Post-disturbance haulout behaviour of harbour seals

WILLIAM D. PATERSON[a], DEBBIE J. F. RUSSELL[a], GI-MICK WU[a], BERNIE McCONNELL[a], JOHN I. CURRIE[c], DOMINIC J. McCAFFERTY[b] and DAVE THOMPSON[a]

[a] *Sea Mammal Research Unit, Scottish Oceans Institute, University of St. Andrews, St. Andrews, Fife, KY16 8LB, UK*

[b] *Scottish Centre for Ecology and the Natural Environment, Institute of Biodiversity, Animal Health and Comparative Medicine, MVLS, University of Glasgow, Rowardennan, Glasgow G63 0AW, UK*

[c] *School of Engineering and the Built Environment, Edinburgh Napier University, Merchiston Campus, Colinton Road, Edinburgh, EH10 5DT, UK*

Corresponding author:

WILLIAM D. PATERSON

Postal address:

Sea Mammal Research Unit, Scottish Oceans Institute, University of St. Andrews, St. Andrews, Fife, KY16 8LB, UK

Email address:

wdp1@st-andrews.ac.uk

Telephone number:

07709602314

1. ABSTRACT

1. We investigated the impact of anthropogenic activity associated with marine renewable developments on harbour seals (*Phoca vitulina*) using controlled disturbance trials.
2. Hauled out seals were approached by boat until all seals had entered the water and this was repeated approximately every three days (weather permitting). The time taken for seal counts to return to pre-disturbance levels was determined by monitoring haulout sites using time-lapse photography.
3. Mean post-disturbance counts of hauled out seals returned to 52% (95%CI 35-69%) of pre-disturbance counts within 30 minutes. However, mean counts only returned to 94% (95%CI 55-132%) of pre-disturbance counts after four hours.
4. Eight seals were tagged with GPS phone tags to provide information on haulout location and at-sea movements, allowing investigation of how disturbance may influence haulout site choice and seal distribution.
5. Telemetry tagged seals displayed a high degree of haulout site fidelity. Disturbance trials did not have a significant effect on the probability of seals moving to a different haulout site.
6. When seals hauled out again within the same low tide period after disturbance trials, the proportion of time spent hauled out was high indicating that when seals are motivated to haulout they will do so despite past disturbance.
7. As there was no large scale re-distribution after disturbance we suggest that monitoring effort to determine the effects of short-term increases in levels of disturbance caused by boat activity can be spatially localized. However, where disturbance is likely to be longer-term or impact on important haulout sites for breeding and/or moulting, monitoring may be required over a larger geographical area.

KEYWORDS

Anthropogenic activity, coastal, intertidal, behaviour, disturbance, mammals, hydropower, phocid, renewable energy

2. INTRODUCTION

The spatial and temporal overlap of marine habitats used by humans and marine mammals is an issue of growing concern. Development of marine renewable energy technology has led to increased levels of construction activity in the marine environment that, in some cases, results in avoidance behaviour by marine mammals (Dahne et al., 2013; Russell et al., 2016). This could lead to barrier effects that exclude animals from areas regularly used for foraging and, in the case of seals, for hauling out. The commitment of many countries to an increased reliance on marine renewable energy is likely to lead to an increase in the development of technologies that potentially have a negative impact on the marine environment. Of those technologies, tidal turbine arrays are expected to become an established technique with several projects already at an advanced stage (Lewis et al., 2011). Tidal turbine deployments are best suited to areas where tidal streams are restricted topographically resulting in faster currents and therefore a higher energy yield (Lawn, 2009), meaning that sites identified for deployment are often close to shore. For species where marine habitat use overlaps with inshore areas identified as suitable for tidal turbine deployments there is a need to assess the impact on these species before the construction phase commences.

In the UK a number of tidal turbine projects are under development (Uihlein & Magagna, 2016). Permitting such developments requires a realistic assessment of their likely impact on marine mammals. Research aimed at meeting these requirements has quantified the effects of marine renewables solely within the marine environment itself (Hastie et al., 2015; Hastie et al. 2017; Thompson, Onoufriou, Brownlow & Morris, 2016; Wilson, Benjamins & Elliott, 2013). However, the habitat use of harbour seals (*Phoca vitulina*) includes terrestrial haulout sites that are important at various stages of their annual life cycle (Thompson, Fedak, McConnell & Nicholas, 1989). Harbour seals have been shown to forage relatively close inshore in some areas (Sharples, Moss, Patterson & Hammond, 2012; Thompson et al., 1996) and display a high degree of site fidelity for particular haulout sites (Cordes & Thompson, 2015; Dietz, Teilmann, Andersen, Riget & Olsen, 2013). Inshore developments are likely to spatially and temporally overlap with habitat regularly used by harbour seals. There is therefore potential for the construction, operational and decommissioning phases of inshore marine renewable developments to affect how harbour seals use the area in the vicinity of those developments for transit, foraging and hauling out.

Several studies have described the normal haulout pattern of harbour seals in relation to environmental conditions (Grellier, Thompson & Corpe, 1996; Watts, 1992), tidal state (Pauli & Terhune, 1987), diurnal activity (Russell et al., 2015; Watts, 1996) and seasonal events such as the breeding and moult periods (Thompson et al., 1989). Where a novel stimulus resulting from increased anthropogenic activity creates a behavioural response that results in a deviation from that normal haulout pattern, animals can be considered to have been disturbed. Previous studies looking at the causes of disturbance of seals at haulout sites have focused on the causes of disturbance, looking into factors such as the distance at which seals are disturbed by boats (Jansen, Boveng, Dahle &

Bengston, 2010), the type of boat activity that causes disturbance (Johnson & Acevedo-Gutierrez, 2007) and disturbance by pedestrians (Osinga, Nussbaum, Brakefield, & Haes, 2012). However, having identified the causes of disturbance it is important to then quantify the consequences in terms of behavioural changes. UK harbour seals are listed as a protected species under Annex II of the European Habitats Directive. Particularly in Scotland, Section 117 of the Marine (Scotland) Act 2010 states that it is an offence to "intentionally or recklessly harass seals" at designated haulout sites. Understanding what happens when a normal haulout pattern is disrupted by anthropogenic activity is key to meeting monitoring requirements aimed at mitigating against the impact of disturbance on seals.

Changes in levels of anthropogenic activity have been shown previously to alter the haulout behaviour of harbour seals. For example, Henry & Hammill (2001) suggest that increased leisure activity increased the number of occasions harbour seals flushed into the water in Métis Bay, Canada. Similarly, Lonergan, Duck, Moss, Morris & Thompson (2013) suggest that harbour seals on the west coast of Scotland haul out less at the weekends as opposed to during weekdays. Harbour seals may also switch to a nocturnal haulout pattern to avoid hauling out during the day when daytime anthropogenic activity is high (London, Hoef, Jeffries, Lance & Boveng, 2012). Increased anthropogenic activity can therefore be a factor when observing broad-scale changes in the timing and frequency with which harbour seals haul out. As well as quantifying how seal activity is affected at particular sites it is also important to determine whether or not seals transit from one location to another in response to disturbance (Andersen, Teilmann, Dietz, Schmidt & Miller, 2014) which may require monitoring over a larger spatial scale. This is particularly true where disturbance results in animals being displaced from sites designated for protection. The spatial scale of monitoring should necessarily include the area in the immediate vicinity of any proposed marine renewable development but also the geographical range over which it is determined that increased anthropogenic activity may have an effect.

One such development is the tidal turbine array granted permission for deployment in the Sound of Islay, Scotland (Paterson, Russell, Wu, McConnell & Thompson, 2015; Sparling, 2013). In terms of impact on marine mammals, this site is of particular importance due to its proximity to the South East Islay Skerries SAC designated to protect harbour seals that use the site to haul out throughout the year. Harbour seals in this area are known to transit between the South East Islay Skerries SAC and the Sound of Islay in which the tidal turbine array is to be deployed. As well as being a regular transit route for seals there are a number of harbour seal haulout sites within the Sound of Islay that are in close proximity to the proposed development (Paterson et al., 2015; Sparling, 2013). Here we describe a study to assess the behavioural responses of harbour seals to disturbance from boat traffic within the Sound of Islay. By implementing a series of controlled disturbance trials where hauled out seals were repeatedly approached by boat until they entered the water, this study quantifies the associated effects in terms of changes in haulout patterns and haulout site fidelity. The results are used to determine the spatial extent of monitoring required when assessing changes in harbour seal haulout behaviour affected by boat disturbance.

3. METHODS

Study sites

Two sites on the eastern shore of Islay (55°45'N, 06°16'W), an island off the west coast of Scotland, were chosen as focal haulout sites for this study (Figure 1). Both haulout locations, Rubha Bhoraraic (RBR) and Bunnahabhain (BHN), were determined to be regularly used by harbour seals based on aerial survey data collected between 1990 and 2009 and a previous telemetry based study of seal movements and haulout site use in 2011 and 2012 (Sparling, 2013). Those data also indicated that RBR and BHN are two of the most frequently used harbour seal haulout sites close to a proposed tidal turbine development within the Sound of Islay. None of the haulout sites targeted in disturbance trials were on the list of sites designated to provide additional protection from intentional or reckless harassment of seals under Section 117 of the Marine (Scotland) Act 2010. RBR and BHN are tidally influenced haulout sites with tidal ranges of between 1.0m and 1.5m during neap tides and 0.3m and 2.2m during spring tides. This results in both haulout sites being fully submerged during spring high tides and remaining partially available during neap high tides.

Monitoring haulouts using remote cameras

Time-lapse photographs were collected at one minute intervals between 23/04/2014 and 22/07/2014 at both BHN and RBR. Both camera systems consisted of two Canon EOS 1100 DSLR cameras in a single weatherproof housing. Each housing had one camera equipped with an 18-55mm lens and the other with a 70-300mm lens. This system provided both a wider scale view of vessel activity around the haulout site to record when disturbance events occurred and a narrower view more focused on the haulout site itself to determine the number of seals hauled out. When conditions permitted, counts were made each minute between the hours of 04:00 and 22:00 each day. Counts of seals were grouped by month and each seal count was assigned values for three tidal state variables based on the time since low water (LW), tidal height at the time of counting and tidal amplitude (difference between predicted high water (HW) and LW heights). Counts were designated as high tide or low tide if they occurred more or less than three hours from LW respectively and as spring tide or neap tide if the tidal amplitude was in the upper or lower half of the amplitude range for that spring/neap cycle. Tidal values were taken from the nearest local reference port (Port Askaig; 3.8km from both RBR and BHN sites) in the POLTIPS tidal prediction package (version 3.2.4, Proudman Oceanographic Laboratory).

GPS/GSM phone tag deployment

In April 2014 eight adult female harbour seals were captured for telemetry tag deployment at either RBR (n = 2) or BHN (n = 6). Seals were captured using a pop-up net that could be deployed underwater at low tide and remotely triggered to float to the surface when seals hauled out in front of it during a subsequent low tide. Seals were weighed before being anaesthetized with a 1:1 combination of Tiletamine and Zolazepam (Zoletil® 100). GPS/GSM phone tags (McConnell, Fedak, Hooker & Patterson, 2010) were then glued to the seals' fur using Loctite® 422 Instant Adhesive. All procedures were carried out under Home Office Animals (Scientific Procedures) Act licence number 60/4009.

GPS/GSM phone tags were programmed to record an animal as having hauled out when the on-board wet/dry sensor was continuously dry for >10 minutes. GPS location fixes were collected while seals were at sea as well as on land. Data collected by the tag were sent back to SMRU via the GSM mobile phone network providing daily updates of the most recent location fixes. Recent movement patterns were used to assess the likelihood of a seal being at or close to haulout sites in the study area. Table 1 gives the latitude and longitude of all haulout locations used by telemetry tagged seals during this study. Figures 1 and 2 present those locations on maps to show the relative distance between visited haulout sites.

Controlled disturbance trials

Disturbance of seals at focal haulout sites

Harbour seals at the South East Islay Skerries SAC and other haulout sites around Islay generally come ashore on small rocky outcrops that are only accessible by boat. The type of disturbance most relevant to the proposed tidal turbine array at the Sound of Islay is a higher than normal exposure to boat traffic during the construction, operational and decommissioning phases. To simulate this type of increased anthropogenic activity, experimental disturbance trials were carried out by approaching hauled out seals in a 4.3m RIB at a speed of five knots. Direct approaches were initiated at a distance of approximately 300m and continued in a straight line until the haulout site was reached and all seals were flushed into the water. Seals were approached at an angle that provided the clearest line of sight between animals on the haulout and the approaching boat. Disturbance of seals from their haulout site was restricted to one trial per day, approximately two hours before low tide to allow time for animals to haul out again within the same low tide period. The first controlled disturbance trials were carried out on 26/05/2014 and continued on a three day cycle thereafter, dependent on navigable weather conditions, until 15/07/2014. Disturbance trials at focal haulout sites were carried out whenever harbour seals were present, regardless of whether any of the telemetry tagged seals were present. The number of seals hauled out at the point of disturbance was used as a reference for estimating the percentage recovery of hauled out seals after disturbance trials.

Disturbance of telemetry tagged seals

Telemetry tagged seals were disturbed into the water at RBR and BHN when present on trial days. However, in order to maximize the number of disturbance trials with telemetry tagged seals the recent movements of seals were examined to identify additional sites where telemetry tagged seals were likely to be hauled out. Those sites were then visited approximately two hours before low tide and wherever telemetry tagged seals were found the same method of approach by boat used at RBR and BHN was applied.

Haulout transition rates

Haulout events recorded by the tag were assigned a location. When multiple GPS points were recorded while a seal was hauled out the median coordinates were used to assign the location of the haulout event. However, the time series of GPS fixes were irregular and so there were haul out events during which no locations were obtained. When this happened, an approximate location was calculated using linear interpolation of GPS locations immediately preceding and immediately following the haulout event. In parallel, a list was accumulated of 'known haulout' sites that had been visited at some time by these or previously tagged seals. Note that haulouts (as defined by >10 minutes continuous dry rule) occasionally occurred at sea due to animals resting at the surface for prolonged periods with the tag exposed to the air. Such at-sea (here defined as >2km from the shore) haulouts were omitted from this analysis. In this study a haulout event was defined as having ended when the tags were wet for >10 minutes. An animal was then defined as being on a trip. The location and time until a subsequent haulout event then determined if an animal had returned to the same haulout site or transited to a different haulout site and in what timeframe either of these events occurred.

The first week's data were excluded from the final dataset. This allowed time for any behavioural changes associated with seals being captured to return to normal (McKnight, 2011). All statistical analyses were carried out using the statistics package R (R Development Core Team, 2014). The modelling approach used examined how the probability of hauling out at a different haulout site was influenced by time of year, site fidelity, whether or not seals hauled out on the same or a subsequent low tide between trips, and whether or not a disturbance event had taken place. The response variable transition was binary in that having embarked on a trip to sea seals either transited from one haulout site to another (1) or returned to the same haulout site (0). Both Julian day and site fidelity were included as smooth terms (thin plate regression splines) to capture the non-linear effects of both variables. Julian day was included to test for seasonal effects. Levels of site fidelity vary by individual through time thus the percentage of haulout events in the previous week that were at the current haulout location was used as a measure of site fidelity for that particular site. Whether or not seals hauled out during the same or a subsequent low tide period was included as a factor to determine to what extent seals enter the water then haul out again at the same site or switch haulout sites within a single low tide. In the context of disturbance this is relevant in that once disturbed into the water, seals could either; (i) haul out within the same low tide period at the same haulout site, (ii) haul out again within the same low tide period at a different haulout site, (iii) haul out on a subsequent low tide period at the same haulout site, or (iv) haul out on a subsequent low tide period at a different haulout site. Disturbance was included as a factor, defined as whether or not seals were flushed into the water during a haulout event while carrying out controlled disturbance trials. The full model also included an interaction between site fidelity and tidal cycle because the effect of site fidelity on transition probability may depend on whether animals haul out in the same or a subsequent low tide period. A Generalized Additive Mixed Model (GAMM) framework within the mgcv library (Wood, 2004) was used for analyses. An AR1 correlation structure from the nlme library (Pinheiro, Bates, DebRoy, Sarkar & R Core Team, 2018) was incorporated to account for temporal autocorrelation within individuals. The error family used in all models was binomial. Backward model selection was carried out using Akaike's Information Criterion (AIC) selection.

Disturbance effect on proportion of time hauled out at low tide

To investigate whether seals were in a cyclic pattern of hauling out more or less when disturbance trials were carried out the proportion of time spent hauled out was compared over the consecutive low tide periods preceding, during and following disturbance. To do this a generalized linear mixed effects model approach was implemented using the R package glmmTMB (Brooks et al., 2017). The full model included the fixed factors consecutive low tide period (three levels; pre-disturbance, disturbance, post-disturbance), seal reaction i.e. whether they hauled out again within the same or during a subsequent low tide after disturbance trials (two levels; same, different) and the interaction between the two. To account for non-independence of data within individuals, individual ID was included as a random effect. Binomial model selection was performed by backwards selection using AIC. *Post hoc* pairwise comparisons to investigate differences in the proportion of time spent hauled out over consecutive low tide periods were made using the R package lsmeans (Lenth, 2016).

4. RESULTS

Monitoring haulouts using remote cameras

Mean counts relative to low tide are summarized for BHN and RBR in Figures 3 and 4 respectively. For both sites combined, the overall mean number of seals hauled out was significantly lower (t-test, $p < 0.01$) at spring high tide ($\bar{x} = 0.12$, SE = 0.05) compared with at neap high tide ($\bar{x} = 1.00$, SE = 0.16). This is due to the largest spring high tides resulting in haulout sites occasionally being completely submerged resulting in increased counts of zero. Mean seal counts were not significantly different ($p = 0.33$) at spring low tide ($\bar{x} = 1.45$, SE = 0.24) compared with at neap low tide ($\bar{x} = 1.79$, SE = 0.20). During neap high tides haulout sites still remained available to seals to haul out but were much reduced in size compared to during low tides. Mean seal counts at neap high tide were significantly lower than at neap low tides ($p < 0.01$) and lower, but not significantly ($p = 0.12$), than at spring low tide.

GPS/GSM phone tag deployment

GPS/GSM phone tag deployment resulted in a total of 626 days of data collected from eight adult female harbour seals. The mean duration of tag deployment was 78 days (range = 41 to 107, SE = 6.98). For all animals there was a total of 634 haulout events separated by more than 10 minutes with a mean trip duration of 18.54 hours (range = 0.17 to 267.17, SE = 1.15) between haulouts. Overall, 16 haulout sites were used throughout the study with individual seals using a mean of five haulout sites (range = 3 to 9, SE = 0.77). The mean duration of haulout events not including those in which disturbance trials were conducted was 5.2 hours (SE = 0.28) (Table 1).

Controlled disturbance trials

Disturbance of seals at focal haulout sites

At BHN a total of 17 disturbance trials were recorded using time-lapse photography with an average of 3.3 days (range = 3 to 4, SE = 0.11) between trials. Figure 5 shows the mean number of seals counted post-disturbance expressed as a percentage of the original number of seals counted immediately before disturbance trials were carried out. Mean pre-disturbance counts of seals at BHN were 3.25 (range = 1 to 5, SE = 0.53) during spring tides and 3.89 (range = 2 to 7, SE = 0.48) during neap tides. The difference in means of pre-disturbance counts of seals during spring and neap tides at BHN were not different (t-test, $p = 0.39$) and so data were pooled when assessing recovery rate. Other than the telemetry tagged seals, it was not possible to identify individual seals to determine whether seals that hauled out post-disturbance were the same as those present before disturbance. It may therefore be that post-disturbance counts were inflated by the presence of non-disturbed seals. However, the number of seals on the haulout returned to 52% (95%CI 35-69%) of pre-disturbance levels within 30 minutes and 94% (95%CI 55-132%) of pre-disturbance numbers within four hours. Beyond that time, the influence of the rising tide caused mean counts to decline. Time-lapse photography showed that BHN was regularly used as a haulout site throughout this study with zero seal counts on only two days in May, three in June and one in July. Seals were therefore available for disturbance trials on almost every occasion the site was visited.

At RBR a total of 10 disturbance trials were recorded with an average of 6.2 (range = 3 to 27 days, SE = 2.62) days between trials. The low number of trials recorded at RBR compared with BHN was due to the fact that on several occasions when disturbance trials were due to be carried out there were no animals on the haulout. On each occasion when disturbance trials were undertaken only one seal was present at RBR. At RBR there were 11 days in May, 17 days in June and 11 days in July when time-lapse photography showed there to be no seals hauled out at low tide. This low level of haulout activity was also reflected in the telemetry data as only one of the telemetry tagged animals in this study visited RBR after April. In all 10 disturbance trials at RBR no seals hauled out again within 30 minutes post-disturbance.

Disturbance of telemetry tagged seals

A total of 15 disturbance trials were carried out at sites with telemetry tagged seals between 29/05/2014 and 16/07/2014, by which time the majority of GPS/GSM phone tags had ceased transmitting data. On four occasions more than one telemetry tagged seal was present at the site where disturbance trials took place resulting in 22 seal disturbance events overall. Table 2 summarizes the haulout sites at which telemetry tagged seals were disturbed and whether they hauled out within the same or on a subsequent low tide period. In 13 of the trials, animals hauled out again within the same low tide period. On 12 of those occasions seals returned to the same haulout location and only once did a seal transit to a different haulout site within the same low tide period. The remaining nine seal disturbance events resulted in seals starting a trip that included at least one high tide period. On eight of these occasions, seals later returned to the haulout site from which they departed and on only one occasion did a seal haul out at a different site on a subsequent low tide.

Haulout transition rates

A total of 626 trips (at sea periods of over 10 minutes) were identified. Trips that resulted in seals transiting from one haulout site to another totalled 162 (26%) and had a mean trip duration of 34.10 hours (SE = 4.58). The remaining 464 trips that resulted in seals returning to the same site had a mean trip duration of 14.25 hours (SE = 0.95). Overall, the maximum trip duration undertaken by a seal was 11 days. However, 75% of trip durations lasted less than 24 hours. For trips that resulted in a transition to another haulout site, the mean number of times that seals had hauled out at that site in the previous week was 2.6 (SE = 0.27) compared to 7.2 (SE = 0.28) when it was a return trip.

For the 162 trips that resulted in a transition, only 13 were transitions to a different site within the same low tide period. Two of those trips occurred after a controlled disturbance trial. The remaining 149 trips were transitions that occurred on a subsequent low tide which suggested that seals travelling from one haulout site to another were more likely to do so having been at sea for a longer period. Of the 464 return trips, 51 occurred within the same low tide period. Additionally, 11 of these trips were undertaken directly after controlled disturbance trials. The remaining 413 return trips occurred on a subsequent low tide period. Overall, whether trips were transitions or returns, 90% were separated by at least one high tide period.

Backwards AIC selection on the initial full model (AIC = 3010) resulted in Julian day and disturbance being excluded as explanatory variables. This suggests that the probability of seals transiting from one haulout site to another did not significantly change over the course of this study and that overall, transition probability was not significantly affected by disturbance trials. The final model (AIC = 2808) retained the interaction between site fidelity and tidal cycle with significant smooths fitted separately for transition probability dependent on level of site fidelity for seals hauling out during the same ($p = 0.02$) or a subsequent ($p<0.01$) low tide period. An AR1 correlation structure that accounted for temporal autocorrelation within individuals was also retained in the final model. Figure 6 shows that probability of transition decreased as seals' fidelity for the site at which they were hauled out increased. However, when a trip in between two haulout events included at least one high tide period, the probability of transition was generally higher than if that trip was completed within the same low tide period.

Disturbance effect on proportion of time hauled out at low tide

In the full model (AIC = -65) the inclusion of the interaction of consecutive low tide period and seal reaction did not improve the model fit and was therefore excluded. When treating consecutive low tide period and seal reaction as separate explanatory factors seal reaction was also found not to improve the model fit and was therefore also excluded. This resulted in only consecutive low tide period being retained as an explanatory variable in the final model (AIC = -66). Post-hoc pairwise comparisons of the proportion of time spent hauled out over consecutive low tide periods showed that during low tide periods when seals were disturbed they spent a higher proportion of time hauled out compared to the low tide periods immediately preceding ($p < 0.01$) and following ($p = 0.04$) disturbance trials. The proportion of time spent hauled out during the low tide periods prior to and following disturbance trials were not different from one another ($p = 0.64$). GLMM model predictions of the mean proportion of time spent hauled out during low tide periods with 95% confidence intervals are summarised in Figure 7.

5. DISCUSSION

The normal haulout pattern of seals in this study was similar to previous studies in which a high tidal range resulted in preferred haulout sites only being periodically available (Da Silva & Terhune, 1988; Granquist & Hauksson, 2016; Pauli & Terhune, 1987). Time-lapse photography revealed that focal haulout sites in the vicinity of the proposed tidal turbine array in the Sound of Islay were either completely submerged or greatly reduced in size during spring high tide and neap high tide respectively. During spring tides, disturbance events that cause seals to enter the water from their haulout site reduces the amount of time available to haul out at that site within a low tide period. Post-disturbance there is a finite time within which disturbed seals can haul out again before the flooding tide makes the haulout site unavailable. Also, the high site fidelity shown by seals during this study meant that seals were unlikely to move to alternative locations that continued to be available at high tide. During neap high tides, focal haulout sites were not fully submerged and remained available to seals in a much smaller capacity. This resulted in smaller groups occasionally hauling out over the high tide period. However, seals in the Sound of Islay hauled out in larger numbers over low tides when the time and space available for hauling out was maximal compared with high tide when space on haulout sites was limited or non-existent. This effect was more pronounced during spring tides compared with neap tides.

The purpose of this study was to quantify behavioural changes associated with a stimulus that would have been perceived as novel by animals, such as that created during a marine renewable development. The type and frequency of disturbance seals were exposed to during trials represents the extreme scenario that all approaches by boat result in seals flushing from the haulout site. However, it is important to note that approaches by boats associated with a tidal turbine deployment in the Sound of Islay are unlikely be in such close proximity to the haulout site and so are not be expected to elicit the same response seen during disturbance trials. Indeed, time-lapse photography indicated that at the two focal haulout sites no boat activity other than that used during trials caused animals to flush into the water suggesting that seals in the Sound of Islay are not currently exposed to disturbance by boats that would be of concern. It may be that harbour seals in the Sound of Islay are already habituated to existing levels of boat traffic as observed in other studies (Johnson & Acevedo-Gutierrez, 2007; Mathews et al., 2016). In the present study, individuals on focal haulout sites could not be identified using time-lapse photography meaning that it was not possible to quantify whether the response of individual seals changed over time as a result of habituation. However, disturbance trials that included telemetry tagged seals showed that no behavioural change was observed over time in terms of the use of preferred haulout sites. This was despite there being alternative haulout sites around Islay that seals could travel to. Site faithfulness of seals remained high throughout even in the presence of a novel stimulus that periodically caused those individuals to flush from their haulouts.

Disturbance trials were implemented at focal haulout sites two hours before low tide to allow time within that same low tide period for the numbers of seals to recover towards the original hauled out group size. It may have been the case that seals hauling out post-disturbance were different to those exposed to disturbance trials. However, given the high levels of site fidelity shown by seals during this study it is likely that at least some of the seals returning to the haulout site post-disturbance were the same as those pre-disturbance. At the more regularly used site (BHN) the rate of recovery was relatively quick as haulout numbers returned to half that of pre-disturbance levels in the first half hour post-disturbance. Haulout numbers did not approach the original state until approximately four hours later indicating that time spent hauled out over the low tide period would have been reduced for some individuals. The mean haulout duration of undisturbed telemetry tagged seals was 5.2 hours (SE = 0.19) which is in line with a previous study at the same site (Cunningham *et al.,* 2009). Seals flushed into the water during disturbance trials would not have had this time available to them for a continuous haulout either between the end of the preceding high tide or the start of the following high tide and the point at which disturbance trials took place. Suryan & Harvey (1998) showed that groups of hauled out harbour seals exposed to disturbance events that caused them to enter the water were more likely to return to their original number when disturbance events occurred earlier, compared to later in the low tide period. Disturbance trials in the present study may therefore have had a greater impact in terms of whether seals returned to haul out or not had they been implemented at a later stage of the low tide period.

The timing of the implementation of disturbance trials may generally have affected the results of this study dependent on how motivated seals were to haul out at particular times. Despite haulouts being interrupted the proportion of time spent hauled out was higher over low tide periods when disturbance trials were implemented compared to during the immediately preceding and following low tide periods. When the reaction of seals to disturbance trials was to haul out again within the same low tide period motivation to haul out could already have been higher on those occasions. However, it does not seem that this was linked to seals spending a higher proportion of time hauled out over consecutive low tide periods. Seal reaction was not retained as an explanatory variable during model selection suggesting that when seals hauled out again after disturbance trials that decision was not motivated by a cyclic pattern of hauling out more. Motivation to haul out can also be influenced by at-sea activities in the lead up to a haulout (Thompson et al., 1989). Trip duration at sea prior to the haulout period in which disturbance trials were implemented was highly variable, making it difficult to associate motivation to haul out with the need to rest after longer periods at sea or indeed with any cyclic pattern of at-sea activity. The variability in trip duration leading up to a haulout period was evident both when the response of animals to disturbance trials was to haul out again within the same low tide ($\bar{x} = 19.38$, SE = 6.49, range = 1.49 to 68.48) or on a subsequent low tide ($\bar{x} = 30.39$, SE = 11.40, range = 1.16 to 110.38). Regardless, when seals hauled out again after being disturbed they were motivated on those occasions to do so, with the net effect of disturbance being to disrupt what may otherwise have been a continuous haulout.

Reducing the time available for seals to haul out or increasing the frequency with which animals enter the water has important implications for periods when harbour seals haul out more often, such as during the breeding season (Cordes & Thompson, 2015) or during the moult (Thompson et al., 1989). Being disturbed into the water may be particularly important for pups that risk hypothermia due to lower insulation compared with adults. Harbour seal pups primarily suckle while on land (Renouf & Diemand, 1984) and where haulout sites are only tidally available there is a limited amount of time during which suckling events can occur (Reijnders, 1981). If the frequency with which mother pup pairs are forced into the water is sufficiently high then this could have energetic consequences for pups (Jansen et al., 2010). A negative energy balance will affect mass at weaning which has been shown to correlate with reduced over-winter survival in young harbour seals (Harding, Fujiwara, Axberg & Harkonen, 2005). There may also be consequences for adult seals that are moulting as repeated immersion due to disturbance will increase heat loss and reduce skin temperature which may impede the growth of new hair (Paterson *et al.* 2012). Disturbance trials in this study were not undertaken at sites identified as being important habitat for breeding or moulting and so a tidal turbine deployment in the Sound of Islay is not likely to have a significant impact on harbour seals during these periods. However, it is essential that assessments of the impact of marine renewable deployments on haulout behaviour of harbour seals take into account proximity to habitat used by seals at different times of the year.

Disturbance trials of the type and frequency carried out during this study did not influence the transit of seals from one haulout site to another. This resulted in disturbance not being an explanatory factor in the final transition model. Site fidelity was retained showing that seals were more likely to make a transition from a haulout if they had visited it infrequently in the previous week. This agrees with other harbour seal studies in which fidelity for particular haulout sites was high (Cordes & Thompson, 2015; Dietz et al., 2013). Seals embarking on trips that included at least one high tide period were also more likely to switch haulout sites. This suggests that unavailability of preferred haulout sites during high tides and/or longer trip duration influenced transition probability. Where seals showed a high level of fidelity for a particular site in the previous week the probability of transition was very low regardless of the tidal cycle when seals hauled out again. Andersen et al. (2014) also found that harbour seals in the

Kattegat Sea showed a high degree of site fidelity when exposed to repeated disturbance trials. However, small tidal amplitudes meant that haulout sites were available to seals at all states of the tide post-disturbance, meaning the option of returning to the original haulout site was always possible. Large tidal amplitudes at the Sound of Islay caused preferred haulout sites to become unavailable, presenting a temporal and spatial challenge to seals disturbed from haulout sites. Despite preferred haulout sites having limited availability in each tidal cycle and even with repeated exposure to disturbance, seals still chose to return to preferred haulout sites when they were available.

Our results show that at least on the time-scale of a few months harbour seals do not make large scale movements between haulout sites in response to boat disturbance. The level of disturbance in this study was likely greater than from the proposed tidal development or from other anthropogenic sources in the Sound of Islay at the present time. We therefore expect that increased anthropogenic activity associated with marine renewables in the Sound of Islay would not change the distribution of harbour seals in the short-term. However, previous studies have shown that harbour seals can be displaced from haulout sites when exposure to anthropogenic activity is continued over several years (Becker, Press & Allen, 2009; Becker, Press & Allen, 2011). Monitoring harbour seal haulout sites during and beyond the construction phase of a marine renewable development may therefore be necessary. In the case of harbour seals in the Sound of Islay, the nearest habitat identified as being important for breeding and moulting is the South East Islay Skerries SAC. In all SACs designated as such by the presence of harbour seals, general advice to the public to avoid disturbing seals includes not approaching animals to the point that they flush from their haulouts and maintaining an appropriate distance when using recreational boats (Scottish Marine Wildlife Watching Code, 2017). Dependent on the expected level of disturbance and how habituated animals are to boat traffic this general advice may also be sufficient for marine renewable developments. None of the telemetry tagged seals in this study visited the South East Islay Skerries SAC and for these animals at least the effect of disturbance was spatially localized to the haulout sites outside the SAC. Nevertheless, where disturbance events associated with future marine renewable developments exceed the type, frequency or duration imposed during this study, monitoring harbour seal haulout behaviour may be required on a larger geographical and temporal scale to establish the effect of those disturbance events.

6. ACKNOWLEDGEMENTS

We are grateful to Simon Moss, Matt Bivins and all field team members who took part in the 2014 telemetry deployments. A special thank you to Gus Newman and the team at StormCats who provided boats and skippers as well as logistical help throughout. Thank you also to Chris Morris and Callan Duck for assistance with generation of aerial survey data on maps and to Ben Goss for assistance in image processing. This study was funded by Scottish Natural Heritage, Marine Scotland and The Marine Alliance for Science and Technology for Scotland (MASTS).

7. REFERENCES

Andersen, S. M., Teilmann, J., Dietz, R., Schmidt, N. M. & Miller, L. A. (2014). Disturbance-induced responses of VHF and satellite tagged harbour seals. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24, 712-723.

Becker, B. H., Press, D. T. and Allen, S. G. (2009). Modeling the effects of El Niño, density-dependence, and disturbance on harbor seal (*Phoca vitulina*) counts in Drakes Estero, California: 1997–2007. *Marine Mammal Science*, 25, 1-18.

Becker, B. H., Press, D. T. and Allen, S. G. (2011). Evidence for long-term spatial displacement of breeding and pupping harbour seals by shellfish aquaculture over three decades. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 21, 247-260.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M. & Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Mixed Modeling. *The R Journal*, 9, 378-400.

Cordes, L. S. & Thompson, P. M. (2015). Mark-resight estimates of seasonal variation in harbor seal abundance and site fidelity. *Population Ecology*, 57, 467-472.

Cunningham, L., Baxter, J. M., Boyd, I. L., Duck, C. D., Lonergan, M., Moss, S. E. & McConnell, B. (2009). Harbour seal movements and haul-out patterns: implications for monitoring and management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 19, 398-407.

Da Silva, J. & Terhune, J. M. (1988). Harbor Seal Grouping as an Anti-Predator Strategy. *Animal Behaviour*, 36, 1309-1316.

Dahne, M., Gilles, A., Lucke, K., Peschko, V., Adler, S., Krugel, K., Sundermeyer J. & Siebert, U. (2013). Effects of pile-driving on harbour porpoises (*Phocoena phocoena*) at the first offshore wind farm in Germany. *Environmental Research Letters*, 8.

Dietz, R., Teilmann, J., Andersen, S. M., Riget, F. & Olsen, M. T. (2013). Movements and site fidelity of harbour seals (*Phoca vitulina*) in Kattegat, Denmark, with implications for the epidemiology of the phocine distemper virus. *ICES Journal of Marine Science*, 70, 186-195.

Granquist, S. M. & Hauksson, E. (2016). Seasonal, meteorological, tidal and diurnal effects on haul-out patterns of harbour seals (*Phoca vitulina*) in Iceland. *Polar Biology*, 39, 2347-2359.

Grellier, K., Thompson, P. M. & Corpe, H. M. (1996). The effect of weather conditions on harbour seal (*Phoca vitulina*) haulout behaviour in the Moray Firth, northeast Scotland. *Canadian Journal of Zoology*, 74, 1806-1811.

Harding, K. C., M. Fujiwara, Y. Axberg & T. Harkonen. (2005). Mass-dependent energetics and survival in harbour seal pups. *Functional Ecology*, 19, 129-135.

Hastie, G. D., Russell, D. J. F., McConnell, B. J., Moss, S., Thompson, D. & Janik, V. M. (2015). Sound exposure in harbour seals during the installation of an offshore wind farm: predictions of auditory damage. *Journal of Applied Ecology*, 52, 631-640.

Hastie, G.D., Russell, D.J.F., Lepper, P., Wilson, B., Elliot, J., Benjamins, S. & Thompson, D. (2017). Harbour seals avoid tidal turbine noise: Implications for collision risk. *Journal of Applied Ecology*, 55, 684-693.

Henry, E. & Hammill M. O. (2001). Impact of small boats on the haulout activity of harbour seals (Phoca vitulina) in Metis Bay, Saint Lawrence Estuary, Quebec, Canada. *Aquatic Mammals*, 27, 140-148.

Jansen, J. K., Boveng, P. L., Dahle, S. P. & Bengston, J. L. (2010). Reaction of Harbor Seals to Cruise Ships. *Journal of Wildlife Management*, 74, 1186-1194.

Johnson, A. & Acevedo-Gutierrez, A. (2007). Regulation compliance by vessels and disturbance of harbour seals (*Phoca vitulina*). *Canadian Journal of Zoology*, 85, 290-294.

Lawn, C. J. (2009). Technologies for tomorrow's electric power generation. *Proceedings of the Institution of Mechanical Engineers Part C-Journal of Mechanical Engineering Science*, 223, 2717-2742.

Lenth, R. V. (2016). Least-Squares Means: The R Package lsmeans. *Journal of Statistical Software*, 69, 1-33.

Lewis, A., Estefen, S., Huckerby, J., Musial, W., Pontes T. & Torres-Martinez, J. (2011). IPCC special report on renewable energy sources and climate change mitigation. *Renewable Energy Sources and Climate Change Mitigation* (pp. 497-533), Cambridge (New York), USA: Cambridge University Press.

London, J. M., Hoef, J. M. V., Jeffries, S. J., Lance, M. M. & Boveng, P. L. (2012). Haul-Out Behavior of Harbor Seals (*Phoca vitulina*) in Hood Canal, Washington. *Plos One*, 7, e38180. DOI: 10.1371/journal.pone.0038180.

Lonergan, M., Duck, C., Moss, S., Morris, C. & Thompson, D. (2013). Rescaling of aerial survey data with information from small numbers of telemetry tags to estimate the size of a declining harbour seal population. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 23, 135-144.

Mathews, E. A., Jemison, L. A., Pendleton, G. W., Blejwas, K. M., Hood, K. E. & Raum-Suryan, K. L. (2016). Haul-out patterns and effects of vessel disturbance on harbor seals (*Phoca vitulina*) on glacial ice in Tracy Arm, Alaska. *Fishery Bulletin*, 114, 186-202.

Mcconnell, B. J., Fedak, M. A., Hooker, S. K. & Patterson, T. (2010). Telemetry. I. L. Boyd, W. D. Bowen & S. J. Iverson (Eds.), *Marine Mammal Ecology and*

Conservation: A handbook of Techniques (pp. 222-241), New York, USA: Oxford University Press.

McKnight, J. C. (2011). Short-term effects of capture and tag attachment in common seals, *Phoca vitulina* (Masters thesis). University of St. Andrews, Scotland.

Osinga, N., Nussbaum, S. B., Brakefield, P. M. & De Haes, H. A. U. (2012). Response of common seals (*Phoca vitulina*) to human disturbances in the Dollard estuary of the Wadden Sea. *Mammalian Biology*, 77, 281-287.

Pauli, B. D. & Terhune, J. M. (1987). Tidal and Temporal Interaction on Harbour Seal Haul-out Patterns. *Aquatic Mammals*, 13, 93-95.

Paterson, W. D., Sparling, C. E., Thompson, D., Pomeroy, P. P., Currie, J. I. & McCafferty, D. J. (2012). Seals like it hot: Changes in surface temperature of harbour seals (*Phoca vitulina*) from late pregnancy to moult. *Journal of Thermal Biology*, 37, 454-461.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2018). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137.

Paterson, W., Russell, D. J. F, Wu, M., McConnell, B. J. & Thompson, D. (2015). Harbour seal haul-out monitoring, Sound of Islay. *Scottish Natural Heritage Commissioned Report No. 894*.

R Development Core Team. (2014). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

Reijnders, P. J. H. (1981). Management and conservation of the harbor seal (*Phoca vitulina*) population in the international Wadden Sea area. *Biological Conservation*, 19, 213-221.

Renouf, D. & Diemand, D. (1984). Behavioral interactions between harbor seal mothers and pups during weaning (Pinnipeds, Phocidae). *Mammalia*, 48, 53-58.

Russell, D. J. F., McClintock, B. T., Matthiopoulos, J., Thompson, P., Thompson, D., Hammond, P. S., Jones, E. L., MacKenzie, M., Moss, S. & McConnell, B. J. (2015). Intrinsic and extrinsic drivers of activity budgets in sympatric grey and harbour seals. *Oikos*, 124, 1462-1472.

Russell, D. J. F., Hastie, G. D., Thompson, D., Janik, V. M., Hammond, P. S., Scott-Hayward, L. A. S., Matthiopoulos, J., Jones, E. L. & Mcconnell, B. J. (2016). Avoidance of wind farms by harbour seals is limited to pile driving activities. *Journal of Applied Ecology*, 53, 1642-1652.

Scottish Marine Wildlife Watching Code, 2017. Scottish Marine Wildlife Watching Code: A Guide to Best Practice for Watching Marine Wildlife.

Sharples, R. J., Moss, S. E., Patterson, T. A. & Hammond, P. S. (2012). Spatial Variation in Foraging Behaviour of a Marine Top Predator (*Phoca vitulina*) Determined by a Large-Scale Satellite Tagging Program. *Plos One*, 7, e37216. DOI: 10.1371/journal.pone.0037216.

Sparling, C. E. (2013). Sound of Islay Marine Mammal Baseline Data – Year 2 Update. SMRUL-SPR-2013-004 to Scottish Power Renewables (Unpublished).

Suryan, R. M. & Harvey, J. T. (1998). Tracking harbor seals (*Phoca vitulina richardsi*) to determine dive behavior, foraging activity, and haul-out site use. *Marine Mammal Science*, 14, 361-372.

Thompson, D., Onoufriou, J., Brownlow, A. & Morris, C. (2016). Data based estimates of collision risk: an example based on harbour seal tracking data around a proposed tidal turbine array in the Pentland Firth. Scottish Natural Heritage Commissioned Report No. 900.

Thompson, P. M., Fedak, M. A., McConnell, B. J. & Nicholas, K. S. (1989). Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). *Journal of Applied Ecology*, 26, 521-535.

Thompson, P. M., McConnell, B. J., Tollit, D. J., Mackay, A., Hunter, C. & Racey, P. A. (1996). Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth, NE Scotland. *Journal of Applied Ecology*, 33, 1572-1584.

Uihlein, A. & Magagna, D. (2016). Wave and tidal current energy - A review of the current state of research beyond technology. *Renewable and Sustainable Energy Reviews*, 58, 1070-1081.

Watts, P. (1992). Thermal Constraints on Hauling Out by Harbor Seals (*Phoca vitulina*). *Canadian Journal of Zoology*, 70, 553-560.

Watts, P. (1996). The diel hauling-out cycle of harbour seals in an open marine environment: Correlates and constraints. *Journal of Zoology*, 240, 175-200.

Wilson, B., Benjamins, S. & Elliott, J. (2013). Using drifting passive echolocation loggers to study harbour porpoises in tidal-stream habitats. Endangered Species *Research*, 22, 125-143.

Wood, S. N. (2004). Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association*, 99, 673-686.

Site Code	Site Name	Location	Lat. (deg)	Long. (deg)	No. of visits	Haulout duration (hours) ($\bar{x} \pm$ SE)	No. of individuals
BDH	Bagh an Da Dhoruis	Islay	55.93559	-6.15097	87	3.2 ± 0.17	3
BHN	Bunnahabhainn	Islay	55.891175	-6.131105	123	5 ± 0.31	7
BRP	Brein Phort	Jura	55.922896	-6.064843	23	5.3 ± 2.64	3
CAS	Carragh an t-Struith	Jura	55.87061	-6.096444	4	2.3 ± 0.93	2
CON	Colonsay North	Colonsay	56.1253	-6.1626	2	4.7 ± 0.08	1
EGH	Eileanan Gainmhich	Islay	55.864512	-6.110327	59	3.9 ± 0.36	6
EGR	Eilean Gleann Righ	Jura	55.968332	-5.986099	230	6.2 ± 0.66	6
EST	Eileanan Stafa	South Uist	57.39659	-7.288119	35	6.9 ± 0.63	1
HAU	Haun	South Uist	57.090523	-7.296631	8	3.5 ± 0.76	1
HOU	Hough Skerries	Tiree	56.52	-7.020000047	1	0.6 ± 0.00	1
HRT	Hairteamul	South Uist	57.084119	-7.229136	1	1.1 ± 0.00	1
ISL	Nave Island	Islay	55.8991244	-6.34078397	1	0.5 ± 0.00	1
RBL	Rubha Liath	Jura	55.962461	-5.950904	22	5.6 ± 0.53	2
RBR	Rubha Bhoraraic	Islay	55.819718	-6.103997	4	1.6 ± 0.87	3
SAN	Sanda Island	Kintyre	55.284856	-5.571027	4	2.9 ± 0.86	1
SGB	Sgeiran a Bhudragain	Jura	55.958036	-5.946192	22	4.5 ± 0.76	3

Table 1. Listed are site code abbreviations for the site names of haulouts visited by telemetry tagged seals at locations around Islay. Latitude, longitude coordinates define exact positions of haulouts. Also given are the number of visits, mean haulout duration and the number of individuals that visited each site.

		Arrive			
		BHN	BDH	EGR	BRP
Depart	BHN	5			1
	BDH		1		
	EGR			6	
	BRP				
	BHN’	5		1	
	BDH’		1		
	EGR’			2	
	BRP’				

Table 2. Haulout/trip transition matrix showing where tagged seals departed from and where they arrived and hauled out again after simulated disturbance trials. The total number of disturbance trials resulting in each scenario are given. In the upper part of the matrix (grey) are locations where seals hauled out again within the same low tide period after being disturbed into the water. In the lower part of the matrix (pink) are locations suffixed with **‘ ,** where seals hauled out again in any subsequent low tide period having started a trip after being disturbed into the water. See Table 1 for full names of abbreviated haulout locations.

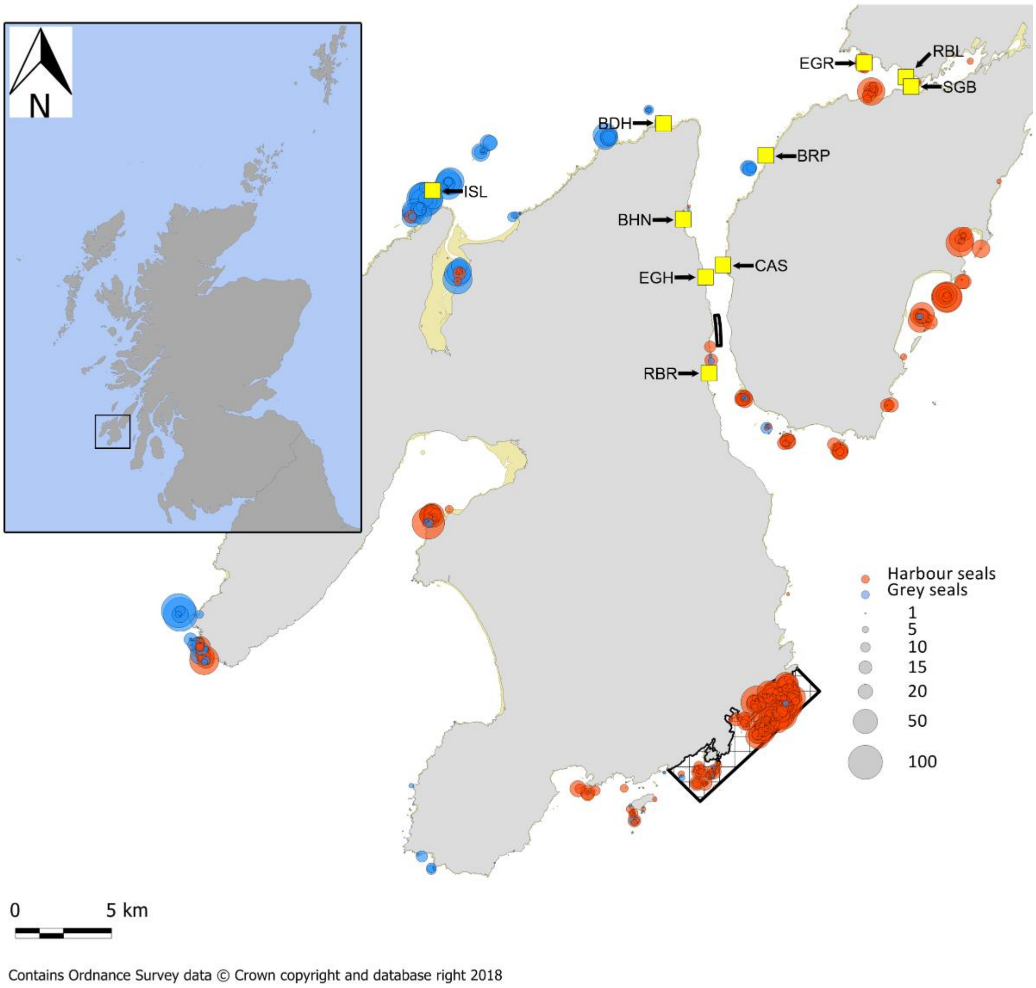

Figure 1. The Sound of Islay and the South-East Islay Skerries SAC haulout sites. The South-East Islay Skerries SAC is delineated and shaded black. Boundaries of the proposed tidal turbine development within the Sound of Islay are also delineated in black. Yellow squares mark haulout sites visited by telemetry tagged seals in this study (See Table 1 for full names and latitude/longitude coordinates). Seal counts were taken from aerial survey data collected during the moult periods between 1990 and 2009. All aerial survey counts were carried out during a window of two hours either side of low tide.

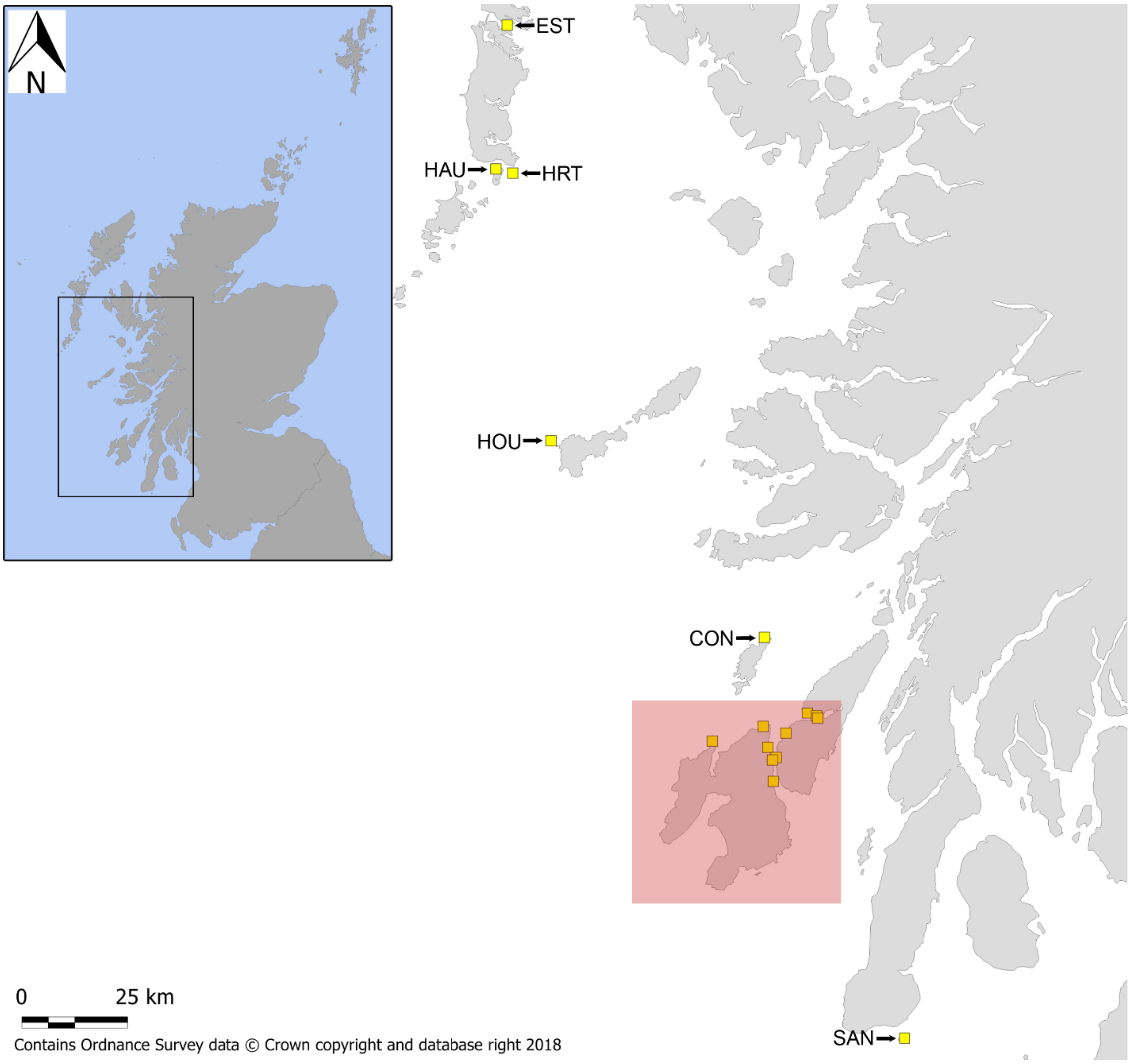

Figure 2. Wider geographical range of haulout sites visited by telemetry tagged seals marked by yellow squares (See Table 1 for full names and latitude/longitude coordinates). Haulout sites visited within close proximity of the Sound of Islay (pink shaded area) are presented in Figure 1.

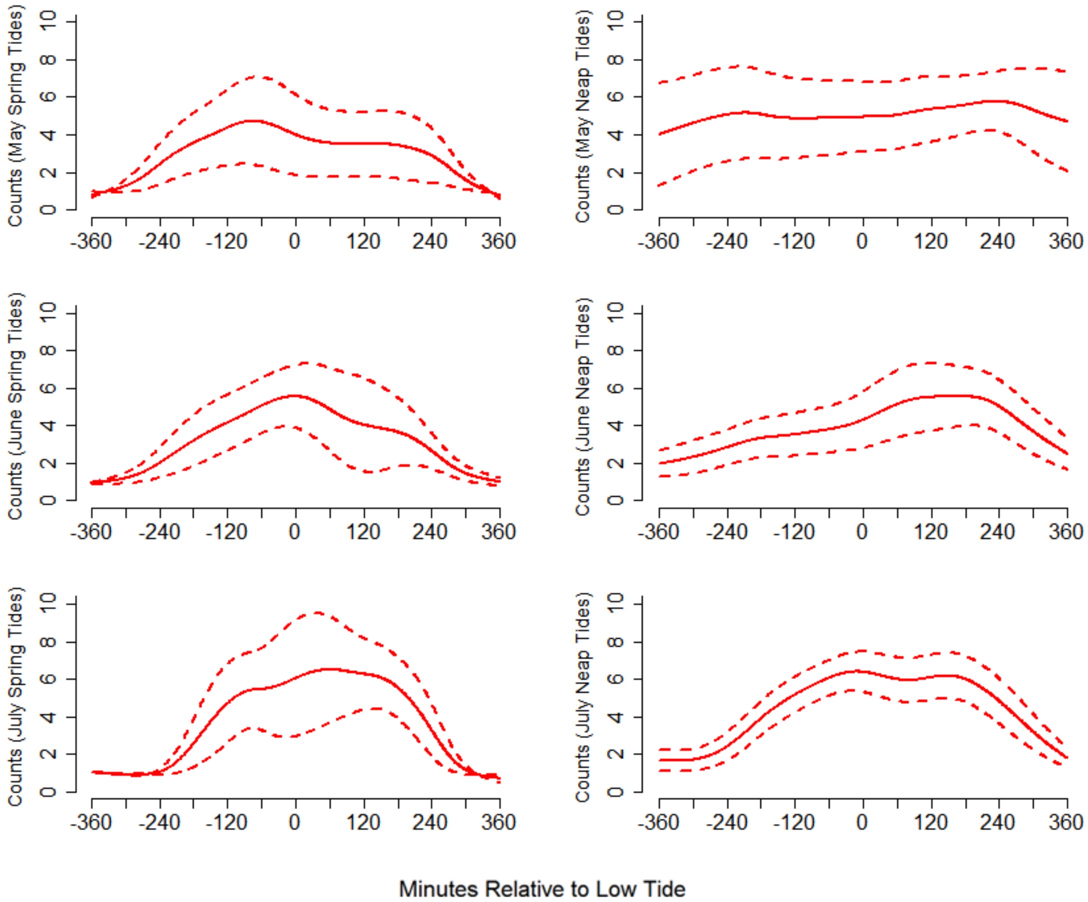

Figure 3. Mean counts of hauled out seals (solid red) with 95% confidence intervals (dashed red lines) with time relative to low tide at Bunnahabhain (BHN). Data are divided into spring and neap tide periods for May, June and July.

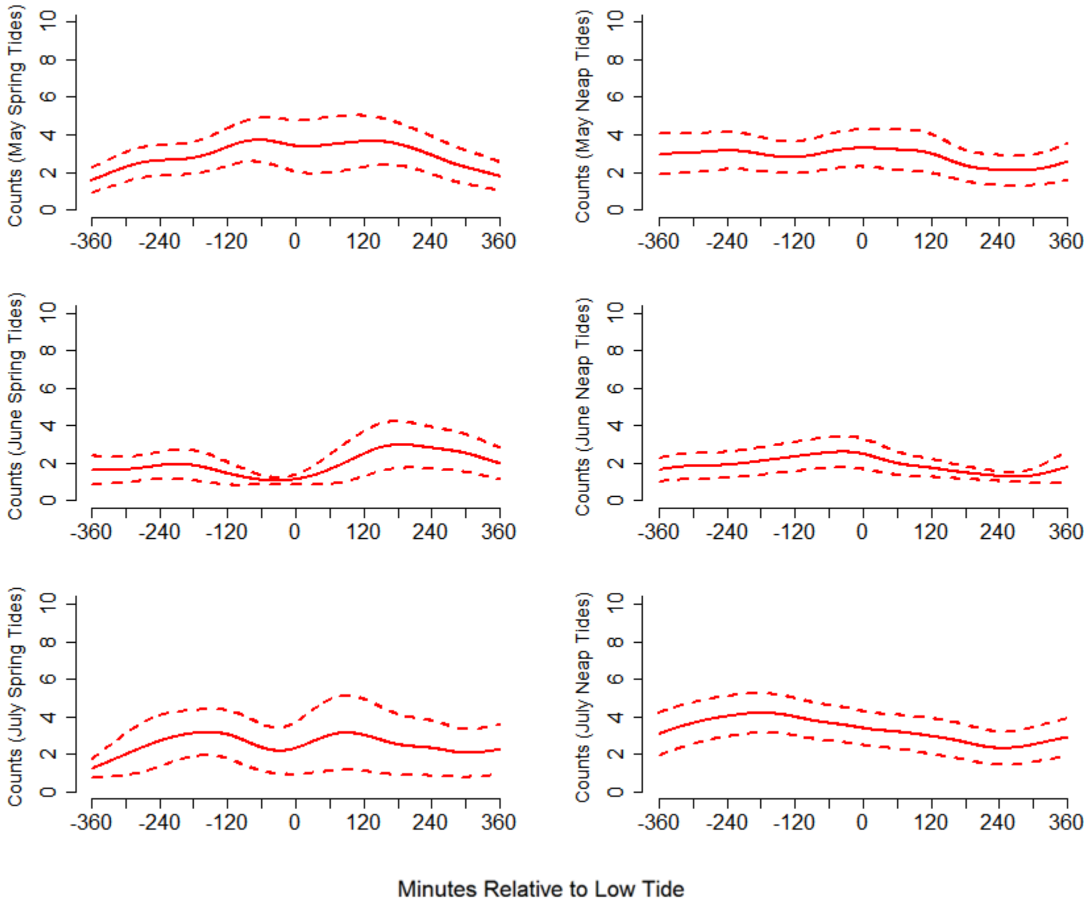

Figure 4. Shown are the mean counts of hauled out seals (solid red) with 95% confidence intervals (dashed red lines) over minutes relative to low tide at Rubha Bhoraraic (RBR). Data are divided into spring and neap tide periods for May, June and July.

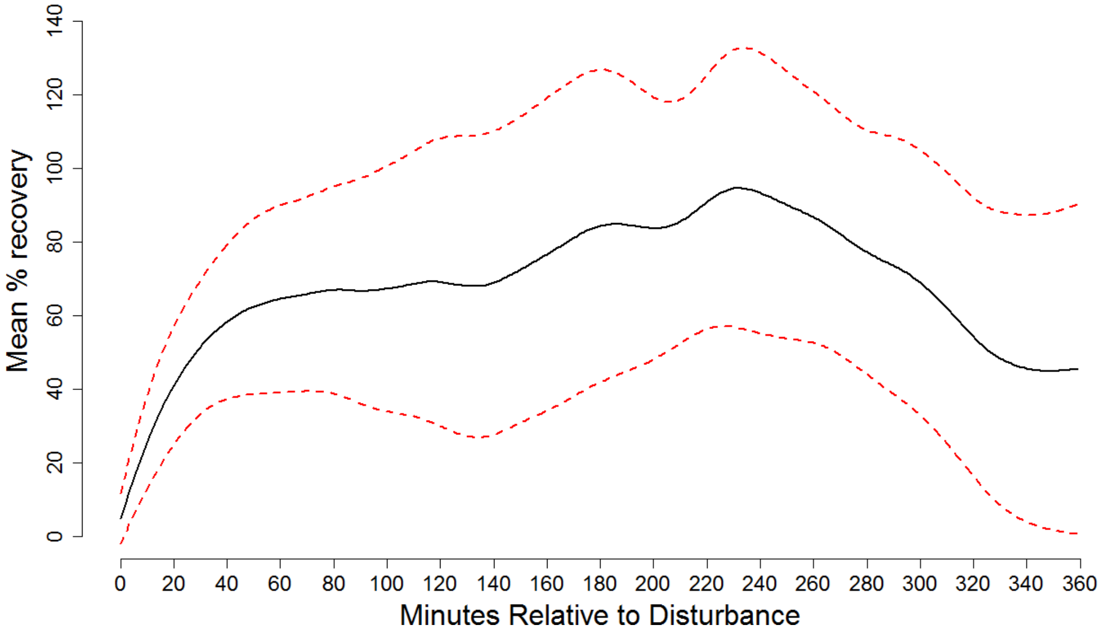

Figure 5. Mean percentage recovery of the number of hauled out seals (solid black line) with 95% confidence intervals (dashed red lines) against time (minutes) since disturbance trials. Data are for Bunnahabhain (BHN).

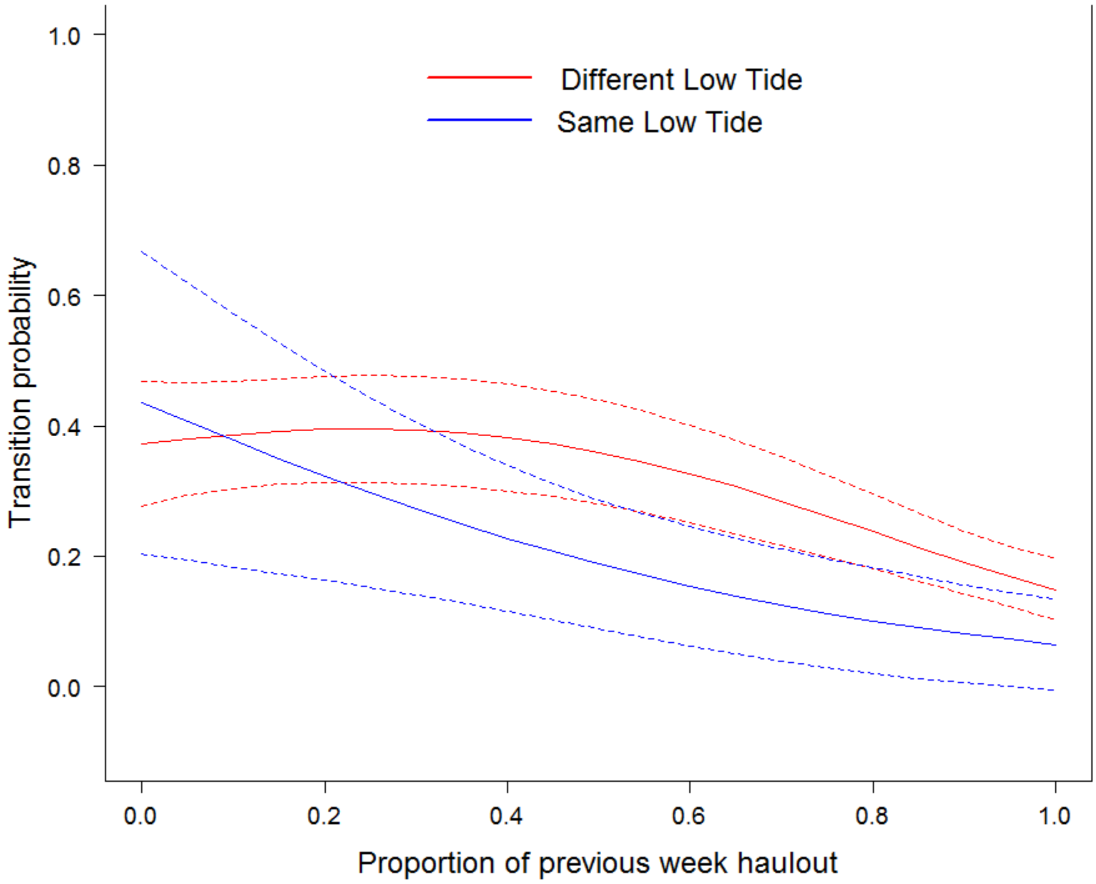

Figure 6. Transition probability i.e. having left a haulout site a seal then hauls out at a different haulout site (y-axis) is shown dependent on the proportion of haulouts in the previous week that were also at the haulout site a seal arrives at (x-axis). Transition probabilities are shown for the two scenarios of having ended a haulout a seal then hauls out again on the same (blue) or on a subsequent (red) low tide. Solid lines are model predictions with 95% confidence intervals as dashed lines.

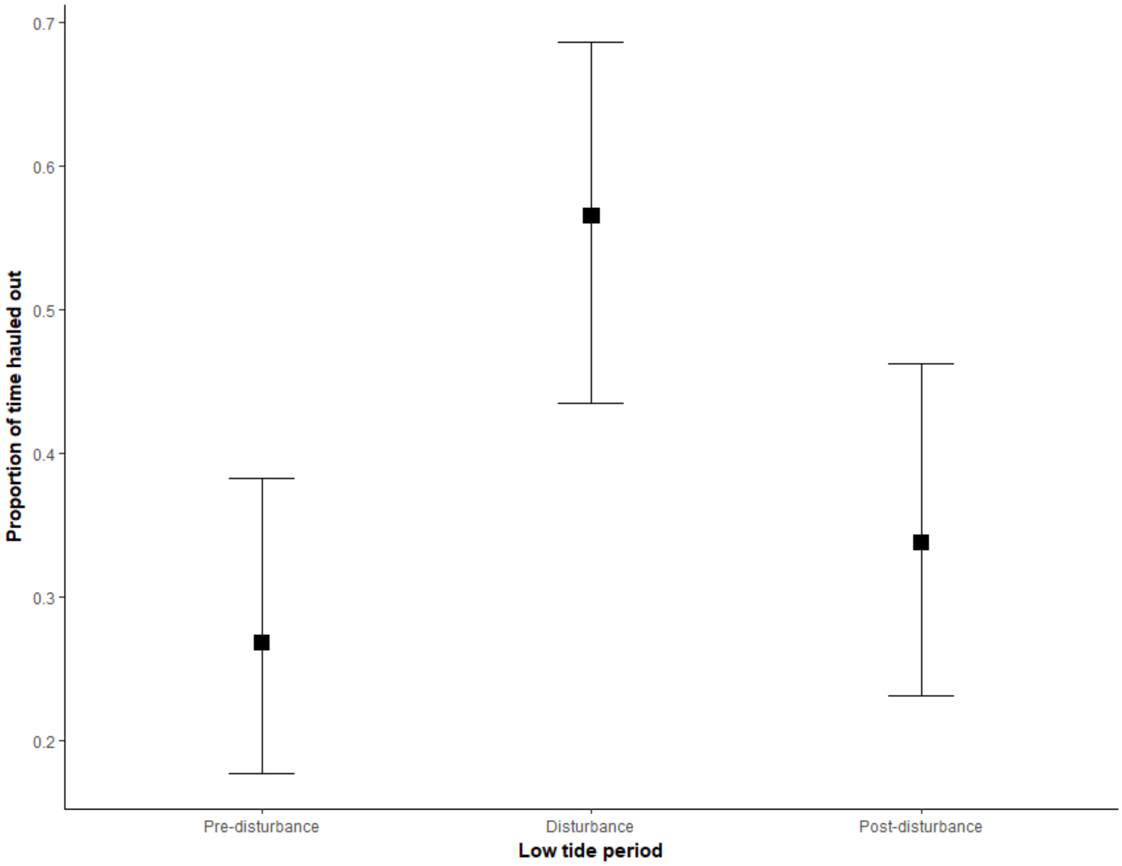

Figure 7. GLMM model predictions of mean and 95% confidence intervals for the proportion of time spent hauled out during pre-disturbance, disturbance and post-disturbance low tide periods.