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Possible Behavioural, Energetic and Demographic Effects of Displacement of Red-throated Divers

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Summary

Red-throated divers (*Gavia stellata*) use marine areas in the North Sea, Irish Sea and Baltic Sea during the non-breeding season. They are known to be displaced by various marine industry activities, including construction and operation of offshore wind farms. However, the consequences of displacement for individuals and consequently on the population as a whole are unknown. On 2nd May 2017, seven scientists with particular expertise in red-throated diver ecology and/or the energetic and demographic consequences of displacement for marine birds were invited to a workshop. Using their expertise and knowledge of divers and other marine birds, plus fundamental ecological principles, some generalisations about how red-throated divers might be affected by displacement were sought. This report comprises the main points of discussion and agreement during the workshop.

For displacement to cause a population-level change the following needs to occur. Divers need to show a behavioural response to anthropogenic marine structures, leading them to forage in a different area. This needs to cause a change in energy budgets either through increased energy costs of displacement and barrier effects or decreased energy intake through reduced prey acquisition and assimilation. This, in turn, would lead to poorer body condition with associated impacts on demographic rates, e.g. reduced breeding success or survival. Finally, a sufficient number of individuals need to have altered demographic rates for it to affect population growth rate and size.

It is difficult to draw concrete conclusions about how displacement will affect individuals and populations of red-throated divers, in the absence of empirical evidence. Based on our understanding of the ecology of red-throated divers and similar species, the following would seem to be likely.

Red-throated divers appear capable of utilising a range of marine habitats and prey species. They also tend to occur at relatively low densities and not in large aggregations. Consequently, reduced prey intake caused by increased density-dependent competition or interference would seem unlikely. Red-throated divers are highly mobile in winter which may mean they are able to find alternative foraging sites following displacement. However, individuals tend to be relatively site faithful in winter and in their choice of staging/moulting areas (even though there is large variation among individuals in choice of site). Red-throated divers show a strong stress response and this could temporarily limit their ability to exploit new locations following displacement, even if prey is abundant. Given patchy and ephemeral seascape environments and mobile seabirds, it is not possible to infer the energetic consequences of displacement with any certainty.

Year-round energetic budgets of red-throated divers are unknown but this information is key to understanding the possible consequences of displacement. An understanding of red-throated diver time budgets during winter, e.g. proportion of time spent foraging, would indicate when individuals are struggling to find sufficient food and might be in poorer condition. If red-throated divers tend to be in poorer condition in the non-breeding season when displacement is occurring, displacement could have an impact on survival and productivity. However, if individuals are in relatively good condition during the non-breeding season and spend only a small proportion of their daily activity budget foraging, they may have the capacity to buffer against any additional energetic expense of displacement and barrier effects.

Contents

1 Introduction

Red-throated divers (*Gavia stellata*) breed at high latitudes and migrate south to winter in entirely marine environments (Wernham *et al* 2002). In Europe, substantial offshore wind development has either already taken place or is planned for areas around the North Sea and Irish Sea, often in locations used by wintering red-throated divers (Dierschke *et al* 2012). Post-construction monitoring of diver numbers and distribution indicates almost all individuals to be displaced from the wind farm footprint, as well as from an area around the outside of the wind farm (Halley & Hopshaug 2007; Furness *et al* 2013; Petersen *et al* 2006, 2014; Percival 2014; Welcker & Nehls 2016; Dierschke *et al* 2016; Webb *et al* 2016; unpublished data, German diver tracking study). However, the consequence of displacement is not known. Are displaced individuals able to adapt to utilising a different area or does displacement severely challenge those displaced individuals and potentially others in the population too?

Acknowledging that empirical data on the consequences of displacement for individual red-throated divers and the population as a whole are lacking, JNCC and Vattenfall jointly organised a workshop in Edinburgh on 2nd May 2017 to discuss how displacement might affect individuals and the population. Seven scientists with particular expertise in red-throated diver ecology and/or the energetic and demographic consequences of displacement for marine birds were invited to the workshop (all are co-authors on this report). Using their expertise and knowledge of divers and other marine birds, plus fundamental ecological principles, some generalisations about how red-throated divers might be affected by displacement were sought. This report comprises the main points of discussion and agreement during the workshop, with additional information added by the scientists following the workshop.

1.1 A conceptual framework

For displacement of red-throated divers to cause a change in population size or growth rate, divers need to change their behaviour, choosing to move to a different marine area from the wind farm footprint. In turn, this would need to impair their ability to acquire prey in some way, altering their energetic budgets, resulting in a decrease in body condition. Individuals in poorer condition may not migrate, may have reduced breeding success or may even die. These demographic changes would lead to reductions in annual survival and productivity of the population and consequent decreased population growth rate and size.

Using this sequence of events as a conceptual framework, this report considers how displacement of individual red-throated divers could bring about population-level changes, looking for evidence supporting the plausibility of different mechanisms identified at each stage.

2 Displacement

Drewitt and Langston (2006) defined displacement as the consequence of disturbance of birds caused by the presence of the turbines, or through visual, noise and vibration impacts, or as a result of vehicle/vessel and personnel movements related to site maintenance. Such disturbance would result in reduced densities of birds up to a certain distance from wind farm structures and can therefore be considered a form of habitat loss. Indeed, avoidance behaviour exhibited by some seabird species to offshore wind farms has resulted in displacement from key foraging areas and flight pathways through changes in their local distribution, abundance and flight patterns, i.e. barrier effects (Petersen *et al* 2006).

This workshop did not aim to discuss exactly what causes displacement in detail but rather to take that as a given and consider what the consequences of displacement might be. Displacement occurs due to activities of multiple marine industries and so this report is of relevance to all those industries. However, offshore wind farms are known to cause relatively large scale and permanent (at least for several years) displacement of some seabirds (Dierschke *et al* 2016).

Displacement is known to occur on wintering grounds, where shallow sandy areas favoured by wintering red-throated divers are also ideal locations for constructing offshore wind farms. Red-throated divers move away from a variety of structures in the marine environment, including wind turbines. There is also evidence of red-throated divers being displaced by shipping on their wintering grounds (Schwemmer *et al* 2011). It is known that they take off from an approaching vessel when it is still far away (several kilometres) (Schwemmer *et al* 2011; Bellebaum *et al* 2006). The reasons for this are not understood at all.

Red-throated divers use staging areas during migration between breeding and wintering grounds. In particular, divers often spend a few weeks undergoing a post-breeding moult, during which they are flightless. Displacement occurring in staging and moulting areas may have different consequences to displacement in wintering areas. This is discussed in more detail below.

3 Behaviour

Displacement of an individual is the consequence of a change in that bird’s behaviour. The individual is deciding to move from one area to another area, presumably as a reaction to the presence of a structure in the marine environment. This change in behaviour might alter their foraging behaviour, including prey choice and acquisition, which will be influenced by their choice of alternative habitat and its availability. Prey acquisition might also be influenced by competition with conspecifics and other species. Site fidelity and ability to move easily to new locations will also influence the consequences of displacement, as will their willingness and ability to forage in novel locations.

The scale and degree of such displacement on populations may vary considerably among species, and, is influenced by wind farm location, its proximity to important habitats, and the availability of alternative habitats (Drewitt & Langston 2006). The number of birds reliant on the area, as well as their patterns of use according to season, time of day, and life cycle stage also contribute to the overall effect of displacement at the population level.

3.1 Feeding ecology

3.1.1 Prey choice, availability and acquisition

Red-throated divers wintering in the North Sea and Baltic Sea are thought to feed predominantly on small fish such as herring (*Clupea harengus*), sprats (*Sprattus sprattus*) and sandeels (*Ammodytes marinus*) (Cramp & Simmons 1977; Guse *et al* 2009). However, they are believed to switch to alternative small prey, depending on the species of fish available, e.g. cod (*Gadus morhua*) and flounder (*Paralichthys dentatus*). Whilst the lipid content of different prey species is likely to differ (Ball *et al* 2007), they probably have similar protein content. Red-throated divers generally feed on small fish, approximately 20-30g body mass. It would seem unlikely that red-throated divers are feeding on schooling fish as they feed individually and not in close proximity to conspecifics, as do other species of marine bird that prey on schools of fish.

Red-throated divers forage using a ‘pursuit diving’ tactic, whereby they swim on the water surface and look below the water surface in search of prey fish, and then dive below the water to pursue detected prey (Eriksson 1985). Visually-oriented aquatic predators that pursue prey under water rely on light; however, they may benefit from some degree of water turbidity if it provides cover when approaching prey (Ainley 1977; Skov *et al* 2016), possibly so that fish cannot see them approaching.

At night, great northern divers (*Gavia immer*) congregate in communal flocks (Shackleton 2012) but there is no evidence for red-throated divers doing this. It is unknown whether red-throated divers forage at night but some individuals remain at relatively high latitudes (e.g. around Iceland) during winter where day length is very short. If they do not forage at night, they would need to be very efficient at catching prey during the short period of daylight in mid-winter. Evidence suggests great northern divers do not feed at night (Barr 1973; McIntyre 1978). Shags (*Phalacrocorax aristotelis*) and cormorants (*Phalacrocorax carbo*) forage at night in some areas and guillemots (*Uria aalge*) forage at night in winter. The proportion of time that red-throated divers spend feeding at different times of year is unknown but great northern divers spent up to 70% of daylight hours foraging (McIntyre 1978; McIntyre & Barr 1983).

3.1.2 Habitat

Winter habitat of red-throated divers has been described as nearshore, sandy, shallow marine waters (Guse *et al* 2009; O’Brien *et al* 2008; Skov *et al* 2016). In the Baltic Sea, Skov *et al* (2011) noted that the greatest densities occurred within a water depth zone of 5 to 30m. Core use areas of red-throated divers wintering offshore of the mid-Atlantic U.S. had a mean water depth of 12m and ranged up to 42m (Gray *et al* 2017). Around the UK they tend to occur over sandy substrate of depth less than 20m, in both the breeding and non-breeding season (S. O’Brien, unpublished data; Black *et al* 2015). Selective use of relatively shallow and sandy habitats indicates divers are feeding on the sea bed. This is supported by the fact that the larger great northern diver regularly occurs over water up to 40m depth as its larger size permits greater diver depths (Haney 1990). The red-throated diver’s upturned beak could be adapted for probing sandy substrates for prey (D. Okill, pers. comm.).

Red-throated divers are also known to exploit estuarine fronts in the North Sea (e.g. Thames Estuary: Skov *et al* 2016, and the German Bight: Skov & Prins 2001; unpublished data German Diver Tracking study). Similar behaviour is observed in western North America (Schmutz, unpublished data). Prey of wintering red-throated divers tends to be patchy, mobile and unpredictable. Estuarine fronts, however, reliably predicted red-throated diver distribution, with densities of red-throated divers being relatively high around fronts. Presumably, fronts concentrate prey in a relatively predictable location, enabling red-throated divers to find prey more easily.

Red-throated divers also occur over water deeper than 20m and with no obvious hydrographic feature. Additionally, McIntyre (1975) and C. Gray (pers. comm.) observed small groups of wintering red-throated divers feeding in fast-moving currents of channels connecting coastal bays with ocean waters.

Winter habitat of red-throated divers is difficult to define because it appears they use a wide range of habitat types, such as near river mouths, bays, and open water, including a variety of depths on continental shelf habitats.

3.1.3 Density dependence

When individuals are displaced from a presumably preferred habitat to somewhere else, as a consequence of activity by offshore industries, they may end up in an area already used extensively by other individuals, both conspecifics and other species. If prey acquisition is density-dependent, meaning it is harder to obtain prey when numbers of conspecifics or other species are high, displacement might cause a reduction in prey acquisition for both displaced red-throated divers and others occupying the area they move to.

Red-throated divers do not usually occur in large tightly-aggregated flocks. Their distribution tends to be at relatively low densities (e.g. up to 4 birds.km^{-2} from visual aerial surveys of the Outer Thames Estuary, Webb *et al* 2009) with normally single birds or very small groups seen together. Even in the spring staging area in the German Bight, the density only occasionally exceeds 5 birds.km^{-2} (Garthe *et al* 2015). Consequently, it is difficult to envisage how interference by conspecifics could reduce prey intake for this species. Occasionally large flocks of more than 50 birds do occur (V. Dierschke, pers. obs.), but birds may be aggregating for reasons other than feeding, e.g. in preparation for migration.

There is little information on possible heterospecific competitors. Auks are unlikely to be using the same habitat as red-throated divers, generally preferring deeper water and different prey. Harbour porpoise (*Phocoena phocoena*) might feed in similar habitats on similar small prey concentrated around estuarine fronts (Skov & Thomsen 2008) but it is difficult to envisage a mechanism by which interference from harbour porpoises could reduce prey intake for red-throated divers.

Importantly, it seems unlikely that red-throated divers and other species could deplete their prey resource. The abundance of prey species and the ability of divers to switch to alternative prey would suggest that depletion would not limit prey intake for red-throated divers.

3.1.4 Summary

Red-throated divers appear to be willing to take a range of prey species and to utilise a range of habitats. Additionally, it is difficult to envisage how inter- or intraspecific competition could reduce prey acquisition through interference or depletion. This implies that displacement might not reduce prey intake through either reduced prey availability, reduced habitat availability or competition. However, there are other mechanisms that could cause reduced prey intake (see below).

3.2 Movements

3.2.1 Passage/moult

Tagged red-throated divers breeding at high latitudes have been found to use staging areas while on both spring and autumn migration. Major spring and fall staging and stopover locations of red-throated divers along the North American Atlantic Flyway include: Nantucket Shoals, Gulf of St. Lawrence, Hudson Bay, and the lower Great Lakes (Gray *et al* 2017). In Europe, red-throated divers use the Gulf of Riga and northern Baltic Sea (Lithuanian Diver Tracking study, unpublished data) as well as the German Bight and Pomeranian Bay (East Germany, Baltic Sea) for spring staging (German Diver Tracking study, unpublished data; Garthe *et al* 2015; Boertmann & Mosbech 2011). Staging areas used by the population as a whole can cover a large area but the few individuals that have been tagged for more than one year show high site fidelity, i.e. there is a large amount of variation among individuals but an individual diver will tend to do the same thing each year (German Diver Tracking study, unpublished data).

Birds breeding at lower latitudes, e.g. Scotland and Iceland, tend to remain close to their breeding grounds through the winter (Okill 1994; Wernham *et al* 2002). High latitude breeders appear to undergo a 'leapfrog' migration strategy of wintering further south than their lower latitude breeding conspecifics. This phenomenon has been observed in North American great northern divers, whereby populations in interior Canada undergo extensive migration distances to the most southern part of the winter range, while north-eastern United States populations overwinter in the northern end of the range (Gray *et al* 2014). By contrast, red-throated divers in North America migrate as three different populations, with the most northerly breeding population wintering at the most northerly location (McCloskey *et al* 2017). Birds are capable of undergoing long distance migrations, moving up to 1300km in a single movement (German diver tracking study, unpublished data). Hypothetically, it is possible that numbers of individuals undertaking long distance migration might decrease in future years due to climate change driving a reduction in sea ice extent during winter that enables divers to remain relatively close to their breeding grounds. This has been seen for some seaduck species that now winter in the Baltic rather than the North Sea (Austin & Rehfisch 2005; Pearce-Higgins & Holt 2013) or winter in the Barents Sea instead of the Baltic (Aarvak *et al* 2013). However, currently red-throated divers continue to migrate from areas irrespective of whether they are free of ice or not, e.g. from Norwegian coasts.

Red-throated divers undertake a post-breeding moult during the autumn whereas other diver species undertake a winter moult (Woolfenden 1967; Johnsgard 1987; Pyle 1997). Hypothetically, this difference could possibly be due to red-throated divers having to fly more during the breeding season. They fly from their nest site to nearby lakes and marine waters to obtain food for their young and so by autumn migration their feathers are heavily worn (J. Schmutz, pers. comm.). During the post-breeding moult period, red-throated divers become flightless and move relatively little for a period of about three weeks. Some satellite-tagged individuals in both North America and Europe were observed to use the same pre- and post-breeding staging/moulting sites while others use different sites in the spring and autumn. This has been seen in other species too, e.g. diving ducks are very site faithful to post breeding moult locations over multiple years; yellow-billed divers (*Gavia adamsii*) also return to use the same moult location (J. Schmutz, pers. comm.). This is presumably a successful strategy because individuals know these sites have adequate food resources, low predation risk, *etc*. Red-throated divers also have a second pre-breeding moult into breeding plumage but this less substantial moult does not include replacing flight feathers.

Juveniles do not moult in autumn and thus do not have a flightless phase in their first migration. There is a paucity of information on movements of juvenile and immature birds but one satellite-tagged immature bird in its second year did move north from its winter capture location off the coast of Delaware in the U.S. to lower New York Harbor before suffering mortality in late May (C. Gray, pers. comm.).

3.2.2 Winter

During winter, some individuals tend to remain in particular areas whereas other individuals move continuously throughout the non-breeding season (Lithuanian Diver Tracking study, unpublished data; German Diver Tracking study, unpublished data). It is unknown what drives this variation. Optimal quality habitat is often indicated by the persistent annual occupancy of an area by individuals of a given species (Faaborg *et al* 2010) and so perhaps the mobile individuals are failing to find sufficient prey and are obliged to keep moving. On the other hand, perhaps the two different strategies are both successful, with one successfully exploiting a single area and the other exploiting multiple prey patches. Such floating behaviour, where some individuals occupy disproportionately larger areas relative to the average winter home range size, is a strategy that perhaps allows an individual to remain in high quality habitat throughout winter (Brown & Long 2007).

Why are red-throated divers generally so highly mobile? Food availability is presumably the most important constraint affecting habitat use during the nonbreeding season (Hutto 1985) but direct correlation between seabird and prey distributions is constrained by the hierarchical patch structure of prey, such as pelagic schooling fish and crustaceans (Fauchald 2000). So, do divers need to continually sample the environment for their sparse patchy mobile prey? Individuals that are foraging around estuarine fronts are known to be highly mobile, as they track the front, and they are faithful to the hydrodynamic feature as that moves. Furthermore, tagged birds have been observed to make short compensation flights to account for being pushed by currents (German diver tracking study, unpublished data).

The extent of site fidelity of individuals will strongly influence the consequences of displacement. A highly site faithful individual may find it much harder to accommodate being displaced than one that is highly mobile and is familiar with multiple other sites. Even if prey is abundant in the new site, an individual that cannot readily adapt to the new site may still find it difficult to forage successfully. Intimate knowledge of a particular site and how to exploit prey at that site might greatly increase foraging efficiency, meaning a displaced individual might struggle to successfully exploit a new site. Juveniles have lower survival than adults (Hemmingsson & Eriksson 2002; Horswill & Robinson 2015), suggesting there is some period of learning to forage successfully, which not all individuals manage to achieve. Whether this learning is site-specific or can be applied in any habitat with abundant prey is unknown.

If a particular area in which a wind farm is constructed is used by many mobile individuals rather than just a few site faithful individuals, more of the population will be exposed to displacement effects. However, it is difficult to assess the consequences of this; if mobile individuals are better able to cope with displacement than individuals faithful to one or two sites because they are familiar with alternative foraging locations, then having more of the population exposed to displacement effects will have less impact than if fewer site faithful individuals are displaced.

Red-throated divers are capable of making long distance flights across land. For a species that is highly immobile on land, these individuals must be confident of finding water and presumably prey at the end of their flight. This indicates some knowledge of distant but productive foraging areas.

If there is age or sex segregation in use of wintering areas, displacement effects might impact certain segments of the population more severely than others. In red-throated divers, and in other seabird species, juveniles tend to be more mobile and travel further south than adults, potentially sampling many different locations through random movements before wintering location becomes fixed in subsequent years (Wernham *et al* 2002). Ring recoveries show juveniles winter further from breeding grounds than adult birds, e.g. red-throated divers ringed in Iceland and Scotland were recovered in France, while adults tended to remain near to their breeding grounds (Wernham *et al* 2002). This difference between age classes is also seen in many other species of marine bird (Wernham *et al* 2002), e.g. common guillemot (Bairlein *et al* 2014); common gull (*Larus canus*) (Bønløkke *et al* 2006; Bairlein *et al* 2014). Sex segregation in choice of wintering areas is seen in some seabirds, e.g. male wandering (*Diomedea exulans*) and black-browed albatrosses (*Thalassarche melanophrys*) winter further south than females (Phillips *et al* 2005; Jimenez *et al* 2015). A sex bias of 3:1 females:males was found in red-throated divers caught off the east coast of the United States and in the German Bight. Individuals by-caught in fishing nets in Pomeranian Bay (Baltic Sea) showed no sex bias (105 females: 95 males, Guse *et al*

2009). However, bycatch was dominated by immature birds (80%) probably due to those individuals either being inexperienced at avoiding nets or being in poorer condition and so compelled to forage close to nets. Speculatively, males could favour the eastern Baltic in the non-breeding season, closer to the breeding grounds, and females favour marine areas further east, such as the German Bight. There may also be sex-biased selection of areas for spring pre-breeding aggregations, such as the German Bight, but clear evidence for sex segregation in selection of wintering areas is lacking and may be confounded by females being more readily captured than males.

Birds breeding at high latitudes spend longer on wintering grounds whereas those breeding at lower latitudes, tending to arrive on wintering grounds later and to leave earlier. Extent of ice, particularly on breeding lakes, restricts the ability of birds breeding at high latitudes to return earlier. As a consequence, birds breeding at high latitudes could be exposed to displacement effects for longer although this doesn’t necessarily mean consequences for those individuals will be more severe as it depends on their response to displacement and ability to compensate for it.

3.2.3 Breeding

Individual red-throated divers are highly site faithful to individual breeding locations, going back to the exact same nesting location in multiple years (Okill 1992). In Sweden, individuals were found to recruit to within 60km (in one case 98km) of their natal site (Hemmingsson & Eriksson 2002), while the average distance of dispersal of Shetland breeders was only 2km in males and 38km in females (Okill 1992).

Red-throated divers will compete for high quality nest sites. In one location in Iceland, many pairs bred around a few lakes that were near to the sea. It appears that individual birds were competing for nest sites close to ideal habitat supporting prey suitable for their chicks.

Generally, red-throated divers nest within foraging distance of the sea but some do nest far in land, e.g. in Siberia, away from marine habitats, relying on freshwater prey for both adults and chicks.

3.2.4 Summary

There are large amounts of variation among individuals in movements, both local movements within a season and long-distance migration. Both timing/duration of migration and choice of staging location and wintering area show substantial variation among individuals. However, individuals tend to be site faithful, using similar staging, moulting and wintering sites in different years, although sample sizes are small. During winter, some individuals are highly mobile while others are more faithful to particular areas. It is unknown whether both of these strategies are successful or whether individuals move continuously as they are failing to find sufficient prey at each location. The extent of site fidelity will influence the consequence of displacement, with highly site faithful individuals probably finding it more challenging to deal with being displaced than mobile individuals with a choice of sites. Birds breeding at high latitude spend more time on wintering grounds than those breeding at lower latitudes so could be more affected by displacement. It is likely that both males and females have the potential to be affected by displacement. Juveniles tend to winter further south so are less likely to encounter offshore wind farms but are likely to be less successful than adults at foraging and so the consequences of displacement might be more severe for them.

3.3 Stress response

Red-throated divers show a strong behavioural (and likely hormonal) stress response to anthropogenic disturbance (Lokki & Eklöf 1984). They are highly sensitive to shipping (Bellebaum *et al* 2006) and show a stronger reaction than other seabird species to the presence of anthropogenic structures in the marine environment (Furness *et al* 2013). When handled, divers can become highly stressed very quickly and are prone to disturbance at nest sites, although the response of incubating or chick-rearing adults can vary enormously from pair to pair. Being sensitive to the presence of predators at nest sites is advantageous as divers are slow and vulnerable on land and could not easily escape a predator such as a fox. Their life history strategy relies on them maintaining high adult survival and having many breeding attempts over a long reproductive lifespan (Rizzolo *et al* 2014; Schmutz 2014). Consequently, it is adaptive for a diver to readily flush from the nest rather than sitting tight. However, being highly sensitive to structures in the marine environment does not appear to be advantageous. This 'stress response' would seem to be non-adaptive, i.e. there is no benefit to the individual in being so wary of new structures in the marine environment whilst there is obviously a cost to stopping feeding and to flying a considerable distance away. Perhaps divers simply have not evolved to deal with anthropogenic disturbance in the marine environment and their extreme reaction to anthropogenic structures has no advantage. Behaviour of individuals following displacement is unknown; they may spend a period of time not feeding due to exhibiting a stress response or may begin foraging immediately.

4 Energetics

An individual's energetic budget will be determined by its behaviour through a combination of energy expenditure (flying, foraging, maintenance, *etc*) and energy acquisition (prey intake). Energetic demands vary across the year. At certain times of year, energy acquisition will exceed expenditure and birds will lay down fat stores, while at other times of year they will be in energy deficit, using up fat stores. Periods of high energetic demand will most likely be chick rearing, migration and moult. Red-throated divers must be capable of laying down energy reserves to support long distance migration. They are known to undertake long distance journeys of up to 1300km in a single flight (R. Zydelis, pers. comm.) which would require considerable energy reserves stored just before the migration starts (costs may be estimated using a modelling framework developed by Pennycuick 1989). During moult, birds have a reduced ability to move to new foraging locations as they are flightless. Additionally, energetic and protein demands of replacing flight feathers will be high. However, foraging success might be increased during moult as drag may be reduced by lack of flight feathers.

Mid-winter may also be a critical period, when foraging time is limited due to short daylength and energy expenditure is high due to cold ambient temperature and prevalent stormy sea conditions. Displacement might affect energetic expenditure during this period. There will be an immediate effect of displacement with increased energy expenditure from moving away from the wind farm and reduced energy acquisition due to impaired foraging although this could be a very brief, temporary phenomenon. Barrier effects increase travel distance and flying time for individuals moving around a wind farm to reach favoured foraging areas although this is likely to be less for wintering birds that are not central-placed foragers (Searle *et al* 2014). For instance, if a red-throated diver deviated 15,000 meters to get past an ocean-based windfarm, this diver would expend an extra 42kJ of energy to do so (Speakman *et al* 2009). This increases energy expenditure and reduces foraging time. Additionally, individuals may expend additional energy avoiding wind farms when currents, tides and wind push them towards them. Furthermore, staging in the vicinity of anthropogenic structures and associated disturbance sources may make birds more vigilant and in this way affect overall activity budget. Masden *et al* (2010) indicated that when comparing seabird species with contrasting morphologies, species with high wing-loading ratios, such as divers, would incur the greatest energetic costs associated with additional foraging distances. The cumulative energetic cost to an individual likely becomes more significant as the number of wind farms increases (Speakman *et al* 2009). However, without understanding how the presence of anthropogenic structures affects behaviour, it is difficult to speculate on how energy budgets might be altered.

A maximal estimate of red-throated diver energetics suggested individuals may need up to approximately 630g of fish per day during winter. This estimate was derived using the following rules and assumptions: basal metabolic rate (BMR) of a diver weighing 1650 grams is 659kJ/day (BMR = $3.201m^{0.719}$; Ellis & Gabrielsen 2002); assumed field metabolic rate FMR_{winter} = 4 BMR = 2,276kJ/day; assumed food assimilation efficiency 80%; average caloric value of fish is 5kJ/g fresh weight. This estimate of energy expenditure may be biased high, as provisioning prey to young in summer is likely more energetically expensive than provisioning one's self on the open ocean. Energy density of fish prey is variable over time and space, which affects productivity (Ball *et al* 2007; Rizzolo 2014).

Although they may not fly much while foraging, red-throated divers are highly mobile in winter (unpublished data, German diver tracking study) despite their relatively large wing loading which makes flight energetically expensive. Therefore, there must be some advantage, in terms of increased energy acquisition, associated with being highly mobile.

5 Body condition

An individual's energetic budget determines body condition. Body condition determines demographic rates (see below) but is very difficult to measure in wild birds. To assess body condition at different times of year, it is necessary to catch healthy individuals. This can be done by tagging studies, or possibly by birds that have been shot (in previous decades), or by birds caught in fishing nets, though these types of samples may be biased towards birds in poorer body condition or towards younger age classes (Guse *et al* 2009), so may not be directly comparable to live samples caught at sea.

Red-throated divers have substantial sub-cutaneous fat. This could have the same functional purpose as blubber in marine mammals, acting as insulation against cold water and might not be a useful measure of body condition. Fat may be stored in other locations in the body that is then burnt off during periods of high energy use such as migration.

Whilst it is very difficult to measure body condition, there is some evidence in some species that individuals must reach a threshold body condition before undertaking energetically demanding activities such as breeding and migration (Monaghan *et al* 1989; Davis *et al* 2005). Birds that do not achieve a minimum body condition during winter may not migrate, may not breed or may do so late and have reduced breeding success (Ebbinge & Spaans 1995). Reduced energy intake caused by displacement could result in birds during winter failing to achieve the minimum necessary body condition to migrate and breed successfully.

Body mass is not a reliable indicator of body condition, due to wide variation in body size among individual great northern divers (C. Gray, pers. comm.). Furthermore, body mass data collected during the breeding season is biased towards successful breeders. Birds in poorer condition may still migrate to the breeding grounds but their mate may have already paired with an earlier-arriving individual. Body mass data is therefore not generally available for individuals that did not breed as a result of failing to obtain a breeding territory or mate, which may be related to poor body condition. Similarly, body mass data are lacking for individuals that experienced nest failures or predation of young before ringing/capture activities could be conducted. Even if they do breed, late arrivals often have higher predation rates of chicks and lower post-fledging survival. Generally, seabirds follow a life history strategy which requires them to maintain high adult survival, achieved through them favouring maintenance of their own body condition over successful fledging of their offspring (Booth & McQuaid 2013).

Juveniles and immature birds in other species tend to have poorer body condition than adults, e.g. immature gannets at Bass Rock were, on average, 20% lighter than adults (R.W. Furness, unpublished data).

6 Demographics

6.1 Adult survival

Seabirds have high adult survival and presumably have some means of buffering themselves to survive through winters of reduced prey availability. However, those adults that do die each year tend to die in winter.

Adult survival is generally high. Hemmingsson and Eriksson (2002) estimated annual adult survival to be 0.84 and Schmutz (2014) found adult survival to be 0.92. One ring recovery was from a bird that was 28 years old (BTO ringing data). Like all long-lived species, small changes in adult survival can result in significant population declines for species, such as divers, with low reproductive capacity and a relatively late age at first breeding (Mitro *et al* 2008; Grear *et al* 2009). In a modelling approach, Rebke (2005) found that an increase of only 0.4% in adult mortality caused significant reductions in population size after 25 years (and 0.1% increase in mortality would significantly reduce population growth rate).

Great northern divers in North America undergo episodic mass die-off associated with the moult period in winter. Sixty-six percent of great northern divers found dead along the coast of Florida from 1970 to 1994 died from emaciation syndrome, characterized by muscle atrophy, abnormally low body weight, and depleted body fat (Forrester *et al* 1997). The stress of moulting flight feathers, limited food resources and inclement weather were all cited as contributing factors to mass die-off events. The mass mortality might be attributed to disease events coinciding with periods when birds are already in poor body condition due to moult and winter conditions.

The observed high adult survival means that adults are unlikely to die in winter. However, displacement could push individuals into poor condition, reducing adult survival. One study noted a possible link between adult survival during winter and oceanographic conditions (Schmutz 2014). Key information that would help with understanding this is knowledge of year-round energetic budgets of red-throated divers and the times of year when body condition is likely to be poor. If this coincides with birds being displaced, then they may struggle to cope with the additional energetic costs of displacement and barrier effects.

6.2 Juvenile/immature survival

There is very little information on juvenile and immature survival, other than a small amount of ring recovery and colour-ring sighting data. Juvenile survival is likely to be relatively low and variable, compared with adult survival. Piper *et al* (2012) determined that the survival estimate for juvenile great northern divers was 0.81 across all of the first three years of life until it reaches adulthood, resulting in an overall annual juvenile and immature survival rate of 0.53. Hemmingsson and Eriksson (2002) estimated annual juvenile survival to be as low as 0.37. However, Horswill and Robinson (2015) estimated juvenile survival from the data presented by Hemmingsson and Eriksson (2002) at 0.60, and immature survival (1-2 years old) at 0.62.

Juvenile and immature birds have lower survival than adults and so are presumably less efficient at obtaining prey than adults. Displacement could affect juvenile and immature birds that are already in poor condition and struggling to survive the winter, more than adults.

6.3 Productivity

Productivity can be highly variable among sites and years. For example, productivity in west Iceland is much lower than productivity in north Iceland (I.K. Petersen, pers. comm.). This could be caused by sandeel and capelin (*Mallotus villosus*) availability but additionally, predation is often high at red-throated diver nests. Productivity at breeding sites in southern Finland averaged 1.15 young per nest, for the period from egg laying to fledging. Variation in productivity was due to nest location on (floating) small islets or on shores, probably related to flooding, predation and human disturbance (Lokki & Eklöf 1984). In 2010, average breeding success was 1.13 (Eklöf *et al* 2011), with an estimate of 0.90 needed for a stable population (Pakarinen & Järvinen 1984). In south and central Sweden, average breeding success was 0.82 (large chicks per pair and year), without an effect of water chemistry in the fishing lakes or total fish abundance (but probably related to the abundance of cyprinids and/or salmonids) (Eriksson 2006). In a later analysis (based on partly the same data), Eriksson (2012) found average productivity to be 0.71 in southern Sweden, 0.69 in central Sweden, 0.97 at freshwater lakes in northern Sweden and 0.91 for pairs foraging at sea in northern Sweden, i.e. breeding less than 10km from the coast. Hemmingsson and Eriksson (2002) estimate that a productivity of 0.86 is necessary to compensate for annual mortality.

Productivity at Scottish breeding sites (mostly in Orkney and Shetland) was reported as averaging 0.571 (S.D. 0.222) chicks reared per pair (Horswill & Robinson 2015). In Shetland, productivity was between 0.24 and 1.19 chicks per pair in years 2005 to 2014 (Pennington 2016), variation among years being attributed mainly to changes in fish availability, predation rates and fluctuations in rainfall (Pennington *et al* 2004).

Carry over effects have been demonstrated for other seabirds where productivity is related to winter conditions from the previous season (Daunt *et al* 2014). Equally, winter survival can be affected by conditions during the breeding season (Fayet *et al* 2016). However, discerning these effects is not straightforward as winter and breeding conditions may be correlated. Effects can even be carried over from one breeding season to the next, e.g. removal of great skua eggs, causing repeated laying and reduced body condition, resulted in poorer body condition, later breeding and reduced productivity in the following year (Kalmbach *et al* 2004), and similar carry-over effects have been reported in gulls (Nager *et al* 2001).

Displacement will not directly affect productivity as, for most red-throated divers, offshore wind farm development does not happen in areas used for foraging in the breeding season, although breeding sites in Norway were abandoned when terrestrial wind turbines were built close-by (Halley & Hopshaug 2007). However, displacement could reduce breeding success through carry-over effects of individuals being in poorer condition at the end of the winter season.

6.4 Other demographic parameters

Poor body condition is highly likely to influence other demographic parameters, such as age at first breeding and the likelihood of an individual missing a breeding season. However, obtaining empirical measures for these parameters is highly challenging for a species such as red-throated divers.

6.5 Other sources of mortality

Besides displacement from marine industries including shipping, aggregate extraction and marine renewable energy possibly increasing mortality or reducing productivity, significant other natural and anthropogenic sources of mortality already exist during the non-breeding season. These include energetic costs of migration and feather replacement during the annual moult (Forrester 1997), exposure to contaminants such as mercury, PCBs and PFCs (Eriksson *et al* 1992; Schmutz *et al* 2009; Rubarth *et al* 2011), oil spills (Sperduto *et al* 2003; Camphuysen *et al* 2009), and as bycatch in fishing nets, particularly gill nets (Warden 2010; Zydelis *et al* 2013; Pott & Wiedenfeld 2017).

Climate change may considerably alter breeding conditions for red-throated divers but whether for better or worse is unknown. The birds may benefit from greater availability of open water due to thawing of permafrost sections (e.g. breeding sites in thermokarst lakes, Vincent *et al* 2008). Or suitable breeding lakes may disappear due to erosion from the rising sea level or due to drying-out (Prowse & Brown 2010). Climate change is also likely to change prey species and availability but again, how this will affect red-throated divers is unknown.

The cumulative effect of all these sources of increased adult mortality could be substantial.

6.6 When is the population limited?

Great northern divers are known to undergo periodic mass die-off during winter, suggesting that the population might be limited at this time of year for this species. Red-throated divers do not appear to be limited by density-dependent competition during the winter (see section 3.1.3 above). The population could be limited by density-independent processes in winter, e.g. weather conditions driving reduced prey availability causing increased mortality. The population could be limited on the breeding grounds through competition for high quality nesting sites. Given the highly variable but frequently low productivity rates, there may be competition for optimal nest sites. However, there is evidence from Scotland, Sweden, Iceland and Alaska that breeding red-throated diver numbers are increasing, indicating no limitation on suitable nest sites, although a report on numbers of divers wintering in the Baltic indicated substantial declines (Skov *et al* 2011). Dickson and Beaubier (2011) detected very little change in the number of breeding pairs in the Canadian Beaufort Sea region between the 1985-1989 and 2007-2008 survey periods. Most of the red-throated diver population breeds in Siberia and status of the population there is unknown.

7 Conclusions

It is difficult to draw concrete conclusions about how displacement will affect individuals and populations of red-throated divers, in the absence of empirical evidence. Furthermore, this report did not consider cumulative impacts of any wind farm effects along the red-throated divers' flyway. At each wind farm, effects may be minor but cumulative effects could substantially alter demography.

Based on our understanding of the ecology of red-throated divers and similar species, the following would seem to be likely:

- Red-throated divers exhibit displacement behaviour, moving away from anthropogenic structures in the marine environment;
- they are capable of switching to feed on a variety of prey species, many of which are relatively abundant in the North Sea;

- Red-throated divers can use a variety of habitats but prefer estuarine fronts and shallow water over sandy substrate;
- density-dependence with conspecifics and other species would appear to be unlikely to limit prey intake for displaced individuals and those already present in areas to which displaced individuals move;
- Red-throated divers are highly mobile in winter. Some individuals move constantly while others spend longer in one area. It is unknown whether these are both successful strategies or whether the more mobile individuals are failing to find adequate prey and keep moving to new locations looking for better foraging;
- individuals tend to be relatively site faithful in winter and in their choice of staging/moulting areas. However, there is large variation among individuals in choice of site and thus both relatively sedentary and highly mobile behaviours are observed;
- Red-throated divers show a strong stress response which could temporarily limit their ability to exploit new locations following displacement, even if prey is abundant;
- annual energetic budgets of red-throated divers are unknown but this information is key to understanding the possible consequences of displacement;
- poor body condition caused by displacement could result in carry-over effects causing individuals to have reduced breeding success;
- an understanding of red-throated diver time budgets during winter, e.g. proportion of time spent foraging, would indicate when individuals are struggling to find sufficient food and might be in poorer condition;
- if red-throated divers tend to be in poorer condition during winter and spring pre-migration periods, displacement could have an impact on survival and productivity; if individuals are in relatively good condition during winter and early spring and spend only a small proportion of their daily activity budget foraging, they may have the capacity to buffer against any additional energetic expense of displacement and barrier effects.

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9 Appendix 1: Future work

9.1 Habitat availability and red-throated diver density distribution across Europe

Red-throated divers occur at surprisingly low densities and generally don’t aggregate in large flocks during the winter season. It would be useful to investigate whether individuals are randomly distributed around habitat features or are uniformly distributed. If the latter, it would imply that individuals are deliberately avoiding foraging in close proximity with conspecifics, suggesting there may be some interference effect, which is a prediction if density-dependence was operating on winter feeding grounds. Digital aerial survey data would allow analysis of distribution of birds but without a good understanding of the habitat features they are using, it is difficult to know whether their observed distribution is determined by underlying habitat or by distribution of conspecifics.

If it was possible to evaluate and quantify suitable red-throated diver habitat across Europe, it would also be possible to estimate the numbers of displaced individuals and the consequent increase in mean densities of birds across remaining habitat. If the increase in density caused by displaced individuals moving in to remaining areas is very small, it might suggest that displacement has minimal effect. However, as discussed above, it is unlikely that density dependence would drive a reduction in body condition for displaced individuals; rather that the increased energetic costs associated with displacement and barrier effects, including a lack of familiarity with the new site, could reduce body condition in displaced individuals.

9.2 Body condition throughout year

Assessing body condition of wild birds is very difficult, particularly obtaining measures from representative individuals. Possible data sources for body condition of red-throated divers in winter are:

- birds that have been caught and have internal transmitters fitted – in the process of operating on the bird the vet would probably have noted the body condition (including measurements of body size) of the bird;
- post-mortems of fisheries by-catch individuals could provide information on body condition, although those individuals that end up being by-caught may be younger or in poorer condition than healthy adults so the sample might be biased. However, if these individuals are all in good condition, it would suggest that the rest of the population is also in good condition at that time of year;
- birds caught for ringing on the nest for population or telemetry studies would have been measured and weighed (preferably at different stages of incubation); measures of body mass and other biometrics from the breeding period could infer body condition of breeding birds.

This information could be fed into an energetics model, described below.

9.3 Tracking and time budget study of short and long-distance migrants

Individuals that are struggling to meet their energetic requirements and are in poorer condition are likely to spend more time foraging than those that are easily able to meet their energetic requirements. Consequently, attaching time depth recorders (TDR) to individuals would give insight into frequency of diving and daily activity budgets, particularly the proportion of their day that divers spend foraging. If they are only spending a small amount of time foraging it would imply they are not in poor condition and are struggling to meet their energetic requirements.

Breeding birds could be tagged in several locations including at high latitude (north Norway?) and at lower latitudes (Iceland/Scotland). The intention of tagging birds in different locations would be to tag some birds that use the North Sea, as well as individuals that undergo long-distance migration compared with relatively short distance. As well as attaching archival TDRs, use of geolocators would give coarse resolution information on location of birds as well as time budgets (the latter giving an index of flight activity based on salt-water switch data). Additionally, it would show whether birds forage at night. This information could be fed into an energetics model, along with any data obtained on body condition.

GPS-GSM tags with depth logging capabilities can be fitted to non-breeding birds as an alternative to archival data loggers, which can only be deployed on breeding birds and need to be recovered by recapturing the same individuals. Current technology requires GPS-GSM tags to be implanted in the bird’s body cavity (e.g. German diver tracking study) whereas archival loggers can be attached to leg rings.

9.4 Build model of annual energetic budget

A key knowledge gap with respect to displacement of red-throated divers is understanding when in their annual life cycle the ‘pinch points’ occur, i.e. when are they in energetic deficit and struggling to meet their energetic requirements. To investigate this would require development of an energetic model. The model could be parameterised with information on body condition and time budgets obtained from the projects listed above. By understanding when and where the pinch points occur, we can make qualitative judgements about the ability of individuals to accommodate the additional energetic demands of displacement and barrier effects on the wintering grounds.