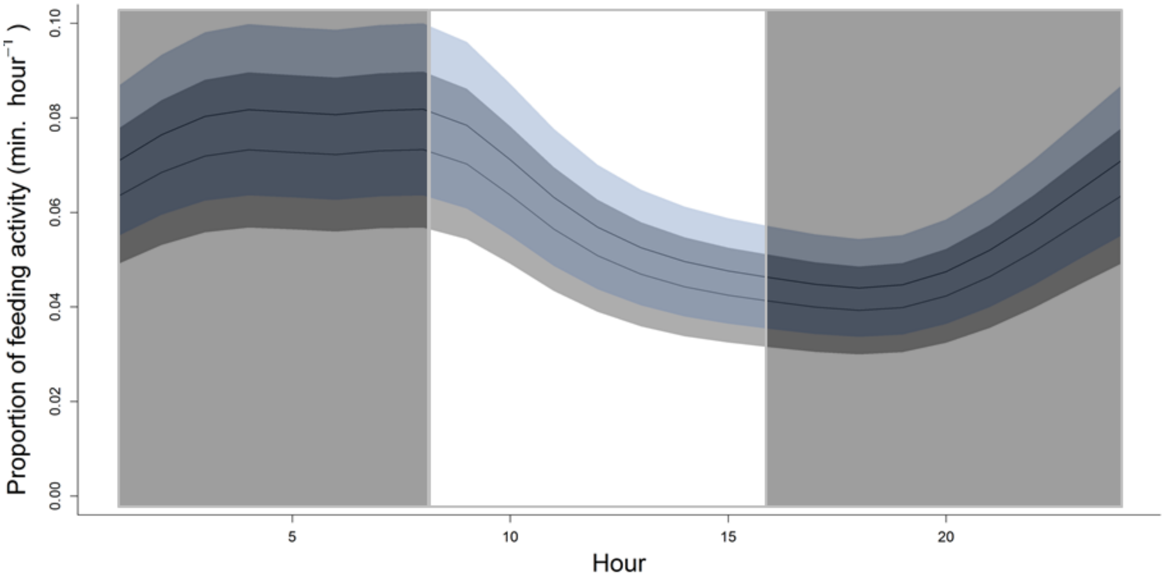

Figure 5.6 Trend in proportion of feeding activity during the day (minutes hour^{-1}) of adult (dark grey smoother) and juvenile (blue smoother) great black-backed gulls on experimental carcasses; shaded area on smoother line represents the 95% CIs. Hours of darkness are grey-shaded, while daylight hours are white-shaded.

Competition

A total of 99 competitive events were detected. There was a difference in proportion of competitive events between juvenile and adult gull: 59 (59.6%) were competitions between a juvenile and an adult, 15 (15.2%) between two juveniles and 25 (25.3%) between two adults. Adults were more successful than juveniles in competing for the carcass ($X^2 = 20.55$, df = 1, $P = 0.001$).

Consumption states of carcasses

The mean cumulative mass loss (in %) for consecutive consumption states observed on experimental carcasses was calculated (Table 5.2). Small changes in the carcass mass were visible also when the body appeared still intact (state A). Generally, scavenging gulls consumed the eyes of the dead seals first. Following, they accessed the internal organs by pecking and breaking the abdominal skin (state B). The latter process was facilitated when the neonatal umbilicus was still present (first development stage of seal pups). It was observed that other openings rather than, or in addition to, the umbilicus were produced when the carcass position did not expose the abdomen. The areas most targeted after the abdomen were the scapula and axilla regions (state C). The seal's head was strongly consumed by gulls which emptied the orbital cavity and softened the area of the neck, provoking its disarticulation and creating additional access to internal parts. At this late stage, the continuous scavenging activity would have depleted most of the body organs, also from the thorax (state D). The maximum consumption of the carcass, represented solely by seal remains, was often associated with the gull's ability to turn the seal body inside out through the openings generated before in order to exploit the carcass completely (state E). Scavenging activity of mice was characterised by wounds generated often on soft tissues, such as the seal's eyes, nose and gums, but also on other parts of the body surface, as observed for carcass number 1.

Mass loss depicted by consecutive measurements on experimental carcasses during time were owed only to scavenging activity rather than decomposition, as the variable Experimental Day was significant when modelling the mass loss of experimental carcasses ($P < 0.0001$) (Figure 5.7a), whereas it was not significant when explaining variation in mass loss of those carcasses deployed in cages (control carcasses, $P = 0.4037$) (Figure 5.7b). Feeding activity of scavengers caused an average loss of 0.3 kg per day. The small changes observed in the mass of both un-scavenged experimental and control carcasses were probably due to wetting and drying according to weather.

Table 5.2 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

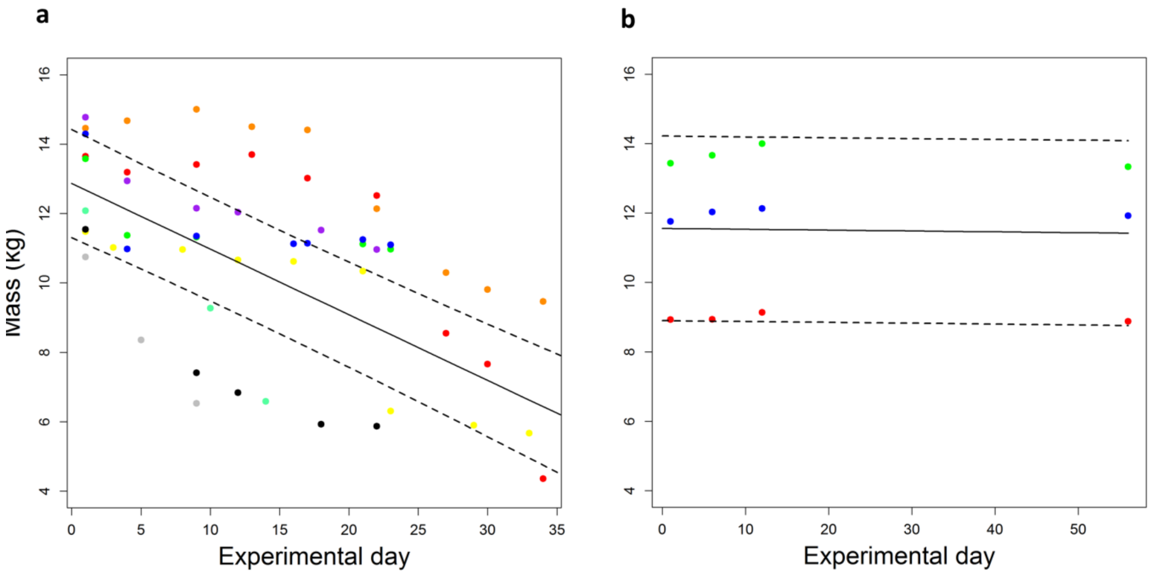

Figure 5.7 Mass (kg) of experimental carcasses (N = 11) (a) and control carcasses (N = 3) (b) as function of experimental day (where 1 = first day of deployment of each carcass). Each colour identifies a carcass.

5.5.2 Placenta

Gulls detected the afterbirth in 15 out of 16 events, reaching the area surrounded the placenta on average after 7.1 minutes (SE = 3.59). Avian scavengers were attracted to female grey seals already before the placenta was available showing a slightly earlier first arrival of gulls than during experimental events, but this difference was not significant (Wilcoxon rank sum test : W = 18, P = 0.2910) (Appendix D.7). The maximum number of gulls attending all events was similar for adult and juvenile individuals (W = 174.5, P = 0.0800). Excluding the event where placenta was not detected by any bird (observation 1), adult gulls did not take part on three other occasions (observations 4, 11 and 12). Overall, feeding activity per event (minutes bird^{-1}) of adults was less than juveniles (W = 190.5, P = 0.0191), but the swallowing rate (number of swallows minute^{-1} bird^{-1}) was similar (W = 140, P = 0.2598) (Figure 5.8).

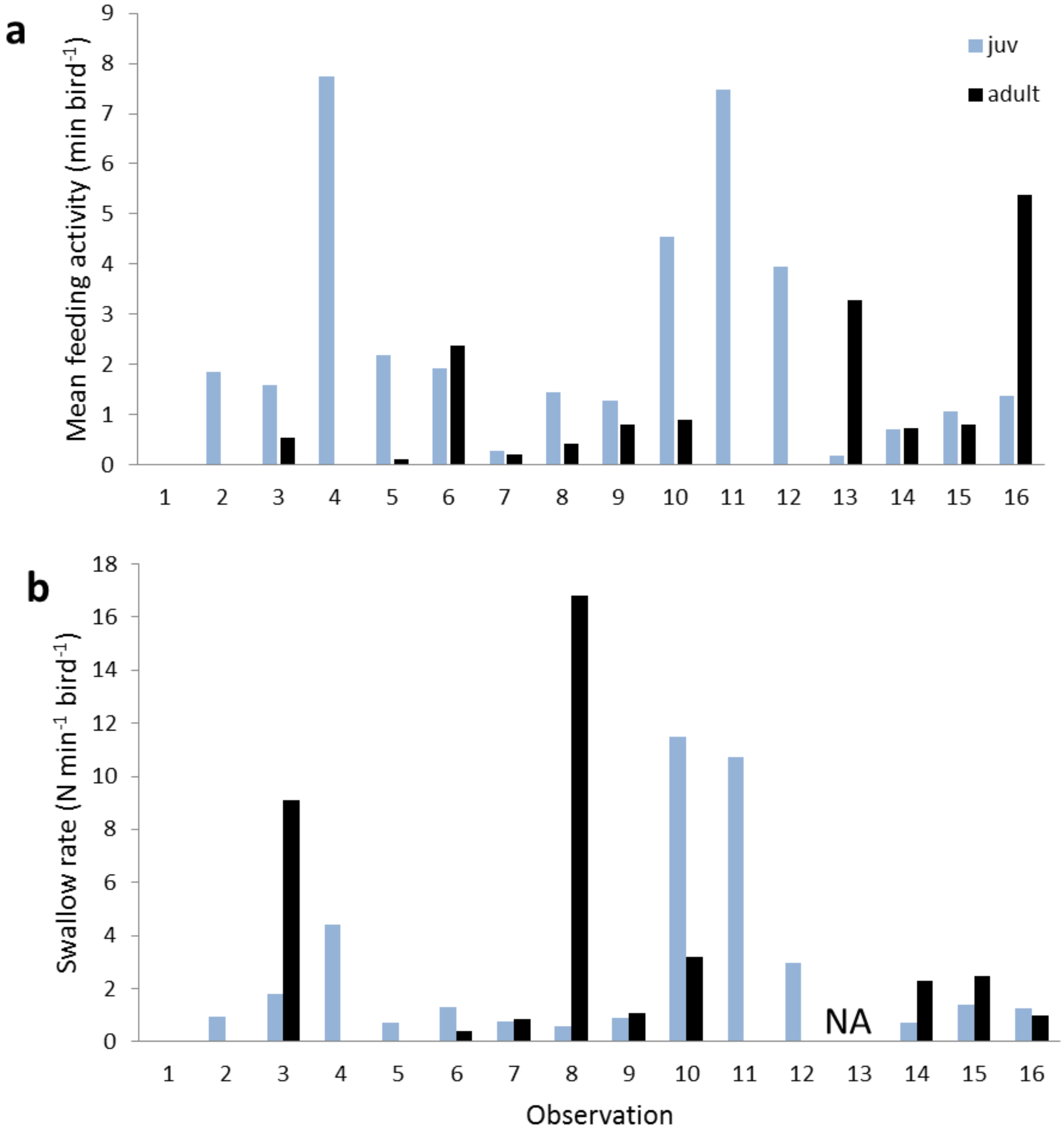

Figure 5.8 a) Mean feeding activity per bird (minutes bird-^{1}) and b) Swallow rate (number of swallows minute^{-1} bird^{-1}) of adult (black) and juvenile (blue) great black-backed gulls on placenta observations.

Competition

A total of 273 competitive events were observed among gulls feeding on placenta during 879 minutes of observation: 116 involved a juvenile and an adult (42.5%), 132 two juveniles (48.4%) and 25 two adults (9.2%). Intraspecific competition showed that again adult gulls were more successful in competing than juvenile gulls (adult: 79.6% and juvenile: 20.4%).

5.6 Discussion

As predicted, results show that in conditions of predictable and abundant carrion availability a similar trend in feeding activity on experimental carcasses occurred between adult and juvenile great black-backed gulls, suggesting that both stages take advantage of this resource evenly without monopolisation by adult individuals to the detriment of juveniles. Opposite to the expectations, adult great black-backed gulls did not show to spend feeding a greater amount of time than juveniles, even if it was predicted that they would have had more access to this type of carrion with greater energy density being competitively superior.

At the carcass, despite adult and juvenile great black-backed gulls exhibiting similar feeding rates, the scavenging efforts of young gulls slightly exceeded that of adults on later stage of carcasses: juvenile birds can, in fact, spend more time feeding to overcome their lack of feeding skills or inexperience (Greig et al. 1983; Forero et al. 2005), showing overall to be less efficient than the older stage. Both juvenile and adult gulls increased the time spent feeding towards the end of the experiment; this may reflect the easier consumption for gulls after the carcass was opened. However, variation in scavenging activity among carcasses was also evident, but generally the extent of feeding time was similar between the two gull life history stages, even if different trends during time occurred for different carcasses. It appeared, in fact, that the first three carcasses to be deployed were seldom visited in the first twenty days, but feeding activity drastically increased afterwards, while other experimental dead pups, deployed later, were detected and scavenged immediately. Temporal variation in scavenging activity on different carcasses reflected also changes in their mass loss. This discrepancy could be associated with a preference for placenta rather than carcasses in the period just after the mean pupping date, but also lower abundance of gulls at the beginning of the seal season (see Chapter 4). Other reasons might include their locations on the colony or human disturbance. Decomposition can result in a less valuable resource, more repulsive to scavengers (DeVault et al. 2004; Selva et al. 2005; Parmenter and Macmahon 2009), but our results showed that older carcasses were also consumed suggesting that lower temperatures during winter inhibit bacterial growth and insect activity making them still palatable. Finally, the lack of mass loss in caged carcasses as opposed to the other experimental carcasses demonstrated that scavenging activity, and not decomposition, had a significant effect on reducing the mass of carcasses in winter conditions.

Because of its energy density and reduced handling time necessary for its consumption, placenta was considered *a priori* the preferred food by gulls. Despite this resource being valuable in energy density (twice that of carcass), juvenile great black-backed gulls spent more time feeding, regardless they were competitively inferior. However, due to a similar number of adult and juvenile gulls attending birth events, kin interactions between individuals might have helped the younger ones to have greater access to the food item (Pierotti and Murphy 1987). Furthermore, considering that observations were carried out only during daylight, it is possible that also feeding efforts of gulls on placenta were higher during night, as was the case for carcasses.

It is often assumed that gulls are diurnal (Hailman 1964; Garthe and Hūppop 1996), whereas in this study the great black-backed gulls fed more on seal carrion during nocturnal hours. Herring and great black-backed gulls were active scavenging at fish offal provided by fishing vessels not only during the day, but also during night (Garthe and Hüppop 1996), while ring-billed gulls (*Larus delawarensis*) preying were predominantly active at night when nocturnal anti-predatory behaviours to protect their chicks were less intense (Hebert and McNeil 1999). Opportunities can therefore drive gulls' behaviour, enabling them to be active also during hours of darkness. Seal carrion is spatially predictable and may represent a convenient food source in a safer environment when visibility decreases. Nocturnal consumption may suggest that gulls did not feed enough during the day, because of reduced number of daylight hours during winter, or reduced availability of other food resources. Rubbish tips, fishery discards and coastal invertebrates are plausible food options available to these scavengers (Greig et al. 1986; Furness and Monaghan 1987; Buckley 1990; Rome and Ellis 2004). The energy value of the latter resources are similar to seal carcasses, but lower than placentae (placenta: 21.8 MJ kg^{-1}; carcass: 14.1 MJ kg^{-1}; garbage: 6.28 MJ kg^{-1}; capelin: 7.95 MJ kg^{-1}, round fish: 5.5 MJ kg^{-1}, shrimps: 4.3 MJ kg^{-1}, flatfish: 4 MJ kg^{-1} and marine invertebrate: 3 MJ kg^{-1}) (Kamil et al. 1987; Walter and Becker 1997) more energetically costly as they require movement from the colony where they roost. A recent European ban of fishery discards (EU Regulation 1830/2013) is decreasing the availability of this type of resources, but gulls might still using it, explaining the reduced feeding time observed during the day on the Isle of May. Seal carrion, however, may be an alternative food resource for gulls, because of its incomplete utilisation and lower number of gulls observed in the island during the day (see Chapter 4).

Regardless abundance of carrion occurring on the Isle of May, the herring gull and the carrion crow were rarely observed feeding. It is known that the great black-backed gull outcompetes the smaller herring gull (Rome and Ellis 2004), however their low scavenging activity on seal carrion suggests that, between the two, the great black-backed gull is specialised in exploiting carrion. Ronconi et al. (2014), also found that in the seal colony of Sable Island (Canada) the diet of herring gull was different from the great black-backed gull, composed mostly of invertebrates rather than seal remains. Carrion crows scavenged very little and always in pairs, a fact which can be explained by the low number of individuals inhabiting the island (one nest recorded in 2010) and by their tolerance of conspecifics during foraging when food abundance is high (Miller et al. 2014).

The house mouse was another active scavenger of seal carrion on the Isle of May. Mice are invasive on this island and were probably introduced here more than once during human occupation. The population was estimated to range from 450-3250 animals occurring in all areas of the island including Rona and North Ness which are isolated at high tide (Triggs 1991). In this study it was found that mice visited at all the carcasses and surprisingly at least one carcass was accessed and opened solely by the action of the small rodents, usually starting from just after dusk. The use of marine inputs by terrestrial rodents has already been highlighted in other studies (Polis and Hurd 1996b; Stapp and Polis, 2003) and the smaller the island, the greater the transfer inland of marine nutrients by the mice population (Stapp and Polis, 2003). Owing to the small geographical size of the Isle of May and presence of mice at seal carcasses located at different distances from the littoral zone, it is possible that the seal carrion represents a fundamental component of the diet of the overall mice population in the island during winter. Moreover, on the Isle of May other carrion is available throughout the year, including the ten species of seabirds which breed there during summer (SNH 2012). Brown et al. (2015, in press) found that the invasive red fox (*Vulpes vulpes*) had large effects in the coastal scavenging community occurring on a sand barrier island in eastern Australia. The presence of foxes, in fact, modified the nature of the scavenging process as they consume the largest part of the carrion available to detriment of raptors which also feed on beach-carrion. Because of their size compared to gulls, it is possible that mice do not reduce carrion availability to a detrimental extent to the scavenging birds wintering on the Isle of May. However, they can enhance their abundance because of seal carrion and could affect gull breeding productivity of the local population during summer by predating on chicks, as already observed for the critically endangered Tristan Albatross (*Diomedea dabbenena*) (Davies et al. 2015). In this study it is believed that this is the first documented case of mice scavenging pinniped carcasses.

The impact of carrion on the ecosystem is probably underestimated (DeVault et al. 2003; Wilson and Wolkovich 2011) as the energy flow derived from carcasses is often associated with predation instead of the alternative foraging strategy represented by facultative scavenging (Wilson and Wolkovich 2011). Weak links established in the trophic web, as defined by McCann et al (1998), can be crucial for the stability of the ecosystem. Among them there are those originated between facultative scavengers and the resource carrion (Selva and Fortuna 2007), such as gulls and seal carrion of the present study. Competition between consumers is one of the factors influencing any scavenging process as it shapes the structure of the scavenging assemblage gathering around the food source.

Competition requires energy and it can be avoided when resources are abundant and predictable: consumers in fact can have access to multiple resource opportunities, of equivalent energy value, occurring simultaneously in the same environment. In these conditions food is not required to be defended (Houle et al. 2006), competition is reduced (Wilmers et al. 2003b) and dominance effects can be weakened, resulting in “shared” exploitation by competitors. Aggressive social interactions can be detrimental for less dominant species or individuals whose access to the resource can be reduced or temporally adapted to avoid competition (Moreno-Opo et al. 2015). On the Isle of May, competitive events have been recorded during the scavenging processes of both carcasses and placentae, and adult gulls were competitively superior over their younger counterparts. However, the aggressive behaviour displayed by the two gull stages did not lead to a temporal and spatial segregation of subordinate individuals or a lower carrion consumption. Investigations into the interactions between species and age classes at feeding stations, which are important for conservation of vultures, highlight the need for consideration of the effect of dominance in order to be effective in safeguarding the more endangered species (Moreno-Opo et al 2015). In light of the results of this study, seal carrion provided a relevant feeding opportunity for the great black-backed gull, which is currently Amber listed endangered in Birds of Conservation Concern 3 (Eaton et al. 2015), without detrimental effects on subordinate juveniles. Considering the lower relative abundance of juvenile great black-backed gulls wintering on the island comparing to adults (see Chapter 4), carrion provided by seal colonies is a crucial resource during winter for young gulls in particular, easy to exploit and potentially enhancing chances of survival (Sanz-Aguilar et al. 2015) and stabilising pre-adult population (Votier et al. 2008; Margalida et al. 2011). The great black-backed gull could therefore benefit from this resource and its population potentially recover. Finally, the importance of seal carrion can increase over time: a recent study made in Sable Island (Canada) showed that this species is now consuming more seal remains than forty years ago (Ronconi et al 2014) due to an increasing seal population, but possibly also because of changes in fish availability, reduction of scavenging via fishery discards and alterations in the surrounding ecosystem. These same changes are also true throughout the UK, so it is expected that gull populations here may increasingly use seal carrion in the near future.

Chapter 6: Discussion

The thesis set out to investigate the role of marine mammal carrion in the ecology of coastal systems. This was addressed by providing first a detailed documentation of the fate of a grey seal (*H. grypus*) pup carcass with insights on the scavenging ecology existing in both terrestrial and marine ecosystems (Chapter 2). Then the predictability of the resource carrion, specifically carcasses and placentae, was defined in the largest single-island grey seal colony of the UK examining its timing, spatial distribution, biomass and energy released during the pinniped pupping season (Chapter 3). Finally, the impact of this predictable and abundant subsidy was determined by exploring the spatial and temporal distribution of scavenging gulls (Chapters 4) and their behavioural dynamics (Chapter 5).

In the terrestrial ecosystem a distinct shift in the relative proportions of bird groups feeding at the carcass was observed over the duration of the experiment: great black-backed gulls (*Larus marinus*) fed first, followed by juvenile gulls and ravens (*Corvus corax*). Against the expectations, the deployment of the carcass did not influence the spatial and temporal distribution of the scavenging birds. Difference in the relative abundance of marine scavengers occurred on the two periods of monitoring of the underwater carcass, as a drop in the number of starfish characterised the later stage of the experiment, while crabs were present in similar number to the early stage. It was clear that the daily mass loss of carrion was lower in the marine ecosystem than in the terrestrial one, with a ratio of 1:8, and bacterial activity occurred in both systems (Chapter 2). In one of the largest grey seal colony in the UK, inter-annual variability of seal carrion availability was below 34% of Relative Standard Errors (RSE%), similarly to other resources, such as salmon runs, which appear to be predicted by consumers (Chapter 3). For the seal carrion feeding species, great black-backed gull, the presence of carrion affected their abundance and behaviour at scales from the region to the patch: the analysis of their spatial and temporal distribution and behavior show that the great black-backed gulls, which fed on carrion, increased in abundance at the Isle of May while they were falling in the surrounding region. The herring gull, instead, which did not feed on the seal carrion, fell in abundance in the same way as abundance in the surrounding region (regional scale). The latter were also more likely to leave the island in the morning than great black-backed gulls, rather than staying close to the carrion (local scale). Areas with carrion were visited in higher number by great black-backed gulls than areas without carrion, while no such difference was seen for herring gull (patch scale) (Chapter 4). Juvenile and adult great black-backed gulls scavenged carcasses at similar extent without showing temporal shift in the access of these abundant and predictable resources. Dominance of adults, instead, was expected to be displayed during the consumption of placentae, but results showed that juvenile gulls spent more time feeding than older more dominant individuals, despite these were competitively superior (Chapter 5).

The potential impact of carrion inputs occurring on the coastal area can extend to both the marine and terrestrial ecosystems. However, the processes dominating carrion decomposition and the dynamics in scavenging activity can notably differ in the two systems (Beasley et al. 2012; Chapter 2). Slower consumption was evident on the seal carcass deployed in the water, in comparison to the carcass placed in the littoral zone, due to differences in the scavenging community. Bacterial activity was noticeable in both environments. However, the deterrent effect of decomposing matter and toxin production on the behaviour of terrestrial scavengers (DeVault et al. 2004; Selva et al. 2005; Parmenter and Macmahon 2009) was not observed, as the carcass was not abandoned prior to complete consumption. This was observed also on the Isle of May, as dead pup remains were recorded at the end of the seal pupping season during the ground visual census. However, decomposition was not as advanced as the one detected on the experimental carcass deployed during summer, probably because of the lower temperatures characterising the winter season. Gulls habits in scavenging on animal carrion and at landfills suggest that these birds have a natural tendency of feeding on rotting organic matter and their tolerance is high. This behaviour exposes them to toxins and microbiological diseases, such as botulism (e.g. Macdonald and Standring 1978). However, it was found that the proliferation of this bacterium and the incidence of the disease on gulls is not only related to warm weather, but also to landfill sites which generate heat (Ortiz and Smith 1994), implying that feeding on natural seal carrion might be a less risky alternative, especially during winter in Scotland. Temporal shifts in the access of the carcass by scavenging birds was likely to be driven by the dominance structure established by inter and intra-specific competition. In the underwater experiment, instead, bacterial activity possibly induced changes in the scavenging community during time as observed by Burkepile et al 2006. Differently from deep waters where carrion is preserved against decomposition (Beasley et al. 2012) because of temperature and pressure conditions (Jannasch 1978), in shallow waters bacterial action appeared to be an important factor driving the fate of the experimental seal carcass.

After simulating the unpredictable availability of marine mammal carcasses on both the marine and terrestrial ecosystems, the study then examined a predictable carrion resource provided at the seal colony of the Isle of May (Chapter 3). The predictability of the food resource is, in fact, one of the critical determinants shaping the structure of a community, ultimately inducing some response by consumers at a population level (Polis et al. 1996) such as changes in behaviour, ecology and adaptation (Overington and Lefebvre 2011). Considering that predictability is a measure of ecosystem stability explained by low variability in its properties both temporally and spatially (McGrady-Steed et al. 1997), inter-annual variation of seal carrion according to its timing and spatial distribution were evaluated together with its released biomass and energy. Using data on pup production and ground visual censuses of carcasses for multiple years, seal carrion was found to be predictable (Chapter 3). Similar to other predictable resources such as salmon carcasses derived by mortality at spawning areas, which are notably responsible for the co-evolution between feeding strategy and food input in black bears (Reimchen 2000), seal carrion may therefore influence the behaviour of scavengers.

Activity and distribution patterns of scavengers can be driven by the temporal and spatial predictability of the food (Cama et al. 2012; Allen et al. 2014). This was also demonstrated for seal carrion which affected the distribution of scavenging great black-backed gulls at regional, local and patch scales (Chapter 4). Moreover, higher searching efforts were displayed at the peak of placenta and carcass availability, while number of scavengers was directly related to the amount of the resource as previously found for vultures (Bosè and Sarrazin 2007; Moreno-Opo et al. 2010). The herring gull was included in the study as a potential scavenger, but it was evident that its behaviour was not affected by seal carrion at any scale. The higher number of individuals counted at dusk at the roosting sites of the island suggested that the herring gull may pursue other resources rather than carrion during the day. This species is, in fact, more urbanised than the great black-backed gull (Camphuysen 2013) and it was observed feeding at landfills in higher number (Greig 1984), so that differences in food preference together with the higher position of great black-backed gull in the dominance hierarchy may explain the resource partitioning between the two species.

On the Isle of May the annual amount of energy available as placentae and dead seals to potential scavengers was estimated to be 110.5 x 10^3 MJ, corresponding to more than 42 thousand daily gull meals. The fact that only 32.5% (9.1 x 10^3 MJ) of the resource carcasses was consumed at the end of the pupping season (Chapter 3), suggests that the ecosystem was saturated by carrion. In environmental conditions of food saturation competition among consumers may reduce (Wilmers et al. 2003b; Houle et al. 2006) weakening the structure of dominance, so that subordinate individuals can also access the resource (Chapter 5). Juvenile great black-backed gulls in fact fed on carcasses to a similar extent as adult conspecifics and did not adopt any alternative foraging strategy such as temporal and spatial segregation to avoid the superior competitors. At feeding stations where carrion is predictable, instead, dominant vultures species monopolise the carrion (Cortés-Avizanda et al. 2012). Differing from the seal colony, where carcasses were dispersed over large areas, feeding opportunities at feeding stations for vultures are highly clustered making it difficult to avoid aggression. Moreover, number of vultures is higher than scavenging gulls of the Isle of May. It was also found that the younger gulls spent more time than adults feeding actively on placenta, highlighting the potential significance of this resource for juvenile stages of this species during winter. Continuous monitoring using infrared cameras revealed that gulls are highly nocturnal, counter to what it is often assumed (Hailman 1964; Garthe and Hūppop 1996). This behaviour may also explain that carrion may be a safer and easier alternative resource to capitalise on once back around roosting sites. Finally, the presence of the house mouse and its ability to actively open the pup carcasses was unanticipated; it is likely that this is the first study documenting this small rodent feeding on dead pinnipeds. The seal carrion, therefore, may be an important resource for mice, especially during winter.

Outside of the seal pupping season, other types of carrion may be available on the Isle of May for scavenging mice and gulls. During spring and summer, twelve species of seabirds breed there (SNH 2012) providing chick carcasses to scavengers as result of natural mortality or predation. Also marine scavengers may take advantange of this source of food, as some dead birds may fall into the sea from the western cliff of the island where some species nest. Outbreaks of myxomatosis, an infectious and usually fatal viral disease, experienced by the population of rabbits living on the island, during summer may also contribute to the carrion pool.

In light of the findings of the present thesis, seal carrion is likely to influence the coastal systems as unpredictable events such as a strandings, but also as predictable, abundant and high energy resources at the seal colony. In both cases, its impact is not only limited to the terrestrial ecosystem, but also to the marine one, where it would affect a different scavenging community. According to our estimates, 32.5% of the total amount of edible matter derived from seal carcasses on the Isle of May was taken by terrestrial scavengers such as great black-backed gulls and mice by the end of the seal pupping season. The uneaten remaining carrion could be possibly be further consumed by these vertebrate scavengers later during winter or finally become available to invertebrates and soil, which would receive additional nutrients released by the inedible skin and bones (34.8% of the total seal carcass biomass) (Chapter 3). Because most of the pups are born far from the sea, placentae are for the major part available to the terrestrial system. Placenta intake by gulls was estimated to be 67.9% (Chapter 5), while insects can probably have access to the dry remains. Carcasses found on the area between mean high and low tide represented 13.1% of the total number of carcasses recorded during the ground visual census. At sea carrion biomass, when negative buoyant, is transferred to benthic invertebrate scavengers such as crabs and starfish which can feed at a rate of 0.07 kg day^{-1} (Chapter 2). However, knowledge on the fate of seal carcasses in shallow waters is still limited. Internal decomposition, body composition, currents and tides, but also type of substrate and depth can in fact all contribute to generate different scenarios of biomass transfer to the scavenging community or nutrients to the abiotic factors in the marine system.

When predictable, seal carrion has an effect on the distribution of scavengers, but also on their behavioural dynamics, favouring a weaker dominance structure and diminishing competition. It is therefore likely to be of particular significance to juveniles unable to compete for other high quality resources. Carrion availability coincides with the wintering months when food is usually scarce. This may be crucial for the declining great black-backed gull (Foster and Marrs 2012) as survival of early life stages during the cold season can mitigate the current endangered status of this species (Sanz-Aguilar et al. 2015). Due to global changes in the environment and the high level of carrion availability, there is the potential for gulls (and other facultative scavengers) to rely more heavily on carrion in the future.

6.1 Lessons for future research

Various approaches were used to address the range of ecological questions forming the basis of this work (Chapter 1) with the aim of overcoming both technical and circumstantial challenges. Ecological research has recently been enhanced by the development of numerous non-invasive methods, such as camera traps to monitor wildlife at any time of day or year (O'Connell and Nichols 2010) and underwater cameras for marine monitoring (Willis and Babcock 2000). Infrared time-lapse cameras were therefore used when exploring the scavenging activity on seal carcasses in the terrestrial ecosystems (Chapter 2 and 5) as they permitted a 24/7 monitoring instead of limited intervals of observations performed by individual researchers. In this way, human disturbance was minimised, while data collection of wildlife was maximised, including hours of darkness which eventually revealed fascinating aspects of the ecology of scavengers. Similarly, the underwater camera permitted the continuous surveying of the decomposition and consumption of a pup carcass without repeated inspections by divers, representing a time consuming and expensive alternative. However, technical problems are inherent to cameras, to the extent that they have been even addressed in a study aiming to guide sampling design in ecology when using camera-traps (Hamel et al. 2013): environmental conditions, humidity and battery exhaustion were some of the reasons identified. To maximise a "problem-free" monitoring, silica gel sachets (1 x 2cm) were inserted in the cameras to reduce humidity, electrical tape used to seal them and new batteries deployed regularly. Seal movements also interfered with instrumentation causing camera displacement, and eventually also re-placing it in the exact position. Circumstances like these were avoided when cameras were located on man-made structures such as the small stone walls occurring on the Isle of May. However, the absence of trees on the island and the necessity to deploy cameras and experimental carcasses as close as possible to the main aggregations made the installation difficult. In the marine system, instead, corrosion, oxidation and leakage can cause malfunction of underwater instruments. In our case the underwater camera failed twice: the first time because of leakage and the second time because the buoy was hauled up breaking the camera housing off. This damage could have been avoided by a different design of the mooring. A lesson learnt. In order to limit these problems, the infrared camera functioning was checked regularly, while the underwater camera was replaced once the problem had been identified.

The experiments simulating the unpredictable events of a stranding and availability of seal carrion in the marine system (Chapter 2) were limited to two single carcasses, or observations. Among the reasons there were time and budget constraints and technical challenges (also experienced by Hobischak and Anderson 2002). To increase the sample size of the terrestrial experiment, multiple grey seal carcasses should have been used on different islands located on the west coast of Scotland, over the same period during summer. Seabirds, such as gulls, in fact, move seasonally and in order to obtain comparable results it would have been appropriated to carry out simultaneous experiments. Unfortunately, this was not feasible. As this sample size can restrain the inference of the results obtained, even if they were in line with previous studies, further experiments might be useful to increase their significance.

To study the spatial distribution and temporal trend of the gull populations different types of data were used: counts directly carried out on the Isle of May were compared with long-term databases provided by JNCC as best compromise between economy of collection effort and completeness of data to be used. In particular, for the purpose of this thesis counts data were a sensible alternative of more expensive methods such as telemetry (Franco et al. 2007), which would have been prohibitive if applied at a population level. Moreover, counts of different types were not modelled together, because of the risk of making an incorrect statistical interpretation, but only the temporal trends obtained from different models were compared.

The use of the Isle of May as a study site had the advantage of possessing the largest grey seal colony in the UK and a history of ecological research, however it would be prudent to expand the research present in this thesis beyond into other islands and mainland colony sites, during both day and night. This would elucidate the role of marine mammal carrion in different ecosystems each with potentially varying or unexpected endemic facultative scavengers (e.g. house mouse in Chapter 5) and anthropogenic interactions. As such the importance of carrion on coastal ecosystems is likely global but care should be taken in extrapolating the specific findings of this thesis into significantly different ecosystems.

6.2 Implications, applications and future investigations

Scavenging is documented globally in both extant and even in extinct species, such as *Tyrannosaurus rex* during the Cretaceous era (Ruxton and Houston 2003) and the Ice Age spotted hyena (*Crocuta crocuta spelaea*) during the Late Pleistocene (Diedrich 2015), meaning that it is a well-established foraging strategy. New evidence on the use of carrion by carnivore species, which utilise this resource opportunistically as an alternative to predation, brought attention to the importance of scavenging behaviour in the food web (Moleón et al. 2014), emphasizing its role in stabilising the ecosystem (Selva and Fortuna 2007). This thesis elucidated the relationship between carrion and facultative scavengers, which is generally underestimated 16-fold in food webs, suggesting that the energy transferred through scavenging is likely to be greater than that gained by predation (Wilson and Wolkovich 2011).

Despite recent research focusing on carrion ecology, the current scientific literature lacks studies evaluating the role of pinnipeds as key species in coastal systems, providing potentially abundant and high energy resources, such as carrion, to the surrounding marine and terrestrial ecosystems and their scavengers. Seals occur worldwide, from the Northern to the Southern Hemisphere: of the 33 species of pinnipeds existing, 20 breed on land, and the remaining 13 breed on ice (Cappozzo 2001). The latter statistics could be already indicative on how carrion derived from these marine mammals may be a crucial resource in many biomes, whose impact is still little understood. In the present work the study species considered as the carrion provider was the grey seal as it is the marine mammal likely providing the highest number of carrion inputs onto coastal ecosystems in the UK. In the absence of obligate scavengers, the great black-backed gull was the main scavenger feeding on seal carrion in land. The present thesis quantifies for the first time the amount of carrion released during the pupping season in the shape of placentae and carcasses and determined its predictable nature highlighting its impact on the main scavenging gull benefitting from this resource. The great black-backed gull is an Amber listed species in the UK (Eaton et al. 2015), which declined in the UK during the last decades. Human persecution, botulism and viral infection, and predation by brown rats (*Rattus Norvegicus*) and American mink (*Neovison vison*) are the possible main threats that acted upon the population (Zonfrillo 2007). The actual decline in fishery discard opportunities, due to the landing obligation of the whole catch by fishing vessels, may represent an additional threat to this species which sustain itself by using this resource. However, the reduction of discards together with the increasing of the UK grey seal population (SCOS 2013), may lead to a higher consumption of seal carrion as alternative resource by great black-backed gulls. Ronconi et al. (2014) found that the same species, living in Sable Island, the largest grey seal colony in the world, notably increased the use of seal remains during the last forty years due to alterations in the offshore waters of Atlantic Canada and the increasing of breeding grey seals. The English *Nephrops norvegicus* fishery during the fishing season in 2001 to 2002 disposed of an estimate of 4,780 tonnes of discards, of which 57% were taken by seabird scavengers. The energy equivalent was 11,647 10^3 MJ (Catchpole et al. 2006), which is three orders of magnitude higher than the energy released annually on the Isle of May as seal carrion. Although grey seal colonies can not provide such amounts of energy, it is possible that seal carrion will become a relevant alternative of fishery discards, at least for the great black-backed gull. Monitoring the proportion of pup carcasses consumed at a seal colony may therefore represent a valuable method to evaluate changes in the feeding habits of scavengers such as the great black-backed gull. Moreover, knowing the temporal trend in consumption of seal carrion during consecutive years may help in determining which other variables should be included or excluded from the list of possible causes for the decline in the population. Restaurants for vultures represent a reasonable solution for conservation purpose, as they rebalance the lack of carrion caused by regulation of livestock carcasses, helping the productivity to increase. However, now it is clear that there are also some side effects such as changes in the behavior and ecology for these obligate scavengers (Deygout et al. 2009), which were used to forage on unpredictable resources (Ruxton and Houston 2004a). On the contrary, seal colonies are natural providers of predictable carrion, whose impact on the consumers is not caused by a perturbation of anthropogenic origin. PAFS (predictable anthropogenic food subsidies) may have some negative effects: landfills, for instance, have been shown to provide some exotic species with junk food and pollutants, making them obese, ill and incapable to react to predators (e.g. Carrete et al. 2009). It is possible that this type of diet could compromise also the health of gulls.

Investigating carrion consumption on other seal colonies could also reveal differences in behavioural dynamics of gulls established by the relation between carrion availability and number of scavenger consuming it: for instance, if carrion is completely depleted by scavengers at the end of the pupping season, this would probably imply that the food resource was limited on that seal colony, and a higher level of competition between age classes occurred. The latter would indicate that the juvenile gulls wintering on that area might have less access to the resource carrion, eventually negatively affecting their survival. Considering that seal aggregations occur in eighteen out of 29 great black-backed gull colonies located on the north eastern coast of Scotland (SMRU unpublished data), it is possible that seal colonies may enhance productivity of the local gull population.

Seals and birds can act as disease vectors (e.g. Higgins 2000; Fuller et al. 2012) facilitating the transmission to the human population and viceversa. The enteropathogenic *Escherichia coli* was found, for instance, in the Antarctic fur seal pups *Arctocephalus gazelle* (Hernandez et al. 2007), while the foraging area of herring gulls carrying *Salmonella* corresponded to the incidence of salmonellosis in humans living nearby (Monaghan et al. 1985). The link between gulls and seal carrion, explored in this thesis under a pure ecological prospective, can therefore have some health implications.

More attention should be also devoted to the impact of predictable seal carrion occurring in the intertidal system around the seal colony: in this study, in fact, 13.1% of carcasses occurred in the area between the mean high and low water boundaries, suggesting that marine scavengers, such as benthic invertebrates, may exploit this resource as well. Moreover, as the effect of carrion is not limited only to terrestrial and marine scavengers, but also to other biotic and abiotic compartments of the ecosystem, such as plants and soil (Erskine et al. 1998; Koyama et al. 2005), additional research can be pursued in this direction.

The future looks promising for taking advantage of entering the “golden age for scavenging research”.

Appendix A: Chapter 2 Statistical outputs

A.1 Seabird surveys details.

AREA	PERIOD	DATE	TIME	TIDE
control	before	18/07	17:30	low
		20/07	06:20	low
		24/07	15:55	high
		26/07	17:10	high
study	before	19/07	12:35	high
		19/07	18:20	low
		25/07	09:40	low
		25/07	16:30	high
control	after	26/07	17:10	high
		29/07	08:10	high
		02/08	17:50	low
		03/08	13:15	high
		04/08	07:10	low
		14/08	15:47	low
		15/08	09:45	high
		20/08	19:05	low
		21/08	08:15	low
		29/08	16:00	low
		30/08	08:20	high
study	after	27/07	10:30	low
		29/07	14:00	low
		30/07	09:35	high
		02/08	12:25	high
		03/08	17:50	low
		04/08	14:05	high
		05/08	07:30	low
		14/08	15:35	low
		15/08	09:35	high
		20/08	14:50	high
		21/08	08:30	low
		29/08	16:15	low
		30/08	09:00	high

A.2 Mini DVR system with IR camera.

Featuring small size and lightweight, the Mini SD DVR's compact dimensions mean it requires very little space, fitting easily into restrictive spaces.

Ultra-compact pocket size digital video recorder with enhanced features that is ideal for surveillance.

1. PLAYBACK

Recordings can be played back via the AV output to a compatible display. Alternatively video clips can be exported to a PC via the USB port or simply by removing the SD card.

2. FEATURE

   - DC 12V Adapter
   - One Video in, one video out
   - Support TF card of max 16G Storage, video is recorded in real time monitoring.
   - Smart detector to moving objects, to save the storage space. 1 Frame/sec when moving Objects detected, and 1Frame/2min when no moving Objects detected
   - AV cables to Monitor, Real-time monitoring and playback with switch button shifted
   - Timetable adjustable supported
   - Work with Special PC Software, convenient and friendly to user

3. . SPECIFICATION

   - TV Format NTSC/PAL
   - VIDEO IN (CVBS) 1Channel
   - VIDEO OUT (CVBS) 1Chanbel
   - Resolution 352*288

4. NORMAL WORKING STATUS

- The MINI DVR will shoot automatically 1 frame images in every two minutes and store them if there aren’t any moving objects appears in the view.
- The MINI DVR will shoot continually until the moving targets disappeared and freeze completely if there has any moving object appears in the view.

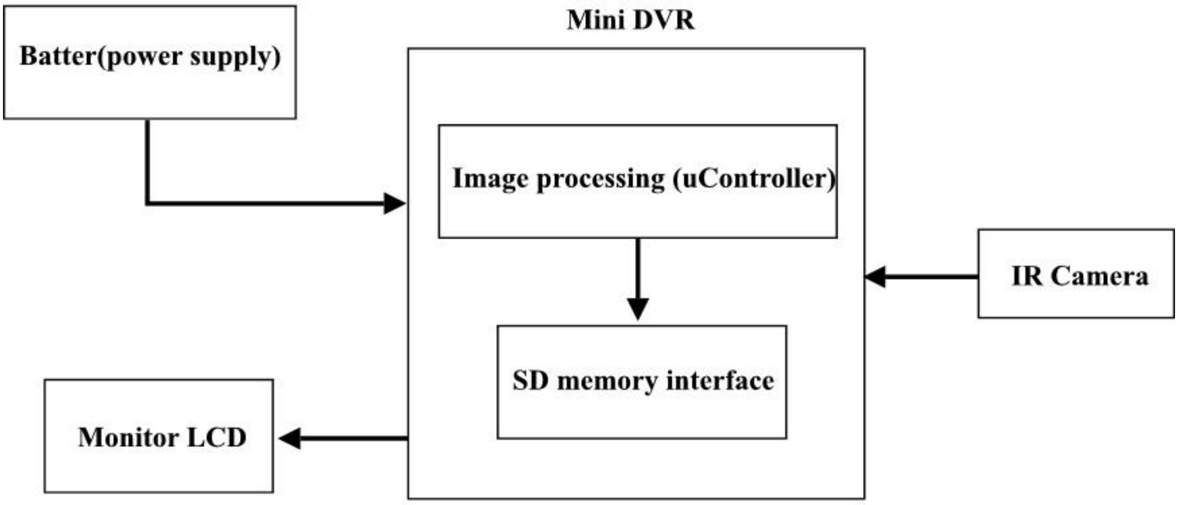

Image recording (Mini DVR) System Bioelectronics unit CMVLS Glasgow university 2014

A.3 – Times of bad visibility during the underwater experiment.

Period 1		Period 2	
Date	**Time**	**Date**	**Time**
02/08	05:00 / 08:50	17/09	23:40
02/08	22:30	18/09	02:20
03/08	04:40 / 07:10	18/09	03:30
03/08	22:50	18/09	20:50 / 21:30
04/08	01:10	19/09	00:30
04/08	03:30	19/09	05:20
04/08	23:30	19/09	21:50 / 22:00
05/08	01:20 / 01:40	19/09	22:30 / 23:20
05/08	02:20	20/09	00:00 / 00:20
05/08	13:20	20/09	04:00 / 04:20
05/08	22:40 / 23:40	20/09 - 21/09	14:40 / 14:00
06/08	00:00	21/09	21:30
06/08	00:50 / 01:20	23/09	03:20
06/08	02:40	24/09	02:40 / 03:00
06/08	03:30	24/09	05:30
06/08	04:00 / 04:20	25/09	00:50
06/08	23:10	25/09	04:10 /04:20
06/08	23:40	25/09	05:40
07/08	02:00		
07/08	04:.30		
07/08	23:00		
08/08	01:20		
08/08	02:00 / 02:20		
09/08	04:30		
10/08	02:00		
10/08	02:40 / 02:50		
10/08	05:00 / 05:10		
11/08	00:00 / 00:20		
11/08	02:40		
11/08	23:00		
12/08	14:00 / 15:00		
13/08	01:00		
13/08	01:50 / 02:10		
14/08	12:00		
14/08	20:00 / 23:00		
15/08	03:10 / 03:30		

A.4 Terrestrial experiment: summary of results obtained by individual negative binomial GLMs for each group of birds.

Count of bird passages (GBBG = great black-backed gull, HG = herring gull, LBBG = lesser black-backed gull, JUV = juveniles gulls) undertaken at the study and control sites both before (Period 1) and after (Period 2) the deployment of a single grey seal pup carcass. Formula = Log (Total Number of Bird Passages) ~ Tide + Time of the day + Area : Period.

GBBG (likelihood ratio test: X^2 (df = 3) = 25.98, P < 0.001)

	Estimate	Std. Error	Z value	Pr (>|z|)
Intercept	-2.3401	0.8343	-2.805	0.0050
Tide - Low	0.5789	0.2818	2.055	0.0399
Area - Study	1.2523	0.2951	4.244	< 0.0001
Period - 2	1.4395	0.4120	3.494	0.0005

HG (likelihood ratio test: X^2 (df = 4) = 15.54, P = 0.0037)

	Estimate	Std. Error	Z value	Pr (>|z|)
Intercept	3.8625	0.6382	6.052	< 0.0001
Tide - Low	0.8318	0.2191	3.797	0.0001
Area - Study	-1.1621	0.8955	-1.298	0.1944
Period – 2	-0.7410	0.3554	-2.085	0.0371
Area – Study : Period - 2	0.7798	0.4988	1.563	0.1180

LBBG (likelihood ratio test: X^2 (df = 3) = 4.32, P = 0.2290)

	Estimate	Std. Error	Z value	Pr (>|z|)
Intercept	4.9236	0.7949	6.194	< 0.0001
Area - Study	-2.0490	1.1334	-1.808	0.0706
Period – 2	-0.8293	0.4459	-1.860	0.0629
Area – Study : Period - 2	1.1116	0.6317	1.760	0.0785

JUV (likelihood ratio test: X^2 (df = 1) = 2.51, P = 0.1130)

	Estimate	Std. Error	Z value	Pr (>|z|)
Intercept	3.8410	0.2253	17.0510	< 0.0001
Area - Study	-0.4921	0.3055	-1.6110	0.1070

A.5 Underwater experiment: summary of results obtained by the Poisson GLM.

Maximum number of individuals (MaxN) observed for the classes Actinopterygii (fish), Asteroidea (starfish) and Malacostraca (crabs) in the periods of monitoring (1 and 2) at day and night time. Formula = Log (MaxN) ~ Period + Time + Class + Period : Class + Time : Class.

	Estimate	**Std. Error**	**Z value**	**Pr (>|z|)**
Intercept	2.39795	0.08115	29.550	< 0.0001
Period - 2	-1.08606	0.16804	-6.463	< 0.0001
Time – Night	-0.61826	0.12657	-4.885	< 0.0001
Class - Asteroidea	0.07745	0.11157	0.694	0.4876
Class - Malacostraca	-2.12147	0.22680	-9.354	< 0.0001
Period – 2 : Class - Asteroidea	-1.18476	0.30052	-3.942	< 0.0001
Period – 2 : Class - Malacostraca	0.88407	0.32279	2.739	0.0062
Time – Night : Class - Asteroidea	0.46377	0.16840	2.754	0.0059
Time – Night : Class - Malacostraca	0.90308	0.28691	3.148	0.0016

Appendix B: Chapter 3

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

Time (a)

Reference	*Resource*	*Mean*	*SE*	*RSE%*	*Effect*
Present study	Seal pupping	30th Oct	0.58	1.97	Scavengers: great black-backed gulls

Quantity (b)

Reference	***Resource***	***Mean***	***SE***	***RSE%***	***Effect***
Present study	Dead seals (ground visual census)	N = 209.0	22.03	10.54%	Scavengers: great black-backed gulls
		3777.7 kg	720.87	19.08%	
	Afterbirths (aerial survey)	N = 1,988.1	47.72	2.40%	
		3,124.3 kg	74.99	2.40%	
Reimchen 2000	Salmon spawning run	N = 4,000	1,011.60	25.00%	Black bears (*Ursus americanus*) predation
Bouchard and Bjorndal 2000	Sea turtle nesting	N = 14,305 (1.6 · 106 eggs) 9,841.84 kg			Raccoon and ghost crab 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%	Scavengers: great black-backed gulls
	Afterbirths (aerial survey)	68.1 10^3 MJ	1.64	2.41%	
Bouchard and Bjorndal 2000	Sea turtle nesting	267.8 10^3 MJ			Raccoon and ghost crab predation

B.2 Comparison between the Isle of May seal carrion availability and apparently predictable pulses in resource availability according to space (d).

Space (d)					
Reference	***Resource***	***Mean***	***SE***	***RSE%***	***Effect***
Present study	Dead seals (ground visual census)	0.005 carc m-$^{2\ \mathrm{A}}$	0.001	20.00%	Scavengers: great black-backed gulls
		0.09 kg m$^{-2\ \mathrm{A}}$	0.03	33.33%	
	Afterbirths (aerial survey)	0.04 plac ·m$^{-2\ \mathrm{B}}$	0.001	2.50%	
		0.07 kg m$^{-2\ \mathrm{B}}$	0.002	2.86%	
Hocking and Reimchen 2009	Salmonids	16.3 Kg m^{-1}	5.00	1.67%	Marine enrichment in riparian food webs
Polis and Hurd 1996b	Chick carcasses	0.77 carc m^{-2} 0.16 Kg m^{-2}			Land animal species observed in coastal areas
	Pelican chick carcasses	0.09 carc m^{-2} 0.17 Kg m^{-2}			
Bouchard and Bjorndal 2000	Sea turtle nesting	0.032 Kg m$^{-2\ \mathrm{C}}$ 0.85 MJ m$^{-2\ \mathrm{C}}$			Raccoon and ghost crab predation
Davenport 1995	Calanoid copepods, chaetognaths and pteropods	<4 Kg m^{-2}			Kelp gulls, sheathbills and terns

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 considering 21 km stretch of beach (11m beach width) in Brevard County Florida

Appendix C: Chapter 4 Statistical outputs

C.1 Model selection for feeding activity of gulls during seal pupping season using negative binomial general additive model (NB GAM).

BG = Bird group (great black-backed gull and juvenile gulls), Site = East Tarbet and Loan.

Feeding activity		
Model	df	AIC
1 ~ f BG + f Site + s Carrion	**7.752840**	**528.371153**
2 ~ f BG + f Site + s Time	5.001181	537.9466
3 ~ f BG + f Site + s SeaLevel	6.339486	542.671953
4 ~ f BG + f Site + s Date	9.386395	532.6151
1 ~ f BG + f Site + s Carrion + s SeaLevel	10.010854	528.207551
2 ~ f BG + f Site + s Carrion + s Date	**10.010854**	**517.3300**
3 ~ f BG + f Site + s Carrion + s Time	8.915908	520.8179
1 ~ f BG + f Site + Carrion + s Date	9.868550	522.940951
2 ~ f BG + f Site + Date + s Carrion	**8.877449**	**517.7664**
1 ~ f BG + f Site + s SeaLevel + s Carrion s Date	12.48696	515.6323
2 ~ f BG + f Site + s Time +s Carrion + s Date	**10.62407**	**513.9346**
1 ~ f BG + f Site + Date + S Carrion + s Time	**9.846593**	**513.4144**
2 ~ f BG + f Site + Carrion + s Date + s Time	10.716321	1518.5358
1 ~ f BG + f Site + Date + s carrion + s Time	9.846593	513.414451
2 ~ f BG + Date+ s Carrion + s Time	8.896637	511.4690
3 ~ f BG + Date + Time + s Carrion	**8.896434**	**511.4688**
1 ~ f BG + Date + Time + s Carrion	8.896434	511.46889
2 ~ f BG + Date + s (Carrion, by = BG)	**11.971145**	**510.9466**

C.2 Model selection for crossing activity of gulls during seal pupping season using negative binomial general additive model (NB GAM).

BG = Bird group (great black-backed gull and juvenile gulls), Site = East Tarbet and Loan.

Crossing activity		
Model	df	AIC
1 ~ f BG + f Site + s Carrion	7.911940	1029.146
2 ~ f BG + f Site + s Time	8.713801	1027.428
3 ~ f BG + f Site + s SeaLevel	7.076107	1024.117
4 ~ f BG + f Site + s Date	**10.494497**	**1008.095**
1 ~ f BG + f Site + s Date + s SeaLevel	12.77685	999.6510
2 ~ f BG + f Site + s Date + s Carrion	**18.65041**	**987.8856**
3 ~ f BG + f Site + s Date + s Time	13.59967	997.0193
1 ~ f BG + f Site + f Carrion + s Date	**11.075330**	**1005.986**
2 ~ f BG + f Site + Date + s Carrion	9.050258	1030.625
1 ~ f BG + f Site + s SeaLevel + s Carrion s Date	**19.90647**	**978.9979**
2 ~ f BG + f Site + s Time +s Carrion + s Date	18.26077	983.4252
1 ~ f BG + f Site + f Carrion + s SeaLevel + s Date	**12.56086**	**996.3519**
2 ~ f BG + f Site +f Date + s SeaLevel + s Carrion	13.10045	1018.0026
1 ~ f BG + f Site + f Carrion + s SeaLevel + s Date	12.56086	996.3519
2 ~ f Site + f Carrion + s SeaLevel + s Date	11.61642	994.3872
3 ~ f Site + f Carrion + s SeaLevel + s Date	**11.61192**	**994.3793**
1 ~ f Site + f Carrion + s SeaLevel + s Date	**11.61642**	**994.3872**
2 ~ f Site + f Carrion + s SeaLevel + s(Date, by Site)	14.98552	999.7193

Appendix D: Chapter 5 Statistical Outputs

D.1 Details of experimental carcasses.

Carcass N	Group	Collection date	Original Location	Deployment date	Experimental Location	Sex	Development stage	Consumption stage	Weight (kg)	Girth (cm)	Length (cm)	Nose to scalpo (cm)	Blubber thickness (mm)
1	1	27-Oct	Rona	28-Oct	Cross park	F	1	A	13.7	52.6	91.0	36.0	7.0
2	1	27-Oct	Rona	28-Oct	Cross park	F	1	A	14.5	55.2	85.0	32.0	8.0
3	1	29-Oct	Kirkhaven	29-Oct	Far Cross Park	F	1	A	11.5	47.4	84.5	32.0	7.0
4	2	06-Nov	Rona	08-Nov	Rona	M	Starveling	A	13.6	49.6	99.0	45.0	1.5
5	/	07-Nov	Pilgrim Haven	08-Nov	Rona	M	2	A	13.6	50.0	93.0	43.0	1.5
6	2	07-Nov	Pilgrim Haven	08-Nov	Rona	M	1	A	14.3	48.0	102.0	43.0	1.8
7	2	08-Nov	Rona	09-Nov	Loan	M	2	A	14.8	59.2	101.0	45.0	7.0
8	2	09-Nov	Loan	09-Nov	Loan	M	1	B	11.5	50.6	95.0	36.0	8.0
9	/	11-Nov	Rona	14-Nov	Rona	M	Starveling	B	12.4	49.6	102.0	40.0	1.0
10	3	22-Nov	Loan	22-Nov	Loan	M	1	B	10.8	50.8	95.0	38.0	9.0
11	3	25-Oct	Rona	17-Nov	Kirkhaven	M	2	B	12.1	52.0	97.0	43.0	10.0
12	cage	18-Nov	Pilgrim Haven	19-Nov	Byres	M	1	A	12.4	48.1	93.5	36.0	6.5
13	cage	18-Nov	Pilgrim Haven	19-Nov	Byres	M	1	A	9.4	41.8	90.0	37.0	3.0
14	cage	18-Nov	Pilgrim Haven	19-Nov	Byres	F	1	A	14.3	51.8	99	38.0	5.0

D.2 Details of placenta events.

Observation	Event type	Location	Date	Mass (kg)	Energy Density (MJ kg^{-1})	Start time (hh:mm)	Duration (hh:mm)
1	experimental	Rona	02-Nov	1.42	22.17	10:22	05:34
2	experimental	Loan	03-Nov	1.42	22.47	09:47	00:04
3	experimental	Loan	04-Nov	1.91	22.10	09:23	00:53
4	experimental	Loan	10-Nov	1.46	20.30	10:44	00:13
5	experimental	Loan	15-Nov	1.19	20.33	10:38	01:23
6	experimental	Loan	17-Nov	1.81	23.49	11:45	01:50
7	experimental	Rona	21-Nov	1.63	21.81	10:19	00:03
8	natural	Loan	03-Nov	1.57	21.81	15:47	00:30
9	natural	Loan	03-Nov	1.57	21.81	10:42	00:16
10	natural	Loan	05-Nov	1.57	21.81	14:33	01:04
11	natural	Cross Park	07-Nov	1.57	21.81	16:28	00:1
12	natural	Loan	07-Nov	1.57	21.81	15:50	00:22
13	natural	Rona	08-Nov	1.57	21.81	11:57	00:16
14	natural	Rona	11-Nov	1.57	21.81	10:44	00:13
15	natural	Loan	14-Nov	1.57	21.81	15:15	00:52
16	natural	Loan	26-Nov	1.57	21.81	12:29	00:42

D.3 Details of the scavenging activity performed by adult and juvenile great black-backed gulls on experimental carcasses.

Carcass N	Group	Opener	Adult MaxN	Juvenile MaxN	Adult feeding time (min)	Juvenile feeding time (min)	Consumed carcass (kg)	Competition		
								Adult VS Juvenile	Juvenile VS Juvenile	Adult VS Adult
1	1	mice	1	1	3928	2704	9.29	13	3	5
2	1	adult GBBG	2	1	1282	2978	4.99	1	1	1
3	1	juv GBBG	1	2	261	808	5.81	2	3	1
4	2	adult GBBG	1	1	955	262	2.61	4	0	5
5	/	not opened	/	/	115	86	0.42	1	1	1
6	2	juv GBBG	1	1	162	857	3.19	8	4	1
7	2	juv GBBG	2	1	1048	1679	3.81	2	0	3
8	2	adult GBBG	2	1	1926	1116	5.67	9	0	1
9	/	not opened	/	/	9	59	0.31	0	0	1
10	3	mice and adult GBBG	2	1	3045	375	4.22	9	0	4
11	3	unknown	1	1	529	3437	7.01	5	3	1

D.4 Model selection for mass loss (kg interval^{-1}) of carcasses VS feeding activity (minutes interval^{-1}) of gulls using Linear mixed effect model (LMM).

LMM Mass loss VS Feeding activity

Model	df	AIC	BIC	LogLik	Test	Chisq df	L. Ratio	p-value
1 ~ Feeding * Stage + random (Carcass)	6	259.4406	273.732	-123.7203				
2 ~ Feeding + Stage + random (Carcass)	5	243.948	255.9206	-116.9742	1 vs 2	1	27.642207	<.0001
3 ~ Feeding + random (Carcass)	**4**	**240.5538**	**250.1806**	**-116.2769**	**2 vs 3**	**1**	**1.394554**	**0.2376**
4 ~ 1 (null) + random (Carcass)	3	266.1960	273.4525	-130.0980	3 vs 4	1	13.492236	0.0002

D.5 Model selection for feeding activity (minutes day^{-1}) of gulls VS experimental day (1/34) using General linear mixed model, family Poisson (GLMM).

GLMM Feeding activity VS Experimental day

Model	df	AIC	BIC	LogLik	Test	Chisq df	Chisq	Pr (>Chisq)
1 ~ Stage * Expday + random (Carcass)	**5**	**52408.5**	**52428.3**	**-26199.3**				
2 ~ Stage + Expday + random (Carcass)	4	52458.1	52474.0	-26225.0	1 vs 2	1	51.583	6.863e-13
3 ~ Expday + random (Carcass)	3	52540.8	52552.7	-26267.4	2 vs 3	1	84.689	< 2.2e-16
4 ~ 1 (null) + random (Carcass)	2	57907.6	57915.5	-28951.8	3 vs 4	1	5368.771	< 2.2e-16

D.6 Model selection for feeding activity (minutes hour^{-1}) of gulls VS hours of the day (1-24) using general additive mixed model, family binomial (GAMM).

GAMM Feeding activity VS Hour

Model	df	AIC	intercept
1 ~ f Stage + s Hour	7.368	155864.05	3.2673
2 ~ f Stage + s Hour + random(Carcass)	4.286	45129.36	2.83571
3 ~ f Stage + s Hour + random(Carcass) + AR1	**3.858**	**45063.82**	**2.8347**
4 ~ f Stage + s (Hour, by = Stage)	Ad: 3.870 Juv: 6.423	45197.54	2.8186

D.7 Details of the scavenging activity performed by adult and juvenile great black-backed gulls during experimental and natural placenta events.

Obs	**Type**	**First Arrival (min)**	**Adult MaxN**	**Juvenile MaxN**	**Adult feeding time (min)**	**Juvenile feeding time (min)**	**Consumed placenta (%)**	**Adult VS Juvenile**	**Competition Juvenile VS Juvenile**	**Adult VS Adult**
1	experimental	/	0	0	0.00	0.00	0	0	0	0
2	experimental	0.00	1	11	0.00	3.68	100	0	0	0
3	experimental	41.50	1	6	0.55	9.48	100	6	13	0
4	experimental	2.00	0	1	0.00	7.73	20	0	0	0
5	experimental	6.58	2	3	0.22	6.55	100	2	8	0
6	experimental	8.65	3	5	7.10	9.65	95	7	6	0
7	experimental	0.00	6	5	1.18	1.33	50	12	1	2
8	natural	0.00	1	11	0.42	15.82	95	8	57	0
9	natural	0.00	4	6	3.18	7.73	95	16	31	1
10	natural	2.92	3	1	2.72	4.53	33	3	0	0
11	natural	1.78	0	1	0.00	7.47	10	0	0	0
12	natural	2.63	0	2	0.00	7.53	80	0	0	0
13	natural	0.00	5	6	16.45	1.15	NA	22	2	3
14	natural	0.00	4	15	2.97	10.45	100	7	1	0
15	natural	39.85	3	5	2.42	5.33	50	5	11	0
16	natural	0.00	6	4	32.27	5.45	90	28	2	19

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