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RESEARCH ARTICLE

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Creating wetland islands to enhance shoreline habitat for fish recruitment in a modified shallow lake

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Abstract

1. Soft shoreline engineering is increasingly used to combine shoreline fortification with the enhancement of biodiversity and biological production of land–water transitions. From 2016 to 2021, the large-scale ecosystem restoration project Marker Wadden has created new multiple wetland islands from local sediments in the highly modified Lake Markermeer, the Netherlands. Instead of replacing steep rip-rap shorelines with soft shorelines, new islands with soft land–water transitions were engineered to offset the marked declines in bird and fish populations in this Natura 2000 area, protected under the European Union Birds and Habitats Directives.
2. This new approach was evaluated by assessing the added value of the newly created wetland islands with soft shorelines to the existing steep rip-rap fortified shores of the lake, for the enhancement of fish spawning and nursery habitat.
3. Young-of-the-year fish densities at the Marker Wadden islands were highest in sheltered bays and wetlands with nutrient-rich silt sediments, and lowest at wind-exposed sandy beaches. Both newly engineered soft shorelines and existing rip-rap shorelines contributed to habitat diversity, although fish densities declined considerably with increasing exposure to wind-induced wave power.
4. Building soft shorelines as a new archipelago instead of replacing existing shoreline habitats increased the total length of the land–water transitions in the lake. The 800 ha Marker Wadden archipelago covers only 1% of the 70,000 ha lake surface area, but provides a 16% increase in shoreline habitat and a fivefold increase in soft shoreline for the lake.
5. We conclude that designing wetland islands as a means of lake restoration can contribute effectively to sheltered habitat enhancement for fish spawning and nurseries, and thereby to the potential conservation of fish communities. The approach of building islands achieves this without compromising the complementary functionality of the original, more mature, shorelines of the lake.

KEYWORDS
fish larvae, Marker Wadden, soft shoreline engineering, nursery habitat, rip-rap, land-water transition

1 | INTRODUCTION

Gradual land–water transition zones are key habitats for natural processes in lake ecosystems (Strayer & Findlay, 2010; Vadeboncoeur et al., 2011; Winfield, 2004). Such zones are often covered with submerged and emergent vegetation, which support biological production and biodiversity (Duncan & Kubečka, 1995; Wetzel, 2001). The shallow waters of such transition zones are important for spawning and nurseries for many different fish species (Radinger et al., 2023; Vadeboncoeur et al., 2011; Winfield, 2004). However, the gradual land–water transition zones of rivers, lakes, and coastal wetlands around the world are increasingly replaced and surrounded by hard rip-rap constructions, to prevent shoreline erosion for water safety purposes (Gittman et al., 2015; Strayer & Findlay, 2010). Shoreline hardening, with unnaturally steep land–water transitions, offers limited space for natural shallow-area conditions, such as overhanging vegetation, input of terrestrial nutrients, and physical structures that function as feeding and refuge habitat for young fishes. Therefore, the diversity and density of young fishes are typically reduced in aquatic systems dominated by rip-rap shores (Duncan & Kubečka, 1995; Kornis et al., 2018; Massey et al., 2017; Purcell et al., 2013).

Restoration efforts in many lake systems increasingly call for reversing this process by replacing rip-rap with more natural, gradual land–water transition zones, often called 'soft shoreline engineering' (Hartig et al., 2011). These new habitats are typically constructed of sand deposited with gradual slopes along the existing steep shorelines (Hartig et al., 2011; Munsch et al., 2015; Toft et al., 2013). Fish communities can benefit from such gradual connections between terrestrial and aquatic ecosystems, because wider shallow zones along the shores provide food and shelter for young fishes of many species, especially if these zones are enriched habitats in which emergent and submerged vegetation becomes established (Radinger et al., 2023; Winfield, 2004). However, as rip-rap shore protection is primarily applied at locations with strong wind and wave exposure, the effectiveness of the restoration may be conditional on where the engineering takes place (Duncan & Kubečka, 1995). Long fetch lengths, i.e. the distances over which wind can travel over the lake surface, are common in large freshwater lakes, with strong winds able to create waves with destructive forces for the littoral environment (Mason et al., 2018; Ton et al., 2023). Even after wind speeds have decreased, residual water movement continues for many hours or even days, and shorelines not protected by rip-rap may erode and continue to change dynamically. This is of great significance for the morphological development of low-energy, nontidal beaches in shallow, wind-driven water bodies (Ton et al., 2023). Climate change predictions include an increase in storm frequency and magnitude, affecting the physical conditions in lakes, the water chemistry, and the aquatic food webs (Jabbari et al., 2021). Replacing rip-rap shorelines with more gradual natural shorelines should therefore be studied together with the effects of wind exposure.

Lake Markermeer in the Netherlands is a large 70,000 ha shallow lake in which biological processes are dominated by the wind-induced dynamics of sediment suspension and steep rip-rap shoreline protection (De Lucas Pardo et al., 2013; Van Leeuwen et al., 2021; Van Riel et al., 2019). Fetch lengths in the lake may exceed 25 km, and mean annual wind speeds in the Netherlands are between 2 and 5 m s^{-1} (Ton et al., 2023). Lake Markermeer is part of the larger Lake IJsselmeer system that was created through the construction of a large rip-rap dyke in a former marine estuary of the river Rhine in 1932 for flood protection, and then subsequently divided into two lakes by another rip-rap dyke in 1975. The isolation of Lake Markermeer from the river also implies reduced nutrient inputs and the recirculation of fine sediments that were formerly transported to the sea. Combined with a strong decrease in phosphate levels (from water purification and residuals from washing detergents and agriculture), biological productivity has declined since 1980 (Van Leeuwen et al., 2021; Van Riel et al., 2019). Consequently, young fish stocks have gradually declined (Figure 1), as have the yields of commercial fisheries (De Leeuw et al., 2008). In addition, many bird species protected by the European Union (EU) Birds Directive (Council of the European Communities, 2010) have declined in numbers (Van Rijn & Van Eerden, 2021).

Low nutrient levels and high concentrations of fine sediments in the water column of the lake have been proposed as causes of declining lake productivity, both in the benthic communities (Van Riel et al., 2019) and in the pelagic communities (Jin et al., 2022). One restoration measure that could potentially address both factors simultaneously is to construct natural shallow shore zones enclosing sheltered zones in the lake (Van Leeuwen et al., 2021). Creating gradual land–water transition zones can be expected to reinforce habitat coupling between terrestrial and aquatic ecosystems, via processes such as the run-off of terrestrial organic matter and nutrients into the water column (Schindler & Scheuerell, 2002). In addition, shoreline construction is likely to create sheltered sections in the lake, where wind-induced resuspension would decrease to create more transparent and warmer shallow zones in spring (Čech et al., 2012; Finlay et al., 2011; Trochine et al., 2022). The designation of Lake Markermeer as a Natura 2000 protected area in 2009, under the EU's Birds Directive (Council of the European Communities, 2010) and Habitats Directive (Council of the European Communities, 1992), further stimulated large restoration projects aiming to increase the length of productive, gradual shore zones and the surface area of sheltered zones, with a specific goal to enhance fish stocks and populations of protected wetland bird species.

These restoration approaches included a unique project, called Marker Wadden. Beginning in 2016, a new archipelago of five

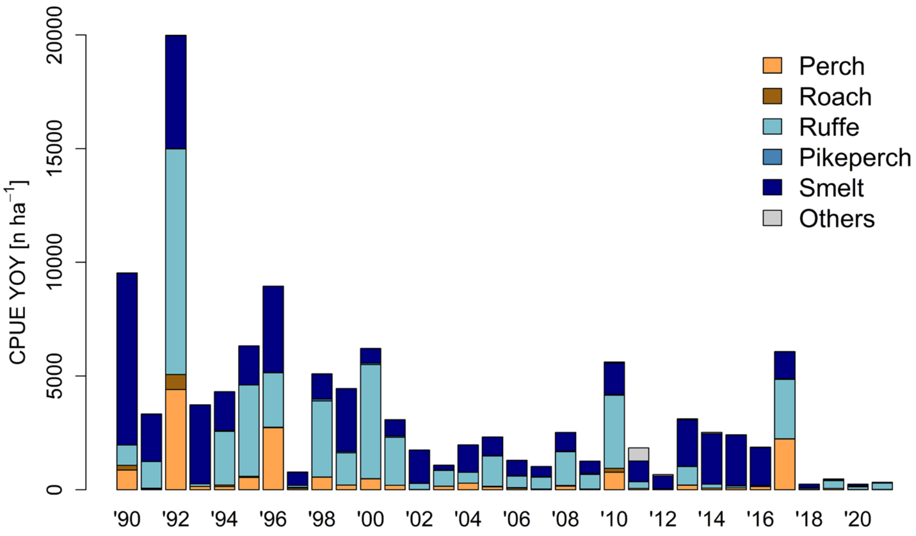

FIGURE 1 Trends in young-of-the-year fish index (catch per unit of effort, number per ha swept area, as indicator of stock size) in Lake Markermeer based on the annual open water bottom trawl survey in October/November. Note that bottom trawls are selective for bottom-dwelling species, whereas more pelagic species, especially smelt (*Osmerus eperlanus*) are underrepresented in the catches.

wetland islands of 800 ha has been constructed in the most wind-exposed area of the lake (Van Leeuwen et al., 2021). The islands of Marker Wadden were created as ring dykes from locally extracted deep Pleistocene sand layers, filled with local former marine Holocene clays and silts from the top 6–7 m layer of the lake bottom. The use of nutrient-rich marine silt layers and the creation of sheltered bays and wetlands in the manmade archipelago supported the rapid colonization of a large diversity of organisms (KIMA, 2022). In addition, several other nature development projects were carried out in the vicinity of Marker Wadden, including the deposition of sand and the creation of wetlands in 2018 along the dyke separating Lake IJsselmeer and Lake Markermeer. A unique feature of the Marker Wadden project is that it added soft shorelines to the lake without replacing existing rip-rap shoreline habitats.

The aim of this study is to assess the added value for fish recruitment of constructing novel islands consisting of sheltered wetlands with gradual shorelines in a shallow lake that is strongly influenced by wind and is dominated by rip-rap shore protection. We hypothesized that: (i) young-of-the-year fish densities in coastal habitats in Lake Markermeer would be higher at shorelines that are more sheltered from wind and wave exposure; and (ii) the highest densities of young-of-the-year fishes would occur in the newly created sheltered shallow wetland areas of the Marker Wadden islands.

2 | METHODS

2.1 | Shoreline alterations

2.1.1 | Lake Markermeer

Shoreline habitats were identified in Lake Markermeer by combining analyses of satellite images and aerial photographs with ground-truthing during the annual surveys of young fishes near the shoreline. Four shoreline habitats were distinguished: (i) rip-rap basalt blocks with steep slopes to the lake bottom at approximately 2.0–4.5 m of water depth; (ii) reeds growing on rip-rap shores; (iii) sandy beaches with a more gradual slope; and (iv) shallow, sheltered wetlands with pioneer vegetation (Figure 2a). The length of each type of shoreline habitat was assessed over two periods of time: (i) the time between 2007 and 2016, during which no major soft shoreline restoration projects were carried out on the shorelines (with alterations on less than 2% of the total shore length of the lake); and (ii) the time between 2016 and 2021, during which 1400 ha of soft-shoreline wetland islands and peninsulas were newly created, which increased the total shoreline of the lake from 284 km in 2016 to 370 km in 2021 (a 30% increase) and the total soft shoreline from 8 to 89 km (an 11-fold increase) (Figure 3).

These shoreline habitat enhancements included predominantly: (i) sand supplementation on rip-rap shores (9.6 km, mainly in the north-western and north-eastern part of the lake, along the dyke separating Lake Markermeer and Lake IJsselmeer), often accompanied by rip-rap breakwater dams at some hundreds of metres parallel with the shore to protect the sandy beaches from wave action. (net increase of rip-rap shores amounting to 13 km) (a 4.6% increase); and (ii) novel construction of wetland islands (Marker Wadden archipelago, 800 ha, representing 1.1% of the surface area of the lake) and wetland peninsulas (Trintelzand in the north-eastern part of the lake, 530 ha, representing 0.8% of the surface area of the lake).

2.1.2 | Marker Wadden

The construction of Marker Wadden between 2016 and 2021 added 45.8 km (16%) of additional shoreline to Lake Markermeer, estimated on a scale of approximately 100 m (given that the vegetated shores especially follow an almost fractal geometry). This resulted in a fivefold increase in the length of soft shoreline present in the lake. The new area included 14.1 km of exposed shoreline of mostly sandy beaches and 31.7 km of new sheltered gradual shorelines along bays and sheltered shorelines between the islands, as well as shorelines of the wetlands on the islands. The nutrient-rich sheltered wetland shore zones were rapidly colonized by the pioneer vegetation of marsh

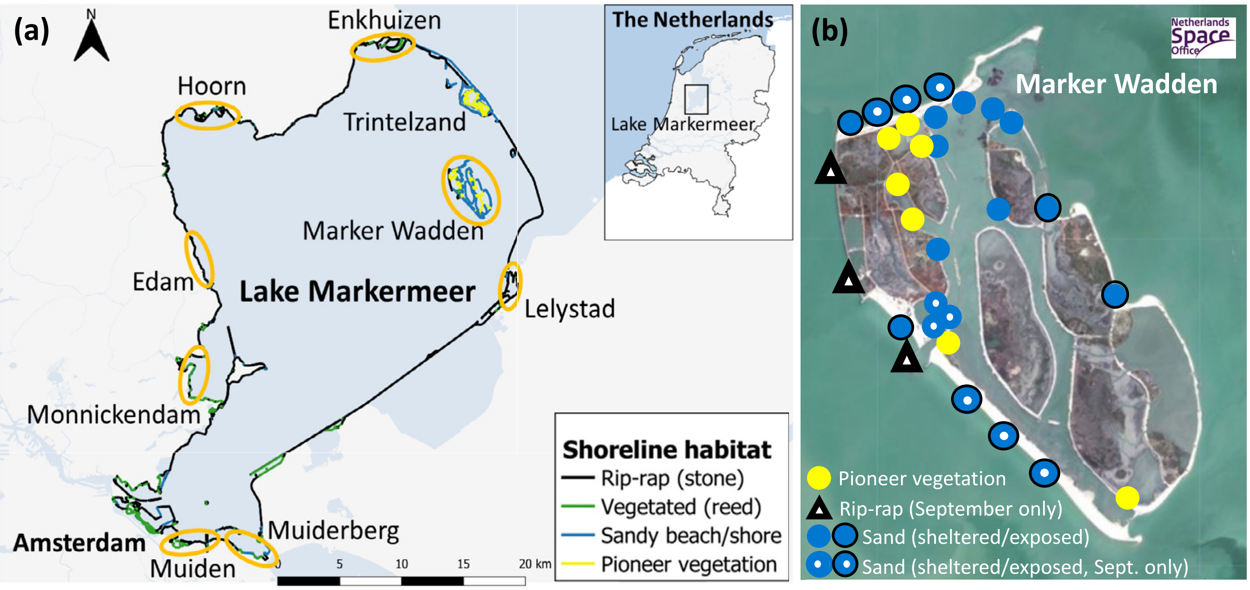

FIGURE 2 Study area: (a) shoreline habitats and sampling sites (orange ovals) in Lake Markermeer; and (b) sampling locations at Marker Wadden (colours represent habitats; closed symbols, entire growing season; open symbols, September only; round dots, beach seine; triangles, electrofishing; symbols with a black outline, exposed sites). The islands in the north-western part of the archipelago were created in 2016 and 2017, with the remaining islands created in subsequent years.

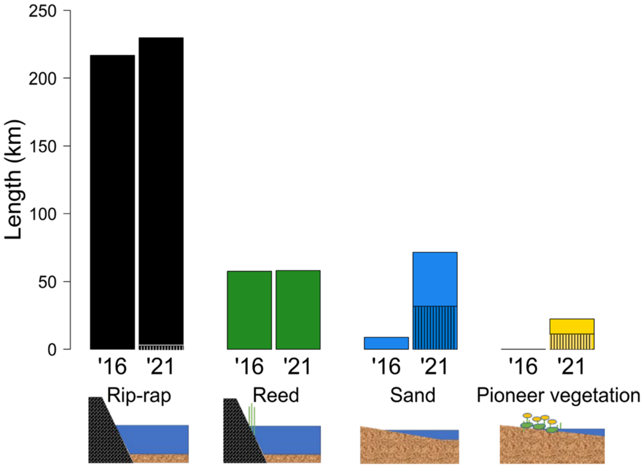

FIGURE 3 Length of shoreline habitat in Lake Markermeer in 2016 and in 2021, before and after the creation of the Marker Wadden islands (hatched part of bars) and other shallow shore zones in the lake, respectively. Note that rip-rap and reed (growing mostly on rip-rap) refer to steep shores to water depths of 2.0–4.5 m, whereas sand shores and shore zones with pioneer vegetation have shallow slopes.

fleawort (*Tephroseris palustris*) and locally the settlement of reed (*Phragmites australis*) and cattail (*Typha latifolia*).

2.2 | Wave power

Wave power was calculated to assess the effect of wind exposure on fishes. Wave power (also known as 'wave energy flux') expresses the power of water movement (W m^{-1}). Wave power is based on wind fetch, i.e. the distance over which wind travels over a water surface, wind speed, and water depth. The length of wind fetch at any given location typically depends on the wind direction. Therefore, a line shapefile of Lake Markermeer was created in QGIS 3.4.3 (https://www.qgis.org). This line shapefile and the sampling locations were imported into R (R Development Core Team, 2023). Fetch lengths of every sampling location were calculated for every wind direction (over 1–360°). Wind data were downloaded from the open data source of the Royal Dutch Meteorological Institute (KNMI) for the location 'Houtribdijk'. This included wind directions per day (1–360°) and the mean daily wind speeds over the study period. The water depth in Lake Markermeer was assumed to be 4 m on average for all locations. For some shallower shores at more sheltered locations (i.e. with low wave power) this assumption may slightly overestimate the wave power, resulting in conservative estimates of the differences in wave power between sheltered and exposed sites.

With the above-described parameters, wave power was calculated using the function 'wave energy' in the 'waver' package of R (Marchand & Gill, 2018). First, this function gives an estimate of significant wave height and wave period. Second, the wave power is calculated per day per location in kW m^{-1}, which was converted to W m^{-1}. Third, wave power was averaged over the period from 1 March to 30 June for all separate locations during both study years (2020 and 2021). This was the period when fish larvae were present, which were assumed to be the life stage most vulnerable to wave action. For all analyses, wave power was natural log(x+1) transformed to approach normality of residuals.

2.3 | Fish surveys

Standardized annual surveys of young fishes in the open water of Lake Markermeer have been carried out in October/November since 1990 using a 7-m (until 2012) or 4-m (since 2013) wide bottom trawl (mesh size 60 mm, decreasing to 20 mm at the cod end) to sample 14 locations per year with hauls of approximately 1 km. Bottom trawls are selective for bottom-dwelling species, whereas more pelagic species, especially smelt (*Osmerus eperlanus*), are under-represented in the catches (Mous, 2000). From each haul, fishes were sorted to species level and the total body length was measured to the nearest cm below, either for the whole catch or from subsamples in the case of large numbers of small fishes.

Surveys of young fishes along the shorelines of Lake Markermeer have been carried out annually in late August and early September since 2007. Boat electrofishing has been used along the steep rip-rap shores (13 locations per year, on average 670 m per location) and a 20-m wide beach seine (mesh size 18, 10 mm at the cod end) has been used on sandy beaches (five locations per year, on average 300 m^2 per location). Length distributions per fish species were assessed as described in the open water survey. Surveys of young fishes along the shorelines of the new Marker Wadden archipelago were performed once or twice per month between April and August in 2020 and 2021. Fish larvae and larger young-of-the-year fishes were captured with fine mesh larvae nets (width 25 cm, 0.3 mm mesh size), coarse young fish nets (RAVON, width 70 cm, 3 mm mesh size), and small-mesh beach seines (width 3 m, mesh size 3 mm; width 15 m, mesh size 10 mm) (Figure 2b). Sampling conditions in shallow habitats varied owing to unstable (quicksand) sediments, especially in the first years after the creation of the islands. Most sampling operations were carried out by wading along the shore. Beach seining was usually supported by a small boat setting out the net. Sampling effort for larvae nets varied between 20 and 100 m shoreline; sampling effort for beach seines typically covered surface areas of approximately 160 m^2. In September 2020 and 2021, additional fish sampling was carried out at Marker Wadden using boat electrofishing along the rip-rap shores (three locations) and using beach seining at gradual sand beaches (nine locations) (Figure 2b).

During the sampling of fish larvae and larger young-of-the-year fishes, fishes were identified in the field and total body lengths were measured to the nearest cm below to determine age classes. Fish larvae caught early in the season during sampling campaigns at Marker Wadden could not all be identified immediately in the field. Therefore, these larvae were stored in 4% formaldehyde solution and analysed within 6 months under a Leica M205C stereomicroscope (Leica Microsystems, Wetzlar, Germany). Species identification of these early life stages was primarily based on pigmentation, number of fin rays, preanal and postanal myomeres, and body lengths, measured to the nearest mm below under the microscope (Pinder, 2001).

The young-of-the-year age class was identified by analysing length–frequency distributions for the presence of peaks representing cohorts of fishes in the population. The first peak with the smallest fishes was assumed to represent young-of-the-year fishes; for most species the young-of-the-year fishes are easily discernable from older fishes during the growing season. However, for some benthic species, such as ruffe (*Gymnocephalus cernua*) and gobiids, some overlap with older age groups might occur by the end of the growing season in August/September. Fishes were only classified as young-of-the-year if their body lengths were below a species-specific demarcation length ('maximum size', listed in Table S1).

2.4 | Statistical analyses

Data were analysed using multiple statistical models (Table S2) in R for statistics (R Development Core Team, 2023). Models were constructed with package lme4 (Bates et al., 2015) and glmmTMB (Brooks et al., 2017), where there were nonnormal distributions of the dependent variables. To determine which predictor variables contributed significantly to a model, model selection procedures were performed based on the Akaike Information Criterion (AIC). During model selection, models with ΔAIC values of >2.0 were considered to be different, and models with the lowest AIC value were selected for further analyses of effect sizes for the terms of interest (Burnham et al., 2011; Burnham & Anderson, 2002). All continuous explanatory variables were centred by subtracting their means from all values (following Raudenbush & Bryk, 2002). Durbin–Watson tests were used to assess the possible influence of temporal autocorrelation, and model residuals were analysed for possible heteroscedasticity, overdispersion, and zero inflation with the package 'DHARMa' in R (Hartig, 2022).

Data on trends in young-of-the-year fishes in the open water of Lake Markermeer were analysed with model 1. Model 1 was a generalized linear mixed-effects model with fish counts as the dependent variable, modelled with a Poisson error distribution and log link function – as appropriate for count data. Fish counts were dependent on 'year since the start of fish surveys' as the continuous predictor variable of interest to analyse whether there were temporal trends, whereas 'swept area' and 'sampling location' were included as random intercepts to account for variation in fishing effort and repeated sampling at the same locations over different years, respectively. Model 1 was first run with the counts of all fish species combined as the dependent variable, and with 'fish species' included as an additional random intercept with eight levels (after the removal of rare species with <50 captured fish to allow models to converge). Second, to detect species-specific trends, the model was run separately for counts of perch (*Perca fluviatilis*), smelt, and ruffe as the dependent variable (without fish species included as a random intercept).

Data on trends in young-of-the-year fishes in the shore habitats of Lake Markermeer were analysed with models 2 and 3. Model 2 was a generalized linear mixed-effects model with fish counts as the dependent variable, modelled with a Poisson error distribution and log link function. To analyse trends in fish counts over time, 'year since the start of fish surveys' was the continuous predictor variable in model 2a. In model 2b, 'year' was included as a random intercept to create a repeated-measures model, and the focus was on analysing how fish counts depended on the fixed factor 'habitat type' (two levels: 'rip-rap shore with reed' and 'bare rip-rap shore') and the continuous explanatory variable 'wave power'. In both models, 'surface area (seine)/shore length (electrofishing) fished' was included as a random intercept to account for variation in fishing effort. The interaction between 'habitat type' and 'wave power' was also included in model 2b. However, this inflated the variance of the model owing to collinearity. To further interpret this interaction, the effects of wave power on reed establishment were investigated directly with model 3, by using reed presence as the binomial dependent variable (present, yes/no), depending on 'wave power' as the continuous predictor variable. 'Year' was included as a random intercept.

Data on wave power and young-of-the-year fishes in the shore habitats of the new Marker Wadden islands were analysed in models 4 and 5. Model 4 was a general linear model, with the natural log of wave power as the dependent variable, with a Gaussian error distribution, depending on 'habitat type' as the fixed factor. Model 5 was a generalized linear mixed-effects model with fish counts of all species as the dependent variable, modelled with a zero-inflated Poisson error distribution and log link function. Explanatory predictor variables were 'habitat type', 'month', and their interaction. In model 5, the effects of year and catching effort were accounted for by including these variables as random intercepts. Model 5a was computed on counts of all species combined, and models 5b and 5c were computed for data for perch and ruffe separately, respectively. These three models yielded identical results and therefore only the results of model 5a are further specified. Species-specific data for species other than perch and ruffe were not sufficient for the models to converge.

Model 6a and 6b further explored the impact of wave power and shore habitats of Marker Wadden and Lake Markermeer on young-of-the-year fish densities in two generalized linear mixed-effects models with Poisson error distributions and log link functions. The models used all sampled sites in August and September 2020 and 2021. In model 6a the dependent variable was fish counts at steep rip-rap shores sampled with boat electrofishing, and in model 6b the dependent variable was fish counts at soft shorelines sampled with beach seines. 'Year' and 'fishing effort' were included as random intercepts, and the focus was on analysing how fish counts depended on the fixed factor 'lake or islands' (two levels: Lake Markermeer or Marker Wadden islands) and the continuous explanatory variable 'wave power'.

3 | RESULTS

3.1 | Young fishes in the open water of Lake Markermeer

In the open water of Lake Markermeer, the young-of-the-year fish species composition in October/November was dominated by perch, ruffe, and smelt, as these three species together made up 97% of all fishes captured (Figure 1). Between 1990 and 2021, the total number of individual young fishes declined significantly (model 1: $Z = -390.1$, $P < 0.001$, with a back-transformed effect of a decrease of 9.33% (95% CI = 9.28%–9.38%) every year). These declines were also significant ($P < 0.001$) when analysed for each of the three most dominant species separately: perch (−13.8%), smelt (−11.0%), and ruffe (−7.3%) (models 1b, 1c, and 1d; Table S2). This effect size can be illustrated by the decline in mean young-of-the-year fish counts (all species) per haul from 663 fishes in the first decade (1990–2000), 190 fishes per haul in the second decade (2000–2010), and 105 fishes per haul in the last decade (2010–2021).

3.2 | Young fishes along the shorelines of Lake Markermeer

Along the shore zones of Lake Markermeer, the young-of-the-year fishes in August were dominated by roach (*Rutilus rutilus*) (60.1%), perch (12.9%), and round goby (*Neogobius melanostomus*) (11.4%) (Figure 4; Table S1). The occurrence of species along sandy beaches varied among years owing to the occurrence of large numbers of species such as bream (*Abramis brama*) or ide (*Leuciscus idus*) in some years. The invasive round goby has become abundant since 2013 (Figure 4; Table S1) along the rip-rap shores (Table S1). Total young-of-the-year fish counts have declined significantly since 2007 (back-transformed effect size: decrease of 3.8% (95% CI = 3.65%–4.13%) every year, $Z = -30.9$, $P < 0.001$; model 2a in Table S2).

Young-of-the-year fish counts along the shores of Lake Markermeer were negatively affected by exposure to wave action,

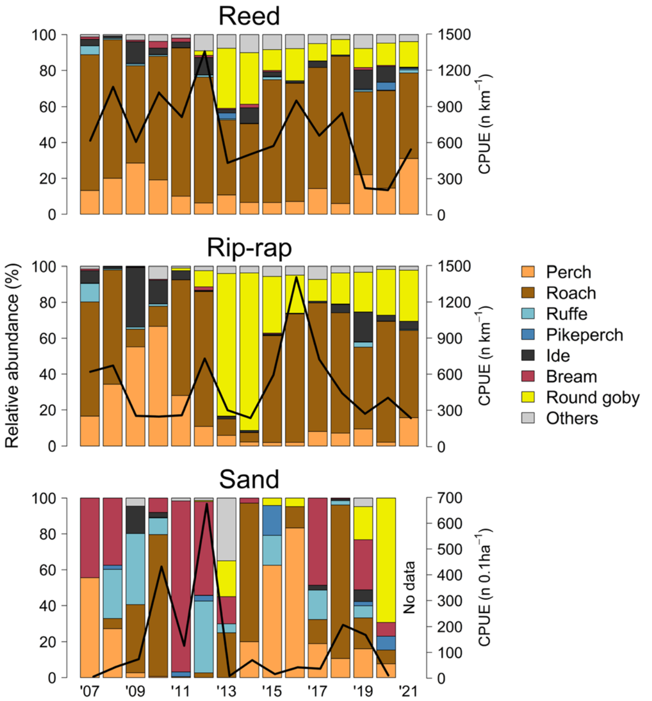

FIGURE 4 Relative abundance (stacked bars) and total catch per unit of effort (CPUE of all species; black line, secondary axis) of young-of-the-year fishes per shore habitat type in Lake Markermeer from 2007 until 2021, based on the annual shoreline survey in August, not including the recent novel habitats. Note the different units for electrofishing (n km^{-1}, upper two panels) and beach seine (n 0.1 ha^{-1}, lower panel).

expressed as ln(wave power + 1). The back-transformed effect size was 21.2% (95% CI 20.7%–21.8%) fewer young fishes when ln(wave power + 1) increased by 1.0 (model 2b; Table S2). Averaged over all years, young-of-the-year fish counts were almost three times lower at the most exposed shores compared with the most sheltered shore zones (Figure 5a). The interactive effect of vegetation and wave power on fish counts was collinear, and thus difficult to separate in model 2b; therefore, the direct response of vegetation (reed presence on rip-rap) to wave power was investigated separately. This showed that reed establishment was negatively affected by wave power: mean ln(wave power + 1) for rip-rap shores with reeds, 1.65 ± 1.10 SD W m^{-1}; mean ln(wave power + 1) for bare rip-rap shores, 2.98 ± 1.27 SD W m^{-1} (logistic regression, $Z = -11.9$, $P < 0.001$; Figure 5b; model 3 in Table S2). Therefore, no further disentangling of the isolated effect of reeds on young-of-the-year fish densities was attempted.

3.3 | Young fishes along newly created shorelines of Marker Wadden

The mean wave power at the sheltered shallow shorelines between the islands with sand or pioneer vegetation (2.6 W m^{-1}) was lower than at the exposed shore zones at the western, eastern, and northern parts of the archipelago (79.8 W m^{-1}) (Figure 6; model 4 in Table S2; $P < 0.001$). The mean wave power in the sheltered habitats did not differ significantly between pioneer vegetation and sheltered sand shorelines (Table S2; $P = 0.48$).

The fish surveys at the new shorelines of Marker Wadden revealed strong variation in young-of-the-year fish densities between the exposed and the sheltered shorelines and over time in the year. This resulted in a significant interaction between habitat type and sampling month (model 5 in Table S2, $\chi^2 = 1169.3$, $df = 8$, $P < 0.001$). For most of the year, the young-of-the-year fish densities at sheltered sandy beaches were similar to the densities in sheltered habitats on nutrient-rich silt with pioneer vegetation. Only in July and August were the densities observed in pioneer vegetation higher (Table S2). In both habitats, densities could be up to 10 times higher than in the exposed shore zones. Densities in all habitats varied over the season from May until September (Figure 6; Table S2), associated with the ontogenetic development and greater mobility of the growing fishes. Densities of young-of-the-year fishes in the sheltered shallow shore zones declined sharply in August. Roach larvae dominated in May, young-of-the-year perch and pikeperch (*Sander lucioperca*) mostly appeared in June and July, whereas ruffe appeared in larger numbers in July and August. Newly hatched perch and ruffe (occurring in May) were rarely observed in both years.

3.4 | Lake versus island shore zones

The densities of young-of-the-year fishes sampled with electrofishing in August and September at rip-rap shorelines were significantly higher at sheltered rip-rap slopes (with or without reeds) than at exposed shores around the lake (model 6a in Table S2; $P < 0.001$). This pattern was found irrespective of whether these shores were at

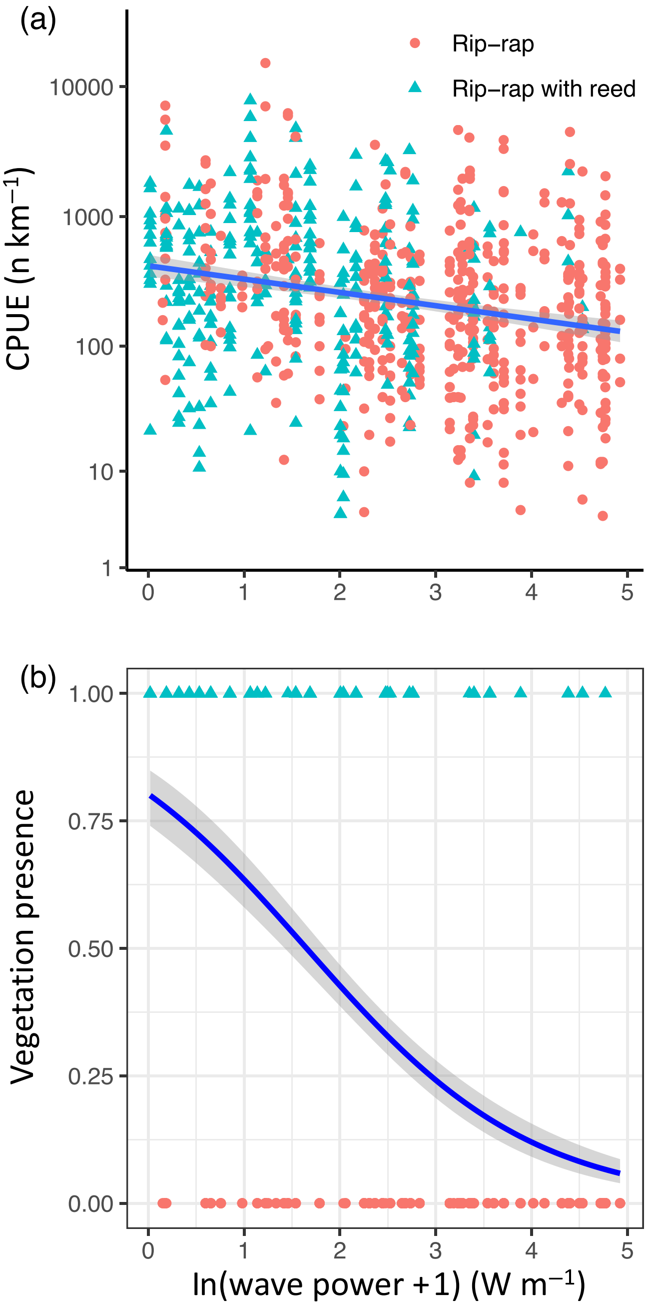

FIGURE 5 (a) Effect of wave power on catch per unit of effort (CPUE) of young-of-the-year fishes (i.e. number of fishes captured per km shoreline) along the shorelines in Lake Markermeer sampled annually between 2007 and 2021. Wave power negatively affected the number of fishes, with 21.2% (95% CI 20.7%–21.8%) fewer young fishes when ln(wave power + 1) increased by 1.0 (model 2b, Table S2), according to the fitted line with shaded standard errors. (b) Effect of wave power on the presence and absence of reeds on the rip-rap shores of Lake Markermeer. Reed establishment was negatively affected by wave power (logistic regression, $Z = -11.9$, $P < 0.001$, model 3 in Table S2, according to the fitted line with shaded standard errors).

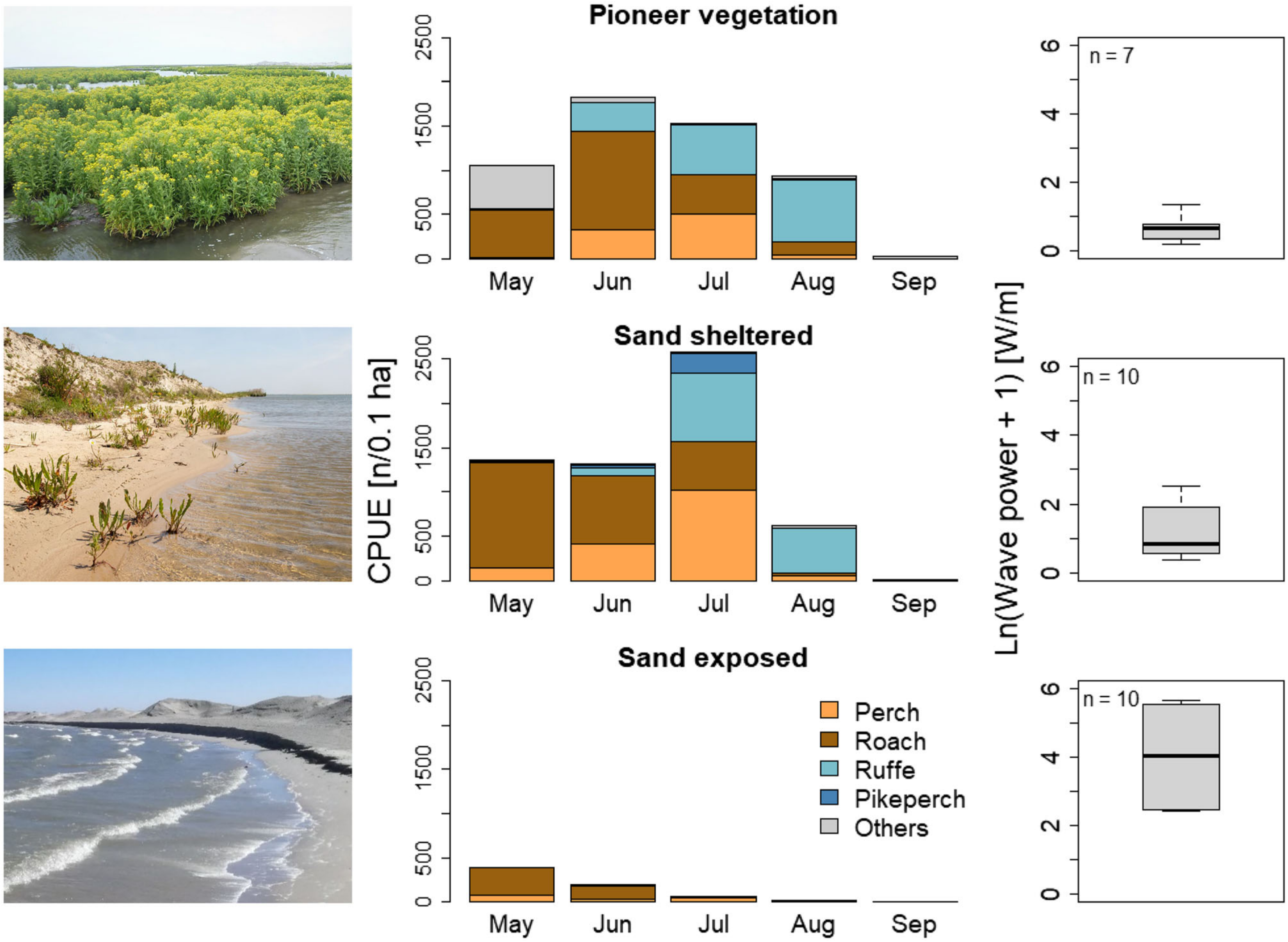

FIGURE 6 Seasonal dynamics of species composition and densities of young-of-the-year fishes (left panels) and wave power (right panels) in different habitats within the Marker Wadden archipelago (beach seine sampling, average 2020 and 2021). Box plots indicate variation in ln(wave power + 1) among the three habitat types, with the boxes in the plot representing the middle 50% of the data for each habitat type, and with the line inside the box representing the median value. The top and bottom of the boxes represent the 75th and 25th percentiles. Whiskers represent maximum and minimum values of the data.

the lake or at the new islands. Young-of-the-year fish densities sampled with beach seines at soft sandy shorelines in August and September were significantly lower at the exposed new shorelines of Marker Wadden than at the sheltered shore zones of the islands (Figure 7; model 6b, Table S2; $P < 0.001$). Soft sandy lake shores and shorelines with pioneer vegetation showed patterns that were consistent with the wave power-related pattern observed (Figure 7).

4 | DISCUSSION

The novel, gradual land–water transitions that were created as the sheltered wetland islands of Marker Wadden have rapidly developed as spawning and nursery areas for fishes. In contrast, similar gradual shoreline constructions at the exposed sides of the newly created islands were inhabited by only low densities of young fishes. This observation corroborates our hypotheses and earlier studies demonstrating the beneficial effect of shelter on the spawning and nursery function of wind-protected shore zones (Duncan & Kubečka, 1995; Radinger et al., 2023; Winfield, 2004). As such, it has important implications for the design of ecosystem enhancement measures aimed at increasing gradual shore zones, whether through replacement of unnatural steep rip-rap shores by gradual sandy shores, or by creating novel wetland islands.

4.1 | Mosaic landscape habitat use

The newly created wetlands and shallow shore zones of the Marker Wadden islands offered suitable habitat for young-of-the-year fishes, especially in the sheltered inshore bays with extensive aquatic–terrestrial transition zones. As the spawning period for most species is in late April and May, seasonal differences in occurrence of species between April and August probably represent differences in habitat use. Species such as roach were predominantly caught right after the spawning season in May and seemed to prefer these habitats for

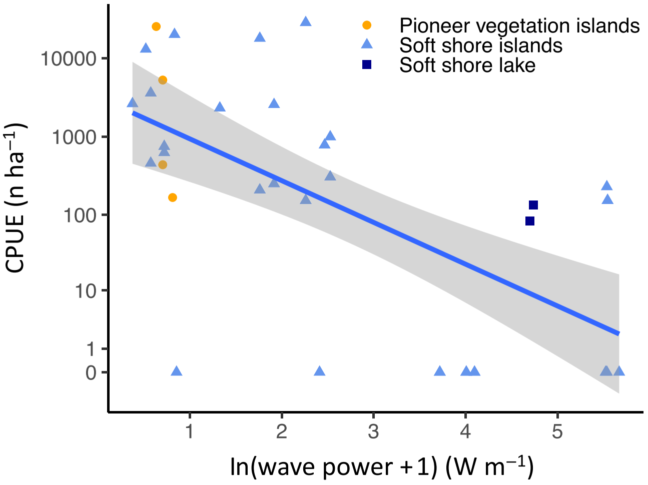

FIGURE 7 Effects of wave power on catch per unit of effort (CPUE) of young-of-the-year fishes in Lake Markermeer and Marker Wadden islands in August and September 2020 and 2021 at soft shore habitats fished with beach seines. CPUE declined significantly in response to increases in wave power, as shown by the fitted line (with shaded standard errors, model 6b, Table S2, $P < 0.001$). Soft sandy lake shores and shorelines with pioneering vegetation at the new islands showed patterns that were consistent with this pattern.

spawning and nursery in their earlier life stages, whereas other species such as perch and ruffe mostly appeared in July and August. The latter two species presumably spawned elsewhere and used these habitats as nursery areas somewhat later in their development. These observations are in line with other studies showing that early larval stages of perch prefer pelagic habitats before shifting to more nearshore habitats, typically when they attain a body size of 1–3 cm, whereas roach generally prefer nearshore habitats throughout their larval and early juvenile stages. Alternatively, ontogenetic diet shifts during summer (e.g. from cladocerans to chironomid larvae or macrocrustaceans, such as *Neomysis integer* or *Gammarus* spp.) have been observed for ruffe upon attaining a body size of approximately 3 cm (Bergman & Greenberg, 1994; Ogle, 1998), which may also have incurred a habitat shift towards nearshore zones. Changes in competition for food, predation pressure, and physical conditions such as turbidity can incur considerable interspecific and intraspecific variation in the occurrence of ontogenetic habitat shifts (Persson & Eklöv, 1995; Byström et al., 2003; Trochine et al., 2022; Urho, 1996).

In August, the densities of young-of-the-year fishes sharply declined. Occasional observations suggest that young fishes moved from the most shallow shoreline habitats to the adjacent sheltered bays and shallows (up to 1 m deep) between the islands, with submerged water plants (e.g. *Myriophyllum*, *Potamogeton*, and *Zanichellia*; Scirpus Ecologisch Advies, 2020). This movement could not be further substantiated because of limited options to sample small fishes in these habitats; unstable sediments (quicksand) limited accessibility, and dense vegetation limited the use of seine nets. Many other studies, however, demonstrated that young-of-the-year fishes may benefit from submerged macrophytes as a refuge against predators (Čech et al., 2012; Quirino et al., 2023; Radinger et al., 2023). Recent telemetry studies demonstrate that piscivorous fishes (van Leeuwen et al., 2023a) and piscivorous wading birds such as the spoonbill (*Platalea leucorodia*) and herons *Ardea* spp. (Dreef et al., 2021) forage on small fishes in the shallow shore zones of Marker Wadden. The predation risk in the shallows with dense, submerged vegetation further offshore is presumably considerably lower (Jacobsen & Perrow, 1998), although great-crested grebes (*Podiceps cristatus*) and black-necked grebes (*Podiceps nigricollis*) forage in these shallow waters between the islands. Littoral vegetation and submerged macrophytes may also contribute to favourable benthic and pelagic food conditions for young-of-the-year fishes (van Leeuwen et al., 2023b), especially for perch (Čech et al., 2012). Such habitat diversity may lead to complex interactions between food availability and predation risk, including the occurrence of diel movements of young fishes that depend on macrophyte cover and turbidity (Quirino et al., 2023). Generally, a mosaic landscape of shallow sheltered shore zones combined with shallow sheltered bays with submerged vegetation thus offers important spawning and/or nursery habitats for a variety of fish species. These habitats provide suitable water temperatures for growth in spring, high food availability, and shelter both from wave action and predators (Čech et al., 2012; Jennings et al., 1999; Quirino et al., 2023; Radinger et al., 2023; Winfield, 2004).

4.2 | Added value of newly created shore zones

Young-of-the-year fishes were widespread along the existing shores of Lake Markermeer, despite the steep and unnatural rip-rap shores exposed to wave action. Rip-rap shores in general are overgrown with epibenthic algae and associated communities of plankton and macrofauna that provide a potential food source for small fishes (Nunn et al., 2012; Reid & Church, 2015; Van Dam et al., 2002). The spaces between the basalt rip-rap blocks can also provide some shelter from both wave action and predation by piscivorous fishes (e.g. perch and pikeperch) and piscivorous birds (e.g. great-crested grebes, gr cormorants (*Phalacrocorax carbo*), or aerial pursuit divers such as common terns (*Sterna hirundo*)). Other studies have also recorded many fish species (and not only young-of-the-year fishes) along rip-rap shores (Kornis et al., 2018; Purcell et al., 2013; Trial et al., 2001). Rip-rap appears especially favoured by gobiid species such as the round goby and the bighead goby (*Ponticola kessleri*), and by eel (*Anguilla anguilla*), in Lake Markermeer (Van Rijssel et al., 2022). The dominance of non-native gobiids is common along rip-rap shorelines (Sindilariu et al., 2006; Zarini et al., 2019), and rip-rap has even been considered as a major driver for the invasion of round goby (Roche et al., 2021). Species such as perch are known to spawn in deeper littoral zones when shorelines are exposed to wave action (Čech et al., 2012; Probst et al., 2009). In the shallow Lake Markermeer, the options to spawn deeper are limited, as the depth of the lake at the rip-rap shores is only about 2.5–4.5 m. Nevertheless, the destructive forces of wave action are less pronounced in the deeper parts of steep rip-rap shores of Lake Markermeer than at exposed shallow shore zones with sandy beaches (Ton et al., 2023), where the densities of young-of-the-year fishes were lowest in this study.

It is tempting to compare the fish densities between the steep, 'hard', rip-rap shores of the lake and the novel, shallow, 'soft' sandy shores of Marker Wadden. However, direct comparisons of the densities of young fishes in shore zones of the lake and of the islands should be made with care for methodological reasons. The steeper shore zones of the lake were mostly sampled using boat electrofishing, whereas the shallow sandy beaches, with or without vegetation, were sampled using beach seine nets. Catch efficiency of boat electrofishing at steep rip-rap shores might differ considerably from catch efficiency using seines at sandy beaches with shallow slopes. In addition, the effects of dispersal of young-of-the-year fishes in summer to adjacent habitats might also differ between the lake (rip-rap shores bordering deep, usually unvegetated, open water) and the islands (gradual shore zone bordering sheltered shallow bays with submerged vegetation).

Irrespective of the densities of young fishes observed along the rip-rap shores of the lake and at the newly created soft shorelines, the added value of the novel creation of high-quality habitat for fish recruitment at Marker Wadden, and at other soft engineering projects in the lake, is the considerable increase of the productive shore length of Lake Markermeer by more than 30% in recent years. Despite the added recruitment potential of the lake, the densities of young fishes have been relatively low in the open water since construction on the new islands started. This, together with sand supplementation to create new beaches over a 5-year period, has also incurred side effects (KIMA, 2022). A temporary increase of suspended particles in the water column during island construction works may have had an adverse impact on plankton production and on the grazing efficiency of zooplankton, and therefore could have limited the food available for planktivorous young-of-the-year fishes (Jin et al., 2022). In addition, the extra sediment load may have adversely affected the benthic foodweb and increased oligotrophication (Van Riel et al., 2019). Another reason for low densities of young-of-the-year fishes in open water since 2018 might be the delayed impact of a significant reduction in the gillnet fishery since 2014 and a strong year class of pikeperch in 2017, which has brought about a high predatory fish stock since 2018 in Lake Markermeer (Van Rijssel et al., 2022; Volwater et al., 2022). Therefore, any immediately noticeable effects on fish recruitment at the scale of the whole lake were not yet to be expected.

4.3 | Implications for conservation and ecosystem restoration

The high densities of young-of-the-year fishes observed in the sheltered shallow wetland habitats of the newly created archipelago demonstrate the enhancement of the fish recruitment function in the lake. This finding has several important implications for conservation and ecosystem restoration. First, rip-rap shores are typically created for conditions in which shorelines are highly exposed to wave action. As shown, wave action has an adverse impact on young-of-the-year fish densities. In more sheltered areas, reed vegetation creates extra habitat structure which might further support young-of the-year fish densities. Second, the replacement of rip-rap by gradual sandy shorelines does not itself enhance fish densities in the short term. Exposed shallow sandy beaches offer no shelter for young fishes, in contrast to steep rip-rap, which offers both open spaces between basalt blocks, allowing smaller fishes to hide, and deeper water, where wave action is less than that at the surface. Third, constructing sandy gradual shorelines instead of rip-rap as an ecosystem restoration measure is most useful in sheltered locations, and is less valuable in wind-exposed areas. However, sandy shorelines protected from wave action by rip-rap breakwaters some hundred metres away not only protect sandy shorelines from erosion but can also provide shelter for fishes and enrich habitat structure through the development of submerged vegetation. Lastly, the concept of adding completely new additional shorelines through creating sheltered wetland islands greatly enhances fish recruitment opportunities because it adds extensive, productive, sheltered shore zones with a small lake surface area without sacrificing existing shorelines.

4.4 | Future perspectives for fish recruitment in the lake

The creation of islands and shallow shore zones elsewhere around Lake Markermeer is continuing, making it difficult to determine the long-term added value of the shore zones created since 2016, compared with the lake shores before 2016. Moreover, the shallow shore zones are typical pioneer habitats, where marsh fleawort dominates, and succession to more diverse vegetation has only just begun. This also includes the establishment of a richer benthic habitat, with more organic material accumulating in sheltered littoral zones, favouring the production of benthic organisms, and as a consequence the conditions for higher trophic levels, including fishes (Brauns et al., 2011; Kallasvuo et al., 2011; Kornis et al., 2018; Peterson et al., 2000; Vadeboncoeur et al., 2011).

The littoral zones of the wetland islands of Marker Wadden will probably be developed further when the reed beds are more fully established. Since 2020, the area of submerged vegetation has expanded rapidly in the shallow sheltered waters between the islands, which is likely to increase the nursery area as both food supply and shelter increase with plant cover (Duncan & Kubečka, 1995; Kallasvuo et al., 2011; Trial et al., 2001).

Future developments that can be envisaged therefore include higher biological production and habitat structure, both in the shore zones and in the shallow waters between the islands of the archipelago. Successive changes in vegetation, benthic fauna, and fish fauna will, over time, probably offer favourable conditions for long-lived species such as unionid mussels and the symbiotically related spawning conditions of bitterling (*Rhodeus amarus*), as well as conditions for other limnophylic fish species such as pike (*Esox lucius*), tench (*Tinca tinca*), and rudd (*Scardinius erythrophthalmus*), which occur in Lake Markermeer in only small numbers. The comprehensive monitoring of a variety of organism groups, and more detailed studies on ecological functioning and biological production, need to be implemented to fully appreciate and evaluate the long-term potential of creating these sheltered wetland islands as a means of lake restoration.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data on fish surveys of Lake Markermeer are openly available at https://wmropendata.wur.nl/site/zoetwatervis/. Other data that support the findings of this study are available from the corresponding author, upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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