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Grey seal *Halichoerus grypus* breeding sites contribute substantial carrion biomass to the Firth of Forth

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ABSTRACT: Decomposing organic matter is central to the recycling of energy and nutrients in all ecosystems. Few studies have investigated the role of animal carrion biomass in ecosystem functioning, and quantitative data on carrion biomass are lacking. The role of carrion inputs in the marine environment specifically is poorly understood. The grey seal *Halichoerus grypus* breeding colony on the Isle of May in the Firth of Forth, Scotland, provides insight into the contribution of regular carrion pulses to the surrounding marine ecosystem. This study analysed 3 breeding locations with a range of topographies, elevations and tidal influences. Carcasses were mapped from aerial images and ground visual surveys in the 2008 and 2012 breeding seasons. Generalised linear mixed models were used to explore the degree to which breeding location and the position of a carcass influenced its availability to marine scavengers. Carcasses closer to shore were more likely to be completely displaced to the marine environment, and this effect varied with breeding location. An approximate 0.9 to 1.3 tonnes of biomass per hectare of breeding site per year were released into the marine system. For carcasses that were below the high-water spring tide range but remained on shore, we quantified the typical duration of submersion to range from 5% to 44% of the time carcasses were ashore. Additionally, up to 808 kg of carrion was accessible to marine scavengers while washed by tides. Our results suggest breeding colonies of grey seals may contribute significantly to the carrion biomass available in local marine systems.

KEY WORDS: Marine carrion · Carcass · Grey seal · *Halichoerus grypus* · Pinniped · Scavenging

1. Introduction

Decomposition of organic matter contributes to nutrient and energy cycling through ecosystems (Barton et al. 2019). The role of plant decomposition as a central component of ecosystem functioning is broadly recognised (Gessner et al. 2010). Yet, the significance of dead animal (carrion) biomass to ecosystem functioning and nutrient budgets is not well understood (Barton et al. 2019, Benbow et al. 2020). Although carrion forms a minor component of the dead biomass resource pool, it is likely to have a disproportionate effect on ecosystems relative to equivalent amounts of plant biomass (Parmenter & Macmahon 2009, Barton et al. 2013, 2019). This is because carrion is a comparatively nutrient-rich, ephemeral and spatially patchy contribution to ecosystems and an important resource for many specialist species (Barton et al. 2013, 2019). Carrion, as a heterotrophically derived resource, should therefore be considered separately from plant biomass for a clearer understanding of ecosystem function (Barton et al. 2019). While carrion inputs to other ecosystems have been more widely documented (e.g. freshwater rivers, forests and marine pelagic systems; Barton et al. 2019), the extent and importance of carrion input to coastal marine systems is poorly understood.

The importance of marine carrion inputs in supplying energy varies across different marine systems (Davenport et al. 2016). Large vertebrate carcasses falling into the nutrient-poor deep sea from surface waters represent a large energy resource, particularly for scavenging communities (Higgs et al. 2014, Smith & Baco 2021). The role of marine scavengers in coastal waters is being increasingly studied in light of human activities such as fishing and associated discards, which lead to high carrion input (Ramsay et al. 1997, Groenewold & Fonds 2000, Link & Almeida 2002, Davenport et al. 2016, Depestele et al. 2018). In productive shallow-water systems, carrion inputs may be a minor ephemeral resource exploited by facultative rather than obligate scavengers (Britton & Morton 1994, Davenport et al. 2016). However, the influence of carrion availability in shallow waters on community structure is not well known (Ramsay et al. 1997) and the prevalence of scavenging is greatly underestimated in the marine environment (Wilson & Wolkovich 2011).

Regular pulses of carrion associated with breeding aggregations of animals in coastal systems may contribute a significant, predictable food resource for local scavenger communities (Quaggiotto et al. 2018). The potential of coastal marine mammal aggregations as a regular source of carrion to local marine communities is not well understood (Watts et al. 2011). Yet, marine mammals can at particular times be significant carriers of energy and nutrients across ecosystem boundaries (Ellis et al. 2003, King et al. 2007). Carrion biomass from marine mammals may be located in the terrestrial, intertidal or marine area, and therefore has the potential to support both terrestrial and marine scavenging communities.

There are limited studies on the composition of coastal marine scavenging communities along with a general lack of knowledge on carrion in the context of ecosystem functioning in this system (Schlacher et al. 2013, Quaggiotto et al. 2018). Quaggiotto et al. (2016) represents one of the few experimental studies documenting the successional pattern of scavenging on marine mammal (seal) carrion in the subtidal marine environment. Results from this study show that the composition of a subtidal scavenging community may be dominated by benthic invertebrates (e.g. Echinodermata and Malacostraca), with coastal fish species and bacterial activity also present as part of the scavenging community. However, there has been limited research on the effect of carrion on energy and nutrient flows in food webs (Benbow et al. 2020).

Grey seals *Halichoerus grypus* aggregate in seasonal breeding colonies, with pups remaining ashore until after weaning. Breeding colonies of grey seals produce a predictable influx of high-quality carrion for surrounding ecosystems in the form of pup carcasses and afterbirth (Quaggiotto et al. 2018). This potential resource has been increasing in the Firth of Forth in recent years as the seal colony expanded, from 30 pups in 1977 (Harwood & Wyile 1987) to 1875 pups born in 2008 (Russell et al. 2017). Given mean annual pup mortality rates of $13.3 \pm 0.9\%$ (mean ± SE), there were approximately 3200 deceased pups produced between 2000 and 2012, representing a potentially considerable quantity of carrion (Quaggiotto et al. 2018). However, tidal action, weather conditions and coastal topography may affect the transfer of seal pup carrion to the local marine system. Extreme weather conditions, steep shore gradients and strong currents could also facilitate the transfer of carrion further offshore into deeper waters.

The present study aimed to quantify the input of grey seal pup carrion biomass over 2 pupping seasons (2008 and 2012) to the Isle of May marine system in the Firth of Forth, Scotland. We quantified the carrion available from pup carcasses at 3 distinct locations and assessed what proportion of carrion enters the marine system through carcass displacement and submersion by tidal action. The biomass from seal carcasses available to marine scavengers was estimated during the breeding seasons of 2008 and 2012. We discuss the importance of this carrion input into the marine coastal system.

2. Materials & Methods

2.1. Study area

The Isle of May (56°11.202'N, 2°33.342'W) is located 8 km from the southeast coast of Fife, Scotland, at the mouth of the Firth of Forth. The island is 1.9 km long and 0.5 km wide (45 ha), with the west and southeast coasts surrounded by cliffs (Fig. 1). The island is designated a Special Area of Conservation (SAC) (EC Habitats Directive 92/43/EEC) because of the grey seal breeding colony. The northern part of the island mainly consists of low-lying rocky terrain and is the primary area of pup production (Pomeroy et al. 2000a). As the colony has grown, other areas have been occupied including the tussock grass areas and rocky cliff-lined beaches of the south. Three site locations – East Tarbet on the northeast of the island, The Loan on the southeast of the island and Pilgrim's Haven on the southwest (Fig. 1b) – were chosen to study the effect of proximity to shore in varying topographies and tidal influences on the entry of seal carcasses into the marine system. East Tarbet is relatively sheltered from wave and tide action in some areas, yet possesses a long, thin channel stretching to the breeding colony, which effectively increases the coastline and offers little protection from extreme tidal surges and waves. The Loan, although on the east coast of the island and therefore more affected by easterly storms, is relatively sheltered from tidal action. Most breeding females and pups at The Loan are located on the elevated grassy areas behind raised rocky outcrops separating them from the sea. Pilgrim's Haven is a low-lying rocky beach influenced by tidal action and surrounded by cliffs. There is limited overland mixing of seals between the sample locations due to distance between locations, and the presence of natural barriers such as walls and cliffs.

2.2. Data collection

Aerial surveys covering the island and a walked visual census that systematically searched seal breeding locations were used to count seal pup carcasses in 2 pupping seasons on the Isle of May (October – December 2008 and 2012). Images from aerial surveys were supplied by the Sea Mammal Research Unit (SMRU, University of St Andrews). Adult grey seals and pups were identified from digitised aerial images captured between 14 October and 28 November 2012 and from microfiche images captured between 18 October and 30 November 2008. Both sets of aerial images consisted of 5 surveys flown during each season. Examples of portions of the high-resolution stitched imagery are available in the Supplement (Fig. S1, www.int-res.com...). Using this method, the locations of carcasses were estimated to be accurate to ±3 m (Pomeroy et al. 2000b). Walked visual censuses of carcasses were carried out at the end of both breeding seasons (late November to early December). The geographic locations of carcasses were therefore identified at 6 time points in both breeding seasons: the 5 dates on which aerial surveys took place and a final catalogue of carcass locations from the final walked visual census (Table S1 in the Supplement, www.int-res.com...). During walked visual census, when a carcass was encountered, sex (where possible), developmental stage, geographic location and any water influence acting on the carcass were recorded. In 2012, aerial carcass identification was also verified by data collected by visual census. These visual censuses were conducted from hides near the colony areas of East Tarbet and The Loan, and a remote camera at Pilgrim's Haven (to avoid disruption to the seal colony at this location). Each carcass was tracked from the point it first appeared in the photographic record either until it was absent from images or until the final walked visual census.

To differentiate dead from live pups in the aerial images and microfiche, a set of 6 weighted criteria were developed (Table 1). Evidence such as bloodstains on pelage and the attendance of gulls were weighted as more reliable indicators of a dead pup than other categories such as possible entrapment. Each pup or carcass identified in the aerial images was assessed on this basis with some requiring several criteria to be fulfilled (as described in Table 1) before they were designated as a carcass.

2.3. Statistical analysis

The vertical and horizontal distances from carcasses to the shore (defined as Admiralty Chart Datum; ACD) were calculated. Horizontal measures were taken from the carcass to ACD by the shortest downhill route and vertical distance was derived from the elevation of the carcass above ACD. The duration carcasses remained present was calculated from the time of first observation to the survey in which the carcass was recorded as no longer present. Two statistical models were used to understand the influence of the proximity to shore and then tidal influence on pup carcasses. A binomial GLMM was used to verify that carcasses closer to shore were more likely to be removed as the pupping season progressed. A negative binomial GLMM was then used to predict the length of time carcasses remained ashore and predict the average length of time a carcass remained in each tide strata.

All statistical analyses were carried out in R v.3.6.1 (R Core Team 2018). Published data and code used in these analyses are available for download (Burns 2022). A mixed effects modelling approach was adopted to include ‘year’ as a random intercept in all models to account for the repeated measures at each colony location in both years. Generalised linear mixed models (GLMMs) were fitted in the lme4 package (Bates et al. 2015). A binomial GLMM was fitted to the data to estimate the probability of a carcass being present (or absent) as a function of colony location and the carcass’s proximity to shore (calculated as the vector distance from ACD of horizontal and vertical components). For carcasses identified as absent after an initial sighting, a negative binomial GLMM was used to model the duration carcasses remained visible as a function of tide stratum and colony location. Variance inflation factors (VIFs) were used to identify collinearity in the explanatory variables. All VIF values for the 3 variables tested were <3, and so were retained in the model selection process (Zuur et al. 2009). Backwards stepwise model selection was used to identify the optimal models by Akaikes’ information criterion (AIC) (Table S2 and Table S3 in the Supplement). We selected models based on the rules: (i) more parsimonious models are preferable, (ii) smaller AIC is preferable, and if these contradict, (iii) the more complex model was selected when $\Delta AIC > 2$. The models were validated by visually analysing residual plots to check for normal distributions and the absence of any patterns (Figs S2 and S3 in the Supplement).

2.4. Calculation of carrion biomass entering the marine system

The mass of all carcasses was estimated from the earliest image in which the carcass was present. The developmental stage was assessed for each carcass from the aerial images. Three categories of developmental stage were possible to identify. Categories, displayed in Table 2, were adapted from Boyd & Laws (1962) and Kovacs & Lavigne (1986). The mass (kg) of carcasses at each developmental stage (Table 2) was calculated using the equations (reproduced in Equations in the Supplement) provided by Kovacs & Lavigne (1986). The mean age of each developmental category was used in the equations and a mass was calculated for each category by taking a mean between male and female values. These values were assumed to be the maximum carcass mass given that they are based on live pups. Minimum masses were calculated from Quaggiotto et al. (2018), where estimated masses were adjusted by 8.02 kg, the average difference in mass measured between alive and dead pups. Estimated values were calculated as the mean of female and male pups at each developmental stage. Stages I and II were indistinguishable in the present study and pooled average mass was calculated across both stages for male and females.

For carcasses assumed to be washed away during the breeding season, the 2 mass values were used to estimate the total carrion biomass. To also understand the quantity of carrion available to marine scavengers when carcasses were still ashore but inundated by tide, tide heights for the duration of each breeding season were used to define tide strata (Fig. 2). The hourly tide heights for both breeding seasons were sourced from the British Oceanography Data Centre (www.bodc.ac.uk) for the port of Leith, approximately 44 km west of the Isle of May. Tide strata were defined as: Dry above High Water Spring (HWS), HWS to High Water Neap (HWN), HWN to Low Water Neap (LWN) and LWN to Low Water Spring (LWS). The measures of elevation were used to allocate individual carcasses to a particular tide stratum. Carcasses identified in the Dry tide stratum were considered to not contribute carrion to the marine environment. Conversely, all carcasses in the lowest tide strata (LWN–LWS) were considered continuously submerged and available to marine scavengers. The mean elevation of carcasses in the 2 middle tide strata (HWS–HWN and HWN–LWN) were calculated and used to estimate the tidal influence on an 'average' carcass. The total time submerged was then calculated for the mean carcass elevation in each of the 2 middle tide strata. Carcasses were assumed to be submerged when tide height was equal to or greater than their elevation.

3. Results

3.1. Carcass abundance

A total of 253 carcasses were identified in all 3 study sites: 133 carcasses in the 2008 breeding season and 120 carcasses in 2012 (Table 3). However, there were distinct differences in carcass density between sites. Carcass density was much higher at Pilgrim's Haven, producing densities of 80.6 to 124.9 carcasses per hectare, compared to the other sites (The Loan and East Tarbet), which exhibited densities of 6.2 to 9.9 carcasses per hectare (Table 3). Of the total 253 carcasses identified, 59% were still present by the end of the breeding season (60% in 2018; 58% in 2012).

3.2. Effect of carcass proximity to shore on availability to marine scavengers

All of the predictor variables (location and proximity to shore) and the interaction term (location: proximity to shore) were retained during model selection (Tables S2 and S4 in the Supplement). At all 3 locations, carcasses first observed closer to chart datum had a higher probability of being absent from later surveys (Fig. 3). Pilgrim's Haven and The Loan displayed similar trends, and carcasses in these locations had significantly lower probability of being washed to sea compared with East Tarbet (Fig. 3). As expected, the duration seal pup carcasses remained on land decreased significantly in tide strata closer to chart datum (Fig. 4). Colony location was dropped during model selection, indicating that this effect was similar across all 3 locations (Tables S3 and S5 in the Supplement). Carcasses that remained in the Dry stratum, above HWS, remained visible in aerial images for about 20 d. Carcasses that were influenced by tidal action remain for shorter periods of 13 d or fewer. Closer to chart datum, carcasses were washed away from the lower 2 strata after 11 and 8 d, respectively.

3.3. Biomass input to the marine system

The estimated biomass of seal pup carrion, remaining on land and displaced to the sea, was calculated across the 3 study locations for the 2008 and 2012 breeding seasons (Table 4). These 3 areas produced a total mass of carcasses between 2234.60 and 2990.60 kg in 2008 and between 1941.43 and 2660.79 kg in 2012. This is equivalent to between 2273.54 and 3114.07 kg ha–1 in 2008 and between 1597.82 and 2193.14 kg ha–1 in 2012. In both seasons, approximately 930 to 1296 kg ha–1 of these seal pup carcasses were displaced into the marine environment (Table 4). Additionally, prior to carcasses fully entering the marine environment, some were available to marine scavengers at the shoreline when located between HWN and HWS, and between LWN and HWN inundated by the tide (Table 5). Carcasses submerged in this way provided additional access for marine scavengers to this resource for up to 44% of the time they remained on shore.

4. Discussion

The range of estimated of carrion biomass entering the marine system from the 3 study sites presented here on the Isle of May is equivalent to approximately 0.9 tonnes to just less than 1.3 tonnes per hectare annually. This figure represents the first time carrion biomass entering the marine environment has been calculated for this coastal ecosystem. The estimated 0.9 to 1.3 tonnes is based on only 2 years of data, and further study would be required to confirm the annual variation in carrion biomass entering the marine system. The regular, predictable influx of seal pup carrion likely constitutes an important energy subsidy for marine scavengers in this region (Quaggiotto et al. 2016, 2018). Observations of individual seal carcasses have provided insights into scavenging community assemblages in both the coastal terrestrial and marine environment (Quaggiotto et al. 2016). Further studies have demonstrated seal carrion sustains avian scavengers thereby affecting ecosystem structure and function as an important energy transfer pathway (Quaggiotto et al. 2018, Mills et al. 2021). However, there is limited understanding of how individual carcasses scale with mortality at population and community levels, as quantitative data are lacking on carrion contribution to ecosystems. Carrion contributions, especially in the coastal marine environment, have been difficult to quantify due to the rapid turnover of this labile resource (Benbow et al. 2020). Modelling studies have also demonstrated that carrion biomass may be a large natural source of food compared to other carrion inputs, for example, fisheries discards (e.g. Depestele et al. 2018). It is important to quantify natural carrion from seal colonies at a larger seascape scale to more fully understand the role of carrion biomass in wider ecosystem functioning and in ecosystem energy and nutrient budgets (Benbow et al. 2020).

The overall abundance of grey seal pup carcasses was similar in both the 2008 and 2012 breeding seasons. Pup carcass abundance was also similar across the 3 study locations (Pilgrim's Haven, The Loan and East Tarbet), but with substantially higher carcass densities recorded at the Pilgrim's Haven site, even though this site had smaller available space. Breeding aggregations of grey seals maintain relatively constant densities, through threat displays and aggressive behaviour (Caudron et al. 1998). On the Isle of May, this is one adult female to 10 m2 (Pomeroy et al. 2000b). Therefore, the high carcass densities recorded at Pilgrim's Haven are likely a consequence of higher mortality rate at this location as a result of being a lower quality breeding site, rather than a higher density of pupping mothers (Twiss et al. 2003).

Whether a site is prime or sub-optimal habitat can be influenced by local topography. In the elevated locations observed in our study (East Tarbet and The Loan), pup mortality rates tend to be higher, where these areas are further from sources of water and further from access to the sea (Twiss et al. 2001, 2003). In these elevated areas, higher mortality rates tend to produce carcasses further from the sea and are relatively sheltered from tidal action; therefore, they are less likely to contribute carrion to the marine system. Sub-optimal, low-lying sites, surrounded by cliffs with little tidal refuge, such as Pilgrim's Haven in this study, will produce high carcass numbers as advancing tides increase seal densities, and increase the likelihood for aggressive interactions and the potential for pups to be crushed. Sites that are closer in proximity to the sea also display an increased probability that pups are washed away at high tides. High tide events will have a twofold effect by increasing both pup mortality and readily displacing carcasses to the marine system. As seal numbers increase, terrestrial environmental heterogeneity within and between breeding sites will create carrion hot spots, influence scavenger abundance and affect the distribution of marine organisms.

There are 3 main scenarios in which carcasses were identified as being detectable in one survey and then undetectable in subsequent surveys: (1) the lack of detection may result from consumption by terrestrial scavengers; (2) carcasses may be buried by the movements of other members of the colony; or (3) carcasses are washed away by tide and wave action. Carcasses identified in one survey, which were then consumed by terrestrial scavengers or buried, were sometimes still partially visible, but often classified as undetectable in subsequent surveys. In both breeding seasons (2008 and 2012) and across all 3 study locations, we showed a direct positive relationship between proximity to shore and the likelihood of carcass disappearance. This means it is likely that if carcasses are identified in one survey and are then undetectable in subsequent surveys that they have been washed into the sea.

Pup carcasses from both The Loan and Pilgrim's Haven study sites showed a similar probability (80% chance at 48–49 m from ACD) of being washed into the sea. Pilgrim's Haven is a low-lying site often inundated at high tide and had the potential for large numbers of carcasses to be removed by wave and tide action. The Loan is likely to be strongly affected by easterly storms and swells. At East Tarbet, carcasses were considerably more likely to be washed away at greater distances from ACD (80% chance at 123 m from ACD). A long, thin channel at East Tarbet stretches to the breeding colony, which effectively increases the coastline and offers little protection from extreme tidal surges and waves, meaning carcasses could be washed away at greater distances. Carcasses that were more influenced by tidal action remained visible for shorter periods (≤14 d), in contrast to predominantly terrestrial areas, where carcasses remained visible for approximately 20 d.

The contribution of carrion is not solely limited to carcasses washed directly into the sea. Carcasses within reach of the tide, but left dry, will also contribute to shoreline habitat diversity, retaining moisture and influencing the microclimate of their surroundings (Quaggiotto et al. 2019). Tide and wave action will submerge carcasses regularly, allowing access for marine and intertidal zone scavengers, many of which will synchronise foraging activity with high tides (Watts et al. 2011). The results from this study, based on an 'average' carcass within each stratum, showed that between approximately 0.25 and 1.6 tonnes of carrion were available to marine scavengers, partially or fully submerged in the intertidal zone.

This study has demonstrated that the contribution of carrion biomass from a grey seal breeding colony to the coastal marine system may be substantial. The data presented here were collected in 2008 and 2012, as such, further studies using more recent data that reflects anecdotal population increases on the Isle of May could dramatically increase the pup carrion input. Additionally, potential variability in pup births between years could be accounted for by using additional data across multiple years. Future studies are also needed to quantify this input at a larger scale across other grey seal breeding colonies. The proximity to shore and the likelihood of carcass disappearance is a clear indication that carcasses within the reach of tide and wave action are being washed out to sea. This predictable source of energy may subsidise the diets of numerous marine scavengers. Carrion from dead seal pups is available to marine scavengers not only from pups washed out to sea but also through being submerged by tidal action. The comparison of 3 study sites allowed inferences to be drawn about how site characteristics, including topography, influence of tidal action and available pupping space, can influence the probability of seal carcasses entering the marine environment. Further studies would provide insight into the carrion contribution of other colonies of grey seals, and indeed other pinnipeds, to marine scavenger communities. Importantly, more research is needed to understand how these baseline quantities of carrion resource affect ecosystem energy and nutrient budgets, vital for ecosystem modelling.

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Table 1. Identification criteria for seal pup carcasses

Criterion	Weighting of criterion
I: Several gulls in attendance close to a suspected carcass and visibly pecking	Accept as carcass based on this alone
II: Bloody patches on pelage, especially at anterior end	Accept as carcass based on this alone
III: No obvious shadow being cast from raised limbs, head or body	One more criterion required from any category
IV: Obvious flattening of body, loss of '3-dimensional' body form	One more criterion required from any category

V: Suspected carcass trapped in particularly inaccessible area	More criteria required other than VI
VI: Suspected carcass separated from mother or alone	More criteria required other than V

Table 2. Descriptive age categories, based on Kovacs & Lavigne (1986), of neonatal seal pup masses from the Isle of May. Dashed lines indicate divisions between the 3 categories used to assess pup carcasses. Masses display a minimum and maximum estimate. Maximum carcass mass was based on live pup mass from the equations of Kovacs & Lavigne (1986). Minimum masses were calculated from Quaggiotto et al. (2018), where estimated masses were adjusted by 8.02 kg based on the measured difference between alive and dead pups

Developmental stage	Description	Mean age (d)	Mass (kg)
I	White coated pups with yellowish tinge; small; neck, hips and ribs visible	2-5	14.48 – 20.07
II	White coated pups; fore and hind flippers often visible; more blubber deposition than stage I		
III	White to light grey coat; body barrel shaped with obvious blubber layer; white pelage still covering body but slight loss in facial areas	12	23.40 – 31.29
IV	Lanugo being shed exposing some areas of juvenile pelage	16 – 21+ (weaning age of 18 d used for calculation of mass)	34.35 – 39.21

Table 3. Numbers of carcasses identified at 3 breeding locations (Pilgrim's Haven, The Loan and East Tarbet) on the Isle of May in the 2008 and 2012 breeding seasons. N_c: total number of carcasses; N_a: number of absent carcasses; D_c: carcass density (N_c ha^{-1}).

	2008				2012			
Location	N_c	N_a	Area (ha)	D_c (ha^{-1})	N_c	N_a	Area (ha)	D_c (ha^{-1})
Pilgrim's Haven	47	20	0.376	125.00	34	22	0.422	80.57
The Loan	34	14	5.506	6.18	41	9	4.125	9.94
East Tarbet	52	19	5.357	9.71	45	19	5.132	8.77

Table 4. Distribution of grey seal pup biomass and density between marine and terrestrial environments in 3 breeding locations (Pilgrim's Haven, The Loan and East Tarbet) in 2008 and 2012. Masses display the minimum and maximum estimates calculated as live pup mass for maximums (max.) and adjusted down by 8.02 kg as per Quaggiotto et al. (2018) for minimum (min.) masses.

Location	2008				2012			
	Remaining terrestrial		Displaced to marine		Remaining terrestrial		Displaced to marine	
	(kg)	(kg ha^{-1})	(kg)	(kg ha^{-1})	(kg)	(kg ha^{-1})	(kg)	(kg ha^{-1})
Pilgrim's Haven								
Maximum	597.99	1590.40	435.06	1157.07	263.28	623.89	486.42	1159.65
Minimum	435.56	1158.40	316.36	841.38	191.60	454.03	354.24	839.43
The Loan								
Maximum	475.55	86.37	314.64	57.14	737.55	178.80	191.85	46.51
Minimum	369.93	67.19	229.48	41.68	542.31	131.47	139.24	33.76
East Tarbet								
Maximum	759.99	141.87	435.06	81.21	566.70	110.42	414.99	80.86
Minimum	566.91	105.83	316.36	59.06	412.16	80.31	301.88	58.82
Total								
Maximum	1833.53	1818.64	1157.07	1295.43	1567.53	913.11	1093.26	1280.03
Minimum	1372.40	1331.42	862.20	942.12	1146.07	665.81	795.36	932.01

Table 5. Carcass tidal submersion for the 2008 and 2012 grey seal breeding seasons. HWS: high water spring; HWN: high water neap; LWN: low water neap. Carcasses in the upper stratum (Dry) were assumed to never be submerged and those in the lowest stratum (LWN–LWS) were assumed to be constantly fully submerged. Total carcass submersion times were calculated from the GLMM used to predict the duration (d) carcasses remained visible in the 4 tide strata

Tidal stratum	No. of carcasses	Mean (± 1 SD) carcass mass (kg)	Total biomass (kg)	Modelled median duration (d)	Total carcass submersion time (h:min) | Proportion of time spent submerged
2012					
HWN–HWS	7	21.95 ± 4.1	153.65	14	35:23 | 0.11
LWN–HWN	36	20.20 ± 0.0	727.20	12	114:56 | 0.40
2008					
HWN–HWS	12	22.20 ± 4.3	226.40	12	15:08 | 0.05
LWN–HWN	36	22.44 ± 5.0	807.84	10	104:43 | 0.44

Fig. 1. Grey seal colony study locations on the Isle of May in the mouth of the Firth of Forth. (a) Location of the Isle of May (Scotland). (b) Aerial image of the Isle of May, with red polygons showing the location and extent of the 3 study sites: (i) East Tarbet, (ii) The Loan and (iii) Pilgrim's Haven. (c) Topographic map of the Isle of May with red polygons showing the 3 study sites: (i) East Tarbet, (ii) The Loan and (iii) Pilgrim's Haven. The dark blue contour line shows mean low water, light blue contour line shows mean high water and brown lines show land elevation from 5 to 50 m at 5 m intervals

Fig. 2. Tide heights above chart datum for the (a) 2008 and (b) 2012 breeding seasons. Each *x*-axis tick mark displays one day between the dates shown. The 4 colour bands indicate the 4

tide strata used (orange: Dry – above High Water Spring; yellow: HWS–HWN – between High Water Spring and High Water Neap; light blue: HWN–LWN – between High Water Neap and Low Water Neap; dark blue: LWN–LWS – between Low Water Neap and Low Water Spring). Blue horizontal lines indicate the mean carcass elevation for carcasses influenced by tidal action

Fig. 3. GLMM prediction of the probabilities of grey seal pup carcasses being washed away as a function of distance from Admiralty Chart Datum (ACD). The solid lines indicate the prediction for carcasses in a ‘typical’ year at each of the 3 survey sites. The shaded areas show the model variation from the random and fixed effects equivalent to a 95% prediction interval. Each survey site is indicated by 1 of 3 colours: purple line and shading represent East Tarbet, red line and shading represent Pilgrim’s Haven, and green line and shading represent The Loan

Fig. 4. Tidal influence on the duration that carcasses remained visible in aerial imagery in a ‘typical’ year predicted from data from the 2008 and 2012 breeding seasons. Black diamonds show the fixed effect prediction in a ‘typical’ year and the intervals show medians of the upper and lower bounds of the random effects. Tide strata are: Dry – above High Water Spring; HWS–HWN – between High Water Spring and High Water Neap; HWN–LWN – between High Water Neap and Low Water Neap; LWN–LWS – between Low Water Neap and Low Water Spring