

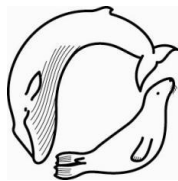
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Report

Inter-haul-out transition rates

Sea Mammal Research Unit
Report to
Scottish Government

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**Sea Mammal
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**The Scottish
Government**



McConnell, B. J., Wu, M. & Thompson, D.

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

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1 Executive summary

The aim of this study was to predict the changes in the number of seals hauled at the South-East Islay Skerries Special Area of Conservation (EIS SAC) in response to disturbance at other haul-out sites.

Telemetry data from 25 harbour seals (*Phoca vitulina*), tagged between 2011 and 2014 at capture sites close to the Sound of Islay, were used to populate a movement model based on individual haul-out transition matrices. This model generalised the matrices in order to represent population movements. Disturbance was modelled as the serial permanent closure of one of the 35 haul-out sites used by the tagged seals. The model excluded movement during the breeding season. The modelled response was the change in numbers hauled out at the Ardmore haul-out site within in the EIS SAC. The varying effect of disturbing different haul-out sites reflected the complexity of the haul-out network.

Most disturbances had a positive effect of the number of seals at Ardmore (range: -0.5% to +21%). Haul-out sites with the largest effects were within 50 km of Ardmore and there was little or no effect when the disturbed site was more than 150 km away, though the response was variable and within 50km distance did not predict which disturbed haul-outs affected Ardmore, as many sites within 50km had little or no effect. Thus the power to infer the effect of remote haulout disturbance by distance alone was limited, other than to say that the effect was greatest within 50 km of the haulout of interest.

However, within a range of 50km, the shortest network path between the disturbed haul-out site and Ardmore provided more information about which sites had an effect. Haul-out site networks adjacent to Ardmore (such as Machrihanish and Eilean nan Coinein) had a larger influence. There was no significant effect when a disturbed haul-out site was more than two transition jumps (connections) from Ardmore. Such network path information can be efficiently obtained in other areas with a simplified and cheaper telemetry system.

The effect of disturbance on the entire EIS SAC depended on the representativeness of the 25 tagged seals' usage within the EIS SAC. The distribution of haul-outs in the August moult survey differed from the haulout usage of the tagged seals in this study. However, this may be due in part to redistribution during the breeding season. If the tagged seals were representative, the proportional effect of a disturbance to the EIS SAC would be similar. If, however, seals that used other haul-out sites in the EIS SAC were part of a completely different network of haul-out sites then the effect reported here would be reduced.

Whilst useful in this study, the model that was developed was essentially mechanistic. The limitations of this approach are reviewed and recommendations about future work using Individual Based Models are made.

2 Introduction

Quantifying large-scale movement patterns in harbour seals is necessary to predict and manage anthropogenic risk. Specifically, it allows the sensitivity of seal counts at one haul-out site to disturbance at other (perhaps distant) haul-out sites to be predicted. In addition, such information aids the determination of the geographic extent of haulout monitoring programmes.

Assessing the risk from potential injurious activities (for example, piling operations and tidal turbine activity) requires an assessment of the geographical overlap between seals and the area affected, but this is not sufficient. Harbour seal foraging is often local (within 50 km) of a haul-out site (Cunningham *et al.*, 2008; Sharples *et al.*, 2012) but they can occasionally travel longer distances and move (transit) to more distant haul-out sites. Seal counts at a specific haul-out site can therefore include individuals that travel far, and are thus vulnerable to distant risk.

In this study, harbour seal movement data obtained from telemetry was used to assess the rates of movement (transition) from one haul-out site to another. The analysis was restricted to one geographic region centred on a proposed tidal turbine array site, the Sound of Islay (Inner Hebrides, Scotland) (Figure 1). The EIS SAC (Figure 2) is located just south of the Sound and is one of the nine UK Special Areas of Conservation where harbour seal conservation is one of the primary reasons for designation. A simulation model of seal movement was built and used to predict the effect of disturbing distant haul-out sites on the changes in the expected numbers of seals hauled out at Ardmore, a haul-out site inside the EIS SAC. The consequences of changes with the entire EIS SAC are also discussed.

The simulation model was built as a network of haul-out sites with transitions between them so some terminology in this report is borrowed from network analysis. Their definitions in the context of this study are as follows:

- A *connection* is the transition from one haul-out site to another, without stopping at another haul-out site en route.
- Two haul-out sites are *adjacent* if they are directly joined with a *connection*.
- *Connectivity* is the number of *connections* to or from a given haul-out site.
- *Shortest network path* is the minimum number of *connections* required to go from one haul-out site to another.

Inter-haul-out transition rates

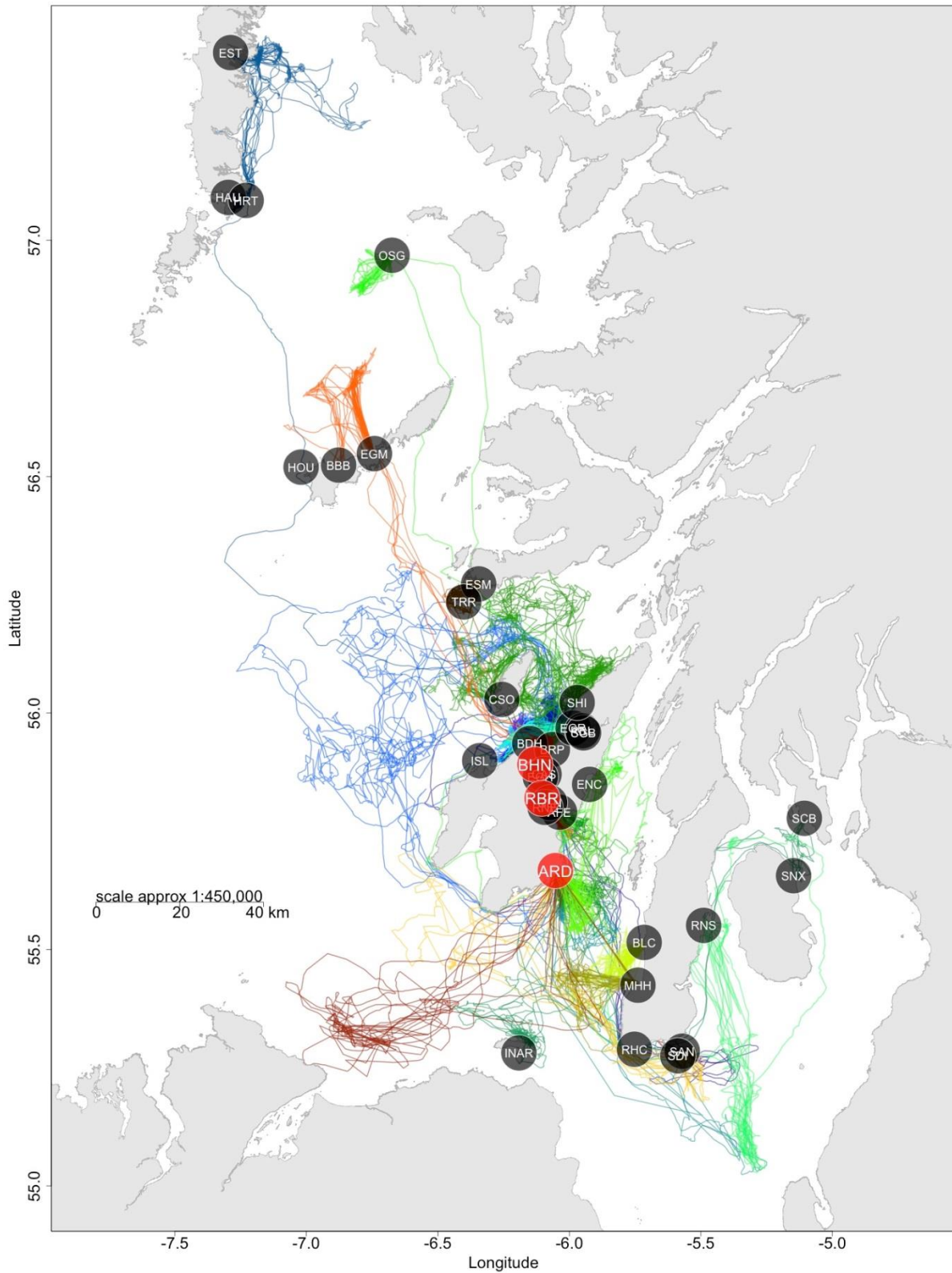


Figure 1. Tracks from 25 harbour seal tags, each illustrated with a unique colour. Circles represent the 35 sites where these seals hauled out (see Table 2 for details). Red circles show the haul-out sites (Ardmore (ARD), Rubha Bhoraraic (RBR) and Bunnahabhainn (BHN)) where the seals were captured and tagged.

Inter-haul-out transition rates

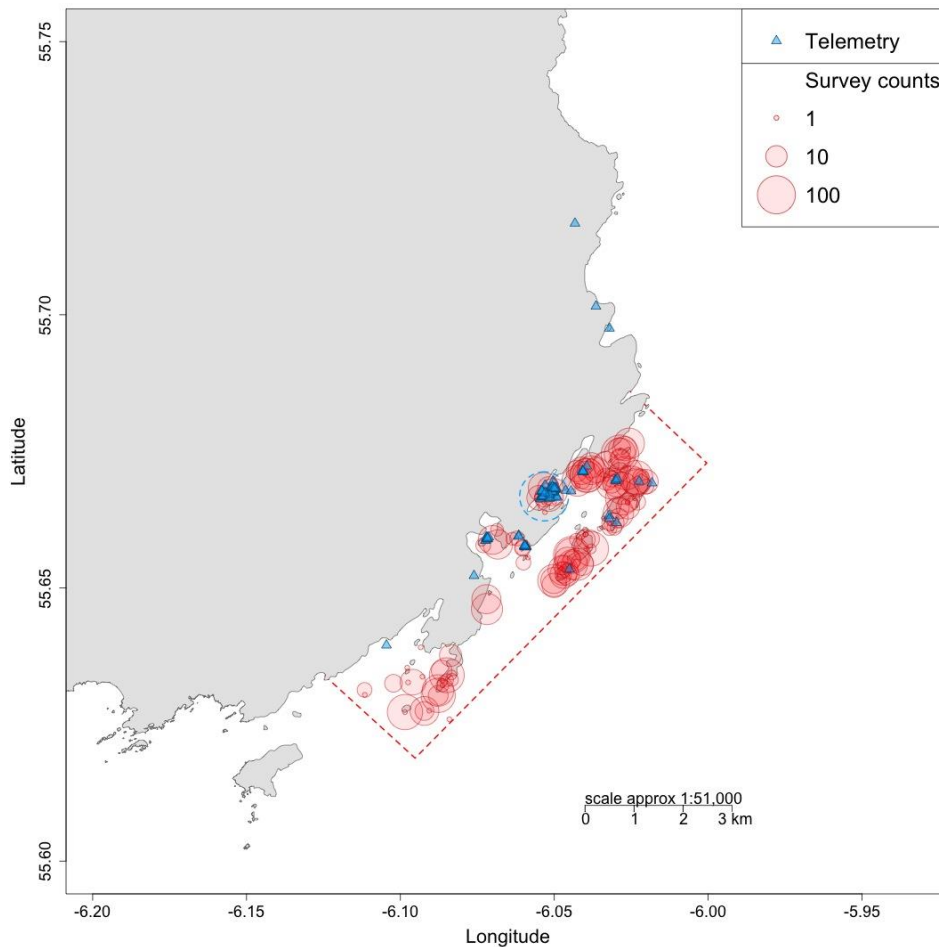


Figure 2. The boundary of the South-East Islay Skerries Special Area of Conservation (EIS SAC) is shown by the red dashed line. Red circles show the relative size of the harbour seal survey counts conducted in August. The blue dashed line shows those survey counts within a 500 m radius of the Ardmore (ARD) haul-out site. The blue triangles show the locations of haul-outs events relayed from tagged seals that are all snapped (see Methods section) to the Ardmore haul-out site.

3 Methods

3.1 Data collection

Three harbour seal telemetry tagging deployments were carried out in the vicinity of the Sound of Islay: (7 in 2011, 10 in 2012, and 8 in 2014). Deployment details are shown in Table 1 and a summary of the resulting tracks is shown in Figure 1. The locations of haul-outs of tagged seals and the August aerial moult survey of haul-out counts within the EIS SAC are shown in Figure 2.

Inter-haul-out transition rates

Table 1. Details of the 25 harbour seals tagged near the Sound of Islay. Capture site abbreviations are explained in Table 2.

Tag ID	Start date	End date	Mass (kg)	N-T length (cm)	Axial girth (cm)	Sex	Capture site
pv41-107-11	05/10/2011	03/12/2011	67.2	146	98	M	ARD
pv41-130-11	07/10/2011	01/12/2011	81.6	151	105	M	ARD
pv41-137-11	05/10/2011	18/11/2011	84.8	153	108	M	ARD
pv41-140-11	06/10/2011	22/11/2011	87.0	145	112	M	ARD
pv41-152-11	05/10/2011	25/11/2011	78.6	153	103	M	ARD
pv41-141-11	07/10/2011	08/02/2012	56.4	133	91	M	ARD
pv41-154-11	07/10/2011	25/01/2012	76.8	149	104	M	ARD
pv41-125-11	05/03/2012	31/05/2012	65.4	118	103	F	RBR
pv41-136-11	11/03/2012	31/05/2012	92.0	142	113	F	RBR
pv41-138-11	05/03/2012	31/05/2012	80.6	146	106	M	RBR
pv41-139-11	06/03/2012	31/05/2012	104.8	146	123	F	BHN
pv41-143-11	06/03/2012	31/05/2012	103.0	142	112	F	BHN
pv41-x1-12	12/03/2012	31/05/2012	94.4	143	111	F	RBR
pv41-x2-12	05/03/2012	01/05/2012	52.6	127	91	M	RBR
pv41-x3-12	12/03/2012	21/04/2012	83.4	138	113	M	RBR
pv41-x4-12	12/03/2012	31/05/2012	88.6	145	111	F	RBR
pv41-x5-12	11/03/2012	24/04/2012	90.2	136	111	F	RBR
pv55-102-14	17/04/2014	31/05/2014	84.4	147	111	F	BHN
pv55-103-14	13/05/2014	31/05/2014	92.6	144	113	F	BHN
pv55-105-14	18/04/2014	31/05/2014	73.4	141	109	F	RBR
pv55-106-14	13/05/2014	31/05/2014	75.6	143	103	F	RBR
pv55-107-14	18/04/2014	31/05/2014	80.0	141	107	F	BHN
pv55-108-14	17/04/2014	31/05/2014	72.4	137	100	F	BHN
pv55-109-14	20/04/2014	31/05/2014	72.6	141	99	F	BHN
pv55-110-14	20/04/2014	31/05/2014	75.2	143	102	F	BHN
pv55-108-14	17/04/2014	31/05/2014	72.4	137	100	F	BHN

The GPS/GSM tags that were used provide detailed at-sea locations and dive information. They also record and relay haul-out behaviour. Individual haul-out events are defined within the tag as: start, > 10 mins continuously dry; end, > 40 s continuously wet. An illustration of such haul-out patterns for one seal is shown in Figure 3. In this example, haul-out events, shown as red horizontal lines, occur primarily during the day-time, and are modified by tidal height. The inter-haul-out intervals vary from hours to weeks. Other tagged seals show a similar pattern of haul-out behaviour.

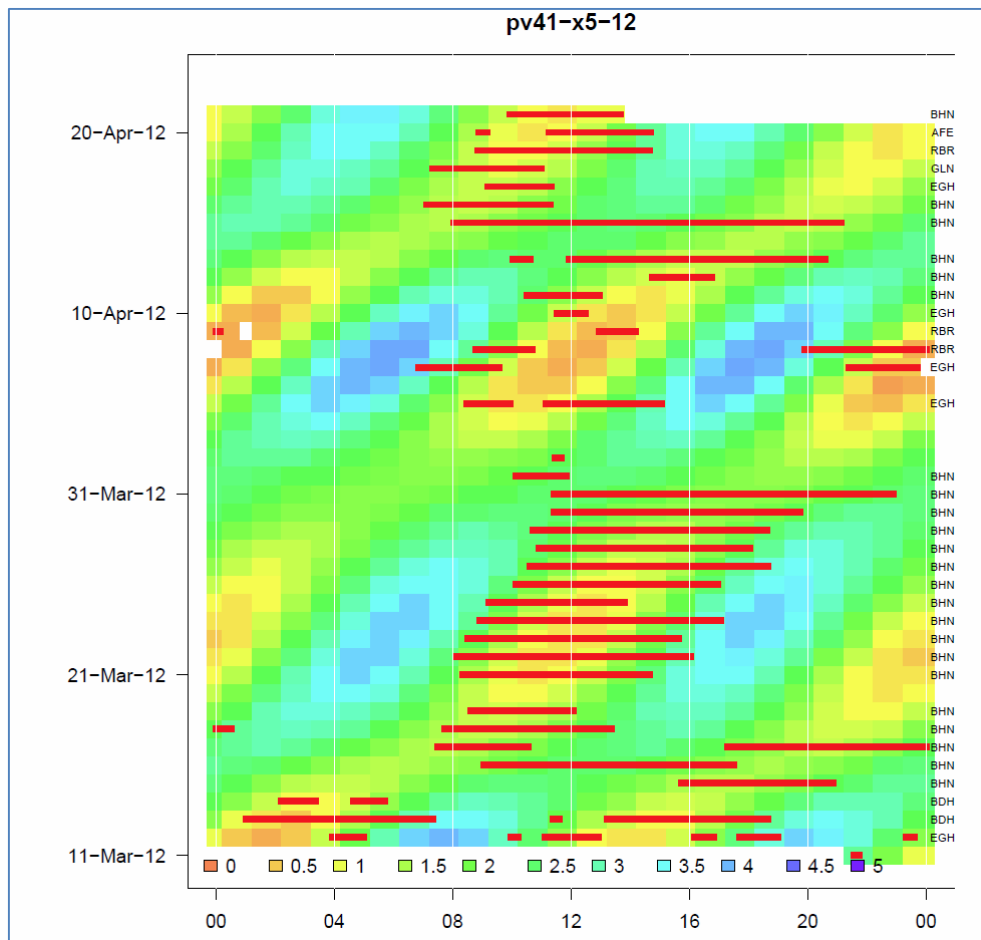


Figure 3. Haul-out events for seal pv41-x5-12. The vertical axis is date and the horizontal axis is time of day (GMT). The red bars indicate the duration of individual haul-out events. The underlying colours show local tidal height (the legend shows height (m) above chart datum) for the current location of the tagged seal. The text at the right hand side of the vertical axis shows the abbreviation (see Table 2) of the haul-out site used that day.

3.2 GPS data filtering

GPS tracks were filtered using ‘residuals’ of the locations to exclude locations of lower quality. Excluding locations with residuals > 25 was estimated to result in 95% confidence intervals within 81m of the reported location (henceforth ‘GPS 95% C.I.’). Start and end dates were also trimmed by visual inspection to exclude inappropriate locations (e.g. locations after tag failure/detachment). The average usable lifespan of the tags was 84d (range: 40d to 146d).

3.3 Haulout location, snapping and verification

Using the track data, each time-stamped haul-out was assigned a location. If there were any valid GPS locations during a haul-out, their median coordinates were used for the haul-out. If there were none, the GPS locations immediately preceding and immediately following the haul-out were used to interpolate (linearly) the haul-out location. A list of *standard* haul-out sites that were visited at some time by the tagged seals was generated by visual inspection of the haul-out events (Table 2). The Ardmore haul-out site (ARD) is situated in the EIS SAC. The estimated haul-out locations were then snapped to the nearest *standard* haul out. The distance between the estimated and snapped location was termed the ‘snap distance’.

Inter-haul-out transition rates

Table 2. Thirty-five standard haul-out sites shown in Figure 1 with abbreviation codes and coordinates. The survey counts columns shows the average (\pm SD) count and number of counts from aerial surveys between 2007 and 2011. The Ardmore haul-out site (ARD, shown in red) is located the EIS SAC. No other haul-out site is within the EIS SAC.

Site code	Site name	Latitude	Longitude	Survey counts	
				mean \pm SD	N
AFE	Am Fraoch Eilean	55.79009	-6.03733	18 \pm 5.7	2
ARD	Ardmore	55.66676	-6.05331	82.5 \pm 48.8	2
BBB	Balephetrish Bay	56.52428	-6.87751	0	1
BDH	Bagh an Da Dhoruis	55.93559	-6.15097	2 \pm 2.8	2
BHN	Bunnahabhainn	55.89118	-6.13111	1.5 \pm 2.1	2
BLC	Bellochantuy	55.51487	-5.71561	6.5 \pm 9.2	2
BRP	Brein Phort	55.92290	-6.06484	3 \pm 4.2	2
CAS	Carragh an t-Struith	55.87061	-6.09644	0.5 \pm 0.71	2
CSO	Colonsay 1	56.02884	-6.25692	32 \pm 25.5	2
EGH	Eileanan Gainmhich	55.86451	-6.11033	5 \pm 7.1	2
EGM	Eilean Ghreasamuill	56.54853	-6.74130	0	1
EGR	Eilean Gleann Righ	55.96833	-5.98610	23.5 \pm 4.9	2
ENC	Eilean nan Coinein	55.84909	-5.92313	75.5 \pm 3.5	2
ESM	Eilean na Seamair	56.27299	-6.34486	25 \pm 2.8	2
EST	Eileanan Stafa	57.39659	-7.28812	22.5 \pm 31.8	2
GLN	Glas Eilan	55.81048	-6.07503	33 \pm 5.7	2
HAU	Haun	57.09052	-7.29663	0.5 \pm 0.71	2
HOU	Hough Skerries	56.52000	-7.02000	0	1
HRT	Hairteamul	57.08412	-7.22914	3 \pm 2.8	2
INAR	Rathlin	55.28132	-6.19186	18	1
ISL	Islay	55.89912	-6.34078	0 \pm 0	2
MHH	Machrihanish	55.42436	-5.73928	5 \pm 7.1	2
OSG	Oig-sgeir	56.96802	-6.67440	180	1
RBL	Rubha Liath	55.96246	-5.95090	9 \pm 8.5	2
RBR	Rubha Bhoraraic	55.81972	-6.10400	6.5 \pm 4.9	2
RHC	Rubha Clachan	55.28889	-5.75252	0 \pm 0	2
RNE	Rubha nan Earachan	55.80051	-6.09249	0 \pm 0	2
RNS	Rubha nan Sgarbh	55.55086	-5.48960	88	1
SAN	Sanda Island	55.28486	-5.57103	0.5 \pm 0.71	2
SCB	Scalpsie Bay	55.77741	-5.10650	26	1
SDI	Sanda Island Scotland	55.27506	-5.58763	111 \pm 73.54	2
SGB	Sgeiran a Bhudragain	55.95804	-5.94619	3.5 \pm 4.9	2
SHI	Shian Island	56.02225	-5.97046	51 \pm 11.3	2
SNX	Sannox	55.65598	-5.14770	4	1
TRR	Torran Rocks	56.23493	-6.40173	0	1

Some interpolated haul-out locations were far from the coast (up to 20km). This could be due to the linear interpolation being carried out on GPS locations that occurred long before and long after the seal had hauled out, or to extended surface intervals (ESI's (Ramasco *et al.*, 2014)) at-sea that appear as haul-out events. Haul-out locations within 581m from the nearest coastline were considered to be on land. This threshold was defined by the sum of the GPS 95% C.I. (81m) and the approximate resolution of the "World Vector Shoreline" (500m) used to build the coastline maps (National Imagery and Mapping Agency, 1999). Interpolated haul-out locations further than 581m away from the nearest coastline were also considered on land if the seals could have travelled from the haul-out location to the nearest coast and back. This was assumed to be feasible if the seal could have covered this distance during the available time (time interval between the GPS locations and the haul-out) with a maximum speed of 2m/s. The remaining haul-out locations (less than 1%) were considered at sea and excluded from further analyses because this study was only concerned with haul-outs that are on land.

3.4 Trip assignment

A trip was defined as 'not-hauled-out for at least 10 min', and having moved 162m away from the last haul out (twice the GPS 95% C.I.) as smaller changes in locations could be simple location error. Thus the entire track of a seal was divided exclusively into trip and haul-out states.

Trips occurring between the 1st June and 1st September were excluded to avoid the harbour seals breeding period. The average duration of data remaining was 57 d (range: 17d to 121d).

3.5 Transition matrix construction

The trip data were used to construct matrices of transition probabilities among haul-outs to model the movement of seals. These probabilities are shown in matrix form in Figure 4 and as a directed network graph in Figure 5. Individual seals showed great variability in their movement patterns and

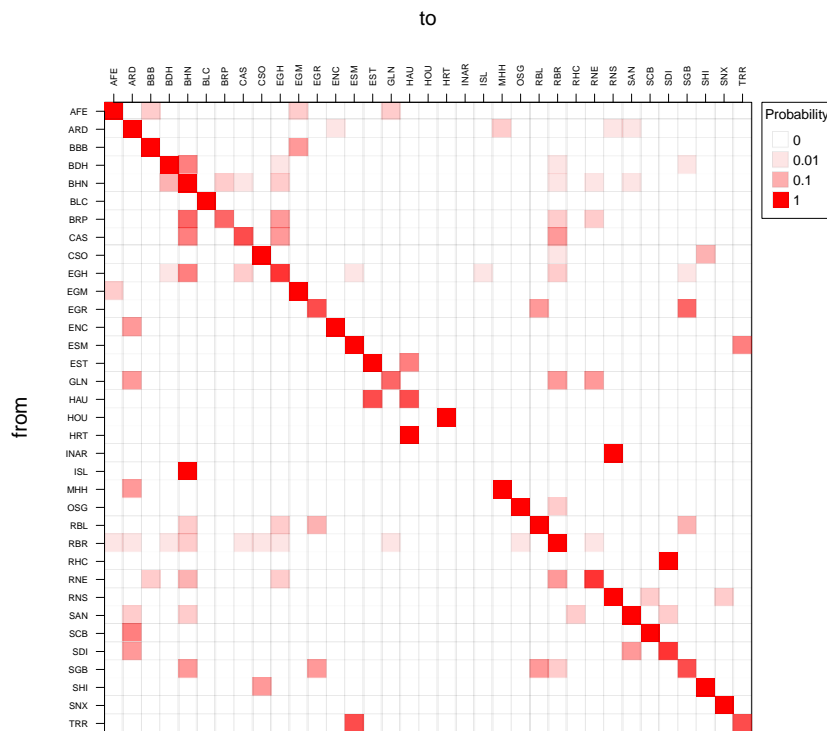


Figure 4. The probability of transitions from one haul-out site (rows) to another (columns) using data from 25 harbour seal tracks. The haul-out site abbreviation codes are expanded in Table 2.

haul-out usage. In order to model variability in the movement pattern of the *population* due to individual differences, a different transition matrix was constructed for each of the 25 tagged seals. The simulated population was then drawn randomly (with replacement) from these 25 matrices.

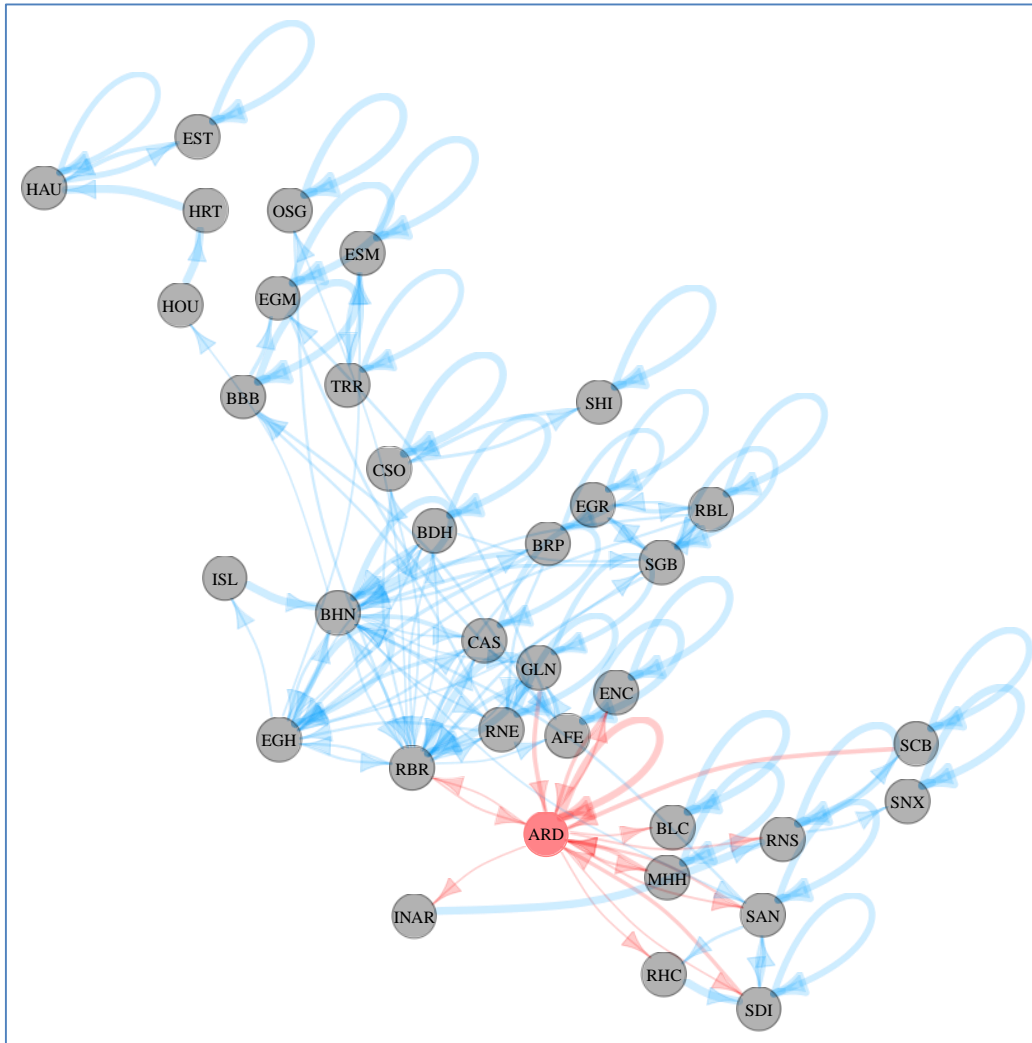


Figure 5. The transition probabilities among haul-outs shown as a directed network graph. Each node is a haul-out site and arrows show transitions (connections) from one haul-out site to the next haul-out site. The thickness of arrows is proportional to the transition probability from the departing haul-out site. The red node represents the Ardmore haul-out site (ARD) within the South East Islay Skerries Special Area of Conservation (EIS SAC) and the red arrows are transitions (connections) directly to or from it.

3.6 Adjusting zero transition elements

Because GPS tracks are only available for a limited time (~ two months), only a sample of the ‘population’ transitions were observed. The transition matrices of the 25 seals contain a large number of zero probabilities (pairs of haul outs with no trips observed). It is possible, however, that these trips occurred and that they would have been observed if the animals had been tracked for a longer time period. The number of unique trips that were missed (zeros in the transition matrix) was estimated for each seal track by fitting a discovery curve. The number of unique trips (N_{unique}) was modelled as a function of the number of trips realised (N_{realised}) using the equation

$$N_{\text{unique}} = \beta_0 - e^{-\beta_1 * N_{\text{realised}}},$$

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where β_0 is the maximum number of unique trips that an animal makes and β_1 is the rate of discovery of unique trips. For each seal, the model was fitted on 1000 bootstrap samples of trips (with replacement) to obtain a frequency distribution for the expected maximum number of unique trips. The observed number of unique trips was subtracted from this distribution to obtain a distribution for the number of missed unique trips. This distribution was truncated so there was at least one missed unique trip. At the start of each simulation iteration the number of missed unique trips (n_{missed}) was drawn randomly from this distribution. The matrices of transition probability were recalculated by adding $(n_{\text{missed}} / n_{\text{zero}})$ to the frequency of unobserved trips (zero in the matrix), where n_{zero} is the number of zeros in the matrix. Consequently, all transitions were possible, albeit mostly with a small probability. Seals departing from a haul-out for which there are very few trips, however, had an almost equal probability to transition to any haul-out.

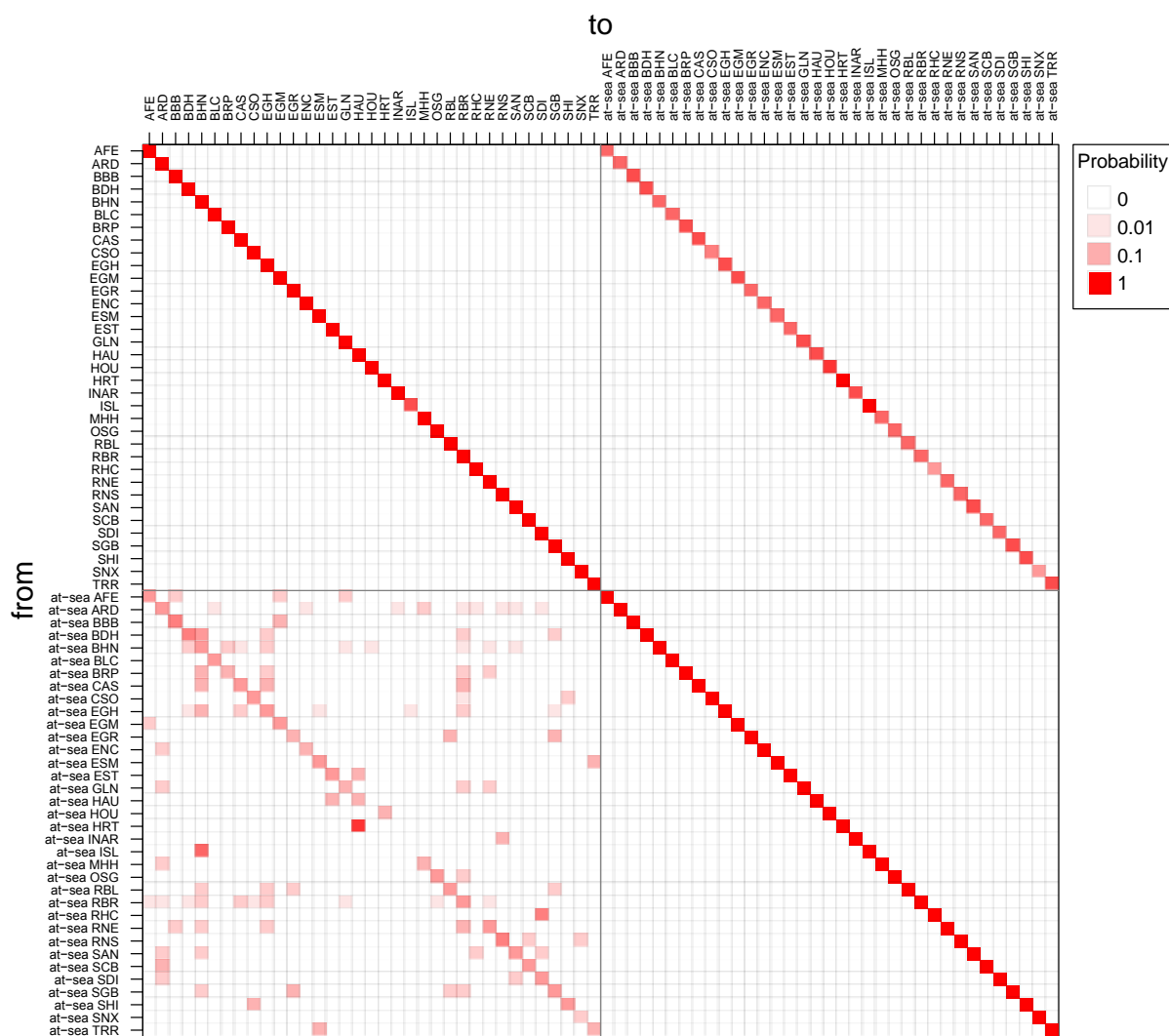


Figure 6. Example of a two-class (haul-out and at-sea) transition matrix. The elements represent the hourly probability of state transition. Upper left quadrant: probability of remaining at a haul-out. Upper right quadrant: probability of leaving a haul-out and entering the at-sea state indexed by the location of the departure haul-out site. Lower right quadrant: probability of remaining in an at-sea state (remaining at sea). Lower left quadrant: probability of hauling out at a site given the previous site; these probabilities were smoothed by resampling the discovery curve at each iteration.

3.7 Adding a temporal dimension

In order to account for variable haul-out and trip durations, at-sea states indexed by the haul-out site of departure were added to the transition matrices. For each of the 25 matrices, the median durations of haul-outs and at-sea trips were used to estimate the hourly probability of remaining in each state. These *time-based* transition probabilities were then used to populate a haul-out/trip transition matrix as illustrated in Figure 6. The upper left quadrant of the matrix refers to the probability of remaining at a haul-out (diagonal with probabilities close to 1). The upper right quadrant refers to the probability of leaving a haul-out and entering the appropriate at-sea state indexed by the location of the departure haul-out site (diagonal with probabilities close to 1). The lower right quadrant refers to the probability of remaining in an at-sea state (diagonal with probabilities close to 1). The lower left quadrant refers to the probability of hauling out at a site given the previous site. Seals cannot directly transit from one haul-out site to another without first having transitioned via an at-sea state (indexed by its departure haul-out site).

3.8 Transition simulation

The simulations were run for a population size estimated by aerial surveys data (mean counts of 2007-2011; (Duck & Morris, 2012)). Aerial survey counts for the *standard* sites (within 500m radius of each) totalled 836 seals. Because only 72% (95% C.I.: 54 – 88 %) of seals are estimated to be hauled out during survey periods (Lonergan *et al.*, 2013), the total population should be approximately 1162 (836/0.72) seals.

At the start of a simulation, each virtual seal was randomly assigned to one of the 25 different transition matrices and to one of the 35 haul-out sites. This yielded 25 different vectors of abundances, each representing the distribution of virtual seals at the 35 haul-outs and each with their respective transition matrix. At each (hourly) time step, these vectors of abundances were updated by drawing transition events from their respective matrix of transition probabilities to simulate seal movements. Simulations were run for a period of 12 weeks to obtain a steady state distribution of seals over haul-out sites. Confidence intervals for the seal counts at each haul-out site were obtained by running 1000 iterations of the simulations.

3.9 Disturbing the haul-out network

The primary aim of the study was to simulate disturbance at a particular haul-out site in turn to predict the effect at another (target) site. Here, a disturbed site was made unavailable for hauling out as would be the case if the site itself was altered or its access blocked by anthropogenic activity e.g. piling or habitat change. This site closure was achieved by setting each element in the ‘to column’ for this site to zero. Each ‘from row’ was then appropriately adjusted so that the ‘from row’ probabilities still summed to one. The disturbance was set to start on week 8 so that the distribution of virtual seals with and without the disturbance could be compared for a period of 4 weeks. The disturbance was simulated for each of the haul-out sites in turn. For each disrupted site, the change in the number of hauled out seals at the Ardmore haul-out site (ARD) was recorded over four weeks post-disruption.

3.9.1 Scaling of predictions

Predicted changes at the Ardmore haul-out site are provided as a proportional change at the EIS SAC so that the effect can be scaled to different population estimates. In addition, an approximate observable change in count was provided for the estimated population size and scaled for tidal patterns in haul-out behaviour. The model predictions did not take into account tidal factors (the simulated seals can haul-out at any state of tide) whereas harbour seals can show a preference for hauling out at low water (approximately 40% of the day; (Thompson *et al.*, 2005)). If the animals that are predicted to be hauled out in a day are constrained to do so within that period, the number of seals observed at low water will be greater. The number of seals predicted to be hauled out by the model was therefore divided by 0.4 to obtain changes in numbers of seals observable during a typical survey period.

Within the empirical model used in this study the closure of a site necessarily resulted in the redistribution of seals to other sites and so the latter should experience a small net increase (expected number of seals at closed site / number of sites remaining). In order to find effects beyond this simple redistribution, the expected mean increase (number of seals at disturbed site / number of remaining sites) was subtracted from the simulated change in number of seals. A reported change of 0% was therefore no different from an equal redistribution of seals.

4 Results

4.1 Simulation model

The simulation model of seal movements reached a “stable state” after about 8 weeks, when the median number of seals at each haul-out did not change significantly (Figure 7). The Ardmore haul-out site stabilised at approximately 100 hauled out seals (95% C.I. of approximately 70-130).

4.2 Effect of disturbance

The effect of disturbing (closing) a single haul-out varied depending on which site was disturbed. Figure 8 shows two very different effects of disturbance on Ardmore (ARD). Disturbing Machrihanish (MHH) increased the number of simulated hauled out seals from 100 to 125, a 25% increase (Figure 8a). Disturbing Bagh an Da Dhoruis (BDH) on the other hand, had no visible effect on the number of simulated seals hauled out at Ardmore; instead, it increased the number of simulated seals at Bunnahabhainn (BHN) (Figure 8b). For most sites, the change in simulated hauled out seals at Ardmore after correcting for simple redistribution was small (range: -0.5% to +21%).

Figure 9 shows no obvious pattern in the magnitude of the effect of closing down a haul-out site in relation to its location. Larger changes tended to occur when the disrupted site was close, but many nearby sites had no effect on the changes in number of seals at Ardmore (Figure 10a). In addition, the magnitude of the effect was also not related to the number of seals hauled out at the disturbed site. In fact, the most frequented site (Bunnahabhainn (BHN)) was one of the least influential sites (Figure 10b).

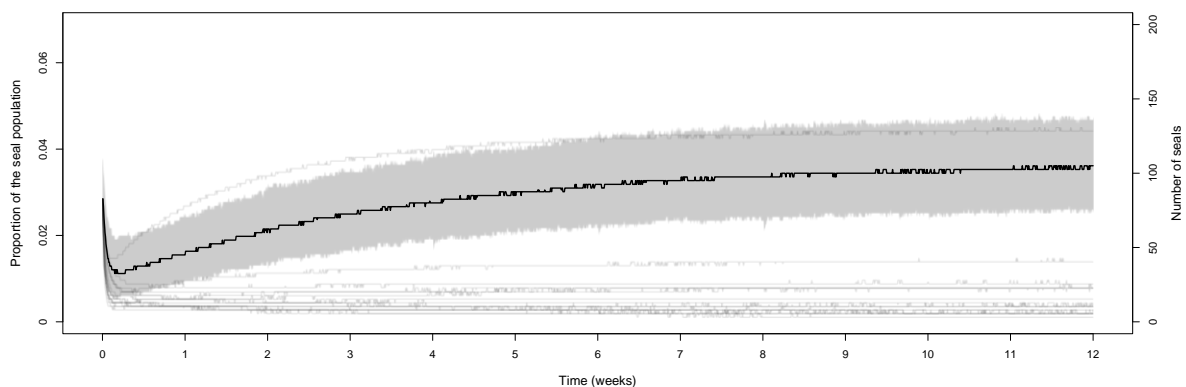
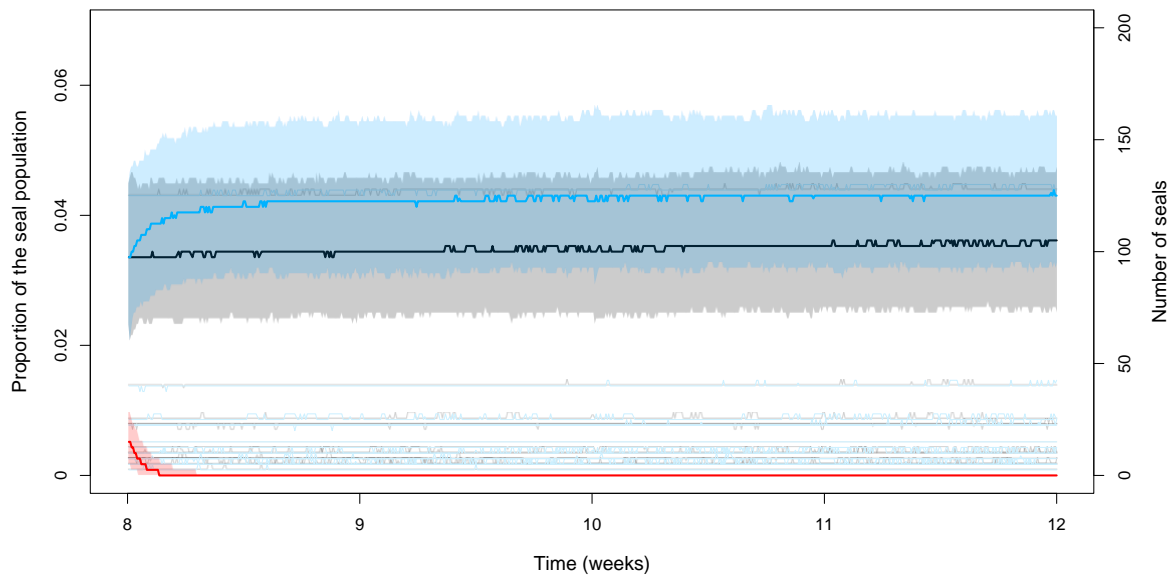


Figure 7. Simulated numbers of seals hauled out over a period of 12 weeks (proportion of simulated population at each haul-out). Each grey line shows the median number of simulated seals at each of the 35 haul-out sites over 1000 iterations. The Ardmore haul-out site is shown in bold and the shaded area represents its 95% confidence interval.

Inter-haul-out transition rates

a.



b.

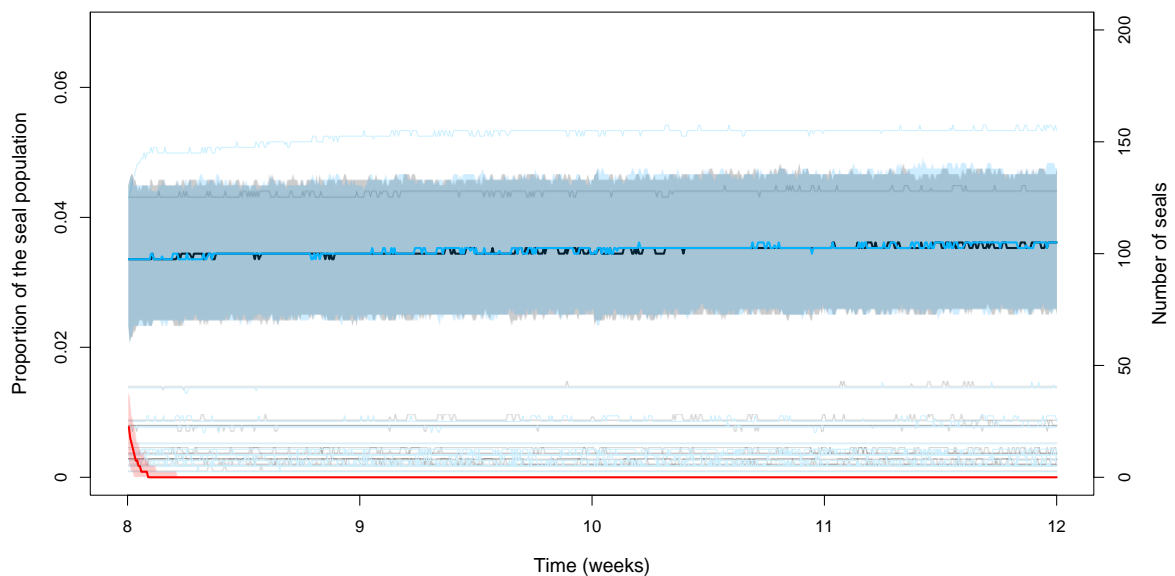


Figure 8. Simulated distribution of numbers of seals hauled out over a period of four weeks. Lines represent the median number of hauled out seals at each site with and without the disturbance (grey and blue, respectively). The Ardmore haul-out site (ARD) is shown in bold lines with shaded 95% confidence intervals. The disturbed site is shown in red (a. Machrihanish (MHH), and b. Bagh an Da Dhoruis (BDH)). Disturbing Machrihanish had an effect on Ardmore while Bagh an Da Dhoruis had little effect on Ardmore, but affected a different site (Bunnahabhain (BHN): top blue line > 150 seals).

Inter-haul-out transition rates

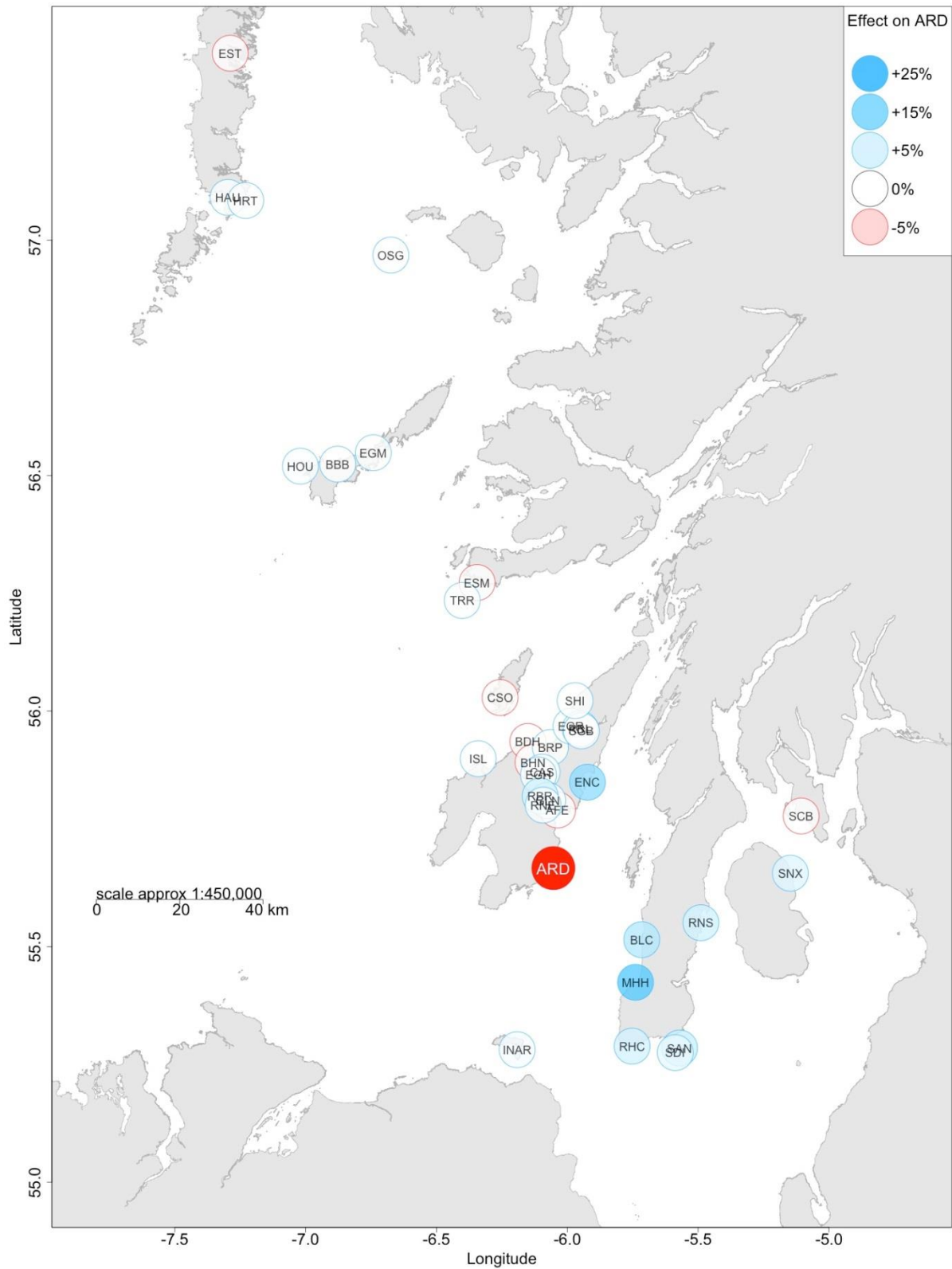
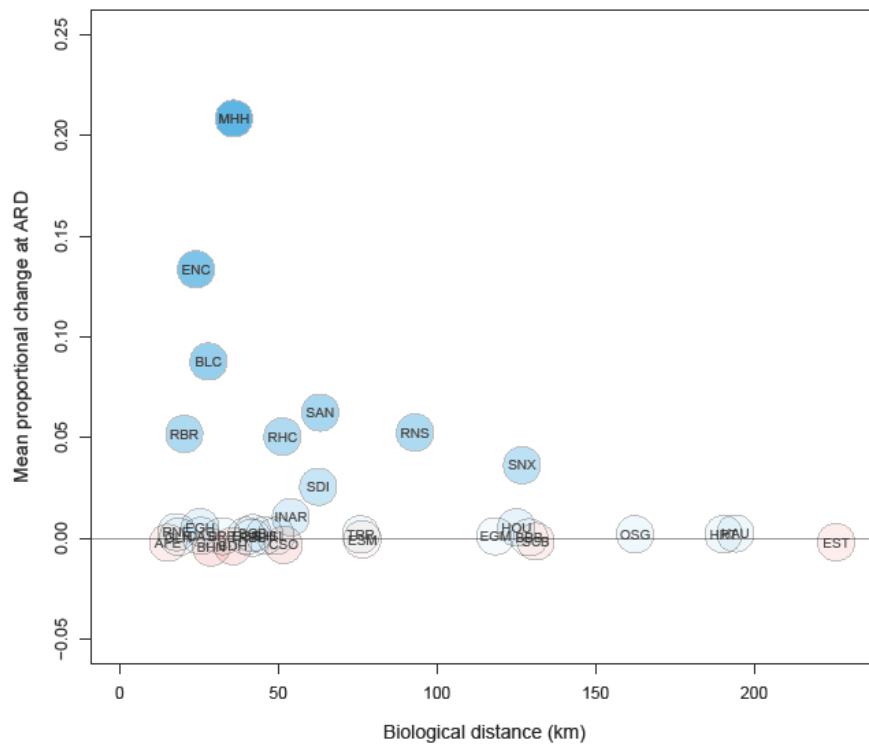


Figure 9. The effect of disturbing (closing down) each haul-out site in turn on the Ardmore haul-out site (ARD). The effect is shown in terms of mean proportional change in counts at Ardmore on a given day post-disturbance.

Inter-haul-out transition rates

a.



b.

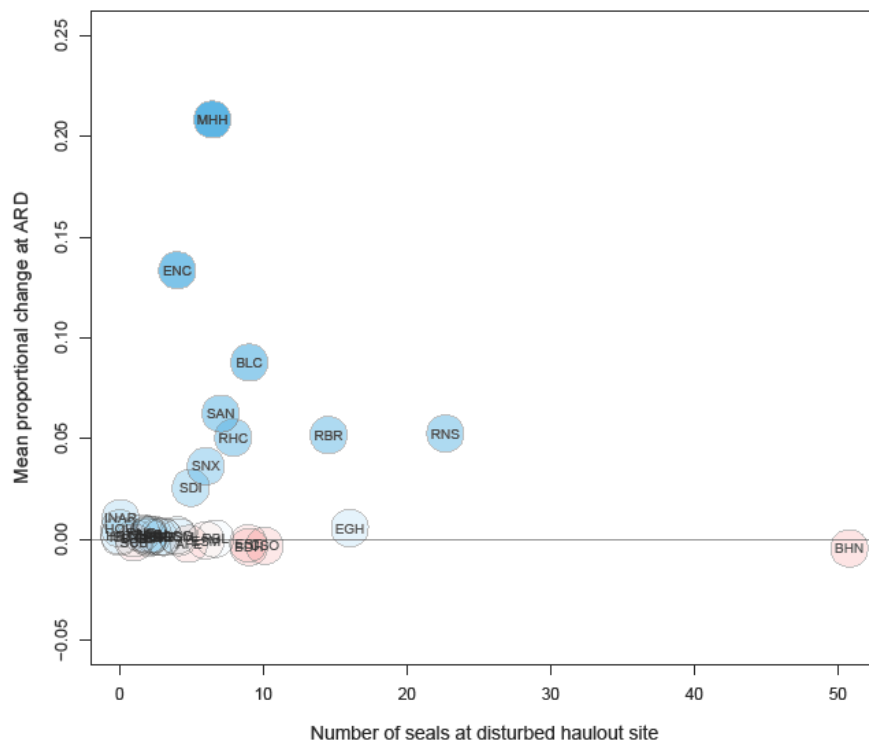
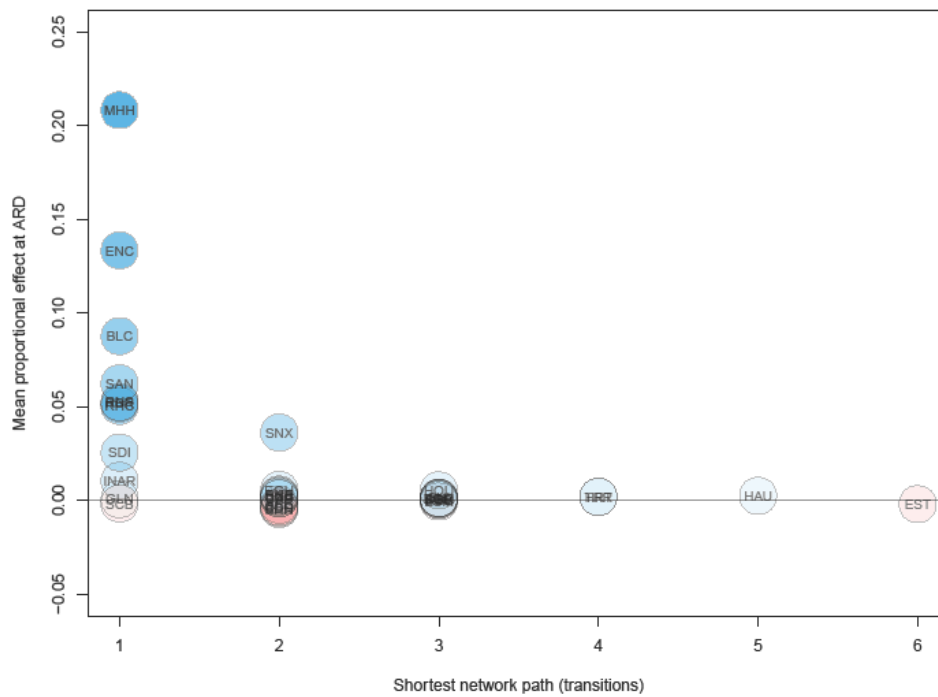


Figure 10. The effect of disturbing a site on seals hauled out at Ardmore (mean proportional change on a given day post-disturbance) as a function of a. the biological distance (shortest path by sea) between the disturbed site and the Ardmore haul-out site, and b. the predicted number of seals at the disturbed site (median of 1000 iterations). The points are colour-coded: blue is a positive change and red is a negative change.

Inter-haul-out transition rates

a.



b.

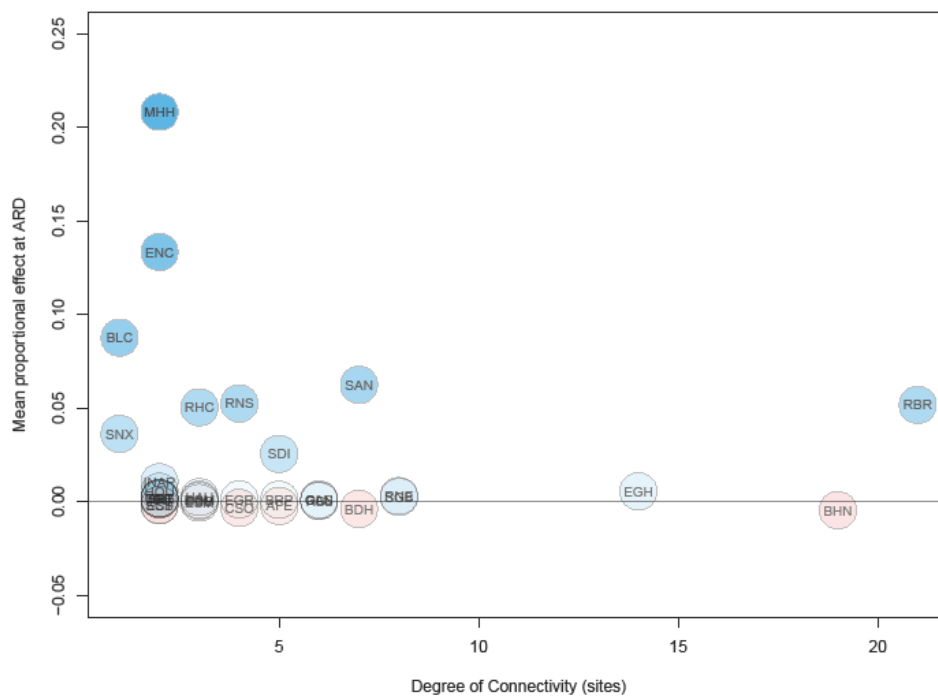


Figure 11. The effect of haul-out network properties (for the unsmoothed population transition matrix) on the effect of remote disturbance at the Ardmore haul-out site (mean proportional change of seals). The haul-out sites are colour-coded: blue is a positive change and red is a negative change. (a) the shortest network path (smallest number of connections) from Ardmore for each haul-out site. (b) the degree of connectivity for each haul-out site (number of connections to other sites).

The best predictor of the effect size was the shortest network path (the number of connections to go from the disturbed haul-out to Ardmore). Figure 11a shows that disturbed sites with an effect on Ardmore are essentially one connection away from Ardmore. The degree of connectivity of the disturbed haul-out was not clearly related to the magnitude of the effect (Figure 11b).

5 Discussion

The inter-haul-out movements of tagged harbour seals captured in the vicinity of the Sound of Islay were modelled as transitions within a network of haul-out sites. Within this modelling framework, each haul-out site was disturbed (closed) in turn and the effect was recorded at one specific haul-out site on Islay – Ardmore (ARD) within the EIS SAC. The effects are first discussed with respect to this single haul-out site. Then the relevance of the results to the whole of the EIS SAC is discussed. The modelling framework is critiqued and then future developments are recommended.

5.1 The effects of disturbance

The response variable used in this study was the *change* in haul-out numbers at Ardmore (not total numbers expected at the haul-out). The model framework dictated that the seals that were excluded from each closed haul-out site in turn would still haul out for the same amount of time, but at one less haul-out site. The effect size was corrected for an equal redistribution of the disturbed seals so that the results are due to redistribution of the seals among haul-outs in the model. Most disturbances had a positive effect of the number of seals at Ardmore (range: -0.5% to +21%).

Haul-out sites with the largest effects were within 50 km of Ardmore and there was little or no effect when the disturbed site was more than 150 km away. These results are in accord with a number of other studies of UK harbour seal movement (Cunningham *et al.*, 2008; Sharples *et al.*, 2012). Within a range of 50km however, distance did not predict which disturbed haul-outs affect Ardmore, as many sites within 50km had little or no effect. Thus the power to infer the effect of remote haul-out disturbance by distance alone was limited, other than to say that the effect was greatest within 50 km of the haul-out of interest.

However, within a range of 50km, the shortest network path (minimum number of connections) between the disturbed haul-out site and Ardmore provided more information about which sites had an effect. The adjacent (in network terms) haul-out sites to Ardmore had a larger influence (Figure 6.11a). There was no significant effect when a disturbed haul-out site was more than two transition jumps (connections) from Ardmore. In practice this shortest network path may be readily obtained from conventional GPS/GSM telemetry. In this model framework, no information about travelling routes and foraging areas are used, so simpler (and thus cheaper) telemetry systems could be used. For example, a tag that simply relayed the location and duration of haul-out events would be sufficient. Such technology is feasible, and its low cost (perhaps low hundreds of pounds per tag) compared with conventional tag costs (approximately three thousand pounds per tag) permitting sufficient seals to be tagged in regions where recent movement data are sparse.

Ardmore has a high degree of connectivity (Figure 5). This may explain why many disturbed haul-out sites resulted in little change in seals numbers at Ardmore; haul-out sites with greater connectivity will be more dampened in their response to disturbance at a single site. When assessing the impacts of distant disturbances at other sites (for example in another SAC), results might change depending on the connectivity of the site in question

5.2 Inference to the EIS SAC

This analysis predicted effects of disturbances at a distant haul-out for the haul-out site Ardmore (ARD). However, annual moult surveys identified other haul-out sites within the EIS SAC (Figure 2). The EIS SAC extends over 15 km² and harbour seals haul out on both the coastline and offshore Skerries over its 8 km length as shown by survey counts (Figure 2). Scaling the predictions to effects on the entire EIS SAC depends on how representative the tagged seals are of all seals in the SAC.

The tagged seals used in this analysis tended to haul out at, or close to, Ardmore more often than elsewhere in the EIS SAC. The difference in the distribution of haul-outs between the survey data and the behaviour of the tagged seals may be due in part to the fact that the survey was conducted during the moult period (August) when haul-out usage may differ from the period of the tagging data (truncated at 1st June) used in this analysis. Nevertheless, it is worth considering the implications of the representativeness of the behaviour of the tagged seals to the counts of seals within the entire EIS SAC.

If all the seals hauling out in the rest of the EIS SAC behaved in the same way as the tagged seals, the proportional effect of a disturbance would be similar. At one extreme case, any seals hauling out at other sites in the EIS SAC could behave completely differently and move to haul-outs not included in this analysis and the proportional effect of a disturbance would then be much smaller. For instance, the analysis predicted a 20% change at Ardmore when disturbing Machrihanish (MHH). This was about 20 animals for a simulated count of 100 at Ardmore. Because the August aerial survey counts for the entire EIS SAC were much greater than Ardmore alone (704 ± 53), the proportional change would be much smaller ($20/704 = 2.8\%$). The effect of disturbing MHH would be almost impossible to detect using aerial surveys counts. In this scenario however, the SAC would be susceptible to disturbance at the sites not included here. At the other extreme, seals hauled out in the rest of the EIS SAC could be hauling out at MHH even more often than the tagged seals. In that case, the proportional change at the EIS SAC would be even larger than predicted.

At the moment, it is unclear how representative the tagged seals are of the entire EIS SAC. Tagging seals at other haul out sites within the EIS SAC that were not used by the tagged study seals would help reduce this uncertainty.

5.3 Critique of methods

The modelling framework presented here is simplistic and incorporates assumptions which may be challenged. A critique of some aspects of the framework and their practical relevance follows.

5.3.1 Uncertainty of predictions

Whilst the median of the 1000 simulations of the changes in counts at Ardmore showed no long term after the first two weeks of disturbance at remote sites there was considerable variability in individual simulations (as shown by the shaded 95% confidence intervals in Figure 8). This was due to the fact that individual seals in the simulation were randomly assigned a transition matrix generated by individual study seals. However, the resulting variability was not uncharacteristic of the behaviour of seals observed in the wild, where the pattern of hauling out ashore and the choice of haul-out sites are variable – both from seal to seal and day to day.

The last three harbour seal aerial moult counts for the Ardmore haul-out site were 25 in 2000, 117 in 2007, and 48 in 2009. Moreover, previous harbour seal counts in the Sound of Islay (Sparling, 2013) and counts in the Sound of Islay (BHN & RBR) using time lapse photography, show large day to day variability at a given haul-out site. The point here is that, with this magnitude of observation variability, even a predicted change of 20% at the Ardmore haul-out site will be difficult to differentiate from natural variability using conventional survey methods.

5.3.2 Nature of the disturbance

In this study, disturbance was defined as the act of forcing each haul-out in turn to become permanently unavailable (closed), forcing seals to redistribute. Alternative disturbance scenarios could also be coded: for example, periodic unavailability or simultaneous unavailability of a geographic cluster of haul-out sites. Disturbance could also affect the paths that seals have to travel across so that certain haul-outs require longer travel times or are only accessible through certain haul-outs. This could be the case for the installation of a turbine array in a narrow channel.

5.3.3 Measures of disturbance

The effect at the target haul-out (in this study the Ardmore haul-out site) was recorded was the average *change* in seals hauled out at the EIS SAC over a period of a month. The absolute numbers of seals at haul-out sites were not predicted. However, other measures could have been applied. These include the time to recovery within 95% of the historical mean, to quantify the capacity of the system to recover after a temporary effect. However, it is likely that the general finding of this study would apply to such alternative measures of the effect of disturbance because they are linked to the connectivity of the haul-out sites.

This study makes no inference about any secondary individual consequences caused by changes in haul-out usage. For example, it is quite feasible that disturbance of a haul-out site close to areas of high prey availability could reduce the overall nutritional condition of the disturbed seals.

5.3.4 Data extent

In order to increase the sample size, seal tracks from the 2014 deployment were included in this study. During this 2014 deployment, seals were occasionally deliberately disturbed as part of a related study. These data were included since the effect of deliberate disturbance was small. Seals that left their haul-outs due to the deliberate disturbances often remained close to the site, and these ‘trips’ are likely to have been excluded by the trip assignment algorithm used in this study.

5.3.5 Bias due to capture location

The 25 study animals were all captured and tagged near the Sound of Islay. If it is assumed that actual home ranges may vary from seal to seal there is a risk that the sample of seals may under represent the movements of seals for whom the Sound of Islay was at the edge of their distribution. Furthermore the accuracy of the predictions of the effect of disturbance will reduce as the distance from the Sound of Islay increases. However, since both the location of capture and the focus of interest in the response to disturbance (Ardmore) are nearby, it is likely that any such biases are of little significance in this study.

5.3.6 Recommendations for model development

The simulation model in its current state has proved a useful tool to predict the effect of disturbance on changes of numbers seals hauled out at a specific site – in this study Ardmore within the EIS SAC. However, it is essentially an empirical model. That is, it uses the data generated by the study animals to simulate disturbance scenarios without reference to the biological and environmental drivers and modifiers of seal movements. The main biological driver is the need to maintain both short-term condition (through foraging–resting cycles) and long-term condition (sufficient to produce viable offspring). The behaviour seals use to attain these goals is both enabled and constrained by their physiology (for example ingestion/ digestion rates (Sparling *et al.*, 2007) and swimming speeds), information (spatial memory map of the status of *known* foraging and haul-out sites) and possibly the behaviour of conspecifics. All this is set within the dynamic availability of prey fields.

One approach is to develop the simulations in this study into a biologically informed individual based model (IBM) of movement, such as that carried out on Danish harbour porpoises by Nabe-Nielsen *et al.*, (2014). Whilst such IBMs are challenging to build and data hungry to run, they do offer an opportunity to synthesise environmental and biological processes and data over a spectrum of temporal and spatial scales, and thus offer the prospect of more credible predictions of the effect of environmental change (Grimm & Railsback, 2012).

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