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Shifts in fine-scale distribution and breeding success of boreal waterbirds along gradients in ice-out timing and habitat structure

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Abstract

1. Climate change and other anthropogenic stressors affect freshwater ecosystems worldwide. A prominent manifestation of climate change impacts on aquatic systems at high latitudes is the advance of ice-out date (IOD). Earlier IOD should be advantageous for species such as migratory waterbirds that are dependent on open water to initiate breeding; earlier breeding usually means higher reproductive success.
2. However, advance of IOD may induce phenological mismatches that have negative impacts on the species involved. This may alter habitat dynamics, challenging habitat selection by breeding individuals. An additional challenge is imposed by changes in habitat quality, particularly if preferred habitats deteriorate.
3. Here, we investigated how the fine-scale distribution of breeding individuals and breeding success have changed along gradients in IOD and habitat structure (richness of emergent vegetation) in a boreal waterbird assemblage in southeastern Finland from 1991 to 2018.
4. IOD varied considerably between nearby lakes. The distribution of breeding individuals of the common teal (*Anas crecca*) and horned grebe (*Podiceps auritus*) shifted toward lakes with relatively late IOD while Eurasian wigeon (*Mareca penelope*) and tufted duck (*Aythya fuligula*) shifted toward lakes with sparse emergent vegetation. Also, breeding success in common teal showed a decreasing trend at lakes with relatively early IOD, while it increased on lakes with relatively late IOD. Success in tufted duck breeding decreased on lakes with rich emergent vegetation, while the opposite was true on lakes with sparse emergent vegetation. The mallard (*Anas platyrhynchos*) was the only species that did not show a shift in breeding distribution or breeding success along either of the environmental gradients.
5. The findings suggest that a potentially positive climate-driven impact on breeding phenology (earlier IOD) was over-ridden by negative changes in habitat quality. The results underline the need to understand the complexity of the effects of multiple stressors in boreal freshwater ecosystems for their successful management.

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KEYWORDS

climate change, habitat quality, habitat selection, migratory species, waterfowl

1 | INTRODUCTION

Global climate change has impacted species and their habitats in terrestrial and aquatic ecosystems throughout the globe. Numerous studies have documented shifts in species' phenologies, such as advancement of flowering in plants and spring migration and breeding in birds (Parmesan & Yohe, 2003; Walther et al., 2002). Changes in geographical distribution of species due to climate change are also widely documented (Chen et al., 2011; Parmesan & Yohe, 2003; Pecl et al., 2017). Less attention has been paid to climate change impacts on fine-scale distribution of individuals and how these impacts may affect demographic rates of populations. Still, local effects on niche breadth and plasticity may fundamentally affect forecasts of species site occupation and range shifts under a warming climate (Peterson et al., 2019; Valladares et al., 2014).

Freshwater ecosystems are particularly vulnerable to global changes such as climate change, eutrophication and land-use change (Dudgeon et al., 2006; Heino et al., 2009; Reid et al., 2019). The highest concentration of freshwater bodies occurs in boreal and arctic latitudes (Verpoorter et al., 2014). Climate change has been identified as the main threat to freshwater biodiversity at these latitudes, although other anthropogenic stressors may also play an important role (Heino et al., 2009; Yeung et al., 2019). One of the prominent manifestations of climate change impacts in these areas is the decreased period of ice cover in lakes (Benson et al., 2012; Sharma et al., 2019). Ice breakup is occurring earlier throughout the Northern Hemisphere (Benson et al., 2012; Lopez et al., 2019; Magnuson et al., 2000), although the sensitivity of lakes to global warming may differ between regions (Weyhenmeyer et al., 2011). The inter-annual dynamics of ice breakup are usually coherent between lakes within a region, but the date of ice breakup within a year may still differ considerably between nearby lakes (Arp et al., 2013; Magnuson et al., 2004). However, local variation in the timing of ice-out and, particularly, its consequences for the distribution and reproductive success of species dependent on ice-free conditions, have not been studied.

The timing of ice breakup not only determines habitat availability for species dependent on open water but also affects the fundamental processes in aquatic ecosystems and food webs (Berger et al., 2014; Prowse et al., 2011; Thackeray et al., 2013). For example, lake ice has a controlling influence on water temperature, and earlier ice breakup causes earlier and stronger thermal stratification and increases the period over which the lake warms over the summer months (Austin & Colman, 2007; Winder & Schindler, 2004). These changes affect the dynamics of primary production and increase the risk of algal blooms, particularly in nutrient-rich lakes (Winder & Schindler, 2004), with fundamental implications to lake food webs and the functioning of aquatic freshwater ecosystems

(Shuvo et al., 2021; Woolway et al., 2020). Hence, changes and local variation in the timing of ice breakup may critically alter habitat dynamics and quality, thus challenging the habitat selection of species dependent on open water. This is particularly the case with migratory species such as waterbirds breeding at high latitudes, where the timing of ice breakup may affect the onset of breeding and, hence, reproductive output. However, temporal ice dynamics are obviously not the only factor determining the suitability of a lake for waterbirds. For example, many species breeding in boreal areas show a strong affinity to lakes with rich and complex emergent vegetation (Elmberg et al., 2020; Kauppinen, 1993; Nummi & Pöysä, 1993), with rich vegetation affording cover for nests and probably reflecting profitable forage conditions. On the other hand, shallow lakes with rich emergent vegetation typically are eutrophic (Ranta & Toivonen, 2008; Toivonen & Huttunen, 1995), and the amount of emergent vegetation, such as the extent of common reed (*Phragmites australis*) beds, generally provides a useful indicator of the ecological status of lakes under human-caused eutrophication (Kolada, 2016; Lawniczak-Malińska & Achtenberg, 2018). It has been found for boreal lakes in Finland that naturally eutrophic lakes are more sensitive to anthropogenic stressors, such as fertiliser inputs, than nutrient-poor, oligotrophic lakes (Tammelin & Kauppila, 2018). Moreover, a recent analysis suggests that total phosphorous and total nitrogen loads originating from diffuse sources, especially those from agriculture, have not decreased in Finland during the recent decades (Räike et al., 2020). This suggests that the ecological status of eutrophic lakes in Finland has not improved despite considerable water protection measures (Räike et al., 2020). The finding that waterbird species and populations associated with eutrophic lakes have decreased more than those breeding on oligotrophic lakes points in the same direction, suggesting that the quality of eutrophic lakes as a breeding habitat has decreased (Lehikoinen et al., 2016; Pavón-Jordán et al., 2017; Pöysä et al., 2013; see also Elmberg et al., 2020; Pöysä et al., 2019).

Here, we study the impacts of changes in ice-out date (IOD) in spring on the local distribution of breeding individuals in a boreal waterbird community in southeastern Finland. We will also consider possible habitat structure-dependent shifts in local distribution while doing this. Consistent with the findings from a wide range of high-latitude lakes (see above), ice breakup in the lakes in this area has become progressively earlier during the last 3 decades (Pöysä, 2019). Given this long-term trend and considering the gradual increase of temperature during the spring months (Mikkonen et al., 2015), impacts of continuously advancing IOD may change in lakes with very different average breakup dates. In this paper, we will first study whether the lakes in the area differ in the timing of ice breakup. Considering that many waterbirds breeding in boreal areas track year-to-year variation in IOD and occupy

individual lakes soon after ice breakup (Oja & Pöysä, 2007; Pöysä, 1996, 2019; Väisänen, 1974), we studied (1) whether the distribution of breeding individuals has changed with respect to the timing of ice breakup (i.e. shift along the IOD gradient). For example, if the timing of ice breakup has advanced strongly, migratory waterbirds may not have been able to match their arrival with the IOD in the earliest lakes, probably resulting in changes in the local (between-lake) distribution of breeding individuals (i.e., proportionally more individuals may settle in lakes with later ice breakup). Changes in breeding distribution may also result if impacts of climate warming on ecological conditions differ between lakes with early versus late ice breakup, potentially resulting in phenological mismatches that reduce reproductive output (Durant et al., 2007; Thackeray et al., 2013). Furthermore, we may expect that the habitat-specific, broad-scale population trends of waterbirds in Finland (i.e., overall decline in eutrophic lakes but not in oligotrophic lakes; see above) are reflected locally as changes in the habitat distribution of breeding individuals, because broad-scale population trends generally mirror processes operating at the local level, particularly habitat selection and individuals' breeding performance (Pulliam, 1996; Pulliam & Danielson, 1991). Hence, considering the eutrophic status-indicator function of rich emergent vegetation and the overall decline of waterbirds at eutrophic lakes (see above), we studied (2) whether the distribution of breeding individuals has shifted toward lakes with less rich emergent vegetation (i.e., shift along a habitat structure gradient). Finally, because changes in population size often stem from changes in reproductive output (Coluccy et al., 2008; Hoekman et al., 2002) and may be associated with changes in the timing of breeding or the quality of habitat (Arzel et al., 2014; Drever & Clark, 2007), we examined (3) if breeding success, measured as the number of broods, has changed with respect to IOD and habitat structure gradients. The measure of breeding success in this study captures changes in total brood loss, being caused, for example, via increased nest and duckling predation or via impaired feeding conditions for newly hatched ducklings, increasing mortality.

2 | METHODS

2.1 | Study area and species

The study area in southeastern Finland (61°35N, 29°40E; see Figure S1 for a map of the study area and location of the study lakes) is about 59 km² (the area of a four-sided polygon within which all study lakes are situated) and dominated by pine *Pinus sylvestris* L. or mixed (pine, birch *Betula* spp., and spruce *Picea abies* (L.) Karst) forests interspersed with lakes of varying size and luxuriant, emergent vegetation (see Pöysä, 2001). The 37 study lakes (mean size 3.5 ha, range 0.05–24.0 ha) are covered by ice during winter, have a relatively stable water level in summer and are only used by waterbirds for breeding. Hence, waterbirds breeding in the study area are migratory, and the habitat selection process is repeated

each spring. The maximum distance between any two of the 37 lakes is 11.8 km.

We focused on five ground-nesting species in this paper, viz. the horned grebe (*Podiceps auritus*), the Eurasian wigeon (*Mareca penelope*), the common teal (*Anas crecca*), the mallard (*Anas platyrhynchos*), and the tufted duck (*Aythya fuligula*). Based on breeding densities and habitat distribution, all these species show a preference for eutrophic lakes with rich emergent vegetation (Elmberg et al., 2020; Kauppinen, 1993; Kauppinen & Väisänen, 1993). The mallard and common teal are early settling species, while the tufted duck and horned grebe are late settlers; the Eurasian wigeon is somewhere between these two groups (Pöysä, 2019). These are the most abundant ground-nesting waterbird species in the study area (Pöysä, 2019) and generally represent the core species in boreal waterbird communities (see Elmberg et al., 2020; Pöysä et al., 2019).

2.2 | Waterbird and IOD data

Annual (1991–2018) lake-specific bird and IOD data are from Pöysä (2019) in which all the methodological details are explained. While Pöysä (2019) addressed relationships between IOD and the phenology of settling and breeding success using landscape-level data, this study uses lake-level data and focuses on processes that take place within the landscape. A standard waterbird point count was made (Koskimies & Väisänen, 1991; see also Koskimies & Pöysä, 1989) on each lake four times in April–May at an interval of approximately 7 days (mean survey interval = 7.0 days, SE = 0.1) each year from 1991 to 2018. In the point count, a lake is surveyed for waterbirds from one or more fixed vantage points so that all the shoreline and open water areas are visible and carefully observed. All lakes were monitored within a few days (mean range 2.5 days, SE = 0.1) on each of the four surveys. The first survey in each year coincided with an early stage of ice breakup in the study area (i.e., some lakes had some open water, while other lakes were still fully ice covered), while all the lakes were free of ice during the last (fourth) survey (see below and Supplementary material appendix 1 figure A1 in Pöysä, 2019). Waterbird observations from each survey and lake were interpreted as *pair numbers* using the species-specific criteria of Koskimies and Väisänen (1991; a summary of the species-specific criteria is presented in Table S1; see Dzubin, 1969, and Kauppinen, 1983, for further information). The annual number of breeding pairs for each species and lake was estimated as the mean of the pair numbers from the survey when the lake was free of ice and the survey before or after the ice-free survey, whichever had a higher pair number; i.e., in each year and for each species and lake, data from two consecutive surveys, adjusted to year-specific timing of ice breakup, were used to estimate the annual number of breeding pairs.

Three brood surveys were made on the lakes each year between mid-June and late July/early August using the standard waterbird point count method to obtain a habitat-specific demography measure (Koskimies & Väisänen, 1991). The total number (sum) of broods

from the three surveys was calculated for each species, lake, and year. A *brood* means a separate group of unfledged ducklings of any age, with or without a female. The total number of broods from the three surveys was used to measure breeding success (see below), although we did not identify broods individually.

During each of the four waterbird surveys in April–May (see above), the progress of the breakup of ice cover on each lake was marked on a field map and later scored as follows (open water score; see Pöysä, 1996): 0 = lake fully ice-covered; 1 = small openings along shoreline, central parts fully ice-covered; 2 = half of the shoreline open, central parts fully ice-covered; 3 = more than half of the shoreline open; central parts partially (<50%) open; 4 = shoreline fully open, small ice rafts or scattered build-ups; 5 = lake fully open. An annual IOD for each lake was estimated as the mean of the dates of two consecutive surveys when the open water scores were 4 and 5; if the lake was already free of ice (score 5) during the first visit, the IOD was estimated as the date of the first survey minus 3.5 days (i.e., the mean difference in days between two consecutive surveys divided by 2).

The IOD gradient consisted of lake-specific average IODs; the 37 IODs were first centred within each year and mean of the lake-specific centred IOD values from 1991 to 2018 was calculated and used for each lake (see Figure S2 for photos illustrating differences between lakes in IOD). Note that, because the lakes were free of ice when lake-specific pair numbers were derived for each species (see above), between-year variation in IOD per se could not affect the distribution of individuals along the IOD gradient.

2.3 | Habitat structure

We used the lake-specific habitat structure index in Pöysä (2001), which is based on the abundance of emergent (helophyte) and floating-leaved vegetation and shore water depth (the index was developed in Elmerg et al., 1993; Nummi & Pöysä, 1993). Details of vegetation classification and field procedures are described in Nummi and Pöysä (1993). In brief, the structure of emergent vegetation along the shore line of each lake was described using six variables for the type of the vegetation—(1) forest and bog, (2) *Phragmites* on dry land, (3) *Carex* on dry land, (4) *Phragmites*, (5) *Carex*, (6) *Equisetum/Typha*; shores belonging to the first three types did not have clear zones of emergent vegetation extending to the water, whereas types 4–6 did—and four variables for both the width—(1) 0–1 m, (2) 1–5 m, (3) 5–10 m, (4) >10 m—and height—(1) 0–25 cm, (2) 25–50 cm, (3) 50–100 cm, (4) >100 cm—of the vegetation. The cover of floating vegetation was estimated using four classes: (0) 0%, (1) 1%–5%, (2) 5%–15%, (3) >15%. Water depth was measured at the distance of 0.5 m from the shoreline, the number of measurement sites per lake varying from 5 to 10 depending on lake size. The mean of these measurements was used to classify the shore water depth of each lake as one of the three classes: (1) 0–50 cm, (2) 50–100 cm, (3) >100 cm. We used principal component analysis (Pimental, 1979) to derive a single gradient of habitat

structure, along which the lakes were ordered (i.e., habitat structure gradient). The first principal component (PC) axis represented a gradient from deep-shore lakes with low and narrow belts of sparse, emergent vegetation and little floating-leaved vegetation (high negative values on the first PC axis) to shallow-shore lakes with tall, wide and heterogeneous emergent vegetation and abundant floating-leaved vegetation (high positive values on the first PCA axis), the mean of the 37 lake-specific values being zero (range from –3.117 to 4.218; see Table S2 for variable component loadings and Figure S3 for photos illustrating differences in habitat structure between lakes; see also Elmerg et al., 1993; Nummi & Pöysä, 1993). Specifically, lakes with a high positive score typically had large stands of common reed, water horsetail (*Equisetum fluviatile*), broadleaf cattail (*Typha latifolia*), or sedges (*Carex* spp.), whereas lakes with a strongly negative score were characterised by shores with barren moraine and forest or narrow belts of poor bog or open fen. Hence, this habitat index reflects the eutrophic status of the lakes (Kolada, 2016; Lawniczak-Malińska & Achtenberg, 2018; Toivonen & Huttunen, 1995). The habitat index has been successfully used in studies addressing habitat quality as well as habitat affinity and distribution of breeding waterbirds and species richness in waterbird communities in boreal landscapes (Elmerg et al., 1993, 2020; Nummi & Pöysä, 1993; Pöysä, 2001; Pöysä et al., 2019; Suhonen et al., 2011). Moreover, Suhonen et al. (2011) found few long-term changes (between 1989 and 2009) in relative distribution of lakes along this habitat structure gradient in another study area in southern Finland, indicating that the habitat index is robust enough also for long-term studies (see also supplementary information in Pöysä et al., 2019).

2.4 | Statistical analyses

Kendall's coefficient of concordance was used to study whether the ranking of the lakes in terms of IOD was consistent throughout the 28 years of the study. Considering the bird data, we were particularly interested in the question whether the distribution of breeding individuals and broods on the IOD and habitat structure gradients showed a directional shift over the study period (1991–2018). In the case of breeding individuals (pair abundance data), we fitted for each species a model in which *year*, *IOD*, and *habitat structure* were included as main effects and *year*IOD* and *year*habitat structure* as interaction terms. Brood models had a similar structure, except that *pair number* was included as an additional fixed effect to account for variation in breeding numbers as lake-specific pair numbers may affect lake-specific brood numbers. Site (lake) identity was included as a random effect in all models. Year was expressed as a series of numbers running from 1 (1991) to 28 (2018), while habitat structure and IOD values were z-transformed (standardised and centred) for the analyses. In a priori diagnostics, we inspected the data and tested several error distributions to optimise model performance (e.g. no convergence problems) and to find the most appropriate modelling approach in each

case (Brooks et al., 2017; Ives, 2015; Warton et al., 2016). It turned out that linear mixed-effects models (LMMs) with $\log(x + 1)$ transformed response (pair number) and Gaussian distribution worked best for the pair abundance data and we used the LMM (function `lme` in package `nlme` version 3.1.151; Pinheiro et al., 2017, see also Pinheiro & Bates, 2000) for pair number analyses. Residuals of full models were visually inspected for the functionality of the models. In the brood data, we found serious excess of zero counts in all species. Therefore, for the brood abundance data, we used zero-inflated generalised linear mixed-effects models assuming negative binomial distribution and the most simple one parameter model (intercept) for zero inflation (i.e., ZINB modelling approach; family = `nbinom1` and `zi = ~1`, package `glmmTMB` version 1.0.2.1; Brooks et al., 2017). Simple ZINB settings appeared to be a robust approach and were used in all brood analyses. The dispersion and residuals of all full models was checked using the `DHARMA` package (version 0.4.1; Hartig, 2018) and functions `testDispersion()` and `testUniformity()` (see also Brooks et al., 2019). We checked collinearity between the predictor variables by calculating variance inflation factors for each predictor in different models; collinearity appeared not to be a problem as all variance inflation factors were <1.69 (Table S3). Spatial autocorrelation of residuals for each full model was checked with Moran I test for each species-specific pair and brood data; no statistically significant spatial autocorrelation was detected (Table S3). We used the simple slope analyses tool in package `interactions` (version 1.1.3) and function `interact_plot()` for visual inspection of statistically significant interaction terms in the models. In the plots, the interactions between the continuous parameter (i.e. $year \times IOD$ and $year \times habitat\ structure$) were expressed by holding all other predictors in their mean and setting meaningful values for the interaction terms; i.e., mean (zero) and mean ± 1 standard deviation were used for the standardised values of the environmental gradients (IOD and habitat structure). We let the function `interact_plot` find the appropriate scale for the responses in each case. Note, that back transformed responses of a ZINB model (log-link) are not linear and the responses of pair numbers are log scaled according to the original LMM. All statistical analyses were carried out in R version 4.0.2. (R Development Core Team, 2020).

3 | RESULTS

3.1 | Variation in IOD

Ice-off day varied considerably between lakes, with the difference between the earliest (24 April) and latest (6 May) mean IOD being 12 days (lake-specific mean IODs calculated over the whole study period). There was a strong concordance in the order of lakes along the early-late IOD continuum across the study years (coefficient of concordance, $W = 0.548$; $\chi^2 = 552.38$, $df = 27$, $p < 0.001$); in other words, a lake with relatively early IOD in year t had relatively early IOD also in year $t + n$.

3.2 | Relationship between IOD and habitat structure

There was a relationship between the two gradients (IOD gradient vs. PC axis 1 score on the habitat structure gradient: $r = -0.527$, $df = 35$, $p = 0.001$); lakes with early IOD had a more complex habitat structure (rich emergent vegetation) than lakes with late IOD.

3.3 | Shifts of breeding pairs along IOD and habitat structure gradients

The mean number of breeding pairs per lake and year during 1991–2018 ($n = 1,036$ lake-year cases) varied from 0.2 (range 0–4) in the horned grebe to 0.6 (range 0–8) in the mallard, the other three species having mean values between these two. Long-term changes in the distribution of breeding individuals along the IOD gradient varied depending on the species. The distribution of breeding individuals among the common teal and horned grebe shifted toward lakes with relatively late IOD over the 28-year study period (Table 1). Specifically, while there was no overall decline in the breeding abundance of the common teal, breeding numbers on lakes with early IOD decreased, whereas those on lakes with late IOD increased (Figure 1). Breeding abundance of the horned grebe in turn showed an overall decline during 1991–2018; however, the decline was apparent only on lakes with relatively early IOD (Figure 1). The other species showed no statistically significant directional shift along the IOD gradient (Table 1).

The species showed differences in long-term shifts along the habitat structure gradient, as with the IOD gradient. No statistically significant directional change was found in the common teal, mallard, and horned grebe (Table 1), while the distribution of breeding individuals of the Eurasian wigeon and tufted duck shifted toward lakes with poor emergent vegetation (Table 1; Figure 1). In the Eurasian wigeon, breeding abundance showed contrasting trends between lakes with rich emergent vegetation and lakes with poor emergent vegetation: decrease on the former and increase on the latter. In the tufted duck, breeding numbers declined more on lakes with rich emergent vegetation than on lakes with poor emergent vegetation.

3.4 | Shifts of broods along IOD and habitat structure gradients

The mean number of broods per lake and year during 1991–2018 ($n = 1,036$ lake-year cases) varied from 0.04 (range 0–7) in the tufted duck to 0.2 (range 0–7) in the mallard. Brood abundance models included the variable *pair number* as a fixed effect; hence, the effect of pair number on brood abundance was controlled for, and brood abundance as such can be considered as a measure of breeding success. Success in common teal breeding showed a decreasing trend

TABLE 1 Linear mixed-effects models for testing changes in the abundance of breeding pairs with ice-out date (IOD) and habitat structure (Habitat) gradients over the study years, 1991–2018, for five waterbird species ($n = 1,036$ for each species; 37 lakes, 28 years)

Species	Year	IOD	Habitat	Year*IOD	Year*Habitat
<i>Horned grebe</i>					
β	-0.0015	-0.1047	0.0194	0.0013	-0.0005
SE	0.0005	0.0459	0.0459	0.0006	0.0006
t	-3.062	-2.283	0.423	2.210	-0.883
p	0.002	0.029	0.675	0.027	0.378
Full model versus null model:			$\chi^2 = 23.266$, $df = 5$, $p = 0.0003$		
<i>Eurasian wigeon</i>					
β	-0.0002	0.0150	0.1770	-0.0010	-0.0027
SE	0.0009	0.0384	0.0384	0.0011	0.0011
t	-0.260	0.390	4.606	-0.989	-2.535
p	0.795	0.699	0.0001	0.323	0.011
Full model versus null model:			$\chi^2 = 22.169$, $df = 5$, $p = 0.0005$		
<i>Common teal</i>					
β	0.0013	-0.0298	0.2039	0.0032	-0.0028
SE	0.0013	0.0499	0.0499	0.0015	0.0015
t	1.027	-0.597	4.088	2.099	-1.811
p	0.305	0.555	0.0003	0.036	0.070
Full model versus null model:			$\chi^2 = 11.576$, $df = 5$, $p = 0.041$		
<i>Mallard</i>					
β	0.0038	0.0214	0.2314	0.0012	-0.0001
SE	0.0013	0.0540	0.0540	0.0015	0.0015
t	2.942	0.396	4.287	0.773	-0.051
p	0.003	0.694	0.0001	0.440	0.959
Full model versus null model:			$\chi^2 = 13.028$, $df = 5$, $p = 0.023$		
<i>Tufted duck</i>					
β	-0.0042	0.0013	0.1075	-0.0003	-0.0033
SE	0.0009	0.0384	0.0384	0.0011	0.0011
t	-4.544	0.033	2.798	-0.279	-3.024
p	0.0000	0.972	0.008	0.780	0.003
Full model versus null model:			$\chi^2 = 10.170$, $df = 5$, $p = 0.071$		

Note: While the focus was on the interaction terms Year*IOD and Year*Habitat, all main effects are given. Statistically significant effects are in bold. Likelihood-ratio chi-squared tests for differences between the full model and null model (a model including only the intercept) are also given.

on lakes with relatively early IOD, while it increased on lakes with relatively late IOD (Table 2; Figure 2). Success in tufted duck breeding in turn showed a decreasing trend on lakes with rich emergent vegetation, while the opposite was true on lakes with poor emergent vegetation (Table 2; Figure 2). No significant associations between long-term breeding success trend and IOD and habitat structure gradients were found in the other species (Table 2).

4 | DISCUSSION

Mean IOD varied considerably between nearby lakes, the greatest between-lake difference being 12 days; however, the order of lakes along the early-late IOD continuum across the study years

was consistent. Factors explaining differences between lakes in IOD are out of the topics of this study and will be addressed elsewhere (H. Pöysä, manuscript in preparation). Nevertheless, it is interesting to note that the between-lake variation in mean IOD is correlated with the richness of emergent vegetation in the lakes, the latter constituting another important environmental gradient for waterbirds breeding in boreal lakes (see below). This is a new finding as earlier studies exploring factors that could explain differences between lakes in mean IOD have not considered the role of aquatic vegetation but focused on other characteristics such as lake size and depth (e.g. Arp et al., 2013; Vavrus et al., 1996).

The degree of between-lake variation in IOD occurring at a local spatial scale (<12 km) should be biologically relevant to

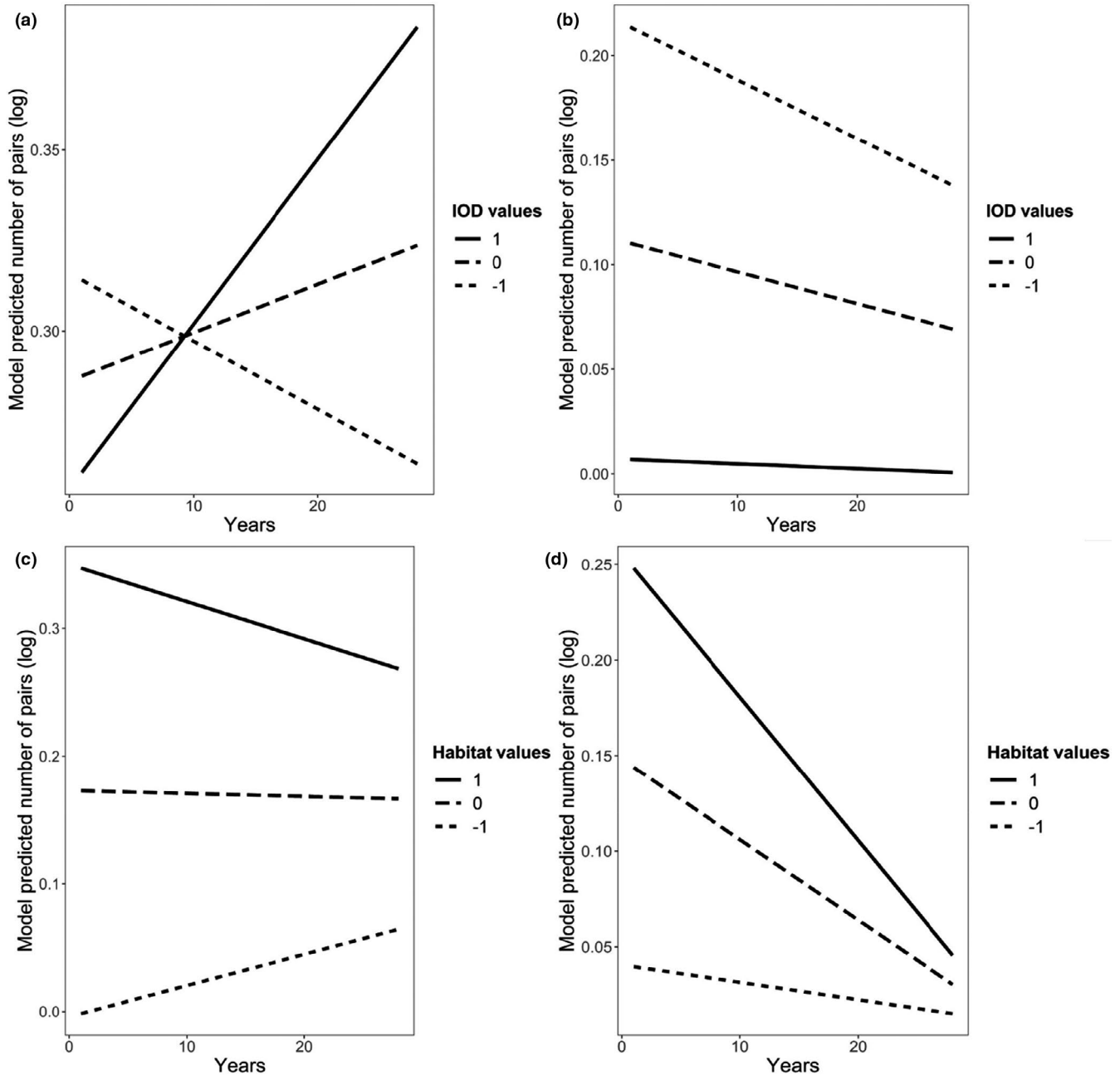


FIGURE 1 Plots of statistically significant interactions in linear mixed-effects models explaining changes in the distribution of breeding pairs along environmental gradients: (a) common teal, $year \times IOD$; (b) horned grebe, $year \times IOD$; (c) Eurasian wigeon, $year \times habitat$; (d) tufted duck, $year \times habitat$ (models are given in Table 1). Ice-out date (IOD) gradient values were fixed at 1 (lakes with late ice breakup), 0 (lakes with average ice breakup) and -1 (lakes with early ice breakup) and habitat structure gradient values were fixed at 1 (lakes with rich emergent vegetation), 0 (lakes with average emergent vegetation) and -1 (lakes with poor emergent vegetation). Note that the scale of the y-axes differs between the sub-figures. See Section 2.4 for further explanation

habitat-selecting migratory waterbirds, which are fully dependent on open water when preparing for breeding. That early IOD generally did not increase the attractiveness of lakes was surprising, given that the settling phenology of breeding individuals of all the studied species tracks closely with the year-to-year variation in IOD at the study area level (Pöysä, 2019) and considering that early breeding is generally advantageous in terms of reproductive success (Clark et al., 2014; Morrison et al., 2019; Verhulst & Nilsson, 2008). On the

contrary, the distribution of breeding individuals of the common teal and horned grebe shifted toward lakes with relatively late IOD. In the common teal, the shift of both breeding pairs and broods away from lakes with early IOD indicates that these lakes have become worse as breeding habitat. Given the large variation between the lakes in average IOD and considering that average IOD in the study lakes has advanced about 8 days between 1991 and 2018 (Pöysä, 2019), it is possible that negative impacts of climate warming have

TABLE 2 Generalised linear mixed-effects models for testing changes in the abundance of broods along ice-out date (IOD) and habitat structure (Habitat) gradients over the study years, 1991–2018, for five waterbird species ($n = 1,036$ for each species; 37 lakes, 28 years)

Species	Pair	Year	IOD	Habitat	Year*IOD	Year*Habitat
<i>Horned grebe</i>						
β	0.0530	-0.1539	-0.4930	0.2589	-0.0534	-0.0175
SE	0.2187	0.0759	1.5989	1.1837	0.0889	0.0375
z	0.242	-2.028	-0.308	0.219	-0.601	-0.465
p	0.809	0.043	0.758	0.827	0.548	0.642
Full model versus null model:				$\chi^2 = 20.893$, $df = 5$, $p = 0.0008$		
<i>Eurasian wigeon</i>						
β	0.2472	0.0060	-0.2301	1.0708	-0.0270	-0.0140
SE	0.0774	0.0279	0.5251	0.5218	0.0239	0.0226
z	3.196	0.214	-0.438	2.052	-1.128	-0.617
p	0.001	0.831	0.661	0.040	0.259	0.537
Full model versus null model:				$\chi^2 = 21.340$, $df = 5$, $p = 0.0007$		
<i>Common teal</i>						
β	0.1696	0.0078	-1.4871	0.4259	0.0575	-0.0152
SE	0.0628	0.0191	0.4654	0.3719	0.0231	0.0169
z	2.703	0.409	-3.195	1.145	2.489	-0.899
p	0.007	0.682	0.001	0.252	0.013	0.369
Full model versus null model:				$\chi^2 = 33.062$, $df = 5$, $p = 0.0000$		
<i>Mallard</i>						
β	0.1422	0.0027	0.0741	1.1819	-0.0162	-0.0140
SE	0.0560	0.0158	0.3836	0.3788	0.0174	0.0160
z	2.539	0.172	0.193	3.120	-0.932	-0.876
p	0.011	0.864	0.847	0.002	0.351	0.381
Full model versus null model:				$\chi^2 = 21.436$, $df = 5$, $p = 0.0006$		
<i>Tufted duck</i>						
β	0.0740	-0.0322	0.9116	2.2413	-0.0476	-0.1058
SE	0.0614	0.0363	1.2501	1.2064	0.0573	0.0441
z	1.204	-0.885	0.729	1.858	-0.830	-2.402
p	0.229	0.376	0.466	0.063	0.406	0.016
Full model versus null model:				$\chi^2 = 14.885$, $df = 5$, $p = 0.0101$		

Note: While the focus was on the interaction terms Year*IOD and Year*Habitat, all main effects are given. Statistically significant effects are in bold. Pair was included as a fixed effect to control for the effect of the number of breeding pairs on brood abundance. Likelihood-ratio chi-squared tests for differences between the full model and null model (a model including only the intercept) are also given.

been relatively stronger in early-IOD lakes than in late-IOD lakes. Considering possible climate change impacts, advanced IOD per se may have negatively affected ecological conditions in the lakes, for example, via phenological mismatches (e.g. Durant et al., 2007). Such mismatches are possible in freshwater ecosystems (Thackeray et al., 2013), but evidence is still limited for waterbirds breeding in boreal lakes (see Clark et al., 2014; Guillemain et al., 2013; Pöysä, 2019). However, several routes to such negative impacts are possible. For example, with the warming climate, the duration of ice cover in boreal lakes has shortened, both due to later ice freeze and earlier ice breakup (Hewitt et al., 2018; Sharma et al., 2019). This may have enhanced fish survival and increased fish abundance, resulting in higher fish predation on zooplankton and benthos

(Gyllström et al., 2005; Jeppesen et al., 2010). Increased competition for aquatic invertebrates between fish and common teal (e.g. Nummi et al., 2016) in early-IOD lakes may have forced the latter to move to late-IOD lakes. Furthermore, many aquatic invertebrates that are accessible and important food for nesting duck females start to increase in numbers soon after ice breakup and decline again towards the summer (Pehrsson, 1984). The abundance peak may have advanced in early-IOD lakes so much that common teal females no longer are able to use the dynamic food source efficiently, particularly if competition from other taxa such as fish and large invertebrate predators has increased. Impaired ability to use temporal peaks in food abundance in early-IOD lakes may also concern newly hatched common teal ducklings, for which emerging aquatic insects,

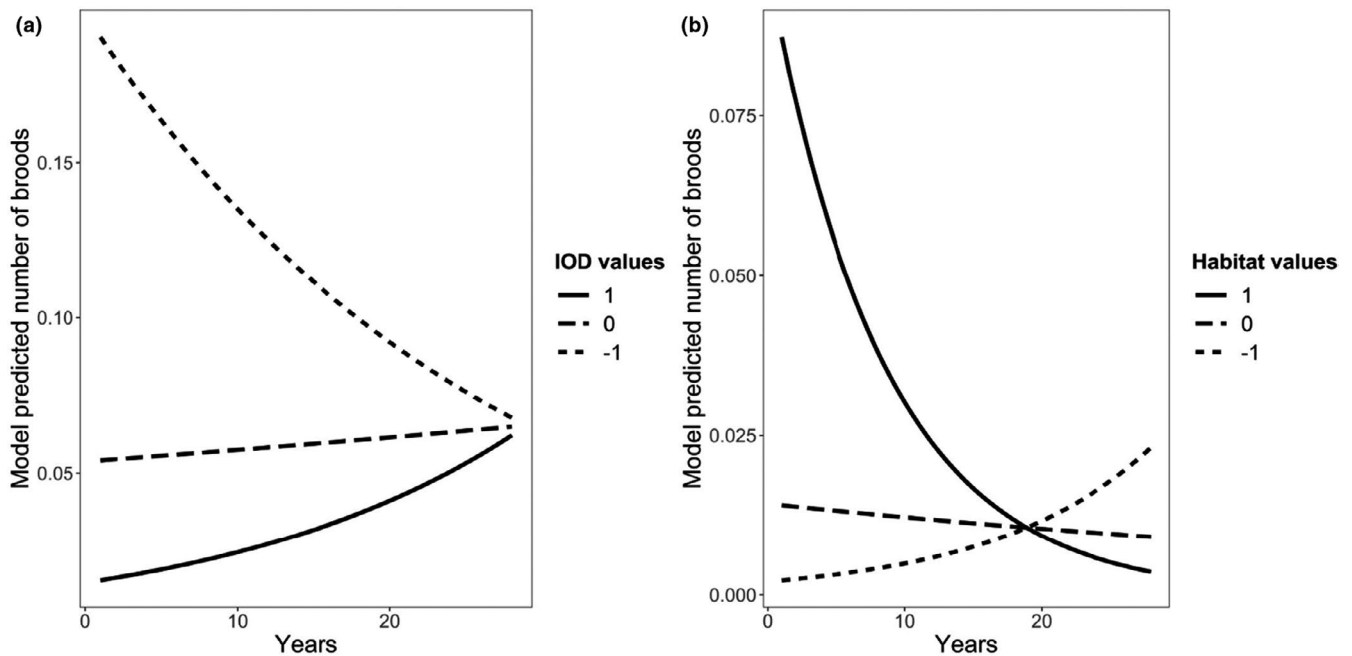


FIGURE 2 Plots of statistically significant interactions in generalised linear mixed-effects models explaining changes in the distribution of broods along environmental gradients: (a) common teal, $year \times IOD$; (b) tufted duck, $year \times habitat$ (models are given in Table 2). Ice-out date (IOD) gradient values were fixed at 1 (lakes with late ice breakup), 0 (lakes with average ice breakup) and -1 (lakes with early ice breakup) and habitat structure gradient values were fixed at 1 (lakes with rich emergent vegetation), 0 (lakes with average emergent vegetation) and -1 (lakes with poor emergent vegetation). Note that the scale of the y-axes differs between the sub-figures. See Section 2.4 for further explanation

especially Chironomidae, are an important food source (Danell & Sjöberg, 1980). It has been found that the peak emergence of chironomids either precedes or coincides with the hatching of ducklings in a shallow boreal lake in northern Sweden (Danell & Sjöberg, 1977; but see Dessborn et al., 1999). Whatever the actual impacts and mechanisms of earlier IOD are, the findings of this study suggest that common teal may be particularly vulnerable to climate warming-driven changes in boreal lake ecosystems. Clearly, more research on the role of changes in lake IOD in affecting the habitat distribution and breeding success of common teal is needed, particularly because breeding numbers of the species in Finland and probably elsewhere in boreal lakes are declining (Elmberg et al., 2020; Laaksonen et al., 2019).

That the breeding numbers of the horned grebe decreased more on early-IOD lakes than on late-IOD lakes amplifies the findings of Pöysä (2019). In that work, an overall population decline was demonstrated for the horned grebe, together with a negative impact of earlier IOD (measured at the study area level) on annual breeding success. The findings of this study in turn demonstrate that, while early-IOD lakes have been preferred by horned grebe pairs, ecological conditions particularly there have deteriorated, resulting in population decline. Increased nest predation may have been the main cause for the population decline of the horned grebe as discussed in Pöysä (2019).

The distribution of Eurasian wigeon and tufted duck pairs, in turn, shifted toward lakes with less rich emergent vegetation. The

observed shifts of breeding individuals of these species along the habitat structure gradient are in line with the prediction based on habitat-specific, long-term changes in breeding population sizes of waterbirds in Finland (Lehikoinen et al., 2016; Pavón-Jordán et al., 2017; Pöysä et al., 2013). Interestingly, breeding success of the tufted duck showed contrasting patterns along the habitat structure gradient: clear decrease on lakes with rich emergent vegetation but a slight increase on lakes with poor emergent vegetation. This suggests that lakes of the former type have lost attractiveness and quality as brood habitat.

Given that the IOD and habitat structure gradients were inter-correlated (i.e., lakes with early IOD had more rich emergent vegetation than lakes with late IOD), the findings concerning shifts along the two environmental gradients for different species together suggest that a presumably positive IOD-related impact (i.e., early IOD should allow earlier habitat settlement and breeding; Clark et al., 2014; Elmberg et al., 2005; Pöysä, 2019) was over-ridden by negative changes in habitat quality at lakes with rich emergent vegetation (and early IOD). Eutrophication and brownification (i.e. processes that affect water quality) probably have occurred in at least some of the lakes in the study area. For example, local fishermen have reported increased water turbidity and cyprinid fish abundance, both of which are associated with eutrophication (Rask et al., 2010). These changes could be due to diffuse nutrient loading from agriculture (lakes typically surrounded by arable land and having rich emergent vegetation) and forest cutting (lakes

typically surrounded by forests and having poor emergent vegetation). Forest cutting may also increase the amount of dissolved organic matter, causing browning of surface water (Kritzberg, 2017; Škerlep et al., 2019) with fundamental consequences for primary production and functioning of aquatic food webs (reviews in Creed et al., 2018; Kritzberg et al., 2020), including changes in the abundance of aquatic invertebrates that are a critical resource for breeding ducks and ducklings (Arzel et al., 2020). Finally, the effects of eutrophication and brownification on aquatic ecosystems may be accelerated by climate change via increased temperature and precipitation and shorter ice duration (Moss et al., 2011; Williamson et al., 2017; Woolway et al., 2020). The effects of these water-quality changes on waterbirds are not well known, but presumably they are mediated via impacts on the food web as discussed above in the case of common teal.

Interestingly, the mallard was the only species that did not show a shift along either of the environmental gradients for either of the studied life stages (i.e. breeding pairs and broods). Amongst the five species studied here, mallard is the only species that has a stable or increasing long-term population trend in Finland, breeding numbers of all the other species show a long-term decrease (Laaksonen et al., 2019; Lehikoinen et al., 2016; Pöysä et al., 2013). Breeding numbers of the mallard have also been relatively stable in other Nordic countries (Dalby et al., 2013). It is possible that the mallard is particularly adaptable to environmental changes such as those driven by climate change and eutrophication (e.g. Messmer et al., 2021; Sjöberg et al., 2011). Indeed, the high adaptability of the mallard is expressed in its capability to use a wide variety of habitats throughout the globe, even to such an extent that it is considered an invasive species in some parts of the world (Guillemain et al., 2020).

In conclusion, IOD varied considerably between nearby lakes. Surprisingly, the distribution of breeding individuals of two out of the five species shifted toward lakes with relatively late IOD. At the same time, breeding success in one of these species, the common teal, showed a decreasing trend on early-IOD lakes, while it increased on late-IOD lakes. The distribution of two other species shifted from lakes with rich emergent vegetation toward lakes with poor emergent vegetation, a shift consistent with habitat-specific, long-term changes in breeding population sizes of waterbirds in Finland. In one of these species, breeding success decreased on lakes with rich vegetation. The habitat shifts for different species together suggest that a presumably positive, climate-driven impact on breeding phenology was over-ridden by negative changes in habitat quality at lakes with rich emergent vegetation. The findings of this study underline the need to understand the complexity of the effects of multiple anthropogenic stressors in freshwater ecosystems in order to arrest their degradation and the decline of inhabiting species.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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