

## Durham Research Online

---

### Deposited in DRO:

05 October 2015

### Version of attached file:

Accepted Version

### Peer-review status of attached file:

Peer-reviewed

### Citation for published item:

Stewart, J.E. and Pomeroy, P.P. and Duck, C.D. and Twiss, S.D. (2014) 'Finescale ecological niche modeling provides evidence that lactating gray seals (*Halichoerus grypus*) prefer access to fresh water in order to drink.', *Marine mammal science.*, 30 (4). 1456-1472 .

### Further information on publisher's website:

<http://dx.doi.org/10.1111/mms.12126>

### Publisher's copyright statement:

This is the accepted version of the following article: Stewart, J. E., Pomeroy, P. P., Duck, C. D. and Twiss, S. D. (2014), Finescale ecological niche modeling provides evidence that lactating gray seals (*Halichoerus grypus*) prefer access to fresh water in order to drink. *Marine Mammal Science*, 30(4): 1456-1472, which has been published in final form at <http://dx.doi.org/10.1111/mms.12126>. This article may be used for non-commercial purposes in accordance With Wiley Terms and Conditions for self-archiving.

### Additional information:

## Use policy

---

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a [link](#) is made to the metadata record in DRO
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the [full DRO policy](#) for further details.

1 Finescale ecological niche modeling provides evidence that lactating gray seals (*Halichoerus*  
2 *grypus*) prefer access to fresh water in order to drink.

3

4 Authors: Stewart, J.E.<sup>1</sup>, Pomeroy, P.P.<sup>2</sup>, Duck, C.D.<sup>2</sup> and Twiss, S.D.<sup>1</sup>

5 1. *School of Biological and Biomedical Sciences, Durham University, DH1 3LE, UK.*

6 2. *Sea Mammal Research Unit (SMRU), Scottish Oceans Institute, University of St. Andrews,*  
7 *St. Andrews, Fife, KY16 8LB, UK.*

8

9 Key words: pinniped, phocid, habitat preference, Ecological Niche Factor Analysis, ENFA,  
10 thermoregulation, water balance, water drinking, salinity.

11

12 ABSTRACT

13 Many phocids are capital breeders, relying on stored reserves to sustain energetic  
14 requirements whilst on land. Their large body size, high energy expenditure during lactation,  
15 and the insulative effects of the blubber layer can lead to thermal stress from overheating,  
16 especially in warm and temperate climates. Thermal stress can influence fine-scale site  
17 choice on breeding colonies, and behavioral thermoregulation has been proposed as an  
18 explanation for the clear preferences shown by breeding female gray seals for proximity to  
19 pools of water. However, anecdotal observations suggest that pools of water may also be  
20 preferred for drinking, though water intake is difficult to verify without real-time  
21 physiological monitoring. Here, an alternative approach demonstrates that gray seals also  
22 require access to water for drinking. Using Ecological Niche Factor Analysis to examine fine-  
23 scale physical determinants of pupping site choice at North Rona, Scotland, we found that  
24 lactating mothers showed preference for lower salinity pools. This is most pronounced early  
25 in the season, when ambient temperatures and presumably thermal stress are greatest. Given  
26 that the cooling effect of fresh and salt water should be equivalent, the most parsimonious  
27 explanation for this preference for fresh water pools is that lactating females use these pools  
28 for drinking.

29 INTRODUCTION

30 Many phocids are capital breeders, and therefore fast continuously throughout the  
31 breeding period (Riedman 1990). During their time on the breeding colony, postpartum  
32 mothers obtain their energy from the metabolism of stored reserves including lipids in their  
33 thick blubber layer (Pomeroy *et al.* 1999). These reserves are also mobilized to provision the  
34 pup with a lipid-rich milk in a short lactation period (approximately 18 d in the gray seal,  
35 *Halichoerus grypus*; Boness and James, 1979; Pomeroy *et al.* 1999). This results in high  
36 energy expenditure during lactation, as demonstrated by increased basal metabolic rates  
37 (BMR); for example, the BMR of lactating gray seal mothers is typically approximately 2.3  
38 times that of nonlactating females (Reilly *et al.* 1996). This dramatic increase in BMR during  
39 lactation can lead to thermal stress from overheating (Twiss *et al.* 2002) as a result of the  
40 insulative effects of the blubber layer and large body size, while the burden of lactation can  
41 contribute to water stress (Reilly *et al.* 1996). Phocids are unable to pant or sweat (Riedman  
42 1990) and cooling on land is primarily achieved by thermal radiation *via* poorly insulated  
43 “thermal windows” such as the flippers (Ronald *et al.* 1977, Øritsland *et al.* 1978, McCafferty  
44 *et al.* 2011, Paterson *et al.* 2012). However, this can be insufficient to prevent thermal stress  
45 on warm days, generating a requirement for behavioral thermoregulation, for example by  
46 seeking shade (Campagna and Le Beouf 1988) or bathing in pools of water (Twiss *et al.*  
47 2002). These behaviors are common in pinnipeds breeding in warm and temperate climates  
48 (Gentry 1973, Campagna and Le Beouf 1988, Twiss *et al.* 2002, Wolf *et al.* 2005) and  
49 involve individuals actively seeking fine-scale, heterogeneous landscape features, such as  
50 shady cliffs or pools of water. Behavioral thermoregulation has been proposed as an  
51 explanation for the clear preferences shown by breeding female gray seals for proximity to  
52 pools of water (Redman *et al.* 2001, Twiss *et al.* 2002).

53           It has previously been assumed that gray seals meet their water requirements while  
54 hauled out through the metabolism of fat reserves (Schweigert 1993), with no clinical  
55 evidence having been found for dehydration during this time (Irving 1935, Kooyman and  
56 Drabek 1968, Ortiz *et al.* 1978). However, at the Scottish colony of North Rona (59.10°N,  
57 5.83°W; Fig. 1), lactating female gray seals incur a negative water balance (Reilly *et al.*  
58 1996) and have been observed drinking from pools of water of varying salinities (Reilly *et al.*  
59 1996, Redman *et al.* 2001, PPP and SDT, personal observation). Similar drinking behavior  
60 has been observed at other UK colonies, including Donna Nook (53.47°N, 0.15° E, JES,  
61 personal observation) and the Isle of May (56.18° N, 2.56° W, PPP and SDT, personal  
62 observation). Therefore, it is also possible that proximity to water is important because  
63 lactating gray seals may need to drink from pools of water to maintain a positive water  
64 balance and avoid the water stress that develops during lactation (Reilly *et al.* 1996, Redman  
65 *et al.* 2001). The difference between these observations and those of Schweigert (1993) at  
66 Sable Island, Nova Scotia (43.93°N 59.92°W) could be a result of the higher average  
67 temperatures (approximately 7°C difference) at North Rona (Redman *et al.* 2001) relative to  
68 Sable Island (Schweigert 1993), which may be enough to induce additional water  
69 requirements. However, despite behavioral observations showing that seals submerge their  
70 mouths and appear to drink (PPP and SDT, personal observation), it is difficult to state  
71 conclusively, without real-time physiological monitoring, that free-living seals drink water  
72 whilst hauled out. However, an alternative approach is to examine the fine scale habitat  
73 preferences of individuals, particularly with regards to proximity to pools and to pool salinity.  
74 If seals require pools solely for thermoregulation they should not differentiate between salt  
75 and fresh water pools. Therefore, we examined the fine spatial scale terrestrial habitat  
76 preferences of adult female gray seals based on preestablished preferences (proximity to  
77 access points to the sea and to pools of water; Twiss *et al.* 2000, 2001) and introduced pool

78 salinity as a new parameter. If gray seal mothers do require access to fresh water for  
79 addressing water stress, we predict that proximity to pools and positioning relative to access  
80 points to and from the colony will remain key determinants of pupping site choice, but that  
81 pool salinity will also contribute substantially to pupping site preferences.

82

## 83 METHODS

84

### 85 Study Site and Population

86 North Rona is a small island located 75.5 km NNW of Cape Wrath, Scotland, and  
87 covers an area of approximately 1.2 km<sup>2</sup>. The gray seal breeding colony at North Rona is  
88 concentrated on the Fianuis peninsula, and forms annually between September and November  
89 (Pomeroy *et al.* 1999), with individual females generally remaining ashore for approximately  
90 22 d. The study site is a 287 m<sup>2</sup> area in the south of this peninsula (Fig. 1). Due to the  
91 locations of cliffs surrounding the island, that rise up to 108 m, access to the study site from  
92 the sea is limited to a series of gullies in the east (Fig. 1), which lead to a relatively low-lying,  
93 open and boulder-strewn grassy slope. North Rona experiences a decline in daily air  
94 temperature over the breeding season (Fig. 2). Adult females tend to give birth within four  
95 days of arriving on North Rona (Pomeroy *et al.* 1999), and the colony typically expands  
96 inland, further from access points throughout the season (Pomeroy *et al.* 1994). Due to the  
97 distance of pupping sites from the sea, females at North Rona typically do not return to the  
98 sea during lactation (Pomeroy *et al.* 1994, 1999). The time spent on the colony prepartum is  
99 thought to be spent in site selection before individuals give birth to a single pup (Pomeroy *et*  
100 *al.* 1999). Adult females show both site fidelity, returning to sites within a median distance of  
101 55 m from the previous years' pupping site, and temporal fidelity, pupping within a few days  
102 of their pupping date in the previous year (Pomeroy *et al.* 1999).

103

104 Eco-Geographical Variables

105         The study site was characterized in terms of three key eco-geographical variables  
106 (EGVs), chosen for their known or hypothesized influence on seal distribution and behavior  
107 (Pomeroy *et al.* 1994; Twiss *et al.* 2000, 2001, 2002, 2007; Redman *et al.* 2001): “cost-  
108 distance” to access (CACC), “cost-distance” to nearest pool (CPOOL) and pool salinity.  
109 Study site topography was quantified using a submeter-accurate Digital Terrain Model  
110 (DTM), previously generated from high resolution aerial photogrammetry (Mills *et al.* 1997,  
111 Twiss *et al.* 2000). The DTM was stored as a grid of elevation values across the study site,  
112 including information on slope and aspect between neighboring 0.2 m × 0.2 m grid cells, and  
113 was integrated with a grid of the same resolution and extent depicting land extent and access  
114 point availability to provide the CACC surface. The CACC surface represents a cell-by-cell  
115 index of the cumulative “cost” incurred from travelling from any location within the study  
116 site to the “nearest” (least “costly”) access point to the sea, where cost is a function of the  
117 slope traversed between neighboring grid cells, and is represented as a relative index ranging  
118 from zero to 100 (Twiss *et al.* 2000, 2001).

119         High resolution aerial photographs of the study site (taken by SMRU for the annual  
120 pupping census; Hiby *et al.* 1988) were available for four dates, hereafter “focal dates”,  
121 during the 2010 breeding season. These focal dates are referred to by the “stage” of the  
122 breeding season to which they relate: 30 September 2010 (“Beginning”), 12 October 2010  
123 (“Mid”), 24 October 2010 (“Late”) and 03 November 2010 (“End”). Using a geographic  
124 information system (GIS; ArcInfo Version 9.3, Environmental Systems Research Institute  
125 Inc., Redlands, CA), digital copies of these aerial photographs were georectified. We then  
126 digitized as polygons all pools of standing water across the study site. These polygon  
127 coverages were converted to a grid of the same resolution and extent as the study site DTM

128 and used in conjunction with the DTM to create a CPOOL surface for each focal date. The  
129 cost-distance surfaces provide a representation of the potential relative costs incurred by  
130 individuals moving across the study site towards access points or nearest pools of water, and  
131 do not imply a knowledge of the physiological cost to individuals seals (Twiss *et al.* 2000,  
132 2001). Based on personal observations of the locomotory abilities of adult gray seals (PPP  
133 and SDT), the cost-distance maps also assume that any feature (*e.g.*, stone walls) resulting in  
134 a 2 m vertical change in elevation between neighboring grid cells act as impassable barriers  
135 to movement (Twiss *et al.* 2000, 2001). Separate CPOOL surfaces were generated for each of  
136 the four focal dates due to the spatially and temporally variable nature of the pools, which  
137 form as a result of variable rainfall and sea spray throughout the season (Twiss *et al.* 2007),  
138 though only one CACC surface was generated as the terrain and positions of access points  
139 remain unchanged across the season.

140         Seals have previously been observed drinking from pools of water at North Rona and  
141 therefore salinity was quantified to assess whether a preference for less brackish water  
142 influenced seal distribution. We recorded pool salinities from seven days of sampling (29  
143 September; 5, 9, 10, 11, 19 and 31 October) during the 2010 breeding season on base maps of  
144 pools, providing a map of pool salinities for beginning, mid and late in the 2010 breeding  
145 season. Salinity was measured in parts per thousand (‰), based on the refractivity index of  
146 the water sample. These salinity maps were transferred to the GIS and the salinity at  
147 unmeasured locations was predicted using spatial interpolation of salinity values at known  
148 locations for each stage of the 2010 season. Interpolation was carried out using a smoothed  
149 inverse exponential distance-weighted (IDW) interpolation. The IDW interpolation method  
150 operates using the assumption that locations close to each other are more similar than those  
151 that are further apart. Measured points close to the prediction location are therefore assigned  
152 a higher weighting than those further away, which have relatively little influence on the



153 predicted value (Ball and Luk, 1998). The salinity surface for late 2010 was also used for the  
154 end of 2010, as salinity patterns were the same for late and end of season. It was important to  
155 quantify CPOOL and salinity over a range of dates during the breeding season due to the  
156 changing availability and distribution of pools, and the varying contributions of rainwater and  
157 seawater spray to the pools. Generally, the most saline areas are in the northwest of the study  
158 site and around access points, due to high seawater contributions from sea spray and runoff  
159 from seals arriving to the colony (Fig. 3). Though SAL and CACC are therefore negatively  
160 correlated across the study site at each stage in the breeding season (Pearson's product  
161 moment correlation,  $n = 82,221$ ,  $P < 0.001$ ; early,  $r = -0.225$ ; mid,  $r = -0.050$ ; late and end,  $r =$   
162  $-0.178$ ), both variables were retained within the model as the effect sizes were very small.

163

#### 164 Seal Location Data

165 Daily locations (28 September to 3 November) of all seals, including adult females  
166 with pups, during the 2010 breeding season were recorded on a fine-scale base map of the  
167 study site from a hide overlooking the southern half of Fianuis peninsula (Pomeroy *et al.*  
168 1994). The number of seals observed on focal dates is summarized in Table 1 (see methods  
169 below for an explanation of terminology). All data were recorded with submeter accuracy  
170 with the aid of a 10 m  $\times$  10 m grid overlay, using the head of each individual as a standard  
171 reference point. Resulting maps were digitally transferred to a GIS database and georectified  
172 to real-world coordinates. Points depicting seal locations were digitized to form a point  
173 coverage within the GIS for each stage of the 2010 breeding season (Twiss *et al.* 2000, 2002).  
174 These points were associated with the age, sex, and, where available, identity (Hiby *et al.*  
175 2012) of each individual, allowing coverages to be created depicting the locations of adult  
176 females on all focal dates.

177

178 Ecological Niche Factor Analysis (ENFA)

179 Earlier studies of gray seal pupping site choice (*e.g.*, Anderson and Harwood 1985,  
180 Twiss *et al.* 2001) have been based on qualitative habitat descriptions or simplistic models  
181 utilizing hierarchical selection procedures, rather than using factor analyses of all variables  
182 simultaneously, and none have considered the influence of pool salinity. Ecological Niche  
183 Factor Analysis (ENFA) was chosen to further investigate gray seal habitat preferences,  
184 including the influence of pool salinity. ENFA requires presence-only rather than presence-  
185 absence species location data (*i.e.* a knowledge of species' occurrences within a study area,  
186 not whether they are consistently absent from specific locations). Presence-absence  
187 techniques such as Generalized Linear Models (GLMs; Gu and Swihart, 2004) are not  
188 applicable here, as the absence of seals at a given location on the North Rona colony cannot  
189 confidently be assumed to be a result of poor suitability at that location, because the colony is  
190 in decline (Pomeroy *et al.*, 2010). Absence from a location could therefore occur simply  
191 because not all the breeding space is required. Furthermore, the fine-scale nature of our  
192 environmental data means that there are many potential locations for individuals to be  
193 "absent" from, and assuming that these "false absences" represent actual absences could bias  
194 the predictions of the niche model (Hirzel *et al.* 2002, Kéry 2002, Gu and Swihart 2004).

195 EGV maps and Boolean seal presence maps were converted and aggregated to 1 m ×  
196 1 m grids, to make the resolution of all maps uniform. Boolean seal presence maps indicated  
197 simple presence or absence (1/0) rather than the actual number of seals in each cell. All grids  
198 were converted to ASCII files and imported into IDRISI32 (Version I32.11; Clark Labs,  
199 Worcester, MA) for conversion into raster maps suitable for Ecological Niche Factor  
200 Analysis (ENFA) analysis in BioMapper (Version 4.0.7.373; Hirzel *et al.* 2007). For ENFA  
201 analyses on all focal dates one adult female seal presence map was used alongside one of  
202 each EGV map for the corresponding date.

203           The ENFA process has been described in detail elsewhere (Hirzel *et al.* 2002) but, in  
204 summary, ENFA assesses habitat usage and preferences by comparing the species'  
205 distribution on the EGVs (*i.e.*, the values of EGVs at locations with adult female seals  
206 present) with the global set of EGV values (the EGV values in all cells of a raster map of the  
207 study site). In doing so, it defines the ecological niche in the terms of Hutchinson (1957): an  
208  $n$ -dimensional hypervolume that encompasses the ecological requirements of a species. In  
209 order to define habitat preferences, ENFA extracts all information relevant to the species  
210 niche from the input EGVs whilst discarding the correlations between these variables. It does  
211 so by computing two types of uncorrelated factors from the input set of possibly correlated  
212 EGVs (composite “global marginality”,  $M$ , and composite “global specialization”,  $S$ ). These  
213 factors are ecologically relevant in that they formally describe some aspect of the species  
214 niche relative to the “global” availability of the modelled set of EGVs. Therefore, these  
215 factors are easier to interpret in ecological terms than those produced by traditional factor  
216 analyses such as principal components analysis (PCA), another method commonly used to  
217 assess habitat preferences (Hirzel *et al.* 2001, 2002). The first factor to be extracted is the  
218 marginality,  $M$ , which summarizes the difference between the species and global mean on all  
219 EGVs and ranges between 0 and 1; the larger the value of  $M$ , the further the mean of the  
220 species distribution lies from average conditions available across the study site.  $M$  is  
221 composed of marginality coefficients ( $coMs$ ) for each EGV, which express the degree of  
222 correlation between  $M$  and each EGV. EGVs with large  $coMs$  contribute more to  $M$  than  
223 those with small  $coMs$ ; a low  $coM$  value (close to 0) indicates that the species tends to live in  
224 average conditions in relation to that EGV, whilst values closer to  $\pm 1$  indicate a tendency to  
225 live in “extreme” habitats. Positive  $coMs$  indicate that the species prefers EGV values that are  
226 higher than the global mean, whilst negative coefficients indicate the opposite.

227           The marginality factor accounts for all of the marginality and a certain proportion of  
228 the specialization; the residual specialization is accounted for by the subsequently extracted  
229 global specialization factors ( $S$ ), which describe the species' specialization in relation to the  
230 range of available EGVs. The  $\nu$ - $I$  specialization factors (where  $\nu$  is the number of EGVs) are  
231 extracted according to decreasing amounts of explained variance.  $S$  is composed of  
232 specialization coefficients ( $coS$ ) for each EGV which range between 0 and  $\pm 1$ , with a high  
233 absolute  $coS$  value indicating a narrow niche breadth relative to the range of available  
234 conditions. Note that the sign associated with each  $coS$  is redundant and is simply a product  
235 of its computation.  $S$  is not bounded between zero and one but ranges from one to infinity,  
236 with any value exceeding unity indicating a degree of specialization. Thus, the higher the  
237 absolute value of  $coS$ , the more restricted the species is on the corresponding EGV. As  $S$   
238 ranges between one and infinity, it is difficult to interpret meaningfully. Instead it is easier to  
239 define the species niche breadth in terms of the computed tolerance value,  $T$ .  $T$  is simply the  
240 inverse of  $S$  and, as such, ranges between 0 and 1, with low values indicating lower tolerance  
241 (high specialization) and vice versa. Thus, a species with a high  $T$  value has a particularly  
242 wide niche and is generally widespread across the study site.

243

## 244 RESULTS

245

246           ENFA showed that female gray seals occupy habitat close to the average of all EGVs  
247 (*i.e.*, are only slightly marginal; Table 1) but that they tend to occupy a restricted range of  
248 EGV values relative to those which are available (Table 1). That is, females are relatively  
249 specialized in terms of their site choice, as shown by  $S$  and  $T$ . The marginality and  
250 specialization displayed is a consequence of avoidance of extreme values, with females  
251 typically occupying intermediate values for all EGVs, but avoiding both high and low

252 extreme values (Fig. 4, Table 2). CPOOL contributes the most to female gray seal  
253 marginality, and females are typically found closer to pools than would be expected on  
254 average (Fig. 4, Table 3).

255 Table 1 shows that all composite marginality values are greater than zero, though  
256 none exceed 0.5. There is an overall decrease in composite marginality (*e.g.*, beginning 2010,  
257  $M = 0.479$ , end 2010,  $M = 0.221$ ; Table 1) and specialization (*e.g.*, beginning 2010,  $S =$   
258  $5.951$ , end 2010,  $S = 1.434$ ; Table 1) across the season, as individuals are increasingly found  
259 in more average locations across a wider range of EGV values (Fig. 4). Female specialization  
260 is especially pronounced at the beginning of the season when the first arrivals are selecting  
261 sites on the colony; this is also reflected in the lower tolerance ( $T$ ) displayed earlier in the  
262 season (Table 1).

263 All EGVs influenced gray seal habitat selection (Tables 3 and 4); the *coMs* for each  
264 EGV indicate that female gray seals prefer sites close to pools of low salinity near to access  
265 points. Throughout the season, CPOOL is the EGV on which the female distribution differs  
266 most from the study site average, as indicated by the large and negative CPOOL marginality  
267 coefficients, which demonstrate a preference for proximity to pools of water (Table 3).  
268 Though salinity contributes less to marginality than does CPOOL (Table 4), what is clear is  
269 that individuals avoid those areas with the highest salinity (Fig. 4, Table 2). CPOOL  
270 contributes the most to specialization during the beginning and middle stages of the season,  
271 though later in the season CACC is the EGV with the greatest contribution to  $S$  (Table 4); at  
272 the end of the season seals are typically further from access points than earlier in the season,  
273 though opt for sites at intermediate rather than extreme high or extreme low CACC and  
274 CPOOL values (Fig.3, Table 2). Salinity contributes more to specialization at the beginning  
275 of the season (Table 3), when temperatures are higher (Fig. 2), than does CACC, indicating  
276 the importance of pool salinity over CACC to the first females to come ashore at the onset of

277 the breeding season, and all EGVs have a demonstrable impact on the marginality and  
278 specialization of female distribution throughout the season (Table 4). The results presented in  
279 Tables 3 and 4 also suggest that low CACC and salinity are less important to females later in  
280 the season, when temperatures are typically lower (Fig. 2), as they are found nearer to the  
281 study site average over a wider range of CACC and salinity conditions (are less marginal, less  
282 specialized, and more tolerant). The change in CACC and salinity *coMs* demonstrate a shift  
283 towards higher values of CACC and salinity closer to the study site average as the season  
284 progresses, suggesting that females either prefer or are forced into areas of higher salinity and  
285 further from access points as the season progresses (Table 3).

286

## 287 DISCUSSION

288

### 289 Habitat Preferences

290 The ENFA has confirmed previous indications that adult female gray seals show a preference  
291 for sites near to pools of water at intermediate distances to access points (Pomeroy *et al.*  
292 1994, 2000; Twiss *et al.* 2000, 2002, 2003, 2007; Redman *et al.* 2001, Stephenson *et al.*  
293 2007). Furthermore, there is a clear preference for fresh rather than brackish or seawater  
294 pools, particularly early in the season, when temperatures are typically higher; this has been  
295 discovered despite the range of salinity values across the study site being deceptively low (0-  
296 10‰). The interpolation technique results in lower salinity values across the study site than  
297 were actually observed (max. observed = 32‰), meaning that the results presented here are a  
298 conservative metric of the avoidance of high salinity areas, which in reality is likely to be  
299 more pronounced. It is concluded that, though pools are demonstrably important for  
300 thermoregulation (Redman *et al.* 2001, Twiss *et al.* 2002), they are also likely important  
301 sources of drinking water, potentially to avoid a negative water balance. Indeed, it may be

302 that the requirements for thermoregulation mask the requirements for drinking water, with  
303 females bathing in any given pool to cool off regardless of the salinity, but showing a  
304 preference for lower salinity pools given the option. The water in the more saline pools is  
305 more frequently replenished (by sea-spray) than that in less saline pools, and is therefore  
306 likely to be relatively cleaner (*e.g.* less concentrated buildup of fecal material). Despite this,  
307 individuals show a clear preference for the less saline, potentially more contaminated pools; it  
308 may be that amongst these low salinity pools there is a finer scale of selection, with seals  
309 avoiding more contaminated pools, though no quantitative data are available to test this.

310         It is likely that females can actively distinguish between the fresher and more saline  
311 pools; Friedl *et al.* (1990) demonstrated that California sea lions (*Zalophus californianus*) can  
312 discriminate between freshwater and salt water at salinities at least as low as 3.6‰ (0.1M  
313 NaCl). Though there are likely some interspecific differences in gustatory threshold, this  
314 suggests that gray seals at North Rona are indeed basing their site choices partially on  
315 avoidance of high salinity areas, which exhibited salinity readings of over 10‰. Schweigert  
316 (1993) suggested that the metabolism of stored lipid reserves was sufficient to offset water  
317 losses through lactation, evaporation and urine, and proposed this as an explanation for why a  
318 highly concentrated urine or increased osmotic level in blood plasma was not found.  
319 However, the oxidation of stored lipids does not contribute to increased urinary water content  
320 (Schweigert 1993), further suggesting a likely input from exogenous water to account for  
321 additional urinary water output.

322         The evidence presented here concurs with results of previous studies (Twiss *et al.*  
323 2003) and indicates that females choose sites near to, but not necessarily within, pools as a  
324 means of addressing the pup-pool trade-off (Redman *et al.* 2001). This trade-off arises since  
325 newborn pups are vulnerable when the mother is absent whilst travelling to and from pools,  
326 for example, to attacks from gulls or starvation if permanent mother-pup separation results

327 (Redman *et al.* 2001) but pups in locations too near to pools may suffer trampling from  
328 nearby conspecifics also utilizing the pools (Twiss *et al.* 2003). Similarly, females likely  
329 choose sites at intermediate distances to access points to avoid areas directly next to access  
330 points which experience greater traffic associated with seals arriving to or leaving the colony,  
331 whilst they also avoid greater locomotory costs associated with travelling further inland  
332 (Twiss *et al.* 2003, Stephenson *et al.* 2007).

333

### 334 Change in Preferences Across the Season

335

336         The decrease in composite marginality values across the season may be informative,  
337 and is due to females being found in increasingly average sites as the season progresses. Later  
338 in the season, maps of females are likely to contain some females in late lactation that are  
339 moving to seek mating opportunities or are in the act of departing from the island. These  
340 females are likely to be less influenced by pool proximity or salinity, though we expect their  
341 contribution to the decrease in marginality values to be minimal. This is because females on  
342 North Rona typically depart rapidly after weaning, and only a small proportion (<10%) of  
343 females exhibit movements outside the home range of their local male to seek matings (Twiss  
344 *et al.* 2006).

345         The decrease in composite marginality may therefore be interpreted in one or more of  
346 three ways: (1) as the season progresses, more females choose sites with EGV values closer  
347 to the average available across the study site; (2) as the season progresses, more females are  
348 forced into more average areas by the presence of females at preferred sites; or (3) as the  
349 season progresses, fewer sites with more extreme EGV values are available (for EGVs that  
350 vary across the season *i.e.* salinity and CPOOL), with each site having EGV values closer to  
351 the global average; as a result the range of sites that females can choose from is less variable.



352 These alternative interpretations are not necessarily mutually exclusive, though for salinity  
353 there was generally greater variability, with larger variances and greater spread of values later  
354 in the season (Fig. 4, Table 2) so explanation (3) seems unlikely with regards to salinity.  
355 Furthermore, the minimum EGV values across the study area did not increase between stages  
356 within the breeding season, whilst at no point in the season did the maximum EGV values in  
357 occupied areas approach the maximum values seen across the study site, suggesting that a  
358 change in availability of preferred sites has not necessitated female movement into less  
359 preferred areas. This suggests that the decrease in marginality over each season is due to  
360 female choice or exclusion from more preferred sites, rather than declining availability of  
361 preferred sites as a result of EGV changes.

362

### 363 Broader Implications for Gray Seal and Wider Mammalian Reproductive Ecology

364

365 Throughout its range, the gray seal breeds on a variety of substrates. Given the preference for  
366 proximity to low salinity pools demonstrated here it is interesting to note that many of these  
367 substrates, such as the porous sands of Donna Nook, do not support extensive or widespread  
368 pool formation, whilst those pools that do form may be more ephemeral and spatially  
369 unpredictable than those at North Rona. This highlights the fact that these are really habitat  
370 preferences, as opposed to immutable requirements. The ability to address water deficits by  
371 drinking seawater (mariposia) has been recorded in otariids (Gentry 1981, Costa and  
372 Trillmich 1988) and phocids, including harp seals, *Pagophilus groenlandicus* (Storeheier and  
373 Nordøy 2001, How and Nordøy 2007), hooded seals, *Cystophora cristata* (Skalstad and  
374 Nordøy 2000) and harbor seals, *Phoca vitulina* (Hedd *et al.* 1995). Therefore, it is intriguing  
375 that this current study demonstrates a preference for freshwater among lactating gray seals. It  
376 is possible that, given the option, addressing a water deficit by drinking freshwater is

377 physiologically less costly, and therefore preferable. It is interesting to question what the  
378 effects are of a lack of freshwater pools on female distribution, behavior, and physiology (and  
379 therefore reproductive success), especially at sites with similar weather patterns to those at  
380 North Rona. Conditions at such sites are known to induce thermal stress (Twiss *et al.* 2002),  
381 though even gray seals in colder climates may exhibit similar habitat preferences. For  
382 example, water ingestion has even been observed at sites such as Sable Island, where gray  
383 seals eat snow and drink from tide pools (SDT, personal observation; D. J. Boness, personal  
384 communication<sup>1</sup>). Records of pinnipeds specifically ingesting freshwater are rare (*e.g.*  
385 Antarctic fur seal, *Arctocephalus gazella*, Lea *et al.* 2002), but such findings raise the  
386 question of why seals would choose to breed at sites with limited freshwater availability, and  
387 what, if any, advantages are conferred to those that drink freshwater during lactation  
388 compared to those that have access only to salt water.

389

390 Acknowledgements

391

392 JES was funded by the Grevillea Trust Scholarship at Durham University, UK. SMRU's gray  
393 seal aerial survey program is funded by NERC. Original development of the North Rona GIS  
394 was carried out during a NERC Research Fellowship to SDT (GT59401MS), and fieldwork  
395 was supported by grants from NERC (NE/G008930/1 to PPP, Lex Hiby and SDT) and the  
396 Esmée Fairbairn Foundation (08-1037 to PPP). Thanks to Gordon Smith and Bill Giles of  
397 Giles Aviation Ltd. for piloting their Piper Aztec aircraft. PPP would like to thank all  
398 involved in fieldwork. Thanks also to two anonymous reviewers and both the Editor and  
399 Associate Editor for providing valuable comments on the initial draft.

400

401

402 <sup>1</sup>Personal communication from Daryl J. Boness, University of New England, Department of  
403 Marine Science, c/o Green Acres Road, Hartford, ME, October 2013.

404

405 Literature Cited

- 406 Anderson S. and J. Harwood. 1985. Time budgets and topography: how energy reserves and  
407 terrain determine the breeding behaviour of grey seals. *Animal Behaviour* 33: 1343-1348.
- 408 Ball, J. E. and K. C. Luk. 1998. Modeling spatial variability of rainfall over a catchment.  
409 *Journal of Hydrological Engineering* 3: 122-130.
- 410 Boness, D. J. and H. James. 1979. Reproductive behaviour of the grey seal (*Halichoerus*  
411 *grypus*) on Sable Island, Nova Scotia. *Journal of Zoology* 188: 477-500.
- 412 Campagna, C. and B. J. Le Boeuf. 1988. Thermoregulatory behaviour of southern sea lions  
413 and its effect on mating strategies. *Behaviour* 107: 72–90.
- 414 Costa, D. P. and F. Trillmich. 1988. Mass changes and metabolism during the perinatal fast: a  
415 comparison between Antarctic (*Arctocephalus gazella*) and Galapagos fur seals  
416 (*Arctocephalus galapagoensis*). *Physiological Zoology* 61: 160–169.
- 417 Friedl, W.A., P.E. Nachtigall, P.W.B. Moore, N.K.W. Chun, J.E. Haun, R.W. Hall and J.L.  
418 Richards. 1990. Taste reception in the pacific bottlenose dolphin (*Tursiops truncatus gilli*)  
419 and the California sea lion (*Zalophus californianus*). Pages 447-454 in J.A. Thomas and R.  
420 Kastelein, eds. *Sensory abilities of cetaceans*. Plenum Press, New York, USA.
- 421 Gentry, R. L. 1973. Thermoregulatory behaviour of eared seals. *Behaviour* 46: 73-93.
- 422 Gentry, R. L. 1981. Seawater drinking in eared seals. *Comparative Biochemistry and*  
423 *Physiology Part A* 68: 81–86.
- 424 Gu, W. and R. K. Swihart. 2004. Absent or undetected? Effects of non-detection of species  
425 occurrence on wildlife habitat models. *Biological Conservation* 116: 195-203.
- 426 Hedd, A., R. Gales and D. Renouf. 1995. Use of temperature telemetry to monitor ingestion  
427 by a harbour seal mother and her pup throughout lactation. *Polar Biology* 15: 155-160.
- 428 Hiby, A. R., D. Thompson and A. J. Ward. 1988. Census of grey seals by aerial photographs.  
429 *Photogrammetric Record* 12: 589-594.

430 Hiby, L., W. D. Paterson, P. Redman, J. Watkins, S. D. Twiss and P. Pomeroy. 2012.  
431 Analysis of photo-ID data allowing for missed matches and individuals identified from  
432 opposite sides. *Methods in Ecology and Evolution*, DOI: 10.1111/2041-210x.12008

433 Hirzel, A. H., V. Helfer and F. Metral. 2001. Assessing habitat-suitability models with a  
434 virtual species. *Ecological Modelling* 145: 111-121.

435 Hirzel, A. H., J. Hausser, D. Chessel and N. Perrin. 2002. Ecological-niche factor analysis:  
436 How to compute habitat-suitability maps without absence data? *Ecology* 83: 2027-2036.

437 Hirzel, A. H., J. Hausser and N. Perrin. 2007. Biomapper 4.0. Laboratory for Conservation  
438 Biology, Department of Ecology and Evolution, University of Lausanne, Switzerland. URL:  
439 <http://www2.unil.ch/biomapper>.

440 How O. J. and E. S. Nordøy. 2007. Seawater drinking restores water balance in dehydrated  
441 harp seals. *Journal of Comparative Physiology B* 177: 535-542.

442 Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbour Symposium on*  
443 *Quantitative Biology* 22: 415-427.

444 Irving, L., K. C. Fisher, and F. D. MacIntosh. 1935. The water balance of a marine mammal,  
445 the seal. *Journal of Cellular and Comparative Physiology* 6: 387-391.

446 Iverson, S. J., Bowen, W.D., Boness, D.J. and Oftedal, O.T. (1993). The effect of maternal  
447 size and milk energy input on pup growth in grey seals (*Halichoerus grypus*). *Physiological*  
448 *Zoology* 66: 61-88.

449 Kéry, M. 2002. Inferring the absence of a species—a case study of snakes. *Journal of*  
450 *Wildlife Management* 66: 330–338.

451 Kooyman, G. L. and C. M. Drabek. 1968. Observations on milk, blood, and urine  
452 constituents of the Weddell seal. *Physiological Zoology* 41: 187-194.

453 Lea, M. A., F. Bonadonna, M. A. Hindell, C. Guinet and S. D. Goldsworthy. 2002. Drinking  
454 behaviour and water turnover rates of Antarctic fur seal pups: implications for the estimation

455 of milk intake by isotopic dilution. *Comparative Biochemistry and Physiology A* 132: 321-  
456 331.

457 McCafferty, D. J., C. Gilbert, W. Paterson, P. P. Pomeroy, D. Thompson, J. I. Currie and A.  
458 Ancel. 2011. Estimating metabolic heat loss in birds and mammals by combining infrared  
459 thermography with biophysical modelling. *Comparative Biochemistry and Physiology, A*  
460 158: 337-345.

461 Mills, J. P., I. Newton and S. D. Twiss. 1997. Photogrammetry from archived digital imagery  
462 for seal monitoring. *Photogrammetric Record* 15: 715-724.

463 Øritsland, N. A., D. M. Lavigne and K. Ronald. 1978. Radiative surface temperatures of harp  
464 seals. *Comparative Biochemical Physiology* 61: 9-12.

465 Ortiz, C. L., D. Costa and B. J. Le Boeuf. 1978. Water and energy flux in elephant seal pups  
466 fasting under natural conditions. *Physiological Zoology* 51: 166-178.

467 Paterson, W., C. E. Sparling, D. Thompson, P. P. Pomeroy, J. I. Currie and D. J. McCafferty.  
468 2011. Seals like it hot: Changes in surface temperature of harbour seals (*Phoca vitulina*) from  
469 late pregnancy to moult. *Journal of Thermal Biology* 37: 454-461.

470 Pomeroy, P. P., S. S. Anderson, S. D. Twiss and B. J. McConnell. 1994. Dispersion and site  
471 fidelity of breeding females grey seals (*Halichoerus grypus*) on North Rona, Scotland.  
472 *Journal of Zoology* 233: 429-447.

473 Pomeroy, P. P., M. A. Fedak, P. Rothery and S. Anderson. 1999. Consequences of maternal  
474 size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland.  
475 *Journal of Animal Ecology* 68: 235-253.

476 Pomeroy, P. P., S. D. Twiss and C. D. Duck. 2000. Expansion of a grey seal (*Halichoerus*  
477 *grypus*) breeding colony: changes in pupping site use at the Isle of May, Scotland. *Journal of*  
478 *Zoology* 250: 1-12.

479 Pomeroy, P. P., S. Smout, S. Twiss, S. Moss and R. King. 2010. Low and delayed  
480 recruitment at two grey seal breeding colonies in the UK. *Journal of Northwest Atlantic*  
481 *Fisheries Science* 42: 125-133.

482 Redman, R., P. P. Pomeroy and S. D. Twiss. 2001. Grey seal maternal attendance patterns are  
483 affected by water availability on North Rona, Scotland. *Canadian Journal of Zoology* 79:  
484 1073 – 1079.

485 Reilly, J. J., M. A. Fedak, D. H. Thomas, W. A. A. Coward and S. S. Anderson. 1996. Water  
486 balance and the energetics of lactation in grey seals (*Halichoerus grypus*) as studied by  
487 isotopically labelled water methods. *Journal of Zoology* 238: 157-165.

488 Riedman, M. 1990. *The Pinnipeds. Seals, sea lions and walruses*. University of California  
489 Press, Berkeley and Los Angeles, California, USA.

490 Ronald, K., R. McCarter and L. J. Selley. 1977. Venous circulation in the harp seal  
491 (*Pagophilus groenlandicus*). Pages 235-270 in R.J. Harrison, ed. *Functional anatomy of*  
492 *marine mammals*. Volume 3. Academic Press, London, UK.

493 Schweigert, F. J. 1993. Effects of fasting and lactation on blood chemistry and urine  
494 composition in the grey seal (*Halichoerus grypus*). *Comparative Biochemistry and*  
495 *Physiology A* 105: 353-357.

496 Skalstad, I. and E. S. Nordøy. 2000. Experimental evidence of seawater drinking in juvenile  
497 hooded (*Cystophora cristata*) and harp seals (*Phoca groenlandica*). *Journal of Comparative*  
498 *Physiology B* 170: 395–401.

499 Stephenson, C. M., J. Matthiopoulos and J. Harwood. 2007. Influence of the physical  
500 environment and conspecific aggression on the spatial arrangement of breeding grey seals.  
501 *Ecological Informatics* 2: 308-317.

502 Stewart, J. E. 2013. Fine scale determinants of female grey seal (*Halichoerus grypus*)  
503 pupping site and habitat preferences at North Rona, Scotland. MSc thesis, Durham  
504 University, Durham, U.K. 229 pp. Available at <http://etheses.dur.ac.uk/7296>.

505 Storeheier, P. V. and E. S. Nordøy. 2001. Physiological effects of seawater intake in adult  
506 Harp seals during phase I of fasting. *Comparative Biochemistry and Physiology* 128A: 307–  
507 315.

508 Twiss, S. D., A. Caudron, P. P. Pomeroy, C. J. Thomas and J. P. Mills. 2000. Finescale  
509 topographical correlates of behavioural investment in offspring by female grey seals,  
510 *Halichoerus grypus*. *Animal Behaviour* 59: 327-338.

511 Twiss, S. D., C. J. Thomas and P. P. Pomeroy. 2001. Topographic spatial characterization of  
512 grey seal *Halichoerus grypus* breeding habitat at a sub-seal size spatial grain. *Ecography* 24:  
513 257-266.

514 Twiss, S. D., N. C. Wright and N. Dunstone. 2002. Behavioural evidence of thermal stress  
515 from overheating in UK breeding seals. *Marine Mammal Science* 18: 455-468.

516 Twiss, S. D., C. D. Duck and P. P. Pomeroy. 2003. Grey seal (*Halichoerus grypus*) pup  
517 mortality not explained by local breeding density on North Rona, Scotland. *Journal of*  
518 *Zoology* 259: 83-91.

519 Twiss, S. D., P. P. Pomeroy, J. A. Graves and V. F. Poland. 2006. Finding fathers – spatio-  
520 temporal analysis of paternity assignment in grey seals (*Halichoerus grypus*). *Molecular*  
521 *Ecology* 15: 1939-1953.

522 Twiss, S. D., C. J. Thomas, V. F. Poland and J. A. Graves. 2007. The impact of climatic  
523 variation on the opportunity for sexual selection. *Biology Letters* 3: 12-15.



524 Wolf, J. B. W., G. Kauermann and F. Trillmich. 2005. Males in the shade: habitat use and  
525 sexual segregation in the Galápagos sea lion (*Zalophus californianus wollebaeki*). Behavioral  
526 Ecology and Sociobiology 59: 293-302.

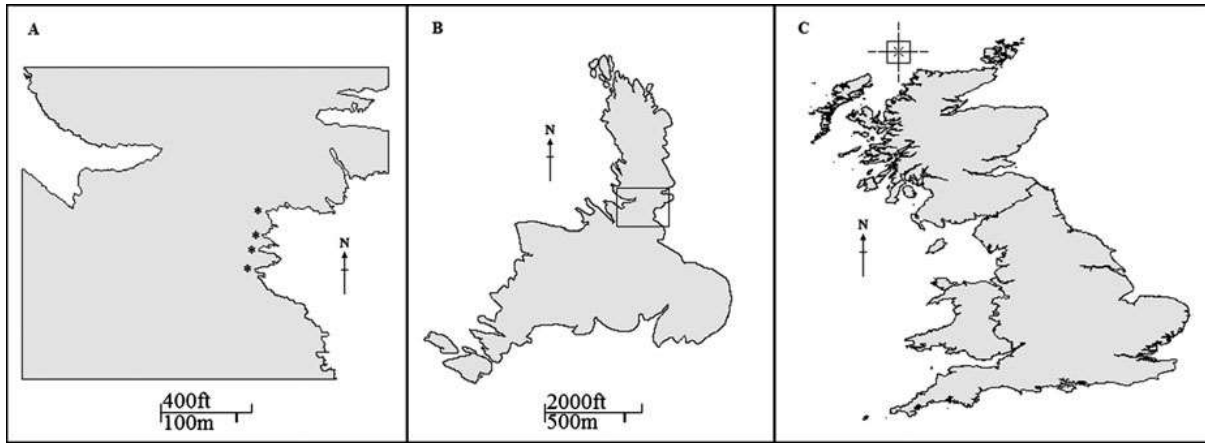


Figure 1: (A) An outline of the Study Site at North Rona; asterisks (\*) indicate the location of the main access gullies to and from the sea (B) Location of the Study Site in relation to the rest of North Rona and (C) relative to the rest of the United Kingdom, indicated by crosshairs at  $59.1^{\circ}$  N,  $5.83^{\circ}$  W. Areas of land shaded gray. A: outline of Digital Terrain Model of the study site (Stewart, 2013), B: adapted from Google Maps outline view of North Rona (Stewart, 2013), C: adapted from a shapefile of the UK coastline (Stewart, 2013).

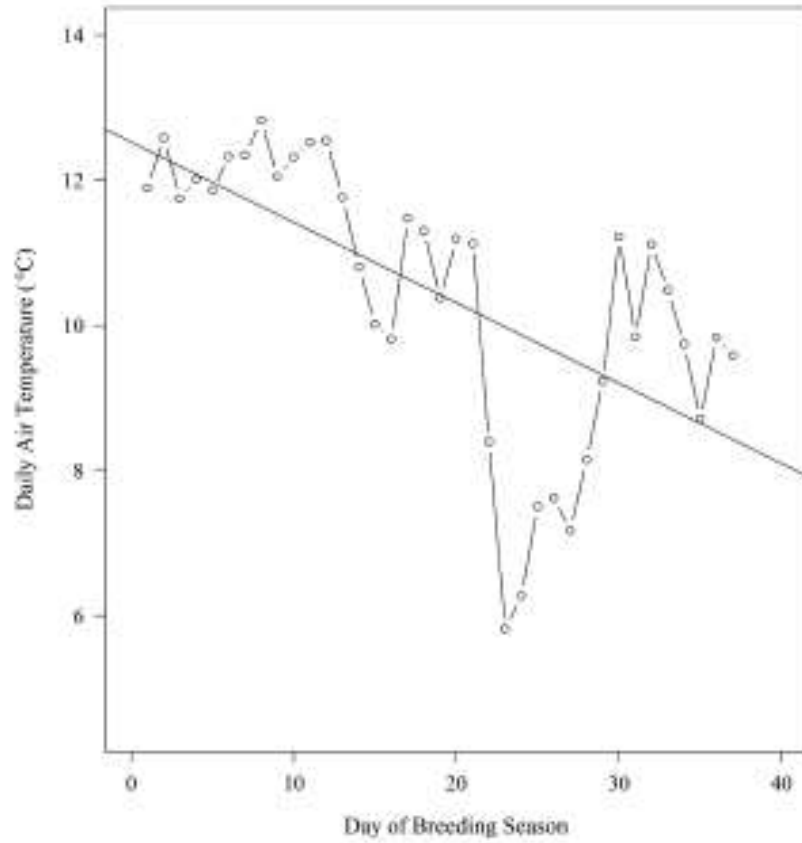


Figure 2: Change in air temperature (°C) over the 2010 breeding season. Day 1 = 28 September. Spearman's rank correlation demonstrates a negative correlation between air temperature and day of breeding season ( $r = -0.746$ ,  $n = 36$ ,  $P < 0.001$ ).

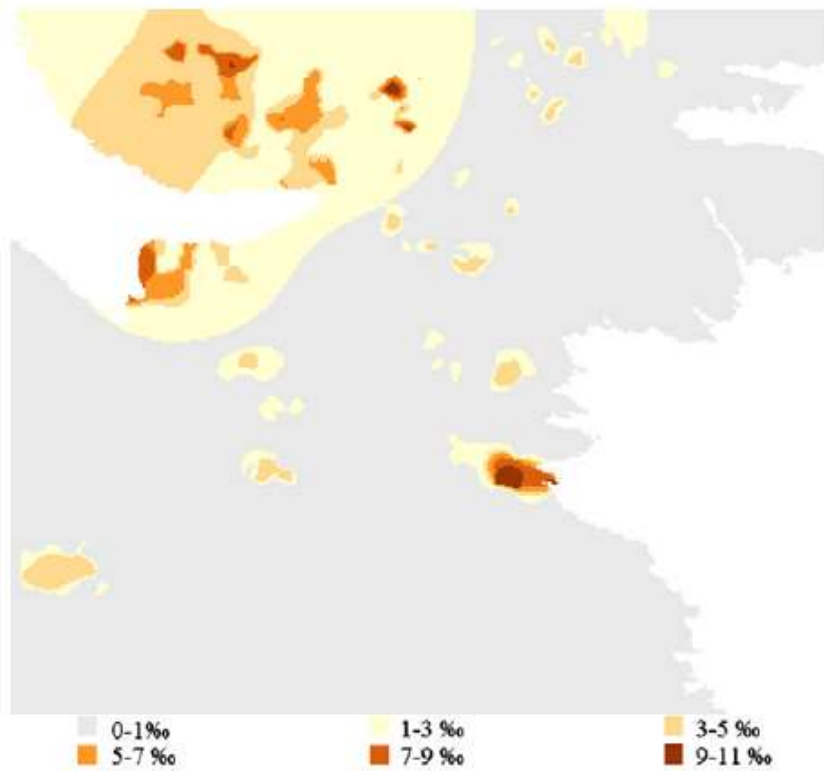
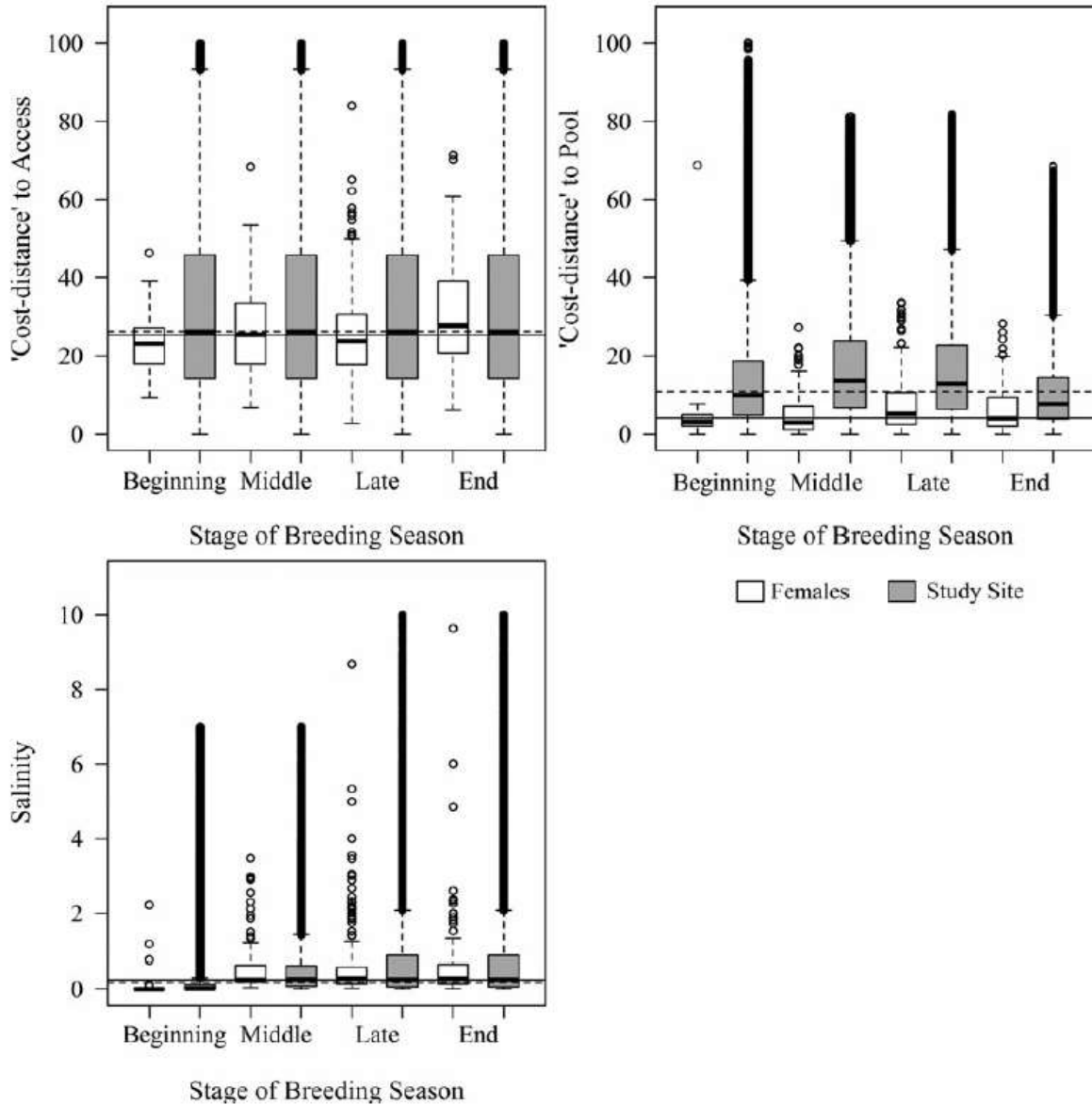


Figure 3: Distribution of salinity values (‰) across the study site on 03 November 2010 (“End” 2010). Dark shades represent high salinity whilst the lower values are represented by lighter shades. Pools are present across the study site, and are not restricted to colored areas.



**Figure 4:** CACC, CPOOL and salinity (%) values at female locations and across the study site in all four stages of the 2010 breeding season. The horizontal dashed line represents the study site (global) median for all focal dates in 2010, whilst the solid horizontal line represents the median across all four focal dates for female locations. Outliers have been included as these represent real measurements from within the study site at locations accessible to seals.

Table 1: Numbers of females in the study site on focal dates, and composite marginality, specialization and tolerance values for females on all focal dates.

<b>Parameter</b>	<b>Stage of Breeding Season</b>	
<b>Number of females</b>	Beginning	48
	Mid	135
	Late	176
	End	106
<b>Marginality (M)</b>	Beginning	0.479
	Mid	0.472
	Late	0.355
	End	0.221
<b>Specialization (S)</b>	Beginning	5.951
	Mid	1.856
	Late	1.557
	End	1.434
<b>Tolerance (T)</b>	Beginning	0.168
	Mid	0.539
	Late	0.642
	End	0.697

**Table 2:** Summary statistics for CACC, CPOOL and salinity values at female locations and across the study site in all four stages of the 2010 breeding season; CACC = “Cost-distance” to nearest access; CPOOL = “Cost-distance” to nearest pool; SAL = Salinity.

	Females (used habitat)				Study Site (available habitat)			
	Max.	Min.	Median	IQR	Max.	Min.	Median	IQR
<b>(a) CACC</b>								
<b>Beginning</b>	46.28	9.25	23.17	9.52	100.00	0.00	26.17	31.66
<b>Mid</b>	68.38	6.76	25.39	15.57	100.00	0.00	26.17	31.66
<b>Late</b>	83.92	2.64	23.73	12.98	100.00	0.00	26.17	31.66
<b>End</b>	71.42	6.06	27.69	18.51	100.00	0.00	26.17	31.66
<b>(b) CPOOL</b>								
<b>Beginning</b>	7.62	0.00	3.08	2.86	100.00	0.00	9.92	13.82
<b>Mid</b>	27.26	0.00	2.90	6.05	81.28	0.00	13.57	17.09
<b>Late</b>	33.65	0.00	5.14	8.16	81.71	0.00	12.90	16.33
<b>End</b>	28.26	0.00	4.01	7.29	68.48	0.00	7.71	10.63
<b>(c) SAL</b>								
<b>Beginning</b>	1.17	0.00	<0.01	<0.01	7.00	0.00	0.02	0.12
<b>Mid</b>	3.47	0.04	0.25	0.45	7.00	0.00	0.26	0.54
<b>Late</b>	8.67	0.02	0.27	0.45	10.00	0.00	0.25	0.81
<b>End</b>	9.63	0.01	0.27	0.51	10.00 <sup>†</sup>	0.00	0.25	0.81

<sup>†</sup>The maximum value for salinity was not equal to the maximum measured value (32.00) due to the interpolation technique used to create the salinity surface, which reduced the maximum salinity across the study site.

**Table 3:** Coefficients of Eco-Geographical Variables (EGVs) on each ENFA (Ecological Niche Factor Analysis) factor for female gray seals on each focal day. The marginality factors (M) explain 100% of the marginality and a certain amount of specialization; “%S” indicates the amount of specialization (S) accounted for by each factor; CACC = “Cost-distance” to nearest access; CPOOL = “Cost-distance” to nearest pool; SAL = Salinity. Bold numbers indicate the EGV with the largest coefficient value on each factor.

Stage of Breeding Season	ENFA Output	EGV			
		CACC <sup>3</sup>	CPOOL <sup>3</sup>	SAL	(% S)
<b>Beginning</b>	<i>coM</i> <sup>1</sup>	-0.402	<b>-0.843</b>	-0.357	60
	<i>coS1</i> <sup>2</sup>	0	0.376	<b>0.926</b>	31
	<i>coS2</i> <sup>2</sup>	<b>0.872</b>	0.472	0.132	9
<b>Middle</b>	<i>coM</i> <sup>1</sup>	-0.269	<b>-0.963</b>	0	49
	<i>coS1</i> <sup>2</sup>	<b>0.957</b>	0.271	0.104	39
	<i>coS2</i> <sup>2</sup>	0.148	0	<b>0.989</b>	12
<b>Late</b>	<i>coM</i> <sup>1</sup>	-0.365	<b>-0.921</b>	-0.138	34
	<i>coS1</i> <sup>2</sup>	<b>0.928</b>	0.371	0	46
	<i>coS2</i> <sup>2</sup>	0	0.16	<b>0.987</b>	20
<b>End</b>	<i>coM</i> <sup>1</sup>	-0.131	<b>-0.973</b>	-0.191	37
	<i>coS1</i> <sup>2</sup>	<b>0.991</b>	0.132	0	46
	<i>coS2</i> <sup>2</sup>	0.133	-0.209	<b>0.969</b>	16

<sup>1</sup> Positive marginality coefficients indicate that the species was found in locations with higher than average values whilst negative coefficients indicate lower than average EGV values at species locations. A value of 0 indicates no significant differentiation from the global mean.

<sup>2</sup> Specialization factors (S) one and two (S1 and S2) convey niche breadth. There are two specialization factors because one factor is extracted for each of the three EGVs, one of which is the marginality factor. S will be > 0 whenever female seals were found to occupy a narrower range of conditions than was available across the study site; the greater the absolute value of the coefficient, the more restricted the females’ range on the corresponding EGV.

<sup>3</sup> Avoidance of large values of “cost-distance” to a feature (indicated by negative marginality coefficients) may be understood as a preference for proximity to this feature.



**Table 4:** Eco-Geographical Variable (EGV) contributions to female composite marginality and specialization throughout 2010. CACC = Cost-distance to nearest access; CPOOL = Cost-distance to nearest pool; SAL = Salinity. Bold numbers indicate the EGV with the largest contribution to each factor. Absolute values only reported, sign is unimportant to interpretation.

Stage of Breeding Season	ENFA Output	EGV		
		CACC	CPOOL	SAL
Beginning	$M^1$	0.402	<b>0.843</b>	0.357
	$S^2$	35.111	<b>70.527</b>	54.634
Middle	$M^1$	0.269	<b>0.963</b>	0.029
	$S^2$	5.416	<b>5.969</b>	1.792
Late	$M^1$	0.365	<b>0.921</b>	0.138
	$S^2$	<b>4.037</b>	3.770	1.847
End	$M^1$	0.131	<b>0.973</b>	0.191
	$S^2$	<b>3.268</b>	2.836	1.431

<sup>1</sup> Absolute values for EGV contributions to marginality have been reported; a higher  $coM$  indicates a greater contribution to  $M$  by that EGV whilst a value of 0 indicates no significant difference between the mean at occupied sites and the global mean.

<sup>2</sup> Specialization factor, which indicates how narrow the range of conditions occupied by the species is (essentially niche width).  $S$  varies between 1 and infinity and will exceed unity whenever female gray seals were found to occupy a narrower range of conditions than was available across the study site; the higher this value, the more restricted the females' range on the corresponding EGV.