JNCC Report
No. 638

Red-throated Diver Energetics Project: Preliminary Results from 2018/19

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January 2020

ISSN 0963-8091

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This report should be cited as:

Duckworth, J., Green, J., Daunt, F., Johnson, L., Lehikoinen, P., Okill, D., Petersen, A., Petersen, I.K., Väisänen, R., Williams, J., Williams, S. & O'Brien, S. 2020. Red-throated Diver Energetics Project: Preliminary Results from 2018/19. *JNCC Report No. 638*, JNCC, Peterborough, ISSN 0963-8091.

EQA:

This report is compliant with the JNCC Evidence Quality Assurance Policy http://jncc.Defra.gov.uk/default.aspx?page=6675.

Peer-review of this report was undertaken by Dr Kyle Elliot and Dr Allison Patterson (Peer Review in JNCC Evidence and Advice Provision Level 4: External Independent Peer Review). All authors and Red-throated Diver Energetics Project partners were invited to comment on an earlier version of this report, prior to publication.

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Summary

Red-throated divers (*Gavia stellata*) are known to be displaced by marine industries, including offshore wind development and vessel traffic. Displacement is analogous to habitat loss, with areas used by divers prior to displacement no longer being available to them. However, the energetic, physiological and demographic consequences of displacement are currently unknown. If divers are already energetically constrained in the non-breeding season, they may struggle to meet the additional energetic demands following displacement. The aim of the Red-throated Diver Energetics Project (https://jncc.gov.uk/our-work/rtde-project/) is to collect and compare novel data on foraging and movement behaviour of red-throated divers in the breeding and non-breeding season. Whilst this will not give direct empirical measures of the consequences of displacement for individuals, it will give insight and inference into whether divers are currently energetically challenged in the non-breeding season.

During the 2018 breeding season, 74 red-throated divers breeding in Finland, Iceland and the Northern Isles of Scotland were tagged with time depth recorder (TDR) and geolocator (GLS) bio-logging tags. In 2019, 27 divers were recaptured, and tags removed but, due to tag loss and failure, data from only 21 TDR and 15 GLS were acquired. Tags provided data from June 2018 to March 2019 (TDR) or October 2018 to February 2019 (GLS, avoiding the equinox periods). GLS data were processed to reveal non-breeding season core use areas during October to February. TDR data were processed to extract dive information, with multiple sequential dives classified into dive bouts. TDR data from both the breeding and non-breeding seasons were obtained to compare foraging behaviour in different seasons.

Red-throated divers showed consistency in non-breeding season core use areas amongst individuals from the same breeding site (i.e. country). The divers from Finland for which location information was available (n=4) moved westwards during the non-breeding season, from the Baltic Sea into the North Sea. By contrast, Scottish (n=4) and Icelandic (n=7) divers for which location information was available, remained close to their breeding grounds, with Scottish divers wintering around NW Scotland and Northern Ireland and Icelandic divers remaining around the north coast of Iceland.

From June 2018 to March 2019, a total of 275,091 dives in 14,917 dive bouts were recorded, with a mean of 710 bouts per individual or 16 bouts per day (n=912 days of data, across all individuals). Almost all dives had a maximum dive depth (MDD) of <20 metres, with 2-6 metres being the most frequent MDD. Individual divers showed substantial variation in MDD, dive bout duration (DBD) and daily total dive bout time (TDBT). In Iceland, mean MDD remained relatively consistent between the breeding and non-breeding seasons, whereas in Scotland and Finland, mean MDD increased with birds tending to dive deeper as the non-breeding season progressed. Mean DBD was relatively consistent in Scotland across the whole study period, at around 10-15 minutes per dive bout, whereas in Iceland and Finland mean DBD increased as the non-breeding season progressed to a peak of approximately 25-30 minutes per dive bout. Mean TDBT was lower for Scottish birds, at approximately 3 hours per day, compared with Finnish and Icelandic divers, at approximately 4-5 hours per day. TDBT was relatively consistent across the study period at all sites, showing no substantial changes with season, although there was substantial individual variation in time spent diving each day.

We did not have data on light levels experienced by all birds at all times, so instead inferred diurnal and nocturnal foraging behaviour by assessing diving activity by hour of day, termed here ‘Diel Dive Activity’ (DDA). DDA was found to be consistent among individuals, with no divers diving for long periods either side of midnight. For Icelandic and Finnish birds in mid-winter, almost all divers were diving for a period either side of midday, suggesting that all

birds were foraging only during periods of daylight. This suggests that divers choose to forage only during daylight hours.

During the 2019 breeding season, more TDR and GLS tags were deployed on divers at the same three breeding locations. Attempts will be made to retrieve these tags in the 2020 breeding season. Once these data are available, further analyses will be conducted on the foraging and movement behaviour of red-throated divers during the non-breeding season and conclusions drawn about the behaviour and energetics of this species at this time. The preliminary results presented in this report do not attempt to evaluate whether divers undergo an energetic bottleneck in the non-breeding season as we currently have insufficient data to make this assessment and comprehensive detailed analyses have not yet been undertaken. Consequently, results from this report should not be used to make inference about diver foraging behaviour and energetics.

Contents

1 Introduction

Globally, offshore wind deployment is expected to undergo a massive increase to assist with mitigating climate change impacts. By 2030, the UK could see an increase in installed capacity from the current 8GW up to 30GW of offshore wind, under the Offshore Wind Sector Deal[1]. Whilst the UK is currently the world leader in offshore wind deployment, Europe has also seen substantial offshore wind development, with growth in the offshore wind sector forecast to continue.

Whilst energy generation from offshore wind development clearly helps mitigate climate change, the impact on the environment is less well understood. There is some evidence of marine birds colliding with turbines, being displaced and wind farms acting as barriers to flight paths (Dierschke *et al.* 2016; Drewitt & Langston 2006). Whilst colliding with a turbine results in immediate mortality to that individual, displacement can cause sub-lethal effects that are harder to measure.

Species susceptible to displacement effectively suffer from habitat loss as the area used prior to constructing the wind farm becomes unavailable to them. Displaced individuals have to use alternative habitat which may unfavourably alter an individual's energetic budget. This could be through reduced prey availability due to absolute lower abundance of suitable prey in the alternative habitat or as a consequence of increased intra- and/or inter-specific competition for prey. Following displacement, the density of individuals foraging in remaining habitat must increase, assuming non-displaced individuals do not redistribute themselves. This could affect prey acquisition for both displaced and non-displaced individuals (Dolman & Sutherland 1995). Trevail *et al*. (2019) showed that when environmental conditions force black-legged kittiwakes (*Rissa tridactyla*) to forage together, breeding success is lower, driven by greater overlap among individuals foraging ranges and increased foraging effort, most likely caused in part by greater interference competition. Displacement may also increase energetic costs of foraging if an individual has to find prey in an unfamiliar environment. Evidence from other marine birds shows that individual foraging site fidelity is typically high for adults, with presumed benefits of site familiarity (Votier *et al.* 2017; Wakefield *et al.* 2015). Displacement from familiar foraging sites may reduce foraging efficiency for these individuals. To compensate for any of these consequences, an individual may need to increase foraging effort to meet their energetic demands and maintain body condition. Failure to do so during the non-breeding season may result in increased risk of mortality for an individual. There may also be carry-over effects to the subsequent breeding season such as reduced breeding productivity (Salton *et al*. 2015). Both of these effects could also operate at the population level, if sufficient numbers of individuals are affected in the same way. However, the mechanistic links from displacement to demographic consequences are not known, especially during the non-breeding season.

Red-throated divers (*Gavia stellata*) are known to be displaced by offshore wind farms (e.g. Dierschke *et al.* 2016; Irwin *et al.* 2019). Among species that are displaced by marine activities, they are considered to be the most sensitive (Furness *et al.* 2013), with evidence of displacement effects up to 8-16km from the edge of an offshore wind farm (Mendel *et al.* 2019; Webb *et al.* 2016). Red-throated divers favour marine areas with shallow seas and sandy substrate (e.g. Irwin *et al.* 2019). In the UK, red-throated diver overwintering distribution overlaps with areas ideal for offshore wind development (Bradbury *et al.* 2014; Gove *et al.* 2016; O'Brien *et al.* 2008), with wind farms planned or constructed in areas of high red-throated diver density (The Crown Estate 2018). Consequently, red-throated divers pose a consent risk for offshore wind development and have stopped development in an area of high diver density[2].

[1] https://www.gov.uk/government/publications/offshore-wind-sector-deal
[2] http://www.londonarray.com/the-project-3/phase-2/

Whilst divers are known to be displaced by offshore wind development, very limited evidence currently exists on red-throated diver foraging behaviour and energetics (Duckworth *et al.*, *in press*) and they are a poorly understood species compared with other European marine diving birds, e.g. common guillemot (*Uria aalge*) (Dunn *et al.* 2019). In particular, prior to this study, nothing was known about foraging behaviour of red-throated divers in the non-breeding season. Whilst it is not feasible to obtain direct measurements of the behavioural, physiological and demographic consequences of displacement on individuals and populations (Dierschke *et al*. 2017), understanding when during the year divers are most energetically constrained gives some insight into the potential consequences of displacement. For example, if the period when divers are using areas of offshore wind development is a time of year when individuals can easily meet their energetic requirements, they may be able to increase foraging effort to compensate for the effects of displacement (e.g. Langton *et al*. 2013). Conversely, if displacement occurs at a time when individuals are energetically and behaviourally constrained (Dunn *et al.* 2019; Fort *et al.* 2009), individuals may fail to adequately compensate for displacement effects.

The aim of the Red-throated Diver Energetics (RTDE) Project is to collect novel data on foraging behaviour of red-throated divers in the non-breeding season. Whilst this will not give direct empirical measures of the consequence of displacement for individuals, it will give insight and inference into whether divers are already energetically challenged in the non-breeding season. This report does not attempt to address the overarching aim of the RTDE Project but to simply describe data obtained from the first non-breeding season. Further data will be collected during 2019/20 and a more comprehensive analysis will be carried out in which information on red-throated diver behaviour and energetics from various sources will be integrated. Later publications will include an assessment of whether red-throated divers undergo an energetic bottleneck in the non-breeding season.

2 Methods

2.1 Tag specification, deployment and retrieval

2.1.1 Tag deployment

During the 2018 summer, breeding red-throated divers were tagged in southern Finland (n=31), Orkney (n=17), Shetland (n=14) and Iceland (n=12). Divers were caught at their nest site, either using a nest trap or a wader net if the bird was on their breeding lake. See O'Brien *et al* (2018) and O'Brien *et al.* (2020) for more information on why Finland, Scotland and Iceland were chosen for tagging divers and how divers were caught.

2.1.2 Tag specification

Divers were fitted with leg-mounted archival time depth recorder (TDR) tags (Cefas G5 Standard Time Depth Recorder, dimensions: 8mm x 31mm, weight: 2.7g) and global location sensor (GLS) tags (Biotrack/Lotek MK4083 Geolocator, dimensions: 17mm x 10mm x 6.5mm, weight: 1.8g). Tags were mounted on 2mm thickness red darvic colour rings using cable ties and epoxy resin glue to attach tags to the darvic ring (Figure 1). The rings were specially shaped to fit a red-throated diver leg, which is elliptical and not cylindrical. Tags were mounted and attached according to British Trust for Ornithology (BTO) recommendations.

Figure 1. Time depth recorder (TDR) tag (left) and geolocator (GLS) tag (right) mounted on red darvic rings and attached to red-throated diver legs. GLS tags were put on the same leg as the metal ID ring. Photo: Sue O'Brien.

TDR tags recorded barometric pressure, as a proxy of water depth, every six seconds and temperature every ten minutes for a 24-hour period, every five days. This duty cycle was chosen to obtain maximum detail of individual dives while also sampling for the longest duration possible across the year. GLS tags were set to record maximum light levels every five minutes and saltwater immersion every ten minutes, continuously. MK4083 tags have a battery life of two to five years[3] and so battery life did not limit data collection for the GLS tags.

2.1.3 Tag retrieval

TDR and GLS tags were archival, necessitating recapture of tagged birds to download data from tags. Red-throated divers show high interannual nest site fidelity (Okill 1992), facilitating relocating a tagged individual the following breeding season. During the 2019 breeding season, attempts were made to locate and recapture all tagged divers and remove tags. Divers were recaptured using the same methods as in 2018 (see O'Brien *et al.* 2020 for more information).

2.2 Data analysis

2.2.1 Geolocator data

Light data from the GLS tags was processed using the BASTrack software package. Raw GLS data were decompressed using Decompressor. Annotation of twilight events was undertaken with Transedit and Locatoraid. A light threshold of 15 was used to calculate an individual sun elevation angle for each device (range: -4.6018, -4.3022). To remove daytime shading, a minimum dark period of three hours was applied. Using BirdTracker, two location fixes per day were generated, representing the bird's geographical position at noon and midnight. GLS data do not provide useful latitudinal information on an individual's location around the autumnal and spring equinox. Therefore, only data from 12 October 2018 to 20 February 2019 were used to generate polygons of non-breeding season core use area (50% density kernel) and non-breeding season home range (90% density kernels), in the R software package adehabitatHR

[3] https://www.lotek.com/wp-content/uploads/2017/10/MK-Geolocators-Spec-Sheet.pdf

(https://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf).

50% and 90% density kernels were produced using pooled GLS data from all birds tagged in a site (Finland, Iceland or Scotland), showing general patterns in movement of divers from that site. Kernels were also generated for each individual diver for which adequate data were available. Finally, since birds tagged in Finland appeared to change core use areas during the non-breeding season, unlike those from Iceland and Scotland, data from the October to February period for Finnish birds were subdivided into two or three subgroups. A subgroup was determined by plotting the location of all points over time and looking for a significant change in location.

2.2.2 Time depth recorder data

The baseline surface reading of a TDR can change over an extended study period, so a slightly modified version of the R programme script from Duckworth *et al. (in press*) was used, which shifted the dive profiles to set the surface as zero metres. The minimum value for the detection of a dive at each recording interval was one metre. This excluded any non-foraging dives or residual errors from the shifting baseline (Falk *et al.* 2000). The dives were analysed for maximum dive depth (MDD, lowest depth reached on a dive), duration of a dive bout (dive bout duration, DBD) and cumulative time spent in dive bouts during a 24-hour period (daily Total Dive Bout Time, TDBT). Dives were classified into bouts, defined as a series of dives where the maximum surface time between each dive was less than 60 seconds. A 60 second cut-off was chosen based on the decreased frequency of surface times above 60 seconds (Duckworth *et al.*, *in press*). This method presents each bout as a period of intense activity and provides a good estimate of “time active”, including inter-dive intervals, while avoiding the inclusion of any extended rest periods. At least three sequential dives were defined as a dive bout. This removed the influence of isolated non-foraging dives. TDBT was therefore a measure of daily total time spent in dive activity, including surface time between each dive, rather than daily time submerged which would exclude surface time between dives in a dive bout.

A mean of MDD for each individual in each month was calculated as the mean of all MDDs recorded for that individual across all days of sampling within that month. A grand mean and grand standard deviation of MDD was then calculated across all individuals for a particular site and month. Whilst better methods exist for calculating a weighted mean (e.g. Green *et al.* 2007) the simple approach used here is adequate for the small sample sizes obtained and this preliminary investigation into the TDR data. Grand mean dive bout duration (DBD) and daily Total Dive Bout Time (TDBT) were calculated in the same way.

We did not have both GLS data on light levels experienced by an individual and TDR data for all tagged birds, due to tags failing. Instead, we inferred diurnal and nocturnal foraging behaviour by assessing diving activity by hour of day, termed here ‘Diel Dive Activity’ (DDA). DDA was found by calculating the proportion of tagged divers undertaking a dive bout during each hour of a UTC 24-hour period, from midnight to midnight. When DDA is at 1, all individuals are foraging and when at 0 no individuals are foraging. DDA was reported for each day that the loggers recorded data, during the non-breeding season (October-January) for each site.

3 Results

3.1 Tag retrieval and data acquisition

A total of 27 tagged red-throated divers were recaptured during the 2019 breeding season, 10 from Finland, eight from Iceland, five from Orkney and four from Shetland. Treating

Orkney and Shetland birds as a single ‘Scottish’ population, sample sizes were reasonably equally distributed across the three study areas. It is reasonable to pool data from Orkney and Shetland as there is some evidence of individuals moving between Orkney and Shetland to breed (Okill 1994; *pers. obs*., J. Williams). Additionally, both ringing recoveries and unpublished GLS data from 2007 suggest divers from Orkney and Shetland mostly use the same wintering areas (Okill 1994).

The GLS tags were faulty, with all tags showing signs of water ingress (*pers. comm*., Lotek Wireless Inc.). Five tags failed to record any data and another seven tags failed before the end of October 2018 (tag duration <175 days). Only 15 of the 27 tags retrieved recorded for a sufficient duration to provide some information on the wintering location of individuals.

Four birds (Finland n=2, Iceland n=1, Orkney n=1) had lost their TDR tags. The plastic darvic ring on which the tag was mounted was still present, but the tags appeared to have slipped out of the two cable ties and epoxy resin glue used to hold the tag on the ring (Figure 2). In addition, a further two TDR tags (Iceland n=2) were damaged and recorded no data.

Figure 2. Two darvic rings retrieved in Summer 2019 from divers tagged in Summer 2018. The left ring has a TDR tag still correctly mounted on it; the TDR and one of the cable ties was lost from the right ring.

The quality of data retrieved from GLS and TDR tags varied in duration due to problems with tag integrity (GLS) or battery dying (TDR) (Table. 1).

A combination of difficulty with finding and re-trapping tagged divers (see O’Brien *et al.* 2020), tags being lost and faulty tags failing to record data for a sufficient duration resulted in small sample sizes, with only ten birds carrying tags that obtained sufficient data from both TDR and GLS tags.

Note one diver tagged in Finland in Summer 2018 was found dead in August 2018 (see O’Brien *et al.* 2018 for details). The TDR data were analysed and presented in Duckworth *et al.* (*in press*). Since no non-breeding season data were obtained from this individual and the results are in the process of being published, information from this individual are not reported here.

Table 1. Location, unique metal ring number and date of deployment of tags and number of days from deployment that each tag continued collecting data. Only some GLS tags recorded for a sufficient duration to provide information on winter location of that bird. Four TDR tags were lost from the darvic ring, as indicated by a '-'.

Country	Ring No.	Date	GLS (days)	Data on winter location?	TDR (days)
Finland	GS0811	22/05/2018	175	Yes	231
Finland	GS0814	21/05/2018	368	Yes	-
Finland	GS0815	29/05/2018	366	Yes	214
Finland	GS0822	02/06/2018	2	No	220
Finland	GS0824	03/06/2018	142	No	164
Finland	GS0825	01/06/2018	0	No	-
Finland	GS0829	05/06/2018	370	Yes	212
Finland	GS0832	07/06/2018	109	No	204
Finland	GS0834	07/06/2018	109	No	220
Finland	GS0838	09/06/2018	0	No	208
Iceland	115111	26/05/2018	404	Yes	0
Iceland	115112	26/05/2018	35	No	232
Iceland	115113	27/05/2018	336	Yes	221
Iceland	115115	27/05/2018	380	Yes	231
Iceland	115116	27/05/2018	266	Yes	0
Iceland	115119	30/06/2018	346	Yes	258
Iceland	115120	01/07/2018	368	Yes	-
Iceland	115122	02/07/2018	367	Yes	256
Orkney	1323954	09/07/2018	350	Yes	143
Orkney	1337340	12/06/2018	0	No	200
Orkney	1440402	08/06/2018	374	Yes	-
Orkney	1440403	12/06/2018	92	No	215
Orkney	1440406	13/06/2018	195	Yes	219
Shetland	1173676	28/05/2018	0	No	225
Shetland	1173677	29/05/2018	46	No	224
Shetland	1173687	28/05/2018	395	Yes	230
Shetland	1410844	28/05/2018	0	No	230

3.2 Location of red-throated divers in the non-breeding season

Maps of non-breeding season core use areas and home ranges for all individuals for which sufficient GLS data were available are presented below (Figure 3 to Figure 8). Since Scottish and Icelandic divers did not move long distances in the non-breeding season, a single set of non-breeding season core use area and home range polygons are presented, whereas maps for each individual tagged in Finland with sufficient GLS data are presented. Maps of core use areas and home ranges for each individual diver from Scotland and Iceland are presented in Appendix 1.

Geolocator data do not give precise locations of birds. Each position potentially has a large error of +/- 145-185km (Merkel *et al.* 2016) so the maps below and in Appendix 1 should be viewed as approximate areas used by these tagged divers.

3.2.1 Location of divers breeding in Scotland and Iceland

Divers from Scotland and Iceland remained close to their breeding grounds during the winter, with GLS data suggesting Scottish birds tended to move to the west coast of Scotland or the north coast of Northern Ireland and Icelandic birds wintered along the northern coast of Iceland (Figure 3). Icelandic birds appear to remain particularly close to their breeding grounds, using marine areas to the north and east of Iceland. Some Scottish birds moved further from their breeding grounds to winter off west Scotland and Northern Ireland. Divers occasionally tuck their legs into their plumage while resting on water, causing shading of the GLS tag. When leg-tucking happened at dawn or dusk, the GLS tag recorded truncated day lengths and consequently shifted the location north. Whilst, data from GLS tags deployed on Scottish and Icelandic divers showed leg-tucking to be less prevalent than in Finnish divers, infrequent leg-tucking events could still push the location of density kernels slightly further north. Additionally, there was some evidence of GLS tags coming loose and sliding around the darvic ring such that the tag then sat directly below the diver's body, rather than on the outside of their leg (*pers. obs*., P. Lehikoinen). This could also contribute to shading of tags and consequent northwards shift of GLS locations and kernels.

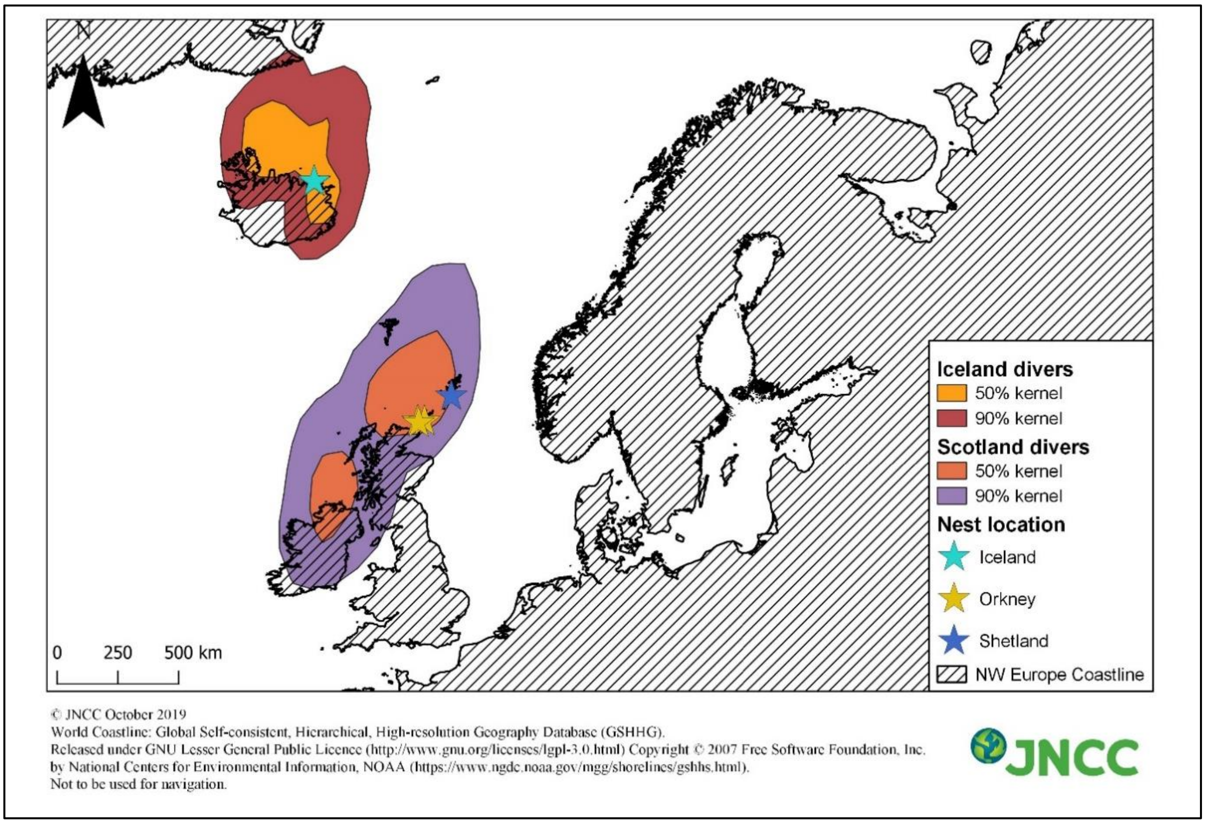

Figure 3. Non-breeding season (October 2018 to February 2019) core use area (50% density distribution kernel) and home range (90% density distribution kernel) for Scotland- and Iceland-tagged birds (n=4 and n=7, respectively) during October 2018 to February 2019.

3.2.2 Location of divers breeding in Finland

Most GLS tags from Finnish divers failed, with only three tags recording for the full winter period and one other recording into November. Non-breeding season core use and home range kernels from these four individuals showed them to be using three distinct areas, two of which are apparently over land (Figure 4). Red-throated divers in NW Europe are known to not spend any time inland during the non-breeding season. Examination of the GLS and

TDR data suggests, as for Scottish and Icelandic birds, these individuals were tucking their legs into their plumage for periods of time, or tags were rotating around the leg to sit beneath the bird's body, causing shading of the GLS tag. Assuming divers were therefore further south than indicated by the density kernels presented here, divers appeared to spend time in the Baltic Sea reasonably close to their breeding grounds, around Denmark and in the southern half of the North Sea.

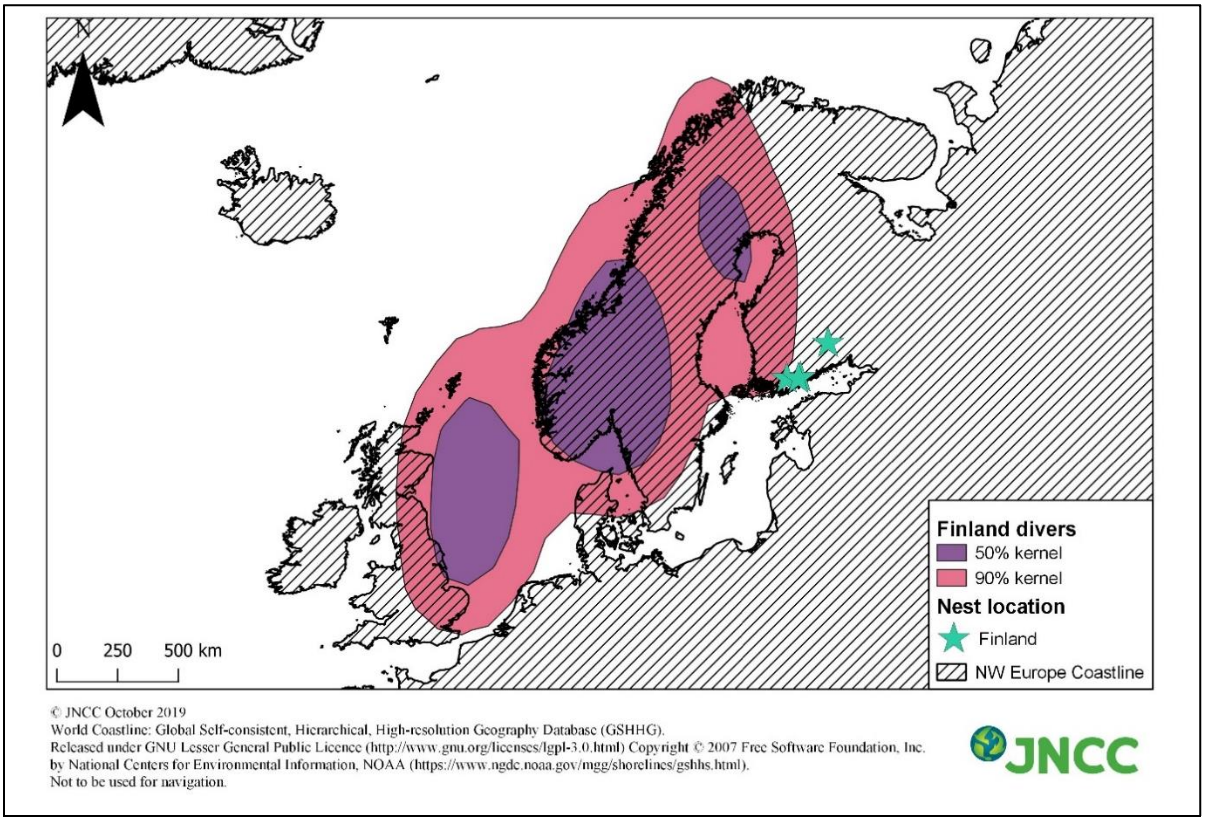

Figure 4. Non-breeding season (October 2018 to February 2019) core use area (50% density distribution kernel) and home range (90% density distribution kernel) for Finland-tagged birds (n=4). Note, the true location of these birds is likely to be further south than indicated by these kernels (see text for more information).

Closer examination of the GLS data for the four Finland divers showed divers to move westwards as the non-breeding season progressed, likely starting in the Gulf of Bothnia, in the Baltic Sea off western Finland, then around Denmark. Finally, in late winter two of the birds moved into the southern North Sea, while one remained around the coast of Denmark (Figure 5 to Figure 8).

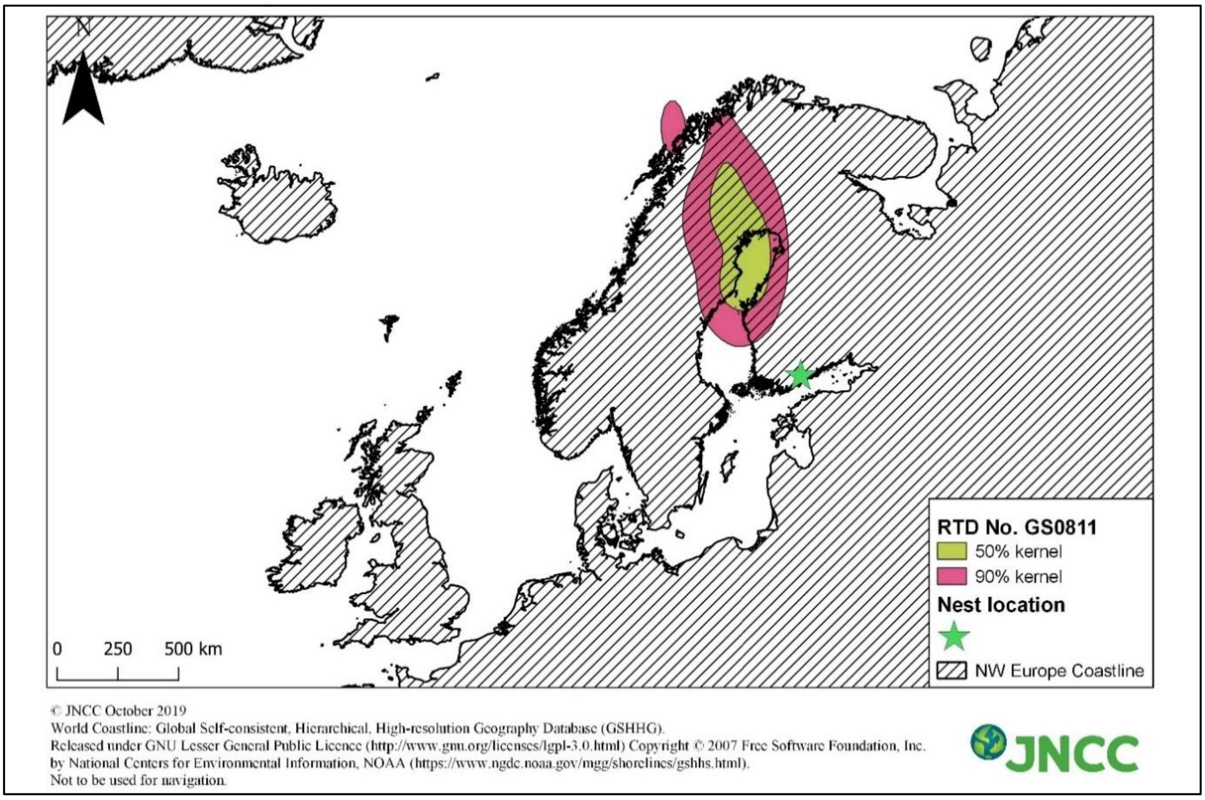

Figure 5. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number GS0811 for 12 Oct to 13 Nov 2018 when the tag failed. Note, the true location of these birds is likely to be further south than indicated by these kernels (see text for more information).

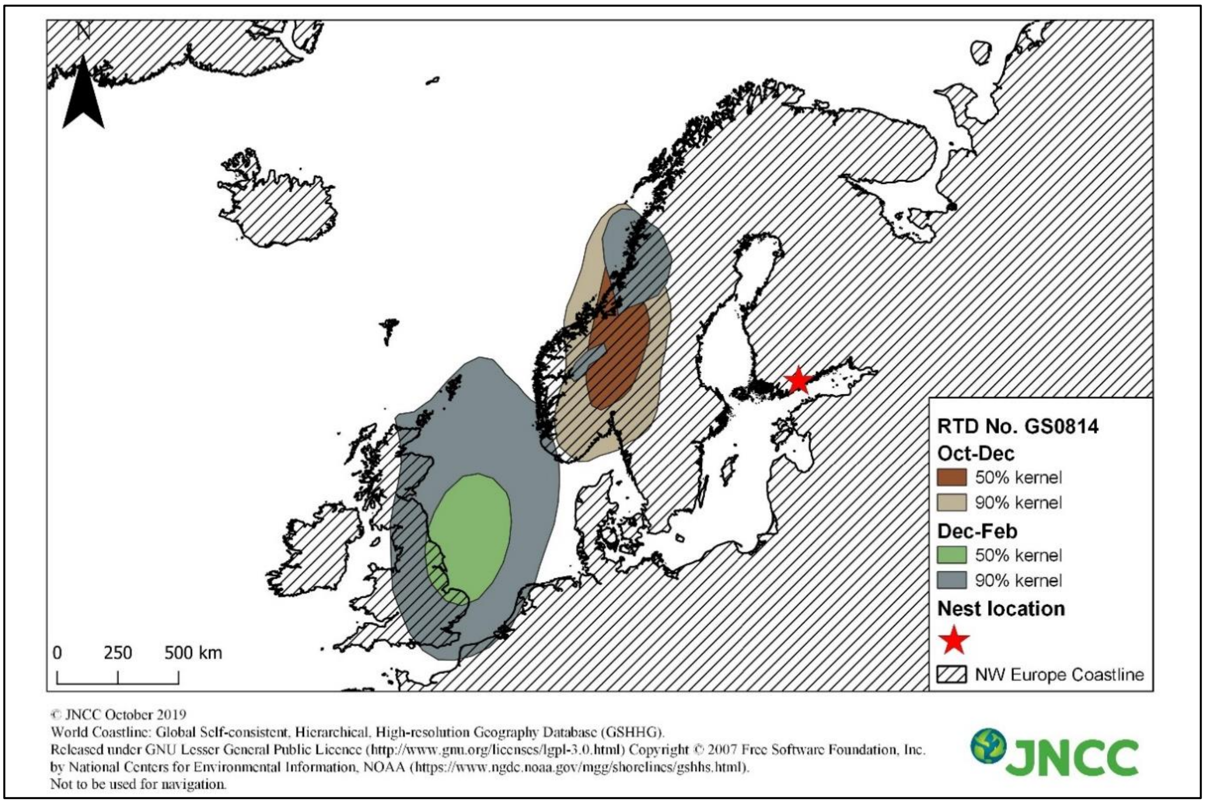

Figure 6. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number GS0814 for Oct-Dec 2018 and Dec 2018 to Feb 2019. Note, the true location of these birds is likely to be further south than indicated by these kernels (see text for more information).

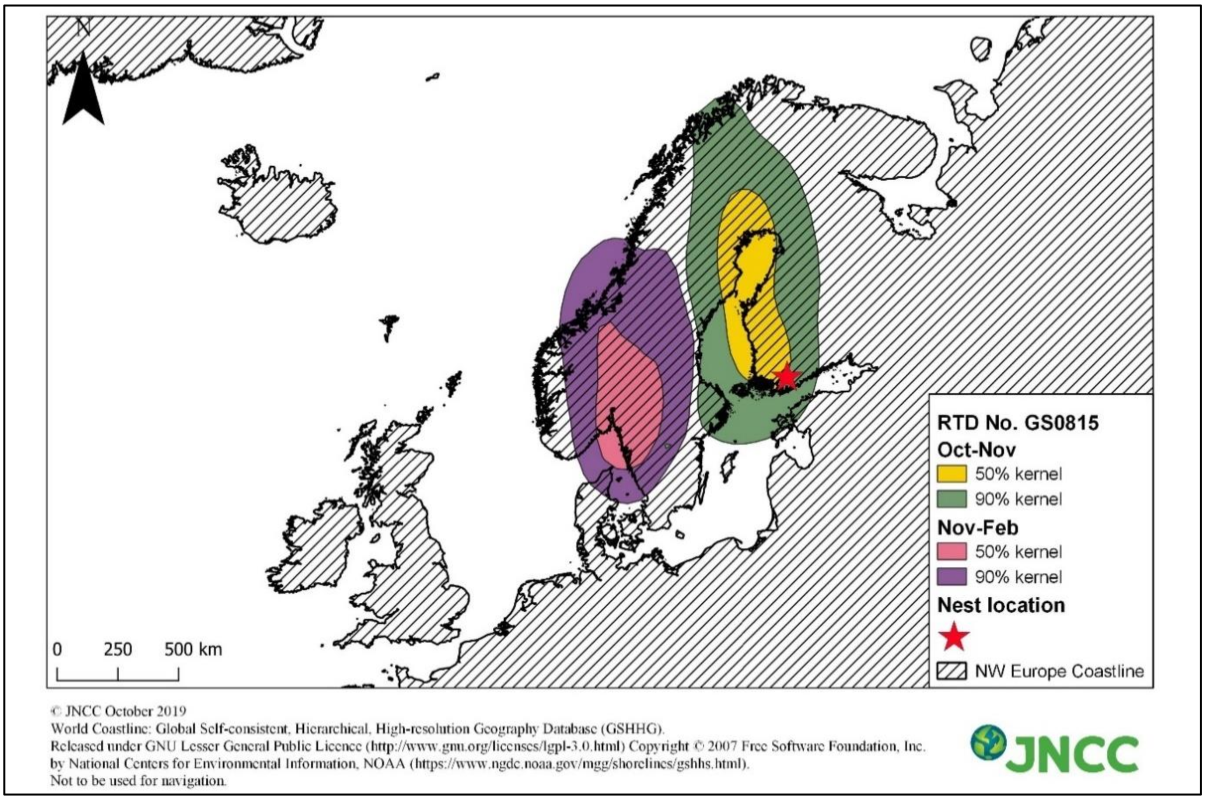

Figure 7. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number GS0815 for Oct-Nov 2018 and Nov 2018 to Feb 2019. Note, the true location of these birds is likely to be further south than indicated by these kernels (see text for more information).

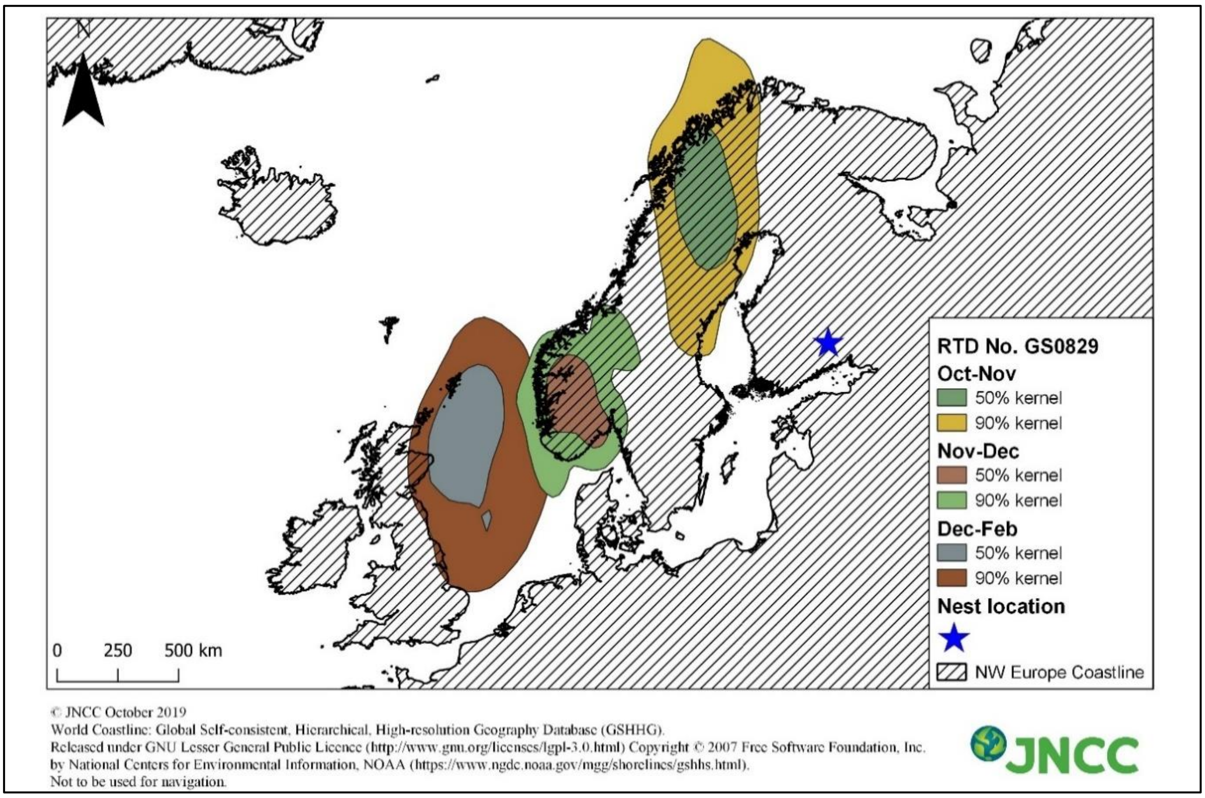

Figure 8. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number GS0829 for Oct-Nov 2018, Nov-Dec 2018 and Dec 2018-Feb 2019. Note, the true location of these birds is likely to be further south than indicated by these kernels (see text for more information).

3.3 Dive behaviour of red-throated divers

This report presents only preliminary descriptions of the TDR tag data. A more in-depth analysis will be undertaken once a second year of data have been obtained from the 2019/20 winter.

3.3.1 Quantity of data

The 21 TDR tags recorded data until the batteries failed. Most tags stopped recording in December 2018 or January 2019, with just two tags on birds from Iceland continuing until March 2019. This resulted in a data collection period of between 143 and 258 days, with an average of 217 days (see Table 1). Most tags recorded between 200 and 232 days of data but two tags failed earlier than expected, recording for 143 and 164 days and failing to record any data beyond the end of November 2018.

Number of days of data obtained from the 21 TDR tags, across all individuals and sites, was fairly consistent during July-November (see Figure 9). Number of data days were lower in June, as tags were deployed during June and so fewer data were recorded for the first part of the month prior to deployment. Most tags started to fail during December, with the number of data days declining by month until February and March when just two tags in Iceland were still recording data. More data days were acquired from birds in Finland and Scotland than Iceland due to more functioning tags being deployed and subsequently retrieved in Finland (n=8) and Scotland (n=8) than Iceland (n=5) (Figure 9).

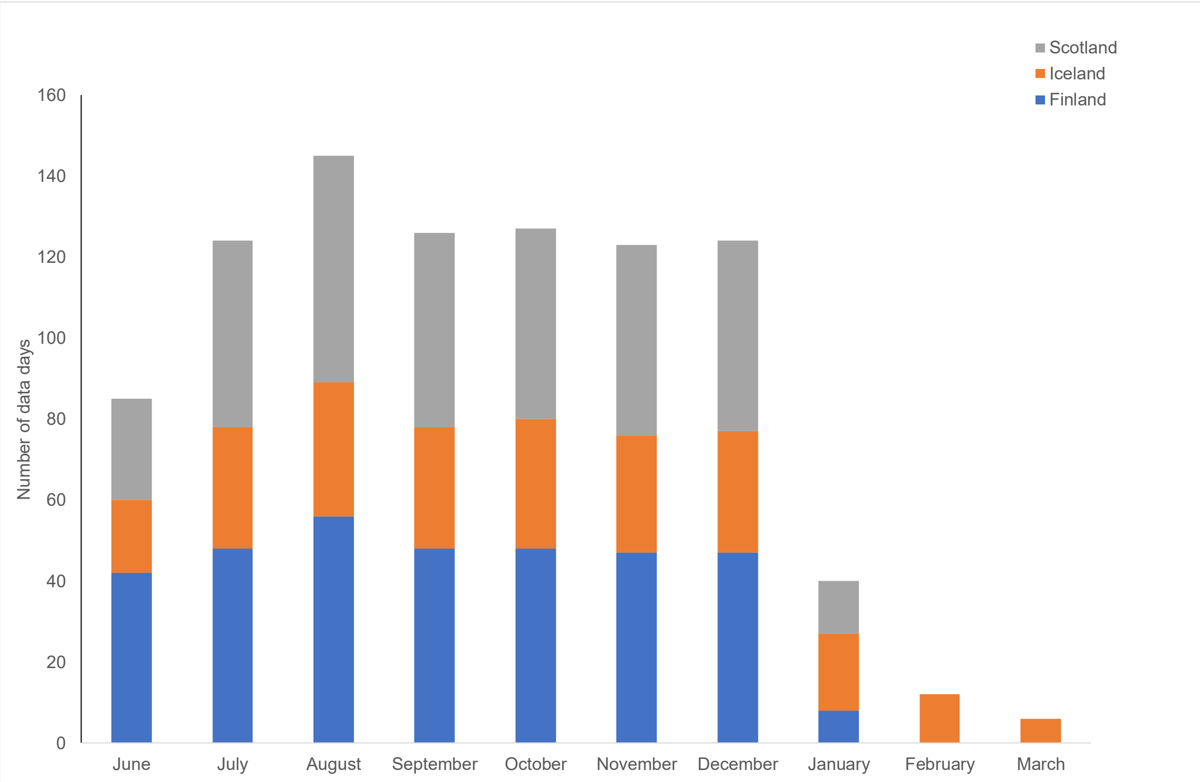

Figure 9. Number of days of data collected each month by TDR tags, across all individuals at each study site.

From June 2018 to March 2019, a total of 14,917 dive bouts from 21 individuals were recorded. The greatest number of dive bouts was from Finland birds (n=5,657 from eight individuals), then Scotland (n=5,442 from eight individuals) and then Iceland (n=3,818 from five individuals). From June 2018 to March 2019, the mean number of dive bouts recorded per individual was 710 bouts (range 440 to 882 bouts).

3.3.2 Dive bouts

The TDRs recorded dives that were grouped into bouts. Figure 11 shows three examples of dive bouts for two divers in winter 2018. These data show divers on these days largely not diving at all before around 09:00 or after around 17:00 or 19:00. Note, ‘Time’ corresponds to the tag’s internal clock, set to GMT+1 and not to local time, so periods of daylight and darkness experienced by these individuals cannot be inferred from ‘Time’. The plots show a marked difference in dive behaviour either side of midnight (no dives) compared with either side of midday (many dives). Dives were sometimes to the same depth (Figure 10a) or to very different depths (Figure 10c). The duration of a dive bout varied, e.g. Figure 10a shows a mix of short and long dive bouts. Rest time between dive bouts also varied with short rests (Figure 10b) or longer rests (Figure 10a and c).

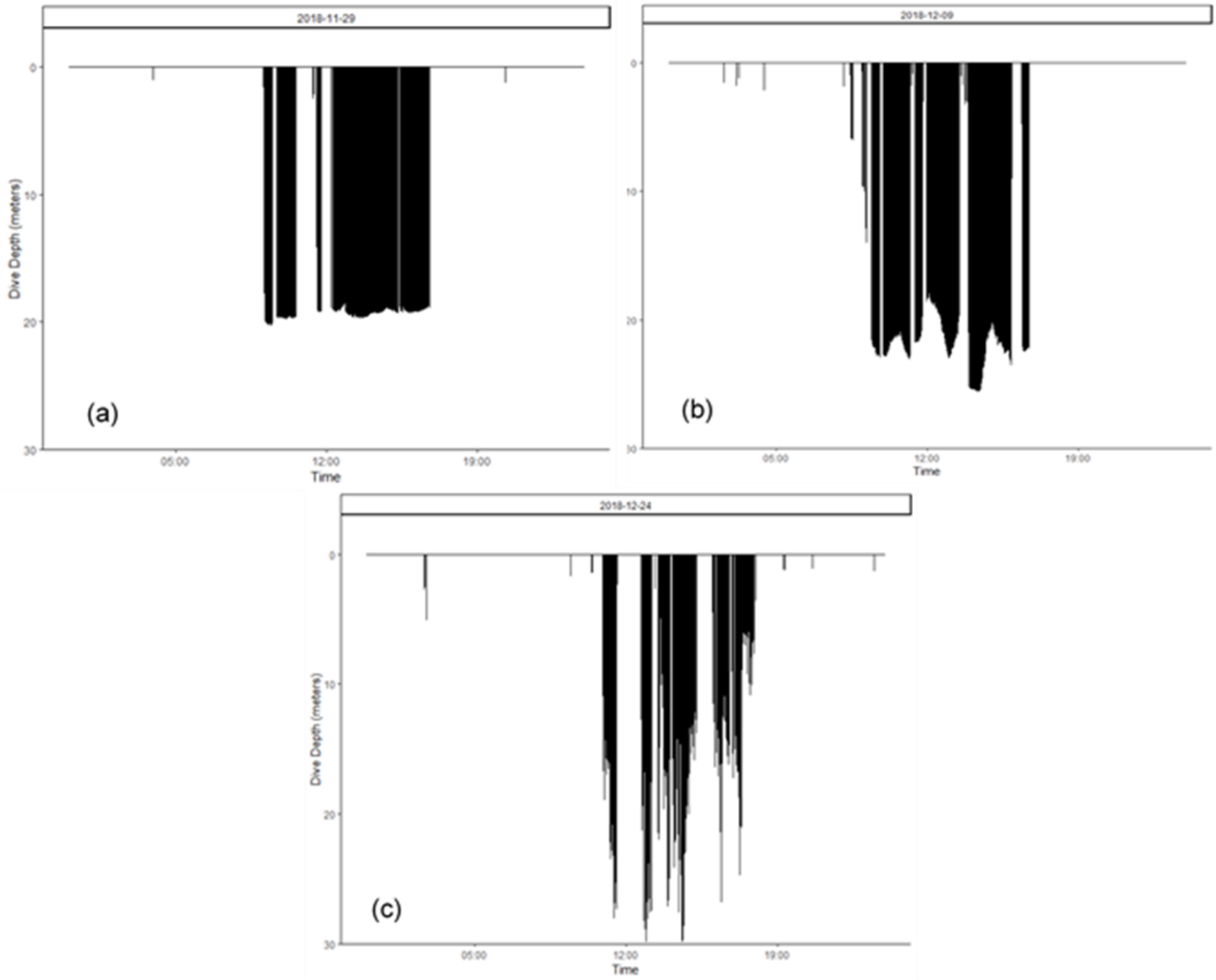

Figure 10. Example dive profiles for Finland RTD ring no. GS024 in (a) November, (b) December and for Shetland RTD ring no. 1173687 in (c) December. Note the inverse *y*-axis with the sea surface at the top of the plots.

3.3.3 Maximum Dive Depth

The frequency distribution of maximum dive depth (MDD) achieved during a dive was similar across all three sites despite divers using different habitat types in both the summer and winter. Divers performed relatively shallow dives, with most frequent MDDs of 2-6 metres (Figure 11). There is slight evidence of bimodality in MDD, with divers showing a second peak in their frequency distributions at slightly deeper depths of approximately 8-10 metres for Scottish and Finnish divers, although this was not seen in dives by Icelandic divers. Most dives (>95%) had an MDD of <20 metres (Finland), <17 metres (Scotland) and <14 metres (Iceland), with dives deeper than 30 metres very rare (0.1% of all dives). The deepest dive recorded was 41 metres.

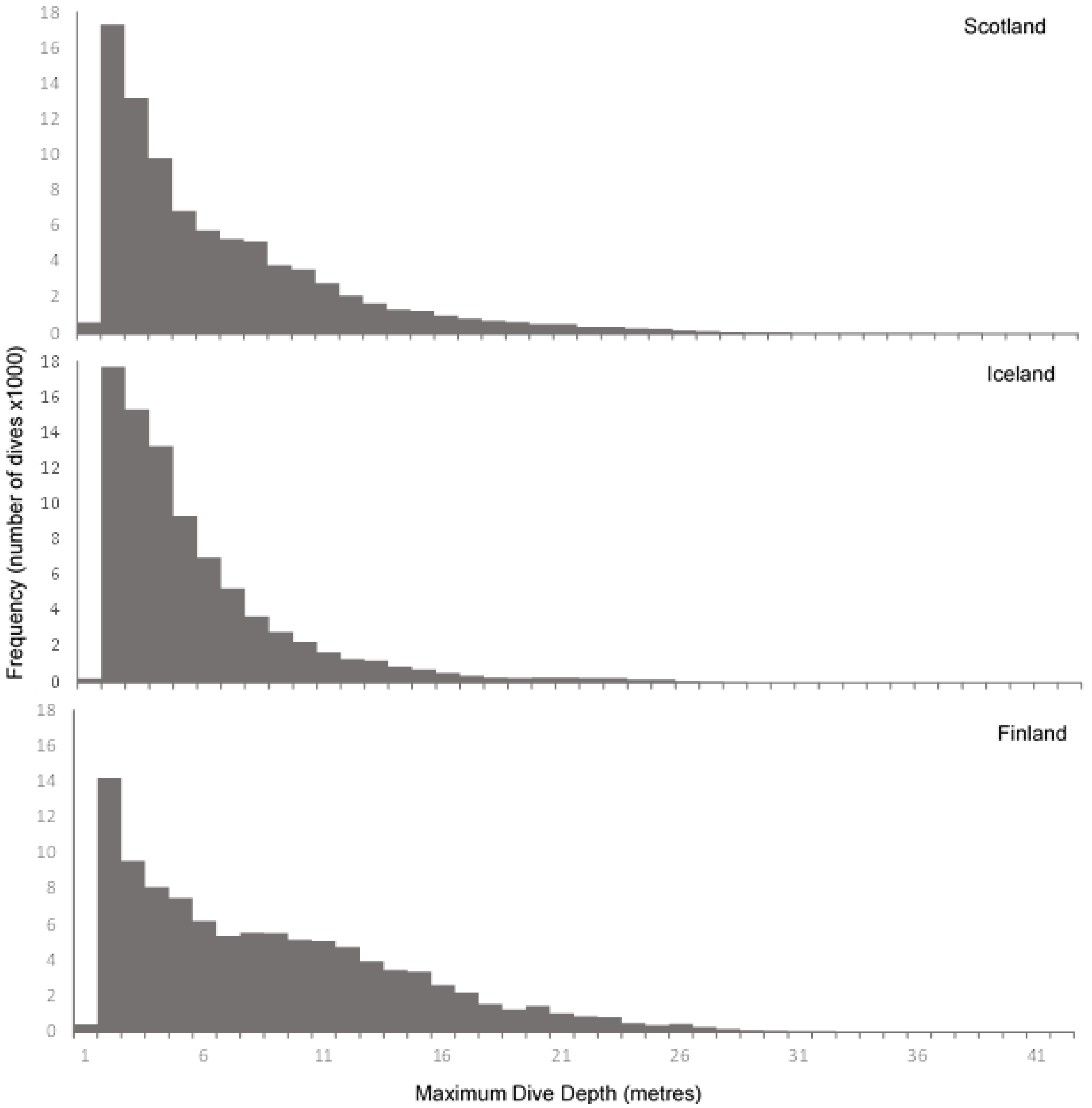

Figure 11. Frequency histograms of maximum dive depth (MDD) achieved during each dive for all individuals pooled across all months (June 2018 to March 2019) for birds in Scotland (n=86,592 dives), Iceland (n=86,024 dives) and Finland (n=102,475 dives).

During the breeding season (June-August), grand mean of MDD was relatively shallow, at around 4-6 metres (Scottish- and Icelandic-tagged divers) and 7-8 metres (Finnish-tagged divers) (Figure 12). Divers from Iceland tended to maintain a similar MDD into the non-breeding season, whereas divers from Finland and Scotland tended to have a progressively deeper MDD as the non-breeding season progressed. Divers from Scotland recorded a mean MDD of 9 metres in January, divers from Finland reaching a deeper mean MDD of 12 metres in December, although individual variation also increased during the non-breeding season for Finnish and Scottish divers. Finnish divers showed a decreased mean MDD in January.

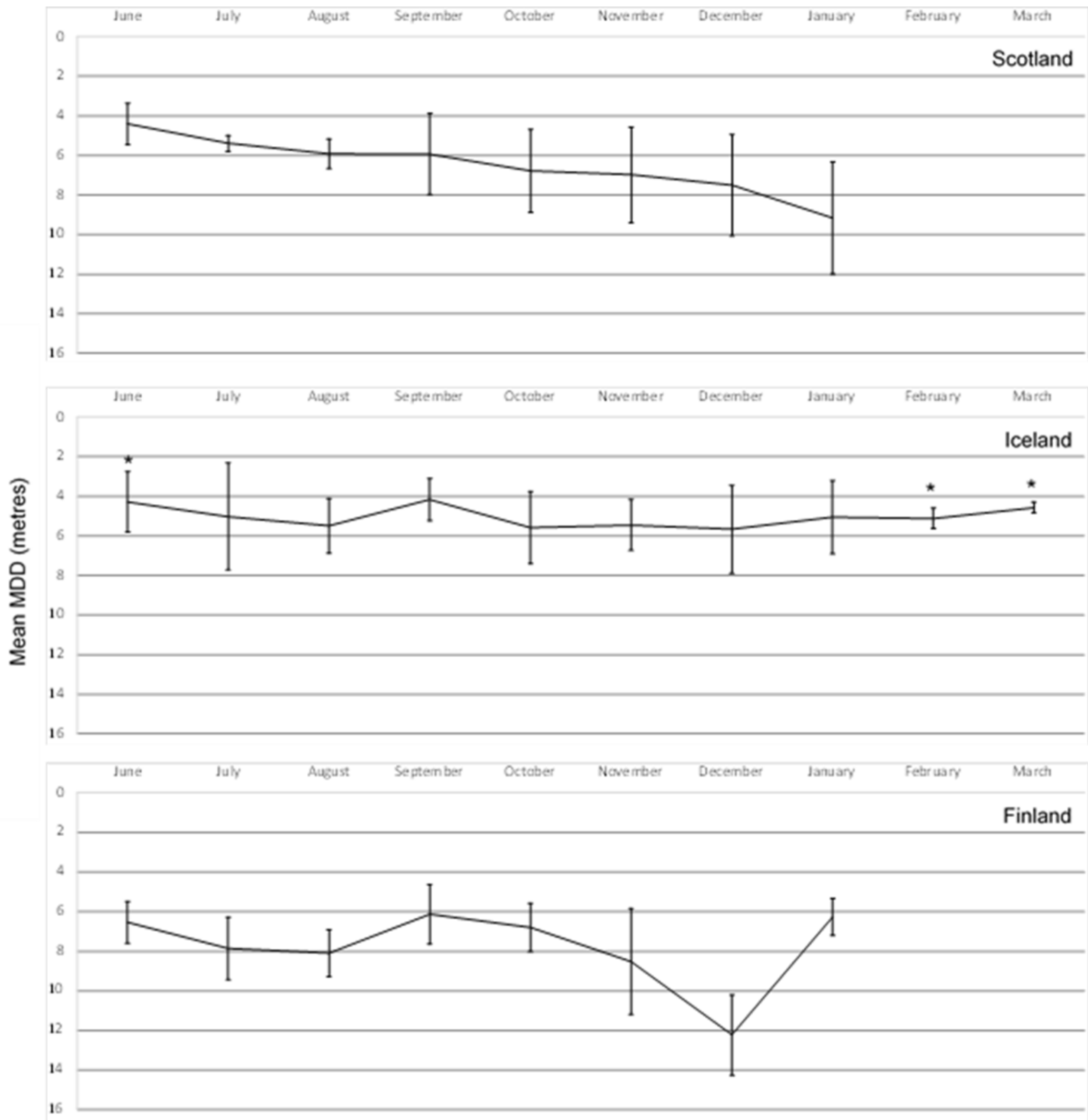

Figure 12. Grand mean and SD of MDD (Maximum Dive Depth) across all individuals from Scotland (n=8), Iceland (n=5) and Finland (n=8), for each month. Note the inverted *x*-axis with the water surface at the top of the axis. *small sample size, data from <5 individuals available for this month.

3.3.4 Dive Bout Duration

Dive Bout Duration (DBD) varied from 30 seconds to 230 minutes with substantial inter-individual variation in DBD in the mid-winter period (Figure 13). The grand mean DBD was approximately 10-15 minutes in the summer in Scotland and Iceland whereas it was longer, around 25 minutes, for divers breeding in Finland. By August and September, when divers are thought to undertake a post-breeding moult, mean DBD across sites was fairly consistent at around 10-15 minutes. However, as the non-breeding season progressed, mean DBD remained relatively constant for Scottish-tagged divers, reaching a maximum of 15 minutes, but gradually increased for Icelandic and Finnish tagged divers, to 25-30 minutes. Mean DBD appears to decline for Icelandic tagged divers in February and March but this may be due to the very small sample size of only two individuals.

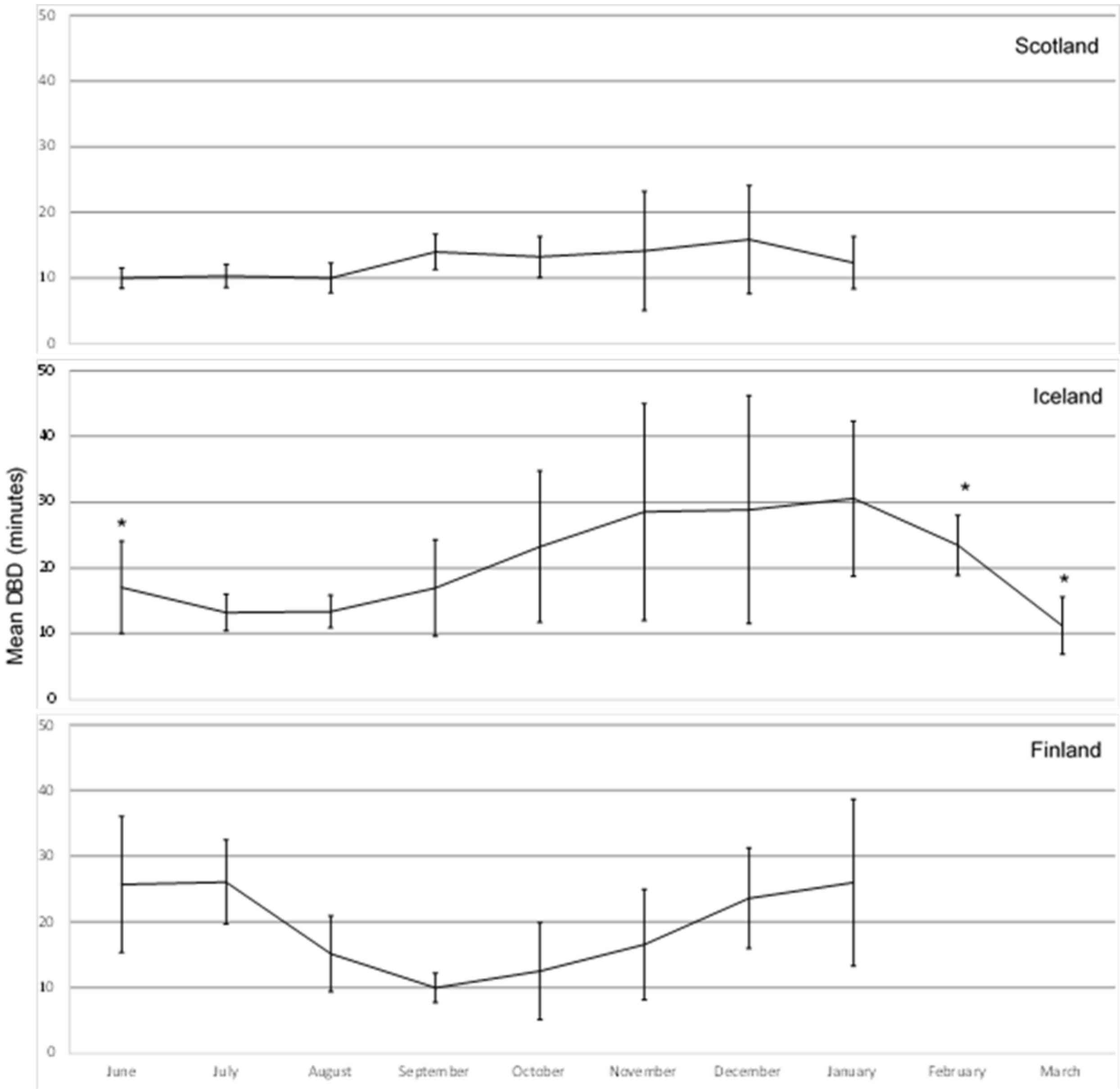

Figure 13. Grand mean and SD of dive bout duration (DBD) across individuals at a site, for each month. *small sample size, data from <5 individuals available for this month.

3.3.5 Daily Total Dive Bout Time

The daily Total Dive Bout Time (TDBT) varied greatly from 90 seconds up to >11 hours. Across June 2018 to March 2019, divers from Finland most frequently had a TDBT of 5-6 hours, from Iceland around 4 hours and from Scotland around 3 hours (Figure 14). Few birds had a TDBT of >8 hours per day, although birds tagged in Finland and Iceland did occasionally dive for up to 12 hours per day, unlike those tagged in Scotland where maximum TDBT was 8.5 hours.

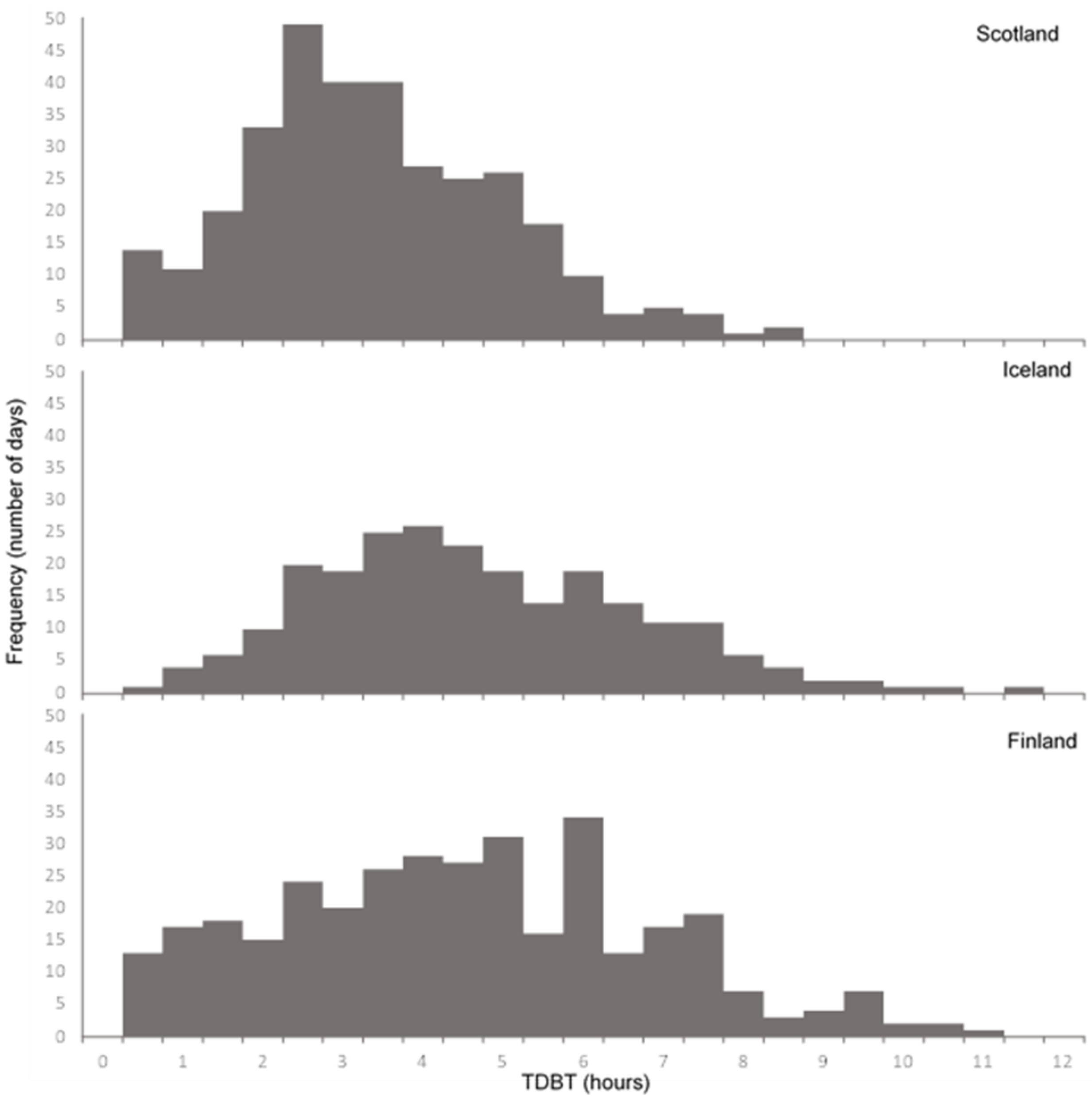

Figure 14. Frequency histograms of daily Total Dive Bout Time (TDBT) for each day for all individuals across all months (June 2018 to March 2019) for divers tagged in Iceland, Scotland and Finland.

Mean daily Total Dive Bout Time (TDBT) showed substantial inter-individual variation but was lower for Scottish tagged divers (mean TDB approx 3 hours per day) compared with Finnish and Icelandic tagged divers (mean TDB approx 4-5 hours per day) (Figure 15). The amount of time tagged red-throated divers spent diving each day was surprisingly consistent through time, especially for Scottish divers which consistently spent around 3 hours per day in dive bouts, across the whole study period. Icelandic and Finnish divers showed more variation in mean TDBT across the study period although not significantly so. The exception was Finnish birds in September, with a smaller standard deviation implying all birds exhibited a reduced TDBT this month.

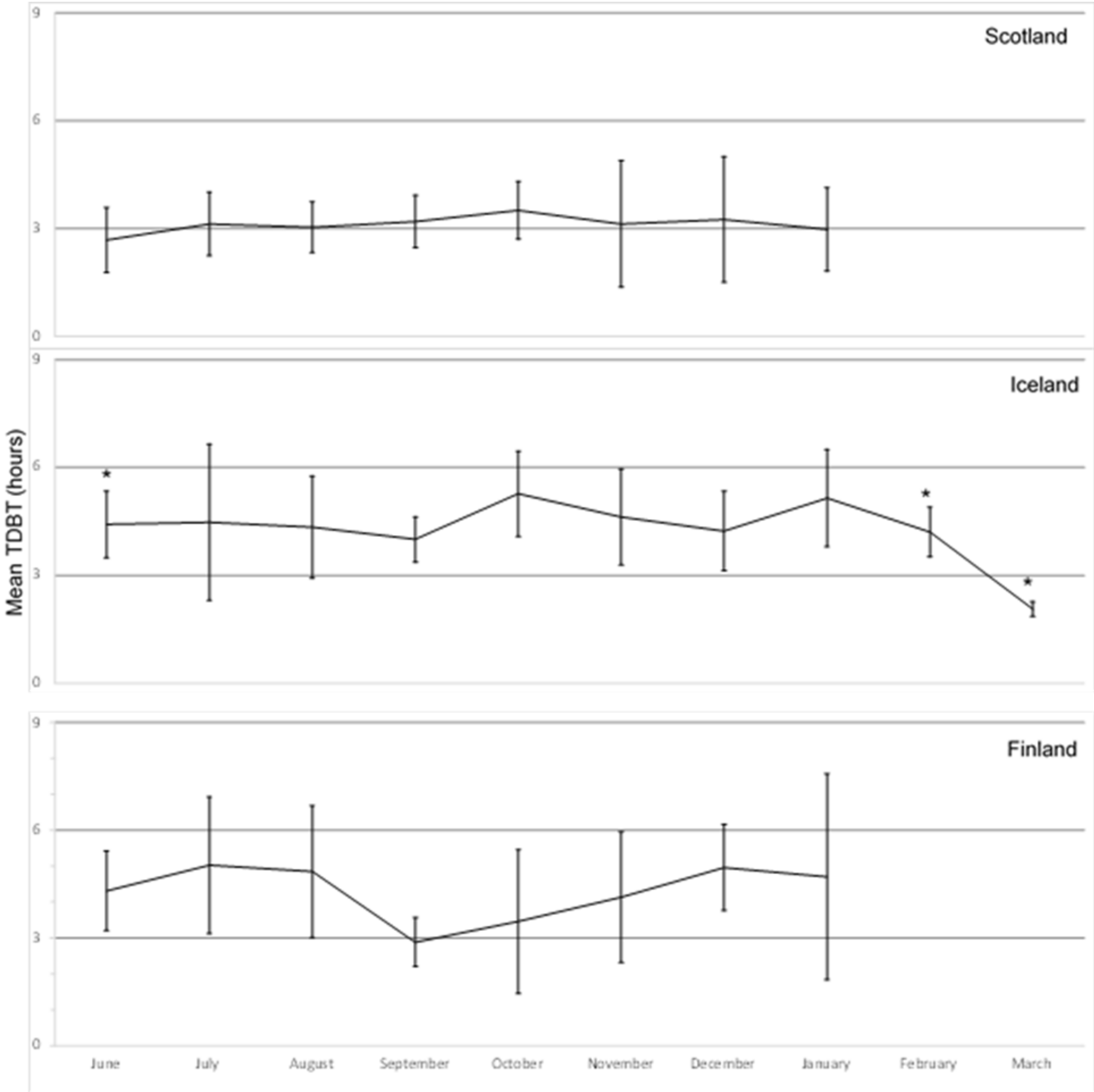

Figure 15. Grand mean and SD of daily Total Dive Bout Time (TDBT) across all individuals at a site, for each month. *small sample size, data from <5 individuals available for this month.

3.3.6 Diel Dive Activity

Diel Dive Activity (DDA) is a measure of consistency in activity among individuals at a site, showing when, in a 24-hour period, they undertake dive bouts. When DDA is at 1, all individuals are foraging and when at 0 no individuals are foraging. The timing of dive activity is recorded by the tag's internal clock, which was set to GMT+1 and so divers in different locations will be experiencing daylight at times that do not necessarily correspond to that of the TDR clock. Without matching GLS data for each tagged individual, light levels in each hour are unknown. DDA is presented for all days the loggers recorded during the non-breeding season (October 2018 to January 2019) (Figure 16). DDA showed a distinct pattern across all individuals and sites, with virtually no birds diving at the start and end of the 24-hour period, around midnight, and almost all birds diving at some points around noon (Figure 16).

There was a tendency for a higher proportion of birds to be diving around midday in December and January, compared with October. In mid-winter, almost all Finnish and Icelandic divers were diving in the middle of the day, whereas a smaller proportion of Scottish birds were diving in each hour. Icelandic divers were active for a shorter period in the mid-winter than Scottish and Finnish divers. Some plots show a slight dip around the middle of the 24-hour period, suggesting more divers tended to dive in the morning and evening around dawn and dusk than in the middle of the day.

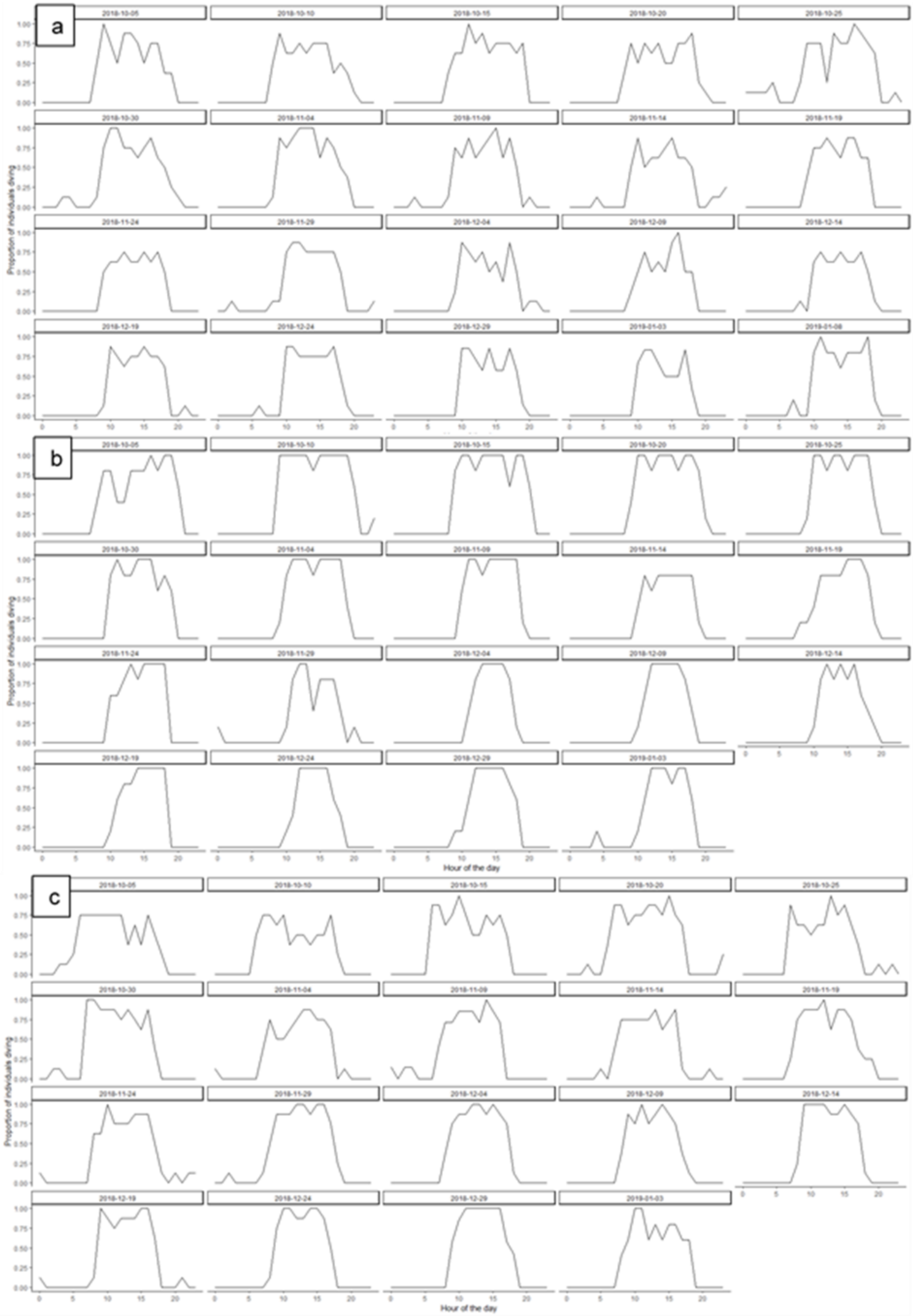

Figure 16. Diel Daily Activity (DDA) showing proportion of tagged individuals diving each hour (midnight to midnight). Each plot is for a 24-hour period, every five days, from 5 October 2018 to 3-8 January 2019, for birds tagged in (a) Scotland, (b) Iceland and (c) Finland.

4 Discussion

Prior to this study, TDR tags had never previously been deployed on red-throated divers in Europe. The Red-throated Diver Energetics Project aimed to obtain information on foraging behaviour of divers to provide insight and inference into the possible consequences of displacement by offshore wind development. This study demonstrates that, although not straightforward, it is possible to obtain empirical data on diving behaviour of divers during the non-breeding season. This information will be of great value in providing insight into the possible effects of displacement by offshore wind development on red-throated divers.

4.1 Location of tagged red-throated divers in the non-breeding season

Red-throated divers breeding in Scotland (n=4) and Iceland (n=7) were found to remain close to their breeding grounds, wintering in north western Scotland/Ireland and northern Iceland, respectively. Divers breeding in Finland (n=4), however, moved westwards from the Baltic Sea adjacent to Finland, to Denmark, as the non-breeding season progressed, with two individuals moving on to the North Sea.

Ring recovery data from the UK agree with the core use area and home range density kernels found for the four Scottish divers for which location data were available, with recoveries of Scottish ringed birds occurring all around northern Scotland (Okill 1994). Additionally, unpublished data on locations of Scottish and Icelandic divers previously tagged with geolocators show agreement with the locations of divers found in this study. Individuals remained close to their breeding grounds with the exception of one Scottish diver that was found to be off the coast of Norway (*pers obs.,* I.K. Petersen & Daunt). Both ringing recoveries and GLS data suggest that Scottish divers are not using Liverpool Bay which regularly supports large numbers of red-throated divers each winter (O'Brien *et al.* 2008). Ring recoveries from divers ringed in Finland show strong agreement with the GLS results found here, with recoveries occurring all along the coasts of the Baltic, around Denmark and the southern North Sea (Saurola *et al.* 2013). Additionally, another three red-throated divers previously equipped with GLS tags, were found to also move through the Baltic in to the North Sea during the non-breeding season (*pers. obs.*, I.K. Petersen).

Finnish divers were probably wintering further south than is indicated by the density distribution kernels presented in this report. Initial investigation of the GLS and TDR data indicate this might be caused by divers' leg-tucking, as also found in auks equipped with TDR tags (Elliott & Gaston 2014). Curiously, leg-tucking seemed less prevalent for Scottish and Icelandic divers and consequently, their core area and home range density kernels are likely to be more representative of actual locations. There is no evidence that divers were preferentially leg tucking around dawn over dusk or vice versa. This is important as if divers tended to leg tuck more at dawn than dusk this would push kernels westwards (i.e. GLS tag would record a later 'dawn' than reality) and conversely, preferentially leg tucking at dusk would push kernels eastwards. Further analysis of leg tucking behaviour will be undertaken, using the wet/dry information on the GLS tag and temperature from the TDR tag in combination. Inference from extent of leg tucking will be used to try and correct predicted locations. Further shading of the GLS tag could also have been caused by tags becoming loose and rotating on the darvic ring to sit beneath the diver's body.

4.2 Diving behaviour of red-throated divers

These novel dive data for red-throated divers in the non-breeding season show that generally, red-throated divers are choosing not to dive to great depths, unlike some other diving birds, (e.g. Green *et al.* 2005). Whilst a maximum dive depth of 41 metres was recorded during the 2018/19 breeding season, most frequently maximum dive depth (MDD) was only 2-6 metres and 95% of MDD were <14-20 metres, depending on the site. Mean MDD was relatively shallow across sites in the breeding season, approximately 4-6 metres in Scotland and Iceland and 7-8 metres in Finland, during June to August. During the breeding season, divers in Finland forage in deep freshwater lakes (*pers. obs*., P. Lehikoinen; Duckworth *et al.*, *in press*) whereas divers in Iceland and Scotland forage in marine habitats, close to the coast in shallow sandy bays (*pers. obs*., S. O'Brien; Black *et al.* 2015) and so would be expected to have lower MDD than Finnish divers. As the non-breeding season progressed, mean MDD remained relatively constant for Icelandic divers whereas mean MDD increased for Finnish and Scottish tagged divers. In January, mean MDD for Finnish divers decreased to six metres. Speculatively, this may relate to a change in habitat and foraging strategy, with some divers moving through to the North Sea in January and February.

There was substantial individual variation in mean MDD suggesting that individuals may have different foraging strategies and/or have preferred individual foraging areas during the non-breeding season. It is not currently known whether red-throated divers are generally pelagic or benthic feeders, but more detailed analysis of dive profiles obtained from the TDR tags should reveal this. Red-throated divers around the UK are most frequently recorded in shallow water with a sandy substrate and rarely in water of >20m depth (e.g. Irwin *et al.* 2019), suggesting they may be benthic feeding. However, divers are also known to aggregate around estuarine fronts, suggesting they are using predictable hydrographic features which increase prey availability (Skov & Prins 2001; Skov *et al.* 2016).

Mean dive bout duration (DBD) was relatively consistent for Scottish birds, across both the breeding and non-breeding seasons, at approximately 10-15 minutes per bout. Mean DBD for Icelandic and Finnish divers increased as the non-breeding season progressed to a peak of approximately 25-30 minutes in January. However, DBD has limited information about how much time divers are spending foraging as a diver might have a few long or many short bouts.

A better metric of foraging effort per day is mean daily Total Dive Bout Time (TDBT) was lower for Scottish birds, at approximately 3 hours per day, compared with Finnish and Icelandic divers, at approximately 4-5 hours per day, although there was substantial individual variation among all sites and months. It is not clear why Scottish birds should need to spend less time foraging than Finnish or Icelandic birds. Individuals from Iceland, wintering further north in colder waters, would be expected to have higher foraging effort and energy expenditure than individuals from Scotland, wintering around the UK, as was seen for Atlantic puffins (*Fratercula arctica*) (Fayet *et al.* 2017). However, observed TDBT for divers tagged in Finland was higher than would be expected, based on their wintering locations in the southern North Sea and western Baltic, i.e. we would expect TDBT for Finnish birds to be similar to Scottish birds and lower than Icelandic birds. TDBT was relatively consistent across the study period, which is as might be expected given the sequential nature of the high energetic demands of breeding, moulting and wintering.

Diel Daily Activity (DDA) was investigated as light levels experienced by all divers at all times was not available. This partly due to failure and loss of both TDR and GLS tags, meaning combined information from both TDR and GLS tags were available for only ten divers. Additionally, marrying GLS and TDR data is a complex procedure and beyond the scope of this preliminary results report. Consequently, whilst dive activity throughout the 24-hour period was known, the times of daylight and darkness were not, as they are location dependent. DDA indicates when all divers from a site are diving at the same times of day. The DDA plots show high consistency among individual divers from a site, with no divers diving for long periods either side of midnight. This strongly suggests that divers are unwilling to dive at night, perhaps because it is too dark for these visual feeders to forage or because prey are unavailable at night. By contrast, during mid-winter, almost all Icelandic and Finnish birds were diving for a period either side of midday. Further evidence for divers being unwilling to forage at night can be seen in the gradual reduction in the hours when any diver was diving during the period from October to December and that the period of activity was of shorter duration for Icelandic birds, wintering at higher latitudes than Scottish and Finnish birds. Actual hours of daylight and darkness will be available for individuals where sufficient data from both the TDR and GLS tag were obtained, once the two data sets are combined. From this, it will be possible to confirm that red-throated divers choose not to dive and forage at night.

As with any novel study, multiple challenges and difficulties were encountered during tag deployment and retrieval. Briefly, recapturing tagged divers proved very time consuming and challenging, particularly where it was necessary to catch divers on the nest. A high proportion of the GLS tags malfunctioned due to a manufacturing fault. Sourcing tags from another manufacturer would avoid this problem and improve the quantity of GLS data obtained. A few TDR tags worked free of the epoxy resin and cable ties holding them onto the darvic rings. Use of self-amalgamating tape would assist with preventing tag loss. TDR tags were not capable of recording for the full 12-month period. The battery life of these small TDR tags currently precludes obtaining data during the March-June period and whilst other tags with longer-life batteries are available, they are significantly larger than tags deployed to date. Some tags were started up to three weeks before deployment in some cases and the sampling regime was relatively frequent (every five days). However, the sampling regime doesn’t greatly alter battery life and whilst tags could be started immediately prior to deployment, it is likely to only extend the period of recording by up to three weeks, into January.

The aim of the Red-throated Diver Energetics Project is to assess whether divers face an energetic bottleneck during the non-breeding season, when they are more likely to be displaced due to using areas of offshore wind development. This requires use of the dive data presented in this report as well as other information, to understand diver energetics at different times of year. This is beyond the scope of this report which only aims to present a descriptive analysis of data collected so far on diver foraging behaviour. With further data collected during the 2019/20 non-breeding season and a more comprehensive detailed analysis that integrates multiple data sources, we will investigate whether divers undergo an energetic bottleneck in the non-breeding season.

5 Conclusions and Recommendations

Sample sizes acquired in this study were small and so conclusions drawn from these data are not as robust as if informed by data from more divers and from multiple years. Results presented in this report are only preliminary analyses of a subset of all data. Analysis of a second year of TDR and GLS data, along with stable isotope analysis of feather samples, as well as a more thorough and sophisticated investigation of these data, will be undertaken during 2020/21. This could change our understanding of red-throated diver foraging behaviour and energetics and consequently, the preliminary results presented in this report should not be used to make inference about the effect of offshore wind development on red-throated divers.

6 Acknowledgements

We are grateful to The Crown Estate, Ørsted, Equinor, Vattenfall and UK Department for Business, Energy and Industrial Strategy’s Offshore Energy SEA programme (via Hartley Anderson Ltd) for providing funding for this project. The Natural Environment Research

Council (NERC), University of Liverpool and JNCC are providing funding, via the ACCE DTP, for a CASE PhD studentship to analyse data collected during this project. Funding for some of the tags deployed in Iceland and fieldwork costs was provided by the Icelandic Ministry for the Environment and Natural Resources.

We are indebted to all the fieldworkers involved with deploying and retrieving these tags, as well as those who advised on and helped with catching and ringing divers and provided us with information on diver breeding success. Guðmundur Ö. Benediktsson (a co-worker with Aevar Petersen), Moray Souter, Mark Lewis, Pete Ellis, George Petrie, Kerstin Kroeger, Karen Hall, Gus Routledge, Ruth Williams, Kerstin Kober, Matt Parsons, Nick Moore, Thomas Cornulier, Julia Sutherland, Marc Illa Llobet, Jari Laitasalo, Tuula Kyllönen, Aleksi Lehikoinen, Jarkko Santaharju, Veli-Matti Väänänen, Petri Nummi, Jani Suua, Markku Vakiala, Kalevi Eklöf, Heikki Helle, Teemu Lehtiniemi, Markus Piha, Jari Valkama.

We are also grateful to all those involved with providing permission to undertake this work including the Centre for Economic Development, Transport and the Environment in Finland, the National Parks, Finland, the British Trust for Ornithology, Scottish Natural Heritage and the Royal Society for the Protection of Birds.

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Appendix 1: Location maps for divers tagged in Iceland and Scotland

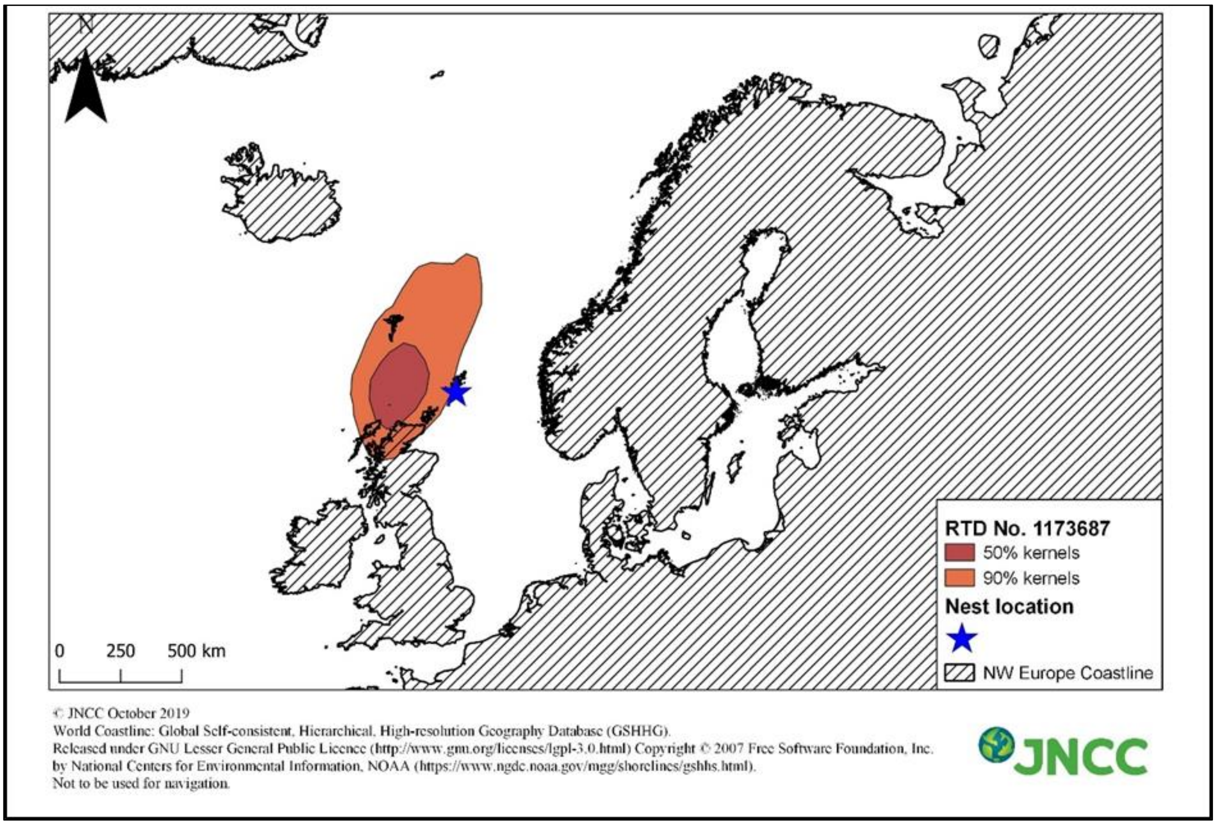

Figure 18. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number 1173687, 0ct 2018 to Feb 2019.

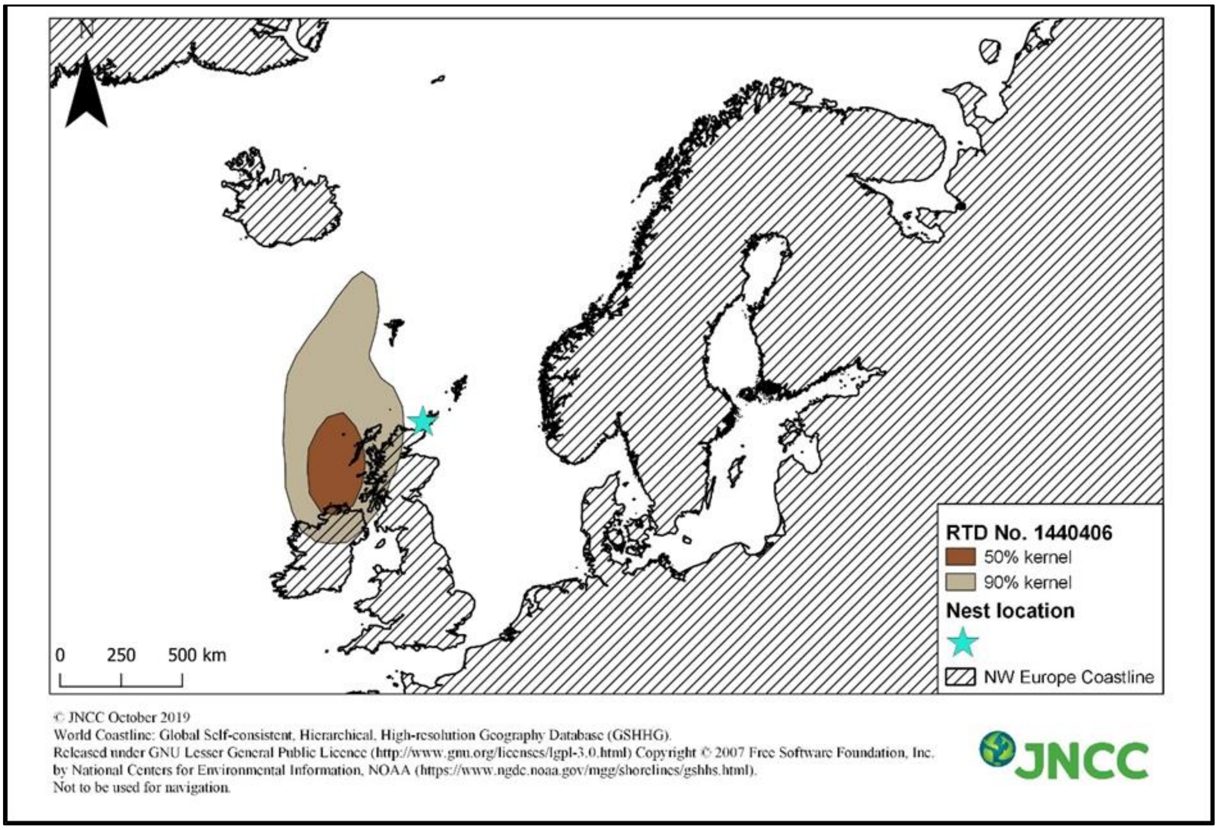

Figure 19. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number 1440406, 0ct 2018 to Feb 2019.

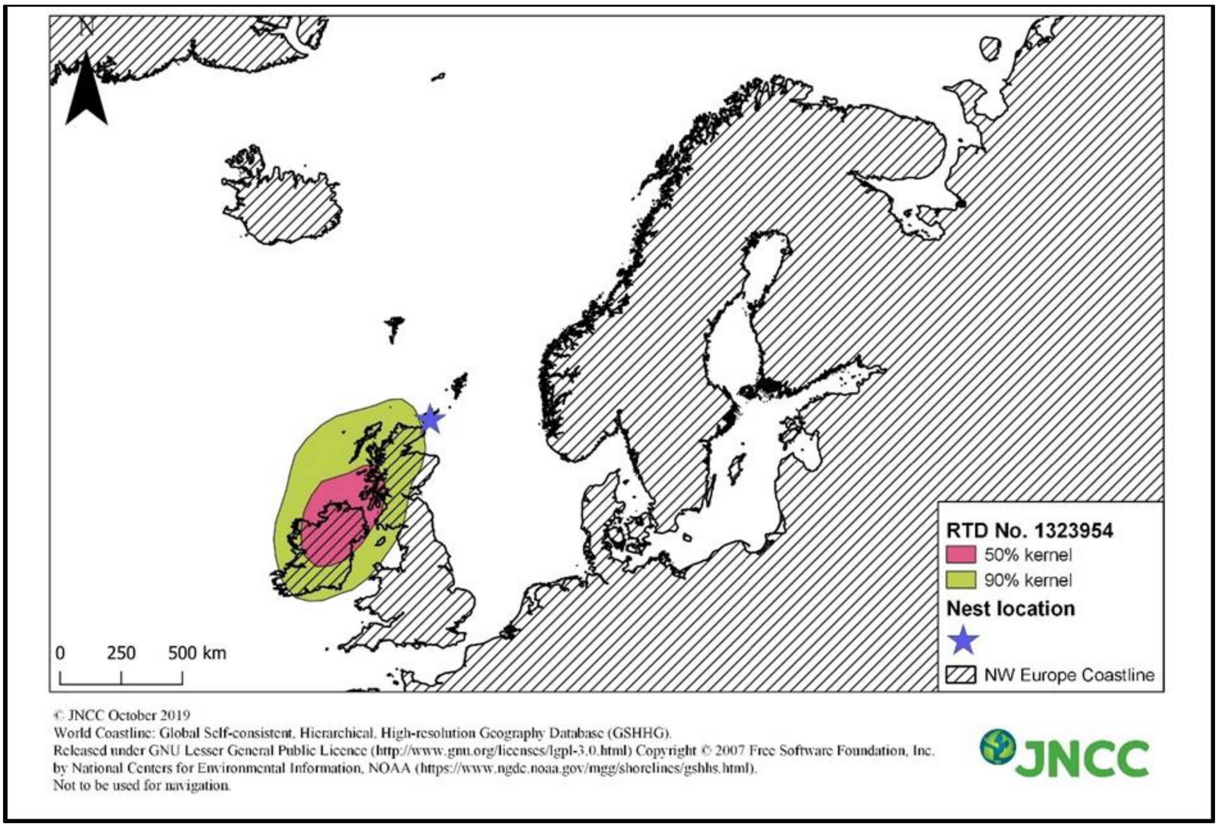

Figure 20. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number 1323954, 0ct 2018 to Feb 2019.

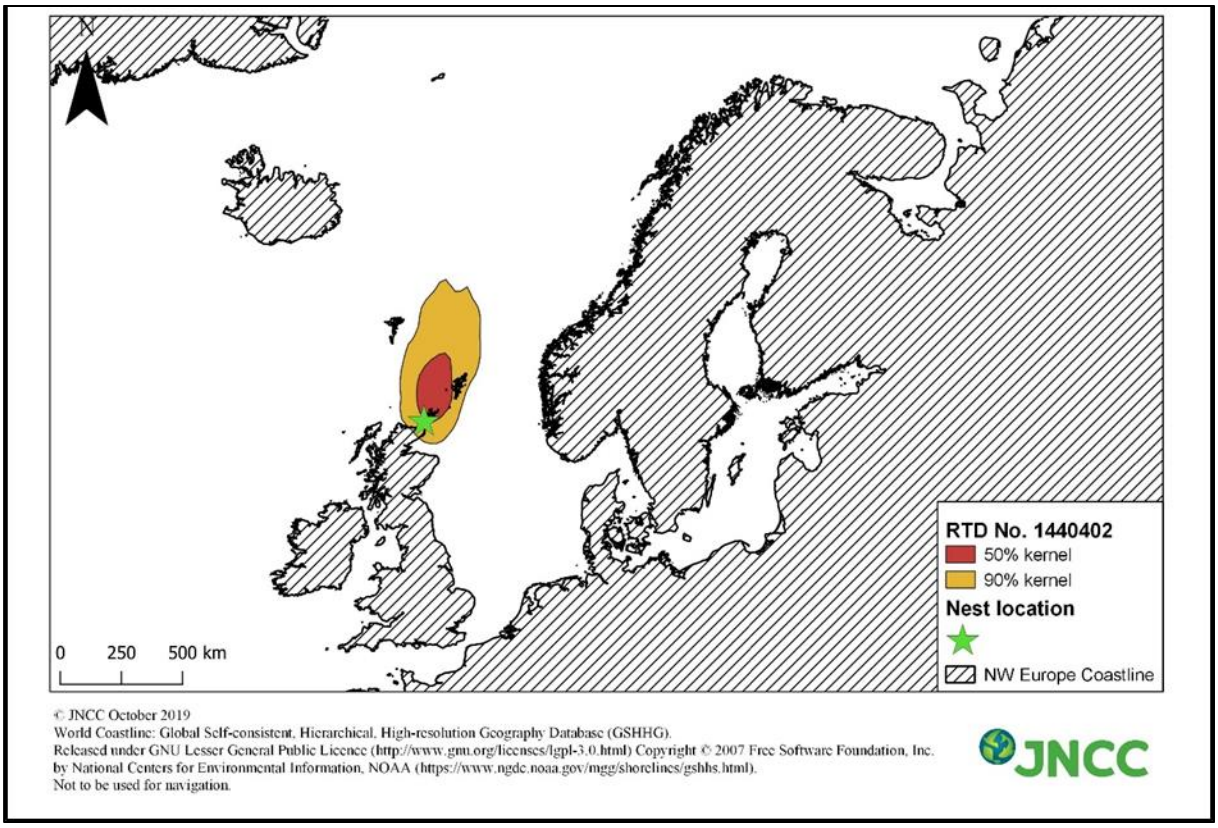

Figure 21. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number 1440402, 0ct 2018 to Feb 2019.

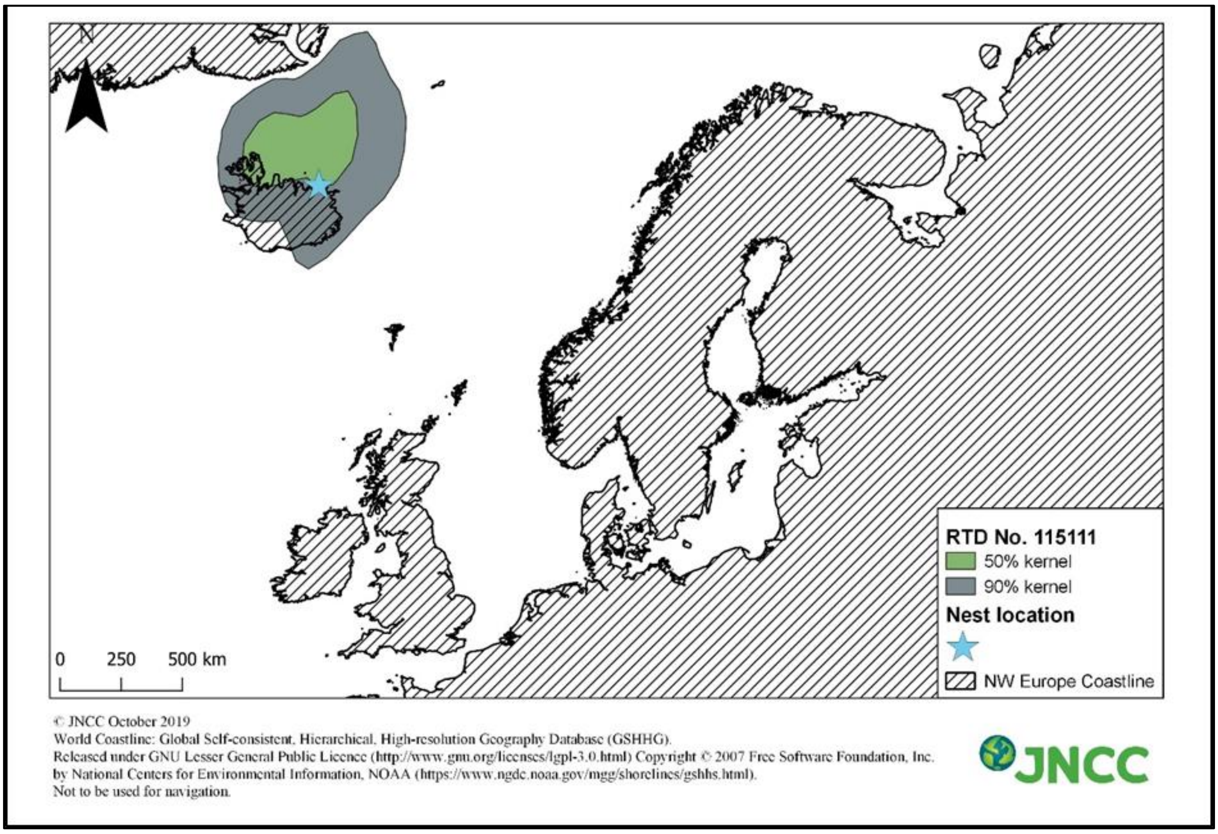

Figure 22. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number 115111, 0ct 2018 to Feb 2019.

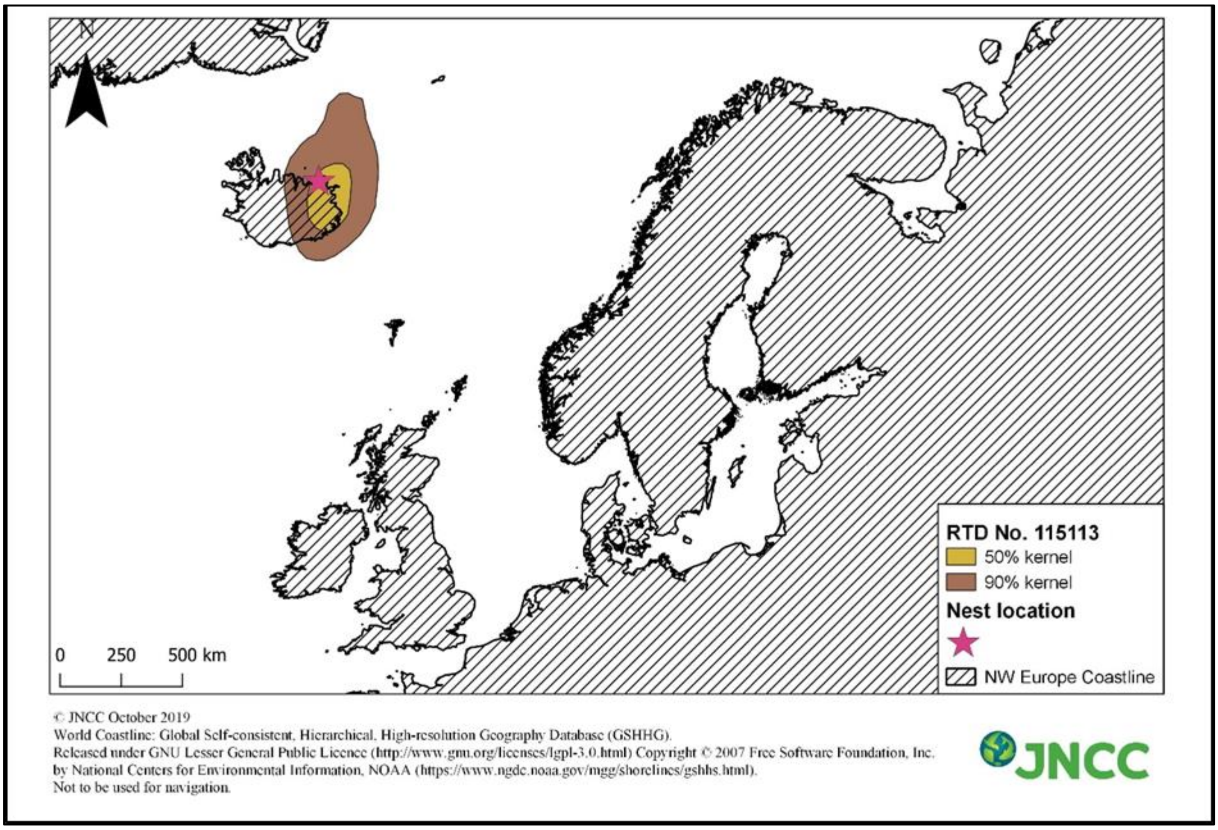

Figure 23. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number 115113, 0ct 2018 to Feb 2019.

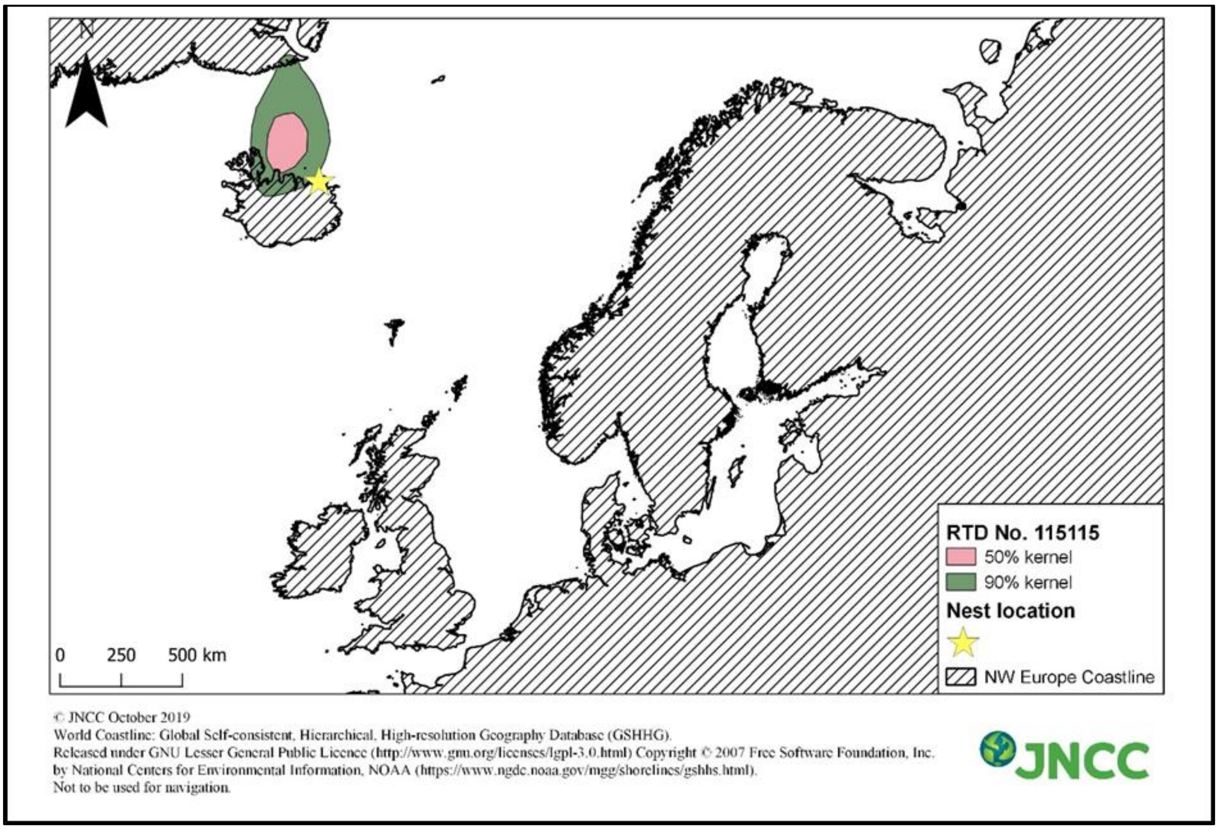

Figure 24. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number 115115, 0ct 2018 to Feb 2019.

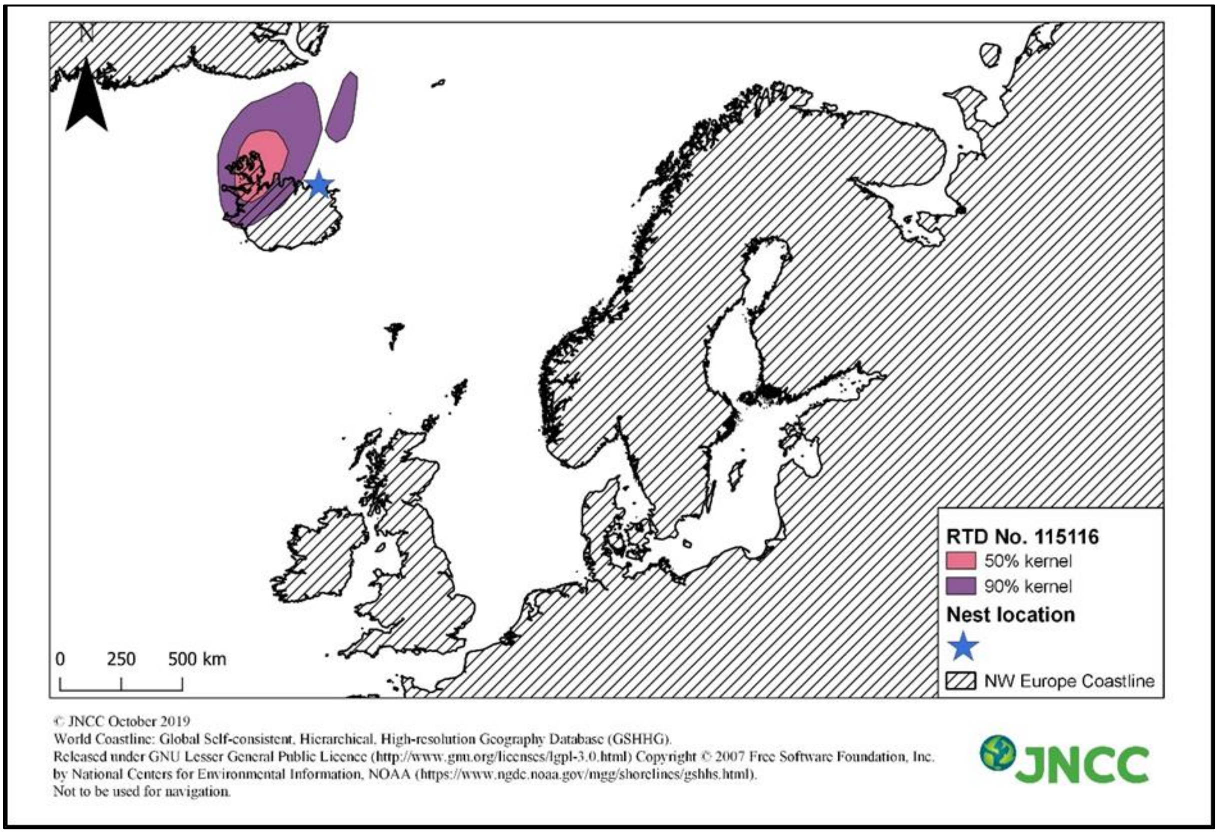

Figure 25. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number 115116, 0ct 2018 to Feb 2019.

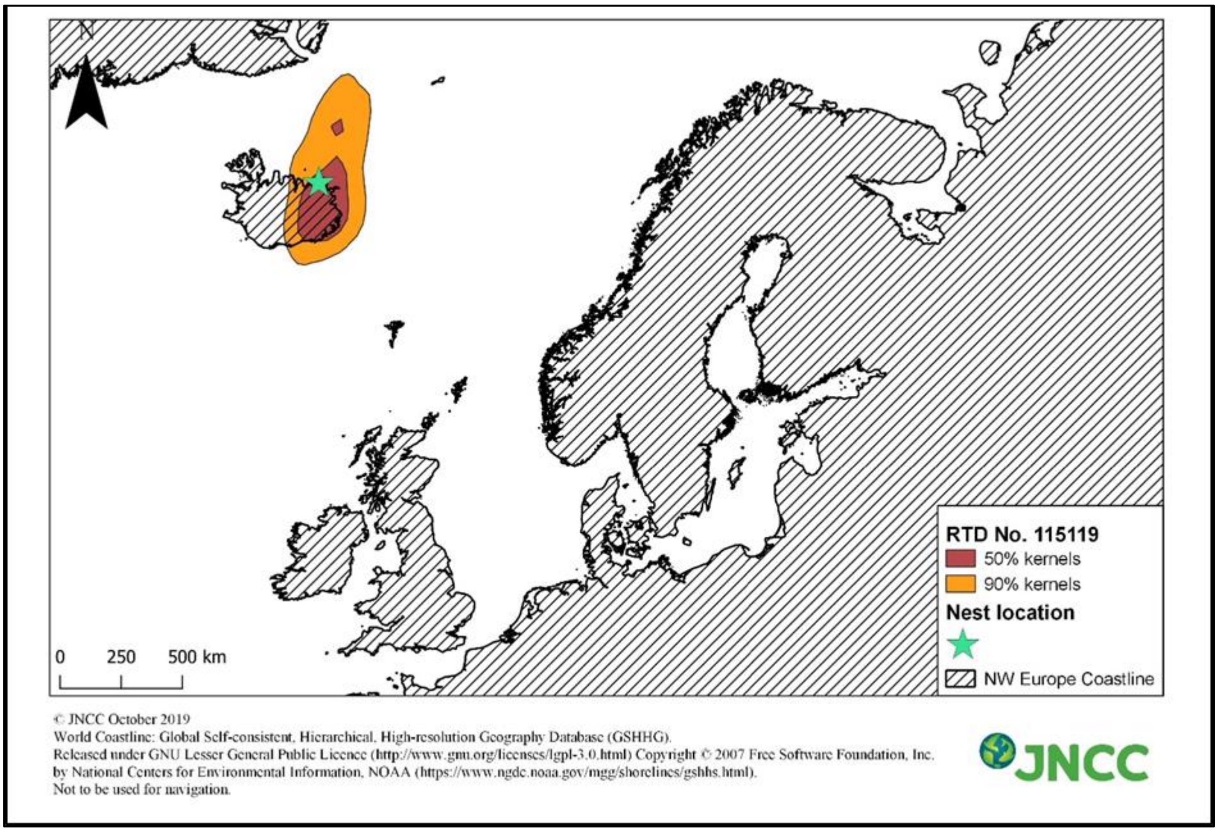

Figure 26. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number 115119, 0ct 2018 to Feb 2019.

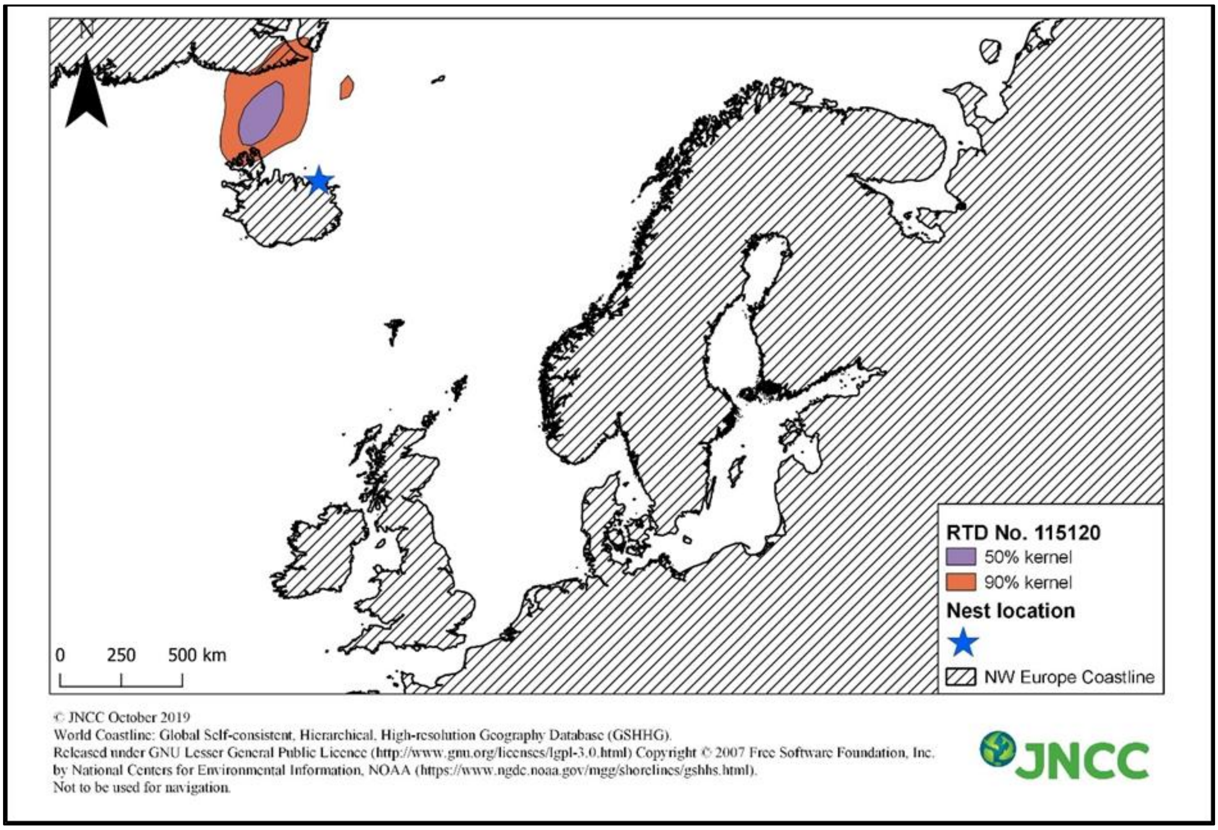

Figure 27. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number 115120, 0ct 2018 to Feb 2019.

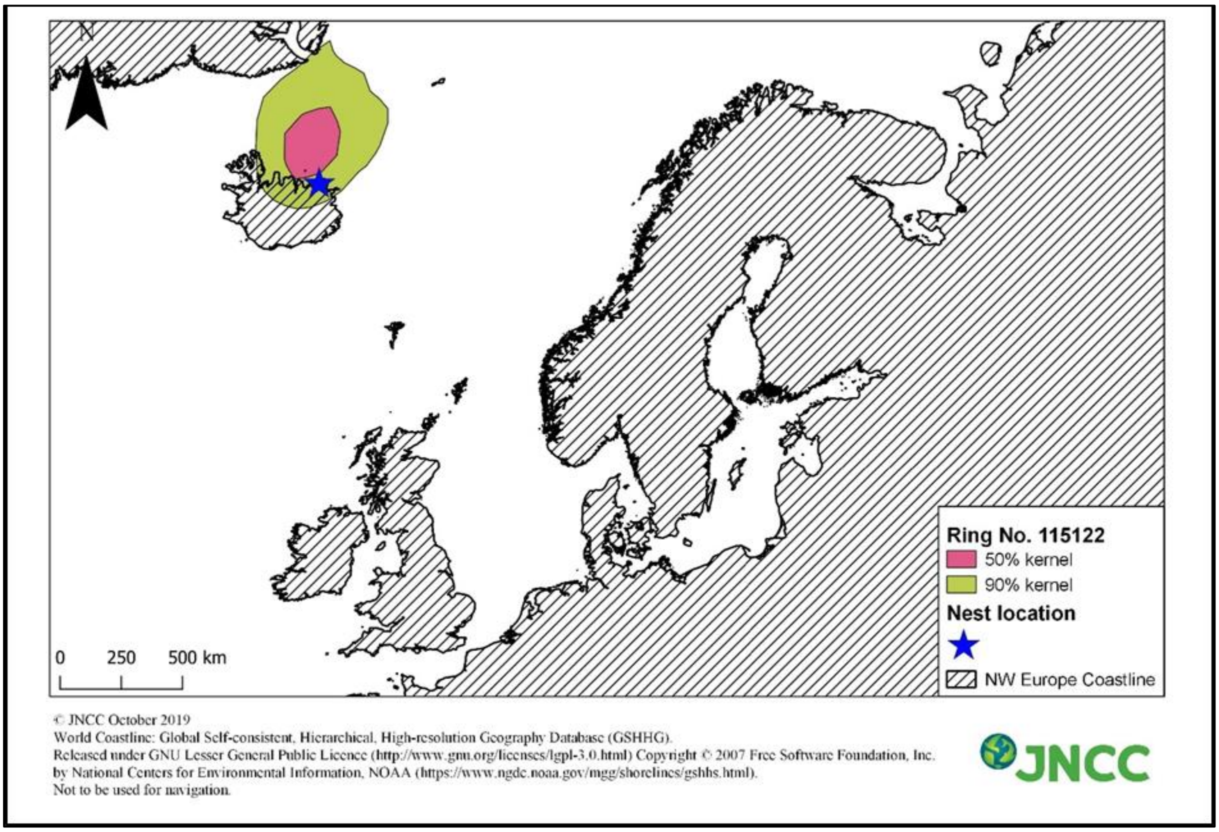

Figure 28. Non-breeding season core use area (50% density distribution kernel) and home range (90% density distribution kernel) for red-throated diver ring number 115122, 0ct 2018 to Feb 2019.