The causes of diving duck population declines on
Lough Neagh, Northern Ireland

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Doctor of Philosophy

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Declaration

I declare that the work contained within this thesis was carried out in accordance with the regulations of the Queen’s University Belfast and complies with the criteria required by the Academic Council as follows:

(i)  the thesis is not one for which a degree has been or will be conferred by any other university or institution;

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Irena Tománková

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Summary

Lough Neagh and Lough Beg Special Protection Area (SPA) was one of the most important non-estuarine sites for overwintering wildfowl in Britain and Ireland. Up to 100,000 individual diving ducks overwintered at the site during the early 1990s, however, by the winter of 2003/04, populations of pochard (Aythya ferina), tufted duck (A. fuligula), scaup (A. marila) and goldeneye (Bucephala clangula) had declined to 23,500 individuals. The changepoint in the temporal trend was the winter of 2000/01 with most of the decline occurring rapidly within 2 winters. These changes in migratory species may implicate extrinsic factors at the flyway-scale yet comparable declines in resident or partially resident species, such as coot (Fulica atra) and mute swan (Cygnus olor), may also implicate intrinsic factors. The density and biomass of benthic macroinvertebrates, the main food source of diving ducks, declined by 66-67% between 1997/98 and 2010. This reduction was correlated with a major decline in chlorophyll a concentrations, taken here as a proxy of primary productivity, suggesting a major shift in the Lough Neagh ecosystem coincident with the changes observed in overwintering bird communities. However, there was no substantial shift in the diving duck diet (derived from oesophagus contents) comparable to the shift observed in the availability of their prey. Stable isotope analysis of duck liver tissue collected throughout 2010-2012 suggested that 57% of birds, mostly 1st winter birds, had fed recently on other waterbodies, indicating high levels of dynamic within-winter movements and population redistribution. Analysis of ringing and recovery data provided support for the phenomenon of migratory short-stopping in goldeneye, where distances between their breeding grounds and winter recovery locations had contracted by 400km from the south-west to north-east Europe. However, this was not the case for the other species. Nevertheless, a meta-analysis of count data suggested rapid climate-driven shifts in the wintering distributions of three common waterbird species including tufted duck and goldeneye in response to increasingly mild winter temperatures, making waterbodies at northern latitudes more suitable as overwintering sites. It is concluded that intrinsic and extrinsic factors coincidentally conspired to make Lough Neagh a less attractive overwintering site, leading to a marked decline in diving duck numbers shortly after the winter of 2000/01.
Chapter 1

Introduction
Global decline of biodiversity

Biodiversity on Earth has been dramatically impacted by human activities that have radically affected ecosystems, leading to an accelerating loss of species and populations. Biodiversity has been depleted as a consequence of human actions, both direct and indirect, in what is sometimes referred to as the ‘sixth major extinction event’ in the history of the planet (Chapin et al. 2000). Recent extinction rates are 100 to 1 000 times higher than background rates and they are expected to increase further (Pimm et al. 1995). Currently, 13% of extant bird, 41% of amphibian and 25% of mammal species are threatened and thus facing a high risk of extinction within the immediate future (IUCN 2013). Threats to biodiversity include habitat destruction (Brooks et al. 2002, Fahring 2003), the spread of introduced and invasive species (Vitousek et al. 1997a, Molnar et al. 2008), overexploitation (Wilkie & Carpenter 1999, Grafton, Kompas & Hilborn 2007), human overpopulation (Vitousek et al. 1997b, Dumont 2012) and climate change (IPCC 2002, Kannan & James 2009). These human induced factors can reduce species to small population sizes, thus making them increasingly susceptible to stochastic events. Increasing public awareness concerning environmental issues led to the development of the concept of conservation biology during the second half of 20th century (Meine et al. 2006). Conservation biology is defined by the Oxford English Dictionary as “the branch of biological science concerned with the conservation, management, and protection of vulnerable species, populations, and ecosystems”. The principal aim of conservation biology is to develop data- or theory-driven applied approaches to prevent species decline and extinction (Wilson 1992).
Chapter 1

Introduction

The problem(s) of migratory species conservation

Migratory species are particularly challenging to monitor and protect because they move large distances across often disparate regions of the world during varying stages of their life cycle. Migration is a trait found amongst all major animal groups, including insects, crustaceans, fish, amphibians, reptiles, mammals and most notably birds (Dingle & Drake 2007). For example, wildebeest Connochaetes taurinus migrate on the African savannah in a roughly circular pattern based on the availability of food and surface water (Boone et al. 2006) and salmonid fishes (Salmo spp. and Oncorhynchus spp.) migrate between freshwater and saltwater at various stages of their life cycle (Dodson 1997). Migration is particularly common in birds; about half of all bird species are migratory (Colombo 1981). Seabirds, geese, ducks and passerines regularly undertake migrations between their breeding and wintering grounds, triggered by climatic variation affecting food availability (Wernham et al. 2002). Among seabirds, the Manx shearwater Puffinus puffinus undertakes a migration of over 10 000 km from its breeding grounds in the North Atlantic to its wintering grounds close to Brazil and Argentina (Guilford et al. 2009). In Europe, many duck (Anseriformes; Anatidae) species migrate from northern and north-eastern Europe, where they breed, to south-western Europe to overwinter (Wernham et al. 2002).

Migratory waterbirds regularly cross international borders during their life cycle, thus international cross-jurisdictional cooperation and collaboration along migration flyways is necessary to effectively protect their populations. Several wetland and waterbird site safeguard programmes are in place to protect migratory waterbirds, including the designation of Special Protection Area (SPA) networks under the EU Birds Directive (2009/147/EC), the designation of Wetlands of International
Importance under the Ramsar Convention and the African-Eurasian Waterbird Agreement. Threats to waterbird conservation, for example habitat loss and fragmentation, climate change and overexploitation, are not unique to any one country but rather concern entire species’ ranges. Incentives to protect migratory waterbirds in one part of a species’ range are less effective, if these are not matched by conservation efforts in other parts of the flyway. The establishment of site safeguard networks along the whole migration route, including the breeding, staging and wintering grounds, is therefore essential to the protection of migratory waterbirds. Central to this approach is the maintenance of the quality and integrity of these sites that contribute to the conservation of species throughout the different critical stages of their annual life cycles.

Study site

Lough Neagh (Fig. 1 & 2) is the largest freshwater lake in Britain and Ireland in terms of surface area (383 km², Carter 1993a) which has been the subject of extensive research and study (Wood & Smith 1993). Despite its size, the lake is relatively shallow with a mean depth of 9 m, and as a consequence usually remains well-mixed (Carter 1993a). Lough Neagh is situated on the boundary of 5 counties and drains 43% of Northern Ireland as well as part of the Republic of Ireland (Fig. 1). Six major rivers flow into Lough Neagh (River Main, Balinderry River, Six Mile Water, Moyola River, River Blackwater and Upper Bann River) and one river, the Lower Bann, drains into the Atlantic Ocean via Lough Beg. The catchment is primarily agricultural dominated by dairy and beef farming (Carter 1993b). Historically, eutrophication has been a major concern at Lough Neagh (Foy, Lennox & Gibson 2003), most recently reflecting agricultural run-off (Bunting et al. 2007).
In the 1970s, Lough Neagh was considered one of the most eutrophic lakes in the world (Wood & Gibson 1973). In an effort to control eutrophication, tertiary sewage treatment works were installed in 1981 at major sewage treatment works in the Lough Neagh catchment (Foy et al. 2003); however, the effect was only temporary (Heaney et al. 2001).

The macroinvertebrate fauna of Lough Neagh is dominated by chironomid larvae, particularly Chironomus anthracinus, C. plumosus and Procladius, and oligochaeta worms, in particular Tubificidae (Carter 1978). Macrophytes, mainly Elodea sp. and Potamogeton sp., are limited to sheltered bays (Carter & Murphy 1993) and the shallower Lough Beg (Davidson 1993).

The site qualified for a Special Protection Area (SPA) status by supporting internationally important numbers of wintering Bewick’s (Cygnus columbianus) and whooper swans (C. cygnus) and nationally important numbers of breeding common tern (Sterna hirundo). Although the SPA includes both Lough Neagh and Lough Beg, all count data used in analyses refer to Lough Neagh only. It also qualified as a Ramsar wetland of international importance by regularly supporting over 20,000 individuals of various waterbird species in winter, in particular pochard (Aythya ferina), tufted duck (A. fuligula), scaup (A. marila), goldeneye (Bucephala clangula), little grebe (Tachybaptus ruficollis), great crested grebe (Podiceps cristata), cormorant (Phalacrocorax carbo), mute swan (Cygnus olor), greylag goose (Anser anser), wigeon (Anas penelope), gadwall (A. strepera), teal (A. crecca), mallard (A. platyrhynchos) and coot (Fulica atra) (DoENI 1998). Finally, it is designated as an Area of Special Scientific Interest (ASSI) under the Environment (Northern Ireland) Order 2002, of interest for its wintering and breeding birds, vegetation which includes a number of rare plant species, and a number of rare species of invertebrates
and fish (DoENI 1992). The lough also contains a number of National Nature Reserves.

Fig. 1 Location map of Lough Neagh, showing location in Ireland (inset top left) and the extent of the total catchment (solid boundary) and individual catchments (defined by lighter lines within) which straddle the border of Northern Ireland and the Republic of Ireland (broken line)
Fig. 2 Aerial photograph of Lough Neagh taken from the south west corner looking north eastwards. The small partly wooded island centre frame is Coney Island (54°31′N 6°33′W) just offshore of the village of Maghery. Note the mixed, but predominantly lowland farmland nature of the catchment immediately surrounding the lough. Photograph taken 12 June 2008 © Northern Ireland Environment Agency.

Declines of diving duck populations at Lough Neagh

Lough Neagh and Lough Beg Special Protection Area or SPA (54°35′N, 6°25′W) is an important non-estuarine site in Britain and Ireland for overwintering wildfowl, of particular significance for its diving duck assemblage. In the late 1980s and early 1990s, Lough Neagh hosted diving ducks numbers in excess of 100 000 (Maclean, Burton & Austin 2006). However, the number of diving ducks on the site has declined dramatically from the late 1980s and early 1990s to the winter of 2003/04, from 40 000 to 8 000 in the case of pochard, 30 000 to 9 000 for tufted duck, 5 000 to 2 600 for scaup and 14 000 to 4 000 for goldeneye (Maclean et al. 2006).
Different explanations for the causes of these declines have been suggested, including site related factors (Maclean et al. 2006) and migratory short-stopping (Allen & Mellon 2006).

Since the relevant statutory agencies are responsible for maintaining the site, it is essential to determine whether extrinsic or intrinsic factors at Lough Neagh are responsible for changes in diving duck abundance. If intrinsic factors are contributing to the declines, it is important to determine whether sympathetic management actions can be implemented to restore conditions and ultimately duck abundance.

**Intrinsic factors**

Intrinsic, or site-related, factors could have a negative impact on waterbird populations at a site. These factors might include, but are not limited to, pollution, disturbance, food availability and competition. Habitat deterioration induced by such factors might cause waterbirds to re-distribute to other, more suitable, wintering sites. The effect of some of these factors has already been investigated. For example, shooting disturbance was shown not to have a major impact on diving duck populations (Evans 2000). As opposed to dabbling ducks, diving ducks moved away from disturbance at the shoreline to areas where they were still able to feed (Evans 2000). The diet of tufted duck at Lough Neagh overlaps with the diet of the introduced cyprinid fish the roach (*Rutilus rutilus*) due to common consumption of molluscs, suggesting possible competition for food resources which may have influenced population dynamics of both species (Winfield & Winfield 1994a).

Lough Neagh is likely attractive to diving ducks because it is large and nutrient rich, therefore, producing abundant food in the form of benthic macroinvertebrates,
and secondly, because it is relatively shallow, allowing diving ducks to exploit the majority of the lough’s benthos. If efforts to control eutrophication and improve water quality are successful, they may lead to declines in macroinvertebrate abundance and changes in the macroinvertebrate community structure, as has happened in other lakes (Schloesser, Reynoldson & Manny 1995, Köhler et al. 2005, Carter, Nalepa & Rediske 2006), with subsequent impacts on the putative diets of diving ducks. Sand extraction is an important industry at Lough Neagh with production at about 1.2 million tonnes of sand per annum (G. Best, QPANI, pers. comm.). It is feasible that disturbance of the sediment by sand extraction might alter the habitat for benthic macroinvertebrates. A potential decline in the macroinvertebrate abundance or biomass due to changes in physiochemical conditions or disturbance of the lough is likely to have a profound impact on consumers from higher trophic levels throughout the system that feed on them, including diving ducks.

An alternative hypothesis, as suggested by Allen & Mellon (2006) is that the decline in diving duck populations at the site does not reflect a real decline but rather is a case of undercounting. On a water body of almost 400 km$^2$, it is possible that ducks may be utilizing areas further off-shore than they previously did and thus might not be detected during Wetland Bird Survey (WeBS) counts, which are conducted from the shore, leading to an apparent decline.

**Extrinsic factors**

The declines in overwintering waterbird species at a site may also be the result of extrinsic factors that impact populations across a larger area, such as the entire flyway or the breeding grounds. One of the most obvious of these distributional
factors is migratory short-stopping (e.g. Hankla & Rudolph 1967, Takekawa et al. 2009), the result of waterbirds (in Northern Hemisphere) reducing the migration distance between their breeding and wintering grounds, utilizing wetlands formerly inaccessible to them in the winter to the north and east of their traditional wintering areas, while retracting from traditional wintering areas further south and west. Such shifts are thought to reflect a biological response to climate change (Appendix I). In Europe, between 2002 and 2011, the average temperature was 1.3˚C above the pre-industrial level (defined here as 1850-1899), making it the warmest on record (European Environment Agency 2012). Ireland is located at the south-western edge of the wintering distribution of many waterbird species that breed in north-eastern Europe and Iceland. These species have recently encountered climatic changes within their distributions, e.g. changes in the extent of winter ice cover of lakes and warmer, shorter winters (European Environment Agency 2012). The largest climate changes have occurred so far in the winter (European Environment Agency 2012). Understandably, such climatic change is predicted to cause changes in species distributions (Parmesan 2006). The wintering distribution of many bird species is responsive to climate (Austin & Rehfish 2005, La Sorte & Thompson 2007). Wintering waterbirds are particularly likely to show distributional shifts due to climate change, as they respond rapidly to weather conditions (Ridgill & Fox 1990, Rainio et al. 2006). In recent years, wading birds (Maclean et al. 2008) and diving ducks (Appendix I) in Europe have shown shifts in the centres of their winter ranges north-eastwards during a period of milder winters, consistent with climate change predictions.

Changes in populations of migratory waterbirds at a site can result not only from shifts in the wintering distribution but can also reflect changes in overall abundance
at the population level as a result of demographic change. For example, pochard numbers have been declining in Northern Ireland (Holt et al. 2012). This downward trend is consistent with Great Britain (Holt et al. 2012), the Republic of Ireland (Boland & Crowe 2012) and the north-east/north-west Europe flyway (Wetlands International 2012). In the case of simultaneous declines across various geographical regions, such as for pochard, it is possible that the downward trend at Lough Neagh reflects genuine population declines across the flyway. These population declines could be triggered by factors such as reduced survival and/or fecundity, which may or may not be connected with the study site.

**Study species**

Diving ducks are highly gregarious during the winter and form large flocks in many areas (Snow & Perrins 1998). Pochard, tufted duck, scaup and goldeneye are predominantly migratory (Wernham et al. 2002). Pochard wintering in Britain and Ireland breed in the region north of about 50°N and east to about 76°E, mostly in the Baltic countries and northwest Russia, but also in Denmark, Fennoscandia, north Germany and Poland (Kershaw 2002). The population of pochard utilizing the north-east/north-west Europe flyway, from which pochard wintering on Lough Neagh are drawn, is classified as decreasing (Wetlands International 2012). Of pochard ringed abroad and recovered in Britain and Ireland, 62% have been ringed in Latvia (Kershaw 2002). Pochard have low fidelity to wintering sites, with considerable movement between Ireland and Great Britain between winters (Kershaw 2002) and with many within-winter movements further up the flyway (Keller, Korner-Nievergelt & Jenni 2009). Pochard feed on both animal (Phillips 1991) and plant matter, with seeds and vegetative parts of plants of primary importance (Snow &

Tufted duck are predominantly migratory (Hearn 2002), but there is a small resident breeding population on Lough Neagh. The majority of tufted ducks wintering in Britain and Ireland breed in Russia, Fennoscandia and Iceland; with birds wintering in Ireland coming mainly from Iceland and birds wintering in Great Britain coming mainly from mainland Europe (Hearn 2002). The population of tufted duck wintering in North–west Europe is classified as stable (Wetlands International 2006). Tufted duck are omnivorous (Olney 1963, Snow & Perrins 1998) and on Lough Neagh have been found to feed primarily on chironomid larvae, molluscs and *Asellus aquaticus* (Winfield & Winfield 1994b, Bigsby 2000, Evans 2000).

Scaup wintering in Ireland breed almost exclusively in Iceland while the British wintering population is drawn mainly from Iceland and to a much lesser extent from Russia, Finland and Lithuania (Campbell 2002a). The population of scaup wintering in Northern and Western Europe is classified as declining (Wetlands International 2012). Scaup are omnivorous, with molluscs of primary importance (Snow & Perrins 1998); however, on Lough Neagh, they feed mainly on chironomid larvae (Winfield & Winfield 1994b, Bigsby 2000, Evans 2000).

Goldeneye wintering in Britain and Ireland are drawn from the Fennoscandian breeding population (Campbell 2002b). The diet of goldeneye consists of molluscs, crustaceans and insect larvae (Olney & Mills 1963, Snow & Perrins 1998). On Lough Neagh, chironomid larvae are the most important prey item (Winfield & Winfield 1994b, Bigsby 2000, Evans 2000).
Aims and objectives

The overall aim of this thesis was to determine the likely causes of recent diving duck population declines at Lough Neagh. Specifically, the objectives of the project were to:

1. Assess temporal changes in composition of the wintering waterbird community at Lough Neagh to identify species or feeding guilds most affected and quantify changes (Chapter 2).

2. Compare population trends of pochard, tufted duck, scaup and goldeneye at Lough Neagh with population trends at greater spatial scales relevant to their flyways (Chapter 2).

3. Assess the feasibility of commercially available sand barge radar for detecting overwintering diving ducks at Lough Neagh (Chapter 3).

4. Describe the contemporary macroinvertebrate community of Lough Neagh in terms of composition and abundance to assess food availability and any temporal changes between 1997/98, i.e. before diving duck declines, and 2010 i.e. after diving duck declines (Chapter 4).

5. Examine the current diet of diving ducks through oesophagus content analysis and stable isotope analysis (Chapter 5).

6. Test, using ringing and recovery data, whether there has been a reduction in recovery distances amongst pochard, tufted duck and goldeneye migrating from their breeding to wintering grounds and whether recovery distances are temperature dependent (Chapter 6).
It was hoped that combining these sources of information may make it possible to determine whether diving duck population declines at Lough Neagh were caused by intrinsic or extrinsic factors or a combination of both. This information is essential to provide an evidence base for local Government to direct the management of designated sites, and in the case of the diving ducks, their designated features. Lough Neagh has the advantage of long-term bird count datasets and might potentially serve as a case study for other lakes at the edge of distributions that exhibit waterbird population declines.
Chapter 2

Assessing the extent to which temporal changes in waterbird community composition are driven by either local, regional or global factors

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Abstract

Lough Neagh and Lough Beg Special Protection Area (SPA, hereafter Lough Neagh) is an important non-estuarine site in Britain and Ireland for overwintering wildfowl. Multivariate analysis of the winter counts showed a state-shift in the waterbird community following winter 2000/1, mostly due to rapid declines in abundance (46-57% declines in the mean mid-winter January counts between 1993-2000 and 2002-2009) of members of the diving duck guild (pochard *Aythya ferina*, tufted duck *A. fuligula* and goldeneye *Bucephala clangula*) and coot (*Fulica atra*), a submerged macrophyte feeder. Only pochard showed correlations between declines at Lough Neagh and those of overall species flyway population indices to suggest global changes could contribute to declines at the site, although indices from the Republic of Ireland showed no overall decline in the rest of Ireland. Tufted duck indices at the site were inversely related with indices in Great Britain. Lough Neagh goldeneye indices were positively correlated with indices in the Republic of Ireland and Great Britain, suggesting short-stopping could contribute to declines at the site. Coot declines at Lough Neagh did not correlate with trends elsewhere, suggesting local factors involved in the decline. These analyses suggest that although there are potentially different explanations for the dramatic declines in these four waterbird species at this site, the simultaneous nature of the declines across two feeding guilds strongly suggest that local factors (such as loss of submerged macrophytes and benthic invertebrates) were involved. An assessment of the food supply, local disturbance and other factors at Lough Neagh is required to find an explanation for the observed adverse trends in wintering numbers of the affected species. This study highlights the potential of waterbird community structure to reflect the status of aquatic systems, but confirms the need to establish site specific factors responsible for the observed changes in abundance of key waterbird species at a site.
Introduction

International agreements and legislation, such as the Ramsar Convention and EU Birds Directive, require that Member States protect their aquatic resources of nature conservation interest. Migratory waterbirds represent a shared but exploited (i.e. huntable) resource, necessitating international co-operation to maximise the effectiveness of conservation actions. Threats to waterbird conservation through habitat loss, fragmentation and degradation, overexploitation and climate change are common across the entire species range/flyway. The effective protection of migratory birds is therefore a particular challenge because it requires the co-operation of all countries involved. A cornerstone of protecting aquatic resources is the establishment of site safeguard networks; in the case of waterbirds, this entails the establishment of a chain of protected areas along the whole migratory route. Fundamental to this concept is the maintenance of the quality and integrity of these sites. For instance, the EC Birds Directive 2009/147/EC requires Member States (Article 4.1) to "...classify...special protection areas for the conservation of ...species” with (Article 4.2) “...particular attention to the protection of wetlands and particularly to wetlands of international importance” and (Article 4.4) “…Member States shall take appropriate steps to avoid pollution or deterioration of habitats...affecting the birds…”

To fulfil these objectives, Member States invariably have waterbird monitoring programmes in place (e.g. Calbrade et al. 2010) that contribute to an overview of population sizes and trends (e.g. Gilissen, Hanstraa & Delany 2002), but that also provide long-term data on bird abundance at the site level to inform local management. Local site monitoring can identify population declines at this spatial scale, but establishing the causes of local declines requires initial comparison with
global population change. Seen from the point of view of a site manager, the first challenge is to determine whether local declines are the result of extrinsic factors impacting the population on a flyway level, or local site-related factors, such as pollution, disturbance or deterioration of habitat. Here, a worked example of such a case study is presented, associated with dramatic declines in some diving waterbird species at one of the most important wintering waterbird sites in Western Europe.

The Lough Neagh and Lough Beg Special Protection Area (SPA) is the most important non-estuarine site in Britain and Ireland for overwintering wildfowl and of particular significance for its diving ducks. While the SPA includes both Loughs Neagh and Beg, Lough Neagh is disproportionally more important for diving ducks, and any count data utilized in the analysis refer to Lough Neagh only. For a description of Lough Neagh, see Chapter 1, pages 4-7.

The number of diving ducks on the site has declined dramatically from the late 1980s and early 1990s to the winter of 2003/04, from 40 000 to 8 000 in the case of pochard (*Aythya ferina*), 30 000 to 9 000 for tufted duck (*A. fuligula*), 5 000 to 2 600 for scaup (*A. marila*) and 14 000 to 4 000 for goldeneye (*Bucephala clangula*) (Maclean *et al.* 2006). The Northern Ireland Environment Agency (NIEA) is the statutory body responsible for establishing and maintaining SPAs in Northern Ireland. In this instance, NIEA needs to determine whether the diving duck declines at Lough Neagh are primarily due to site-specific factors or the results of extrinsic factors acting upon the birds elsewhere away from this site.

In this analysis, multivariate analysis of long term waterbird count data was used to assess the changes in composition of the wintering waterbird community at Lough Neagh during 1989/90-2008/9 in an attempt to identify what feeding guilds and
species have been affected at the site. Then, the role of intrinsic factors in the declines of those species at Lough Neagh was investigated, by comparing declines in these species at the site with the population trajectories at increasingly greater spatial scales (in this case, comparing changes in abundance at Lough Neagh with those in the Republic of Ireland, Britain and in the flyway population as a whole). The null hypothesis would be that the abundance of waterbirds at Lough Neagh would be positively correlated with numbers at greater spatial scales, in which case, the declines at Lough Neagh reflect changes in overall population size and therefore intrinsic factors are unlikely to be responsible. An alternative result, namely an inverse correlation between Lough Neagh numbers and totals elsewhere, implies a redistribution of birds from Lough Neagh. This could suggest site specific factors are responsible for declines at the site, but could also result from extrinsic factors (such as birds wintering nearer to the breeding areas, for instance because of climate change). A total lack of correlation implies more complex relationships, but does not reject the role of intrinsic factors in the decline at Lough Neagh.

Methods

Changes in waterbird community composition

Two methods of multivariate analysis were used to determine whether there was any structuring within the waterbird community on Lough Neagh with respect to temporal changes in overwintering abundance. First of all, the natural log transformed sum of counts from all of Lough Neagh for the months December, January and February combined from the years 1989/90-2008/9 (excluding 2006/7 for which the December counts were missing) was subjected to hierarchical
agglomerative clustering to see if there were discrete differences in the waterbird community across the different years. Simple squared Euclidean distance measures were used to construct a dendrogram of similarity between years using the minimum variance method of clustering (which joins clusters on the basis of giving the least increase in within cluster variation) based on the count data matrix (using MVSP software, Kovach 2007). The Bray-Curtis dissimilarity measure based on furthest neighbour agglomerative clustering (Kovach 2007) was used, but this and other methods gave very similar classification of years by waterbird community composition, so only the squared Euclidean results are presented here.

Principal component analysis (PCA) was used to analyse annual waterbird count data over a series of years, the objective being to show the temporal change in the composition of the waterbird community over the period under consideration, but also to find which changes in abundance of which species contributed most to the overall changes in waterbird community composition. PCA converts species count values into a set of uncorrelated variable values (the principal components) by orthogonal transformation. The first and second principal components account for most variance in the system, and the weightings of the different species on these principal components provide insight into their influence on the relative axes scores through time. PCA was applied on natural log transformed sum of counts from all of Lough Neagh for the months December, January and February combined from the years 1989/90-2008/9.

For the purposes of comparison throughout this paper, these same count data are presented graphically combining species by feeding guilds, namely fish-eaters (little grebe *Tachybaptus ruficollis*, great crested grebe *Podiceps cristatus*, cormorant *Phalacrocorax carbo* and grey heron *Ardea cinerea*), dabbling ducks (*wigeon Anas*
penelope, gadwall A. strepera, teal A. crecca, mallard A. platyrhynchos and shoveler A. clypeata), diving ducks (pochard, tufted duck, scaup and goldeneye) and submerged macrophyte feeders (coot Fulica atra and mute swan Cygnus olor). Species were assigned to their respective guilds based on their feeding habits and requirements following Snow & Perrins (1998).

Index of abundance for feeding guilds of diving duck and submerged macrophyte feeders

Annual index values for the diving duck and submerged macrophyte feeding guilds based on winter counts 1989/90 to 2008/09 were produced using the specialist software programme TRIM (Trends and Indices for Monitoring data; Pannekoek & van Strien 2001). Those two feeding guilds were selected because initial multivariate analysis suggested that they are the main drivers of the waterbird community shift on Lough Neagh. TRIM is traditionally used to account for spatial variation in the number of counts among sites within species to derive an overall temporal trend. However, here the counts from the different species within each waterbird guild at Lough Neagh were combined to produce an overall temporal trend for each guild. TRIM allows trends within time-series to be established prior to or after specific events that may have influenced the data; these time points are referred to as changepoints.

Each year was tested as a candidate changepoint with the fit of the trend before and after each year evaluated using the Akaike Information Criterion value (AIC). The changepoint which produced the lowest AIC was taken as the best approximation on the initiation of any observed decline in numbers. Standard errors
of the indices are also generated based on the assumption of variance proportional to mean, and a pattern of serial correlation which declines exponentially with time between counts. Accounting for overdispersion and serial correlation, TRIM interpolates missing observations (in this case winter 2006/07) using a Poisson general log-linear model (McCullagh & Nelder 1989) assuming the general form:

\[
\log e \mu_{ij} = \alpha_i + \beta_1 (k_2 - k_1) + \beta_2 (k_3 - k_2) + \beta_L (j - k_i)
\]

where \( \log e \mu_{ij} \) is the natural logarithm of the expected counts for species \( i \) at time-point \( j \), with \( \alpha_i \) the effect of species \( i \) and \( \beta_1 \ldots \beta_L \), the slope between changepoints \( k_1 \ldots k_L \), where \( L \) is the total number of changepoints (Pannekoek & van Strien 2001).

Comparing declines in diving species at Lough Neagh with trends at the flyway population, Republic of Ireland and Great Britain levels

To examine whether observed temporal trends in the waterbird guilds that exhibited significant declines were local, regional or global in nature, index values from Lough Neagh were correlated with index values throughout i) the Republic of Ireland, ii) Great Britain and iii) the European flyway. Northern Ireland was not included in the analysis because Lough Neagh is the main driver of the diving duck trends in Northern Ireland: in the winter of 2008/09, over 95% of pochard and scaup in Northern Ireland were wintering on Lough Neagh, and 87% and 71% of goldeneye and tufted duck, respectively.
Indices for the 13 most abundant waterbird species at Lough Neagh (as above but excluding grey heron and mute swan for which insufficient data were available) were generated for Lough Neagh, Great Britain and Republic of Ireland based on count data from the UK WeBS and the Irish I-WeBS databases from the months of September to March, inclusive, for the period 1988/89 to 2009/10 for Lough Neagh, 1982/83 to 2008/09 for Great Britain and 1994/95 to 2008/09 for the Republic of Ireland. Annual index values are expressed relative to the most recent year, which were given an arbitrary value of 100. For months when a site has not been visited an expected count for each species was imputed using the Underhill indexing method (Underhill & Prŷs-Jones 1994), based on the pattern of counts of that species across months, years and other sites. The Underhill indexing method fits a model with site, year and month factors to the incomplete data matrix and imputes values for missing observations using an iterative approach. Where all observations are considered to be of equal status the Underhill method produces the equivalent index to a Generalized Additive Models (GAM) model when fitted specifying (n-1) degrees of freedom (where number of years = n). Generalized Additive Models (GAMs; Hastie & Tibshirani 1990) are then used to fit both index values and a smoothed trend to the WeBS data. Smoothed trends are fitted by reducing the number of degrees of freedom available to the GAMs. As the number of degrees of freedom is decreased from (n-1), the trend becomes increasingly smooth until ultimately with one degree of freedom the smoothed curve becomes a linear fit. WeBS adopts a standard (n/3) degrees of freedom to produce a level of smoothing that, while removing temporary fluctuations not likely to be representative of long term trends, captures aspects of the trends that may be considered to be important.
Flyway population trends

For the calculation of flyway trends for the species showing most critical declines at Lough Neagh, the generated long-term trends created by Wetlands International for the African-Eurasian Waterbird Agreement Conservation Status Report (http://wetlands.org/csr5) were used. This process has summarised the available knowledge about the size and trends of migratory waterbird populations listed in the AEWA Action Plan, including those for pochard, tufted duck, scaup, goldeneye and coot. Counts from sites throughout the Western Palearctic region were assigned to flyways on the basis of ringing recoveries and historical knowledge (see Scott & Rose 1996) and the flyway in which Lough Neagh is situated was selected for each species. Trends were generated from January counts for the years currently available, namely from 1983 to 2007 for pochard, tufted duck, scaup and coot, and from 1983 to 2006 for goldeneye at these sites using the programme TRIM (Pannekoek & van Strien 2001, van Roomen, van Winden & van Turnhout 2011). TRIM can generate trends allowing for missing values to yield yearly index values and associated standard errors by fitting log-linear Poisson regression models to the count data.

Results

Changes in waterbird community composition

Simple squared Euclidean cluster analysis of the waterbird community on Lough Neagh between the winters of 1989/89 and 2008/09 showed a strong dichotomy between the community in the winters up to and including 2001/02 and those since
(Fig. 1). The years 1995/96 and 1999/2000-2001/02 inclusive show some weak signs of intermediate clustering not evident in the PCA ordination (see below).

The PCA of the count data showed that different aspects of the composition of the waterbird community of Lough Neagh were strongly represented on the 5 principal components (Table 1). The first 2 axes of the PCA ordination explained 30.4% and 18.3% of the total variance, respectively. Those species showing the greatest loadings on the first three axes corresponded to trends in the waterbird community according to natural feeding guilds. Variable loadings on Axis 1 included 3 out of 4 diving duck species (pochard $r = 0.937$, tufted duck $r = 0.901$ and goldeneye $r = 0.806$) and the submerged macrophyte feeders (coot $r = 0.873$ and mute swan $r = 0.781$). Greatest variable loadings on Axis 2 included 4 out of 5 analysed dabbling ducks (wigeon $r = 0.679$, gadwall $r = 0.821$, teal $r = 0.786$ and mallard $r = 0.750$) (Table 1). In the ordination of years on the first two principal components, two distinct groupings are apparent – winters from 1989/90 up to and including 2001/02 and winters 2002/03 to 2008/09 (Fig. 2), indicating a marked regime shift in the waterbird community of Lough Neagh.
Chapter 2  Waterbird temporal change

Fig. 1 Simple squared Euclidean cluster analysis of the waterbird community (based on combined counts of individual waterbird species from midwinter December-February inclusive counts) at Lough Neagh, Northern Ireland for the years 1989/90-2008/9. The dendrogram clusters show the strong dichotomy between the waterbird community present in the years up to and including 2001/2 (PRE) and those since (POST).
Table 1 Details of the first 5 principal components and variable loadings of a PCA of the waterbird community (based on combined counts of waterbird species from midwinter December-February inclusive counts) at Lough Neagh, Northern Ireland for the years 1989/90-2008/9. Values shown in bold type indicate those loading of greatest significance on each principal component. Lightest shading indicates members of the diving duck feeding guild, next heaviest shading submerged macrophyte feeders, heavier shading the fish-eating guild and the darkest shading the dabbling duck guild.

<table>
<thead>
<tr>
<th>Species</th>
<th>Principal Component</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Pochard</td>
<td>0.937</td>
</tr>
<tr>
<td>Tufted duck</td>
<td>0.901</td>
</tr>
<tr>
<td>Scaup</td>
<td>-0.310</td>
</tr>
<tr>
<td>Goldeneye</td>
<td>0.806</td>
</tr>
<tr>
<td>Little grebe</td>
<td>0.270</td>
</tr>
<tr>
<td>Great crested grebe</td>
<td>0.007</td>
</tr>
<tr>
<td>Cormorant</td>
<td>-0.437</td>
</tr>
<tr>
<td>Grey heron</td>
<td>-0.194</td>
</tr>
<tr>
<td>Coot</td>
<td>0.873</td>
</tr>
<tr>
<td>Mute swan</td>
<td>0.781</td>
</tr>
<tr>
<td>Wigeon</td>
<td>0.460</td>
</tr>
<tr>
<td>Gadwall</td>
<td>0.060</td>
</tr>
<tr>
<td>Teal</td>
<td>0.335</td>
</tr>
<tr>
<td>Mallard</td>
<td>0.332</td>
</tr>
<tr>
<td>Shoveler</td>
<td>-0.071</td>
</tr>
</tbody>
</table>
Fig. 2 Graphic depiction of a PCA of the waterbird community (based on combined counts of waterbird species from midwinter December-February inclusive counts) at Lough Neagh, Northern Ireland for the years 1989/90-2008/9. The plot shows the strong dichotomy between the waterbird community present in the years up to and including 2001/2 and those since.

**Index of abundance for feeding guilds of diving ducks and submerged macrophyte feeders**

The most marked change in the waterbird guild at Lough Neagh was a dramatic decline in the diving duck and submerged macrophyte feeders group that exhibited a significant changepoint during the winter of 2000/01 (Fig. 3). Between 2000/01 and 2008/09, the overall population of diving ducks and submerged macrophyte feeders on Lough Neagh declined by 63% and 70%, respectively.
Fig. 3 Annual index (+ SE) for diving ducks (pochard, tufted duck, scaup and goldeneye) and submerged macrophyte feeders (coot and mute swan) between 1989/90 and 2007/08 on Lough Neagh, Northern Ireland generated using log-linear Poisson regression models fitted to untransformed count data. The software seeks to generate a best model fit about changepoints in the time series (in both cases 2000/2001, solid line) using the AIC value to differentiate the best model fit when testing each year of the time-series as a candidate change point.

Changes in abundance of individual waterbird species

Based on index values from Lough Neagh during 1988/89 to 2009/10, the fish-eating guild members showed no change (little and great crested grebe) or significant increases (cormorant, Fig. 4a and Table 2). Dabbling duck species have shown modest declines in number over the time period: all species showed between year fluctuations in the index values; gadwall showed no significant trends, whilst the remainder (wigeon, teal, mallard and shoveler) showed significant declines of less than 5% per annum (Fig. 4b and Table 2). Pochard, tufted duck and goldeneye all showed significant declines in index values of 6.5-8% per annum, although in all three species this reflected a slow decline prior to 2000/1, followed by dramatic reductions to lower index values afterwards (Fig. 4c and Table 2). Coot and mute swan showed similar patterns to the three diving ducks (Fig. 4d and Table 2), whilst scaup increased by 5% per annum (Fig. 4c and Table 2). Given the marked changes...
in the composition of waterbird community at Lough Neagh before and after winter 2000/1, the mean mid-winter January counts of all the commoner species for the years 1993-2000 and 2002-2009 are presented in Table 3, where it is evident that the pochard, tufted duck, goldeneye and coot all showed significant declines ($p < 0.01$) in mean January counts in the seven years following 2001 compared to years before. No other species showed significant differences in their mean January counts either side of this season (Table 3).

![Fig. 4](image-url) Natural log-transformed annual index values for a) 3 piscivorous waterbird species, b) 5 dabbling ducks species, c) 4 diving duck species and d) 2 submerged macrophyte feeders wintering at Lough Neagh, 1988/9-2009/10 (1989/90-2008/09 in the case of mute swan). See text for explanation of methods used to generate index values from site count data.
Table 2 Details of simple linear regression models fitted to annual index values based on counts from Lough Neagh during the years 1988/9 to 2009/10 inclusive, showing $r^2$ values for the models, the annual rate of change in the index and $p$ values. Emboldened text indicates significant fits to models, italicised text those species increasing.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>$r^2$</th>
<th>annual %</th>
<th>$p$</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wigeon</td>
<td>0.259</td>
<td>-2.0%</td>
<td>0.016</td>
<td>*</td>
</tr>
<tr>
<td>Gadwall</td>
<td>0.005</td>
<td>+0.2%</td>
<td>0.763</td>
<td>ns</td>
</tr>
<tr>
<td>Teal</td>
<td>0.387</td>
<td>-3.1%</td>
<td>0.002</td>
<td>**</td>
</tr>
<tr>
<td>Mallard</td>
<td>0.270</td>
<td>-1.6%</td>
<td>0.013</td>
<td>*</td>
</tr>
<tr>
<td>Shoveler</td>
<td>0.354</td>
<td>-4.5%</td>
<td>0.004</td>
<td>**</td>
</tr>
<tr>
<td>Pochard</td>
<td>0.836</td>
<td>-8.0%</td>
<td>&lt;0.001</td>
<td>***</td>
</tr>
<tr>
<td>Tufted duck</td>
<td>0.713</td>
<td>-7.0%</td>
<td>&lt;0.001</td>
<td>***</td>
</tr>
<tr>
<td>Scaup</td>
<td>0.404</td>
<td>+5.0%</td>
<td>0.002</td>
<td>**</td>
</tr>
<tr>
<td>Goldeneye</td>
<td>0.790</td>
<td>-6.5%</td>
<td>&lt;0.001</td>
<td>***</td>
</tr>
<tr>
<td>Little grebe</td>
<td>0.040</td>
<td>-0.5%</td>
<td>0.382</td>
<td>ns</td>
</tr>
<tr>
<td>Great crested grebe</td>
<td>0.008</td>
<td>-0.4%</td>
<td>0.696</td>
<td>ns</td>
</tr>
<tr>
<td>Cormorant</td>
<td>0.551</td>
<td>+4.1%</td>
<td>&lt;0.001</td>
<td>***</td>
</tr>
<tr>
<td>Coot</td>
<td>0.592</td>
<td>-6.5%</td>
<td>&lt;0.001</td>
<td>***</td>
</tr>
</tbody>
</table>

Table 3 Mean January counts ($\pm$ SE) of the commoner waterbird species from Lough Neagh during the years 1994 to 2000 and 2002 to 2009, showing the percentage change between the seven year means and $p$ values indicating levels of significance between the means (*** indicate significance level of $p < 0.001$, ** of $p < 0.01$) based on Student $t$ tests. Emboldened text represents significant differences between periods.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>1994-2000</th>
<th>2002-2009</th>
<th>% change</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wigeon</td>
<td>2292 ± 619</td>
<td>1469 ± 295</td>
<td>-36</td>
<td>ns</td>
</tr>
<tr>
<td>Gadwall</td>
<td>72 ± 10</td>
<td>60 ± 7</td>
<td>-17</td>
<td>ns</td>
</tr>
<tr>
<td>Teal</td>
<td>908 ± 75</td>
<td>675 ± 153</td>
<td>-25</td>
<td>ns</td>
</tr>
<tr>
<td>Mallard</td>
<td>2178 ± 158</td>
<td>2206 ± 238</td>
<td>+1</td>
<td>ns</td>
</tr>
<tr>
<td>Shoveler</td>
<td>13 ± 4</td>
<td>22 ± 7</td>
<td>+65</td>
<td>ns</td>
</tr>
<tr>
<td>Pochard</td>
<td>19854 ± 1794</td>
<td>8563 ± 668</td>
<td>-57</td>
<td>***</td>
</tr>
<tr>
<td>Tufted duck</td>
<td>17728 ± 1480</td>
<td>7917 ± 617</td>
<td>-55</td>
<td>***</td>
</tr>
<tr>
<td>Scaup</td>
<td>2453 ± 388</td>
<td>2896 ± 697</td>
<td>+18</td>
<td>ns</td>
</tr>
<tr>
<td>Goldeneye</td>
<td>6461 ± 865</td>
<td>3475 ± 136</td>
<td>-46</td>
<td>**</td>
</tr>
<tr>
<td>Little grebe</td>
<td>239 ± 27</td>
<td>192 ± 19</td>
<td>-20</td>
<td>ns</td>
</tr>
<tr>
<td>Great crested grebe</td>
<td>106 ± 24</td>
<td>138 ± 9</td>
<td>+30</td>
<td>ns</td>
</tr>
<tr>
<td>Cormorant</td>
<td>471 ± 84</td>
<td>715 ± 125</td>
<td>+52</td>
<td>ns</td>
</tr>
<tr>
<td>Coot</td>
<td>3263 ± 341</td>
<td>1544 ± 144</td>
<td>-53</td>
<td>***</td>
</tr>
</tbody>
</table>
Comparing declines in diving species at Lough Neagh with trends at the flyway population, Republic of Ireland and Great Britain levels

Pochard

Pochard indices for Lough Neagh were positively correlated with those for Great Britain ($r^2 = 0.616, p < 0.0001$, Fig. 5a ii) and North-east/North-west Europe flyway ($r^2 = 0.648, p < 0.0001$, Fig. 5a iii); however, there was no relationship with indices for the Republic of Ireland ($r^2 = 0.039, p = 0.480$, Fig. 5a i).

Tufted duck

Lough Neagh indices for tufted duck were inversely related to indices for Great Britain ($r^2 = 0.270, p = 0.016$, Fig. 5b ii). The correlation with the indices for the Republic of Ireland just failed to attain statistical significance ($r^2 = 0.257, p = 0.054$, Fig. 5b i) but there was no significant correlation with the North-west Europe flyway indices ($r^2 = 0.000, p = 0.947$, Fig. 5b iii).

Scaup

Indices for scaup on Lough Neagh were negatively correlated with Northern Europe/Western Europe flyway indices ($r^2 = 0.215, p = 0.046$, Fig. 5c iii). There was no relationship with indices for the Republic of Ireland ($r^2 = 0.153, p = 0.150$, Fig. 5c i) or Great Britain ($r^2 = 0.002, p = 0.863$, Fig. 5c ii).
Goldeneye

Goldeneye indices on Lough Neagh were positively correlated with indices for the Republic of Ireland ($r^2 = 0.543, p = 0.002$, Fig. 5d i) and Great Britain ($r^2 = 0.334, p = 0.006$, Fig. 5d ii); however, no relationship with the North-west and Central Europe flyway indices was found ($r^2 = 0.074, p = 0.273$, Fig. 5d iii).

Coot

There was no relationship of coot indices for Lough Neagh with either the Republic of Ireland ($r^2 = 0.049, p = 0.426$, Fig. 5e i), Great Britain ($r^2 = 0.005, p = 0.752$, Fig. 5e ii) or North-west Europe flyway ($r^2 = 0.013, p = 0.630$, Fig. 5e iii).
Fig. 5 Linear regression between winter index values for a) pochard, b) tufted duck, c) scaup, d) goldeneye and e) coot at Lough Neagh with index values from i) the Republic of Ireland, ii) Great Britain and iii) flyway indices. For comparability between the different plots, all data are here standardised to have a $\bar{x} = 0$ and a $\sigma = 1$. Red lines ($\pm$ 95% CI) indicate a significant linear relationship at $p < 0.05$ whilst blue lines represent a near significant relationship.
Discussion

Cluster analysis and PCA both indicated a major difference in the waterbird community of Lough Neagh during 2002/03–2008/09 compared to 1989/90-2001/02. This shift in the waterbird community structure was caused by the rapid declines of two specific feeding guilds, the diving ducks that feed on benthic macroinvertebrates and the herbivores that feed on submerged macrophytes. Both feeding guilds were relatively stable up to and including winter of 2000/01 but have since collapsed to much lower levels. Since the two affected feeding guilds both feed by diving within the water column, these results suggest a dramatic change in food availability around 2000/01-2001/02. Food availability has been shown to affect diving duck population dynamics (e.g. Gardarsson & Einarsson 2004) and the relationship between macrophytes, macroinvertebrates and waterbirds has been the focus of several studies (Gregg & Rose 1985, Mitchell et al. 1988, Hanson & Butler 1994, Hargeby et al. 1994). Lakes with abundant submerged vegetation generally support a higher biomass of aquatic macroinvertebrates (Gregg & Rose 1985, Blindow et al. 1993, Hanson & Butler 1994) which in turn may have a positive effect on some functional groups of waterbirds (Mitchell et al. 1988, Hanson & Butler 1994, Hansson et al. 2010). This effect has been demonstrated for both diving ducks (Hanson & Butler 1994) and submerged macrophyte feeders (Mitchell et al. 1988, Hargeby et al. 1994). Indeed, it has been suggested that the abundance of macrophytes plays an important role in determining the composition of waterbird community in eutrophic lakes (Milberg et al. 2002) and in a similar study, declines in several tuber-feeding waterbird species coincided with the disappearance of their submerged macrophyte food plants (Fox et al. 2010). In line with these findings, it is plausible that a reduction in the submerged vegetation on Lough Neagh might have had a cascading
effect on several trophic levels, resulting in the steep decline of two feeding guilds. Unfortunately, to our knowledge no studies on the changes in the algal, macroinvertebrate or vegetation communities of Lough Neagh exist, hence the evidence presented here remains circumstantial.

Diving ducks commonly move between different wintering sites within the same winter in response to environmental factors (Kestenholz 1999, Hofer et al. 2005, Keller et al. 2009) and it has been suggested that migratory waterbirds may adjust their migratory routes by avoiding lakes with poor water quality (Hansson et al. 2010). Therefore if Lough Neagh is no longer suitable in terms of food availability, diving ducks and herbivorous waterbirds that formerly used the lake as a wintering site might have re-distributed to more suitable waterbodies.

Analysis of the trends in wintering numbers of individual waterbird species showed that several declined but those of greatest magnitude were pochard, tufted duck, goldeneye, coot and mute swan. It is interesting that of the diving ducks, pochard, tufted duck and goldeneye show very similar population trends on Lough Neagh while the scaup population, which has initially declined alongside those species, has recovered and is currently stable. This could be potentially explained by intrinsic or extrinsic factors, or a combination of both. On Lough Neagh, all diving duck species feed mainly on chironomid larvae (Evans 2000). Shallow areas of Lough Neagh provide inadequate feeding conditions for diving ducks because chironomid larvae are of smaller body size compared to offshore areas (Winfield & Winfield 1994b). According to Winfield & Winfield (1994b), scaup and tufted duck take chironomid larvae of larger body size than pochard and goldeneye. Evans (2000) has also found that scaup, but not tufted duck, consumes significantly larger chironomid larvae than other diving duck species on Lough Neagh. It is therefore
possible that scaup, due to their slightly larger body size, are able to exploit deeper areas of the lake where these chironomids are located. Scaup might therefore respond differently than other diving duck species because a different feeding strategy does not bring it in direct feeding competition with them.

The population trends amongst the different diving ducks could also be explained by extrinsic factors. Pochard and goldeneye wintering in Northern Ireland breed almost entirely in Northern and Eastern Europe, tufted duck originate from Iceland, Ireland, Britain and continental Europe, whereas scaup wintering in Northern Ireland come from Iceland (Wernham et al. 2002). Therefore it is possible that pochard, tufted duck and goldeneye are affected by factors operating on the flyway level, while this is not the case for scaup. To examine this hypothesis, population indices for each migratory species on Lough Neagh were compared with flyway, Great Britain and Republic of Ireland indices. Mute swan was excluded from the analysis because this species is resident at Lough Neagh.

Pochard declines at Lough Neagh were highly significantly correlated with those at the flyway level and Great Britain. This might suggest that the recent declines in numbers at Lough Neagh simply reflected trends in the flyway and in Great Britain were it not for the fact that there was no correlation with the index values in the Republic of Ireland. In the Republic of Ireland, numbers have fluctuated during the period 1994/5 to 2008/9 but have shown no tendency to follow the marked decline at Lough Neagh or in the flyway over all. This is perhaps unusual since Ireland represents the extreme north-western end of the western European flyway for this species, but Lough Neagh holds over half of all the Ireland wintering population (Calbrade et al. 2010, Boland & Crowe 2012). This does rather suggest that declines
at Lough Neagh are more likely linked to overall declines along the flyway, but the possibility of declines resulting from intrinsic factors cannot be ruled out.

Tufted duck have shown declines on Lough Neagh comparable to those of pochard. Tufted duck is unusual in that the population overwintering on Lough Neagh originates from both continental Europe and Iceland (Wernham et al. 2002), and there is also a small resident population on the lough. Index values at Lough Neagh showed no correlation with those at the flyway level, suggesting the declines there are not related to the overall changes in abundance in the flyway. Indeed, there has been no significant change in the index values generated for the North West Europe population of tufted duck between 1983 and 2007. The negative correlations between index values for Great Britain suggest increases in these areas associated with recent declines at Lough Neagh that could be interpreted as a redistribution of birds from this site, supporting the hypothesis of intrinsic factors being responsible for the decline.

Unusual amongst the Lough Neagh diving duck species, scaup have actually slightly increased in recent years. The annual index values for scaup at Lough Neagh showed a negative correlation with those of the flyway. However, it is generally considered from ringing recoveries that the majority of the Lough Neagh scaup originate from Iceland, but the flyway population index values are derived from wintering stocks throughout Western Europe where the majority originate from much larger breeding stocks in Scandinavia and throughout northern Russia (Wernham et al. 2002). There is unfortunately no adequate source of annual abundance data for the Iceland population of Scaup, because in Great Britain, they mix with birds from the continental European flyway (Wernham et al. 2002). There was no relationship between the Great Britain and Republic of Ireland indices and
those of Lough Neagh, showing independence of trends in abundance. Since numbers have increased in recent years at Lough Neagh, this situation strongly suggests that intrinsic factors are either not currently affecting this species at the site or that for some reason, the species is outcompeting other diving ducks.

Goldeneye have declined dramatically at Lough Neagh in recent years and there was no correlation between the index values for goldeneye at Lough Neagh and those from the North-Western and Central Europe flyway from which these birds are considered to draw (Wernham et al. 2002). However, there were significant positive correlations between index values from the Republic of Ireland and Great Britain which suggest the declines observed in these areas have been reflected at Lough Neagh. Goldeneye has shown a decrease in Britain since the late 1990s (after a prior period of increase) and a sustained decline in the Republic of Ireland since counts started in 1993. For this reason, it would be simplest to conclude that the declines at Lough Neagh are associated with declines in Britain and Ireland, potentially associated with “short-stopping”, i.e. where birds simply winter further up-stream along their migratory flyway in response to more favourable conditions there, such as improved food availability or milder mid-winter conditions. This seems likely to be the case since counts in Sweden have increased dramatically in recent years (Nilsson & Månsson 2011) while the population index for the overall wintering numbers in this flyway has also shown a sustained increase during the years 1983-2006.

Coot index values for Lough Neagh showed no correlation with those for the flyway, Great Britain and Republic of Ireland. Even though coot are partial migrants, the majority of the population is resident (Wernham et al. 2002); so a lack of correlation between numbers on Lough Neagh and elsewhere was expected. The fact
that this mainly resident species together with another, the mute swan, declined simultaneously with migratory species is perhaps the most direct indicator that intrinsic factors were operating on Lough Neagh to reduce the food supply to a range of waterbird species present in the non-breeding season.

In summary, the comparison of Lough Neagh trends in individual species with those elsewhere in the flyway, Great Britain and in the Republic of Ireland showed variation between species and no consistent inter-specific trends were detected. While pochard and goldeneye declines at Lough Neagh could be associated with general changes in abundance (either because of population declines or short-stopping along the flyway), this was not the case for tufted duck and coot. However, because short-stopping is a gradual process, it is to be expected that any effects of short-shopping on waterbird populations on Lough Neagh would manifest themselves in a slow and gradual decline. In contrast, the change in the waterbird community on Lough Neagh was sudden and discrete. This evidence suggests that changes in the waterbird numbers were likely the result of an intrinsic regime change, possibly linked with the collapse of submerged plants and macroinvertebrates (changes in the species composition and/or biomass) on Lough Neagh. Benthic invertebrates have been sampled at Lough Neagh in the past, and comparison of pre and post 2000/01 samples of the benthic fauna was carried out to verify if there have been such changes that could potentially contribute to an explanation of the declines in diving ducks and submerged macrophyte feeders at the site (Chapter 4). Only after considering the results of such studies will it be possible to address the potential management consequences of these findings.
Chapter 3

Assessment of commercial sand barge radar for detecting overwintering diving ducks at Lough Neagh

This chapter was submitted as:

Abstract

Lough Neagh Special Protection Area is one of the most important non-estuarine sites in Britain and Ireland for overwintering wildfowl. Wetland Bird Survey (WeBS) counts have revealed a dramatic decline in overwintering diving duck numbers. WeBS counts are conducted from the shore and it has been suggested that on-to-offshore redistribution of ducks may have led to an underestimate of numbers. Diving ducks on Lough Neagh are, with the exception of goldeneye (*Bucephala clangula*), principally nocturnal feeders, and their feeding distribution is unknown. Anecdotal evidence from commercial sand barge skippers suggests that the radar fitted in such craft is able to detect bird flocks. The aim of the study was to determine the diurnal distribution of diving duck flocks at Lough Neagh using visual counts from sand barges and assess the feasibility of using commercially available radar to describe the nocturnal feeding distribution of diving ducks. Sand barge radar was notably poor in identifying diving duck flocks compared to independent visual observations. It was highly sensitive to interference by waves generated during windy conditions. Nevertheless, visual observations were useful in describing their diurnal distribution. The sand barges were positioned on average 1.5 km from the shore when a flock of diving ducks was observed and the probability of detection declined with distance from the shore. This supports the reliability of shore-based WeBS counts in monitoring and surveillance. Given the poor performance of sand barge radar systems in this study, the use of specialised Bird Detecting Radar should be considered to determine the nocturnal distribution of diving ducks on Lough Neagh.
Introduction

Lough Neagh Special Protection Area (SPA) is one of the most important non-estuarine sites in Britain and Ireland for overwintering wildfowl. Wetland Bird Survey (WeBS) counts revealed a dramatic decline in returning diving duck numbers, most notably pochard (*Aythya ferina*), tufted duck (*A. fuligula*) and goldeneye (*Bucephala clangula*). The overall diving duck population declined by 63% between the winters of 2000/01 and 2008/09 (Tománková *et al.* 2013). Diving ducks overwintering on Lough Neagh are, with the exception of goldeneye, principally nocturnal feeders (Evans & Day 2001). Therefore, their feeding distribution is difficult to ascertain as is any shift in the location of their feeding grounds. Attempts have been made in the past to describe the nocturnal distribution of diving ducks at Lough Neagh using land based observations (Evans 2000), however, only those detected visually from the shore were counted and it was concluded that birds may utilize areas offshore. Lough Neagh (383km$^2$) is the largest freshwater lake in Britain and Ireland by surface area (Carter 1993b). WeBS counts are also conducted entirely from the shore and it has been suggested that within-site on-to-offshore redistribution of ducks may have led to overwintering numbers being underestimated (Allen & Mellon 2006). Consequently, further research into the distribution of diving ducks at Lough Neagh, especially their feeding distribution during nocturnal hours, has been recommended (Allen & Mellon 2006).

Bird Detecting Radar (BDR) has become increasingly used to quantify bird numbers and their movements within the vicinity of airports and wind turbine developments to judge collision risk (Liechti & van Gasteren 2010). Sand extraction is an important industry at Lough Neagh with production at about 1.2 million tonnes
of sand per annum accounting for 25% of the Northern Ireland sand supply (G. Best, QPANI, pers. comm.). In winter, sand barges begin operations before dawn during the hours of darkness. Anecdotal evidence from skippers suggests that the commercial radar fitted in such craft, for safety and navigation purposes, is able to detect flocks of birds, primarily ducks, or even large single birds, primarily swans. Currently, twelve barges, operated by six companies, exploit Lough Neagh for sand extraction (G. Best, QPANI, pers. comm.). Such is the level of activity that Lough Neagh is almost certainly completely covered by radar imaging on an almost daily basis providing a potentially cost effective means by which to describe the diurnal and nocturnal distribution of diving ducks using radar readings tested by visual observation.

The aim of this study was to i) determine the post-dawn (diurnal) distribution of diving duck flocks at Lough Neagh using visual counts from the elevated platform of the cabin on sand barges and ii) assess the feasibility of using commercially available radar to describe and map their pre-dawn (nocturnal) feeding distribution.

Methods

The study was carried out in the winter of 2010/11 on Lough Neagh, Counties Antrim, Down, Armagh, Tyrone and Londonderry, Northern Ireland (Grid Ref. J 02357 71723), the largest freshwater lake in Britain and Ireland (Carter 1993b). Three commercial sand extraction companies, namely: Mullholand Bros, Norman Emerson Group and Northstone (NI) Ltd, provided access to their sand barges. A total of five excursions was made during day light hours (Table 1). Depending on the company, barges left from Ardmore, Ballyginniff or Sandy Bay but all travelled to the mouth of the Ballinderry River (Fig. 1a). Sand barge radar readings were recorded using a
standard video camera for the duration of the voyage. In total, 16 hours 29 minutes were recorded. The location of the sand barge was plotted every 60 seconds using a GPS data logger (i-gotU GT-100, MobileAction Technology) and mapped using ArcGIS 10 (ESRI, California, USA). During the hours of darkness, the gain of the radar is normally set between 0.75 - 1.50 nautical miles, depending on the skipper’s preference. Mean wind speed (kph) was recorded for the duration of the voyage.

Radar video recordings were viewed by an independent observer (different than the observer on the sand barge) to eliminate any unconscious bias and ensure a blind experiment. The observer noted presence and time of any flock-like objects on-screen. The location of the barge at each detection was extracted from the time-indexed GPS transponder. The time and approximate size of actual flocks of diving duck and any other bird species was recorded visually from the cabin of the sand barges (by a different observer than that watching the radar footage). This was because radars would only be able to detect a flock of birds and not be able to distinguish between species. However, it is highly likely that the only species forming flocks on Lough Neagh would be pochard, tufted duck, scaup *Aythya marila* and goldeneye. It was assumed that birds present would be recorded by the observer in the cabin of the sand barge. Thus, for daylight hours the rates of true positive, false positive and false negative detections were quantified. True positives were recorded when a diving duck flock was reported on the radar and observed visually on the lough (Fig. 1b). False positives were recorded when a diving duck flock was recorded on the radar but not observed visually on the lough (Fig. 1b) and false negatives were recorded when a diving duck flock was recorded visually on the lough but not reported from the radar.

The probability of detecting a diving duck flock with distance from the shore line was determined using logistic regression. An equal number of pseudo-absences were
generated to match the total number of visual detections (i.e. 23). Pseudo-absences were randomly generated within the extent of the radar gain (i.e. the area within which it was possible to detect ducks) using the Random Point tool in the Spatial Analyst toolbox for ArcGIS. Binary presence / pseudo-absence was fitted as the dependent variable and distance from the shore as the independent covariate. Significance was judged using a $\chi^2$ distribution assuming one degree of freedom. The sensitivity and specificity of sand barge radar in detecting diving duck flocks was evaluated using the Area Under the Curve (AUC) value derived from a Receiver Operating Characteristic (ROC) curve. In order to determine the effect of wind on radar sensitivity, wind speed (kph) was plotted against the rate of false positive detections per hour for each of the sand barge runs using Spearman’s rank correlation. All statistical analyses were conducted using IBM SPSS Statistics 20.

**Results**

A total of 163 visual and/or radar target detections was recorded but only five (3%) were validated as true positives (Table 1). The AUC value = 0.195 substantially below the 0.5 threshold for random classification and thus sand barge radar was notably poor in correctly identifying diving duck flocks compared to independent visual observations. A total of 23 diving duck flocks of up to 1 000 individuals was observed visually from sand barges at an average distance of the sand barge from the shore of 1.5 km (range 0.1 - 3.9 km, Fig. 1c). In all cases, the diving duck flock observed from the sand barge was between the sand barge and the shore. Probability of detecting a diving duck flock decreased significantly with distance from the shore line ($\chi^2 = 10.722$, d.f. = 1, $p = 0.001$, pseudo-$r^2 = 0.277$, $n = 46$). There was a positive
trend for a higher rate of false positive detections during windy conditions \( r_s = 0.67, p = 0.219; \) Fig. 1d).

Table 1 Descriptive statistics for 163 detections using sand barge radar operating at Lough Neagh during winter 2010/11.

<table>
<thead>
<tr>
<th>Date</th>
<th>Company operating barge</th>
<th>Start location</th>
<th>Duration (h:min)</th>
<th>Wind (kph)</th>
<th>True positives</th>
<th>False negatives</th>
<th>False Positives</th>
</tr>
</thead>
<tbody>
<tr>
<td>09/12/2010</td>
<td>Northstone (NI) Ltd.</td>
<td>Ballyginniff</td>
<td>02:41</td>
<td>9.2</td>
<td>1</td>
<td>2</td>
<td>36</td>
</tr>
<tr>
<td>28/01/2011</td>
<td>Norman Emerson Group</td>
<td>Ardmore</td>
<td>01:47</td>
<td>3.2</td>
<td>3</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>09/02/2011</td>
<td>Mullholand Bros.</td>
<td>Sandy Bay</td>
<td>03:25</td>
<td>14.5</td>
<td>0</td>
<td>3</td>
<td>58</td>
</tr>
<tr>
<td>14/02/2011</td>
<td>Mullholand Bros.</td>
<td>Sandy Bay</td>
<td>03:47</td>
<td>17.7</td>
<td>0</td>
<td>0</td>
<td>38</td>
</tr>
<tr>
<td>16/02/2011</td>
<td>Norman Emerson Group</td>
<td>Ardmore</td>
<td>03:46</td>
<td>3.2</td>
<td>1</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>TOTAL / MEAN</td>
<td></td>
<td></td>
<td><strong>16:26</strong></td>
<td><strong>9.6</strong></td>
<td><strong>5</strong></td>
<td><strong>8</strong></td>
<td><strong>150</strong></td>
</tr>
</tbody>
</table>
Fig. 1 a) Distribution of sand barge tracks (black lines) showing the average gain of the radar (grey shading) and the position of the sand barge when diving duck flocks were identified by eye (grey circles, scaled for estimated numbers). b) Screen of a radar fitted to a sand barge. Dot in a red circle represents a true positive, where a bird flock was present on the lough and reported on the radar. Dots close to the centre are false positives, where a flock was recorded on radar but not observed visually on the lough. Consistent colouring at the bottom of the photo represents land. c) Probability of detection with distance from the shore line. d) Relationship between the rate of false positive detection and wind speed.
Discussion

Sand barge radar proved to be highly inaccurate in the detection of diving flocks at Lough Neagh. Specialised Bird Detecting Radar (BDR) is interpreted using sophisticated analytical software which filters out noise and leaves only those objects matching the size and movement speed of the desired target (Liechti & van Gasteren 2010), in this case, ducks. Standard, commercially available radar installed on sand barges operating at Lough Neagh is designed for navigational safety in detecting other boats and preventing collisions during the hours of darkness or in foggy conditions. It is, therefore, unsuited for detailed visual analysis for the purposes of mapping bird distributions. Moreover, it was highly sensitive to interference. Weather degraded its performance. Wind speed is recognised as one of the most important environmental variables determining radar accuracy (Skolnik 2001, Kulemin 2003) although rainfall can also create interference (Moore et al. 1979). Unwanted echoes are almost always present and widespread (Kingsley & Quegan 1992), making the detection of relevant targets difficult (Skolnik 2001).

Another caveat is that it is impossible to distinguish species from radar detections, thus detected flocks may have been single-species or mixed-flocks of the target species: pochard, tufted duck, scaup and goldeneye or non-target species. Consequently, utilizing existing radar fitted to commercial sand barges is not a feasible method to map the nocturnal feeding distributions of overwintering diving ducks at Lough Neagh. Nevertheless, visual observations of diving duck flocks from the elevated platform provided by the cabin of sand barges were useful in plotting their daylight (post-dawn) distribution. Such observations confirmed that during daylight hours diving ducks were detected when the sand barge was positioned about
1.5 km from the shore (compared to a maximum possible distance of about 6km) supporting the reliability of shore-based WeBS counts in monitoring overwintering numbers. It seems unlikely, therefore, that bird numbers are underestimated during the Wetlands Bird Survey. The observed decline in overwintering numbers reported previously is thus a real phenomenon.
Chapter 4

Chlorophyll \( a \) concentrations and macroinvertebrate declines coincident with collapse of overwintering diving duck populations in a large eutrophic lake

This chapter is in press as:

Tománková, I., Harrod, C., Fox, A.D. & Reid, N. (in press) Chlorophyll \( a \) concentrations and macroinvertebrate declines coincident with collapse of overwintering diving duck populations in a large eutrophic lake. *Freshwater Biology.*
Abstract

Lough Neagh is one of the most important non-estuarine sites in Britain and Ireland for overwintering wildfowl. A change in the waterbird assemblage following the winter of 2000/01 was driven mainly by a rapid decline in the population of overwintering diving ducks. Sudden and discrete changes to resident as well as migratory waterbirds may suggest an intrinsic cause. The density and biomass of benthic macroinvertebrates, the food of wintering diving ducks, in 2010 (following the diving duck population decline) was compared with values from a baseline survey conducted in 1997/98 (before the decline in diving ducks). The mean total density of macroinvertebrates declined significantly by 66% from 15 300 m$^{-2}$ in 1997/98 to 5 136 m$^{-2}$ in 2010. There was a concomitant 67% decline in mean macroinvertebrate biomass from 15 667 mg m$^{-2}$ to 5 112 mg m$^{-2}$. In terms of taxonomic composition, the relative contribution of Tanypodinae, Glyptotendipes spp. and Tanytarsini declined while the relative contribution of Chironomus spp. increased. We describe a shift in chlorophyll a concentrations, taken as a proxy for productivity, in the largest freshwater lake in Britain and Ireland coincident with a significant reduction in macroinvertebrate density and biomass with potential implications for ecosystem processes and ecologically and economically important consumer populations, principally waterbirds.
Introduction

Benthic macroinvertebrates are important in many aquatic ecosystems, providing nutrients and energy to a range of predators, including other invertebrates, fish and birds. Many waterbirds act as predators in freshwater ecosystems; for example, diving ducks feed on benthic macroinvertebrates (Snow & Perrins 1998). Chironomid larvae (Chironomidae) are an important constituent of the diet of lacustrine diving ducks (e.g. Bengtson 1971, Nilsson 1972, Winfield & Winfield, 1994b).

As well as providing energy and nutrients to consumers, the abundance and distribution of many benthic macroinvertebrates may reflect changes in physicochemical conditions or system productivity (Krieger & Ross 1993, Schloesser et al. 1995, Carter et al. 2006). Any change in macroinvertebrate abundance or species composition may, therefore, have profound consequences for the whole ecosystem, including waterbirds.

Since 2000, the European Water Framework Directive (Directive 2000/60/EC) has required compliance from European Union member states to introduce monitoring and surveillance of inland and coastal water quality including the implementation of measures to maintain ‘favourable conservation status’ at designated sites. Moreover, the EC Birds Directive (2009/147/EC) provides a framework for the conservation and management of wild birds in Europe and confers protection on some waterbirds populations. To fulfil this objective, Member States invariably have site-based waterbird monitoring programmes in place (e.g. Calbrade et al. 2010) to generate population trends in waterbird species.

Lough Neagh (383 km$^2$) is the largest freshwater lake in Britain and Ireland in terms of surface area (Carter 1993a). It is a Ramsar wetland of international
importance, a Special Protection Area (SPA) and an Area of Special Scientific Interest (ASSI), in part designated for wintering diving duck abundance. Historically, eutrophication has been a major concern at Lough Neagh (Foy et al. 2003), most recently reflecting agricultural run-off (Bunting et al. 2007). Following a large bloom of the blue-green bacterium *Anabaena flosaquae* in 1967, human use of the lough was affected by disruption to water treatment plants, commercial fishing and recreational use (Wood & Gibson 1973). Subsequently, Lough Neagh has received considerable scientific attention (e.g. Wood & Smith 1993) and has been the subject of long-term water quality monitoring and monthly counts of waterbirds during the winter, as part of the UK’s national Wetland Bird Survey (WeBS). However, other components of the ecosystem have been less well studied, and regular macroinvertebrate monitoring is currently restricted to the littoral zone (< 1 m deep). In a lake of almost 400 km$^2$, such monitoring has limited relevance to the greater part of the macroinvertebrate assemblage (e.g. water of a depth < 2 m represents < 8% of the total surface area of the lough bed; Douglas 1997) or to the taxa that consume them, e.g. diving ducks. In addition to macroinvertebrate sampling in the littoral zone, one major lough-wide survey was conducted in 1997/98 (Bigsby 2000).

Chironomid larvae are a major component of the lough’s benthic fauna (Carter 1978) and show seasonal variation, with Carter (1976) reporting larval densities of 4000 m$^{-2}$ in autumn and 2000 m$^{-2}$ in spring. Winfield (1991) produced slightly higher estimates, with a mean density of 6250 m$^{-2}$ in the autumn and 3275 m$^{-2}$ in the spring. In 2005, zebra mussels (*Dreissena polymorpha*) were recorded in Lough Neagh for the first time (McLean et al. 2010); a species that has significantly affected lake ecosystems in lakes throughout Europe and North America (Ward & Ricciardi 2007).
Their impact on Lough Neagh has not yet been established as zebra mussel numbers are still low and the species is localised (McLean et al. 2010).

Any changes in the macroinvertebrate community due to changes in water quality are likely to have an impact on consumers higher in the food web, most notably waterbirds. Indeed, long-term monitoring of waterbirds at Lough Neagh has shown a marked decline in wintering diving ducks, particularly pochard (Aythya ferina), tufted duck (A. fuligula) and goldeneye (Bucephala clangula), since the winter of 2000/01 (Tománková et al. 2013). Between the winters of 2000/01 and 2008/09, the overall population of diving ducks on Lough Neagh declined by 63% (Tománková et al. 2013). Different possible explanations for this decline have included site related factors (Maclean et al. 2006) and migratory short-stopping, where birds reduce the migration distance between their breeding and wintering grounds, resorting to wetlands formerly unsuitable or unavailable to them in the winter to the north and east of their traditional wintering range (Allen & Mellon 2006, Appendix I). Since the relevant statutory agencies are responsible for maintaining the lake and its waterbirds in ‘favourable conservation status’, it is essential to determine whether factors at Lough Neagh are responsible for changes in diving duck abundance and, if so, whether management actions can be implemented to restore their abundance. Recent research suggests that local factors are likely to be at least partially responsible, with reduction in local food supply at the lough being one possible hypothesis (Tománková et al. 2013).

Here, the focus was on changes in the availability and type of benthic prey available to diving ducks before and after their decline, while simultaneously assessing longer term trends in chlorophyll $a$ concentration, taken by some as a proxy for primary productivity (Ware & Tomson 2005, Frank, Petrie & Shackell 2006).
Specifically, the aim was to: i) describe the contemporary macroinvertebrate community in Lough Neagh in terms of composition and abundance, in order to assess food availability for top consumers, including diving ducks, and ii) to assess temporal changes in the composition and abundance of benthic macroinvertebrates between the winters of 1997/98 (Bigsby 2000) and 2010 (this study).

**Methods**

**Macroinvertebrate surveys**

In the absence of routine macroinvertebrate surveys, the densities and biomass from a detailed study of the lough made prior to the decline in diving duck populations during October 1997 and January 1998 (Bigsby 2000) were compared with a contemporary survey during January and October 2010. For consistency, the sampling methodology used by Bigsby (2000) was followed exactly in the current study. This involved core sampling macroinvertebrate communities inhabiting soft sediments in six bays (Washing Bay, Kinnego Bay, Bartin’s Bay, Lennymore Bay, Antrim Bay and Ballyronan Bay) at depths ranging from 3 to 12m (Fig. 1) during October and January. These months were selected to represent the period reflecting the use of the lough by the overwintering diving ducks. Repeated samples \((n = 5)\) of sediment and associated infauna were taken at each site and depth and each month with a Kajak corer \((21.23 \text{ cm}^2)\) attached to either a rope or a hand pole. This method was unlikely to sample more mobile macroinvertebrates effectively, such as *Gammarus* spp., *Asellus aquaticus* and *Mysis* spp., in comparison to other sedentary taxa such as the Chironomidae. Therefore, their numbers are likely to have been underestimated.
However, the main purpose was to compare the macroinvertebrate fauna of Lough Neagh on two occasions, so consistent methodology was important. Samples were washed through a 250 µm sieve to remove sediment. Macroinvertebrates were then picked out, counted and identified. In most cases, chironomid larval head capsules were mounted with either Euparal or Hydromatrix solutions (Brooks, Langdon & Heiri 2007) to allow identification (Wiederholm 1983, Brooks et al. 2007). Not all macroinvertebrates were identified to species; rather, operational taxonomic units were used. This was particularly the case for chironomid larvae which were generally identified to genus. Although relatively abundant, Oligochaeta were excluded from the survey, following Bigsby (2000). Rare taxa were grouped in the category “other”.

All macroinvertebrates were measured to allow biomass to be estimated. Total length ± 0.001 mm was typically recorded but occasionally, head capsule dimensions were taken for chironomid larvae, if only part of the body was found in the sample. Mass-length regressions were then used to convert body dimensions into biomass. In order to make the surveys directly comparable, the mass-length regressions used in this survey were those used by Bigsby (2000). The regressions for chironomid larvae, *Asellus aquaticus*, *Gammarus* spp. and leeches were taken from Bigsby (2000), while regressions for all other macroinvertebrate taxa were obtained from Benke et al. (1999). *Mysis* were weighed, due to the low number of individuals sampled. Both macroinvertebrate counts and dry mass were converted into estimates of density (numbers m$^{-2}$) and biomass (mg m$^{-2}$).

Data from the 1997/98 survey (Bigsby 2000) were extracted from graphs using Plot Digitizer (version 2.5.1: http://plotdigitizer.sourceforge.net/) software, as the original raw data could not be retrieved in any other form. These values were then
converted to density (numbers m\textsuperscript{-2}) and biomass as dry mass (mg m\textsuperscript{-2}) to permit comparison.

**Chlorophyll a concentration**

Concentration of chlorophyll \(a\) (µg L\textsuperscript{-1}) at Lough Neagh was measured from 1995 to 2011. Ten metre composite water samples were collected fortnightly using a flexible tube from a central location in Lough Neagh (54°37’N, 6°24’W) and averaged for each year. Chlorophyll \(a\) was measured after extraction into hot (55°C) methanol (Talling 1969). Data were obtained from the Agri-Food and Biosciences Institute (AFBI), Northern Ireland.

**Statistical analysis**

Variation in total macroinvertebrate abundance and dry mass was examined using Generalized Linear Mixed Models (GLMMs), using a negative binomial distribution with a log link function to account for the large variance of data relative to the mean. Transect ID was fitted as a random factor to account for multiple observations at each sampling site. Survey period, Depth and Season were fitted as fixed factors. Statistics were conducted using SPSS v20 and graphs plotted using Sigmaplot v10.

In order to characterise how the overall macroinvertebrate community differed between the two survey periods, a parallel multivariate analysis was undertaken. Here, the total abundance of each macroinvertebrate taxon was summed for each survey, segregating data by depth (3, 6, 9, and 12 m) and survey transect (Antrim, Ballyronan, Bartin’s, Kinnego, Lennymore and Washing Bays). Abundances were square-root transformed and standardised before a Bray-Curtis dissimilarity matrix was
constructed using PRIMER 6.1.13 and PERMANOVA 1.0.3 (Anderson, Gorley & Clarke 2008). Spatial (Transect, Depth) and temporal (Season, Survey period) influences on the relative abundance of macroinvertebrate taxa were examined using a four-way permutational \((n\) permutations = 9 999) multiple analysis of variance (PERMANOVA). Transect ID was fitted as a random factor and Depth, Survey and Season were fitted as fixed factors. Following the PERMANOVA analysis, those taxa driving the key differences in survey periods were examined using the SIMPER in PRIMER.

Variation in community structure associated with survey period and sample depth was visualised graphically using a Principal Coordinates Analysis (PCO); an unconstrained ordination method also known as metric multi-dimensional scaling (Anderson & Willis 2003, Anderson et al. 2008). Vectors based on multiple correlation (correlation coefficients >0.4) were included to highlight those taxa driving the distribution of data along the first two PCO axes, whilst accounting for variation in the other taxa.

Concentrations of chlorophyll \(a\) were tested before and after the known change point in the temporal trend for diving duck abundance (Tománková et al. 2013) using a \(t\)-test (i.e. pre- and post-2001).
Results

Total macroinvertebrate density decreased significantly (Table 1a) by two thirds between 1997/98 and 2010 (Fig. 2a-d), with an estimated mean ± SD density of 15 300 ± 9 487 m⁻² (mean density averaged for both January and October across all bays and depths) during 1997/98, compared to 5 115 ± 3 944 m⁻² during 2010. Total macroinvertebrate dry mass also decreased significantly (Table 1b) and by a similar order of magnitude between the survey periods (Fig. 2e-h), from a mean ± SD dry mass of 15 667 ± 8 799 mg m⁻² in 1997/98 to 5 275 ± 3 751 mg m⁻² in 2010. Total
biomass was higher in October than in January (Table 1; Fig. 2e-h) in both 1997/98 and 2010 while, for total density, this was the case in the current study but not in 1997/98 (Table 1; Fig. 2a-d). Total density of macroinvertebrates also varied significantly with depth (Table 1). Zebra mussels were not recorded in the current survey; however, it is likely that the species would be under-sampled on soft sediments.

PERMANOVA revealed considerable variation in the relative contribution of different taxa to the macroinvertebrate assemblage associated with three of the main factors examined: Survey (Pseudo-\(F_{1,12} = 6.44, p = 0.009\)), Depth (Pseudo-\(F_{3,12} = 12.89, p = 0.0001\)) and Transect (Pseudo-\(F_{5,12} = 3.3, p = 0.001\)). There was little evidence of any effect of Season on variation in assemblage structure (Pseudo-\(F_{1,12} = 1.41, p = 0.288\)). The relative influence of Survey and Depth on invertebrate assemblage structure is shown in the Principal Coordinates Analysis (Fig. 3).

Comparison of first order interactions suggested strong interactions between Survey*Season (Pseudo-\(F_{1,12} = 10.32, p = 0.0049\)) and Depth*Transect (Pseudo-\(F_{12,12} = 2.16, p = 0.005\)), and a less marked interaction between Survey*Transect (Pseudo-\(F_{5,12} = 2.28, p = 0.025\)). There was no obvious interaction between Survey*Depth (Pseudo-\(F_{3,12} = 1.65, p = 0.132\)) or Depth*Season (Pseudo-\(F_{3,12} = 1.00, p = 0.476\)). Of the second order interactions, only Survey*Depth*Transect was significant at 95% levels (Pseudo-\(F_{12,12} = 1.82, p = 0.03\)).

As the main question of interest in the current study was whether major shifts had occurred in the community structure of the Lough Neagh benthic macroinvertebrate community over the intervening period, the focus was on examining which taxa were responsible for the significant shift in assemblage structure shown between the two Survey periods by our PERMANOVA analysis (see above). A SIMPER analysis
(Table 2) suggested that the relative contribution of Tanypodinae, *Glyptotendipes* spp., Tanytarsini and *Dicrotendipes* spp. to the macroinvertebrate community fell between 1997/98 and 2010, whilst the relative contribution of *Chironomus* spp. and various other taxa increased.

Concentrations of chlorophyll *a* differed significantly between pre- and post-2001 (Fig. 4); taken as the change point in the temporal trend for diving duck abundance ($t_{414} = -6.06, p < 0.001$).

**Table 1** GLMM results describing changes in a) total density and b) total dry mass of benthic macroinvertebrates in Lough Neagh.

<table>
<thead>
<tr>
<th>Model</th>
<th>$F$</th>
<th>df</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Total abundance ($F_{7,78}= 22.703, p &lt; 0.001$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Survey</td>
<td>111.047</td>
<td>1.78</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Depth</td>
<td>7.819</td>
<td>5.78</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Season</td>
<td>6.236</td>
<td>1.78</td>
<td>0.015</td>
</tr>
<tr>
<td>b) Dry mass ($F_{7,78}= 9.656, p &lt; 0.001$)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Survey</td>
<td>60.430</td>
<td>1.78</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Depth</td>
<td>0.371</td>
<td>5.78</td>
<td>0.867</td>
</tr>
<tr>
<td>Season</td>
<td>5.902</td>
<td>1.78</td>
<td>0.017</td>
</tr>
</tbody>
</table>

**Table 2** Results of the SIMPER analysis examining the relative contribution of different taxa to the Lough Neagh macroinvertebrate community in the period 1997/98 and 2010. Also shown for each taxon is the mean dissimilarity between survey dates, and the percentage contribution (individual and cumulative) to the overall dissimilarity between survey periods.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean contribution 97/98</th>
<th>Mean contribution 2010</th>
<th>Mean (± SD) dissimilarity</th>
<th>% contribution to dissimilarity</th>
<th>Cumulative % dissimilarity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tanypodinae</td>
<td>31</td>
<td>21</td>
<td>12.7 (± 0.1)</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td><em>Chironomus</em> spp.</td>
<td>15</td>
<td>27</td>
<td>12.3 (± 1.2)</td>
<td>20</td>
<td>41</td>
</tr>
<tr>
<td><em>Glyptotendipes</em> spp.</td>
<td>21</td>
<td>14</td>
<td>9.7 (± 1.2)</td>
<td>16</td>
<td>57</td>
</tr>
<tr>
<td>Tanytarsini</td>
<td>17</td>
<td>10</td>
<td>9.5 (± 1.0)</td>
<td>16</td>
<td>73</td>
</tr>
<tr>
<td>Other <em>Chironomus</em></td>
<td>6</td>
<td>8</td>
<td>4.1 (± 0.9)</td>
<td>7</td>
<td>80</td>
</tr>
<tr>
<td>Others</td>
<td>2</td>
<td>3</td>
<td>3.6 (± 0.9)</td>
<td>6</td>
<td>86</td>
</tr>
<tr>
<td>Molluscs</td>
<td>2</td>
<td>3</td>
<td>2.0 (± 0.3)</td>
<td>3</td>
<td>89</td>
</tr>
<tr>
<td><em>Dicrotendipes</em> spp.</td>
<td>3</td>
<td>2</td>
<td>1.8 (± 1.0)</td>
<td>3</td>
<td>92</td>
</tr>
</tbody>
</table>
Abundance

Fig. 2 Density (number m$^{-2}$) of total macroinvertebrates during a) Oct 1997 b) Oct 2010, c) Jan 1998 and d) Jan 2010. Dry mass (mg m$^{-2}$), excluding molluscs, during e) Oct 1997 f) Oct 2010, g) Jan 1998 and h) Jan 2010. * sampling was not possible due to the hard nature of the substratum
**Fig. 3** Principal Coordinates Analysis (PCO) ordination showing variation in macroinvertebrate assemblage structure (data square-root transformed, standardised, Bray-Curtis dissimilarity matrix) associated with Depth and Survey. Arrows reflect multiple correlations ($r > 0.4$) between taxa and the two primary PCO axes.

**Fig. 4** Chlorophyll $a$ concentration ($\mu$g L$^{-1}$ ± SE) in Lough Neagh. The periods sampled for benthic macroinvertebrates are shown as asterisks during 1997/98 (Bigsby 2000) and 2010 (*this study*).
Discussion

There were marked differences in the macroinvertebrate assemblage at Lough Neagh in 1997/98 and 2010. The macroinvertebrate fauna decreased significantly in abundance and biomass. Density of macroinvertebrates declined by two thirds, from 15 300 individuals m\(^{-2}\) in 1997/98 to 5 115 individuals m\(^{-2}\) in 2010, with concomitant declines in biomass. These changes coincided with a sustained decline in phytoplankton concentration, and a sudden decline in the overwintering numbers of diving ducks, principally pochard, tufted duck and goldeneye (Tománková et al. 2013).

Chironomid larval densities in 2010 were similar to those reported in the 1969/70 and the late 1980s (Carter 1976, Winfield 1991), highlighting the fact that the densities recorded in the late 1990s appear to have been exceptionally high. The reduction in macroinvertebrate prey by 2010 may have been sufficient to reduce the quantity of food available to overwintering diving ducks, inducing a re-distribution to more suitable overwintering sites. Moreover, Lough Neagh supports dense populations of several fish species (Harrod et al. 2001, Inger et al. 2010), including roach (Rutilus rutilus), and species which are important commercially and for their conservation significance, such as the European eel (Anguilla anguilla), pollan (Coregonus autumnalis) and perch (Perca fluviatilis); all of which feed on macroinvertebrates, including chironomid larvae (Winfield & Winfield 1994a).

The decline of macroinvertebrate abundance and biomass at Lough Neagh was coincident with long-term changes in chlorophyll a concentrations. Lough Neagh has a long and complicated history of cultural eutrophication (Wood & Smith 1993, Bunting et al. 2007), which accelerated during the 20\(^{th}\) century: by the 1970s, it was considered one of the most eutrophic lakes in the world (Wood & Gibson 1973). In an
effort to control eutrophication, tertiary treatment was introduced in 1981 at major sewage treatment works in the Lough Neagh catchment (Foy et al. 2003). Initially, total phosphorus concentrations decreased (Heaney et al. 2001) but the impact was only temporary and, by late 1990s, total phosphorus values exceeded those prior to control efforts, mostly due to non-point source pollution (Heaney et al. 2001) and retention and release of phosphorus from the sediments (Foy et al. 2003). Bunting et al. (2007) noted that, in the 1990s, water column concentrations of NO₃ reached a historical maximum, while P concentrations also remained high, resulting in a historical peak in chlorophyll a concentration. This maximum in algal abundance coincided with Bigsby’s (2000) macroinvertebrate study and a period when large numbers of diving ducks overwintered on the lough. Today, Lough Neagh remains extremely eutrophic, but the recent reductions in chlorophyll a concentrations (and probably underlying primary production) are likely to reflect changes in nutrient availability or dynamics and are clearly worthy of further study.

In other lakes, improvements in water quality have led to shifts in the macroinvertebrate communities (Schloesser et al. 1995, Carter et al. 2006) and decreased total macroinvertebrate abundances (Köhler et al. 2005). In the Firth of Forth in Scotland, attempts to improve water quality by installation of sewage treatment works resulted in declines of wintering diving ducks, namely scaup and goldeneye (Campbell 1984); however, it was unclear whether the declines were caused by the loss of food carried in the sewage or the actual decline of macroinvertebrates associated with the sewage (Campbell 1984). Thus, the decline of macroinvertebrates at Lough Neagh and concomitant changes in overwintering duck populations may well be an unintended consequence of improving water quality.
Unfortunately, suitable data are not currently available to test the long-term interactions between diving ducks and their macroinvertebrate prey, as statutory monitoring extends only to overwintering bird counts at Lough Neagh. Clearly, there is a need to extend monitoring to different components of the ecosystem beyond birds, (at least to benthic macroinvertebrates beyond the littoral zone and fish) in order to identify future shifts in the ecology of the largest freshwater lake in Britain and Ireland.
Temporal changes in diet and contemporary trophic position of overwintering diving ducks in a hyper-eutrophic lake
Abstract

The diving duck population wintering at Lough Neagh declined dramatically following the winter of 2000/01. The abundance and biomass of benthic macroinvertebrates, the main food source of diving ducks, declined significantly between the winters of 1997/98 and 2010. A combination of short-term (oesophagus contents analysis) and longer-term (Stable Isotope Analysis or SIA of liver tissue) was used to characterise the contemporary diet of diving ducks at Lough Neagh. Oesophageal contents were compared with data collected during 1998-99 (Bigsby 2000). Mean δ¹³C and δ¹⁵N duck liver values did not vary between species or sex, but δ¹³C values were significantly more depleted in adults compared to 1st winter birds. Macroinvertebrates were sampled in October 2010 to provide an isotopic baseline with which to compare duck tissue values. Of the 79 ducks sampled (pochard *Aythya ferina* n=1, tufted duck *A. fuligula* n=42, scaup *A. marila* n=9 and goldeneye *Bucephala clangula* n=27), 57% were located outside the SIA food source polygon, indicating that a large proportion of the populations may be dynamic, making within-winter movements and feeding on other waterbodies. The contribution of various prey sources to the diet of diving ducks was examined using a Bayesian mixing model (SIAR). Tufted duck and goldeneye fed primarily on *Valvata* spp. and chironomid larvae, followed by *Asellus aquaticus* and *Gammarus* spp. Scaup were more generalist with all prey occurring at similar frequencies. Analysis of the limited oesophagi contents revealed that tufted duck oesophagi (n=7) were dominated by *Asellus aquaticus* (48%) but also contained molluscs (14%), grain (13%) and chironomid larvae (11%). There were changes in the oesophageal content of tufted ducks between 1998-99 and 2010-12. The contribution of *Asellus aquaticus* to the diet significantly decreased while the proportions of chironomid larvae, grain, *Gammarus* spp. and *Mysis* spp. increased. Diet inferred from oesophagus contents analysis was dominated by *Asellus aquaticus* while SIA indicated a high proportion of chironomid larvae and *Valvata* spp. in the diet.
Introduction

Dietary analysis is a crucial tool for ecological inference, providing information on trophic interactions and food web dynamics within ecosystems (Hughes 1993). On the species level, it provides information on foraging behaviour, habitat use and general ecology (Hyslop 1980). Consequently, temporal variation in diet may contribute to our understanding of population dynamics, particularly in species exhibiting declining populations (Vander Zanden, Casselman & Rasmussen 1999).

For some species, such as diving ducks, diet cannot be inferred from direct observation of foraging and alternative methods of dietary analysis must be employed; typically stomach content analysis. Analysing stomach contents is simple and straightforward, providing a precise snapshot of recent ingestion (Hynes 1950). However, there are limitations associated with the use of this method. Stomach content analysis involves destructive sampling and is often reliant on culling the target species for scientific purposes. Moreover, it provides information on prey selection by the consumer during a brief period of time only (Vinson & Budy 2011). If longer-term time-series data are required on temporal changes in diet, consumers from the target species may need to be lethally sampled over an extended timeframe. Stomach content analysis also tends to be biased towards food items that are hard-bodied, thus taking longer to digest while softer-bodied prey items, which are more easily digested, may be under-recorded (Hyslop 1980). In birds, this can be overcome partly by examining oesophagus contents rather than gizzard contents (Swanson & Bartonek 1970, Guillemette, Bolduc & Desgranges 1994). In ducks, prey items pass through the oesophagus undigested, before they enter the proventriculus and gizzard. Ducks swallow and store large amounts of grit in their gizzards (see Appendix II) to grind up
food and aid digestion, causing prey items to break down rapidly. Swanson & Bartonek (1970) found that, within 10 minutes of ingestion, 100% of amphipods, 82% of molluscs and 24% of diptera larvae in the gizzard were digested beyond recognition.

Stable Isotope Analysis (SIA) is an alternative method of dietary analysis, enabling the evaluation of the relative importance of dietary components to consumers (Inger & Bearhop 2008). Isotopes are forms of the same element that contain equal numbers of protons but differing numbers of neutrons in their nuclei. Isotopic ratios vary across the environment due to the mass difference between heavier and lighter isotopes (Fry 2008), and are reflected in the tissues of consumers synthesised from assimilated foods. While a wide range of elements can be used in SIA, carbon and nitrogen are widely utilized in dietary studies (e.g. Bearhop et al. 1999, Haramis et al. 2001, Inger et al. 2006, Gillespie 2013). Carbon varies between different primary producers (France 1995) and as such is used to infer a consumer’s source of energy, while nitrogen reflects the trophic position at which the consumer feeds (Fry 2008). The isotopic composition of a consumer’s tissue reflects that of its assimilated prey in a predictable manner (DeNiro & Epstein 1981, Tieszen et al. 1983, Peterson & Fry 1987). Typically, consumer tissues are enriched in $^{15}$N and to a lesser degree in $^{13}$C relative to their prey. This differential uptake of isotopes from diet is known as fractionation. Fractionation values differ among species, diets and tissue types (Mizutani, Kabaya & Wada 1991, Hobson & Clark 1992b, Evans Ogden, Hobson & Lanka 2004). If prey sources are sufficiently isotopically distinct, the range of their possible contributions to the diet of the consumer can be estimated through isotope mixing models (Phillips & Gregg 2003, Phillips, Newsome & Gregg 2005). In addition, different consumer tissues have different metabolic turnover rates (Tieszen
et al. 1983, Hobson & Clark 1992a), allowing inferences about a consumer’s diet over varying temporal scales; depending on the target tissue. In birds, tissues with rapid turnover rates (e.g. liver) reflect recent diet over a period of several days while tissues with lower turnover rates (e.g. muscle) reflect longer term diet over weeks or months (Hobson & Clark 1992a, Boecklen et al. 2011).

Due to its probabilistic nature, SIA cannot replace conventional dietary analysis entirely if precise dietary information is required. Ideally, a combination of stomach (or in the case of ducks, oesophagus) contents analysis and SIA would provide a more holistic picture of actual diet and trophic position.

The diet of diving ducks overwintering at Lough Neagh, Northern Ireland was studied in detail in a series of studies during late 20th century (e.g. Winfield & Winfield 1994b, Evans 2000, Bigsby 2000). At the time of study, the diet of pochard, scaup and goldeneye was typically dominated by chironomid larvae (Winfield & Winfield 1994b, Evans 2000) while the diet of tufted duck also contained substantial quantities of molluscs (Winfield & Winfield 1994b). Bigsby (2000) suggested that the predominant prey items in the diet of pochard and scaup were larval and pupal chironomids, while tufted duck fed primarily on *Asellus aquaticus*. Goldeneye took both chironomid larvae and *Asellus aquaticus* in approximately equal proportions. All dietary information for diving ducks at Lough Neagh has been derived from oesophagus or gizzard contents analysis. Until now, no alternative methods of dietary analysis have been employed.

The density and biomass of macroinvertebrates in Lough Neagh declined by ca. 70% between the winters of 1997/98 (prior to observed declines in diving duck numbers; see Chapter 2) and 2010 (after the majority of the decline had occurred; see
Chapter 5. The magnitude of macroinvertebrate reduction was such that it potentially may have reduced the quantity and quality of food resources available to overwintering ducks. Therefore, information on recent diet is required to determine if there have been any significant changes in diving duck diet before and after the observed crash in numbers of both macroinvertebrates and diving ducks.

This study examined the diet of diving ducks overwintering at Lough Neagh using both oesophagus contents analysis and stable isotope analysis of fast turnover tissue, specifically liver. Diet was compared between the time periods 1998-99 (Bigsby 2000) and 2010-12 (this study) to evaluate temporal change.

**Methods**

Diving ducks of the species pochard, tufted duck, scaup and goldeneye were obtained from wildfowlers or fishermen operating at Lough Neagh between the winters 2008/09 and 2011/12. Ducks were aged and sexed based on plumage characteristics (Boyd, Harrison & Allison 1975, Baker 1993). Over the study, a total of 79 individuals of 4 species were collected, of which 75 (95%) had been shot and 4 (5%) accidentally caught in legally set gill nets. The demographic composition of the sample is shown in Table 1.
Table 1 Numbers and percentages (in parentheses) of ducks species collected between the winters 2008/09 and 2011/12, including age and sex classes. Either age or sex could not be accurately determined in one tufted duck and one goldeneye.

<table>
<thead>
<tr>
<th>Species</th>
<th>Male Adults</th>
<th>Male 1st winter</th>
<th>Female Adults</th>
<th>Female 1st winter</th>
<th>Undetermined</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pochard</td>
<td>1 (100)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>1 (100)</td>
</tr>
<tr>
<td>Tufted duck</td>
<td>21 (50)</td>
<td>10 (24)</td>
<td>4 (10)</td>
<td>6 (14)</td>
<td>1 (2)</td>
<td>42 (100)</td>
</tr>
<tr>
<td>Scaup</td>
<td>6 (67)</td>
<td>2 (22)</td>
<td>1 (11)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>9 (100)</td>
</tr>
<tr>
<td>Goldeneye</td>
<td>5 (19)</td>
<td>5 (19)</td>
<td>9 (33)</td>
<td>7 (26)</td>
<td>1 (4)</td>
<td>27 (100)</td>
</tr>
<tr>
<td>Total</td>
<td>33 (42)</td>
<td>17 (22)</td>
<td>14 (18)</td>
<td>13 (17)</td>
<td>2 (3)</td>
<td>79 (100)</td>
</tr>
</tbody>
</table>

Oesophagus content analysis

The oesophagus of each duck was dissected and any prey items removed. These were stored in 80% ethanol and subsequently identified. Chironomid larvae head capsules were mounted with either Euparal or Hydromatrix solutions (Brooks et al. 2007) to allow identification (Wiederholm 1983, Brooks et al. 2007). Results were then compared with the diet of diving ducks investigated in 1998-99 (Bigsby 2000).

Chironomid larvae dissected from the oesophagi of ducks were measured and compared with length frequencies of chironomids found in oesophagi of ducks of the same species collected in 1988-1990 (Winfield & Winfield 1994b), 1998-1999 (Evans 2000) and 1998-2000 (Bigsby 2000). Data from these three studies were extracted from graphs using Plot Digitizer (version 2.5.1) software. Chironomid larvae were pooled irrespective of species or genus.
Stable Isotope Analysis (SIA)

Carbon and nitrogen stable isotope analysis was used to provide an indication of assimilated diet and trophic position. Liver is a metabolically active tissue with a half-life of 2.6 – 7.0 days in birds (Hobson & Clark 1992a, Boecklen et al. 2011); therefore, providing data on relatively short-term diet. Liver samples were dissected out of each individual (Table 1) and dried at 60°C until mass was constant. Duck liver can contain significant amounts of lipid. Lipids are typically $^{13}$C depleted (DeNiro & Epstein 1978, Tieszen et al. 1983) and can, therefore, bias $\delta^{13}$C values and estimates of diet (Kiljunen et al. 2006). Thus, lipids were extracted from one-half of each liver sample using a Soxhlet apparatus with 1:1 chloroform:methanol mixture as the solvent. Both the lipid-free and untreated liver samples were ground into homogenous powders (separately) using a pestle and mortar before being weighed into tin capsules at a mass between 0.45 and 0.60 mg. $\delta^{15}$N of untreated samples and $\delta^{13}$C of lipid-extracted samples were used in the analysis. SIA of duck tissue was carried out at the Centre for Climate, the Environment and Chronology ($^{14}$CHRONO) at Queen’s University Belfast, United Kingdom on a Delta V Advantage Continuous Flow Stable Isotope Ratio Mass Spectrometer. All stable isotope ratios are reported in delta (δ) notation in units of per mil (‰) and normalized to their international standards for carbon (Vienna Pee Dee Belemnite) and nitrogen (air). Standard deviations of carbon and nitrogen standards were less than 0.1 ‰.

In order to provide an isotopic baseline with which to compare duck tissue values, benthic macroinvertebrates, identified as prey items of diving ducks in previous studies (Winfield & Winfield 1994b, Bigsby 2000, Evans 2000), were collected at Lough Neagh during October 2010 (see Chapter 4 for methodology of collection) and similarly processed for $\delta^{13}$C and $\delta^{15}$N values. If invertebrates were not large enough to
be analysed individually, they were grouped together as composite samples. Samples were weighed out at a mass of 0.50 to 0.80 mg and SIA was carried out at OEA Labs Ltd., Callington, Cornwall on an Elemental Analyser EA1110 linked to a Europa Scientific Continuous Flow Isotope Ratio Mass Spectrometer. Standard deviations of carbon and nitrogen standards were less than 0.3 ‰.

**Statistical analysis**

To examine changes in the proportional composition of macroinvertebrates in the diet of diving ducks (extracted from their oesophagi), 2x2 $\chi^2$ contingency tests were used for each prey category between 1998-99 (Bigsby 2000) and 2010-12. To determine whether there was any difference in the size of chironomids consumed, their length frequencies were compared between 1988-1990 (Winfield & Winfield 1994b), 1998-1999 (Evans 2000), 1998-2000 (Bigsby 2000) and 2010-2012 using a Generalized Linear Mixed Model (GLMM) with a fitted gamma distribution and logarithmic link function where chironomid size was fitted as the dependent variable, study as a fixed factor and size category as a random factor to account for the multiple observations per size category, thus avoiding pseudo-replication.

Variation in $\delta^{13}C$ and $\delta^{15}N$ values between age and sex classes of ducks were examined using General Linear Models (GLMs). $\delta^{13}C$ and $\delta^{15}N$ values were fitted as the dependent variables respectively with Species, Sex, Age and all interactions fitted as fixed factors. Temporal variation in annual and monthly $\delta^{13}C$ and $\delta^{15}N$ values was also examined using GLMs where Winter, Month and all two-way interactions were fitted as fixed factors. Statistical analyses were conducted using SPSS v20.
The probable contribution of various prey sources to the diet was examined using a Bayesian mixing model (SIAR) (Parnell et al. 2010). Because fractionation coefficient for liver tissue in wildfowl was not available in the literature, the means of isotopic values for various bird species (including dunlin *Calidris alpina pacifica*, cormorant *Phalacrocorax carbo*, Japanese quail *Coturnix japonica*, domestic chicken *Gallus gallus* and ring-billed gull *Larus delawarensis*) were used (Mizutani et al. 1991, Hobson & Clark 1992b, Evans Ogden et al. 2004). The combined mean (SD) fractionation coefficients used were 0.52 ‰ (0.69) and 2.6 ‰ (0.86) for δ¹³C and δ¹⁵N respectively. Mean and SD elemental concentrations of % C and % N in the tissues of macroinvertebrates were included to refine the model (Phillips & Koch 2002). Macroinvertebrates were further adjusted for ethanol storage as follows: 1 ‰ for δ¹³C and -0.9 ‰ for δ¹⁵N for *Asellus aquaticus*, 1.7 ‰ for δ¹³C and -0.8 ‰ for δ¹⁵N for *Chironomus* spp. and 1.3 ‰ for δ¹³C and -0.9 ‰ for all other invertebrate taxa (Syväranta et al. 2008). Chironomid taxa (*Chironomus* spp., *Glyptotendipes* spp. and Tanypodinae) were grouped together for the purpose of the analysis.

**Results**

**Oesophagus content analysis**

Very few individuals (9%) of 79 ducks examined had prey in their oesophagi: all 4 ducks that had been recovered drowned from gill nets contained prey items in their oesophagi, but only 3 (4%) of the 75 ducks that had been shot contained oesophageal prey items. All 7 individuals were male tufted duck. Their diet (Fig. 1) was
predominantly composed of *Asellus aquaticus* (47.6%), molluscs (14.3%) and grain (13%). Of the chironomid larvae, the most commonly consumed genera were *Glyptotendipes* spp. (5.1%) and *Microtendipes* spp. (4.3%). Molluscs eaten were (in descending order of abundance): *Potamopyrgus antipodarum*, *Lymnaea peregra*, *Valvata* spp., *Planorbis carinatus*, *Physa* spp., *Planorbis corneus* and *Bythinia* spp. Trichoptera larvae belonged to families *Leptoceridae*, *Molannidae*, *Phryganeidae* and *Polycentropidae* while *Hemiptera* were of the family *Corixidae*.

With the caveat of small sample sizes, the oesophagi contents of tufted ducks significantly differed between 1998-99 (Bigsby 2000) and 2010-12 (*this study*). Specifically, the greatest change was the appearance of grain, mostly wheat *Triticum* spp., during 2010-12 (13%) which was entirely absent in 1998-99 ($\chi^2_1= 13.9$, $p<0.001$). The proportion of chironomid larvae (all genera pooled) increased from 3% to 11% ($\chi^2_1= 4.92$, $p=0.027$; Fig. 1), *Mysis* spp. increased from 2% to 9% ($\chi^2_1= 4.71$, $p=0.030$) and *Gammarus* spp. increased from 0% to 4% ($\chi^2_1= 4.08$, $p=0.043$). Conversely, the proportion of *Asellus aquaticus* decreased from 73% during 1998-99 to 48% during 2010-12 ($\chi^2_1= 13.1$, $p<0.001$). Molluscs did not differ with a proportion of 13% during 1998-99 and 14% during 2010-12 ($\chi^2_1= 0.043$, $p=0.836$) nor did the remaining dietary items being 8% in 1998/99 and 2% in 2010/12 ($\chi^2_1= 3.79$, $p=0.052$). There was a strong trend for the size frequency distribution of chironomid prey to vary between studies conducted during 1988-90 (Winfield & Winfield 1994b), 1998-99 (Evans 2000), 1998-00 (Bigsby 2000) and 2010-12 (*this study*; $F_{3,47}= 2.314$, $p=0.088$). Specifically, the median length of chironomid larvae in 1998-99 (Evans 2000) and 2010-12 (*this study*) was smaller exhibiting a normal distribution whilst those during 1988-90 (Winfield & Winfield 1994b) and 1998-00 (Bigsby 2000) were larger exhibiting a bimodal distribution (Fig. 2).
Chapter 5  

Diving duck diet

**Fig. 1** Comparison of tufted duck diet between 1998-99 (Bigsby 2000) and 2010-12. Right braces and percentages indicate the combined contribution of chironomid larvae.

**Fig. 2** Comparison of length frequencies of chironomid larvae from tufted duck diet during 1988-1990, 1998-1999, 1998-2000 and 2010-2012 (re-drawn from Winfield & Winfield 1994b, Evans 2000, Bigsby 2000 and this study).
Stable isotope analysis

The δ^{13}C and δ^{15}N values of duck liver tissue ranged from -33 to -18 ‰ and 10 to 20‰, with a mean of -28‰ and 16‰, respectively. They did not vary significantly between species, sexes or their interactions (Table 2a). δ^{13}C values were significantly depleted in 13C in adults compared to 1st winter birds (Table 2ai), driven predominantly by differences in scaup and tufted duck (Fig. 3a) but δ^{15}N values did not differ between age classes (Table 2aii & Fig. 3b). There was no evidence of monthly or annual variation within or between species for either δ^{13}C or δ^{15}N (Table 2b).

Table 2 General Linear Models (GLMs) describing a) demographic and b) temporal variation in i) δ^{13}C and ii) δ^{15}N. Significant values are denoted in bold and by an asterisk.

<table>
<thead>
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<th>Model/Variables</th>
<th>F</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
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<tr>
<td>i) δ^{13}C (F_{13,65} =0.998, p =0.081, R^2 =0.246)</td>
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<tr>
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<td>0.609</td>
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<td>0.421</td>
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</tr>
<tr>
<td>ii) δ^{15}N (F_{13,65} =0.998, p =0.464, R^2 =0.134)</td>
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<tr>
<td>b) Temporal variation</td>
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</tr>
<tr>
<td>i) δ^{13}C (F_{20,58} =1.450, p =0.137, R^2 =0.345)</td>
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<tr>
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<tr>
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</table>
**Prey isotopes and diving duck diet**

Chironomid larvae and *Valvata* spp. were not sufficiently isotopically distinct in their $\delta^{13}$C (Mann-Whitney $U_{147}$=483.00, $Z$=-0.13, $p$=0.900), $\delta^{15}$N values (Mann-Whitney $U_{147}$=488.50, $Z$=-0.08, $p$=0.939), % C (Mann-Whitney $U_{147}$=365.50, $Z$=-1.18, $p$=0.238) and % N (Mann-Whitney $U_{147}$=425.50, $Z$=-0.64, $p$=0.521) to be differentiated independently. Consequently, they were pooled for the purposes of SIAR dietary analysis. Out of 79 ducks, 45 individuals (1 pochard, 22 tufted duck, 7 scaup and 15 goldeneye), i.e. 57 % of the ducks analysed, were located outside the food source polygon and were excluded from the analysis (Fig. 4). The food source polygon or mixing polygon is a polygon created by the upper limits of the standard
deviation of $\delta^{13}C$ and $\delta^{15}N$ values of putative prey sources, within which the consumer’s isotopic ratios, adjusted for isotopic fractionation, should be located, if consumers feed on the food sources forming the polygon (Phillips & Gregg 2003).

![Diagram](image)

**Fig. 4** Individual carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values for liver of pochard, tufted duck, scaup and goldeneye taken from Lough Neagh and isotopic values of putative prey items from Lough Neagh showing the food source polygon. Ducks outside this polygon were excluded from analysis.

Mixing models based on stable isotope and elemental concentrations indicated that in tufted duck diet (Fig. 5a), chironomid larvae and *Valvata* spp. were of primary importance (mean proportion = 0.45, SD = 0.1), followed by *Asellus aquaticus* (mean = 0.27, SD = 0.2) and *Gammarus* spp. (mean = 0.19, SD = 0.2). *Mysis* spp. contributed little (mean = 0.09, SD = 0.1). In scaup diet, all prey items occurred with a similar frequency (Fig. 5b): chironomid larvae and *Valvata* spp. (mean = 0.28, SD = 0.3), *Asellus aquaticus* (mean = 0.24, SD = 0.2), *Gammarus* spp. (mean = 0.24, SD = 0.2) and *Mysis* spp. (0.24, SD = 0.2). However, it is likely that SIAR could not
reliably estimate diet for scaup, as only two individuals were located inside the food source polygon and thus included in the model. The mixing model indicated that goldeneye (Fig. 5c) largely consumed chironomid larvae and *Valvata* spp. (mean = 0.45, SD = 0.2), followed by *Asellus aquaticus* (mean = 0.23, SD = 0.2), *Gammarus* spp. (mean = 0.20, SD = 0.2) and *Mysis* spp. (0.12, SD = 0.1). Only a single pochard was available for analysis. However, it was located outside the food source polygon and hence was excluded from mixing model analysis.
Fig. 5 Boxplots showing the estimated contribution of food sources (Asellus aquaticus, Gammarus spp., Mysis spp. and chironomid larvae + Valvata spp.) with 25, 75 and 95% credibility intervals in the diet of a) tufted duck, b) scaup and c) goldeneye.
Discussion

Stable Isotope Analysis (SIA) of liver is indicative of a relatively short-term diet because liver is a metabolically active tissue (Hobson & Clark 1992a, Boecklen et al. 2011). In 57% of all ducks analysed, δ\textsubscript{13}C and δ\textsubscript{15}N values were located outside the food source polygon, indicating that they were likely to be either recent migrants having fed elsewhere (en route during migration; for example at sea) within the few days prior to being collected (accounting for 13\,C enriched δ\textsubscript{13}C values) or had not been feeding on the putative food sources examined (accounting for variance in δ\textsubscript{15}N). The former hypothesis would be supported if most of these individuals had been shot early in the season representing recently returned birds; however, this was not the case with samples drawn from throughout each winter. This suggests that the population of diving ducks overwintering at Lough Neagh is dynamic with birds moving between different water bodies within any one winter. Most individuals located outside the food source polygon were 13\,C enriched and 15\,N depleted relative to their putative prey items sampled from Lough Neagh, indicating that they have been feeding in non-nutrient enriched (low δ\textsubscript{15}N) marine (high δ\textsubscript{13}C) habitats (Fry & Sherr 1984, Hobson 1999, Harrod et al. 2005). Indeed, within-winter movements have been described previously in pochard and tufted duck (Keller et al. 2009, Korner-Nievergelt et al. 2009). However, it remains possible that diving ducks were feeding on other food sources not examined here; for example, grain supplied through supplementary feeding as a lure by wildfowlers which could account for the depleted δ\textsubscript{15}N in some individuals: wheat Triticum spp. has a δ\textsubscript{13}C of ca. -28‰ and δ\textsubscript{15}N of ca. 2‰ (Webb, Hedges & Simpson 1998) while barley Hordeum vulgare has a δ\textsubscript{13}C of -28‰ and δ\textsubscript{15}N of 6‰ (Husted et al. 2004) and for maize Zea mays, δ\textsubscript{13}C and δ\textsubscript{15}N values are -13‰ and 3‰, respectively (Webb et al. 1998). Though, if this were the case,
individuals would have to have been eating large quantities in order to significantly alter the values in short-turnover liver tissue, making this hypothesis less likely than within-winter movements. Further evidence against a missed food source is provided by the scale of macroinvertebrate sampling, which was extensive and extended across a range of depths and locations across the lough where diving ducks fed. To the knowledge of the author, all the major representative taxa were included in the analysis.

Adult lipid-free livers were significantly $^{13}$C depleted compared to 1st winter birds in both tufted duck and scaup. This indicates spatial differences in the feeding locations of 1st winter and adult birds. The majority of ducks excluded from analysis due to being outside the food source polygon were 1st winter birds.

Macroinvertebrates sampled from Lough Neagh were collected from a range of depths (3 – 12 m) and locations (all major bays). They were however isotopically similar, making unequivocal interference of diet difficult. This likely reflects Lough Neagh’s hyper-eutrophic status, where primary production is dominated by phytoplankton, and macroinvertebrate production largely reflects this, with little assimilation of $^{13}$C enriched littoral epilithic algae (France 1995) than found in oligotrophic lakes (Harrod, Mallela & Kahilainen 2010). It is, therefore, not unexpected that macroinvertebrates from different taxonomic groups would be more similar isotopically in Lough Neagh than oligotrophic waterbodies. Nevertheless, SIA indicated that tufted duck, scaup and goldeneye at Lough Neagh fed primarily on chironomid larvae and Valvata spp. which is supported by previous studies utilizing oesophagus content analysis (Evans 2000, Winfield & Winfield 1994b). Analysis of the oesophagus contents of male tufted ducks suggested they fed primarily on Asellus aquaticus and to a lesser degree on molluscs. Whilst this analysis was based on a
small sample size ($n=7$), Bigsby (2000) reported a similar diet utilizing a larger, but still limited, sample size ($n=18$) while Evans (2000) and Winfield & Winfield (1994b) found that, although not the dominant prey item, *Asellus aquaticus* appeared more important in the diet of tufted duck than in other diving duck species overwintering at Lough Neagh. Minor differences between the studies may be accounted for by changes in food availability which can influence consumer prey choice (Vickery *et al.* 1995). Grain was found in the oesophagi of shot tufted ducks in 2010-12 while none was recorded in 1998-99 (Bigsby 2000). It is possible that, due to the decline of their macroinvertebrate prey, tufted ducks rely more on supplementary feeding provided by wildfowlers than in the past.

There was a strong trend for the size frequency distribution of chironomid larvae to vary between studies conducted during different time periods. Specifically, the median length of chironomids in 1998-99 (Evans 2000) and 2010-12 (*this study*) was smaller than those during 1988-90 (Winfield & Winfield 1994b) and 1998-00 (Bigsby 2000). Such differences may reflect the timing or location of sampling influencing the population age structure of the macroinvertebrates available to ducks. The majority of ducks sampled in previous studies (Winfield & Winfield 1994b, Bigsby 2000, Evans 2000) had been drowned accidentally in gill nets whilst 3 out of 7 ducks (43%) in the current study had been shot. Therefore, the differences in the size frequencies of chironomids might be due either to the varying depth at which the gill nets were set (which was unknown in most cases) as depth may influence the dynamics and thus size structure of chironomid populations (Winfield & Winfield 1994b). Chironomid larvae were also pooled irrespective of their taxonomic classification, thus compositional differences at the species level may account for differences in the size classes recorded.
In the current study, all ducks that had been drowned contained prey in their oesophagi compared to only 4% that had been shot. Diving ducks at Lough Neagh, with the exception of goldeneye, are primarily nocturnal feeders (Evans & Day 2001), so most birds would have finished feeding several hours before being shot by wildfowlers during daylight hours. Consequently, oesophagus contents analysis of shot ducks cannot be recommended in dietary studies. Ducks accidentally caught in gill nets that are captured while feeding would be the best source of material for oesophagus analysis (Appendix II); though they are more difficult to obtain. Such bias in sampling methods has been reported previously by Winfield & Winfield (1994b) and Bigsby (2000).

In conclusion, the diet of diving ducks at Lough Neagh inferred from SIA was dominated by chironomid larvae and Valvata spp. which is largely in agreement with results obtained from previous studies. The diet of tufted ducks inferred from oesophagus contents analysis was dominated by Asellus aquaticus as it was during 1998-99 (Bigsby 2000); however, this result is based on a limited sample size and therefore potentially not representative. Diving duck populations wintering at Lough Neagh are dynamic and within-winter movements, including to marine areas, appear to be a common phenomenon.
Ringing and recovery data prove poor at detecting migratory short-stopping of diving ducks associated with climate change throughout Europe

This chapter was published as:

Chapter 6  

Climate change and ringing recoveries

Abstract

Climate change has been shown to affect the distribution of many bird species. International Waterbird Census (IWC) data revealed that tufted duck (*Aythya fuligula*) and goldeneye (*Bucephala clangula*) have shifted their European wintering distributions north-eastwards as a direct response to increased winter temperatures. We tested whether it was possible to detect this shift in the wintering distribution of these species as well as pochard (*Aythya ferina*), using ringing and recovery data. Goldeneye conformed to our hypothesis, with its recovery distances decreasing significantly by about 400 km from the south-west to north-east from 1950 onwards, but this change could not be linked to winter temperatures. Conversely, tufted duck directly violated our hypothesis with its recovery distances increasing significantly by about 400 km but again this change could not be explicitly linked to winter temperatures. Pochard in contrast exhibited no change in its recovery distances. Thus, of the three species examined, ringing recoveries showed no trend in one species and of the two species where migratory short-stopping has been well described, one exhibited contraction whilst the other an apparent expansion in recovery distances. It is concluded that ringing and recovery data provide little utility in detecting changes in migratory behaviour of these waterbirds.
Chapter 6  

*Climate change and ringing recoveries*

**Introduction**

In the European Union, considerable effort has been expended on establishing site safeguard networks to protect migratory waterbirds along their flyways, for example, through the designation of *Natura 2000* sites under the EU Birds Directive (e.g. Stroud, Mudge & Pienkowski 1990) and the designation of Wetlands of International Importance under the Ramsar Convention. This is particularly the case for species that are subject to hunting, such as wildfowl, following concerns about their overexploitation in the 1930s (Berry 1941). The wintering distribution of many bird species is plastic and particularly responsive to climate (Austin & Rehfish 2005, La Sorte & Thompson 2007). In former times, severe winter weather in northern Europe resulted in waterbirds shifting their wintering distribution south and west within their normal distributions (Ridgill & Fox 1990). In contrast, in recent years, wading birds have shown shifts in the centres of their winter ranges north and east during a period of milder winters (Maclean *et al.* 2008). Such a trend is likely to challenge the effective maintenance of protected area networks, as birds resort to wetlands formerly unsuitable or unavailable to them in winter to the north and east of their range as these become increasingly ice-free. Concurrently, by decreasing the migration distance along flyways to wintering grounds, given a stable population size, birds will reduce or abandon the use of formerly important wetlands at the south-western edge of their range.

Lough Neagh, Northern Ireland has been designated a Special Protection Area (SPA) and an Area of Special Scientific Interest (ASSI) due to its significance for overwintering wildfowl, in particular diving ducks. The site is also a Ramsar wetland of international importance. However, the numbers of overwintering pochard (*Aythya*
ferina), tufted duck (*A. fuligula*) and goldeneye (*Bucephala clangula*), have dramatically declined at the site since the winter of 2000/01 (Tománková *et al.* 2013), previously attributed to climate change (Allen & Mellon 2006). Lough Neagh is located at the western edge of the European wintering distribution for these species and thus may lose its significance as a major wintering site if birds fail to return due to more favourable wintering conditions closer to their breeding grounds.

During the last three decades, International Waterbird Census (IWC) data have revealed that tufted duck and goldeneye shifted the centres of gravity of their wintering ranges north-eastwards, correlated with a 3.8 °C increase in early winter temperatures in the north-eastern part of their wintering range linked to climate change (Appendix II). We tested whether it was possible to detect this shift in the wintering distribution of both tufted duck and goldeneye, as well as pochard, using ringing and recovery data. Point-source marked individuals were used to determine if there was a reduction in the recovery distances over the period between 1950 and 2010 amongst ducks migrating south and west to their wintering grounds. The effects of climate change may not necessarily be linear with time. Thus, the hypothesis that the mean recovery distances were related to mean daily minimum winter temperatures at the wintering grounds or the difference in mean minimum temperatures between the breeding and wintering grounds each year was also tested.
Methods

Ringing and recovery data for pochard, tufted duck and goldeneye were obtained through the data bank of the European Union for Bird Ringing (EURING) from all European countries with the exception of Russia. Scaup (Aythya marila) was excluded from the analysis because strong circumstantial evidence suggests that the population wintering in Ireland is largely breeding in Iceland (Wernham et al. 2002) and therefore has little opportunity for short-stopping. All the data were coded in the EURING 2000+ code (du Feu et al. 2009). Initially, the aim was to carry out a ringing and recovery analysis for diving ducks wintering on Lough Neagh; however, this proved impossible due to low numbers of individuals recovered on Lough Neagh (Fig. 1). To select only individuals from populations with a known breeding origin, only birds ringed during the breeding season (May, June and July) and recovered during the wintering season (defined here as November, December, January and February) were included in the analysis. It was assumed that adult ducks present at a particular location during the breeding season were breeding nearby, although it is possible that some males ringed in July may have been undergoing a moult migration after breeding at a different location. However, it was deemed that these probably represented only a small proportion of the ringing dataset.

Records were discarded from the analysis to remove potential sources of bias if i) the primary identification method of an individual was not a metal ring, birds were ii) hand-reared, iii) held in captivity for more than 24 hours, iv) manipulated or transported, v) dates and locations of ringing and recovery were not recorded accurately (more than two weeks for date and > 50 km for location) and vi) the distance between ringing and recovery sites was < 100 km. The recovery distance was
calculated according to the loxodrome (constant compass direction) method (EURING 2010). Recovery circumstances were described as a) shot, b) intentionally taken by man using other means, c) taken accidentally and d) taken by other methods. Recoveries were further categorised as i) direct, which were recoveries of birds ringed in the breeding season and recovered in the subsequent winter and ii) indirect, which included recoveries of birds ringed during the breeding season and recovered in any winter after the first winter. The age of each bird at ringing was classed as either a duckling or adult, where a duckling was hatched during the breeding season in which it was ringed and an adult was at least one year old when ringed.

Latvia was selected as a source for breeding data for pochard and tufted duck and Finland for goldeneye because these species were ringed in large numbers in the second half of the 20th century in those countries. Latvia and Finland have been exclusively breeding grounds for those species, unlike countries further south-west which may act as both breeding and wintering grounds for different populations. Only records of individuals recovered from a bearing between 180° and 270° from their breeding grounds were retained for analysis, to ensure that movements were towards their wintering grounds.

The mean daily minimum winter temperature (November to February) was extracted for the centroid of the wintering grounds for each species and daily minimum temperature (May to July) was extracted for breeding grounds. Temperature data were downloaded from the European Climate Assessment & Dataset website (http://eca.knmi.nl/dailydata/index.php) and the weather station closest to the mean ringing location and mean wintering location was selected for each species. For pochard, this was Liyepaya AMSG, Latvia (56° 33.00'N, 21° 01.12'E), on the breeding grounds and Beauvais-Tille, France (49° 26.48'N, 02° 07.42'E), on the
wintering grounds; for tufted duck, Liyepaya AMSG, Latvia, on the breeding grounds and Bad Lippspringe, Germany (51° 47.13’N, 08° 50.23’E), on the wintering grounds; and for goldeneye, Jyvaskyla Lentoasema, Finland (62° 24.08’N, 25° 40.43’E), on the breeding grounds and Copenhagen, Landbohojskolen, Denmark (55° 41.00’N, 12° 32.00’E), on the wintering grounds. The relative difference in the temperatures between the mean ringing and wintering location was also calculated.

Temporal trends in the mean minimum winter temperatures for the centroid of the wintering range of each species were examined using linear regressions. Change in recovery locations over time was visualised by plotting the year of each recovery and spatially interpolating missing areas using the kriging function in the Spatial Analyst toolbox for ArcGIS 10.1 (ESRI, California, USA). Evidence of migratory short-stopping would be taken as a south-west to north-east trend progressing from old to recent recoveries, indicating that the south-western range edge was contracting and the north-eastern range edge expanding, consistent with warming winter temperatures. Variation in recovery distances was examined for i) direct recoveries and ii) all birds (direct and indirect recoveries) for each species using General Linear Models (GLMs). Recovery year was fitted as a covariate to test for change in the recovery distance and sex was fitted as a fixed factor as some species undergo differential migration of the sexes (Nichols & Haramis 1980, Carbone & Owen 1995, Wernham et al. 2002), so females might be expected to migrate further than males. Age at ringing (duckling or adult) was also fitted as a fixed factor but only in models utilizing direct recoveries because, for direct and indirect recoveries analysed together, a bird ringed as a duckling might be either a first-winter bird or an adult when recovered. Days since ringing, winter temperatures and the difference in temperature between the breeding and wintering sites were fitted as covariates. All
possible model permutations were created and ranked using Akaike Information Criteron (AIC) values. The Akaike weight \((\omega_i)\) of each model was calculated within the top set of \(N\) models, where the value of delta AIC \((\Delta_i) \leq 2\) (Burnham & Anderson 2002). The Akaike weight of each model is the relative likelihood of that model being the best within a set of \(N\) models. To calculate the importance of each variable relative to all other variables, the \(\Sigma \omega_i\) of all models within the top set of models that contained the variable of interest was calculated and the variables ranked by \(\Sigma \omega_i\) (McAlpine et al 2006); the larger the value of \(\Sigma \omega_i\) (which varies between 0 and 1), the more important the variable. Multimodel inference and model averaging were used to determine effect sizes \((\beta\) coefficient\) of each variable across the top set of models (Burnham & Anderson 2002). Prior to model fitting, all predictor variables were tested for multicollinearity using ordinary least squares regression to ensure that all tolerance values were > 0.1 and all variance inflation factor values were < 10.0 (Quinn & Keough 2002). To allow the direct comparison of regression coefficients within models, variables were standardized to have a \(\bar{x} = 0\) and a \(\sigma = 1\) prior to analysis. All statistical analyses were conducted using Genstat 15. The recovery distances of those species exhibiting significant temporal trends were plotted against time using Sigmaplot 10.
Results

After the application of the selection criteria, 564 records were included in the analysis for pochard, 230 (41%) of which were direct recoveries; 301 records were included for tufted duck of which 95 (32%) were direct recoveries and 181 records were included for goldeneye of which 31 (17%) were direct recoveries. The distribution of sex and age classes among the birds ringed between May and July, 1950-2010, is given in Table 1. The majority of birds recovered had been shot (Table 1a).

In Latvia, most pochard were ringed on Lake Engure, reflected in the mean ringing position (57° 13.219’N, 23° 18.304’E). The mean recovery position for pochard was in northern France (49° 50.802’N, 2° 12.694’E) but the recoveries were dispersed throughout western Europe. Winter temperatures at this location exhibited a significant positive trend from 1950 to 2010 ($F_{1,59} = 10.590, p = 0.002$; Fig. 2a), but
no spatiotemporal pattern was discernible in the recoveries of pochard throughout its wintering range (Fig. 2d). There was generally poor support for the influence of any variable in describing variation in pochard recovery distances whilst the effects of year, winter temperatures and the difference of temperatures between the breeding and wintering grounds were inconsistent between direct and indirect recoveries (Fig. 3a).

In Latvia, the mean ringing location for tufted duck was 57° 6.042'N, 24° 9.177'E. The mean recovery position for tufted duck was in north-western Germany (51° 51.505'N, 7° 47.527'E) but recoveries were dispersed throughout western Europe. There was no significant change in winter temperatures between 1950 and 2010 at this location but there was weakly positive trend (\(F_{1,58} = 1.856, p = 0.178\); Fig. 2b). However, there was an apparent trend in the spatial location of recoveries with more recent recoveries tending to be near the south-western edge of the wintering range in Iberia, south-western and north-eastern France and Great Britain (Fig. 2e). Thus, there was a significant positive trend in the recovery distances of tufted duck with year using both direct and all recoveries (Fig. 3b) with the strongest trend exhibited by direct recoveries (Fig. 4a-b). On average, the recovery distance of tufted duck extended by approximately 400 km between 1950 and 2010 (Fig. 4b). Tufted duck recovery distances were negatively influenced by days since ringing, suggesting that the longer the period between ringing and recovery the more likely the bird was to be recovered closer to its ringing location (Fig. 3b).

In Finland, the mean ringing location for goldeneye was 62° 7.365'N, 25° 40.471'E. The mean recovery position for goldeneye was located in the Baltic Sea just off the Danish island of Møn (54° 58.629'N, 12° 14.265'E), reflecting a clustered distribution of recovery positions and limited recoveries throughout Europe. There
was a strong trend for winter temperatures to increase at this location between 1950 and 2010 ($F_{1.59} = 3.469, p = 0.067$; Fig. 2c). Moreover, there was an apparent spatiotemporal trend for old recoveries to have been collected from near the south-western edge of the species’ wintering range and more recent recoveries to have been collected near the north-eastern edge (Fig. 2f) whilst there was a significant negative relationship between recovery distances and time using direct and indirect recoveries (Fig. 3c). On average, the recovery distance of goldeneye decreased by approximately 400 km between 1950 and 2010 (Fig. 4c).

None of the species exhibited consistent or significant relationships between their recovery distances and either winter temperatures or the difference in temperatures on the breeding and wintering grounds.

Table 1 Numbers and percentages for a) the recovery circumstances and b) sex and age classes for pochard, tufted duck and goldeneye ringed between May and July and recovered between November and February, 1950-2010.

<table>
<thead>
<tr>
<th></th>
<th>Pochard n (%)</th>
<th>Tufted duck n (%)</th>
<th>Goldeneye n (%)</th>
<th>Total n</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Recovery circumstance</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intentionally by man – shot</td>
<td>504 (89.4)</td>
<td>227 (75.4)</td>
<td>147 (81.2)</td>
<td>878 (83.9)</td>
</tr>
<tr>
<td>Intentionally by man – other means</td>
<td>24 (4.3)</td>
<td>14 (4.7)</td>
<td>1 (0.6)</td>
<td>39 (3.7)</td>
</tr>
<tr>
<td>Accidentally by man</td>
<td>21 (3.7)</td>
<td>51 (16.9)</td>
<td>30 (16.6)</td>
<td>102 (9.8)</td>
</tr>
<tr>
<td>Other known recovery method</td>
<td>15 (2.7)</td>
<td>9 (3.0)</td>
<td>3 (1.7)</td>
<td>27 (2.6)</td>
</tr>
<tr>
<td>Total n (%)</td>
<td><strong>564 (100)</strong></td>
<td><strong>301 (100)</strong></td>
<td><strong>181 (100)</strong></td>
<td><strong>1 046 (100)</strong></td>
</tr>
<tr>
<td>b) Cohort composition</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult female</td>
<td>175 (31.0)</td>
<td>28 (9.3)</td>
<td>127 (70.2)</td>
<td>330 (31.5)</td>
</tr>
<tr>
<td>Duckling female</td>
<td>10 (1.8)</td>
<td>3 (1.0)</td>
<td>0 (0.0)</td>
<td>13 (1.2)</td>
</tr>
<tr>
<td>Adult male</td>
<td>26 (4.5)</td>
<td>12 (4.0)</td>
<td>2 (1.1)</td>
<td>40 (3.8)</td>
</tr>
<tr>
<td>Duckling male</td>
<td>12 (2.1)</td>
<td>8 (2.7)</td>
<td>0 (0.0)</td>
<td>20 (1.9)</td>
</tr>
<tr>
<td>Adult (sex unknown)</td>
<td>2 (0.4)</td>
<td>67 (22.3)</td>
<td>7 (3.9)</td>
<td>76 (7.3)</td>
</tr>
<tr>
<td>Duckling (sex unknown)</td>
<td>339 (60.1)</td>
<td>183 (60.8)</td>
<td>45 (24.9)</td>
<td>567 (54.2)</td>
</tr>
<tr>
<td>Total n (%)</td>
<td><strong>564 (100)</strong></td>
<td><strong>301 (100)</strong></td>
<td><strong>181 (100)</strong></td>
<td><strong>1 046 (100)</strong></td>
</tr>
</tbody>
</table>
Fig. 2 Trends in the mean daily winter (Nov-Feb) temperatures at a) Beauvais-Tille, France, b) Bad Lippspringe, Germany and c) Copenhagen, Denmark, corresponding to the mean centroids of ringing recoveries during winter for d) pochard, e) tufted duck and f) goldeneye respectively. Ringing recoveries are shown as closed circles and their dates of recovery (coloured scale) range from the 1950s (dark blue) to the 2000s (dark red) and have been spatially interpolated using kriging to illustrate any trend. Evidence of migratory short-stopping would be taken as a south-west to north-east trend progressing from red to blue, indicating that the south-western range edge was contracting and the north-eastern one expanding, consistent with global climate change and observed positive trends in winter temperatures.
Fig. 3 Relative importance of explanatory variables in explaining variation in the recovery distance of a) pochard, b) tufted duck and c) goldeneye using i) direct recoveries only and ii) direct plus indirect recoveries. Variables are ranked in order of the sum of their Akaike weights ($\Sigma \omega_i$) within the top set of models i.e. models with $\Delta$AIC≤2. Black bars indicate those variables that were retained in the best single approximating model (i.e. that with the lowest AIC value) and grey bars indicate variables included in all other models within the top set. Variables judged significant at $p<0.05$ in the top model are shown in bold where ** $p<0.01$ and *** $p<0.001$. Notation to the right indicates the strength of the slopes for each standardized covariate.
Fig. 4 Trends in recovery distances for a) direct recoveries of tufted duck, b) all recoveries of tufted duck and c) all recoveries of goldeneye.
Discussion

The recovery distance for goldeneye decreased significantly between 1950 and 2010 but, contrary to our hypothesis, the recovery distance for tufted duck increased and recovery distances for pochard remained variable and unchanged. Although there was wide dispersal from a single breeding source for all three species, there were no species-consistent changes in the winter distribution during the second half of the 20th century. Lehikoinen et al. (2013, Appendix I), using International Waterbird Census (IWC) data, convincingly demonstrated a north-eastern shift, i.e. closer to the breeding grounds, in the wintering distribution of tufted duck and goldeneye during the last 30 years. On the other hand, Švažas, Patapavičius & Dagys (2001), using ringing and recovery data, found no changes in the recovery distance of pochard migrating from their breeding grounds in Lithuania to their wintering grounds. They postulated this may have been due to his small sample size of only 33 individuals. Here, using a much larger sample (564 individuals), there was similarly no evidence of migratory short-stopping in pochard breeding in neighbouring Latvia. Thus, despite evidence for warmer winter conditions throughout Europe and migratory short-stopping of diving duck species using count data, ringing and recovery data provided little utility in capturing and describing movement contraction associated with climatic change.

Recovery distances were independent of mean daily minimum winter temperatures on the wintering grounds and the difference in temperatures between the breeding and wintering grounds. In a comparable study, winter recovery distances for 12 out of 24 bird species were shown to have decreased over the past 70 years and recovery distances were negatively correlated with temperature in the winter of
recovery (Visser et al. 2009). This effect was most pronounced for species from dry and open areas and least so for species from wet and open areas (Visser et al. 2009), such as pochard and tufted duck. Keller et al. (2009) showed that pochard travelled longer distances in harsh winters compared to mild ones, a pattern possibly triggered by the freezing of lakes. This was not the case in this study, as pochard did not shorten their recovery distance even though the mean daily minimum winter temperatures at their wintering grounds significantly increased. Tufted duck, on the other hand, increased their recovery distance while the temperatures at their wintering grounds exhibited only marginal warming. Fiedler, Bairlein & Köppen (2004) demonstrated that, of 30 species of short distance or partial migrants, eight reduced and five increased their migratory distance from their breeding to wintering grounds, while for 17 species migratory distance did not change significantly over time. Whilst a link between recent global climate change and migration distances may be plausible, it has yet to be shown to be causal (Fiedler et al. 2004).

Other studies have shown that European winters have become milder (Moberg & Jones 2005, Appendix I). On a regional scale, the annual and February temperatures in south-western Sweden have increased significantly since the mid 1970s; this was not the case for January temperatures which remained constant (Nilsson et al. 2006). Overall, the majority of studies have demonstrated an effect of warmer winter temperatures on changes in the wintering distribution of migratory species (Austin & Rehfish 2005, Maclean et al. 2008, Visser et al. 2009, Appendix I). Wildfowl in particular have been shown to respond rapidly to short-term climatic fluctuations (Ridgill & Fox 1990, Wernham et al. 2002, Hofer et al. 2005, Rainio et al. 2006). Other factors, however, such as hunting pressure, wetlands availability or availability
of winter feeding are also likely to play an important role in determining the wintering distribution of wildfowl (see Dalby et al. 2013).

Birds ringed or recovered in Russia were not included in the current study as data were not available. It is possible that Russian birds and those nesting further east may exhibit a greater propensity for migratory short-stopping behaviour, especially if they perform a leapfrog migration which would render their breeding and wintering grounds further apart. Leapfrog migration is an unusual migration pattern in which migrants from the northern part of the breeding areas migrate beyond (or “leapfrog”) individuals breeding in a more southern part of the species range during autumn migration, thus overwintering further south (Boland 1990, Kelly et al. 2002). Leapfrog migration has been demonstrated in female pochard (Hofer et al. 2006), and it is plausible that it could apply to the other diving duck species.

Caution is advocated in the use of ringing and recovery data to assess the role of climate change on migratory short-stopping. Ducks as quarry species have a recovery rate of 5-10% (Guillémain et al. 2011) which is much higher than those of species that are not hunted; hence ducks should be ideal candidates for this type of analysis. However, it follows that the distribution of ringing recoveries is heavily influenced by hunting pressure throughout most of Europe (Geis & Atwood 1961, Hofer et al. 2006). For example, the hunting pressure on pochard is higher in western than in central Europe (Švažas et al. 2001); therefore, it would be reasonable to assume that more of these ducks would be recovered from western Europe, biasing analytical results.

Recovery rates vary also temporally (Baillie & Green 1987, Robinson, Grantham & Clark 2009, Guillémain et al. 2011). There was a decline in the number of
recoveries of pochard and tufted duck, with records sparse after 2000. This trend was not as pronounced in goldeneye, which was sourced from a different breeding area and was the only species in which a reduction in the recovery distances could be demonstrated. We have no data on the numbers of goldeneye ringed in Finland, but the numbers of pochard and tufted duck ringed on Lake Engure, where the vast majority of Latvian diving ducks were ringed, decreased steeply towards the end of our study period due to a declining breeding population. During 1980-1995, the mean numbers of pochard and tufted duck ringed per year were 1 544 and 1 150 individuals, respectively. However, during 1996-2011, these numbers fell to 54 and 167 individuals respectively (J.A. Viksne 2012, pers. comm.). Hence, it is clear that the declining number of recoveries from this source was at least partially caused by fewer birds being ringed because of the large decreases in breeding numbers (J.A. Viksne 2012, pers. comm.).

The lack of data for ringing recoveries for pochard and tufted duck in the last 15 years will likely present a problem, as any effect of climate change would be expected to be more pronounced in recent years. A warming of winter temperatures was detected in all three sites examined, which was most pronounced in France and to a lesser extent Denmark. The extent of ice cover in the Baltic has generally decreased in the last 20 years (Nilsson 2008). This seems linked to increasing numbers of pochard, tufted duck and goldeneye wintering in Sweden (Nilsson 2008). Therefore, it might be concluded that the period when a foreshortening in the recovery distance of wintering diving ducks is most likely to occur coincides with the period when both ringing effort and reporting rates of recovered birds have fallen. While changes in the recovery distances for tufted duck and goldeneye were detected, there was no evidence that these changes were temperature dependent and thus causally linked to
climate change. It is possible that this is due to the limitations of ringing and recovery datasets and the confounding variables of uneven hunting pressure and declining recovery rates, rather than to a lack of any clear trend. Therefore, it must be accepted that ringing and recovery data are extremely noisy and potentially of limited utility in studies of this kind.

Continued changes in the distribution and abundance of these waterbirds along the flyway will necessitate vigilance to ensure that protected site networks are modified to take account of the responses of quarry duck species to changes in climate and other associated environmental factors. We would encourage more constant efforts to individually mark diving duck species in the immediate future and to improve reporting rates as we enter a period of accelerating environmental change.
Chapter 7

Discussion
Project Context

Wetlands are among the most threatened ecosystems in the world (Wetlands International 2005). Waterbirds are dependent upon wetlands and are often used as ecosystem sentinels indicative of environmental change (Williamson et al. 2013) as they are essential for aquatic ecosystem functioning by providing a broad range of ecosystem services, ranging from dispersal of plant and animal propagules to their use in pest control and disease surveillance (Green & Elmberg 2013). Waterbirds are also of economic importance in terms of recreation (bird watching), investment in conservation (e.g. The Royal Society for the Protection of Birds - RSPB) and, in the case of ducks, for field sports (e.g. shooting). The conservation and protection of wildfowl is, therefore, of paramount importance in maintaining the biodiversity and functioning of the planet’s wetlands and the public’s engagement with wildlife.

The main threat to waterbirds is habitat loss and degradation, caused by human activities such as agriculture, wetland reclamation or pollution (Sutherland et al. 2012). In Europe, 60-90% of wetlands were lost during the last century due to land reclamation and drainage (Junk et al. 2013). Other threats include the effects of climate change and overexploitation (Kanstrup 2006). Of all extant wildfowl species, 24% are considered endangered by Birdlife International (Butchart et al. 2004). International laws and conventions (e.g. the Ramsar Convention, EU Birds Directive 2009/147/EC and African-Eurasian Waterbird Agreement) protect waterbirds and their habitats, not least because some waterbirds represent a shared exploitable resource (e.g. for hunting). Worldwide, most Ramsar wetlands were recognised using criteria based on their importance for waterbirds (Green & Elmberg 2012). In recent decades, there has been international focus on protecting waterbirds on a flyway scale (Williamson et al. 2013), which is the most efficient approach in the protection and
conservation of migratory species. In Europe, the current network of protected wetland areas for waterbirds has been judged adequate (Williamson et al. 2013).

The aim of the current project was to determine the likely causes of recent diving duck population declines at Lough Neagh, the largest freshwater lake in Britain and Ireland. Lough Neagh has been designated a Special Protection Area (SPA) and Wetland of International Importance partly due to its importance to overwintering waterbirds, and is thus part of an international network of protected areas essential for waterbird protection.

**Population trajectories**

Substantial changes in the waterbird community of Lough Neagh were observed since the beginning of the 21st century. Population declines of migratory diving ducks, in particular, pochard, tufted duck and goldeneye were dramatic and coincided with comparable declines in resident and partially resident submerged macrophyte feeders, such as coot and mute swan following the winter of 2000/01. These declines occurred over a period of 2 winters, after which populations appear relatively stable but at a lower absolute abundance, suggesting the change was rapid and maintained. Some of these changes were correlated with similar changes at larger spatial scales (Republic of Ireland, Great Britain and the European flyway) implicating changes in migratory behaviour (presumed to be related to global climate change). However, other species did not show any correlations across larger spatial scales, while the decline in resident species appeared to implicate local factors associated with Lough Neagh itself (Chapter 2). Use of sand barge radar to determine the distribution of overwintering diving duck flocks throughout Lough Neagh confirmed that during daylight hours, they were generally close to the shore, supporting the view that winter Wetland Bird
Survey (WeBS) counts conducted from the shore are effective in enumerating the majority of the population and thus temporal trends derived from WeBS data were considered largely accurate (Chapter 3).

**Intrinsic factors**

The density of macroinvertebrates, the food source of diving ducks, declined significantly by 66% from 1997/98 to 2010, concomitant with a 67% decline in overall macroinvertebrates biomass. This reduction was correlated with a major decline in chlorophyll \( a \) concentrations, taken here as a proxy of primary productivity, suggesting a major shift in the Lough Neagh ecosystem coincident with the changes observed in overwintering bird communities (Chapter 4).

Diet inferred from SIA indicated that tufted duck and goldeneye feed primarily on chironomid larvae and *Valvata* spp. This was in agreement with results from previous studies utilizing oesophagus content analysis (Winfield & Winfield 1994b, Evans 2000). Here, oesophagus content analysis indicated that *Asellus aquaticus* is the dominant prey item in the diet of tufted ducks, but the result might have been biased due to the small sample size of ducks that contained prey items in their oesophagus. The analyses of temporal changes in the diet and the size frequency of consumed chironomid larvae were contradictory, with some differences and some similarities between 1998-99 (Bigsby 2000) and 2010-12 (Chapter 5). Thus, it cannot be concluded that there has been any substantial shift in the diet of diving ducks comparable to the shift observed in the availability of their macroinvertebrate prey.

It is notable that scaup displayed a different population trend to the other three diving duck species at Lough Neagh (Chapter 2). Scaup have been found to feed on larger chironomid larvae than other diving duck species (Winfield & Winfield 1994b,
Evans 2000). If scaup are able to exploit deeper areas of the lough where these larger size chironomid larvae are located (Winfield & Winfield 1994b), they might have a competitive advantage over other diving duck species. However, according to Winfield & Winfield (1994b), tufted duck also consume larger chironomid larvae, and their populations at Lough Neagh have declined alongside pochard and goldeneye.

Although not examined here, it seems unlikely that the sand extraction would have a major effect on benthic macroinvertebrate abundance across the wider lough-bed, secondarily affecting diving duck populations. The vast majority of sand extraction takes places off the mouth of Ballinderry River in the north-west of Lough Neagh whereas the declines of macroinvertebrates was observed throughout the lough in all six bays sampled. A further factor not examined was the impact of wildfowling activity. Large numbers of diving ducks were shot at Lough Neagh historically which could potentially have impacted returning numbers in subsequent years. However, the data are not available to conduct quantitative population dynamic analyses with respect to the impact of shooting, while the British Association for Shooting and Conservation (BASC) hold the position that diving ducks were historically so common during the winter months that shooting was unlikely to significantly impact numbers (Tommy Maine pers. comm.). Moreover, in recent years during particularly harsh winters (for example, 2010/11) a moratorium was implemented preventing the taking of diving ducks. In addition, wildfowling disturbance has been shown to have little impact on diving duck populations (Evans 2000).

**Extrinsic factors**

Stable isotope analysis suggested that the majority of overwintering diving ducks examined at Lough Neagh, particularly 1st winter birds, had recently fed elsewhere,
most likely in the marine environment. Such birds had been collected throughout the winter and were not restricted to recently arrived individuals during late autumn or early winter. Thus, it seems that populations of tufted duck, scaup and goldeneye currently overwintering on Lough Neagh are notably dynamic, with considerable within-winter movements (Chapter 5) which may implicate extrinsic factors in changes in population dynamics.

A comprehensive European-wide analysis of waterbird count data demonstrated that during the past three decades, the wintering distribution of tufted duck and goldeneye shifted north-eastwards as a response to changes in winter temperature due to global climate change (Appendix I). However, ringing and recovery data were unable to capture this effect perhaps due to trends in ringing rates and difficulties in recovery resulting in relatively small sample sizes that were inconsistent over time (Chapter 6). Nevertheless, recovery distances for ringed goldeneye decreased by a significant 400 km from the southwest to northeast from 1950 onwards, supporting observations using count data (Appendix I), but this change could not be linked to winter temperatures. Thus, waterbird count data appear to be more suitable for analysis of changes in distribution than ringing and recovery data. Indeed, there is evidence for flyway level declines in pochard populations utilizing the north-west Europe flyway (Boland & Crowe 2012, Holt et al. 2012, Wetlands International 2012). If this is the case, the declines of pochard at Lough Neagh may simply reflect population trends across the flyway.

Other potential factors explaining the different population trends in diving duck species at Lough Neagh may be related to species-specific demography. The population of scaup at Lough Neagh is drawn almost entirely from Iceland, whereas pochard, tufted duck and goldeneye migrate either partially or wholly from north-
eastern Europe (Wernham et al. 2002). It is, therefore, conceivable that the factors affecting species at their breeding grounds or during migration may be different and thus responsible for differing trends in their overwintering numbers.

**Conclusion**

Declines in the overwintering diving duck population at Lough Neagh and Lough Beg Special Protection Area (SPA), now classified as in ‘unfavourable condition’, are likely attributable to a combination of intrinsic and extrinsic factors. There was a marked decline in the biomass of phytoplankton at the beginning of 21st century, likely reflecting changes in nutrient availability (Chapter 4) and possibly related to conservation efforts in the second half of 20th century to reduce cultural eutrophication (Foy et al. 2003). The unintended consequence has been a dramatic decline in benthic macroinvertebrate abundance and biomass and thus a reduction in the availability of food resources for diving ducks, which may contribute to frequent within-winter movements and short-distance redistribution. Thus, this study highlights the need for caution in assuming dramatic changes in site populations are always exclusively due to extrinsic factors. Moreover, increasingly milder winter temperatures at higher latitudes caused by global climate change have resulted in migratory short-stopping and thus major redistribution of overwintering duck species throughout Europe (Appendix I). These events appear to have coincidentally conspired, resulting in a rapid decline of diving duck populations at Lough Neagh over just a few years after the winter of 2000/01.

The changes observed here have implications not only for Lough Neagh but also for the Protected Areas Network throughout Europe. Other lakes, on the southern or south-western edge of the wintering distributions of waterbird species, may face
similar problems where climate change may displace populations which retreat further north. Moreover, European-wide efforts to reduce eutrophication generally are likely to alter recent baselines of waterbody productivity, affecting consumer and predator communities. The *Natura 2000* Protected Area Network provides a European-wide approach to site designation and management whilst the EU Birds Directive (2009/147/EC) provides a framework for the monitoring, surveillance and protection of wild birds, in this case waterbird communities of conservation concern. Nevertheless, each designated site is managed locally and there is little scope to account for global level processes, such as climate change, when conducting conservation assessments. Consequently, there is a need for a cross-jurisdictional ecoregion approach to deal with conservation assessments at EU interfaces. Clearly, there is need to periodically re-evaluate conservation objectives in the face of on-going global change. In the specific case of Lough Neagh, as Britain and Ireland’s largest freshwater lake, greater emphasis should be put on developing an integrated monitoring programme for water quality, macroinvertebrates and fish to complement annual bird counts in order to develop a holistic whole ecosystem approach.
Recommendations

Several recommendations are made for further monitoring and research:

1) Currently, chironomid larvae sampling at Lough Neagh carried out by the Water Management Unit (WMU) of the Northern Ireland Environment Agency (NIEA) is shore based and restricted to the littoral zone (less than a metre deep). In a lake of almost 400 km$^2$, this has little relevance to the greatest part of the chironomid community or those taxa that consume them, e.g. diving ducks or fish. Generally, the littoral zone would be expected to be disproportionally important in terms of invertebrate productivity. However, this is unlikely to be the case for Lough Neagh because chironomid larvae and molluscs abundance was found to be low at 1m depth compared to a depth of 3m and more (Winfield & Winfield 1994b). An expansion of the sampling regime to include the macroinvertebrate community of the profundal zone would greatly increase the value of the dataset.

2) More information is needed on natural fluctuations in macroinvertebrate abundance at Lough Neagh between years. Regular annual monitoring of macroinvertebrates on a small number of sites, both in the littoral and profundal zones, would provide information on the extent of natural fluctuations in macroinvertebrate populations.

3) Maintain the current level of wetland waterbird monitoring on Lough Neagh through the WeBS.
4) Review current coverage of all routine survey and monitoring activities on Lough Neagh to determine if appropriate baseline monitoring adequately covers the main physicochemical and biological parameters.

5) Submerged macrophyte sampling is carried out by the WMU of NIEA. If an analysis of this dataset showed a change in the extent or community composition of submerged macrophytes around the time period that the diving duck and submerged macrophyte feeder declines, this would lend further support to the hypothesis that intrinsic factors were affecting waterbird populations at the site.

6) The nocturnal feeding distribution of diving ducks at Lough Neagh remains unknown. The use of specialised Bird Detecting Radar (BDR) is advocated, which can be hired, deployed and analysed by experts (example, the Bird Management Unit at the Animal Health and Veterinary Laboratories or AHVLA) for approximately £1 000 per day. To adequately cover Lough Neagh it should be stationed at about five strategically selected locations around the shore for 24 hours each to capture the movements of all duck-sized targets. Thus, for approximately £5 000 all movements of duck-sized targets throughout the lough could be captured and analysed spatially during mid-winter when diving duck numbers are at their peak.

7) Stable isotope analysis indicated that a large proportion of the overwintering diving duck population at Lough Neagh was dynamic, utilizing other waterbodies, quite likely including the marine environment. GPS loggers or satellite tags deployed on the focal species showing declines (pochard, tufted
duck and goldeneye) would provide information on the frequency and extent of within-winter movements.

8) A review of monitoring and reporting procedures at a European level would ensure that the coverage of protected area networks are appropriate whilst adaptation may be required to reflect recent (and on-going) changes in waterbird distributions.
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References


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References


Appendices
Appendix I

Rapid climate driven shifts in wintering distributions of three common waterbird species

This appendix was published as:

Abstract

Climate change is predicted to cause changes in species distributions and several studies report margin range shifts in some species. However, the reported changes rarely concern a species’ entire distribution and are not always linked to climate change. Here we demonstrate strong north-easterly shifts in the centres of gravity of the entire wintering range of three common waterbird species along the North-West Europe flyway during the past three decades. These shifts correlate with an increase of 3.8 °C in early winter temperature in the north-easterly part of the wintering areas, where bird abundance increased exponentially, corresponding with decreases in abundance at the south-western margin of the wintering ranges. This confirms the need to re-evaluate conservation site safeguard networks and associated biodiversity monitoring along the flyway, as new important wintering areas are established further north and east, and highlights the general urgency of conservation planning in a changing world. Range shifts in wintering waterbirds may also affect hunting pressure, which may alter bag sizes and lead to population level consequences.
Introduction

Several studies have shown range margin shifts in over 20 different taxonomic groups in recent years (Parmesan 2006; Maclean et al. 2008; Brommer & Møller 2010; Chen et al. 2011). To date, such studies have mainly focused on documenting changes at the edges of species’ distributions, and studies concerning shifts throughout entire ranges are rare. The expansion of the northern boundary of European butterfly towards north has been much stronger than retraction of the southern boundary (Parmesan et al. 1999). Maclean et al. (2008) showed that the centre of gravity of wintering distributions of five Northern European wader populations have shifted 95 kilometres northeastwards. Abundance of several European breeding bird species increased along a northern range margin and concomitantly decreased at the southern range margin (Jiguet et al. 2010). La Sorte & Thompson (2007) showed that the northern boundary and centre of wintering bird abundance had shifted northwards, but they did not investigate the southern edge of these distributions, which would be crucial for the determination of spatial shifts of entire ranges.

Although it has been argued that range shifts are caused by climate change, direct links have rarely been demonstrated, and annual variations in the distribution of populations have hitherto not been convincingly linked to climatic fluctuations (Brommer & Møller 2010). The only regional examples of climatic effects on population ranges, of which we are aware, are those showing that fewer wintering waders occurred in southwestern UK during warmer winters (Austin & Rehfisch 2005) and that the wintering distribution of black brent (Branta bernicla nigricans) in Alaska shifted northwards as a response to climatic oscillation (Ward et al. 2009). However, such annual distribution shifts have not been demonstrated for entire
populations at the migration flyway level. The lack of studies demonstrating effects across entire distribution ranges is likely to be because estimating population sizes and trends of most widespread species, over such vast geographical areas, is extremely challenging. This task, however, represents a challenge that researchers must confront, if we wish to conserve populations under changing conditions.

Wintering waterbirds are highly likely to show distributional shifts due to climate change, since they respond rapidly to weather conditions (Ridgill & Fox 1990; Lehikoinen et al. 2006; Rainio et al. 2006). Other environmental changes (e.g. eutrophication or wetland habitat creation) may affect the abundance of birds regionally rather than across entire flyways (Ma et al. 2010). For instance, breeding waterbird populations specifically occupying wetlands subject to excessive eutrophication have recently shown a dramatic decline in breeding numbers in Finland, which cannot be explained by other factors, such as hunting (Rönkä et al. 2005, see also Pöysä et al. 2012).

Waterbirds breeding in Northern Europe and Siberia have increasingly delayed their southward autumn migration, and this delay is thought to be linked to climate warming (Lehikoinen & Jaatinen 2012). Furthermore, spring arrival dates of waterbirds in the same flyway were linked with climatic oscillation (Vähätalo et al. 2004, Rainio et al. 2006), and, for instance, the spring arrival of common eiders to their North European breeding areas has advanced during recent decades (Lehikoinen et al. 2006). Such changes, coupled with indications of past range shifts (Nilsson 2008; Skov et al. 2011), corroborate the notion that waterbirds are highly responsive to changes in climate (Rainio et al. 2006). Based on this background information, we hypothesize that climate change does cause shifts in the centre of the gravity of the
whole flyway population. From this hypothesis we draw two predictions relating to waterbirds in the northern hemisphere: i) that numbers will increase in the northern parts of flyways, coupled with a decrease in the southern parts, and ii) as waterbird numbers respond to temperature, we predict that in mild winters waterfowl numbers will be higher in countries at the northern edge of the flyway and lower on the southern edge, and *vice versa*. To test these predictions, we examine a long-term (31 years, 1980–2010) dataset on the wintering distributions of three common European waterfowl species: the goosander (*Mergus merganser*), the common goldeneye (*Bucephala clangula*; hereafter goldeneye) and the tufted duck (*Aythya fuligula*). We aim to elucidate potential range shifts, their magnitude and their links to temperature fluctuations across the North-West European flyway.

**Material and methods**

**Duck data**

We utilized three decades (1980–2010) of site-based count data to determine the wintering distributions of three common waterfowl species. In this study we track changes in species abundance in nine countries (Finland, Sweden, Denmark, Germany, the Netherlands, Switzerland, Great Britain, the island of Ireland and France) covering a climatic gradient throughout the 3000 kilometre long southwest-northeast flyway of the study species (Perdeck & Clason 1980; Scott & Rose 1996). The data originate from the International Waterbird Census (IWC, coordinated by Wetlands International; Delany 2005) and the Finnish winter bird count scheme (Hildén *et al.* 1991) conducted primarily in January in nine countries during 1980–
2010 (for details of the national count schemes and data, see Table 1). In general, the count data was compiled separately for each country, with the exception of Sweden, which was split into two areas, because the northern and southern parts of this large country differ considerably in terms of winter climate (Nilsson 2008). In addition, the Republic of Ireland and Northern Ireland have been combined, since they are geographically separated from Great Britain.

Our study species are the three common and widely distributed diving duck species in Europe, which exploit both marine and freshwater habitats. The North-West European flyway, to which these species belong, is the best documented of all flyways, with the longest running monitoring schemes. These three study species and the long-tailed duck (*Clangula hyemalis*) are the most abundant wintering diving ducks in the northern edge of the flyway near the edge of the ice cover. However, we excluded the long-tailed duck and other sea ducks from the analyses, because these species are wintering off-shore and majority of the population is not surveyed annually (Skov *et al.* 2011). These three remaining study species are exceptionally suited for studying the impact of climate change, not only because they are common and exhibit relatively stable population sizes (Wetlands International 2012), but also because they are truly dependent on open water as they feed on fish and/or benthic organisms (Cramp & Simmons 1977). Because of this diet, diving ducks may await the onset of winter, and only migrate southward when bodies of water start to freeze over. Dabbling ducks, which feed in shallow water that freezes over rapidly at sub-zero temperatures, also avoid the zero-degree isotherm and do so by rapid and long-distance movements before the onset of winter (Ridgill & Fox 1990, Dalby *et al.* 2013). In addition to this, the population sizes of several species of swans and geese
### Table 1 Duration of study periods used in the data analyses, average number of annually surveyed wintering sites (min-max) and the average number of counted tufted duck, goldeneye and goosander (min-max) in each study area. “—” indicates that these areas were outside of the flyway and thus data were not used in the analyses.

<table>
<thead>
<tr>
<th>Area</th>
<th>Period</th>
<th>Sites (min-max)</th>
<th>Tufted duck</th>
<th>Goldeneye</th>
<th>Goosander</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Individuals</td>
<td>Individuals</td>
<td>Individuals</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Sites</td>
<td>Sites</td>
<td>Sites</td>
</tr>
<tr>
<td>Finland, FIN</td>
<td>1980-2010</td>
<td>94 (46-148)</td>
<td>3,379 (10-44,256)</td>
<td>129 (84-191)</td>
<td>1,740 (77-8,395)</td>
</tr>
<tr>
<td>Denmark, DK</td>
<td>1987–2010</td>
<td>33 (17–44)</td>
<td>81,875 (18,769–147,056)</td>
<td>37 (17–44)</td>
<td>20,609 (6,074–33,071)</td>
</tr>
<tr>
<td>Switzerland, CH²³</td>
<td>1980–2010</td>
<td>83 (73–93)</td>
<td>124079 (81,172–175,679)</td>
<td>60 (54–66)</td>
<td>6,814 (4,150–8,775)</td>
</tr>
<tr>
<td>G. Britain, GB²</td>
<td>1980–2010</td>
<td>1,314 (907–1,512)</td>
<td>50,696 (33,918–61,172)</td>
<td>1,077 (759–1,267)</td>
<td>12,697 (8,282–17,363)</td>
</tr>
</tbody>
</table>

¹ Southern Sweden covers areas of Skåne, Halland, Blekinge, Kronoberg, Jönköping, Västra Götland, and Northern Sweden the rest of the country.

² In the goosander analysis, we used only data from the northern part of Germany (north from latitude 51° N), as South German birds, as well as French, British and Swiss goosanders, mainly belong to other flyway populations (Scott & Rose 1996).

³ Part of the Swiss tufted ducks belong to another flyway population, which also migrates towards north-east (Hofer et al. 2005).
have increased markedly during the recent decades (Wetlands International 2012), which may complicate the investigation of the potential effects of climate change on range shifts. The combined population size of the study species in this flyway is estimated to be more than 2.6 million individuals (Wetlands International 2012) and the estimated annual hunting bag size of the three species throughout Europe is more than 400 000 individuals (Hirschfeld & Heyd 2005).

**Climate data**

We used the average temperature measured in southern Finland by the Finnish Meteorological Institute during a two-month period prior to the censuses (16 November–15 January), as a proxy for early winter temperature at the northeastern edge of the flyway. Data from approximately 100 Finnish weather stations were interpolated to a 10 x 10 km grid of virtual weather stations (Venäläinen *et al.* 2005). From these we calculated the mean early winter temperature in southern Finland (60–64° N; 20–31° E, Supplementary Fig. 1a). The winter temperature in southern Finland correlated with the winter temperature over large spatial areas in northern Europe (Supplementary Fig. 1a). In the northeastern part of the flyway, the early winter temperature increased by 3.8°C during the study period (Supplementary Fig. 1b), which indicates the strong potential for climate driven changes in waterbird wintering distributions.

**Statistical analyses**

Data were analysed by using site-specific duck abundance from each country. The response variables in our analyses, i.e. population trends and annual abundances of goosander, goldeneye and tufted duck, were estimated using the Trends and Indices
for Monitoring data (TRIM) software (Pannekoek & van Strien 2001). This software is commonly used by many European bird monitoring schemes. TRIM uses a generalised estimating equation (GEE) algorithm to estimate a population index from count data taking into account overdispersion and serial correlation in the data. It also interpolates missing observations (sites with lacking censuses in some years) using a Poisson general log-linear model (Pannekoek & van Strien 2001; the software and the manual are freely available on www.ebcc.info).

Because the duck counts were not always repeated at each count-site annually over the study period, we estimated the change in bird abundance in each country by generating annual population indices and using the latest national wintering population estimates (see Table 2 for details). We did this by anchoring the species and country specific wintering number estimate at a particular year in the time series with the abundance indices produced by the TRIM-software. Thus if a population of a species in a given country was estimated to be 50 000 birds in year \( t \), when the annual abundance index had a value of 1, index values of 1.5 and 2.5 in year \( t+n \), where \( n \) is the number of years passed, would mean that the population has increased by 25 000 and 75 000 individuals, respectively. To estimate the change in bird numbers over the study period, we calculated the difference between the averages of the first three, and last three years in the time series (see Table 2 for details on national population estimates). We used an average of three years to balance out the effects of potential single extreme years. We must stress that these abundance estimates are coarse, but we use them here to represent the magnitude of the change in real numbers of individuals.
Appendix I  
Climate change and migratory short-stopping

Table 2 Region wide estimates of wintering tufted ducks, goldeneyes and goosanders including the survey year and the reference of the report, where the results have been published. Values in brackets are not used in the analyses, as they do not concern the birds from the study flyway.

<table>
<thead>
<tr>
<th>Area</th>
<th>Survey year</th>
<th>Tufted</th>
<th>Goldeney</th>
<th>Goosander</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Finland</td>
<td>1990–1992</td>
<td>1,000</td>
<td>1,000</td>
<td>6,000</td>
<td>Koskimies (1993).</td>
</tr>
<tr>
<td>Denmark</td>
<td>2008</td>
<td>162,247</td>
<td>64,977</td>
<td>13,846</td>
<td>Petersen et al. (2010).</td>
</tr>
<tr>
<td>Germany</td>
<td>2000–2005</td>
<td>325,000</td>
<td>65,000</td>
<td>33,500*</td>
<td>Wahl. et al. (in prep.)</td>
</tr>
<tr>
<td>Netherlands</td>
<td>2006–2010</td>
<td>220,000</td>
<td>12,000</td>
<td>11,000</td>
<td>Hornman et al. (in</td>
</tr>
<tr>
<td>G. Britain</td>
<td>2005–2009</td>
<td>110,000</td>
<td>20,000</td>
<td>[12,000]</td>
<td>Musgrove et al. (2011)</td>
</tr>
</tbody>
</table>


We built two different linear autoregressive models to test how the log-transformed annual species and country wide bird abundances are associated with variation in the annual temperature at the northeastern edge of the flyway and bird abundances in the same country year before. The equation adopted in the first approach was:

(1) \( \log(N_{t+1}) \approx \log(N_t) + W_{t+1} \),

where \( N \) is population abundance in year \( t+1 \) and \( t \), and \( W \) is the early winter temperature in South Finland in year \( t+1 \). This model takes into account, and corrects for, temporal autocorrelation when estimating the direct effect of winter temperature on the number of wintering birds (higher temperature increases bird numbers and lower decreases). The second model took the form:

(2) \( \log(N_{t+1}) \approx \log(N_t) + \Delta W_{t+1} \),

which was otherwise similar, except that the effect of weather was modelled on the difference in temperature between two subsequent years. Thus, we expect that
wintering numbers would increase in the case where temperature has been higher in year t+1 than in year t, and \textit{vice versa}. We compared these two models using AICc (Burnham \& Anderson 2002).

**Results**

Over the past three decades, the numbers of all three wintering ducks increased at the northeastern edge of the flyway with a simultaneous decrease in the southwestern edge of their respective distributions (Figs. 1–2). This change was particularly pronounced during the last 15–20 years based on annual fluctuations in the abundance indices (Figs 1–2).

**Fig. 1** Winter percentage change in abundance of (a) tufted duck, (b) goldeneye and (c) goosander in nine north and west European countries in 1980–2010 (slightly shorter periods in some countries; Supplementary Table 1). Significant population changes are bolded in red (increase) and blue (decrease), values in brackets represent no significant change. Relatively few north European goosanders winter as far south and west as France, Great Britain and Ireland (Scott \& Rose 1996), and Swiss birds partly belong to the Central/West European flyway population, so the Netherlands was defined as the south-western edge of the flyway for this population. Estimated population changes in numbers of individuals are shown in Table 4.
In Finland, the number of tufted duck, goldeneye and goosander increased by 24800%, 4320% and 128%, respectively, or by 38 000 birds (Figs 1–2, Tables 3–4). In northern Sweden, the numbers of birds increased by over 80 000 for all three species with 190%, 269% and 124% increases for tufted duck, goldeneye and goosander, respectively (Figs 1–2, Tables 3–4).

At the southwestern edge of the flyway, tufted ducks decreased by 46% in France, 43% in Ireland and 39% in Switzerland or altogether by 104 000 birds. Goldeneyes decreased significantly in Ireland and in Switzerland by 63% and 35%, respectively, representing together a loss of 12 000 birds. Recent short-term declines of goldeneyes (since the mid-1990s) occurred in other southwestern areas; the Netherlands, Great Britain and France (Figs 1–2, Tables 3–4). At the southwestern edge of the flyway, the numbers of goosander decreased by 66%, 41% and 21% in the Netherlands, Denmark and southern Sweden, respectively, or together by 51 000 birds (Figs 1–2, Table 4). In the south-central part of the flyway, Switzerland, the number tufted ducks and goldeneyes decreased by 70 000 birds (Fig. 2, Table 4). Despite these rapid changes in national abundances the combined population size estimate of all three species has remained relatively stable during 1987–2009, when data from all nine study countries were available (Fig. 3).

In half of the country specific analyses, the annual winter abundances were significantly positively dependent on the population abundance in the year before and thus positively autocorrelated (Tables 5–6). This was especially the case in both edges of the flyway: Finland, Sweden in the north and in Netherlands (goosander), Switzerland, UK (goldeneye), Ireland and France in the south (Tables 5–6). The
**Fig. 2** National trends in winter abundance of tufted duck, goldeneye and goosander in Finland, Northern and Southern Sweden, Denmark, Germany, the Netherlands, Switzerland, Great Britain, Ireland and France in 1980–2010 represented as estimated population sizes in each country. The unit of the y-axis is thousands of birds, and it has been calculated using annual population indices of TRIM analysis and national countrywide wintering estimates (see methods and Tables 2 & 4).
Table 3: Annual growth rates of wintering populations of tufted ducks, goldeneyes and goosanders based on TRIM–analyses of annual mid-winter count data from wetlands in all countries. Mean annual growth rate and total change in abundance during the study period in each study area are shown; significant growth rates in bold. “—” indicates areas outside of the flyway of the species, which were not used in the analyses.

<table>
<thead>
<tr>
<th>Area</th>
<th>Study period</th>
<th>Tufted duck Growth rate</th>
<th>Change (%)</th>
<th>Goldeneye Growth rate</th>
<th>Change (%)</th>
<th>Goosander Growth rate</th>
<th>Change (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Finland</td>
<td>1980–2010</td>
<td>0.195 ± 0.028</td>
<td>24797%</td>
<td>0.130 ± 0.005</td>
<td>4320%</td>
<td>0.027 ± 0.003</td>
<td>128%</td>
</tr>
<tr>
<td>Sweden N</td>
<td>1980–2010</td>
<td>0.035 ± 0.004</td>
<td>190%</td>
<td>0.043 ± 0.003</td>
<td>269%</td>
<td>0.026 ± 0.003</td>
<td>124%</td>
</tr>
<tr>
<td>Sweden S</td>
<td>1980–2010</td>
<td>0.022 ± 0.003</td>
<td>98%</td>
<td>0.017 ± 0.002</td>
<td>68%</td>
<td>-0.008 ± 0.003</td>
<td>-21%</td>
</tr>
<tr>
<td>Denmark</td>
<td>1987–2010</td>
<td>-0.013 ± 0.006</td>
<td>-27%</td>
<td>0.013 ± 0.005</td>
<td>36%</td>
<td>-0.022 ± 0.007</td>
<td>-41%</td>
</tr>
<tr>
<td>Germany</td>
<td>1980–2009</td>
<td>0.001 ± 0.001</td>
<td>2%</td>
<td>0.002 ± 0.001</td>
<td>7%</td>
<td>-0.003 ± 0.002</td>
<td>-9%</td>
</tr>
<tr>
<td>Netherlands</td>
<td>1980–2009</td>
<td>0.005 ± 0.003</td>
<td>15%</td>
<td>0.006 ± 0.003</td>
<td>21%</td>
<td>-0.035 ± 0.003</td>
<td>-66%</td>
</tr>
<tr>
<td>Switzerland</td>
<td>1980–2010</td>
<td>-0.017 ± 0.001</td>
<td>-39%</td>
<td>-0.015 ± 0.002</td>
<td>-35%</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>G. Britain</td>
<td>1980–2010</td>
<td>0.006 ± 0.001</td>
<td>20%</td>
<td>0.004 ± 0.001</td>
<td>13%</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Ireland</td>
<td>1986–2010</td>
<td>-0.022 ± 0.003</td>
<td>-43%</td>
<td>-0.039 ± 0.002</td>
<td>-63%</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>France</td>
<td>1980–2010</td>
<td>-0.021 ± 0.001</td>
<td>-46%</td>
<td>0.001 ± 0.002</td>
<td>3%</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>
Table 4 Estimated change in absolute numbers of individuals in each study area between first three and last three study years. ‘–‘–‘ indicates that areas outside of the flyway of the species, not used in the analyses. Note that change in number of individuals and percentiles of growth rate (Table 3) does not necessarily match perfectly, since the trend of the percentiles is counted using all years during the study period but the change in individuals relates directly to the difference between the average of three last and three first study years.

<table>
<thead>
<tr>
<th>Area</th>
<th>First three</th>
<th>Last three</th>
<th>Tufted duck</th>
<th>Goldeneye</th>
<th>Goosander</th>
</tr>
</thead>
<tbody>
<tr>
<td>Finland</td>
<td>1980–1982</td>
<td>2008–2010</td>
<td>22 400</td>
<td>9 800</td>
<td>5 400</td>
</tr>
</tbody>
</table>

*Germany, Switzerland and France share two larger wetlands, where birds could be partly included in estimates from both countries. However, in the trend analyses, the data from these sites have been split between countries.

Fig. 3 Combined population estimates of (a) tufted ducks, (b) goldeneye and (c) goosander, during 1987–2009 when data was available from all nine study countries.
annual fluctuations in duck abundances were more strongly linked to the direct effect of changes in early winter temperatures at the northeastern edge of the flyway (Finland and Sweden), since in six cases the direct effect models were better (ΔAICc > 2) than models where the temperature difference between two subsequent years was used as an explanatory variable, whereas the opposite pattern was found only once (Fig. 4, Tables 5–6, Suppl. Table 1). In Finland, the annual change in abundance of

![Fig. 4](image_url) Annual change in national winter population abundances of tufted duck (a, d), goldeneye (b, e) and goosander (c, f) on the northeastern edge (i.e. Finland, a–c) and southwestern edge (i.e. France, the Netherlands, d–f, respectively) in relation to early winter temperature in Finland in year t+1. (Table 5). The scale of y-axis is log-transformed difference between N_t+1 and N_t. Solid lines represent significant correlation.
tufted duck, goldeneye and goosander increased with increasing early-winter temperatures, and the same was the case with tufted ducks in south Sweden (Fig. 4, Table 5). Compellingly, the southwestern parts of the flyway exhibited the opposite patterns: annual change in French goldeneye numbers and Dutch goosander numbers were significantly negatively associated with the direct effect of early winter temperature at the northeastern edge of the flyway (Fig. 4, Table 5). The difference in temperature between two subsequent years was only significantly associated with wintering numbers of Dutch goosander (Tables 5–6, Suppl. Table 1). In the central part of the flyway, duck abundances were independent of temperature (Tables 5–6).
Table 5 Regression coefficients from linear regressions between wintering waterfowl numbers (in year t) and early winter temperature (in year t; model number 1) in Southern Finland and waterfowl numbers in year t-1 for tufted duck, goldeneye and goosander in each study area. The test-values for the whole model has been shown and significant ($p < 0.05$) relationships are shown in bold, and trend results ($p < 0.1$) are italicized. “–” indicates that areas outside of the flyway of the species, not used in the analyses.

<table>
<thead>
<tr>
<th>Area</th>
<th>Years</th>
<th>B (temp)</th>
<th>Tufted duck</th>
<th>Goldeneye</th>
<th>Goosander</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>B (pop)</td>
<td>F $p$</td>
<td>B (temp)</td>
<td>F $p$</td>
</tr>
<tr>
<td>Finland</td>
<td>n = 31</td>
<td>0.38 ± 0.10</td>
<td>0.37 ± 0.15</td>
<td>16.69 &lt;0.001</td>
<td>0.07 ± 0.03</td>
</tr>
<tr>
<td>Sweden N</td>
<td>n = 31</td>
<td>0.03 ± 0.02</td>
<td>0.58 ± 0.13</td>
<td>17.42 &lt;0.001</td>
<td>0.01 ± 0.02</td>
</tr>
<tr>
<td>Sweden S</td>
<td>n = 31</td>
<td>0.03 ± 0.01</td>
<td>0.41 ± 0.15</td>
<td>6.77 0.004</td>
<td>0.02 ± 0.02</td>
</tr>
<tr>
<td>Denmark</td>
<td>n = 24</td>
<td>0.01 ± 0.02</td>
<td>0.17 ± 0.20</td>
<td>0.64 0.54</td>
<td>0.01 ± 0.02</td>
</tr>
<tr>
<td>Germany</td>
<td>n = 30</td>
<td>-0.00 ± 0.01</td>
<td>0.18 ± 0.20</td>
<td>2.68 0.09</td>
<td>-0.00 ± 0.01</td>
</tr>
<tr>
<td>Netherlands</td>
<td>n = 30</td>
<td>0.05 ± 0.02</td>
<td>-0.11 ± 0.17</td>
<td>3.59 0.042</td>
<td>0.03 ± 0.02</td>
</tr>
<tr>
<td>Switzerland</td>
<td>n = 31</td>
<td>-0.01 ± 0.01</td>
<td>0.77 ± 0.13</td>
<td>18.52 &lt;0.001</td>
<td>-0.02 ± 0.01</td>
</tr>
<tr>
<td>G. Britain</td>
<td>n = 31</td>
<td>0.01 ± 0.01</td>
<td>0.28 ± 0.17</td>
<td>2.89 0.07</td>
<td>-0.01 ± 0.01</td>
</tr>
<tr>
<td>Ireland</td>
<td>n = 25</td>
<td>-0.01 ± 0.02</td>
<td>0.60 ± 0.16</td>
<td>6.62 0.006</td>
<td>0.00 ± 0.02</td>
</tr>
<tr>
<td>France</td>
<td>n = 31</td>
<td>-0.02 ± 0.02</td>
<td>0.55 ± 0.17</td>
<td>8.4 0.002</td>
<td>-0.02 ± 0.01</td>
</tr>
</tbody>
</table>
Table 6 Regression coefficients from linear regressions between wintering waterfowl numbers (in year t) and early winter temperature difference in Southern Finland between year t and t+1 (model number 2) and waterfowl numbers in year t-1 for tufted duck, goldeneye and goosander in each study area. The test-values for the whole model has been shown and significant \((p < 0.05)\) relationships are shown in bold, and trend results \((P < 0.1)\) are italicized. “--” indicates that areas outside of the flyway of the species, not used in the analyses.

<table>
<thead>
<tr>
<th>Area</th>
<th>Years</th>
<th>B (temp)</th>
<th>B (pop)</th>
<th>F</th>
<th>(p)</th>
<th>B (temp)</th>
<th>F</th>
<th>(p)</th>
<th>B (temp)</th>
<th>F</th>
<th>(p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Finland</td>
<td>31</td>
<td>0.25 ± 0.08</td>
<td>0.71 ± 0.15</td>
<td>13.56</td>
<td>&lt;0.001</td>
<td>0.98 ± 0.06</td>
<td>118.49</td>
<td>&lt;0.001</td>
<td>0.11 ± 0.02</td>
<td>12.49</td>
<td>&lt;0.001</td>
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<td>Sweden N</td>
<td>31</td>
<td>0.01 ± 0.01</td>
<td>0.68 ± 0.13</td>
<td>14.25</td>
<td>&lt;0.001</td>
<td>0.80 ± 0.12</td>
<td>22.98</td>
<td>&lt;0.001</td>
<td>0.60 ± 0.15</td>
<td>8.18</td>
<td>0.002</td>
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<tr>
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<td>0.01 ± 0.01</td>
<td>0.46 ± 0.15</td>
<td>4.12</td>
<td>0.027</td>
<td>0.47 ± 0.17</td>
<td>3.6</td>
<td>0.041</td>
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<td>0.003</td>
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<td>24</td>
<td>0.04 ± 0.02</td>
<td>0.22 ± 0.18</td>
<td>2.63</td>
<td>0.97</td>
<td>0.19 ± 0.16</td>
<td>0.76</td>
<td>0.480</td>
<td>-0.02 ± 0.02</td>
<td>1.44</td>
<td>0.260</td>
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<td>0.19 ± 0.19</td>
<td>2.31</td>
<td>0.120</td>
<td>-0.02 ± 0.18</td>
<td>0.89</td>
<td>0.421</td>
<td>-0.00 ± 0.01</td>
<td>0.30</td>
<td>0.19</td>
</tr>
<tr>
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<td>0.01 ± 0.20</td>
<td>1.30</td>
<td>0.290</td>
<td>0.31 ± 0.18</td>
<td>2.26</td>
<td>0.124</td>
<td>-0.08 ± 0.03</td>
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<td>0.15</td>
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<tr>
<td>Switzerland</td>
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<td>0.79 ± 0.14</td>
<td>16.82</td>
<td>&lt;0.001</td>
<td>-0.75 ± 0.15</td>
<td>13.44</td>
<td>&lt;0.001</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>G. Britain</td>
<td>31</td>
<td>0.00 ± 0.01</td>
<td>0.34 ± 0.19</td>
<td>1.72</td>
<td>0.198</td>
<td>0.82 ± 0.12</td>
<td>23.74</td>
<td>&lt;0.001</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ireland</td>
<td>25</td>
<td>0.00 ± 0.02</td>
<td>0.60 ± 0.16</td>
<td>6.61</td>
<td>0.006</td>
<td>0.72 ± 0.15</td>
<td>11.03</td>
<td>&lt;0.001</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>France</td>
<td>31</td>
<td>-0.00 ± 0.01</td>
<td>0.63 ± 0.16</td>
<td>7.46</td>
<td>0.003</td>
<td>0.66 ± 0.14</td>
<td>9.03</td>
<td>0.001</td>
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Discussion

Our results show, for the first time at the flyway level, that the wintering distributions of waterfowl have shifted rapidly northeastward as a response to changes in temperature. The hypothesis for a climate driven shift in the wintering distribution of tufted ducks, goldeneyes and goosanders is supported by the fact that observations of increased duck numbers at the northeastern edge of the flyway were corroborated by those of decreasing duck numbers at the southwestern edge of the flyway. Critically, annual fluctuations in bird numbers were directly linked with early winter temperature at both ends of the flyway, but especially on the northern edge of the distribution in all three species. Our findings also suggest that it is the direct effect of the temperature which drives the population changes and not the difference in temperatures between two subsequent years. Therefore we believe that there are species-specific temperature thresholds, above which wintering abundance increases on the northern side of the distribution and thus increased temperature has key role on large-scale changes in species distribution. Nevertheless, we cannot exclude the possibility that other environmental factors have acted together with global warming.

The wintering numbers were strongly positively linked with the wintering numbers year before in the same region at the edges of the duck distributions. This positive temporal autocorrelation in numbers suggests that large parts of the population likely show wintering philopatry on a larger spatial scale (here manifest at the national level used in this analysis). Nevertheless this does not exclude the possibility that birds can move within winter at smaller spatial scales, as documented for example amongst individually marked tufted ducks (Gourlay-Larour et al. 2012).
In addition, several other waterbirds are known to show winter site fidelity to some extent (Guillemain et al. 2009, Petersen et al. 2012). This implies that some part of the population is responding to new feeding opportunities as these arise from changes in temperature that represent these observed shifts in range. To understand these mechanisms in more detail, we need to know which individuals are more likely to respond to temperature (e.g. are they males, adults, young, good or low quality birds and of which previous wintering provenance?).

The wintering population sizes of the studied species in the two northernmost countries in this study (viz. Finland and Sweden) have increased by more than 140 000 individuals over the past three decades. This number of individuals represents over 5 % of the populations of the three species in the North-West European flyway (Wetlands International 2012). Correspondingly, countries in the southwestern parts of the flyway, the Netherlands, Switzerland, Ireland and France, have lost over 128 000 birds over the same period. In this analysis, we have only analysed count data from three diving ducks, which we consider the most likely to show such range shifts in response to temperature change and hence ice-free habitat up against the northeastern limit of their winter range. There are recent indications that the wintering populations of many waterfowl species have increased in northern Europe (Baltic region; Nilsson 2008, Skov et al. 2011) and decreased in southern and western areas (Crowe et al. 2008, Rendón et al. 2008, Keller 2011). Therefore we believe that climate driven shifts in the central gravity of species distribution could be a general pattern amongst many more European waterfowl species than studied here, and should be examined in more detail.
Waterbird population shifts are of both political and socio-economic importance. They are included in international and national legislations and widely harvested species (Wetlands International 2006). Furthermore, waterbirds are highly dependent on wetlands, including many threatened habitat types throughout the world (Williams 1993). Waterbird abundance is one of the most commonly used designation criteria to protect wetland sites (Wetlands International 2006). There are several wetland and waterbird site safeguard programmes, including the Ramsar Convention, the African-Eurasian Waterbird Agreement and the European Union Special Protection Areas (SPAs) network under the European Union Directive on the Conservation of Wild Birds (Council Directive 2009/147/EC). These programs represent the basis for conserving necessary habitats to safeguard populations of migratory waterbirds. As global warming is predicted to escalate in the near future, particularly so at higher latitudes (IPCC 2007), we can expect increasing numbers of waterbirds staging and wintering in northeastern areas, formerly inaccessible to them. These new staging and wintering areas may become of vital importance for waterbird populations and may not be included in any of the environmental safeguard programmes. Conversely, we can expect to see birds increasingly retracting from sites further south and west within the wintering range, some of which were designated specifically to protect these populations (cf. Kujala et al. 2011). Because of this, local managers should consider climate change as a possible cause of change in the number of birds in their region, in addition to possible changes in total population size and/or changes in habitat suitability. As importantly, new wintering and staging areas may be unprotected, while historical wintering and staging areas may become devoid of birds as distributions are retracting towards north. This creates a major and novel set of challenges for the effective safeguard of
populations, and necessitates a new, more flexible, protection strategy. Such flexible site safeguard programmes need to be underpinned by sound monitoring protocols to inform upon, and deal with, shifting distributions of animals (Pressey et al. 2007, Hodgson et al. 2009), including waterbirds. However, even static networks of protection areas may support climate driven range shifts (Thomas et al. 2012), there is an urgent need to evaluate the importance of the existing networks of conservation areas, now and in the future.

Many waterbird species are highly prized game species and millions are harvested annually throughout Europe (Hirschfeld & Heyd 2005). Redistribution of waterfowl species may affect population management in at least two different ways. Firstly, populations shifting toward the north will exhibit an apparent negative population trend in the south and a corollary, apparent positive population trend in the north (this study). Thus, shifts in the distributions of populations may induce bias in monitoring schemes, and, if not taken into account, may lead to management decisions being made on basis of false information. This effect may be of special importance in the north, where large, apparent population increases may lead to loosened harvesting restrictions, despite populations not actually increasing (or even decreasing), but merely being redistributed in winter during the hunting season. Secondly, the redistribution of one species of waterfowl may have repercussions on the hunting pressure of others. For example, if an abundant quarry species becomes locally rare due to climate driven redistribution, this could shift harvesting pressure to alternative species. On the other hand, a locally rare species may become abundant as a result of climate change, increasing the hunting pressure on that particular species. Such harvesting pressure interactions between species have not yet been recorded in hunting, but they have been suggested to occur in fisheries.
(Cheung et al. 2012). Thus, both local and international wildlife management schemes will need to unite their efforts to monitor the flyway-wide population sizes of waterfowl, as well as the species-specific bag sizes, to avoid overexploitation of locally common species.

Species-specific range shifts may lead to altered interactions both between and within species, either through competition or through changed predator-prey interactions (Bretagnolle & Gillis 2010). The changes in abundance we have documented in this study are likely to affect inter- and intraspecific competition, as all three species are now exploiting winter food resources that were formerly denied them by ice, and hence inaccessible before spring. Several duck species show sexual segregation in wintering areas (e.g. Carbone & Owen 1995), which may lead the sexes to exhibit differential responses to climate change. Such sex-specific effects of climate change may lead to alterations in global sex ratios through differential exposure to mortality (Lehikoinen et al. 2008). The densities of natural predators increase towards the south (Guillemain et al. 2007), wherefore the sex migrating further south may experience increased predation mortality. This predatory pattern may, together with the energetic costs of migration, be a fundamental reason why waterbirds winter as far northeast as climatic conditions allow. We encourage further studies to examine how the effects of waterfowl distribution shifts may ripple through wetland ecosystems, affecting for example, waterfowl species interactions, different predator guilds and hunting bag sizes. Such monitoring efforts need to be put in at both the national and the flyway-levels in order to accurately assess the potential population consequences that may occur as a result of range shifts.
We conclude that the three European duck species examined here have shown rapid northeastward shifts in their wintering distributions, and an exponential increase in abundance at the northeastern edge of their flyways, as a direct response to increased temperatures. These findings show that climate-driven changes in animal distributions may be rapid, are currently ongoing and call for urgent conservation and management actions, as well as further research into the effects of climate change in animal distributions.
Acknowledgements

We acknowledge the selfless contribution of many thousands of volunteers that have collected and submitted waterfowl count data upon which we based our analyses. We also thank all coordinators of the national monitoring programmes to whom data have been submitted. Antti Halkka helped with accessing the Climate Explorer. This project was supported by the NordForsk Top Research Initiative Nordic Waterbirds and Climate Network (NOWAC). The Dutch waterbird census scheme is part of a governmental ecological surveillance (‘NEM’), carried out in association with Dutch Statistics and supported by Dutch Ministry of Economic Affairs and the Ministry of Infrastructure and the Environment. The UK’s Wetland Bird Survey is a partnership of the British Trust for Ornithology, Royal Society for Protection of Birds and Joint Nature Conservation Committee, in association with Wildfowl and Wetlands Trust. The Swiss waterbird census is supported by the Federal Office for the Environment. In Germany the waterbird census is supported by the Federal Nature Conservation Agency (BfN) within the national bird monitoring framework. In Finland, Ministry of Environment has funded winter bird censuses in Åland Islands. It was funded by the Northern Ireland Environment Agency (NIEA) through the Natural Heritage Research Partnership (NHRP) with Quercus, Queen’s University Belfast (QUB) and an Aarhus University AGSoS PhD School Visiting Grant. ADF was part funded by the Danish Nature Agency. KJ was funded by The Finnish Cultural Foundation and The Academy of Finland (grant no. 128039).
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Appendix I

Climate change and migratory short-stopping


Lehikoinen A, Christensen TK, Öst M et al. (2008) Large-scale change in the sex ratio


Appendix I  

Climate change and migratory short-stopping


Supplementary Fig. 1 Early winter temperature in North Europe. a) The spatial correlation of December temperature in southern Finland (defined within the black line on the map) during years 1979 to 2009 based on Climate Explorer of the Royal Netherlands Meteorological Institute (http://climexp.knmi.nl). b) The mean early winter (16 November to 15 January) temperature in southern Finland (defined in map b; mean of daily means of all 10 x 10 km grids in the study area) during winters 1979/1980 to 2009/2010. The line represents the increasing trend in temperature (beta = +0.12 ± 0.06 °C, F = 4.85, df = 29, P = 0.035).

Suppl. Table 1 AICc differences of two different models (Model 1 = direct effect of temperature, Model 2 = temperature difference between two subsequent years) in each country in tufted duck, goldeneye and goosander. Models where ΔAICc was larger than 2 are bolded.

<table>
<thead>
<tr>
<th>Area</th>
<th>Years</th>
<th>Tufted duck</th>
<th>ΔAIC</th>
<th>Goldeneye</th>
<th>ΔAIC</th>
<th>Goosander</th>
<th>ΔAIC</th>
</tr>
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<td></td>
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<td></td>
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<tr>
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<td>n = 31</td>
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<td>Model 1</td>
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<td>Model 2</td>
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<td>1.63</td>
<td>Model 1</td>
<td>0.16</td>
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<td>G. Britain</td>
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<td>Model 1</td>
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<td>0.02</td>
<td>Model 2</td>
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<td>n = 31</td>
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Appendix II

Gizzard contents and morphometrics of overwintering diving ducks shot at Lough Neagh

This appendix was published as:

Appendix II  Gizzard contents and morphometrics

The Lough Neagh Special Protection Area (SPA) is the most important non-estuarine site in Britain and Ireland for overwintering diving ducks (Crowe 2005). Population changes between the winters of 1996/97 and 2006/07 in tufted duck (Aythya fuligula L. 1758) (-69%) and goldeneye (Bucephala clangula L. 1758) (-44%) have triggered a high alert (declines exceeding 50%) and a medium alert (declines between 25-50%) respectively, however, the scaup (Aythya marila L. 1761) population has increased (+77%; BTO 2010).

Lough Neagh is the largest freshwater lake in Britain and Ireland (surface area 383km²) with a mean depth of 8.9m (Wood & Smith 1993). The invertebrate fauna of Lough Neagh is dominated by chironomid larvae and to a lesser extent by oligochaeta worms (Carter 1978). Diving ducks on the lough feed primarily on chironomid larvae and molluscs (Winfield & Winfield 1994b) and it is hypothesized that temporal changes in the benthic invertebrate community within the lough may have contributed to duck population declines. As part of a larger study, we took the opportunity to collect carcasses of shot ducks during winters 2008-09 and 2009-10 to examine their oesophagus and gizzard contents. A total of 6 tufted duck, 4 scaup and 9 goldeneye was collected from wildfowlers and dissected (n=19). Morphometric measurements were also recorded. Eighteen of the ducks (95%) contained no prey items in either their oesophagus or gizzard. Four chironomid larvae identified as Glyptotendipes ssp. were found in the gizzard of a male goldeneye.

Morphometric measurements for the ducks whose sex could be accurately determined based on plumage characters (n=16) are given in Table 1. Large quantities of small stones and grit ranging from 2.0 to 9.4 g were recovered from all gizzards examined. In one case, 0.1 g of grit was recovered from the oesophagus of a male goldeneye. The total mass of stones in each gizzard and the maximum mass of
any one stone was positively correlated with duck body mass (Spearman’s rho = 0.508, \( p=0.044, n=16 \) and Spearman’s rho = 0.631, \( p=0.009, n=16 \) respectively). In general, males were heavier than females and their gizzards contained more grit (Table 1). The total mass of stones recovered from each bird was also positively correlated with bill length (Spearman’s rho = 0.555, \( p=0.026, n=16 \)). Incidentally, body mass was positively correlated with wing length (Spearman’s rho = 0.821, \( p<0.001, n=19 \)), however, bill length was not correlated with any other morphometric measure.

Clearly stones and grit are an important component of diving duck digestion for grinding up food. Diving ducks have a limited capacity to store food in the digestive tract (De Leeuw 1999) and, with the exception of goldeneye, feed predominantly at night (Evans & Day 2001). Thus, ducks shot during the day are of limited value for stomach contents analysis. Other methods, such as stable isotope analysis (Inger & Bearhop 2008) or stomach contents analysis of accidental captures in gill nets, are recommended for future studies of diet.

Table 1 Morphometric measurements (mean ± standard deviation) for male and female diving ducks sampled at Lough Neagh during 2008-09 and 2009-10.

<table>
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<tr>
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<th>Goldeneye</th>
<th>Scaup</th>
<th>Tufted duck</th>
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<tr>
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<td>0.15</td>
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<td>Total mass of stones in gizzard (g)</td>
<td>2.5 ± 0.1</td>
<td>6.4 ± 2.3</td>
<td>2.9 ± 0.8</td>
</tr>
<tr>
<td>Body mass (g)</td>
<td>630 ± 57</td>
<td>1,013 ± 153</td>
<td>780 ± 28</td>
</tr>
<tr>
<td>Wing length (mm)</td>
<td>196 ± 7</td>
<td>226 ± 2</td>
<td>194 ± 5</td>
</tr>
<tr>
<td>Bill length (mm)</td>
<td>28.9 ± 0.6</td>
<td>44.2 ± 2.2</td>
<td>37.5 ± 1.1</td>
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