

1 Perturbation drives changing metapopulation dynamics in a top
2 marine predator

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27 ELC, OEG, AH, AO, DJFR designed the research, AO, AH, DJFR performed research, ELC,
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29

30 **ABSTRACT: 200 words**

31 Metapopulation theory assumes a balance between local decays/extinctions and local
 32 growth/new colonisations. Here we investigate whether recent population declines across part of
 33 the UK harbour seal range represent normal metapopulation dynamics or are indicative of
 34 perturbations potentially threatening the metapopulation viability, using 20 years of population
 35 trends, location tracking data (n=380), and UK-wide, multi-generational population genetic data
 36 (n=269). Firstly, we use microsatellite data to show that two genetic groups previously identified
 37 are distinct metapopulations; northern and southern. Then, we characterise the northern
 38 metapopulation dynamics in two different periods, before and after the start of regional declines
 39 (pre-/peri-perturbation). We identify source-sink dynamics across the northern metapopulation,
 40 with two putative source populations apparently supporting three likely sink populations, and a
 41 recent metapopulation-wide disruption of migration coincident with the perturbation. The northern
 42 metapopulation appears to be in decay, highlighting that changes in local populations can lead to
 43 radical alterations in the overall metapopulation's persistence and dynamics.

44

45 **INTRODUCTION**

46

47 The persistence of spatially-distributed species depends on aspects of local population dynamics
 48 and on dispersal (1). Spatial management of a species therefore needs to consider both
 49 processes simultaneously. The metapopulation paradigm, where local populations are viewed as
 50 relatively discrete spatial entities that interact through migration, has proven very useful in
 51 understanding the interplay between dynamics and connectivity (dispersal) in a wide range of
 52 species including plants, amphibians, insects, birds, fish, and mammals (2–4). As such, the
 53 metapopulation approach is being increasingly applied to management in both the terrestrial and
 54 marine environments (3,5).

55

56 The dynamics of metapopulations are influenced by natural and anthropogenic factors, such as
 57 density dependent natal dispersal and migration rates; (6–9); habitat connectivity, loss and
 58 fragmentation (9,10); and environmental heterogeneity (7,11). At a regional level, it is the balance
 59 between local births and deaths, combined with net migration, which drives local population
 60 dynamics and persistence. Highly variable habitat quality among patches can also lead to source-
 61 sink dynamics (6,12,13). The key idea is that in good quality regions, mortality is lower than
 62 reproduction. Surplus individuals from these 'source' populations emigrate to lower quality
 63 regions, such that even if mortality is higher than natality, these 'sink' populations can persist.
 64 Source-sink metapopulations are of particular interest because they are very susceptible to the
 65 effects of localised but abrupt perturbations affecting source populations, which can lead to
 66 overall metapopulation decline and eventual extinction (14).

67

68 An important implication of metapopulation theory is that, in the absence of exogenous
 69 perturbations, a species may persist regionally despite some local population decay and
 70 extinctions. A balance between these local decays/extinctions and local growth/new colonisations
 71 is expected to maintain the overall metapopulation. Similarly, source-sink dynamics can support
 72 sink populations larger than their source over evolutionary timeframes (13). Therefore, a local
 73 population decline or extinction may be simply the manifestation of normal metapopulation
 74 dynamics but may also indicate more widespread issues with metapopulation health, particularly
 75 when sudden local population declines involve previously stable or growing source populations.

76

77 A prime example of changing dynamics in a metapopulation is the UK harbour seal (*Phoca*
 78 *vitulina*), which has been monitored for decades to provide regional population trends, local
 79 movement and genetic datasets (15–18). The UK-wide abundance of harbour seals is currently
 80 42,100 seals (95% CI: 34,500 – 52,300), which is comparable to the estimate 20 years ago at
 81 45,550 (95% CI: 37,250 – 60,750) (17). In contrast to this stable overall picture, there have been
 82 dramatic declines in abundance in key small areas (e.g., 95% decline between 2002 and 2017 in

83 East Scotland) as well as in large regions, such as Shetland (40% decline between 2001 and
84 2006) and the North Coast & Orkney (85% decline between 1997 and 2016; Figure 1). The
85 reasons for these declines, whilst the populations around the majority of the UK are stable or
86 increasing, are unknown. Factors currently being studied include increased indirect and direct
87 competition (including predation) by grey seals (19) or other marine mammals and exposure to
88 toxins from harmful algae (20). Harbour seal populations exhibit a combination of structure and
89 connectivity that make them suitable for metapopulation analyses. The species' central place
90 foraging tactics mean that individuals generally feed within 100 km of sites at which they haul out
91 (where they are counted) between foraging trips (16), yet there is evidence for large scale
92 movements between haul out sites, and between haul-out and breeding sites; over 50 km apart
93 (16,18,21–23).

94
95 Here we test the hypothesis that the observed regional declines in the UK harbour seal are part of
96 the normal extinction-colonisation dynamics of a single metapopulation, or alternatively, a
97 response to a major perturbation driving changes in metapopulation dynamics. In doing so, we
98 identify which local populations are likely to be sources or sinks. Ideally, metapopulation
99 connectivity and source-sink dynamics would be determined using direct measures of
100 demographic parameters and connectivity among and between local populations, respectively
101 (i.e., survival, reproduction, recruitment and dispersal). However, estimates of these demographic
102 parameters are not available for UK harbour seals, and typically require datasets that follow
103 individuals throughout their lifespan (24), precluding their estimation in a timeframe relevant for
104 management of the current decline. In this context, there are two main difficulties that make
105 assessing source-sink metapopulation dynamics in long-lived species challenging. Firstly, there is
106 no single approach that can determine whether or not movement of individuals among local
107 populations contributes to local dynamics on the short-time scales relevant for conservation.
108 Satellite tracking data can be used to elucidate the level of movement between local populations
109 but cannot determine if dispersing individuals leave descendants in the new location. Genetic
110 data, on the other hand, can estimate per generation migration rates representing real
111 contributions towards local demography but for long-lived species these estimates may cover a
112 period of several years, and therefore may be too coarse-grained to detect sudden changes in
113 migration patterns following a perturbation. Similarly, distinguishing between source and sink
114 populations based on long-term population trends is unfeasible because a sink population may
115 exhibit stable or even increasing census sizes due to the influx of migrants from a source
116 population. On the other hand, genetic data can provide estimates of “retention” (proportion of
117 individuals that remain in their local population), which to some extent are indicative of local
118 recruitment but cannot determine if local birth rate exceeds local death rates, as expected in an
119 “absolute” sink (c.f. 25). In order to make progress despite these challenges, we adopt a
120 framework, bringing together genetic, location tracking and population trend data, to assess
121 metapopulation identity and connectivity in addition to establishing source-sink dynamics.

122
123 We first use population genetics approaches (genetic differentiation index) to establish if all local
124 populations of harbour seals are members of the same metapopulation. Having established that
125 South Eastern UK local populations belong to a metapopulation that extends beyond the British
126 Isles we focus on those found in the North Western and North Eastern UK, all belonging to a
127 separate metapopulation. Specifically, we characterise metapopulation connectivity and source-
128 sink dynamics of local populations in two different time periods, before and after the start of the
129 regional declines (henceforth referred to as pre- and peri-perturbation). Thus, we assess the
130 degree to which local populations are demographically connected by estimating per-generation
131 migration rates pre- and peri-perturbation using multilocus-genotype methods. We seek further
132 support for these results using satellite tracking data providing estimates of short-term movement
133 of adults (>1 year old, non-pups) and pups. Next, we identify putative source populations based
134 on genetic data as those that have both high internal recruitment and display emigration. We then
135 use population trends to further support their “source” status as they should also be stable or
136 growing. Finally, we use a similar procedure to identify putative sink populations as those that are

137 net recipients of immigrants and still declining, in which case mortality is likely exceeding
138 reproduction.
139 The integration of the three data types – genetics, tracking and population trend – allow us to
140 evaluate the viability of putative source and sink populations in the context of changes in
141 connectivity pre- and peri-perturbation and overall trends in abundance. Specifically, we discuss
142 whether or not local population declines and changes in migration patterns are consistent with
143 overall metapopulation persistence or they are indicative of metapopulation decay and potential
144 regional extinction.

145 146 **RESULTS**

147 *Dataset summary and grouping definitions*

148 Our final dataset comprises microsatellite genotypes and animal location tracking data from 269
149 and 380 harbour seals, respectively (Table 1). These data were collected from geographical units
150 known as Seal Management Units (SMUs); eleven SMUs covering the UK were established using
151 harbour seal haul out clusters identified from aerial surveys, and tracking and photo-ID studies
152 (16,21,22). Here we primarily consider the SMUs that hold significant harbour seal populations
153 (>100 individuals counted on surveys) (Fig 1, Table 1). We discuss the results in the context of
154 three different types of groupings: metapopulations, metapopulation subunits called local
155 populations, and SMUs.

156 157 *The UK harbour seal comprises two distinct metapopulations*

158 The pattern of genetic diversity and differentiation, as well as tracking data, suggests that the UK
159 harbor seal SMUs fall into two distinct metapopulations; a northern and a southern. Firstly, the
160 Southeast England SMU showed high and significant levels of genetic differentiation against all
161 other UK harbour seal SMUs ($F_{ST} > 0.2$; Table S1). In contrast, Southeast England showed only
162 weak differentiation against the European samples. The *BayesAss* results confirmed this, with
163 estimates of recent migration between components of the two metapopulations typically being $\leq 1\%$
164 (Table S2 and S3), consistent with demographic independence (26). Therefore, we consider
165 Southeast England and continental Europe part of one southern metapopulation, and all other
166 SMUs part of a northern metapopulation (Northern Ireland and Scottish SMUs) and focus on the
167 latter.

168
169 There was significant genetic differentiation between most of the UK harbour seal SMUs within the
170 northern metapopulation based on pairwise F_{ST} values, although this was not as substantial (F_{ST}
171 from 0.02 to 0.14; Table S1) as between the two putative metapopulations (F_{ST} from 0.18 to 0.30;
172 Table S1). The exceptions to this general pattern were that there was no significant difference
173 between (a) West Scotland and the Western Isles SMUs, which were pooled to form a Northwest
174 local population, and (b) North Coast & Orkney SMU, and the neighbouring Moray Firth SMU, which
175 were pooled to form a Moray Firth, North Coast & Orkney (MFNCO) local population. Thus, the F_{ST}
176 estimates suggest a total of five local populations within the northern metapopulation: Northern
177 Ireland, Northwest, MFNCO, Shetland, and East Scotland. Different haul out sites within SMUs and
178 across SMU subunits (e.g., south and central West Scotland) did not show significant differentiation
179 (Table S1). Although no genetic samples were available from Southwest Scotland SMU, we
180 assume this SMU is part of the Northwest local population: there are similar population trends and
181 no spatial differentiation in haul-out clusters between Southwest and West Scotland SMUs (Figure
182 1).

183
184 The discriminant analysis of principal components (DAPC) clearly separated the northern
185 metapopulation SMUs from Southeast England and Continental Europe along linear discriminant
186 1 (Figure 2). The SMUs within the northern metapopulation were characterised by a pattern of
187 isolation-by-distance along linear discriminant 2, but also indicated some east-west division. The

188 isolation by distance was confirmed by a statistically significant ($p < 0.001$) correlation between F_{ST}
 189 and 'at-sea' distances between haul-out sites (see Supplementary Information (SI) Figure S1).

190
 191 The distinctiveness of the northern and southern metapopulations was also supported by tracking
 192 data from 334 non-pup seals, showing no movement between metapopulations, but some
 193 movement within (Table S4 and S5). For instance, of the 83 individuals tagged in Southeast
 194 England, two travelled to the continent but none to the northern metapopulation. Likewise, in the
 195 northern metapopulation, movements were detected among several haul-outs and SMUs, as
 196 described below, but there was no movement to the southern metapopulation. Overall, these
 197 results provide strong support for defining a northern metapopulation, which excludes the
 198 Southeast England SMU.

199
 200 *Finer temporal scale connectivity of Northern UK harbour seal metapopulation*

201 We assessed connectivity of local populations and SMUs from genetic, movement and
 202 demographic perspectives, using the microsatellites, location tracking, and population trends,
 203 respectively.

204
 205 **Genetic estimates of demographic connectivity:** As the Southeast England SMU and European
 206 samples appear part of a distinct metapopulation, we consider here a *BayesAss* analysis with the
 207 harbour seal dataset covering only the northern metapopulation (Table S6).

208
 209 Overall, migration connects the northern local populations, however, in many cases connectivity
 210 has sharply reduced in the peri-perturbation generation compared with the pre-perturbation
 211 generation. This is evidenced by a lack of first-generation migrants, but a substantial proportion of
 212 individuals with migrant ancestry, during the peri-perturbation period (i.e. descended from parents
 213 that migrated before the perturbation). Median estimates of recent gene flow (past two
 214 generations), inferred from the *BayesAss* analysis, are shown in Table S6. Convergence was
 215 shown by traces and similar results across independent runs, with effective sample sizes for each
 216 parameter > 250 .

217
 218 The Northern Ireland and Northwest local populations are highly connected, as shown by the high
 219 proportion of immigrants from the latter (0.26, 95% HPD:0.19 - 0.31), and the substantial degree of
 220 recent migration based on individual ancestry. In contrast, the Northwest local population appears
 221 to be mostly local recruits, based on individual ancestry data and the high proportion of non-
 222 migrants (0.91, 95% HPD:0.85 - 0.97).

223
 224 There is indication that the MFNCO local population has been a source of migrants to the Northwest
 225 local population based on ancestry and migration rates (0.05, 95% HPD:0.01 - 0.12), but with a
 226 decline from four likely second-generation migrants to two first-generation migrants in the past two
 227 generations. This suggests a decline in migration peri-perturbation compared with pre-perturbation.
 228 The MFNCO local population also has a high proportion of non-migrants (0.95, 95% HPD:0.88 -
 229 0.99) and no evidence of immigrants in the past one generation. In contrast, there is evidence of
 230 past gene flow from the East Scotland local population based on the migrant ancestry of two
 231 individuals. Furthermore, the MFNCO local population is contributing migrants to both the Shetland
 232 (0.20, 95% HPD:0.11 - 0.29) and East Scotland local populations (0.09, 95% HPD:0.01 - 0.18)
 233 based on migration rates over the past 2 generations. For East Scotland, the gene flow from the
 234 MFNCO local population in the current generation shows a decrease from the previous generation,
 235 again supporting a decline in migration peri-perturbation compared with pre-perturbation. For
 236 Shetland, there is also evidence of migration from the Northwest local population, as indicated by
 237 individual ancestry data and relatively high migration in recent years (0.08, 95% HPD:0.01 - 0.16),
 238 despite a moderate and significant F_{ST} value of 0.07 between the two regions.

239
 240 **Regional patterns of movement:** The location tracking data of seals (non-pups) in the non-
 241 breeding season broadly supports the distinctiveness of the five local populations; in total, 21

242 (6.3%) tagged seals moved between SMUs, of which only one (<1%) moved local populations.
 243 None of the individuals tagged in Northern Ireland ($n = 33$), Shetland ($n = 14$) or East Scotland (pre
 244 or peri-perturbation; $n = 33$) moved between local populations. There was movement between the
 245 three SMUs comprising the Northwest local population, particularly between West Scotland and
 246 Southwest Scotland (Table S5). There was also significant movement within the MFNCO local
 247 population, from the Moray Firth to North Coast & Orkney ($n = 4/39$), with 1/53 (1/34 tagged in
 248 southern Orkney) going in the opposite direction. The only movement between local populations
 249 was of one individual tagged in 2003 in northern Orkney, MFNCO local population (of 19), which
 250 moved to Shetland.

251
 252 Pup tracking data indicated a higher degree of connectivity between SMUs and local populations
 253 compared with non-pups, as expected from the dispersing demographic class; in total 11/46 (26%)
 254 moved SMUs, of which 9 (19%) changed local population. Of the 24 pups tagged in Lismore, West
 255 Scotland SMU in the Northwest local population, 4 (17%) moved SMUs within the local population
 256 (2 to Southwest Scotland and 2 to Western Isles), and 1 (4%) moved to Ireland. The latter pup
 257 moved to a region from which we do not have any genetic samples so cannot assess the location's
 258 position in the metapopulation. However, as the seal moved to within 50 miles of the Northern Irish
 259 border its movement could represent a shift between local populations. Of the 22 pups tagged in
 260 Orkney, MFNCO local population, 7 (27%) moved to Shetland and 1 (4%) moved to West Scotland
 261 (Northwest local population).

262
 263 **Demographic trends:** We looked at demographic connectivity by assessing published trends in
 264 population trajectories and identifying which SMUs have similar trends. The Northwest local
 265 population SMUs have shown stable population trends over the time period covered by the study
 266 (Western Isles, West and Southwest Scotland). However, Northern Ireland, a separate local
 267 population, has exhibited a constant gradual decline (Figure 1, Table 2). The SMUs in the MFNCO
 268 local population underwent a sudden change in dynamics in the early 2000s. For instance, North
 269 Coast & Orkney were stable until 2001, whereas the subsequent survey in 2006 showed a dramatic
 270 decline in abundance. Moray Firth stabilised in the early 2000s after a period of decline. Both East
 271 Scotland and Shetland underwent a similar change in dynamics in the early 2000s, but where
 272 Shetland looks to be stabilising at a depleted level, East Scotland continues to decline.

273
 274 *Contemporary dynamics of the northern harbour seal metapopulation*

275 The combined analyses allow us to assess the levels of movement, as well as genetic and
 276 demographic connectivity, within the metapopulation on different timescales and using different
 277 aspects of the harbour seal's biology (Figure 3, Table 2). On the UK west coast, our data suggest
 278 that the Northwest local population (Southwest Scotland, West Scotland, Western Isles SMUs) is
 279 a source population, as it has a high level of retention and substantial emigration to Northern Ireland
 280 (Table 3). Furthermore, population abundance for Northern Ireland has been steadily decreasing
 281 over the study period, despite receiving immigrants from the Northwest local population, suggesting
 282 that it is a sink population.

283
 284 We also hypothesise that the MFNCO is a source population. This local population appears to have
 285 a high level of internal recruitment, based on the *BayesAss* analysis. Furthermore, the genetic and
 286 pup movement data suggests there is emigration from MFNCO to other local populations. In
 287 particular, it seems that MFNCO is a likely source population to both Shetland and East Scotland.
 288 Both latter two local populations have a substantial proportion of individuals with MFNCO ancestry
 289 based on *BayesAss*, and the pup tracking data showed considerable movement from the MFNCO
 290 to Shetland (Table 2, Table S5). Finally, MFNCO, Shetland and East Scotland share similar
 291 population trends, in that they have dramatic declines subsequent to the perturbation. In previous
 292 generations, there appears to have been migration from East Scotland into both Shetland and the
 293 MFNCO local populations; however, there is little evidence of this in the past one generation

294 spanning the perturbation. This decline in emigration coincides with the precipitous decline in the
295 East Scotland local population.

296
297 Overall, the results show that the northern harbour seal metapopulation is highly connected and
298 contains two probable source local populations: MFNCO and Northwest. The decline in the MFNCO
299 local population appears to have reduced connectivity between these local populations as well. For
300 example, there are four individuals (4%) from the Northwest local population ($n = 90$) that are most
301 likely second generation migrants from the MFNCO local population, but only two individuals are
302 likely to be first generation migrants. This could represent a decline in connectivity over the past
303 one generation during which the MFNCO population exhibited a pronounced decline.

304

305 **DISCUSSION**

306 A key tenet of the metapopulation paradigm is that local population decay and decline do not
307 necessarily threaten metapopulation persistence if there is a concomitant balance with new
308 colonisation and growth. Such balanced patterns of extinction and colonisation have been
309 empirically shown in butterflies *Melitaea cinxia* (27) and *Speyeria nokomis apacheana* (28), as
310 well as the American pika *Ochotona princeps* (29). Here we have shown that the northern UK
311 harbour seal metapopulation has been subject to a recent perturbation that has impacted local
312 population connectivity in a way that appears to go beyond the expectations of a simple
313 extinction-colonisation equilibrium. The disruption of migration we see at a local level seems to
314 have wider impacts to the metapopulation, rarely before seen in empirical studies. This change in
315 connectivity could eventually lead to genetic isolation and genetic erosion over time (30), which
316 can be very difficult to detect in the short term given the long generation time of the species (31).
317 Predicting long-term consequences, therefore, requires the use of a thorough population viability
318 analysis integrating both local population demography and migration (32). The migration
319 estimates we provide could be used in such a model once reliable estimates of survival and
320 fecundity are obtained.

321

322 More practically, we demonstrated that there are two distinct harbour seal metapopulations in the
323 UK using genetic data. This confirms previous analyses that showed harbour seals from
324 Southeast UK clustered with samples from France and the Netherlands (18). In addition, it builds
325 on this work by demonstrating that the previously identified Northwest UK genetic cluster
326 represents two local populations (Northern Ireland and Northwest) and the Northeast UK cluster
327 represents three local populations (Shetland, MFNCO, East Scotland) resulting in five local
328 populations in a northern metapopulation linked by gene flow and dispersal (18).

329

330 Furthermore, we have identified putative source-sink dynamics for the northern metapopulation
331 while evaluating if migration patterns had changed between the generations pre- and peri-
332 perturbation. Identifying source-sink metapopulation dynamics and the associated connectivity
333 pattern is of fundamental importance for the management of marine systems (33). However, this
334 is a particularly difficult task in the case of long-lived vertebrate species. No single type of data
335 (population trends, location tracking, genetics) on its own can achieve this goal. Previous studies
336 have used genetic data indicating asymmetric gene flow to support source-sink dynamics (e.g.,
337 34,35) but this is not sufficient evidence as net recipients of individuals could still be self-
338 supporting populations. Our integrative approach, combining genetic, location tracking and
339 population trend information, provides a framework for assessing source-sink metapopulation
340 dynamics in future studies. Specifically, we have placed estimates of local population connectivity
341 from genetic and movement data, as well as genetic migrant ancestry information, in the context
342 of population trends to infer whether local populations could be self-supporting sources or
343 immigration dependent sinks.

344

345 Through this methodology, we show that the putative key source population of MFNCO has
346 shown a decrease in abundance of perhaps 50% and a concomitant reduction in migration to
347 East Scotland and the Northwest population in the past one generation that spans the start
348 perturbation. Extrinsic factors, such as epizootics, can periodically cause declines and impact
349 pinniped population dynamics (36). In the case of the Scottish harbour seal, environmental
350 change, including exposure to toxins from harmful algae (37), competition and predation (17), and
351 prey availability (38) are hypothesised to be contributing to changes in the population dynamics,
352 but there is no evidence for infectious disease (39). Future work should examine habitat loss or
353 fragmentation, which previous studies focused on other species suggest can accelerate
354 metapopulation fragmentation and result in regional extinctions (40).

355
356 Intrinsic factors, such as density-dependent emigration, have been shown as an important
357 determinant of grey seal metapopulation dynamics (6,41). If similar mechanisms operate in
358 harbour seals, then the decline in abundance in the MFNCO population could have led to a
359 concurrent decline in density-dependent emigration to previously connected local populations
360 such as the rapidly declining East Scotland (42). As pups of the year are thought to be the
361 dispersing age class in harbour seals (43–45), facilitating connectivity across the metapopulation,
362 future work should focus on assessing their patterns of movement and recruitment.

363
364 According to genetic and pup-tracking data, seals continue to migrate from MFNCO to Shetland
365 peri-perturbation, likely key to the persistence of the Shetland local population. Rather than a
366 regional issue, the decline in the MFNCO local population has had a ripple effect across much of
367 the northern metapopulation. Indeed, the apparent decline in migration from MFNCO to the
368 Northwest local population could have impacts that are yet to be detected or determined. The
369 Northwest local population is also a likely source population for Northern Ireland, as
370 demonstrated by genetic estimates of migration rates and, potentially, pup dispersal.

371
372 Although the evidence we provide for source-sink dynamics and changes in connectivity are
373 convincing, there are important caveats to consider. Ultimately, our framework uses a range of
374 proxies instead of direct estimates of demographic parameters, such as population trends as an
375 indication that mortality is greater than survival, in the absence of high levels of emigration. As
376 noted earlier, direct estimates of these parameters are needed to definitively assess source-sink
377 and metapopulation dynamics. Furthermore, while we have used genetic data from across the
378 harbour seal's UK distribution to estimate genetic differentiation, migration rates and migrant
379 ancestry, our sample sizes from some locations were small. Future work should assess migration
380 rates using both larger genetic sample sizes and numbers of markers. We also only had pup
381 tracking data from two of five northern metapopulation local populations. However, our inferences
382 from multiple lines of evidence - genetic, pup and non-pup movement data - were consistent,
383 providing confidence in our results. We hope that this prompts other scientists to examine extant
384 datasets on other species for similar analytical opportunities.

385
386 Our study uniquely considers population trend, location tracking and genetic data over a multi-
387 generational timescale for a long-lived mammalian species and provides convincing evidence of
388 source-sink metapopulation dynamics for this top predator. The results suggest that the
389 Southeast England SMU can be assessed and managed independently from those in Scotland
390 and Northern Ireland, with implications for the broader management of the species across
391 Europe. Management across the northern metapopulation should consider connectivity patterns
392 identified here. Continued research into habitat preference for UK harbour seals, combined with
393 patterns of connectivity described here and vital rate estimates, will contribute considerably in the
394 near future to the debate on the metapopulation and habitat paradigms for understanding
395 declines of species (46). More broadly, this work shows that changes in migration and
396 connectivity at a local level can impact wide-scale dynamics, which has important implications for
397 management of the diverse array of terrestrial and marine species that exist as metapopulations.
398 For example, most conservation frameworks assess changes in abundance over time (e.g., the

399 IUCN red list, 47). This work suggests that changes in migration rates and connectivity could
400 foreshadow changes in abundance. Monitoring and identification of reduced connectivity may
401 prompt conservation measures to be put in place that could forestall decline, or could be
402 assessed retrospectively, as has been done here. As anthropogenic activities cause more
403 widespread environmental degradation and habitat fragmentation (48), understanding
404 connectivity could be an important factor in maintaining both populations and biodiversity in the
405 future.

406 **Materials and Methods**

407 **Data collection**

408 *Microsatellite genotyping*

409 In the UK, the Sea Mammal Research Unit (SMRU) and the University of Aberdeen collected skin
410 samples during live-capture of harbour seals across 20 sampling sites between 2003 and 2012,
411 using methods described in Sharples et al. (16). All procedures were carried out under Animal
412 (Scientific Procedures) Act, 1986 Home Office Licences issued to SMRU (PIL nos. 60/3303,
413 60/4009 and 70/7806). In addition to the UK samples, 36 harbour seal samples were included
414 from Norway, Dutch Wadden Sea and France as described in Olsen et al. (18). DNA was
415 extracted using a salt saturated technique (49). Fourteen microsatellite loci were amplified and
416 genotyped by Xelect Ltd (St Andrews, UK). All genotyping previously carried out in Olsen et al.
417 (18) was repeated to ensure complete comparability across the dataset, but was augmented with
418 more loci and UK samples to increase the power of our analyses (See Supplementary Material
419 and Table S7 for full details).

420

421 *Tracking Data*

422 Tracking data provide two sources of information: regional movements of individuals aged one
423 year and older within the non-breeding season and movements of pups, as described below.

424

425 We determined movement behaviour in seals aged one year or older (non-pups) using Argos
426 satellite relay data loggers (SRDLs) or GPS/GSM phone tags (developed and supplied by the
427 SMRU Instrumentation Group) deployed between 2001 and 2017 on 334 harbour seals in eight of
428 the SMUs (Tables 1 and S5). Telemetry tags were attached to the fur at the back of the neck
429 using fast-setting two-part epoxy adhesive or Loctite® 422 Instant Adhesive. Locational data from
430 the SRDLs are subject to location error, so we used a Kalman Filter to estimate locations (50)
431 and any erroneous locations from the GPS/GSM phone tags were also removed (51). The
432 duration of the telemetry tags is less than one year as the tags fall off during the annual moult in
433 August. To minimise bias associated with variations in tag longevity, we excluded deployment
434 durations of less than four weeks with tag durations ranging from 28 to 243 days (mean 95 days).
435 The tags send data remotely and thus do not have to be recovered, such that there is no
436 relationship between movements and data recovery. However, at-sea movements during the
437 summer breeding season may be affected by breeding status, for example, there may be
438 movement between regions associated with breeding. Breeding status of tagged individuals is not
439 known so to ensure estimated movement rates were comparable between regions, we excluded
440 data collected during the breeding season (June to July).

441

442 We considered the movements of tagged pups as an indication of dispersal; juveniles are more
443 dispersive than adults in pinnipeds and the movements of these pups in the first few months of
444 life may be indicative of where they will recruit into the breeding population. However, data were
445 only available from two locations: 46 pups tagged in Orkney, North Coast & Orkeny SMU, and
446 West Scotland SMU (44). The tags (SPOT tags, Wildlife Computers, Redmond, WA, USA) were
447 deployed on flipper tags and thus do not fall off during the annual moult. Pup tag duration was
448 between 31 and 424 days (mean: 155 days).

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453 **Data analysis**

454 *Metapopulation delimitation*

455 We inferred the metapopulation membership of local populations by estimating genetic
 456 differentiation between SMUs, and between sampled haul out sites and subunits within SMUs,
 457 using microsatellite data. We calculated pairwise F_{ST} values (52) using *GENEPOP* (53), with
 458 significance assessed using the exact G test in the same program (100,000 dememorization
 459 steps, 1,000 batches each with 10,000 iterations). Furthermore, we investigated isolation-by-
 460 distance across the UK by regressing $F_{ST}/(1-F_{ST})$ with the log of the 'at-sea' distance between
 461 haul out sites using the *ISOLDE* program implemented in *GENEPOP* (54). To infer recent
 462 connectivity, we also ran the program *BayesAss* ((55), see next section). Finally, we conducted
 463 DAPC using the R package *adegenet* (56) to investigate the genetic differences between SMUs
 464 in a multivariate statistical framework.

465

466 **2.2.2. Northern metapopulation connectivity before and during perturbation**

467 In order to understand migration and genetic connectivity over recent time scales, we used
 468 program *BayesAss* (55). The program estimates immigration rates over the past two generations
 469 using gametic disequilibrium signal generated by immigrant individuals or their descendants. We
 470 conducted four *BayesAss* runs, each consisting of ten million iterations with initial burn-ins of one
 471 million iterations. Parameters were sampled every 1000 iterations and convergence was
 472 confirmed by visual checking in *TRACER v1.6* (57) and by confirming that the independent runs
 473 converged on similar values. We report median migration rates with 95% HPD interval from all
 474 runs and the mean assignment probabilities of individuals across the four runs. The patterns of
 475 connectivity, in terms of migration rates and ancestry of individuals, was used to infer connectivity
 476 over the past two generations. As samples were collected between 2003 and 2012 and the
 477 harbour seal is estimated to have a 14.8 year generation span (58), the approximate timings for
 478 the migration estimates are 1993 to 2007 (taking midpoint of the samples) for the past one
 479 generation, clearly spanning the recent decline (peri-perturbation), and 1977 to 1992 for the
 480 second generation, clearly preceding the recent decline (pre-perturbation).

481

482 We used the tracking data to investigate connectivity through the patterns of movement of UK
 483 harbour seals. For non-pups (tracked within the non-breeding season (September to May), we
 484 calculated the proportion of animals tagged in each unit that moved between local populations,
 485 SMUs or areas within SMUs (north, central and south subunits of West Scotland SMU),
 486 identifying movements using haul out locations rather than at sea locations. Of the SMUs which
 487 have shown decline, only for East Scotland were there data that could reliably represent both pre-
 488 ($n = 10/33$ tagged in late 2001/early 2002) and peri-perturbation (Table S5). The movements from
 489 the Moray Firth represent peri-perturbation (tags deployed from 2004 onwards). For Shetland, all
 490 tags were deployed in late 2003/early 2004; the gap in the surveys synonymous with the 40%
 491 drop in population size. For North Coast & Orkney, 14/53 tags (14/19 of those deployed in
 492 northern Orkney) were deployed during the gap in surveys (late 2003/early 2004), with the
 493 remainder tagged peri-perturbation (2011-2017). All tags deployed in Southeast England were
 494 deployed after the 2002 PDV epidemic (2003 onwards). For pups, the proportion of tagged seals
 495 in each unit that moved between local populations or SMUs, identifying movements using haul
 496 out locations rather than at sea locations, was calculated.

497

498 We also examined population trend data to describe and categorise the trajectories of the
 499 different SMUs as increasing, decreasing, stable, or depleted (defined as a decline and then
 500 stabilisation) using published information (17). Briefly, harbour seal population trend data was
 501 compiled from the ten SMUs, within which >50 individuals have been counted during a survey.
 502 Counts were conducted during the annual moult when the highest proportion of the population is
 503 hauled out (c. 0.72%;(59)), ensuring compatibility of data across survey years and regions and as
 504 described more thoroughly in (17). Although the overall trend for UK harbour seals is stable or
 505 even increasing abundance, the SMUs exhibit strikingly different dynamics (Figure 1).

506

507 **2.2.3. Identifying changes in source-sink dynamics**

508 We made inferences about the source-sink dynamics of the harbour seal metapopulations from
 509 the genetic and short-term movement estimates in the context of the trends in abundance (17;
 510 Figure 1). Specifically, we summarised whether the available data suggested local populations
 511 were (a) genetically distinct, based on the estimates of pairwise F_{ST} and migration rates, (b)
 512 linked by movement of non-pups; and (c) demographically distinct, based on the proportion of
 513 non-migrants from *BayesAss* and dispersal inferred from the pup tracking data (where available).

514
 515 Finally, we considered whether these data suggested that the local populations were putative
 516 sources or sinks in the context of the trend and abundance data. A local population was
 517 considered: (i) putative source region if genetic and demographic (pup movement) data results
 518 indicated high internal recruitment and substantial degree of emigration to other regions and non-
 519 pup tracking data indicated low rates of movement; or (ii) a putative sink region if genetic and
 520 demographic data indicated substantial recruitment from outside the local population and showed
 521 a trend similar to its source population. The long-term viability of putative source populations was
 522 considered in the context of their population size and trend data (17). Ultimately, we consider
 523 whether the totality of the evidence suggests a broadscale metapopulation decline or a regional
 524 decline.

525
 526

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532
 533

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709 **Figures and Tables**

710

711 **Figure Legends**

712

713 **Figure 1.** Map showing the most recent harbour seal count (on 10km² resolution; (17)). The Seal
714 Management Units considered in this paper (as well as Northeast England SMU which has a
715 small population (max count < 100) and for which we do not have any data) are shown as well as
716 associated trends (line and associated 95% confidence intervals) in August counts (points; y-axis)
717 as a function of year (x-axis), extracted from Thompson et al. (17).

718

719 **Figure 2.** Individual genotypes plotted by linear discriminants (LD) from the discriminant analysis
720 of principle components conducted with samples grouped by SMU and haul out site (latter in
721 brackets). Mean values for each sampling partition shown by triangle.

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724 **Figure 3.** Inferred source-sink dynamics of UK harbour seal northern metapopulation. Black lines
725 delineate the SMUs and coloured lines indicate inferred local populations, with arrows indicating
726 movement from putative sources to putative sinks. Dots represent approximate locations of
727 telemetry tag deployment and/or genetic sampling.

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Table 1: Sampling locations and sample sizes used in this study. Locations are shown as metapopulation (M: defined as northern (N) or southern (S)) and local population inferred in this study, United Kingdom Seal Management Unit (SMU) or Area for European samples, and sample types are number of genetic samples (n), number of genotypes (n_{GEN}), number of new genotypes presented here relative to previous work (n_{NEW}), number of tags on seals aged 1+ ($n_{\text{TAGS1+}}$) and pups (n_{TAGSpups}).

M	Local Population	SMU/Area	n	n_{GEN}	n_{NEW}	$n_{\text{TAGS1+}}$	n_{TAGSpups}
N	Northern Ireland	Northern Ireland (NIR)	22	20	20	31	0
N	Northwestern (NW)	West Scotland (WS)	106	75	20	61	24
		Western Isles (WI)	17	15	0	20	0
		Total	123	90	20	81	24
N	MFNCO	North Coast and Orkney (NCO)	62	47	9	53	22
		Moray Firth (MF)	40	32	0	39	0
		Total	102	79	9	92	22
N	Shetland	Shetland (SH)	19	14	0	14	0
N	East Scotland	East Scotland (ESC)	36	28	7	33	0
S	-	Southeast England (SEE)	51	24	5	83	0
S	-	South England (SSE)	6	2	2	0	0
S	-	France (FRA)	12	3	0	0	0
	-	Dutch Wadden Sea (DWS)	9	9	0	0	0
	-	Norway (NOR)	15	0	0	0	0
		EUR Total	37	12	0	0	0
	TOTAL		395	269	63	334	46

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Table 2. Summary distinctiveness and inferred source-sink dynamics between local populations of UK harbour seals, based on movement of non-pups, genetic and demographic data. The demographic distinction criteria are the proportion of non-migrants from *BayesAss* and likely dispersal is from *BayesAss* and pup movement data. These are considered in the context of the trend and abundance for each unit to suggest putative sources and sinks. Depleted trend means there was a period of decrease and then stabilisation a lower abundance level.

Local population (SMU)	Movement between local populations	Genetically distinct	Demographically distinct		Population characteristics		
			Proportion non-migrants	Likely dispersal from:	Trend	Abundance (2011-2016) (95% CI)	Type
Northern Ireland - NIR	None detected	Small, significant difference from NW	0.676 (0.667, 0.703)	NW	Decreasing	1,300 (1,100 – 1,750)	Sink (from NW)
Northwest - NW (WI+WS+SW)	None detected	Yes	0.932 (0.879, 0.976)	MFNCO	Stable/Increasing	26,600 (21,750 – 35,400)	Source (to NIR)
MFNCO (MF+NCO)	To SH	Yes	0.947 (0.885, 0.985)	-	Decreasing	3,200 (2,600 – 4,250)	Source (to SH, ES)
Shetland - SH	From MFNCO	Yes	0.682 (0.667, 0.713)	MFNCO and NW	Depleted	4,700 (3,850 – 6,250)	Sink (from MFNCO)
East Scotland - ESC	None detected	Yes	0.791 (0.705, 0.891)	MFNCO	Decreasing	500 (400 – 700)	Sink (from MFNCO)

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