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RESEARCH ARTICLE

Shorebird responses to fine-scale water level fluctuations and macrofauna biomass in a newly constructed freshwater wetland

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Abstract

Introduction: Restoration of marine and freshwater wetlands for shorebirds is essential for the recovery of their declining populations. An ongoing approach is to restore shorebird habitats by large-scale engineering, expecting the return of birds once suitable abiotic conditions are (re)established. However, this requires science-based knowledge on which abiotic conditions should be (re)constructed.
Objectives: Here, we aimed to identify preferred water-level ranges of a diverse shorebird community by studying shorebird habitat use in a new 1300 ha heterogeneous freshwater wetland with spatio-temporal variation in food availability and water levels (Marker Wadden, The Netherlands). We hypothesized that (1) water levels regulate the attractiveness of wetland sites to shorebirds; (2) shorebird numbers are positively related to benthic and pelagic macrofauna biomass; (3) water level and macrofauna biomass interact, with the effect of macrofauna biomass diminishing as water levels increase.
Methods: We combined artificial intelligence shorebird counting on 86,400 camera trap images with automatic water level registrations and monthly macrofauna biomass sampling.
Results: Statistical modeling identified water level as the key driver of shorebird numbers, and macrofauna biomass as less important during our 1-year study. Optimal water levels ranged between just exposed saturated mudflats and mudflats with 5 cm of water on the sediment surface. Water level-regulated macrofauna accessibility overruled effects of macrofauna biomass on shorebird numbers.
Conclusions: Fine-scale water level management can be a powerful approach to restore habitat suitability for foraging shorebirds, and thus contribute to the recovery of their declining populations.
Implications for Practice: Water levels determine the value of wetland areas for shorebirds at the resolution of centimeters. Two-thirds of all shorebirds were observed when water levels ranged between 10 cm below and 10 cm above the sediment surface. This makes high-resolution water level management a powerful tool for improving shorebird habitat suitability. This is particularly feasible in freshwater wetlands, in the absence of a tidal cycle. Variation in pelagic and benthic macrofauna densities is irrelevant if prey are inaccessible due to unsuitable water levels. Considering water levels during the design phase of wetland restoration can ensure future habitat suitability for shorebirds throughout the annual cycle.

Key words: artificial intelligence, benthic macroinvertebrates, camera trap, Charadriiformes, Marker Wadden, waders

Introduction

Many shorebird species (Charadriiformes, suborder Charadrii, also known as waders) are decreasing in numbers across the globe (Lindström et al. 2015, 2019; Donlan et al. 2023). Among key threats are climate change and habitat loss, which affect their reproduction at breeding grounds, survival at wintering grounds, and the quality of the intermediately located stopover locations they require during their long-distance migrations (van Roomen et al. 2012; Studds et al. 2017; Alves 2020). During most of their annual cycle, shorebird species reside in wet habitats, including wet meadows and tundra for breeding, and mudflats as stopover locations and winter foraging sites (van de Kam et al. 2004). Habitats range from marine to freshwater systems.

Shorebird ecology is especially well-studied in the marine environment, which includes internationally protected areas such as the Wadden Sea, Yellow Sea, and Banc d'Arguin (van de Kam et al. 2004; Piersma 2007; Melville et al. 2016). In these

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systems, identified parameters of suitable shorebird habitat are low predation pressure, high prey density, high prey quality, and suitable water levels for foraging (Pomeroy 2006; van Gils et al. 2015; Bijleveld et al. 2016). At low tide, individuals forage on benthic fauna in the drying mudflats, while they spend their time resting and digesting at roosting sites during high tide (Evans 1976; Dodd & Colwell 1998; Burton et al. 2004). Although the importance of these marine areas for shorebird communities is well-known, it is often complicated to implement conservation or restoration efforts. Socioecological constraints such as coastal protection and the large spatial scale of environmental dynamics (e.g. tidal cycle and global sea level rise) prohibit restoration opportunities, and consequently, many important marine shorebird habitats are degrading globally (Piersma 2007; Pontee 2013; Birchenough et al. 2015). Restoration and conservation may therefore be easier to implement in less dynamic but also important shorebird habitats, such as freshwater wetlands.

Freshwater wetlands are increasingly recognized as important habitats for shorebirds (Foster et al. 2013). Although most shorebird species use both marine and freshwater wetlands, there are also species that almost exclusively reside in freshwater—such as Common snipe (*Gallinago gallinago*) and Ruff (*Calidris pugnax*) (Piersma 2007; Włodarczyk et al. 2007). In freshwater environments, water levels are less dynamic, non-tidal, and they can be regulated by human interventions in many parts of the world. This regulation offers opportunities to manage water levels in favor of the shorebird community, for which water levels are very important (Safran et al. 1997; Colwell & Taft 2000). However, before implementing such management, detailed knowledge is needed on how water levels should best be managed for shorebirds at fine scales, and how shorebirds respond to combinations of water levels and prey availability.

Here, our aim was to quantify how a diverse shorebird community selects foraging sites in a newly constructed freshwater wetland, in relation to spatio-temporally varying water levels and macrofauna prey biomass. We hypothesized that (1) water levels regulate the attractiveness of (newly constructed) wetland sites to shorebirds at the fine scale of centimeters; (2) shorebird numbers are positively related to benthic and pelagic macrofauna biomass; and that (3) there is an interaction between water level and macrofauna biomass, because macrofauna prey species become unavailable when water levels rise too high. We expected a strong role for water levels because in marine ecosystems water levels importantly determine accessibility of prey (van Gils et al. 2015; Bijleveld et al. 2016). However, in contrast to marine studies that typically compare high to low tide situations with a variability of several meters, we here focused on fine-scale water level variation (at the centimeter scale) that is relevant in the context of freshwater wetlands and their management.

Methods

Study Site

This study was carried out in a newly constructed wetland area called "Marker Wadden," situated in the north-east of the 4 m-deep freshwater Lake Markermeer (The Netherlands, 52°35′30.2″N 5°22′43.6″E; Fig. 1A). Marker Wadden was created as a large-scale restoration project in this Natura 2000-protected lake, aiming to add reproduction and foraging habitat to the shallow lake's declining bird and fish communities. Between 2016 and 2020, five islands and a shallow underwater landscape with a total area of 1300 ha were constructed (van Leeuwen et al. 2021). Each island was constructed by creating basins inside oval dikes of coarse Pleistocene sand locally extracted from the lake's own sediment, which provided protection against erosion from wind and waves. The created basins were subsequently filled with soft sediments (i.e. silts and clays) locally extracted from Holocene layers of Lake Markermeer's sediment (van Leeuwen et al. 2021). By strategically distributing these sediments within the basins, mudflats were created with very shallow water depths and gradual land–water transitions. The basins were initially not connected to the larger water body of Lake Markermeer to allow the soft sediments to subside, but after settling of the sediment the basins were connected to the open water of the lake in the winter of 2020–2021.

Water levels in Lake Markermeer are driven by rainfall and evaporation; however, mostly because of water level regulations by the Dutch Water Authorities. As an important lake central in the Netherlands, Lake Markermeer provides many ecosystem services—including recreation, extraction of water for agricultural irrigation and extraction of drinking water (van Leeuwen et al. 2021). The lake's water levels are therefore carefully regulated by weirs and sluices. In spring, high river discharges of the Rhine river allow water levels to be high, and water is actively stored in the lake. Over summer, water levels drop because of surplus evaporation and active water extraction (agricultural irrigation and drinking water, Fig. 2A). During winter, water levels are maintained low for water safety purposes, especially because strong winds in combination with long fetch lengths can cause wind setup of several decimeters on the downwind shore (Calle 2005). As the result of all these active interventions, water levels are artificially reversed to what would be expected in a naturally fluctuating lake (high winter levels and low summer levels). Water levels are partly predictable for birds, but can also suddenly increase substantially in response to changing wind speeds, wind directions, or a surplus in discharge of the Rhine (Calle 2005).

Study Species

A wide variety of shorebird species visited the study area for breeding and feeding throughout the study year (van der Winden et al. 2024). In this study, we were interested in habitat use by the entire shorebird community (Charadriiformes), which included nine different species (Dreef & van der Winden 2023): Pied avocet (*Recurvirostra avosetta*), Common snipe, Ruff, Common ringed plover (*Charadrius hiaticula*), Little ringed plover (*C. dubius*), Common redshank (*Tringa totanus*), Northern lapwing (*Vanellus vanellus*), Black-tailed godwit (*Limosa limosa*), and Black-winged stilt (*Himantopus himantopus*). Of these nine species, we concentrate on the four most dominant ones (Pied avocet, Common snipe, Ruff, and Common ringed plover) to enable working with an artificial intelligence

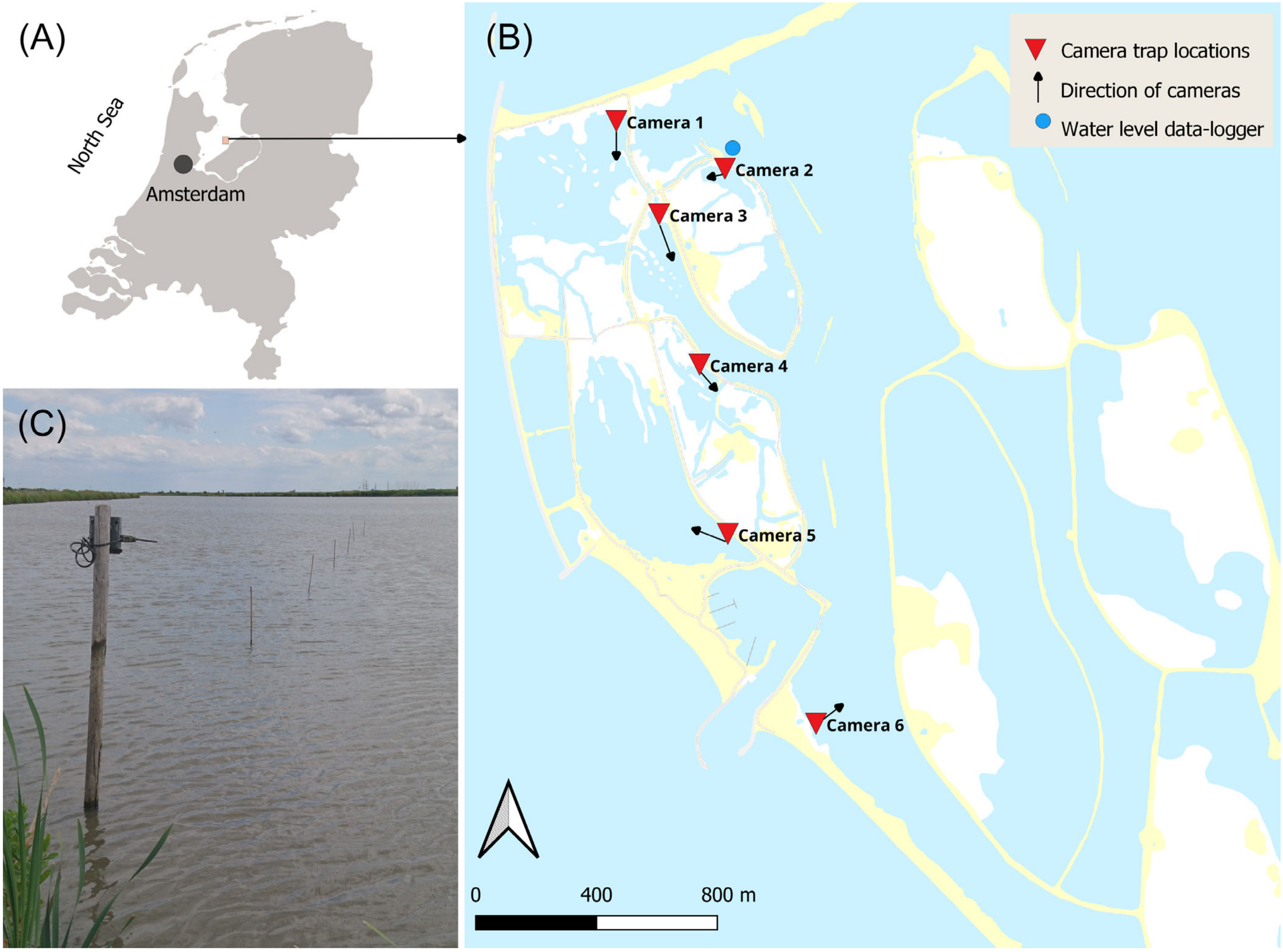

Figure 1. Map of camera trap locations, with (A) the location of the Marker Wadden study area in the Netherlands; (B) a detailed overview of the studied area of the Marker Wadden, with red triangles ($n = 6$) indicating the sampling locations and the black arrows indicating the direction of the camera traps and the transects. The blue circle shows the position of the water level data-logger. (C) Ground image of the setup of one of the camera traps, with the transects indicated by the sticks.

(AI) identification model (see below). These species comprised approximately 63% of the total shorebird community observed on Marker Wadden throughout the study period from May to September in 2022 (Dreef & van der Winden 2023). We here take these four species as representative for the wider range of shorebird species with similar morphological characteristics and preferences.

All four species share that they opportunistically feed on macrofauna, including Oligochaeta, Gastropoda, Chironomid larvae, and fish larvae (Pienkowski 1982; Moreira 1995; Enners et al. 2019). By grouping these species into one focus group (Charadriiformes), we can test general patterns relevant for shorebirds, assuming that individual species within this group respond similarly to changes in water level and macrofauna biomass. However, we know that different shorebird species have slightly different preferences due to, for example, different morphological traits like leg length. Still, we expect more similar intragroup responses to changes in water level and macrofauna biomass as compared to the responses of species in other taxonomic groups (Laridae, Anatidae).

Study Design

To study how shorebirds responded to heterogeneity in water levels and macrofauna biomass, the number of shorebirds was quantified every 5 minutes at six locations on the Marker Wadden islands from May to September in 2022. The six study areas were selected based on the presence of gradual land–water transitions with a gradient of water levels from the shorelines and a soft-sediment substrate, that is, representing mudflat shorebird habitat (Fig. 1B). Sediment slopes of the sites were similar to ensure capturing a consistent range of water levels for our monitoring. At each location we monitored (1) shorebird numbers, (2) water levels, and (3) macrofauna biomass as described in the following sections. Macrofauna sampling dates were 17/05, 07/06, 05/07, 02/08, and 30/08 (for clarity reasons further

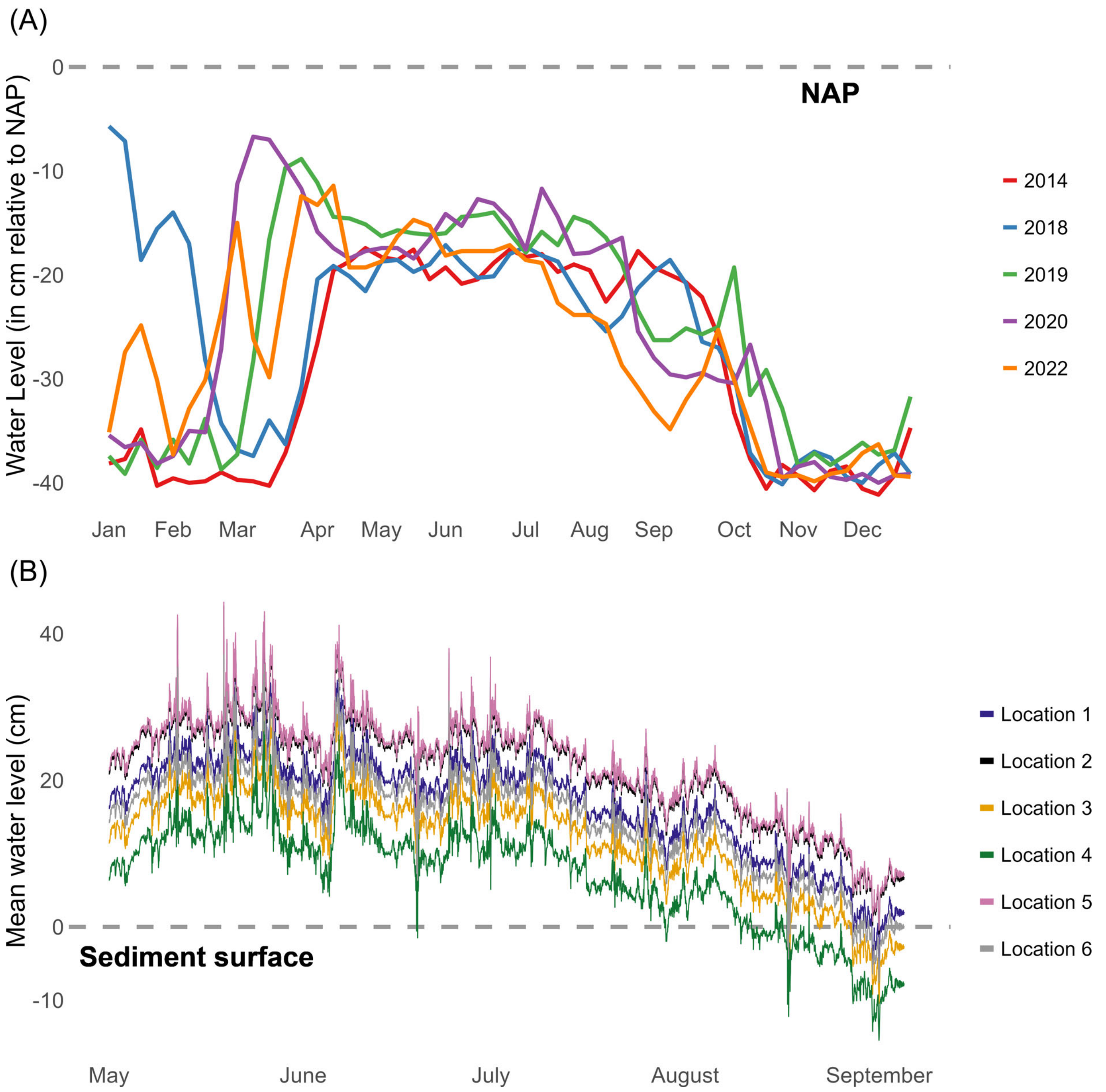

Figure 2. (A) Mean water levels in Lake Markermeer relative to the Amsterdam Ordnance Datum (NAP). Mean water levels were calculated per week for all weeks in 2014, 2018, 2019, 2020, and 2022. Water levels during (early) spring are regulated to be high (notably since a policy change in 2018), and water levels during summer, autumn, and winter are lower and relatively constant over the years. Data: Dutch Water Authorities, https://waterinfo.rws.nl.
(B) Water levels measured at the Marker Wadden study site relative to the sediment surface over time for each location ($n = 6$, sediment surface is at 0). Water levels of all locations are derived as relatives from actual measurements at locations 1.

referred to as the months of May, June, July, August, and September).

Camera Trap Monitoring of Shorebird Numbers

To quantify shorebird numbers, we installed a camera trap at each of the six locations. The camera traps (RECONYX HP2XODG HyperFire 2 Professional Cover IR Camera OD Green) were mounted on a wooden pole and secured in the sediment, leaving the camera approximately 1.5 m above the water level (Fig. 1C). The vertical angle of the camera was such that the horizon would be at approximately one-fifth from the top of the image. The cameras were programmed to take an image every 5 minutes after being installed (26 April 2022), thus producing 288 pictures every 24 hours. All cameras were active throughout the whole study period without malfunctioning. Six bamboo sticks were installed in a straight line in front of each camera, at an interval of five meters, creating a total transect of 30 m (Fig. 1C). The surface area of the water that was captured by the cameras was approximately 200 m^2 (approximately 25 m by approximately 8 m).

Monitoring Water Levels

Water level data were automatically recorded hourly to the nearest mm at one location on Marker Wadden by an Ellitrack data-logger (Leiderdorp Instruments, Leiden, The Netherlands). Water levels in the study area peaked at the start of the study period in May and decreased until early September (Fig. 2B). Mean water levels per location ranged from 7.26 ± 0.04 standard errors (SE) cm to 22.3 ± 0.04 SE cm above the sediment surface. The maximum water level was recorded early in the season at location 5 (44.3 cm above the sediment surface), and the minimum water level was recorded at location 4 (for locations see Fig. 1B) in early September (15.5 cm below the sediment surface, Fig. 2B).

These manual measurements were used to calibrate the water level measurements registered by the data-logger to site-specific values, and programmed to follow the water level fluctuations registered by the data-logger, assuming homogenous water movements over the well-connected and relatively small study area (Fig. 1B). Differences in soil elevation across the transect were assumed to remain constant throughout the study period (i.e. negligible soil subsidence over the 5-month study period, see Alderson et al. 2025). Obtained hourly water level predictions per location were used to calculate mean water levels for each location over each 10-day period around the macrofauna sampling moments. This ensured that the spatio-temporal resolution of the pelagic- and benthic macrofauna biomass matched that of the water levels (see below). We also linearly interpolated the hourly water level data to a 5-minute interval, which could then be used to link water level to wader presence on the 5-minute resolution that images were taken.

Determining Macrofauna Biomass

To quantify macrofauna biomass as a potential food source for shorebirds, samples were collected every 4 weeks throughout the spring and summer season at all six locations ($n = 30$). Benthic macrofauna were collected by taking four sediment cores (diameter = 6 cm) of the top 10 cm at each location, after which the samples were sieved over a 0.72 mm mesh, and obtained macrofauna were pooled and stored in 70% ethanol. In close vicinity of each camera trap, sample locations were selected at a water level of, respectively, 0 and 10 cm, representing the lower and higher end of the water level range in which the selected shorebird species could forage while walking based on their bill lengths (ranging from 4 to 10 cm) and leg lengths (between 1.4 and 10 cm, van de Kam et al. 2004; Karlionova et al. 2007; Meissner 2007; Włodarczyk et al. 2011). Samples were stored at 4°C until visual assessments for the presence of benthic macrofauna using a stereomicroscope (Leica M205C, Germany) within 60 days. Detected macrofauna were counted, their lengths measured to the nearest 0.1 mm, and the individuals were identified up to the taxonomic level of family (except Oligochaeta and Trichoptera, Table S1).

Pelagic macrofauna were collected by securely placing a metal cylinder (diameter = 60 cm, height 50 cm) in the water column on the sediment to prevent mobile macrofauna from escaping. The isolated water column was then sampled with a net (mesh size = 1 mm) to collect all macrofauna. Samples were stored at 4°C on 70% ethanol in 10 mL plastic tubes. This procedure was done at a water level of 10 cm (±2 cm SE) as close to each camera trap as possible, yielding a total of 30 samples throughout the study period. Sample processing and identification were identical to the methods described above for the benthic macrofauna (Table S1). For both benthic and pelagic macrofauna, in samples with more than 30 individuals of a taxonomic group, all individuals were counted but length measurements were only obtained from 30 randomly selected individuals.

To calculate biomass of the macrofauna, length-body mass regressions were applied to each family following the procedure as described in van Leeuwen et al. (2025). By this method, dry body mass was calculated for all individuals of the benthic and pelagic macrofauna group (Table S1). Total biomass was pooled per 4-week period per location.

Data Analyses—Image Processing Using Artificial Intelligence

Each sampling location was visited monthly for 5 months, during which macrofauna biomass was sampled (see above) and images were downloaded from all cameras. To be able to statistically test for relationships between the encountered macrofauna biomass (pelagic and benthic) by the shorebirds on the images, we assumed that pelagic and benthic macrofauna biomass assessed during the field visits would be representative for the macrofauna biomass encountered by the birds captured on the camera images 5 days before and 5 days after the macrofauna sampling. Therefore, for each field visit, images from the 10 days around the visit were selected to be annotated with AI (10 days × 288 images × 5 visits = 14,400 images per location; 14,400 × 5 locations = 86,400 images in total).

Annotation was performed by a two-step AI pipeline. The first step was a YOLOv5 model (trained within the agouti.eu platform [www.agouti.eu]). This is a deep learning model for object detection that can recognize and locate objects in an image in a single step (Redmon et al. 2016). It is trained using labeled images, optimizing a composite loss function that assesses (1) whether or not an object is present, (2) bounding box accuracy (i.e. how good the model is at estimating the location of the object), and (3) classification (i.e. which object is detected), with network weights updated through backpropagation. Once trained, it takes raw pixel values from to-be-classified images and extracts hierarchical features (e.g. edges, textures, and shapes). These features are then used to predict the presence of objects and their location on the image, as well as classifying the objects once detected (Ajayi et al. 2023). We used this YOLOv5 model to detect birds in our images and extract their bounding boxes. Images were cropped around these bounding boxes followed by a manual check of every image, and non-bird objects were all removed to ensure a dataset with 100% bird images (100% specificity).

The second step in the pipeline was aimed at taxonomic classification of these bird images in a second model (ResNet50). A ResNet50 model is a convolutional neural network (i.e. a deep learning model that automatically learns spatial features from images by applying convolutional filters across the images; Habibi Aghdam & Jahani Heravi 2017) with 50 layers that uses residual (skip) connections to enable efficient training of very deep models and improve predictive accuracy. This model recognizes the cropped bird species by adjusting its convolutional filters through backpropagation during training, which minimizes classification error on labeled images. Once trained, it processes new images by extracting hierarchical features (edges, textures, shapes of birds in our case) of the images and uses these to and assign new images to the most likely previously assigned group (bird species in our case; Koonce 2021).

The training dataset for the second (ResNet50) AI model in this pipeline consisted of 8948 randomly selected images (approximately 10%) which were manually assessed for the presence of birds, and each bird was identified up to species level. Individual bird images were extracted and used to train the second AI model using the cnn_learner()-function from the FastAI library (see https://docs.fast.ai/tutorial.vision.html for detailed documentation). The identified birds included several species of shorebirds ($n = 4$; Common ringed plover, Common snipe, Pied avocet, Ruff) but also several others, belonging to the families Anatidae ($n = 4$; Greylag goose [*Anser anser*], Common shelduck [*Tadorna tadorna*], Ruddy shelduck [*T. ferruginea*], *Anas* spec.), Rallidae ($n = 2$; Eurasian coot [*Fulica atra*], Moorhen [*Gallinula chloropus*]), Laridae ($n = 1$; Black-headed gull [*Chroicocephalus ridibundus*]), and Threskiornithidae ($n = 1$; Eurasian spoonbill [*Platalea leucorodia*]). Although this study focused on shorebirds, it was necessary to train the model to classify all (commonly) detected species observed on the camera trap images to avoid misidentifications (L. Ursem,personal observation, NIOO-KNAW, 2025).

Model performance by the ResNet50 in correctly classifying shorebirds (Charadrii group) on the cropped images was evaluated using a subsample ($n = 500$) of the resulting annotations. Manual inspection of AI-classified shorebirds showed that the model was operating with an accuracy of 70% at this taxonomic group level, that is, other bird species were classified as shorebirds or shorebirds were classified as other species in 30% of the cases (i.e. 70% sensitivity). This means that we also obtained information about other taxonomic groups present in the study system (Anatidae and Laridae). These groups showed only weakly directed responses to water levels and/or macrofauna (Colwell & Taft 2000), and in case they did, they showed a relative selection for deeper waters rather than shallow waters (Fig. S1). Therefore, we can safely assume that misidentification at the taxonomic group level (i.e. identifying a duck as a shorebird) would add either non-directional or deep-water-biased noise to the data—and would therefore not interfere with our conclusions on shorebirds (see Section 4).

To further test our assumptions, we performed an additional comparison between AI-annotated images and manually annotated images at the species level. For this comparison, all images from 1 day prior to and 1 day after each sampling visit were manually annotated ($n = 288 \times 2 \times = 2880$ images per sampling site), with detected birds being identified up to species level. This comparison revealed that the AI-annotation was able to accurately predict the shorebird numbers identified by manual annotation with an r^2 of 0.66 (linear regression: manual_shorebird_count = 1.08 × AI_shorebird_count − 7.47, $p < 0.001$; Fig. S2).

Data Analyses—Statistical Models

Effects of the factor "month" on mean macrofauna biomass were tested with analyses of variance (ANOVA) followed by Tukey's honestly significant difference (HSD) tests, separately for benthic and pelagic macrofauna to account for differences in sampling methodologies.

The AI-annotated shorebird numbers per image were summed per location and sampling period, resulting in data with similar temporal resolutions for (1) estimated water level, (2) macrofauna biomass, and (3) shorebird numbers. The main statistical model performed a direct comparison of the effects of water level and macrofauna biomass on shorebird numbers ($n = 30$ datapoints). The model was a generalized linear mixed-effects model (GLMM; Brooks et al. 2017), with shorebird numbers as a count variable depending on (1) mean water level, (2) pelagic- and (3) benthic macrofauna biomass as the three explanatory variables. Interaction terms between water level and the two macrofauna-biomass variables were included in the full model, and sampling location and period were included as random intercepts. A negative binomial distribution was selected because it performed better than a Poisson distribution based on Akaike's Information Criterion (AICc) criteria (Burnham & Anderson 2004; AICc-Poisson: 1274.6, AICc negative binomial: 363.3; dispersion ratio = 31.5, $p < 0.001$). Model selection was performed backwards from full models based on AICc criteria, using maximum likelihood estimation (MLE). If deltaAICc with the best-fit model was less than 2, the most parsimonious model was preferred (Bolker 2009). Models were checked for collinearity using the variance inflation factor (VIF; Lüdecke et al. 2021). r^2-adjusted was calculated by using the predicted values from the best model as an explanatory variable for the observed shorebird numbers in a linear model. Fixed effects were centered around the mean by subtracting the mean value from all values. To test for the robustness and sensitivity of these analyses to extreme values, we also modeled these relationships on subsets of the data, that is, without including the macrofauna data, separately for each location, separately for each month, and on subsets in which we excluded "extreme" values potentially driving the observed relationships (e.g. excluding shorebird numbers >500, excluding September data).

To detect the range of water levels preferred by shorebirds in more detail, mean water levels at a 5-minute interval per location (ranging from 15 cm below to 45 cm above the sediment surface) were binned to intervals of 5 cm (e.g. 0–5, 5–10 cm water depth, etc). For each water level category, the number of occurrences of these depths was determined, as well as how often shorebirds were present (0 for absence vs. 1 for presence). The selection of certain water level categories by shorebirds was then represented as a proportion of the total number of occurrences of the matching bin (i.e. the chance a shorebird is present, given a certain water level category). Using these proportions, a chi-squared test for independence was performed to test for a relationship between shorebird presence and the different water level categories (i.e. testing for non-random site selection by shorebirds based on water levels). Bonferroni post hoc tests were performed to test for differences among water-level categories. An Empirical Cumulative Distribution Function was computed to illustrate the percentage of wader observations in response to increasing water levels.

All analyses were performed using R Statistical Software (v.4.4.3; R Core Team 2025) and the packages glmmTMB (v.1.1.5; Brooks et al. 2017) and lme4 (v.1.1.31; Bates et al. 2015). A significance level of $\alpha = 0.05$ was used for all analyses, and all mean values are provided ± the corresponding SE.

Results

Shorebird Numbers

In total, 27,609 birds were detected and classified on the 86,400 images analyzed via AI. Of these observed birds, 9076 (32.9%) were classified as Charadrii. The other taxonomic groups included in the AI classification consisted of 8154 Anatidae (29.5%), 5445 Laridae (19.7%), and 4934 other bird species (17.9%).

Macrofauna Biomass

Macrofauna biomass varied over time and space. Families found in the benthic and pelagic macrofauna samples included Chironomidae, Gammaridae, Corixidae, Lymnaeidae, Mysidae, and Oligochaeta, with other species comprising less than 5% of the total biomass (Fig. 3). For benthic macrofauna, mean dry biomass was 24.4 ± 3.9 SE mg 0.003 m^{-3}. Biomass ranged from 1.5 to 72.9 mg 0.003 m^{-3}, with lowest biomass in May (mean biomass = 12.7 ± 5.3 SE) and highest biomass in September (mean biomass = 36.9 ± 9.5 SE), but there was no significant effect of time (ANOVA: $F = 1.36$, $p = 0.28$, Fig. 3A). For pelagic macrofauna, dry biomass ranged from 1.2 to 70.2 mg 0.57 m^{-2} respectively, with a mean dry biomass of 31.2 ± 3.7 SE mg 0.57 m^{-2}. May had the lowest biomass of pelagic macrofauna (9.3 ± 4.7 SE mg 0.57 m^{-2}) and June had the highest biomass (47.0 ± 8.6 mg 0.57 m^{-2}), which was significantly different (ANOVA: $F = 4.06$, $p = 0.01$, Fig. 3B); whereas no other differences were observed. Spatially, macrofauna biomass varied up to 25-fold among the study locations (Fig. S3).

Relationship Between Shorebird Numbers, Water Level, and Macrofauna Biomass

We compared the influence of water level, benthic macrofauna biomass, and pelagic macrofauna biomass on shorebird numbers at our six study locations in GLMMs. Model selection on the main model (Table S2) indicated that water level was the main driver of shorebird numbers, with shorebird numbers increasing with decreasing water levels (Table 1; Fig. 4). Generalized linear mixed models including benthic or pelagic macrofauna biomass, or an interaction between pelagic macrofauna biomass and water level, had similar predictive ability as the best model only including water level (deltaAICc <2.0; model M3 in Table S2). Although a marginal positive role of macrofauna biomass was present in these less parsimonious models (M2 in Table 1), their effect sizes were about six-fold smaller compared to the effect size of water level. We therefore identified the model only including water level as predictor as the best model to explain shorebird numbers following (f1) number of shorebirds − mean water level + (1|Location) + (1|Month) (Table 1). With increasing water levels, shorebird numbers decrease following the formula (f2) $N = 609 \times 0.94^x$, where N is the number of shorebirds over a 10-day period and x is the mean water level over the same 10-day period. The effect size of every unit change (on a log scale) was six-fold higher for water level than for benthic or pelagic macrofauna biomass.

A similar negative effect of water level on shorebird numbers was found in the statistical models with only water level included. We found this result when (1) testing the models for temporal variation due to differences in water levels *among months*, as well as when (2) testing within each month for spatial variation *among locations*. The effect of water level due to temporal variation arising within every location was significant for most locations, with the log of all slopes differing significantly from 0 ($p < 0.002$), except for location 3 and location 6 (estimates = −0.02; 0.00, $p = 0.36$; 0.99, respectively; Fig. 4A). The effect of water level due to spatial variation, tested within every sampling month, was significant for the models for May, June, and July ($p < 0.05$), only near-significantly for August, and not significant for September (estimates = −0.07; −0.02, $p = 0.06$; 0.6, respectively; Fig. 4B). Rerunning the model on a subset excluding shorebird numbers greater than 500 and a second subset excluding data from September still showed a significant relationship between shorebird numbers and water levels (estimates = −0.05; −0.07, respectively, $p < 0.001$).

Shorebirds were more often observed in shallow waters than in deeper waters, compared to what was expected under random site selection (Fig. 5; chi-squared test for independence, $p < 0.05$). The highest proportion of images with at least one shorebird present was in the category of 0–5 cm above the sediment surface (Fig. 5). When water levels were between 10 cm below and 10 cm above the sediment surface, we observed 67% of all shorebirds (Fig. 6A & 6B), which was more than two-fold higher than randomly predicted (Fig. 5). Shorebird presence was lower than expected when water levels ranged between 10 and 35 cm, and again relatively higher when water levels increased to more than 40 cm deep.

Discussion

The construction of mudflats with shallow water levels in Lake Markermeer by the Marker Wadden restoration project attracted a great number of shorebirds during the productive spring and summer seasons. However, the presence and numbers of shorebirds on this newly constructed freshwater wetland were highly dependent on the water level. Water levels of less than 10 cm above the sediment surface were strongly preferred, and fine-

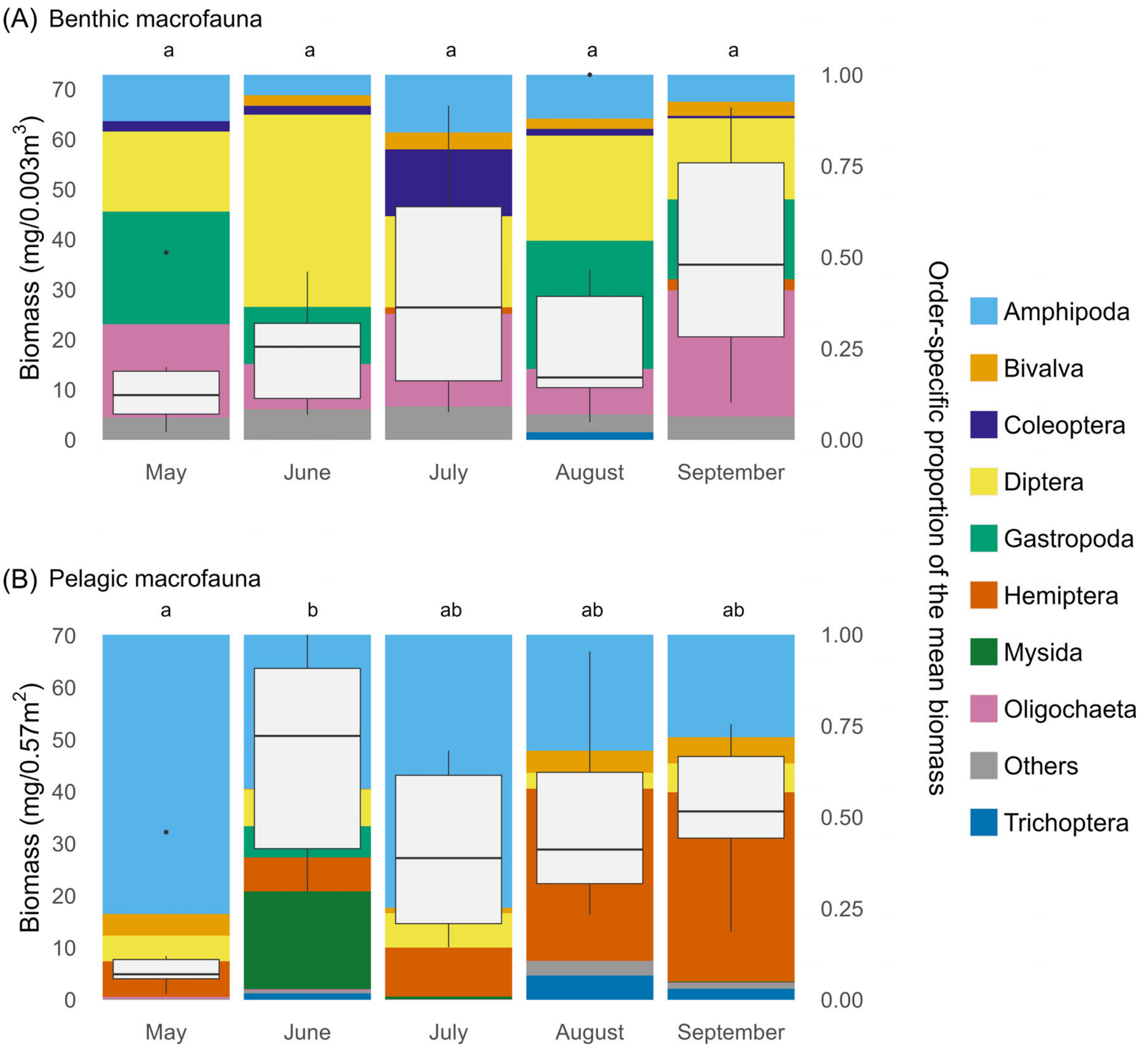

Figure 3. Observed variation over time in (A) benthic macrofauna biomass and (B) pelagic macrofauna biomass. In both panels, boxplots correspond to the left *y*-axis, thus indicating the variation in macrofauna biomass among locations. The colors of the bars in the background correspond to the right *y*-axis and show the proportional representation of the different macrofauna orders in the mean biomass per month. The category "Others" contains the families that together contributed less than 5% of the total macrofauna biomass as calculated over benthic and pelagic macrofauna. Months that share lowercase letters are not significantly different from each other.

scale increases of only a few centimeters quickly reduced the number of birds that were present. Macrofauna biomass also varied extensively over time and among locations in the new restoration area, even within our 1-year study. However, macrofauna biomass was six-fold less important than water level in determining numbers of shorebirds in search of food.

The fine-scale requirement of certain water levels by shorebirds can most likely be explained by their ability to probe in soft and saturated sediments or shallow waters for benthic and pelagic prey. The tactile, visual, or sweeping foraging method of shorebirds to collect prey species is known to be related to their bill and leg lengths (e.g. Dias et al. 2009). The four species selected in this study have bill (approximately 1.4–10 cm) and leg lengths (approximately 4–10 cm) that match the water level ranges that we found these birds to prefer (van de Kam et al. 2004; Karlionova et al. 2007; Meissner 2007; Włodarczyk et al. 2011). These morphological bill and leg length ranges are also typical for the broader shorebird community at the islands and beyond (Chambon et al. 2018; Aarif et al. 2024; Jackson et al. 2024), which suggests that our findings can be applied at the shorebird community level. Deeper waters prohibit reaching benthic prey in the sediment and pelagic prey on the sediment surface. Likewise, probing for prey may be difficult in dryer sediments (Granadeiro et al. 2006; Dias et al. 2009). Therefore, our data suggest optimal water levels ranged between just exposed saturated mudflats and mudflats with 5 cm of water on the sediment surface. Two-thirds of all shorebirds were observed when water levels ranged between 10 cm below and 10 cm above the sediment surface.

By studying water levels and macrofauna biomass in a freshwater ecosystem with regulated water levels and without a tidal cycle, we could detect effects of fine-scale water level

Table 1. Results from generalized mixed-effect models exploring the effects of predictor variables on shorebird numbers using a negative binomial distribution (link function = log). Results are presented for the full model (M1) including all possible terms of interest and their interactions, and results of the best models after model selection within 2.0 deltaAICc from the best model (M5). Estimate and standard errors are given for the predictor variables after centering them by subtracting their mean value from all values.

	Variable	*Estimate*	*Std error*	*Z-value*	p-*value*	*AICc*
M1	Intercept	5.03	0.15	33.52	<0.001	369.7
	Water level: benthic biomass	0.00	0.00	0.32	0.75	
	Water level: pelagic biomass	0.00	0.00	−1.92	0.06	
	Water level	−0.07	0.01	−5.10	<0.001	
	Benthic biomass	0.01	0.00	1.66	0.09	
	Pelagic biomass	0.01	0.01	1.60	0.11	
M2	Intercept	5.05	0.15	34.45	<0.001	364.7
	Water level: pelagic biomass	0.00	0.00	−1.55	0.12	
	Water level	−0.07	0.01	−5.53	<0.001	
	Pelagic biomass	0.01	0.01	1.81	0.07	
M3	Intercept	5.08	0.13	38.85	<0.001	365.2
	Water level	−0.06	0.01	−5.33	<0.001	
	Benthic biomass	0.01	0.00	1.19	0.23	
M4	Intercept	5.05	0.15	33.41	<0.001	363.7
	Water level	−0.07	0.01	−5.16	<0.001	
	Pelagic biomass	0.01	0.01	1.68	0.09	
M5	Intercept	5.08	0.14	37.46	<0.001	363.3
	Water level	−0.06	0.01	−5.44	<0.001	

fluctuations (up to cm) typically not incorporated in marine studies. This adds fine-scale data to the knowledge that shallow water levels are important for probe-feeding shorebirds in freshwater wetlands (e.g. Safran et al. 1997; Colwell & Taft 2000). In marine literature, food availability is typically considered a key variable regulating the spatial distribution of shorebird populations (van Gils et al. 2015; Bijleveld et al. 2016). However, often with the implicit focus on shorebirds foraging during low tides on productive mudflats in which water levels are already in the shallow ranges that we here specifically focused on (Evans 1976; Dodd & Colwell 1998; Burton et al. 2004). The dominant effect of the tidal fluctuations is therefore often not studied directly but rather implicitly included, because during high tides food is simply inaccessible. In freshwater ecosystems, these fine-scale water levels provide the opportunity for management to regulate habitat suitability for shorebirds.

Methodological Challenges With AI Identification

To assess water level preferences of shorebirds at the community level, we trained the AI identification models at the shorebird species level, but finally used the data at the resolution of the community level for improved accuracy (i.e. matching the identified species to the appropriate taxonomic group). This accuracy was analyzed by performing the analysis on all 86,400 images using AI, and additionally manually on 2880 images. This allowed for searching in both datasets for the same patterns and identified an accuracy of about two-thirds. This compares a manually processed much smaller dataset (1 day before and 1 day after sampling) to the AI processed larger database (5 days before, 5 days after) and concludes that both approaches reveal a similar ecological pattern. Both datasets showed clear variation in the numbers of observed shorebirds on the images, which allowed us to analyze the underlying ecological explanatory variables (water level and macrofauna).

There was temporal variation in bird numbers, with most shorebirds counted later in the season (August, September). The AI model overestimated the number of shorebirds mostly early during the year (May), if compared to the manual shorebird counts. This can be explained by the presence of birds from other taxonomic groups at the higher water levels earlier in the season. Particularly the Anatidae and Laridae that were identified showed a bias toward presence at deeper water levels than shorebirds, or had no preference. This implies that several other bird species than shorebirds were also identified by the ResNet model as shorebirds, and that these misidentifications explain a large part of the 30% inaccuracy of the AI model. Knowing this, we can conclude that this bias is unlikely to have contributed to our ecological conclusion that shorebirds prefer shallow waters, as false inclusion of Laridae and Anatidae would have directed our conclusion toward a preference of shorebirds for deeper water. As such, any misidentification of birds by our AI methodology early in the season likely added noise directed toward "shorebirds prefer higher water levels," and thus did not contribute to the overall observed ecological preference of shorebirds for shallow waters.

The accuracy of our approach provides confidence in our choice to use AI bird identifications. However, the AI approach had costs as well as benefits in comparison to traditionally processing images manually. Costs of the AI model include (1) the need to downgrade the data to family level, and thus not yet being able to work with individual species; (2) a loss of accuracy in the identifications, in which bird experts would at present be better; (3) error propagation of mistakes at scale, instead of remaining local mistakes; (4) a loss of serendipity and spotting particularities, that is, by manually processing

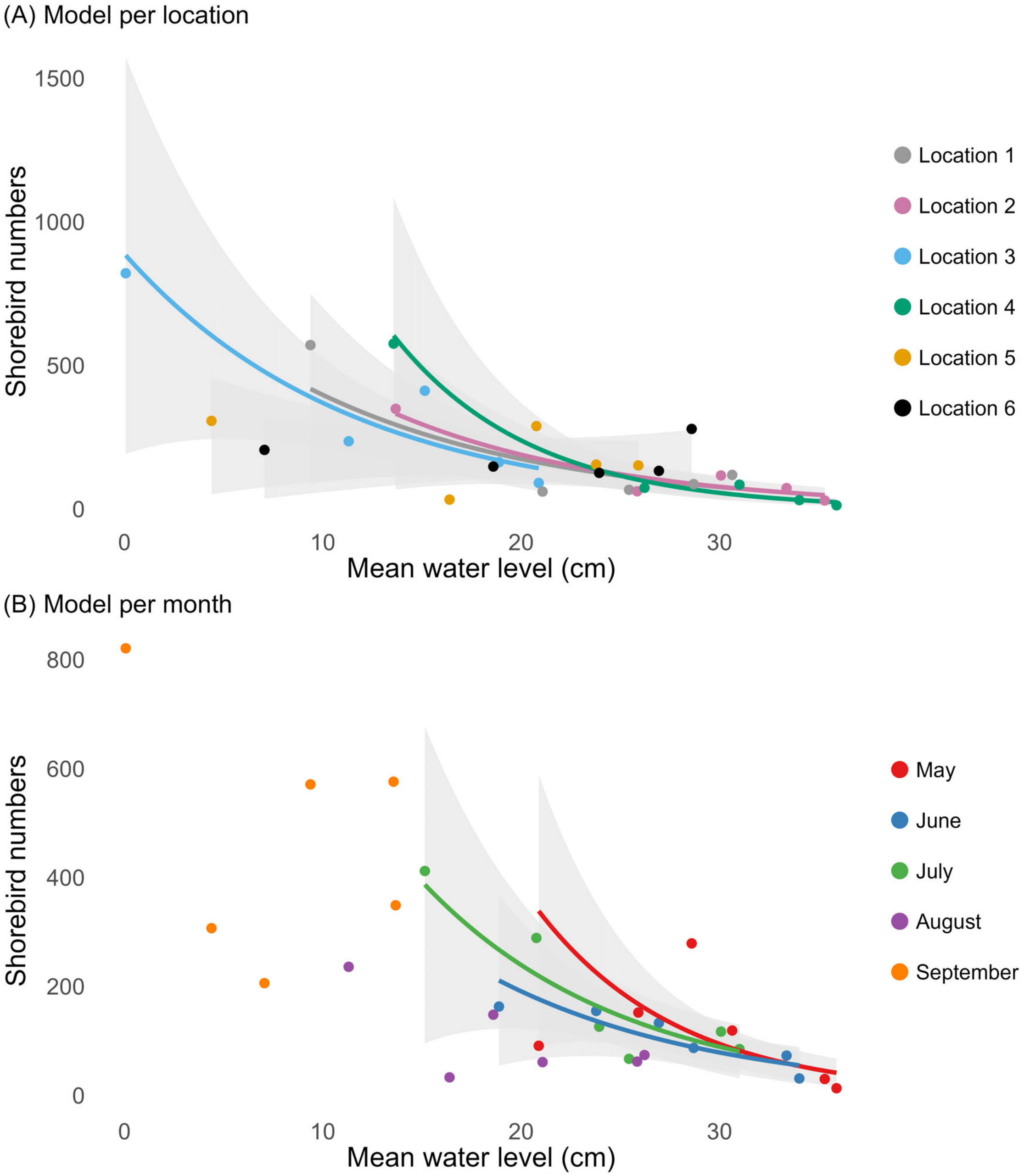

Figure 4. Number of shorebirds present in relation to observed water levels in the study area depicted (A) for each of the six study locations, and (B) for each of the 5 months of the study. In both panels, significant relationships based on individual generalized linear models with a negative binomial distribution are depicted with solid lines with 95% CIs. Non-significant relationships are not shown.

images, scientists also learn about their ecosystem and may make observations that could lead to future research; and (5) the environmental costs of energy-intensive AI models. However, AI approaches can also have many potential benefits, which include (1) an improvement in accuracy due to scalability of the number of processed images, adding confidence to overall observed patterns; (2) a known and consistent error, that is independent of which researcher is processing the images (and for instance at what time of the day, day of the week, increase in experience over time); (3) an objective assessment of the images without unconsciously bias; and (4) exact reproducibility of scientific results. Finally, we also expected the benefit of a lower time investment; however, in retrospect, creating and training of the AI methodology was similarly time-consuming. Choosing to use AI models therefore requires future studies to weigh their time investment for training of AI models based on how many images need to be processed. Still, considering the rapid improvements of AI methodology, the further application of

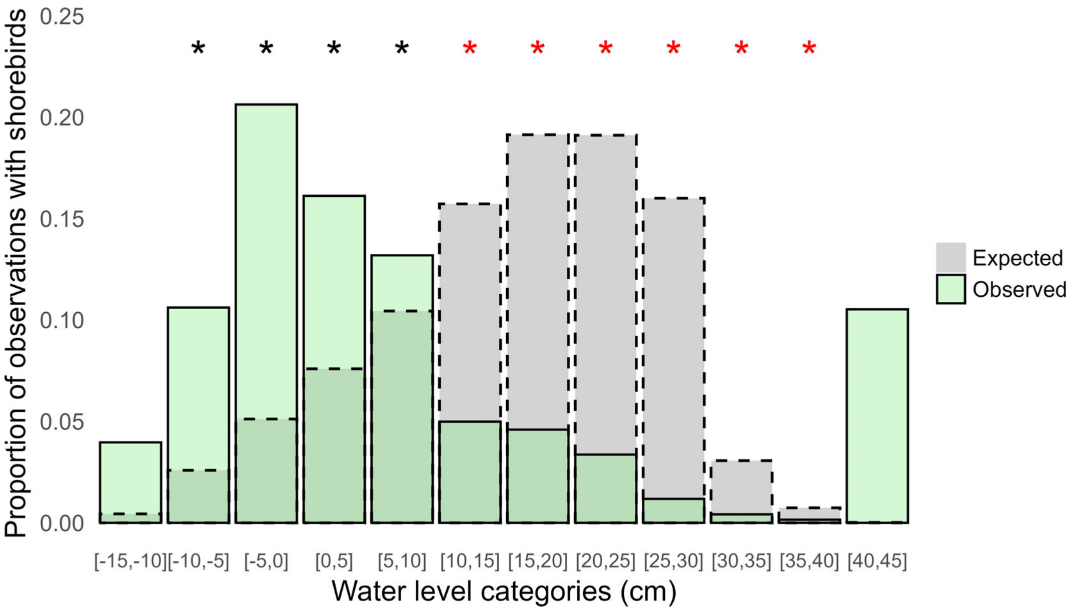

Figure 5. Distribution of observed proportions of shorebird observations per category of 5 cm water levels (green bars), and expected proportions under random site selection (gray bars). Asterisks above the bars indicate a significant difference between observed and expected proportions based on chi-squared tests for independence and Bonferroni corrected Tukey HSD post hoc tests, differentiating between higher (black asterisks) and lower (red asterisks) proportions than expected in the case of random site selections by shorebirds. Negative water levels indicate situations where the water levels are below the sediment surface.

AI identification for studies will without doubt become more user-friendly to set up and make it possible to study specific species of interest with the same methodology in the near future.

Water Level Management in Freshwater Wetlands

The relationship between water levels and shorebirds has long been recognized; however, mostly in relation to tidal fluctuations in situations where management of water levels is impossible. Our study highlights the high potential to improve shorebird habitat by regulating water levels in freshwater ecosystems. These effects of water levels on shorebirds likely stretch far beyond our study system, as, for example, shown for small-bodied shorebirds preferring shallow water on grassland ecosystems during winter floods (Safran et al. 1997; Colwell & Taft 2000), strong preferences for wet conditions by shorebirds in the marine realm (e.g. Helmers 1992), and also linked to studies on a wider range of birds in relation to water dynamics (Lipford et al. 2025). This suggests that the regulation of water levels can be broadly applied in a more global context of shorebird conservation and restoration. We emphasize the importance of the fine scale of this high-resolution management and stress that it needs to be maintained for the full period that (migratory) shorebirds are present in a managed area.

Despite its importance, shorebird foraging habitat quality is not solely determined by maintaining stable water levels within an accessible depth range throughout the annual cycle. Various ecological processes regulate the abundance of resources for shorebirds, and such wetland processes may require a dynamic hydroperiod instead, including times when water levels are lower or higher—and not ideal for shorebirds. By stabilizing water levels to always maintain a range accessible to shorebirds, chemical processes, and productivity by other trophic levels in the food web may be affected (Åhlén et al. 2024), potentially reducing habitat quality despite accessible water depths. In addition, managing water levels to be best for shorebirds locally could have consequences for other wetland birds. In our study, Anatidae were found to be present at practically all observed water levels at similar intensities, while Laridae were more often observed at water levels between 15 and 25 cm. Whether or not this is a result of active or random water level selection and how this relates to habitat suitability at the landscape level are interesting avenues to explore in future studies.

From a restoration context, a dynamic form of water level management that ensures optimal conditions for all biota at each season is more feasible to implement in freshwater systems than in tidal coastal systems. However, also in freshwater wetlands, the regulation of water levels has its limitations. Here we use our own study system of Lake Markermeer as a case study to illustrate this. Our study was carried out in Lake Markermeer in the Netherlands, which is a degrading Natura 2000 protected large shallow lake (van Leeuwen et al. 2021). The new Marker Wadden wetland islands were constructed via engineering in a “building with nature” approach and led to a novel ecosystem of over approximately 1300 ha of marshlands, with the aim and result that bird and fish communities of different life stages profited at local scales (van Leeuwen et al. 2023; Jin et al. 2024; van der Winden et al. 2024). However, because Lake Markermeer also provides ecosystem services such as drinking water supply to a large part of the Netherlands (van Leeuwen et al. 2021), water levels are actively managed as reversed compared to natural fluctuations (see methods for details). That is, water levels

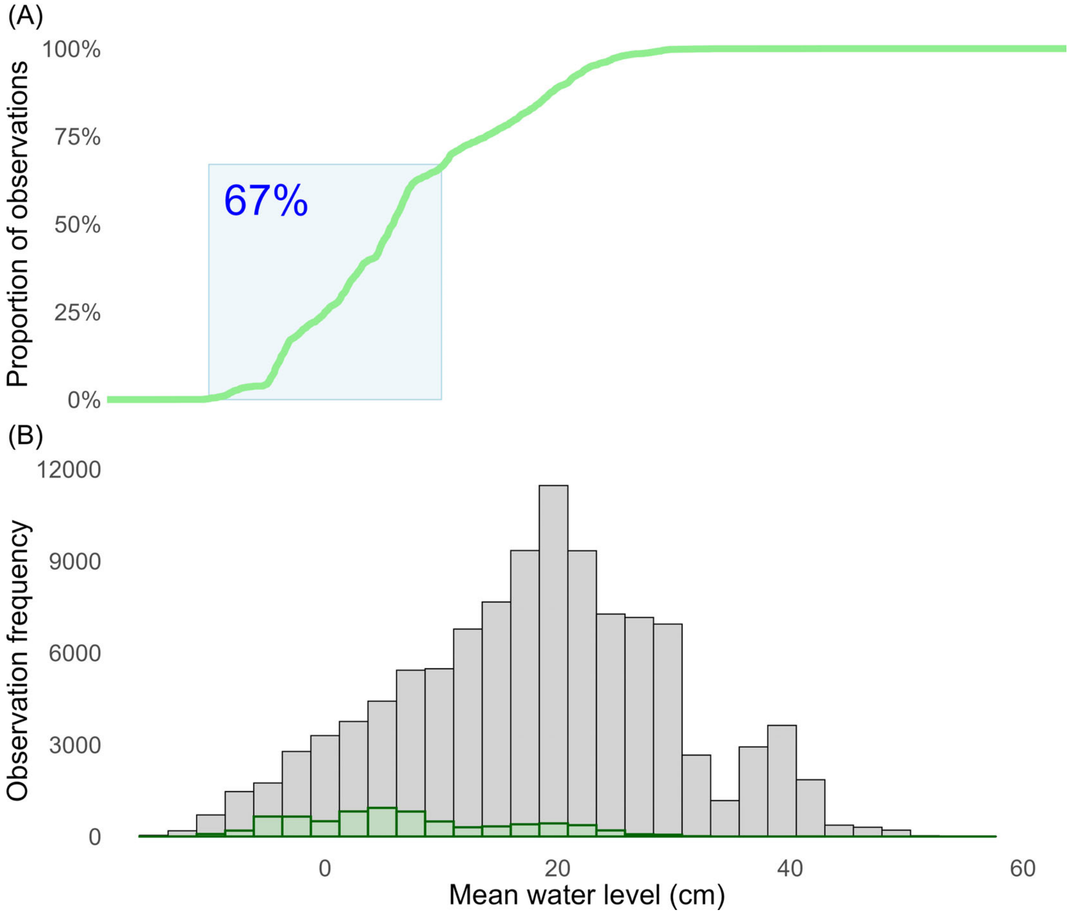

Figure 6. (A) Water level preference of shorebirds visualized as an empirical cumulative distribution function (ECDF) for shorebird numbers as a function of water level. The blue box indicates that water levels ranging from −10 to 10 cm contribute 67% of shorebird observations, matching the peak in shorebird observations in that range of water levels (as displayed in panel B). (B) The distribution of water levels is given for when shorebirds were observed in an image (green bars). The total distribution of water levels is also shown (gray bars) for comparison. This comparison shows that shorebirds were mainly observed when mean water levels ranged from 10 cm above the sediment surface to 10 cm below the sediment surface, although a wide range of water level ranges were commonly observed (notably around 20 cm of water depth).

are higher in summer (water storage for drinking and irrigation) than in winter (for water safety). In recent years, the Dutch water authorities changed their policies, which resulted in higher spring and summer water levels since 2018 compared to previous years. As the nature restoration project of Marker Wadden was constructed while taking into account water level management of years prior to 2018, the aim of creating mudflats with shallow water for shorebirds is challenged. This illustrates that, despite knowledge on optimal water level management for shorebirds, implementation can still be constrained.

These contrasting requirements between humans and nature within one freshwater ecosystem are not unique to our study system, and related to the increased freshwater demand worldwide (Dudgeon et al. 2006). Water extraction for agriculture is, for instance, also known as an important challenge for the renowned wetlands in Doñana National Park in Spain (Green et al. 2024), which makes water shortage a common threat to wetland ecosystems (Huggins et al. 2023). Climate changes will likely worsen future flexibility in water level management, as riverine discharges and rainwater influx become less predictable. Regulating water levels may therefore be a technical and societal challenge in many freshwater ecosystems. We hope that the here provided quantification of how water levels can impact shorebirds can support these discussions and can contribute to better conservation and restoration of wetlands.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Parameters of the regression equations (DM $= a \times L^b$) from linear body dimensions (L, mm) of invertebrates from references used in this study to calculate body biomass (mg).

Table S2. Corrected Akaike’s Information Criterion (AICc) of the fitted models explaining the number of waders observed on the basis of all possible combinations of predictors.

Figure S1. Observations of the four taxonomic groups used in our study were matched with the mean water level at the moment of the observation, for which the distributions are shown.

Figure S2. Relationship between automatic (x-axis) and manual (y-axis) image processing for wader counting.

Figure S3. The variation over space and time is represented for benthic and pelagic macrofauna biomass.

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