ORIGINAL ARTICLE

Limnology for the ornithologist: effects of Lake Maggiore water level on migratory flows

Silvia Giuntini,[1*] Clara Tattoni,[1] Alessandra Gagliardi,[1,2] Alessio Martinoli,[1,2] Nicola Patocchi,[3] Roberto Lardelli,[3] Adriano Martinoli,[1] Damiano G. Preatoni[1]

[1]Environment Analysis and Management Unit - Guido Tosi Research Group, Department of Theoretical and Applied Sciences, University of Insubria, Varese, Italy; [2]Oikos Institute, Milan, Italy; [3]Bolle di Magadino Foundation, Magadino, Switzerland

ABSTRACT

Wetlands are widely recognised as the most critical stop-over locations along migration flyways. Wetland ecology is mostly influenced by water levels and water regimes. This research focuses on Bolle di Magadino (Switzerland), an important stop-over site on Lake Maggiore, artificially regulated by a dam. In this work we examined how the artificial flooding of a wetland affects the use of this stop-over site by migrating passerines during spring. Bird presence in the area was evaluated using both data collected at the ringing station located in the wetlands and the bird traffic rate (BTR) supplied by the BirdScan MR1, an avian vertical-looking radar (VLR) capable of automatically detecting and classifying birds in flight. In an attempt to shed light on the effect of lake level on stop-over quality, we i) simulated with GIS the extent of the flooded area and of the different habitat categories as the lake level changes; ii) calculated the relationship between lake level and the ability of stop-overing birds to acquire trophic resources; iii) verified that the flux of passerines below 500 m above ground level measured by radar could be used as a proxy for the number of stop-overing birds; iv) calculated the relationship between the number of birds leaving the stop-over and the lake level. While the number of ringed passerines has proven to be representative of the migratory flow below 500 meters of altitude at the site of interest, a high lake level seems to have a negative impact on the use by some species of the Bolle di Magadino area as a stop-over site during spring. In particular, two of the target species -the blackcap and the reed bunting- have proven to be sensitive to higher water levels. While taking into account the limitations and the relative nature of the results, could be necessary for the competent authorities to take these results into consideration in order to safeguard the Bolle di Magadino's role as an important stop-over area during spring.

Corresponding author: sgiuntini@uninsubria.it

Key words: stop-over; migration; Lake Maggiore; flooding; GRASS; radar.

Citation: Giuntini S, Tattoni C, Gagliardi A, Martinoli A, Patocchi N, Lardelli R, et al. Limnology for the ornithologist: effects of Lake Maggiore water level on migratory flows. *J Limnol 2022;81:2123.*

Edited by: Angela Boggero, *National Research Council, Water Research Institute (CNR-IRSA), Verbania Pallanza, Italy.*

Received: 30 March 2023.
Accepted: 14 July 2023.

J. Limnol., 2022; 81(s2):2123
DOI: 10.4081/jlimnol.2022.2123

INTRODUCTION

Stop-over sites are locations where birds rest, feed, and seek refuge during their migratory flights (Mehlman *et al*., 2005). Stop-overs, in particular, correspond to critical moments of migratory activity, as they are critical for acquiring the necessary energy to complete the migration while also representing periods of increased vulnerability for birds (Wright *et al.,* 2020). Furthermore, most migratory avian species tend to spend much more time in stop-over sites than on the move (Wikelski *et al.,* 2003). The effectiveness of stop-over sites as "rest and recovery" habitats is largely depending on their geographic location (Tattoni and Ciolli, 2019), the availability of microhabitats (Hutto, 1985; Moore and Aborn, 2000; Tattoni *et al.,* 2019) and the absence of disturbance (Fornasari and Calvi, 2012). Therefore, the en route selection of stop-over sites is of pivotal importance for migratory species (Webb *et al.,* 2010), especially when available habitats and/or habitat quality can vary in time: indeed, even small differences in vegetation or water depth could also mean differences in foraging opportunities and differences in degree of protection from predators. In other words, it is not surprising that most migratory birds end up using a relatively small area after choosing the stop-over site (Liu and Swanson 2015; Wright *et al.,* 2020).

Wetlands are widely acknowledged as the most important stop-over areas along migration flyways (Bonter *et al.,* 2009; Overdijk and Navedo, 2012; Khani *et al.,* 2015). Wetland ecology is primarily determined by water levels and water regimes. As a result, even minor changes in water depth can affect insect biomass production, microhabitat availability and quality, and thus the en route habitat selection process of migratory birds (Hutto 1985; Hu *et al.,* 2010; Jiang *et al.,* 2015), ultimately causing alterations in migratory patterns or even changes in migratory routes on a larger spatial and temporal scale. If birds are forced to stop in unsuitable, low-quality, or unknown areas, they are potentially exposed to high risks, which can have a negative impact on migratory population conservation (Buler and Moore, 2011; Koch and Paton, 2014). This is especially important given that most birds learn, socially and/or individually (Mueller *et al.,* 2013), their own migratory behaviour, which is only partly genetically determined and is indeed highly plastic (Sergio *et al.,* 2014; Verhoeven *et al.,* 2021).

Lake Maggiore is the second largest Italian lake, creating one of the three North to South breaks on the Alpine ridge along with lakes Como and Garda. Lake Maggiore shores, shared between Switzerland and Italy, host an important series of stop-over sites, used by many species of migratory birds: such as the Fondotoce area in Piedmont, or the Sabbie d'oro area and Bruschera marshland in Lombardy (Lardelli, 2006; Saporetti, 2018; Carabella *et al.,* 2022). The water level of the lake is artificially regulated through a dam placed at the outflow (Morabito *et al.,* 2018). Due to short corrivation times and the narrowness of the emissary channel at Sesto Calende, Lake Maggiore shows large variations between minimum and maximum levels (Carabella *et al.,* 2022), and slight variations in the water level are sufficient to cause flooding and draining of large portions of surrounding territory (Inderwildi and Salvietti, 2016). The artificial alteration of wetland dynamics during migration time in this area is likely to affect the usage of this stop-over sites by birds.

Water levels of Lake Maggiore are regulated since 1943 through the Miorina dam located on the Ticino river, 1 km south of the lake, in Italian territory. Lake level regulation is based on the regulatory thresholds established in 1950 through an Italo-Swiss agreement, and is entrusted to a consortium (Consorzio del Ticino) that includes representatives of Italian stakeholders such as the irrigation unions of Lombardy and Piedmont (that control irrigation in the rice growing district), and ENEL, the major producer of electricity in Italy, that owns several hydroelectric plants along the southern course of Ticino river (Interwildi and Salvetti, 2016). The relationships between lake level and its intended uses are therefore complex and often conflicting: for the valley inhabitants on the Italian side, it is expected a sharp seasonal level variation, as high as possible to act as a reservoir to guarantee crops (rice, maize) irrigation in the hottest months, but not so high to cause possible floods e.g., to the city of Pavia. On the other hand, Switzerland would favor lower levels for similar safety reasons, e.g., to guarantee safety from flooding to cities on the lakeshore (e.g., Verbania and Locarno). Other minor stakeholders, at a lesser scale, show the same pattern of conflicting interests: fishermen and anglers as well as environmental associations, both in Italy and Switzerland would opt for a regulation that best approximates natural flows to maintain a good biodiversity level, whereas navigation services both in Switzerland and Italy would prefer a more or less constant level to guarantee safe navigation. In order to try to solve the problem or at least provide information about it, the Interreg Project "Parchi Verbano Ticino" between Italy and Switzerland was conceived.

In our work, we aimed to identify the effect that the artificial regulation of Lake Maggiore level has on stop-over quality using available bird ringing (Lardelli and Scandolara, 2023) and radar data. In particular, we analysed the effect of water level on both the number of stop-over birds and their ability to find trophic resources in that area, in order to propose management measures that could support habitat availability and quality for migratory birds.

We predict that lake level regulation would cause alterations in migratory flows, and in particular in the number of birds that use this area as a stop-over site. We hypothesize that the periods when the water level is higher, and consequently the area of submerged vegetation is larger, coincide with less use of the area by migrating birds and a reduction in stop-over quality in terms of availability of food resources. In fact, a higher level of flooding of the foraging area, particularly grasslands, is thought to be associated with a lower amount of terrestrial invertebrates (Plum, 2005).

METHODS

Study area

The study area is represented by the Bolle di Magadino Natural Reserve (Canton Ticino, Switzerland, 8°51'56.90"E, 46°9'42.17"N, 6.7 km^2 total surface area), a protected wetland located in an estuarine landscape where Ticino river enters Lake Maggiore (Fig. 1). The Bolle di Magadino Foundation has been in charge of site management since 1975, prior to the establishment of the area as Cantonal Natural Reserve in 1974. The area represents an important stop-over and nesting site for numerous bird species (RSIS, 2017; Lardelli and

Scandolara, 2023) and it is enlisted as a Ramsar Wetland of International Importance since 1982, and as an Important Bird and Biodiversity Area (IBA) since 2000. Because of the high transit of birds, Bolle di Magadino is also part of the European-African Songbird Migration Network, a research initiative that focuses on passerine birds migration (Bairlein, 1995).

Lake Maggiore waters are an important natural resource, also exploited for recreation, energy production and agriculture, especially for rice cultivation in the central-western Po plain, immediately South of the Lake. Given the context of "contended resource" of Lake Maggiore briefly described before (see the Introduction section), that dates back since the Middle Ages, acquiring knowledge on the real effects of lake level variation on bird stop-over sites assumes a capital role.

Measurement of bird flow

Bird ringing

At the Bolle di Magadino Reserve, in the Bolla Rossa area, a ringing station for scientific bird ringing has been active since 1994, carrying out capture-mark-recapture (CMR) activities during the spring pass. The Bolle di Magadino Foundation, in agreement with the Swiss Ornithological Station, provided the complete dataset of captures/recaptures for 5 target species, among the most frequently captured ones: the European robin *Erithacus rubecula* (ERIRUB), the Common chiffchaff *Phylloscopus collybita* (PHYCOL), the Eurasian blackcap *Sylvia atricapilla* (SYLATR), the Common reed warbler *Acrocephalus scirpaceus* (ACRSCI), the Common reed bunting *Emberiza schoeniclus* (EMBSCH). Each species

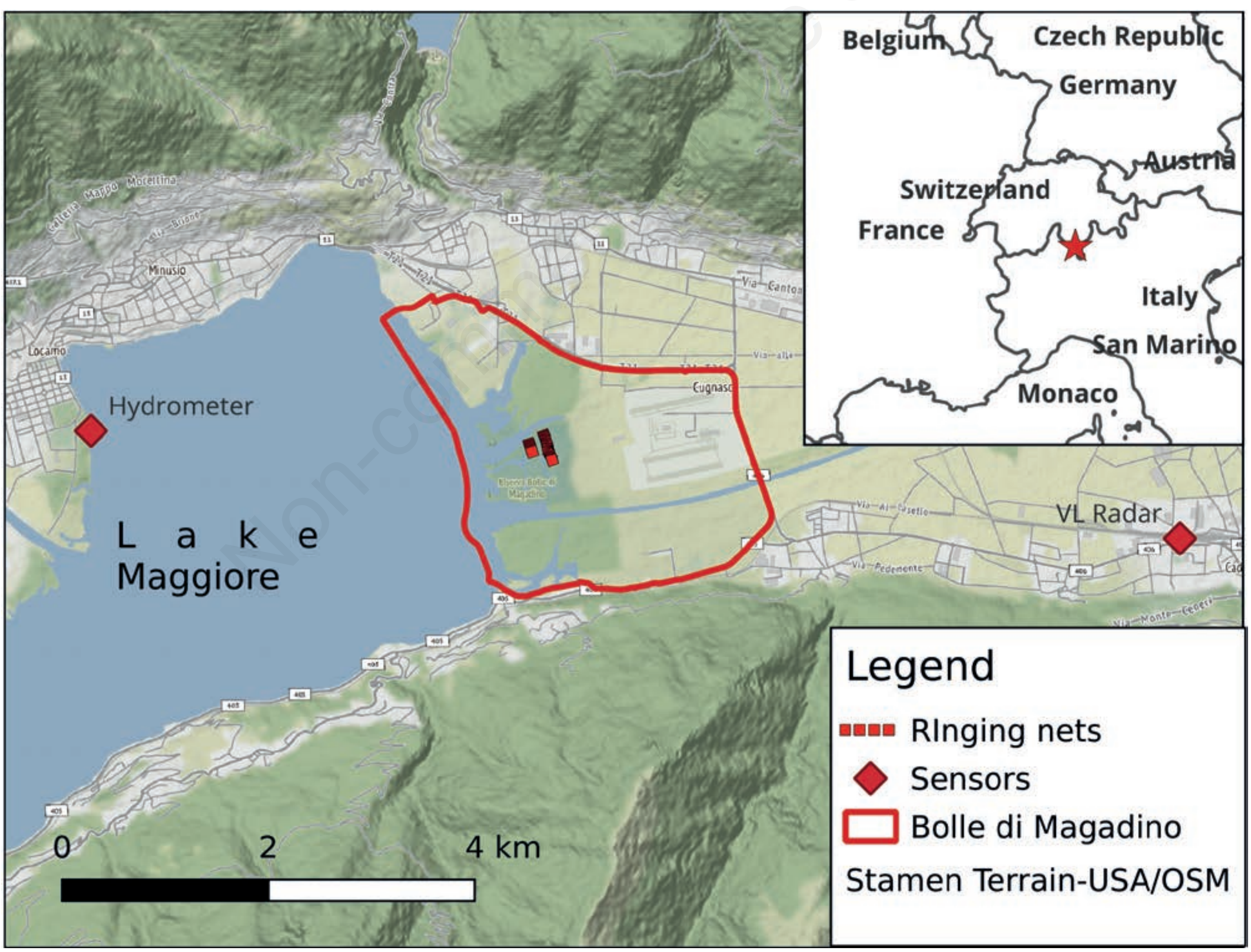

Fig. 1. Bolle di Magadino protected area on the northern shore of Lake Maggiore (Switzerland). Main map: location of the protected area, the ringing station, the vertical looking radar (VL Radar) and the hydrometer. Inlet map: the star shows the location of the study area at the border between Italy and Switzerland. Map data sources: REN water courses/lakes developed by the Federal Office for the Environment (FOEN, WMS by https://opendata.swiss); relief map derived from EUDEM25 DTM (available at https://www.eea.europa.eu); simplified world borders v. 0.3 (available at https://thematicmapping.org/).

has a different feeding ecology and microhabitat utilisation at its stop-over sites (Packmor *et al.,* 2020). The robin feeds mostly on invertebrates, eating on the ground or on the low branches of shrubs in wooded areas or in ecotones (Tsvey *et al.*, 2007). The blackcap has a similar feeding ecology, but shows less frequent ground dwelling behaviour and feeds mainly on shrubs (Brichetti and Fracasso, 2010a). The Common chiffchaff feeds almost exclusively on invertebrates on shrubs, but makes frequent catches of perching dipterans. The reed warbler is strongly associated with reed beds, where it feeds on invertebrates. The reed bunting, on the other hand, can forage both in reed beds and in fields and open areas, feeding on invertebrates and seeds (Brichetti and Grattin, 2012; Brichetti and Fracasso, 2010b). In Tab. 1 the periods referred to in the dataset, which has a total of 15,027 records, broken down as in Tab. 2.

Measurement of bird traffic by radar

To measure the overall bird traffic in the study area, we used the avian vertical-looking radar (VLR) BirdScan MR1 (Swiss Birdradar Solutions AG, https://swiss-birdradar.com), able to automatically detect and classify birds in flight. The radar has been placed in a site near the Bolle di Magadino Nature Reserve, where electrical power and surveillance were granted from the Swiss Federal Agency Agroscope (Cadenazzo, 8°56'2.007"E, 46°9'36.81"N, Fig. 1).

The BirdScan MR1 VLR consists of a self-contained, autonomous vertical pointing X-band pulse radar, with a peak power of 25 kW and an operational range of 0.05–2 km (Nilsson *et al.,* 2018): it records echo signals that are digitized and then processed by an on-board classification proprietary software (Zaugg *et al.,* 2008). Thanks to the wing-flapping pattern analysis, the software classifier can tell non-bird (e.g. insects) echoes and classify them in different subcategories (Schmid *et al*., 2019), storing all the observations in an on-board database. The radar operated at Magadino in May 2019, and from March 1st to May 31st in 2020, 2021 and 2022 (Tab. 3). It always operated in short pulse mode but, for each hour, the radar

Tab. 1. Operation time of the ringing station at Bolle di Magadino wetland (Switzerland).

Year	Start date	End date	Days of survey
2008	9 March	28 May	80
2009	9 April	26 April	17
2010	28 March	2 May	35
2011	23 March	2 July	101
2017	26 March	13 May	48
2018	19 March	12 May	54
2019	18 March	27 May	70
2021	20 March	2 May	43
2022	20 March	10 May	51

Tab. 2. Number of individuals of the 5 target species ringed at the station of Bolle di Magadino (Switzerland).

Species	Number of records
Acrocephalus scirpaceus	943
Emberiza schoeniclus	1919
Erithacus rubecula	6287
Phylloscopus collybita	2199
Sylvia atricapilla	3679
Total	15,027

Tab. 3. Radar operational times at Agroscope Cadenazzo (Switzerland).

Year	Start date	End date
2019	2 May	4 June
2020	1 March	31 May
2021	1 March	31 May
2022	1 March	31 May

was set for 30 min in rotating mode and 30 min in static mode, which allows better classification of echoes, but without information on the speed and direction of flight. Data were analyzed with the BirdScan R package (v 0.1.2 Haest *et al.,* 2023) who returned the Migration Traffic Rate (MTR, Trosch *et al.,* 2005; Welcker *et al.,* 2017), an index that defines the number of individuals crossing an ideal 1 km wide transect, perpendicular to the migration direction, in one hour. In this work, MTR was calculated over an elevation range up to 2500 m above ground level (agl). All calculations were performed in the R environment (version 4.0.5; R Core Team, 2021) with RStudio (version 1.4.1103; RStudio Team, 2020).

Assessment of stop-over site conditions

Land cover and morphology

The Bolle di Magadino Foundation provided a detailed vector map (10 m minimum mappable unit), describing the dominant vegetation types and land cover of the protected area, derived from a phytosociological field survey carried out by the Bolle di Magadino Foundation (Ufficio Protezione della Natura, 2005). The original vector map's more than 100 classes were grouped into 10 main land cover categories using Quantum GIS version 3.3* (QGIS Development Team, 2022). The final habitat map covered an extent of 6.7 km^2, including the Bolle di Magadino actual wetland as well as the rest of the protected area. There are a few infrastructures in the area, including an airport, covering about 23% of the study site. The rest of the area is occupied by bushland, including grasslands (27%); water (22%); trees (17%), agriculture (14%) and, in decreasing order: reeds, high grassland, bushland and brambles, gardens and water vegetation.

We also developed a dedicated Digital Terrain Model (DTM) that included both elevation and lake bathymetry in the study area. Using GRASS GIS version 7.8.2 (GRASS Development Team, 2022) we merged the EU-DEM 25 m Digital Elevation Model (version 1.1, 2017, https://www.eea.europa.eu/data-and-maps/data/copernicus-land-monitoring-service-eu-dem) with a local point elevation measures database (25 cm elevation resolution) created and maintained by the Bolle di Magadino Foundation (Ufficio Protezione della Natura, 2005) and with the data (5 m isobaths) available in the bathymetric study of the northern part of Lake Maggiore produced by Hilbe *et al,.* (2009).

All the GIS data were projected according to the Swiss local reference system CH1903/LV03 (EPSG code: 21781).

Hydrology

We used lake water levels measured at the nearest hydrological station in Locarno (UFAM – Ufficio Federale dell'Ambiente, station n. 2022 "Locarno", 8°48'15.55"E, 46°09'48.77"N). We downloaded the lake water level values, measured every 30 minutes from 1^{st} March to 31^{st} May for 2008-2011 and 2017-2022, from the "Osservatorio Ambientale della Svizzera Italiana" (Canton Ticino Environmental Observatory) web portal (https://www.oasi.ti.ch) and then averaged it to match the temporal resolution of the bird ringing and MTR time series.

We then calculated the inundated area using the r.lake module in GRASS GIS (GRASS Developement Team, 2022, Tattoni *et al.,* 2022). Polygons representing flooded areas were calculated with a step of 0.01 m (1 cm) from a minimum lake level of 191.00 m asl up to 195.00 m asl in order to include all the levels registered in the time span considered (2008-2022).

Data analysis

Relationship between weight gain during daytime stop-over foraging sessions and Lake Maggiore level

The pattern of fat deposition and subsequent weight gain in stop-over birds involves phases of mass increase during the day (due to trophic activity) and mass reduction during the night caused by basal metabolism (Schaub and Jenni, 2000). Effective fat deposition only occurs if the daytime increase in mass is greater than the night-time reduction.

For each target species individually, the effect of the water levels of Lake Maggiore on the ability to find trophic resources was assessed by means of a generalised linear model (GLM) between the height of the lake level and the residuals of the regression between the maximum chord length and the weight of the individuals caught in the late afternoon in the last 3 control rounds. The maximum chord is a standard biometry value measured during ringing operations, corresponding to the length of the flattened and straightened wing from the wing joint - the 'wrist' - to the tip of the longest primary (Demongin, 2016). The inclusion of the mentioned residuals in the analysis, instead of directly including the weight at sunset of the individuals, was done to avoid the birds' intrinsic body size from influencing the analysis.

Relationship between bird traffic rate and number of ringed birds

In order to assess the effectiveness of the BirdScan MR1 radar in quantitatively detecting the flow of migrants departing from the stop-over site, the relationship between the bird traffic rate (BTR) detected by the radar at the centre of the Piano di Magadino above Agroscope (Cadenazzo) and the number of birds captured at the ringing station was analysed. BTR's definition is identical to that of the migratory traffic rate (MTR; Bruderer, 1971), but includes both migratory and non-migratory movements. The latter cannot in fact be excluded a priori as an integral part of the BTR recorded by the radar, since the instrument is located within a wintering and nesting area of several species. The fraction of the BTR corresponding to the departure of migrators from the Riserva Bolle di Magadino stop-over, was identified according to space, time and the taxonomic categories of interest. In terms of space, the detected BTR was divided into two, based on the estimated transit altitude of birds departing from the Riserva stop-over above the radar positioned at Agroscope: low altitude (0-500 m above ground level) and high altitude (>500 m agl). Assuming a passerine climb rate of 6-9% with respect to horizontal displacement (Hedenström and Alerstam, 1992) and given the distance between the ringing station and radar (5500 m), the transit altitude is estimated to be between about 300 and 500 m agl. The hypothesis is therefore that the BTR of the low altitude band is largely composed of birds departing from the stop-over, while the BTR of the high altitude band is made up of individuals in migratory transit, which did not stop at the Bolle di Magadino Reserve. To exclude non-migratory movements, we focused entirely on the departure time of the target species, using only the BTR recorded at a time of 8 h straddling civil sunset (± 4 h), which is commonly used in radar studies (Zehnder *et al*., 2001, Komenda-Zehnder *et al*., 2010) and corresponds to a sun position 6° below the horizon. his choice was made in order to include the departure time of both diurnal migrants (Finches, Emberizidae, *etc*.) and nocturnal migrants, which represent the majority of passerines. In addition, visual inspection of the day-by-day BTR frequently showed a marked increase in the BTR at low altitude in the afternoon, potentially attributable to the departure of daytime migrants. Of the five target species, four are nocturnal migrants (Reed Warbler, Robin, Blackcap, Little Warbler) while one is a predominantly diurnal migrant, but occasionally also nocturnal (Reed Bunting). Finally, because the study's focus is on passerines, and the five target species belong to this group, only the BTR for the class "passerine type" was considered for the analysis. The used dataset is available on Zenodo (doi:10.5281/zenodo.7783993) (Giuntini *et al.,*2023).

The correlation between the BTR, calculated as described above, and the total number of individuals captured at the ringing station, was assessed using 10 Pearson's *r*, each of which considered the sum of the individuals captured on the previous days, from 1 to 10. This way we accounted for the possible effect of arrivals and departures from the stop-over of different magnitude depending on the weather conditions. Due to SARS-COVID restrictions the ringing was not permitted in 2020, thus analysis covered the spring migration periods of 2021 and 2022, the only time frames where there was overlap between the radar and ringing datasets.

Relationship between BTR and Lake Maggiore level

In order to test the hypothesis of a reduced effectiveness of the stop-over under extensive flooding conditions, the relationship between BTR (<500 m agl) and water level was tested by means of a generalized linear mixed model (GLMM), which unlike GLMs, allows the fixed effects (the independent variables of interest) to be evaluated separately from the random effects (other independent variables whose effect on the dependent variable is hypothesised, but not of interest for the purposes of the study). The GLMM allows the effect of the height of the water levels of Lake Maggiore on the BTR to be assessed separately, regardless of the year and month within the three selected to assess spring migration (March, April, May). As far as the "year" factor is concerned, there is potentially a strong collinearity with water levels, the height of Lake Maggiore being strongly influenced by winter precipitation and the speed of change of levels being much lower than that of the BTR. The addition of "month" as a random effect is instead determined by the phenology of the migration itself, which proceeds in an overall Gaussian manner, with a migration peak in April, independent of the flooding of Lake Maggiore. Given the extreme variance of the BTR, the variable was log-transformed to meet the normal distribution requirement of the regression residuals. In order to assess the effect of water levels at a smaller time scale, the same model was replicated separately for each one of the three years analysed (2020, 2021, 2022), including only the "month" variable as a random effect, and at a single month level (March, April, May), including "year" as a random effect. In the overall three-year model, the changepoint of the smoothed GLMM model was finally calculated in order to assess the possible existence of 'critical' water levels, beyond which the BTR drops significantly. All the analysis of this study were performed in the R environment (version 4.0.5; R Core Team, 2021) with RStudio (version 1.4.1103; RStudio Team, 2020).

RESULTS

Flooded area estimation

During the period considered, the lake level fluctuated between 192.54 and 194.29 m asl, with lower levels during the months of April and May, when the water is used for irrigation purposes, while the maximum level was observed in March. The simulated flooded area calculated on the basis of level and cuvette shape varied from 74.95 to 222.89 ha (123.81 ± 0.25 ha). The flooded area maps for each level were superimposed to the same vegetation map, allowing to calculate the amount of flooded habitat for each water level. The lake level of 193.8 m resulted as a threshold point, above which the categories “trees”, “reeds”, “shrubs” and “tall grasses” begin to flood more rapidly than at lower levels. The other categories subject to flooding include beaches and areas without shoreline vegetation and are in fact the first to be covered by water when the lake level rises. Urbanised and cultivated areas within the protected area are less affected by the lake level’s rise as even at very high levels the percentage flooded is less than 10% (Fig. 2).

Relationship between weight gain during daytime stop-over foraging sessions and Lake Maggiore level

The results of the GLMs between sunset weight of ringed birds, measured as the mass of individuals caught during the last three rounds of net-checking, and water level revealed a negative effect of Lake Maggiore level on the foraging capacity during the day of two target species, the blackcap and the reed bunting. For these species, in fact, the correlation was significantly negative (-1.26; $p<0.001$ for the blackcap; -0.71, $p=0.009$ for the reed bunting) (Tab. 4 and Fig. 3).

Relationship between BTR and number of ringed birds

The number of birds caught at the bird station is significantly correlated with the BTR for each of the day intervals considered. Pearson’s *r* increases until it reaches a peak of 0.44 ($p=0.01$) at a time lag of 7 days and then slowly decreases again.

Relationship between BTR and Lake Maggiore level

The explanatory power of the overall “three-year” GLMM model is substantial (conditional $R^2 = 0.43$) although only a fraction can be attributed to the fixed effect of lake height (marginal $R^2 = 0.12$). However, the effect is significant and negative (estimate = -1.28, 95% CI -1.94 / -0.63, $p<0.001$ with Wald t-distribution approximation). The summed variance of the random effects year and month as a whole is quite high (0.75), underlining how migratory phenology and collinearity between year and lake height have a marked effect on the magnitude of the BTR, which is however significantly influenced by the quality of stop-over habitats as shown by the model (Tabs. 5 and 6). The negative effect of water levels can also be observed at the seasonal level, although it is only statistically significant in 2021 and 2022, however with a coefficient comparable to that observed in the three-year model. In this sense, the greater variability of water levels recorded in 2021, compared to 2020 and 2022, could confer greater robustness to the model, reducing the confidence intervals and consequently leading to statistically significant coefficients. The random effect of year and month also emerges quite clearly graphically (Fig. 4). It is particularly noticeable how in May the BTR values remained high even at maximum water levels, strongly influencing the regression. The changepoint analysis conducted shows a threshold value of 193.32 m asl beyond which the BTR decreases significantly.

DISCUSSION

In this work, we used a combination of bird data acquired with two different methods to assess the effect

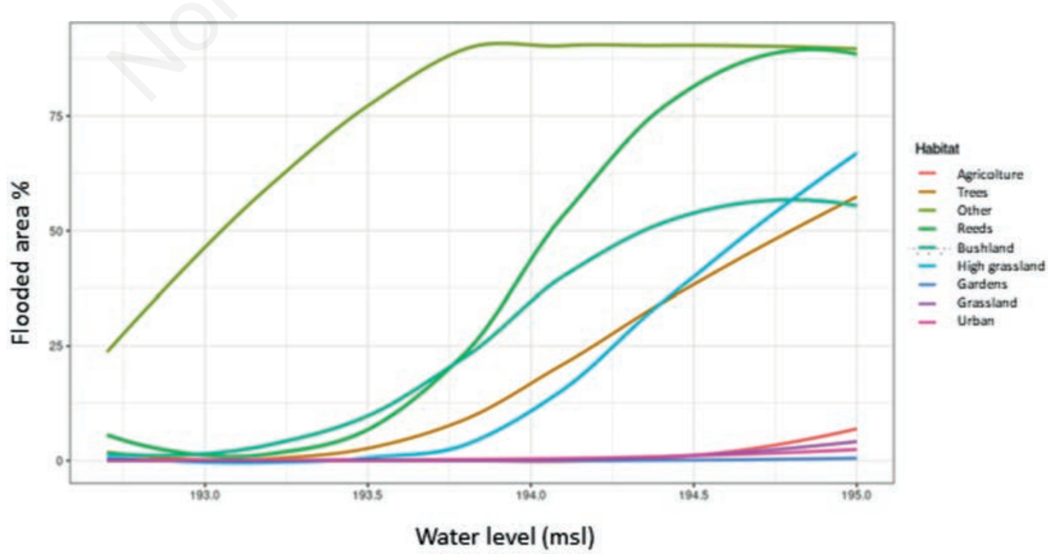

Fig. 2. Flooded percentage of the different habitat types according to the simplified vegetation map as the lake level rises, obtained by 3D modelling.

of Lake Maggiore water levels on both the number of stop-over birds and their ability to find food resources in the area during spring. BTR of passerine birds measured with radar and data recorded at the ringing station proved to have a significant agreement, at least for passerine birds flying <500 m agl and the five most representative species. This result, proving that BTR can be used as a proxy for quantifying stop-over for the given species, allowed us to explore the relationship between Lake Maggiore water levels and BTR, in order to test the initial hypothesis of reduced effectiveness as stop-over of the target area under extensive flooding conditions. This result also support the choice of using the BTR of ±4 hours from sunset, because it reasonably included both nocturnal and diurnal migrants. Despite standardised schemes, counts at ringing stations have limitations due to potential sampling bias, e.g., the possibility that some age categories of bird sare more easily caught than others (Davis, 2005). However, when assessing the intensity of daily migration with catch numbers, it is generally assumed that the number of birds caught is a quantitatively representative sample of migrating birds

Tab. 4. Results of the GLM on the influence of Lake Maggiore water level on the weight of the individuals of the 5 target species caught at sunset (last 3 rounds of net control). The asterisks indicate the level of significance.

		Estimate	SE	T value	PR (>|T|)
Acrocephalus scirpaceus	(Intercept)	48.085	44.174	1.088	
	meanWL	-0.248	0.228	-1.088	0.279
Emberiza schoeniclus	(Intercept)	138.303	52.809	2.610	
	meanWL	-0.714	0.272	-2.610	0.009**
Erithacus rubecula	(Intercept)	32.710	31.405	1.041	
	meanWL	-0.169	0.162	-1.041	0.298
Phylloscopus collybita	(Intercept)	6.385	18.107	0.352	
	meanWL	0.032	0.093	-0.352	0.724
Sylvia atricapilla	(Intercept)	244.480	46.488	5.258	
	meanWL	-1.263	0.240	-5.259	<0.001***

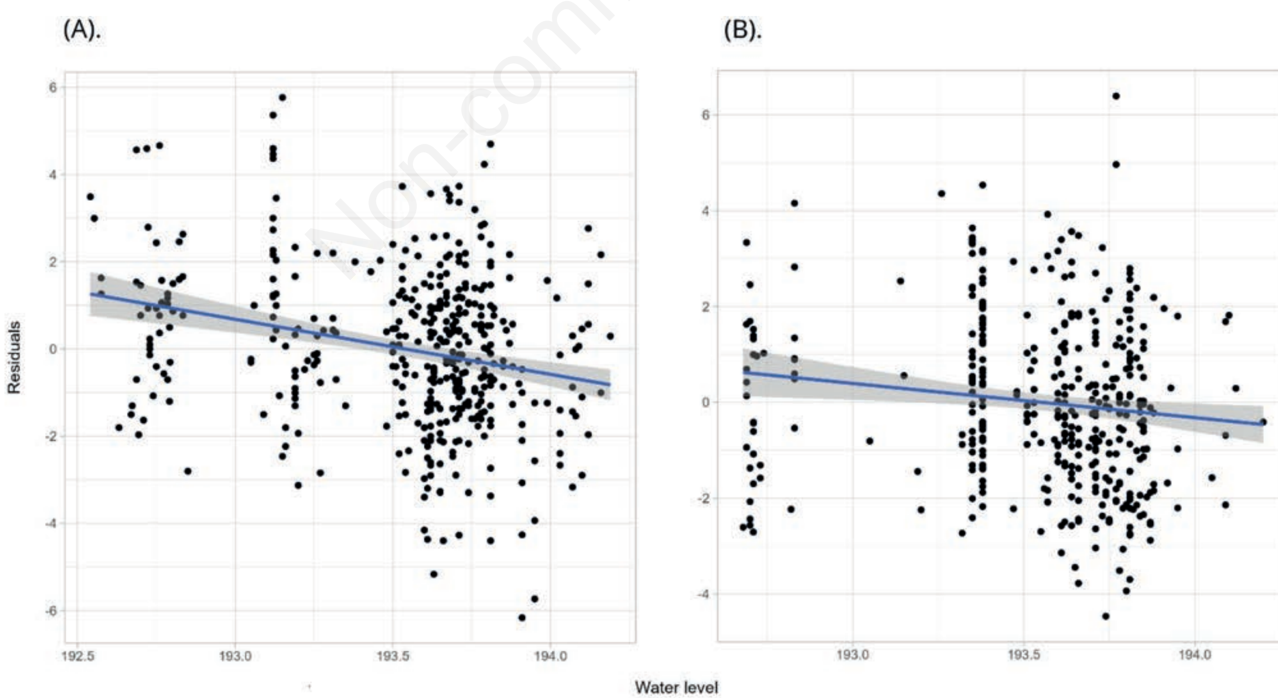

Fig. 3. GLM plots comparing regression residuals between weight at sunset and maximum chord of ringed birds to the average daily level of Lake Maggiore. Residuals are used as a proxy for daily food intake. Only the two significant relationships are shown: *Sylvia atricapilla* (A) and *Emberiza schoeniclus* (B).

(Jenni, 1984; Korner-Nievergelt *et al.,* 2007). A close relationship between daily capture numbers and migratory flux may be more likely at sites where birds are caught outside of active migration with virtually no stop-over time, such as on mountain passes, or at stop-over sites where stop-over time is usually limited to a few hours or a day, such as coastlines and islands that do not offer adequate stop-over conditions, as hypothesised by Komenda-Zehnder *et al*. (2010). However, a less close relationship could be found in stop-over sites where birds stop in appropriate habitats to refuel for several days, such as the Bolle di Magadino Reserve. Nevertheless, it is still an open question whether the numbers of migrants caught reflect those passing through, since birds typically fly at

Tab. 5. GLMM results for BTR (log-transformed) <500 m agl from 1 March to 31 May from 2020 to 2022 (average of the 8 target hours, ±4 h from civil sunset) compared to the average daily water levels of Lake Maggiore. The three-year "overall" model and the models considering only individual years are presented. Estimates, CI and p-value of the fixed effect of the water level are presented. Also presented are overall and individual random effects variance (year and month) and R2 (both marginal - relating to the fixed effect only - and conditional - taking into account both fixed and random effects).

	Full model			2020			2021			2022		
	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
Fixed effects												
(Intercept)	252.29	125.92 | 378.66	<0.001	53.54	-106.48 | 213.55	508	332.73	85.75 | 579.70	9	780.85	162.64 | 1399.06	14
meanWL	-1.28	-1.94 | -0.63	<0.001	-0.25	-1.08 | 0.58	547	-1.70	-2.98 | -0.42	10	-4.03	-7.23 | -0.82	15
Random effects												
σ^2	1.40			0.56			2.21			0.57		
τ_{00year}	0.15											
$\tau_{00month}$	0.60			0.24			3.52			0.16		
ICC	0.35			0.30			0.61			0.22		
N_{year}	3											
N_{month}	3			3			3			3		
Observations	235			90			66			79		
R^2 marginal	115			5			69			142		
R^2 conditional	425			301			641			327		

Tab. 6. The results of the 3-year 'overall' GLMM model (again) and that of the monthly models (cumulative over the 3 years) are shown See caption Tab. 5.

	Full model			March			April			May		
	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
Fixed effects												
(Intercept)	252.29	125.92 | 378.66	<0.001	785.15	290.33 | 1279.97	0.002	225.97	-51.83 | 503.77	0.109	152.23	62.88 | 241.57	0.001
meanWL	-1.28	-1.94 | -0.63	<0.001	-4.04	-6.61 | -1.48	0.002	-1.14	-2.58 | 0.30	0.118	-0.76	-1.22 | -0.30	0.002
Random effects												
σ^2	1.40			1.44			1.28			0.37		
$\tau_{00\ year}$	0.15			2.45			0.11			0.41		
$\tau_{00\ month}$	0.60											
ICC	0.35			0.63			0.08			0.52		
$N_{\ year}$	3			3			3			3		
$N_{\ month}$	3											
Observations	235			81			68			86		
R^2 marginal	0.115			0.393			0.060			0.142		
R^2 conditional	0.425			0.775			0.134			0.590		

altitudes that far exceed the height of the nets. Only a few studies have investigated whether or not capture numbers are quantitatively representative of migration intensity (Peckford and Taylor, 2008). In any case, the positive correlation between the BTR passing over the radar at the expected altitude of stopovering birds leaving the Bolle di Magadino reserve and the number of ringed birds on the previous days suggests that BTR can quantify not only the migratory flux, but also the stopovering fraction of migrants. The increasing robustness of the correlation with the number of ringed birds up to >3 days before may hint at pulses of departures from the stopover, possibly linked to optimal weather conditions (Dänhardt and Lindström, 2001).

The GLMM revealed a significantly negative effect of the lake level on the BTR: In particular, the model for March is the one with the highest estimates (-4.04), with a very pronounced and statistically significant effect of the water level. The result is consistent with what is observed concerning the weight measured at sunset of the target species, among which the blackcap and reed bunting, species with peak migration in March (Spina and Volponi, 2008), are those that are negatively affected by the height of Lake Maggiore, possibly in relation to a reduced ability to find food resources in conditions of persistent flooding (although it is not possible to completely rule out that the reduced appetite of the blackcap may be due to the breeding period, since some of them were captured in April). Interestingly, ongoing research on the productivity of edaphic larvae insects in the reserve is preliminarily pointing out that it is inversely proportional to the days of submergence of the soil in marsh areas, whereas the productivity of aquatic lake habitats (i.e., insects producing larvae that develop on the lake bed) is continuous but starts later than in marshes.

A hypothesis for this mechanism can be sought in the productive capacity of these marsh habitats at the time of submergence: if this occurs early in the season (in March) the aquatic habitat, which is more inert to spring warming than the dry land, may have a delay in the productivity of insects (Chironomidae especially) and not compensate for the loss of productivity of the submerged marshes. While in the second spring transit phase (mid-April to May), the aquatic habitat is also in full production and emergence of midges, which are very abundant, compensating for the lack of production of submerged marshes (Patocchi, *unpublished data*). Indeed, it is particularly noticeable that in May, although there is still a negative effect of the lake level on bird traffic (-0.76), BTR values remain high even at maximum water levels, strongly influencing the

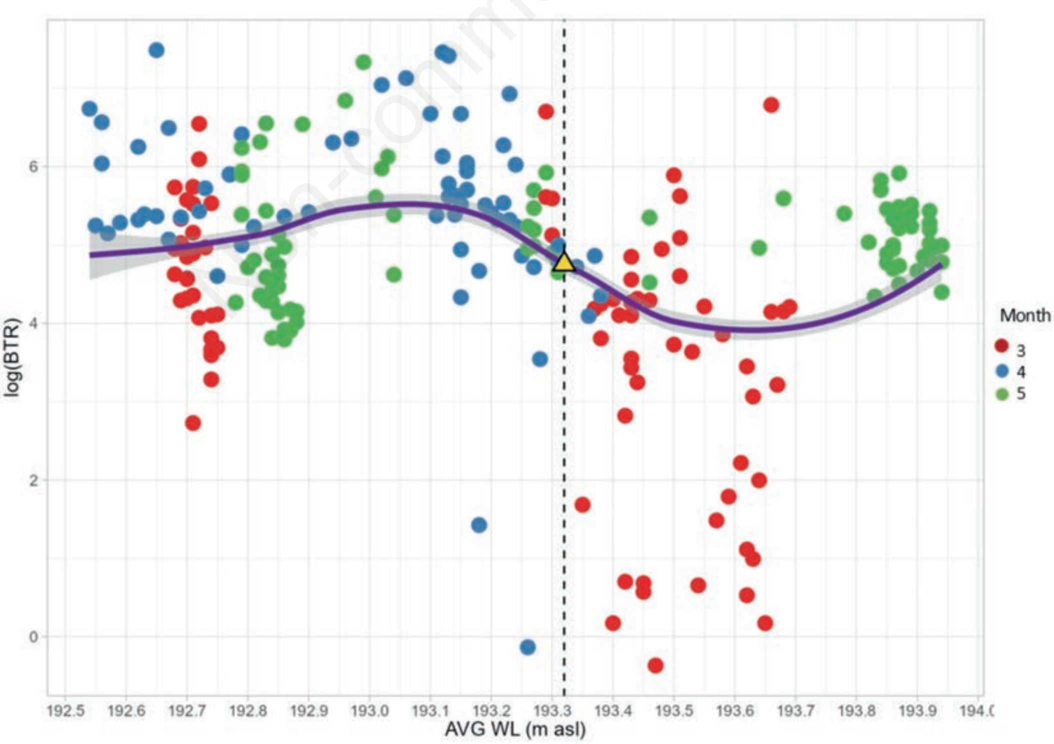

Fig. 4. Bird traffic rate (log-transformed) <500 m agl from 1 March to 31 May from 2020 to 2022 (mean of the 8 target hours, ±4 h from civil sunset) compared to the daily average water level of Lake Maggiore. The colours refer to the monitoring months, as shown in the legend. The blue line represents the regression line of the GLM model (+ CI). The yellow triangle indicates the calculated changepoint.

regression. This is also consistent with the fact that the food intake of the reed warbler, a trans-Saharan migrant whose peak passage occurs in the first two decades of May (Spina and Volponi, 2008), did not prove to be adversely affected by increased water levels. Additionally, other species belonging to the same guild and family (Acrocephalidae) as the reed warbler, well adapted to foraging in flooded reed beds, show similar phenology to the latter, plausibly making up a non-secondary fraction of the BTR observed in May.It is therefore conceivable that the guild of trans-Saharan migratory insectivores may be less sensitive overall - or not at all - to water levels and the consequent degree of flooding of stop-over and foraging habitats at the Riserva Bolle di Magadino.

It is also worth noting, starting from the level of 193.30 m asl, the increase in the flooded area of reed thickets and especially bushes, -i.e. the preferential foraging habitat for numerous intra-Palearctic migratory species such as the Blackcap- which is equal to 7.5% of the total surface area at that water level, as emerges from the GIS analysis. It can be observed, however, that the most noticeable increase in the flooded area of the shrublands, but also of the reed thickets and magnocaricetes, is located approximately 50 cm above the possible threshold value that emerges from the GLMM, and placed between 193.80 and 193.90 m asl. Thus, there is no complete agreement between the results of these two components of the study - the GIS-based flooded areas estimation and the GLMM *changepoint* - but, overall, it can equally be stated that at water levels values between 193.30 and 193.90 m asl the suitability of the Riserva Bolle di Magadino as a stop-over site for intra-Palearctic migratory passerines may be reduced, due to the ineffectiveness of such areas in providing adequate food resources for the fraction of birds feeding on terrestrial, non-flooded habitats, such as to guarantee the necessary fattening for the continuation of the journey towards the nesting grounds.

Equally interesting are the average levels of Lake Maggiore measured in the time interval 1868 - 1942, i.e. before the beginning of the artificial regulation of its waters: 192.5 m for March, 193.0 m for April (Barenghi, 2023). Both values are well below the threshold value that seems to negatively influence the BTR, showing that early migrants such as the blackcap and the reed bunting probably used to find suitable conditions for stop-over before water regulation was introduced. However, it is important to stress that the results, which only concern the spring period, cannot be generalised to the entire migration, as during the autumn the food and microhabitat requirements of stop-overing birds can vary drastically. Moreover, it is highly plausible the same lake level management has opposite effects on different species, or that some species -such as waterbirds for example, not considered in our analysis- simply benefit from stable water levels (Ma *et al*., 2010). Finally, it must be also emphasised that the sample size of the data acquired using the BirdScan MR1 radar, while interesting, is limited to only three migratory seasons. Therefore, more robust conclusions would require further investigation for other seasons in order to increase the sample size of water level/phenology combinations.

CONCLUSIONS

Regarding the spring months, elevated water levels in Lake Maggiore may exert a detrimental influence on a subset of passerine bird species that utilize the region as a stop-over site. A high lake level in fact not only seems to induce a reduction in the number of passerines choosing to use the area as a stop-over, but also reduces the possibilities to find food resources at least for some species. In particular, this outcome seems to affect species with peak migration occurring in March, such as the blackcap, which uses the bushes as a foraging area, and the reed bunting. For these reasons, and for the inherent relativity of the results obtained, we suggest that management decisions ought to be tailored based on the species that need to be preserved.

ACKNOWLEDGMENTS

This research was funded by "Parchi Verbano Ticino" project, supported by Regione Lombardia/EU–INTERREG Italia Svizzera 2014/2020. We would like to thank the Agroscope agricultural competence centre in Cadenazzo for their kind cooperation.

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