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Impacts of shelter on the relative dominance of primary producers and trophic transfer efficiency in aquatic food webs: Implications for shallow lake restoration

Hui Jin[1] | Casper H. A. van Leeuwen[1,2] | Ralph J. M. Temmink[2,3,4] | Elisabeth S. Bakker[1,5]

[1]Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

[2]Aquatic Ecology and Environmental Biology, Radboud Institute for Biological and Environmental Sciences, Radboud University, Nijmegen, The Netherlands

[3]Department Coastal Systems, Royal Netherlands Institute of Sea Research, Den Burg, The Netherlands

[4]Environmental Sciences, Copernicus Institute of Sustainable Development, Utrecht University, Utrecht, The Netherlands

[5]Wildlife Ecology and Conservation Group, Wageningen University, Wageningen, The Netherlands

Correspondence
Elisabeth S. Bakker, Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB Wageningen, The Netherlands.
Email: L.Bakker@nioo.knaw.nl

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Abstract

1. Wind-induced turbulence can strongly impact ecological processes in shallow lake ecosystems. The creation of shelter against wind can be expected to affect both primary producers and herbivores in aquatic food webs. Shelter may benefit particular primary producers more than others by changing relative resource availabilities for different primary producers. Herbivore community compositions may be affected either directly or indirectly as a consequence of changes in their food quantity and quality that, in turn, may affect the transfer efficiency between primary producers and herbivores. A reduction in trophic transfer efficiency resulting from wind-induced turbulence potentially can lead to declines of higher trophic levels, but is generally understudied.

2. Here, we focus on the impact of wind on aquatic primary producers and trophic transfer efficiency. We hypothesised that reducing wind-induced turbulence will stimulate higher trophic production in shallow lakes. However, the multitude of impacts of wind-induced turbulence on aquatic food webs make it challenging to predict the direction of change when creating sheltered conditions.

3. We tested our hypothesis in the shallow waters of a newly constructed archipelago named Marker Wadden in lake Markermeer in the Netherlands. Lake Markermeer has experienced declining numbers of birds and fish. These declines have been related to wind-induced sediment resuspension that potentially limits primary production and trophic transfer efficiency. Marker Wadden is a large-scale restoration project that aims to add sheltered and heterogeneous habitat to the otherwise mostly homogeneous lake, thus targeting the potential problems associated with wind-induced turbulence.

4. We executed a 2-month manipulative field mesocosm experiment in the shallow waters of Marker Wadden to study the effect of reduced wind-induced turbulence (i.e., shelter) on aquatic food webs. Specifically, we studied the effects on primary producers, trophic transfer efficiency between phytoplankton

and zooplankton (using zooplankton biomass divided by phytoplankton Chl *a* as a proxy), and benthic fauna. The experiment consisted of three treatments: *no shelter*, *shelter without macrophytes* and *shelter with submerged macrophytes* (*Myriophyllum spicatum*) *present at the start of the experiment.*

5. Our results clearly showed that under unsheltered conditions phytoplankton was the dominant primary producer, whereas in sheltered conditions submerged macrophytes became dominant. Interestingly, submerged macrophytes appeared rapidly in the sheltered treatment where first no macrophytes were visibly present; hence, at the end of the experiment, there was little difference among the sheltered treatments with and without initial presence of submerged macrophytes. Despite that phytoplankton concentrations were 23-fold higher under the unsheltered conditions, this did not result in higher zooplankton biomass. This can be explained by a five-fold greater trophic transfer efficiency between phytoplankton and zooplankton under the sheltered conditions. Furthermore, under the sheltered conditions the Gastropoda density reached 746 individuals m^{-2}, whereas no Gastropoda were found under the no shelter treatment.

6. These findings indicate that for shallow lakes that are negatively affected by wind-induced turbulence, measures aimed at ameliorating this stressor can be effective in facilitating submerged macrophyte recovery, increasing Gastropoda densities and restoring trophic transfer efficiency between phytoplankton and zooplankton. Ultimately, this may support higher trophic levels such as fish and water birds by increasing their food availability in shallow lake ecosystems.

1 | INTRODUCTION

Ecological processes in shallow aquatic ecosystems can be strongly impacted by wind (Janatian et al., 2020; Stockwell et al., 2020). Wind can directly affect the base of the aquatic food web: the primary producers including macrophytes, benthic algae and phytoplankton. For example, macrophyte establishment may be inhibited directly because of stem breakage, uprooting, or limitations in establishment of their propagules (Jupp & Spence, 1977; Keddy, 1983; Schutten et al., 2005; Van Zuidam & Peeters, 2015). In addition, benthic algae may be unable to colonise exposed habitat as a result of sediment resuspension and instable sediment (Jorge & Beusekom, 1995). As such, wind-induced disturbances may favour phytoplankton dominance by releasing it from otherwise high competition by other primary producers (Hansson et al., 2020; Sand-Jensen & Borum, 1991). Beyond direct wind effects, wind also has indirect effects on shallow lake ecosystem functioning. A key indirect effect of wind in shallow lakes is its effect on sediment resuspension, which can alter relative resource availabilities for distinct primary producers (Tammeorg

et al., 2013). For example, sediment resuspension typically leads to higher nutrient concentrations in the water column coupled with decreased light availability (Blottière et al., 2017; Tang et al., 2020). Consequently, high nutrient availability in the water facilitates the growth of phytoplankton, whereas low light availability created by high phytoplankton abundance and suspended sediments inhibits or restricts the growth of submerged macrophytes or benthic algae (Jäger & Diehl, 2014).

Wind-induced turbulence also can affect secondary producers in shallow aquatic ecosystems. Wind can modify the community of secondary producers (zooplankton) directly (Ohman & Romagnan, 2016; Zhou et al., 2016) as well as indirectly by affecting the quantity and quality of their food (phytoplankton) (Cyr & Coman, 2012; Durham et al., 2013; Tang et al., 2020). Direct effects are, for example, that wind-induced turbulence may inhibit the growth of large-sized zooplankton species when their body size exceeds the Kolmogorov length scale as they are more affected by eddy motion (Peters & Marrasé, 2000). Specifically, organisms larger than the diameter of the smallest turbulent eddy are directly affected by the turbulent

shear forces, which may impair food detection or capture, or directly lead to body damage (G.-Tóth et al., 2011; Visser et al., 2009; Zhou et al., 2016). Although the sediment resuspension process tends to increase phytoplankton biomass (Carrick et al., 1993; Kang et al., 2019), higher inorganic suspended solid concentrations in the water column following this process may pose an indirect constraint on herbivore (zooplankton) feeding, because suspended solids can mechanically interfere with food intake or dilute gut content (Kirk & Gilbert, 1990; Koenings et al., 1990). As a result, wind-induced turbulence potentially may lower the trophic transfer efficiency between phytoplankton and zooplankton – defined as the total production ratio between adjacent trophic levels (Lindeman, 1942) – as a consequence of the dominance of small-sized zooplankton with relatively lower grazing capability and the high suspended solids concentrations (Hall et al., 1976). The decreased trophic transfer efficiency between phytoplankton and zooplankton subsequently might lead to the decline of higher trophic production (Barneche et al., 2021; Kazama et al., 2021).

Shallow lakes may be characterised by two alternative stable states: an aquatic vegetation-dominated clear water state and a phytoplankton-dominated turbid water state (Hargeby et al., 2004; Janssen et al., 2014; Scheffer et al., 1993). Wind-induced turbulence, for example, may maintain the phytoplankton-dominated turbid state by directly favouring phytoplankton to be the dominant primary producer (Blottière et al., 2017; Tang et al., 2020), while indirectly decreasing trophic transfer efficiency between phytoplankton and zooplankton (G.-Tóth et al., 2011; Hall et al., 1976; Zhou et al., 2016). Reducing wind-induced turbulence therefore may be a suitable method to shift a phytoplankton-dominated turbid water state to an aquatic vegetation-dominated clear-water state, thereby stimulating higher trophic production in shallow lakes. However, the complex effects of wind make it difficult to predict the response of aquatic food webs to sheltered conditions. Suspended sediment increases nutrient availability in the water column (i.e., under exposed conditions), and therefore phytoplankton biomass is expected to be lower under sheltered conditions when the sediment settles and phytoplankton growth may become nutrient-limited (Gao et al., 2021; Zhang et al., 2020). Additionally, nutrient limitation may decrease phytoplankton quality because it potentially leads to higher carbon (C):nutrient ratios in primary producers (Ågren, 2004; Sterner & Elser, 2002). Furthermore, if submerged macrophytes or benthic algae establish under sheltered conditions, these will compete with phytoplankton for nutrients (Hansson et al., 2020; Sand-Jensen & Borum, 1991), which may further strengthen nutrient limitation and decrease both phytoplankton biomass and its quality. As such, on the one hand, sheltered conditions seem favourable for larger zooplankton that can profit from easy feeding in a water column with little interference of suspended sediments (Kirk & Gilbert, 1990). However, on the other hand, they may be limited by low phytoplankton production and its quality. As a result, it is questionable whether shelter benefits higher trophic levels by improved trophic transfer efficiency leading to higher zooplankton biomass. Instead, under sheltered conditions, benthic algae and submerged macrophytes

may be the dominant producers, and higher trophic levels may benefit from increased abundances of grazing benthic fauna on benthic algae mats, periphyton on macrophytes and the macrophytes themselves (Karlsson et al., 2009), rather than increased zooplankton production. In the latter case, shelter results in higher food-web complexity, offering alternative pathways to stimulate higher trophic levels rather than strengthening the phytoplankton–zooplankton food chain.

Here, we studied the effects of shelter on the relative dominance of primary producers, trophic transfer efficiency between phytoplankton and zooplankton, and benthic fauna in a 2-month *in situ* manipulative field experiment in shallow water in the newly constructed archipelago Marker Wadden in the Netherlands. We artificially created shelter and manipulated the presence of submerged macrophytes, which resulted in three treatments: (1) no shelter, (2) shelter and (3) shelter with macrophytes. We hypothesised that shelter would: (a) result in shifts in relative dominance of primary producers, expecting a reduction of phytoplankton biomass, and increase in biomass of benthic algae, macrophytes and periphyton; (b) enhance the trophic transfer efficiency between phytoplankton and zooplankton; and (c) increase the abundance of benthic fauna grazing on benthic algae, periphyton and macrophytes.

2 | METHODS

2.1 | Study site

In order to explore the effect of shelter on ecological processes in shallow aquatic systems, we have chosen lake Markermeer as study system. Lake Markermeer is a 3–5 m-deep (mean depth 3.6 m), 680 km^2 delta lake located in the centre of the Netherlands (52°32'23.4"N, 5°13'56.4"E). This freshwater lake has been created in a former estuary due to the completion of two dikes for water safety: a 32 km-long dike called the Afsluitdijk in 1932, and a 27 km-long dike called the Houtribdijk in 1975. These dikes created two adjacent lakes: lake Markermeer and lake IJsselmeer, of which only lake IJsselmeer still receives riverine input from the river IJssel. With the original outlet of lake Markermeer towards the sea blocked, fine silts and clays have been trapped in this essentially land-locked lake and continue to be resuspended by wind action (Kelderman, Ang'weya, et al., 2012). Suspended solid concentrations in the lake ranged from 4.0 to 368.0 mg/L from 1999 to 2016, with an annual average of 45 mg/L (Kelderman, De Rozari, et al., 2012).

Lake Markermeer is a typical example of a shallow lake that has been negatively impacted by wind-induced turbulence, as it has a uniform depth and long fetch length. Even though the water quality has improved since the 1980s by reducing external nutrient loading, the lake's ecosystem continues to deteriorate. The lake is a Natura 2000 area under the Birds Directive and has experienced declining populations of benthivorous and piscivorous birds over the last decades, as well as declines in fish (Noordhuis, 2014). These declines

have been related to wind-induced sediment resuspension, potentially limiting primary production and trophic transfer efficiency, with negative consequences for higher trophic levels in the food web (Van Riel et al., 2019).

In order to improve the ecological integrity of this lake, a large-scale restoration project called "Marker Wadden" was initiated in 2016 by the Dutch Society for Nature Conservation ("Natuurmonumenten" in Dutch). Marker Wadden is a newly constructed archipelago of five islands spread across an area of about 1,000 ha in the northeastern part of lake Markermeer (52°35'02.8"N, 5°21'55.5"E) (Figure 1a–c). The project aims to add sheltered and more heterogeneous habitat to the otherwise rather homogeneous lake. It is expected that these habitats vary in nutrient and light availability, which can result in more diverse types of primary producers to boost the food web in the lake (van Leeuwen et al., 2021). We conducted a field mesocosm experiment in the shallow waters between islands of the Marker Wadden archipelago.

2.2 | Experimental design

In order to study how shelter affects primary producer dominance, the trophic transfer efficiency between phytoplankton and zooplankton, and benthic fauna, we performed an experiment in the shallow waters of Marker Wadden (Figure 1). We used a randomised block design with three treatments: (1) a mesocosm which created

only shelter against wind, (2) a mesocosm that created shelter and in which macrophytes (*Myriophyllum spicatum*) were present (the cylinder was placed over existing patches of *M. spicatum*), and (3) an unsheltered control in the open water, where no macrophytes were visibly present. This design allowed for testing the effects of shelter and the separate effect of macrophyte presence. The treatments were each replicated six times along a 100-m stretch of shoreline, with blocks 20 m apart and plots within a block approximately 3 m from each other (Figure 1).

The mesocosms used for the shelter treatments 1 and 2 consisted of transparent polyethylene cylinders (inner diameter 94 cm, height 200 cm). All cylinders were vertically inserted 100 cm into the sediment and protruded above the water level to ensure no water exchange between the inside and outside of the cylinders. The primary function of the mesocosms was to reduce wind-induced turbulence, however, they may have had other effects as well (that we elaborate on in the Discussion section). Water depth ranged from 0.20 to 0.80 m across the cylinders, probably allowing water column mixing in the enclosures despite the reduction in turbulence. The field experiment started on 24 June 2019 and lasted until 26 August 2019 (c. 2 months), to limit possible accumulation of stochastic enclosure effects over time resulting from the lack of connectivity to the outside water. At the end of the experiment, we measured (as described in detail in the following section): physical parameters of the water column, suspended solids concentrations, seston elemental composition, nutrient concentrations in the water column, types of
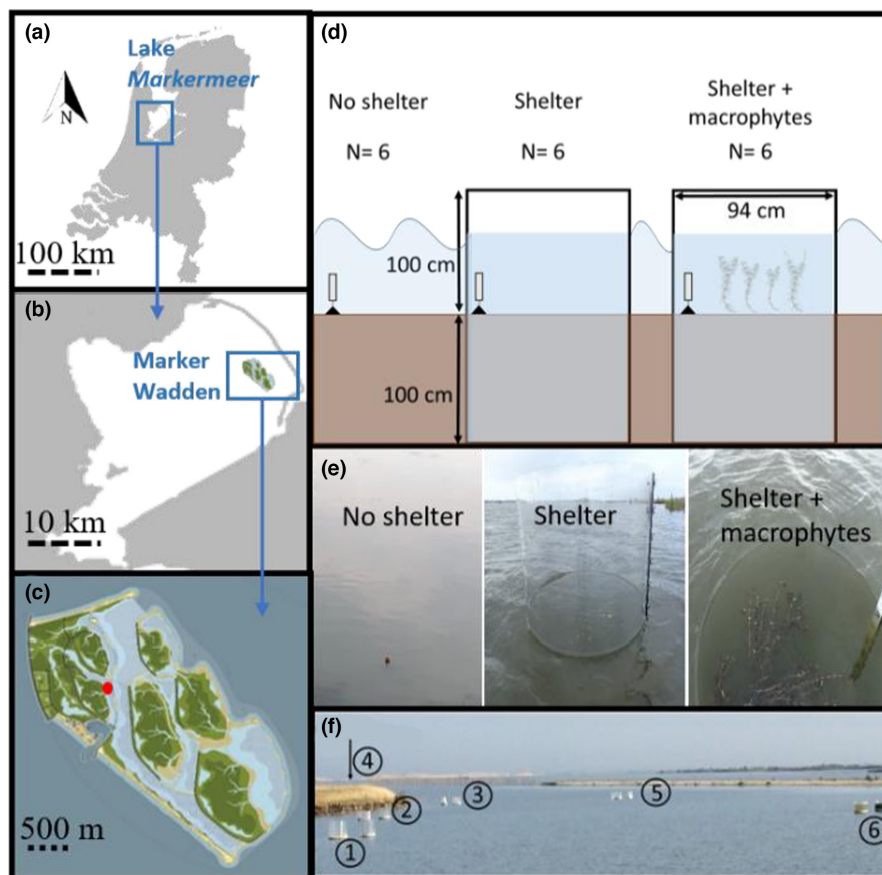

FIGURE 1 Location and design of the study: (a) the Netherlands, (b) lake Markermeer and (c) Marker Wadden; the red dot indicates the location of the experiment. (d) Schematic overview of the experimental design, representing one block. The experiment consisted of six replicate blocks (*n* = 6). The vertical strip in each treatment represents a plastic strip used to measure periphyton growth. (e) Experimental treatments in the field. (f) Overview of the location of the experimental blocks. Photos: Liesbeth Bakker. Map of Marker Wadden: Boskalis

primary producers, the zooplankton community, and benthic fauna composition.

2.3 | Sampling and laboratory analyses

2.3.1 | Physical measurements

Light intensity on the water surface, and 10 cm below the water surface, was measured by UWQ 9146 light sensor (LI-COR Environmental GmbH). The vertical attenuation coefficient, K_d, then was calculated (Lampert & Sommer, 2007). Light at the sediment surface was calculated based on the surface light intensity and the K_d (Lampert & Sommer, 2007).

In order to determine total suspended solids (TSS), inorganic suspended solids (ISS), organic suspended solids (OSS), seston elemental composition, dissolved nutrients, chlorophyll (Chl) *a* concentrations and zooplankton community composition, a depth-integrated 30-L water sample was taken from the centre of the mesocosm with a customised water sampler made of transparent plexiglass (Figure S1), which then was mixed in a 45-L plastic container.

TSS concentrations were determined by filtering 100–200 ml water subsamples over pre-washed and pre-weighed GF/F filters (Whatman), drying these filters at 60°C overnight, and then re-weighing them to determine their weight increase. After weighing, the filters were stored dark in a desiccator for subsequent seston elemental composition analysis (explained in the next section).

To quantify ISS concentrations, 100–200 ml water subsamples were filtered using pre-ashed (2 hr at 550°C) and pre-weighed GF/F filters (Whatman), that then were dried at 60°C overnight, and re-weighed. These filters were combusted in a muffle furnace at 550°C for 2 hr, then cooled in a desiccator, and finally reweighed to determine the ISS concentration. We calculated the OSS by subtracting ISS from TSS.

2.3.2 | Seston elemental composition

In order to determine the quality of seston as food for zooplankton, in terms of C:nutrient ratios, we focused on the edible fraction (size <30 μm) of the seston (Cyr & Curtis, 1999; Haney, 1973). Water samples were sieved through a 30-μm mesh, then 100–200 ml water subsamples were filtered over a pre-washed and pre-weighed GF/F (Whatman), dried at 60°C overnight, and then reweighed. To determine C and nitrogen (N) concentrations of the seston, we extracted two circular disks (5.55 mm diameter) of these dried GF/F filters, folded them into tin cups (Elemental Microanalysis) and analysed the disks for particulate C and N on a FLASH 2000 NC elemental analyzer (Brechbuhler Inc., Interscience B.V.). The remainder of the GF/F filters were used to assess phosphorus (P) contents, by combusting them in a Pyrex glass tube at 550°C for 30 min, adding 5 ml persulfate (2.5%) to the glass tube, and autoclaving them for 30 min at 121°C. Digested P (as PO_4^{3-}) was measured on a QuAAtro39 Auto-Analyzer (SEAL Analytical Ltd).

2.3.3 | Nutrients in the water

Dissolved inorganic nutrients were determined from water subsamples that were filtered using pre-washed GF/F filters (Whatman). GF/F filters were pre-washed by Demi water. The filtrate was stored at −20°C before analyses. Concentrations of dissolved nutrients (ammonium [NH_4^+], nitrate [NO_3^-], nitrite [NO_2^-] and phosphate [PO_4^{3-}]) in the filtrate were determined on a QuAAtro39 Auto-Analyzer (Seal Analytical Ltd). Particulate organic N (PON) was measured by filtering 100–200 ml water subsamples over pre-washed GF/F filters (Whatman), dried at 60°C overnight. Thereafter, the PON and particulate organic phosphorus (POP) were analysed using the same methods as for the seston C, N and P as described before. Total nitrogen (TN) was calculated by summing up of PON, NH_4^+, NO_3^- and NO_2^- concentrations, whereas the total P was calculated as the sum of the POP and PO_4^{3-} concentrations. In our study, we did not measure the DON and DOP fraction, hence these are not included when we calculated the TN and TP.

2.3.4 | Chlorophyll a concentrations

The Chl *a* concentration in the water column was determined from filtered matter retained on GF/F filters (Whatman) after filtering a known volume of water subsamples. For logistic purposes the samples were stored at −20°C for not more than one month. After thawing, the filters were extracted with 80% ethanol in an 80°C water bath, and passed through Millipore Millex FG 0.2-μm membrane filters. Chl *a* concentrations were measured on the filtrate part by means of high performance liquid chromatography (HPLC, UltiMate 3000; Thermo Scientific) equipped with a Hypersil ODS column (25 cm, 5 μm, 4.6 × 250 mm; Agilent) and a RF 2000 fluorescence detector (Dionex/Thermo Scientific). Chlorophyll *a* concentrations were determined in total, and separately for the edible fraction of phytoplankton (<30 μm, by first sieving the water through 30-μm mesh) and inedible fraction (>30 μm, by subtracting the <30 μm concentrations from the total concentrations).

2.3.5 | Zooplankton community composition

Crustacean zooplankton samples were collected by filtering 20-L depth-integrated water samples through an 80-μm mesh size net, whereas rotifer samples were collected by filtering 1 L of depth-integrated samples through a 30-μm mesh size net. To prevent water loss by sampling, we gently poured the filtrate back to the enclosure. All samples were fixed with alkaline Lugol's iodine solution within an hour of collection.

Zooplankton specimens were counted using a stereomicroscope (Leica M205C). Crustacean zooplankton (Cladocera and Copepoda) were counted at magnifications between ×10 and ×40, whereas rotifers were counted at magnifications between ×40 and ×100. Rotifera and Cladocera were identified to the genus level, whereas Copepoda were divided in the two dominant orders in the samples: Calanoida and Cyclopoida. Copepoda in the naupliar stage were counted but not distinguished taxonomically. The zooplankton biomass was estimated by measuring 30 individuals (if there were sufficient individuals to make this possible) of the most abundant genus and deriving biomass from published length–weight relationships (Bottrell et al., 1976; Dumont et al., 1975). Rotifera total biomass was estimated by using geometric formulae that approximate the volume of the individuals, and converting this volume to wet weight under the assumption of a specific gravity of 1. We estimated dry weight as 0.1 * wet weight (*sensu* Doohan, 1973).

2.3.6 | Macrophyte biomass and species composition

In order to determine submerged macrophyte biomass and species composition, all of the plants that grew within the mesocosms were removed carefully with a rake on the final harvesting day (26 July 2019). The plants were transported to the laboratory, washed to remove any attached macrofauna or filamentous algae, and identified to species level. Each macrophyte species and the filamentous algae were dried separately in an oven at 45°C for 2 weeks until constant dry weight, and then weighed. Macrophytes and filamentous algae were blotted dry with paper towels to accelerate the drying process in the oven.

2.3.7 | Periphyton algae biomass

To measure the biomass of periphyton, one plastic strip (length 21.0 cm, width 4.0 cm) was attached by a fishing line to a small metal anchor on the sediment. Strips were installed inside and outside of each mesocosm just below the water surface (Figure 1d). At the end of the experiment, all plastic strips were carefully removed by hand, and immediately stored in plastic zip-lock bags in the dark. In the laboratory, the periphyton attached to the plastic strip was brushed off into a beaker with demi-water, and filtered through GF/F filters (Whatman). The residue subsequently was analyzed using the same method as that for determining Chl *a* in the water column.

2.3.8 | Benthic algae biomass

We determined the biomass of benthic algae, we collected a sediment core of 10 cm depth using a plastic tube (Ø = 5.2 cm); after removing the overlying water in the tube, a small tube (Ø = 1.05 cm)

was used to collect the upper 1 cm sediment once. The collected sediment was stored at −20°C, and liquid chromatographically analyzed as described for determining Chl *a* in the water column. We used the extracted Chl *a* concentration multiplied by the bottom surface of the mesocosm to calculate the benthic algae biomass in each mesocosm.

2.3.9 | Benthic fauna composition

We quantified benthic fauna composition, we collected a sediment core of 10 cm depth using a plastic tube (Ø = 5.2 cm) and analysed the macrofauna washed from the sampled macrophytes. The sediment core was sieved over a 0.5-mm metal mesh, and the materials retained on the mesh were stored in 70% ethanol in 50-ml tubes. In the laboratory, all invertebrates from the sediment cores and attached to the macrophytes were identified to genus or species level. The density of macrofauna attached on macrophytes was estimated by dividing the abundance of each taxon by the bottom surface area of the mesocosm. Total benthic fauna density was calculated by summing up the density in the sediment and the density on the macrophytes.

2.3.10 | Trophic transfer efficiency

In this study, we used Chl *a* as a proxy for phytoplankton biomass. To determine the trophic transfer efficiency (TTE) between phytoplankton and zooplankton, we used the zooplankton:phytoplankton biomass ratio in $\log_{10}$ scale as a proxy (Gaedke & Straile, 1994; García-Comas et al., 2016; Jennings et al., 2002; Yvon-Durocher et al., 2011). We prefer this proxy over the more difficult and time-consuming method based on production ratios first described by Lindeman (Lindeman, 1942). In addition, Ersoy et al. (2017) and previous studies showed that TTE varies mostly with biomass ratios rather than with production ratios (Gaedke & Straile, 1994; García-Comas et al., 2016; Jennings et al., 2002; Yvon-Durocher et al., 2011). In order to make cross-treatment comparisons of TTE based on consumer:resource biomass ratios, we implicitly assumed that the zooplankton consumption rate by fish is similar among the treatments. We did not have data for fish densities in all treatments, but we could test the effects of fish density on the TTE under the shelter and shelter + macrophytes conditions owing to the presence of small fish in these treatments.

2.3.11 | Fish sampling

On the final harvest day, we systematically collected all fish that we observed in (some of) the mesocosms, using a 1-L container. Fish were collected when they came to the water surface during the macrophyte harvest, identified to species, measured (body length) and subsequently released in the open water.

2.4 | Statistical analyses

Linear mixed-effect models were used to analyze the effects of the three treatments (as factor with three levels: no shelter, shelter, and shelter with macrophytes present in the initial stage) on each of the measured parameters as the dependent variable (Table S1). Following the randomised block design, block location (six levels) was included as random intercept in all of the models to account for the dependency structure in our experimental design. Residuals were visually and statistically checked for model assumptions, and in case of model violations the dependent variables were natural log, $\log_{10}$ or square-root transformed (indicated in Table S1). Adjustments of the model intercepts were used to assess differences among the three treatment levels (indicated in Table S2). Block 5 was damaged by wave action, and therefore excluded from the analyses (reducing n from 6 to 5 for the two treatments requiring shelter). Kendall's rank correlation tau was used to analyse the effect of fish number on the measured parameters under the shelter and shelter + macrophytes treatment (Table S3). The analyses were performed with the package nlme (Pinheiro et al., 2022) in R v.3.5.1 (R Core Team, 2021). All data are shown with their mean ± standard error (SE) and in all hypothesis testing procedures the significance level was pre-set at $a = 0.05$ ($p < 0.05$).

3 | RESULTS

3.1 | Primary producers

Shelter significantly affected the abundance of the primary producers. Without shelter, phytoplankton was the dominant primary producer, whereas shelter reduced phytoplankton biomass (indicated by chlorophyll a) 23-fold, regardless of whether macrophytes were initially present or not (Figure 2a; Tables S1 and S2). The quality of phytoplankton for grazing zooplankton was not affected by shelter: no significant effects on C:N or C:P ratios in seston were found; in the treatments with most macrophytes (shelter + macrophytes), C:N ratios were significantly higher compared to the other treatments (Figure S2; Table S1). The edible fraction of phytoplankton was the same among treatments (Table S1). The phytoplankton edible fractions were 75% ± (11; mean ± SE), 93% ± (11) and 75% ± (11) in the no shelter, shelter, and shelter + macrophytes treatments, respectively (Figure S2).

Submerged macrophytes became the dominant primary producers in both shelter treatments and were not present in the no shelter treatment (Figure 2b; Tables S1 and S2). Submerged macrophytes spontaneously developed in all plots of the sheltered treatment where initially no macrophytes were visibly present at the start of the experiment. However, the final biomass in this treatment varied
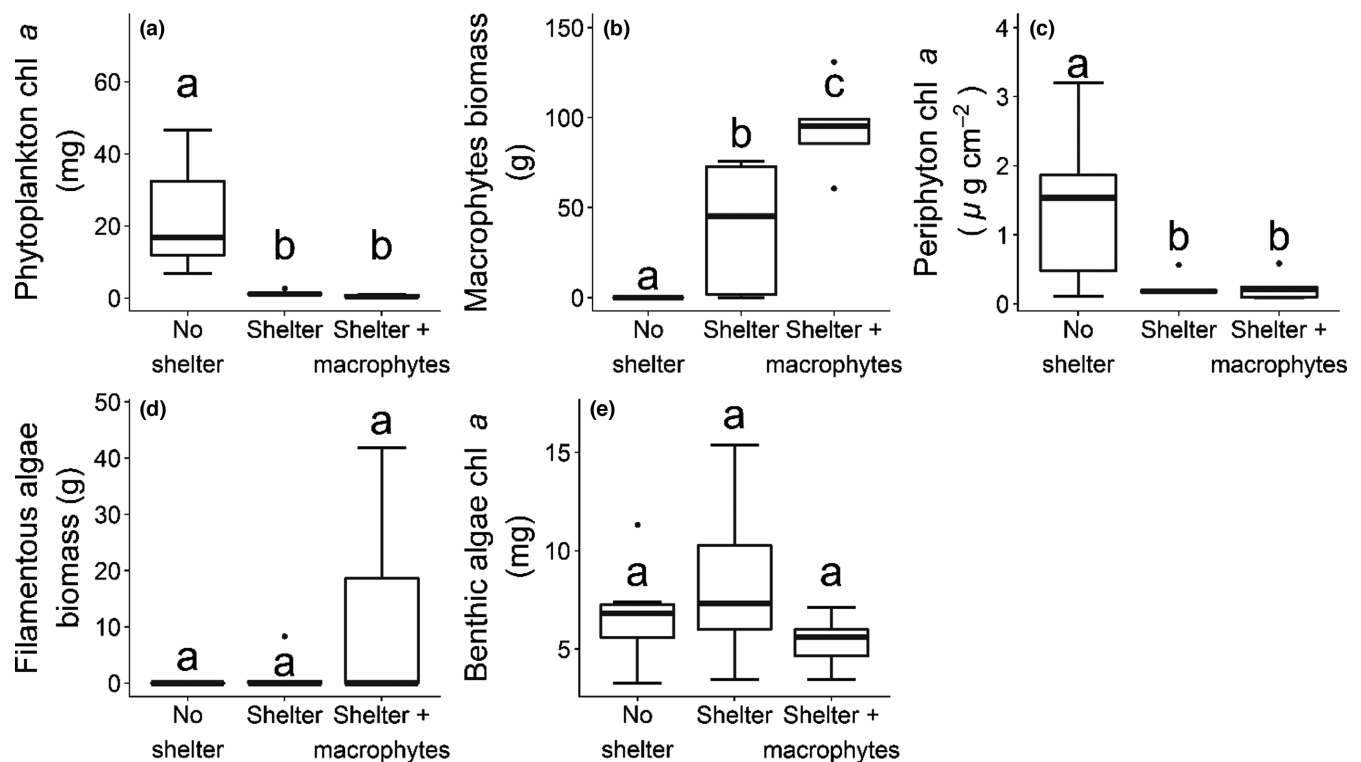
FIGURE 2 (a) Phytoplankton Chl a (mg per plot), (b) macrophytes (g dry weight per plot), (c) periphyton chl a (µg/cm²), (d) filamentous algae (g dry weight per plot) and (e) benthic algae chl a (mg per plot) in the treatments no shelter (n = 6), shelter (n = 5), and shelter + macrophytes (n = 5). Different lowercase letters indicate a significant difference among treatments. Boxplots show the median (middle line), quartiles (boxes), 1.5× the interquartile range (IQR) (whiskers) and extreme values (dots). Dots outside the whiskers are extreme values

considerably. Macrophyte biomass was the highest in the shelter with macrophytes treatment compared to the shelter with initially no macrophytes present treatment and absent in the no shelter treatment (Figure 2b; Tables S1 and S2). Four submerged macrophyte species were recorded in all sheltered treatments – *Myriophyllum spicatum*, *Zannichellia palustris*, *Potamogeton perfoliatus* and *Potamogeton pectinatus* – irrespective of the conditions at the onset of the experiment.

Periphyton algae Chl *a* was six-fold higher in the absence of shelter compared to both shelter treatments (Figure 2c; Tables S1 and S2). The treatments did not affect the biomass of filamentous algae, which were absent without shelter, but highly variable in the shelter with macrophytes treatment. Filamentous algae biomass generally was much lower than the biomass of submerged macrophytes in both shelter treatments (cf. Figure 2b and d). Benthic algae were equally present in all treatments, but at a generally low biomass (Figure 2e).

3.2 | Zooplankton

Total zooplankton biomass was similar among treatments (Figure 3; Tables S1 and S2), but there were differences in the zooplankton community composition (Tables S1 and S2). Specifically, total copepod biomass in the shelter treatment was significantly higher compared with the no shelter treatment, whereas macrophyte presence in the initial stage did not affect copepod biomass (Tables S1 and S2). No significant differences were found in total rotifer biomass, *Daphnia* biomass, nauplii biomass and biomass of small cladocerans among treatments (Table S1).

Thirteen zooplankton taxa were recorded in all treatments, including seven Cladocera genera (*Bosmina*, *Daphnia*, *Chydorus*, *Leptodora*, *Macrothrix*, *Alona* and *Diaphanasoma*), two Copepoda orders (Clanoida and Cyclopoida) and four Rotifera genera (*Brachionus*, *Keratella*, *Polyarthra* and *Lecane*). The total copepod biomass consisted mainly of Cyclopoida, which contributed $100\% \pm 0.2$, $100\% \pm 0$ and $75\% \pm 10$ of the total copepod biomass under the shelter, shelter + macrophytes and no shelter treatments, respectively. The zooplankton community consisted mainly of nauplii ($59\% \pm 9$) in the no shelter treatment, whereas copepods were dominant in the shelter ($42\% \pm 16$) and shelter + macrophytes ($42\% \pm 9$) treatments (Figure 3). Small cladocerans contributed $11\% \pm 2$, $20\% \pm 14$ and $16\% \pm 8$, whereas *Daphnia* contributed $14\% \pm 5$, $14\% \pm 11$ and $13\% \pm 13$ to the total zooplankton biomass under the shelter, no shelter and shelter + macrophytes treatments, respectively. Rotifers contributed less than 1% to the total zooplankton biomass in all treatments.

3.3 | Shelter effect on trophic transfer efficiency

Shelter enhanced the trophic transfer efficiency between phytoplankton and zooplankton five-fold, regardless of whether macrophytes were initially present or not, as indicated by the zooplankton biomass:Chl *a* ratio (Figure 4; Tables S1 and S2).

3.4 | Shelter effect on benthic fauna

Ten benthic macroinvertebrates taxa were recorded across all treatments: Chironomidae, Tubificidae, four Gastropoda genera (*Physella*, *Valvata*, *Bithynia* and *Radix*), two amphipod families (Gammaridae, Corophiidae) and two bivalve families (Sphaeriidae, Dreissenidae). Shelter significantly increased the Gastropoda density: their density reached 746 ± 316 individuals/m^2 in the shelter treatment, whereas no Gastropoda were found under the no shelter treatment (Figure 5; Tables S1 and S2). Macrophyte presence in the initial stage did not affect Gastropoda density (Figure 5; Tables S1 and S2). The shelter treatment where macrophytes were present in the initial stage harboured significantly (46-fold) larger Corophiidae densities, compared with the shelter only treatment. For the other taxa, no differences among treatments were found. Two fish species (European perch *Perca fluviatilis* and a goby species *Neogobius* sp.) with a body length range of 5–10 cm were found in the sheltered treatments, which must have been inadvertently enclosed when placing the cylinders, as we did not add fish after the cylinders were placed. The total fish densities in the cylinders were 0–4 and 0–9 individuals/m^2 in the shelter and shelter + macrophytes treatments, respectively.

3.5 | Abiotic conditions

Shelter significantly decreased the TN concentration in the water column, whereas TP in the water column was not affected by shelter (Figure S3; Tables S1 and S2). Macrophyte presence at the initial stage did not affect TN or TP (Figure S3; Tables S1 and S2). The presence of shelter reduced the DIN, PON and POP by 38-, seven- and five-fold, respectively (Figure S3; Tables S1 and S2). Macrophyte presence in the initial stage significantly increased DIN concentrations nine-fold, whereas there was no significant effect of macrophyte presence in the initial stage on DIP, PON and POP (Figure S3; Tables S1 and S2).

Shelter facilitated the settlement of suspended solids and increased water transparency. Total suspended solids, ISS and OSS were 10-, 12- and six-fold lower in the shelter treatments than in the absence of shelter, respectively (Figure S4; Tables S1 and S2). Within the shelter treatments there were no effects of the presence of macrophytes in the initial stage on suspended solids, whereas macrophyte presence in the initial stage significantly increased K_d (Figure S4; Tables S1 and S2). Shelter significantly also decreased K_d which was two-fold lower in the shelter treatments than in the no shelter treatment (Figure S4; Table S1).

4 | DISCUSSION

We studied the effects of creating shelter in shallow lakes on primary producers, trophic transfer efficiency between phytoplankton and zooplankton, and the availability of benthic food

FIGURE 3 (a) Zooplankton biomass (µg/L), and (b) zooplankton biomass composition (%) in the treatments "no shelter" (*n* = 6), "shelter" (*n* = 5), and "shelter + macrophytes" (*n* = 5). Different lowercase letters indicate a significant difference among treatments. Boxplots show the median (middle line), quartiles (boxes), 1.5× the interquartile range (IQR) (whiskers), and extreme values (dots). Dots outside the whiskers are extreme values
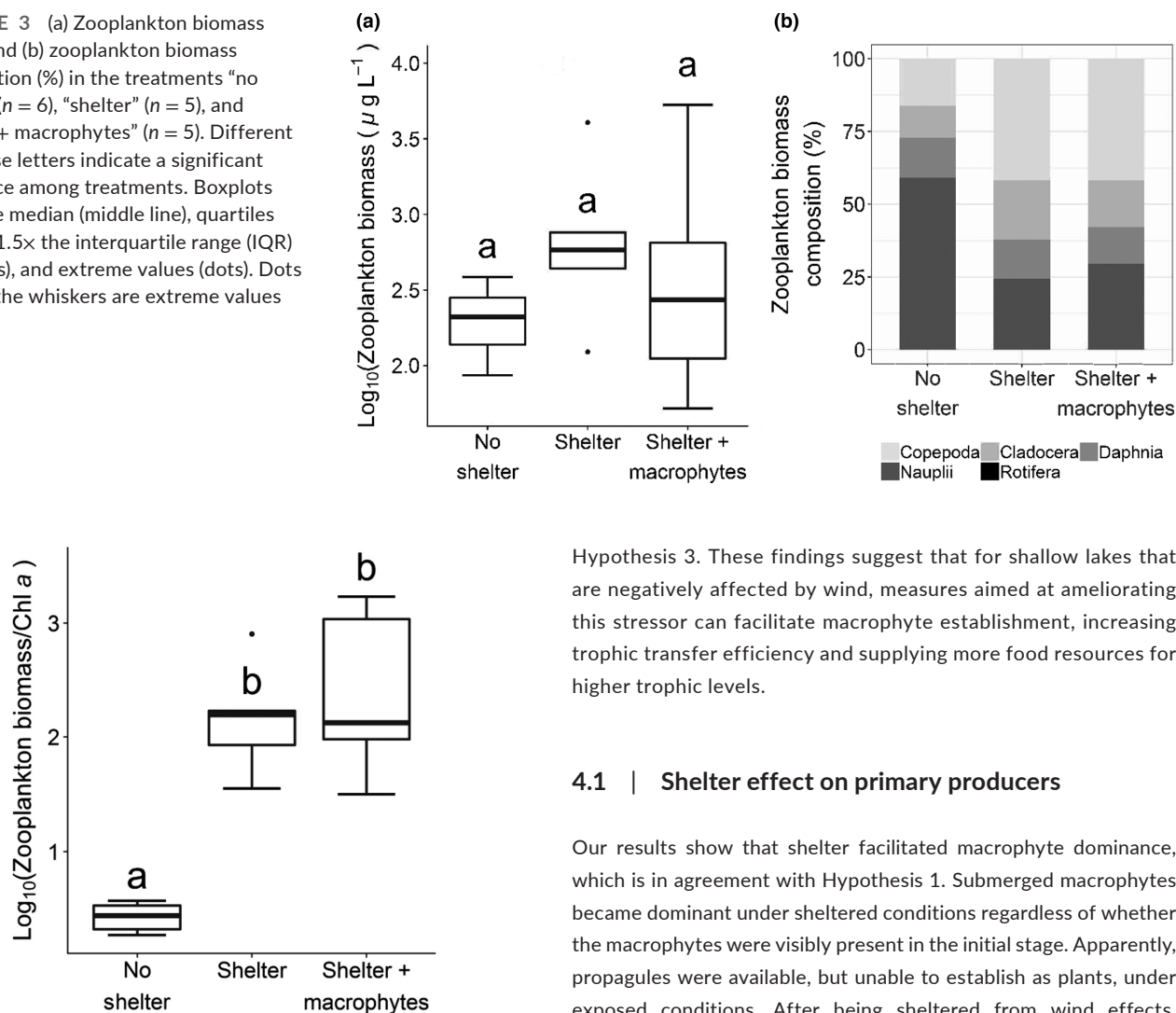

FIGURE 4 Trophic transfer efficiency (log$_{10}$ ratio between the zooplankton biomass and phytoplankton biomass expressed as Chl *a*) in the treatments "no shelter" (*n* = 6), "shelter" (*n* = 5) and "shelter + macrophytes" (*n* = 5). Different lowercase letters indicate a significant difference among treatments. Boxplots show the median (middle line), quartiles (boxes), 1.5× the interquartile range (IQR) (whiskers), and extreme values (dots). Dots outside the whiskers are extreme values

sources for higher trophic levels. Artificially created shelter altered the availability of nutrients and light to primary producers by decreasing resuspension of suspended solids. Under these conditions, submerged macrophytes developed spontaneously, whereas they did not develop under unaltered conditions. At exposed sites, primary production was strongly dominated by phytoplankton, supporting Hypothesis 1. However, the trophic transfer efficiency (estimated with the zooplankton biomass divided by the phytoplankton Chl *a* concentration) of the primary production by phytoplankton towards zooplankton was five-fold higher under sheltered conditions (supporting Hypothesis 2). Gastropoda densities increased in response to shelter, supporting

Hypothesis 3. These findings suggest that for shallow lakes that are negatively affected by wind, measures aimed at ameliorating this stressor can facilitate macrophyte establishment, increasing trophic transfer efficiency and supplying more food resources for higher trophic levels.

4.1 | Shelter effect on primary producers

Our results show that shelter facilitated macrophyte dominance, which is in agreement with Hypothesis 1. Submerged macrophytes became dominant under sheltered conditions regardless of whether the macrophytes were visibly present in the initial stage. Apparently, propagules were available, but unable to establish as plants, under exposed conditions. After being sheltered from wind effects, macrophyte establishment and subsequent growth probably was facilitated by the increased light availability in the water column following the settlement of the suspended materials under sheltered conditions. Indeed, suspended solids concentrations (ISS, OSS and TSS) as well as nutrient availability in the water column (DIN, PON, POP and TN) were significantly lower in the sheltered treatments. The decreased nutrient availability led to low periphyton biomass in the shelter treatment as we observed in our study. As a result, these conditions may release macrophytes from periphyton shading, which is an important factor, as high periphyton shading can even cause collapse of macrophyte populations or inhibit their establishment (Jones & Sayer, 2003; Phillips et al., 1978). Our experimental approach with mesocosms effectively reduced wind-induced turbulence, but also had other effects on the studied food web. Firstly, it should be noted that the walls of the mesocosms provided additional artificial substrate for periphyton, which may have increased resource competition for phytoplankton (Blumenshine et al., 1997). However, we expect this effect to be minor, because periphyton growth on the inner wall of the mesocosm and on the periphyton strips that we installed was minor (Figure 2c), probably related to (a) low nutrient availabilities in the water column (Figure S3), (b) possible shade cast by the macrophytes (Figure S4d), (c) high density of
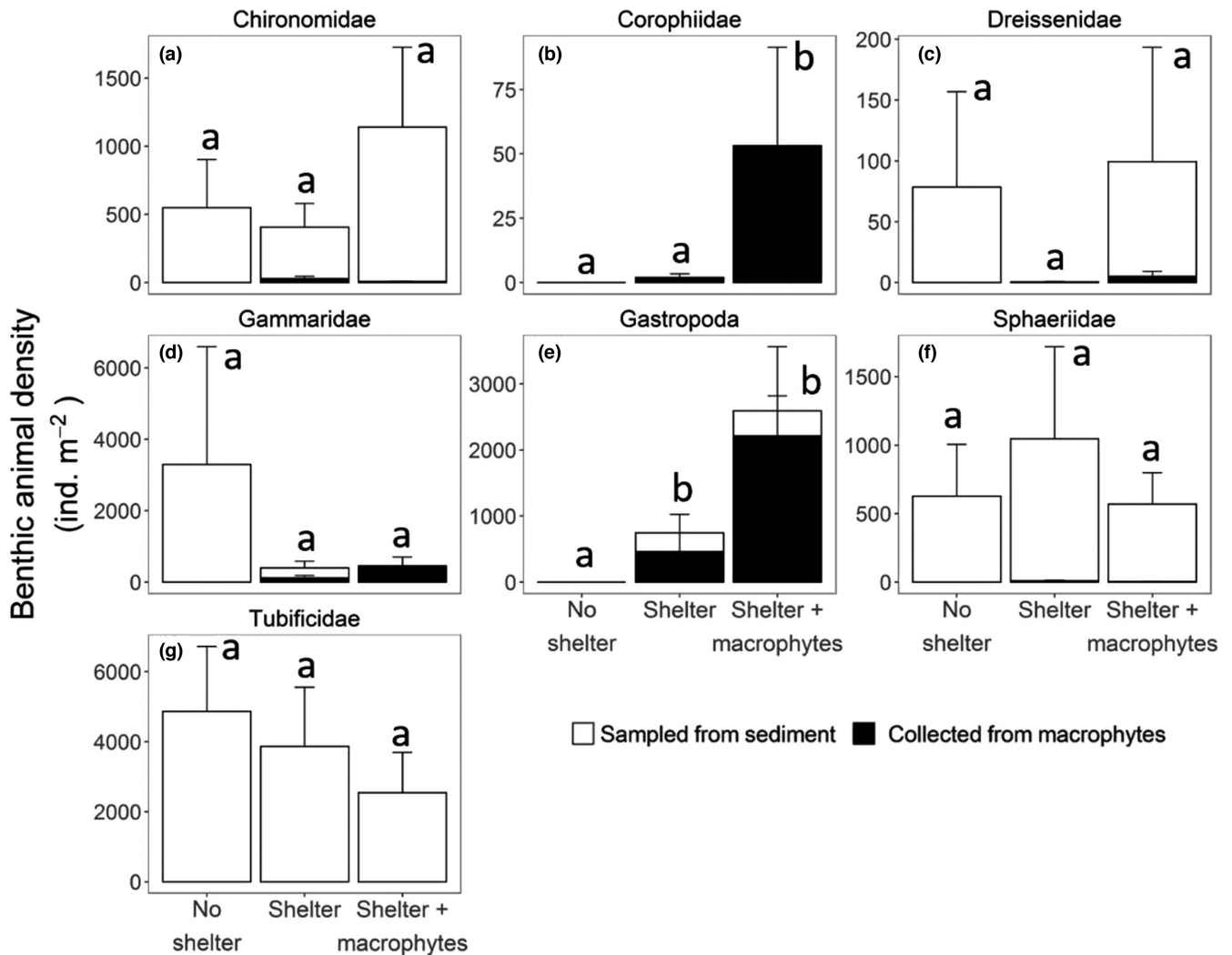
FIGURE 5 Benthic fauna composition (individuals/m²) in the treatments "no shelter" ($n = 6$), "shelter" ($n = 5$) and "shelter + macrophytes" ($n = 5$) separately indicated in panels per family or in case of the Gastropoda for the whole class (panel e). The animals were either collected from the sediment (white bars) or from the macrophytes (black bars). Different lowercase letters indicate a significant difference among treatments

grazing gastropods in the sheltered treatments (Bakker, Dobrescu, et al., 2013), and (d) lack of turbulence that – in open water – would continuously bring new nutrients and inoculums by increasing water turnover and favouring propagule colonization (Cyr, 2016). Therefore, we observed that periphyton biomass was significantly higher under the no shelter treatment compared to the shelter treatments (Figure 2c). Secondly, apart from these indirect effects, wind-induced turbulence also can directly affect macrophytes through the forces that it exerts on macrophytes and their propagules (Jupp & Spence, 1977; Keddy, 1983; Van Zuidam & Peeters, 2015). Shelter, which aims at reducing wind effects, could reduce the wave force which potentially prevents macrophyte damage, whereas it facilitates their anchorage (Schutten et al., 2005) and germination (Fonseca & Kenworthy, 1987; Riis et al., 2003). Consequently, calm conditions in the shelter treatment promote macrophyte abundance as has been observed in our experiment. The mesocosms not only reduce wind-induced turbulence, but also most likely have reduced herbivory by

birds (Bakker, Sarneel, et al., 2013; Bakker et al., 2016), such as mute swans *Cygnus olor* and Eurasian coots *Fulica atra* that are present on the Marker Wadden (H. Jin, personal observations, 6 August 2019). Herbivorous waterbirds not only graze directly on macrophytes, but also may indirectly increase the shading effect by periphyton, which may causes the collapse of macrophytes (Hidding et al., 2016). Besides reducing herbivory by waterbirds, the mesocosms also limited the possible influence of benthivorous fish (Roozen et al., 2007). Benthivorous fish can consume or uproot submerged macrophytes, and increase sediment resuspension that can negatively affect light availability for macrophytes (Roozen et al., 2007; Zhang et al., 2022). Possible effects of herbivorous waterbirds and benthivorous fish in our study remain undetermined and warrant further study.

Shelter significantly increased light availability by decreasing the vertical attenuation coefficient, yet we did not find an effect of shelter on benthic algae biomass. Following the settlement of suspended materials, light intensity at the sediment surface was

estimated to reach $255 \pm 108\ \mu mol\ m^{-2}\ s^{-1}$, which was significantly higher than in the exposed plots (only $44 \pm 32\ \mu mol\ m^{-2}\ s^{-1}$). As benthic algae growth is light-saturated at $100\ \mu mol\ m^{-2}\ s^{-1}$ (Hill et al., 2009), light most probably was not a limiting factor for benthic algae growth in the shelter treatment. However, light availability may have been limiting benthic algae biomass production in unsheltered conditions. Furthermore, the high density of gastropods in the shelter treatment may also have led to lower benthic algae biomass through grazing (Martin et al., 1992; Yang et al., 2019).

4.2 | Shelter effect on pelagic trophic transfer efficiency

Our results show that shelter enhanced the trophic transfer efficiency between phytoplankton and zooplankton, in agreement with Hypothesis 2. This may have been caused partly by the modified zooplankton community in the shelter treatment. Shelter reduced wind-induced turbulence, which may have protected zooplankton from the shear forces, which is especially important for those species with a body size larger than the Kolmogorov length scale (Peters & Marrasé, 2000). If this is true, zooplankton taxa would have a relatively larger body size under sheltered conditions compared to unsheltered condition. Indeed, our data show that Cyclopoida, *Daphnia* and rotifers have a larger body size in the shelter treatments (Figure S5). Specifically, the zooplankton community shifted from being dominated by small-sized nauplii in the absence of shelter to large-sized copepods in the sheltered treatments.

Shelter tended to decrease the quality of phytoplankton as food source for zooplankton in terms of the C:nutrient ratio. In particular, the C:N ratio was significantly higher in the shelter + macrophytes treatment than in the treatments with no shelter and shelter with initially no macrophytes present, which may be attributed to the decreased nutrient availability. A low food quality may drive zooplankton to increase their overall intake rate to compensate for the deficiency of limiting substances (Hessen, 2008). In our experiment, the percentages of the seston available as food to zooplankton were similar in exposed and sheltered conditions. This suggests that food particle size was not inhibiting zooplankton grazing (Burns, 1968; McCauley & Downing, 1985). Although the food quantity (indicated by the Chl *a* concentration) and food quality (the reverse of the C:N ratio) were higher under the exposed conditions, zooplankton may not have been able to benefit from this because the high ISS concentrations could mechanically interfere with food collection or dilute gut content (Kirk & Gilbert, 1990; Koenings et al., 1990).

Fish predation also may inhibit zooplankton biomass build-up by preferential feeding on *Daphnia* in the absence of shelter (Lemmens et al., 2018; Liu et al., 2020) to a point that it limits the trophic transfer efficiency between phytoplankton and zooplankton. In our experiment, we found such an effect in the shelter treatments, in which fish appeared to have been enclosed. Here, we found a significant

and negative correlation (Kendall's tau = −0.60, $p = 0.038$) between the number of small fish and *Daphnia* biomass, that are the most efficient grazers. However, we found no relationship between fish abundance and zooplankton:phytoplankton biomass ratios, suggesting that fish abundance did not affect trophic transfer efficiency between phytoplankton and zooplankton (Table S3).

4.3 | Shelter effect on benthic fauna

We found a higher density of Gastropoda in the sheltered treatments compared to the no shelter treatment, which supports Hypothesis 3. The high gastropod density under sheltered conditions may be attributed to high food availability, especially the presence of macrophytes. Higher macrophyte biomass in the sheltered treatments can be grazed directly by gastropods but can also function as substrate to support periphyton growth, which is an important food resource for gastropods (Ferguson et al., 2021). Although the periphyton biomass in the shelter treatment was significantly lower compared with the no shelter treatment, this may be explained by a high trophic transfer efficiency between periphyton and gastropods – supporting a high density of gastropods under sheltered conditions. Moreover, the gastropods also may directly benefit from the calm conditions in the sheltered treatments as wind-induced turbulence may increase their mortality and/or dislodgement (Brown & Quinn, 1988; Etter, 1989). It should be noted that we also observed the gastropods feeding on the wall of the mesocosm. However, we did not find macroinvertebrate grazers on the periphyton strips and we did not sample them from the walls. In our study, we found significantly higher Gastropoda densities under the shelter treatments compared to the no shelter treatment. If we also sampled Gastropoda attached on the wall, it only increases the gastropod number in the sheltered treatments, which will not affect the final conclusion. In our study, higher Gastropoda densities seemed related to macrophyte abundance, as we observed also elsewhere on Marker Wadden (van Leeuwen et al., 2021). Furthermore, we found that in the shelter + macrophytes treatment more Corophiidae were found. In this case, macrophytes could function as refuge to protect them from predation or physical damage (Clemente et al., 2019; Thomaz et al., 2008). In our study, the large variation in macroinvertebrate abundance and the subsequent lack of significant differences for most of the taxa may be attributed partly to the sampling limitation, as one sediment core may be insufficient to get an accurate estimate of typically patchy distribution of sediment-dwelling benthic fauna (Wetzel & Likens, 2000).

4.4 | Implications for lake management

Our experimental results show that the creation of shelter in shallow lakes can lead to a shift from phytoplankton towards macrophytes as the dominant primary producers, enhance trophic transfer efficiency from phytoplankton to zooplankton, and increase benthic fauna

biomass. This knowledge can be applied in shallow lake management. For example, submerged macrophytes often are a prerequisite for high-quality shallow lake ecosystem services, including drinking water supply and fisheries production, and serve as hot-spots of biodiversity (Hansson et al., 2020; Hilt et al., 2017; Janssen et al., 2020). Therefore, large efforts have been made to shift lakes from a phytoplankton-dominated turbid state to a macrophyte-dominated clear water state by reducing external nutrient loading globally (Abell et al., 2020; Jilbert et al., 2020). However, these efforts are counteracted or weakened as a consequence of the stability of the fish community composition (i.e., more planktivorous and benthivorous fish), waterfowl grazing, sudden rises in water level and high internal nutrient loading (Hargeby et al., 2004; Janssen et al., 2014; Scheffer et al., 1993; Scheffer & van Nes, 2007). Besides these, we find that wind-induced sediment resuspension also tends to maintain the phytoplankton-dominated turbid state, especially for shallow lakes (Tammeorg et al., 2013; Tang et al., 2020). Our results suggest that in these cases the creation of shelter to reduce negative effects of wind could facilitate a shift in primary producer dominance from phytoplankton to macrophytes. Therefore, the creation of shelter could complement other measures such as nutrient reduction and planktivorous/piscivorous fish biomanipulation (Hansson et al., 1998; Moss, 1990; Moss et al., 1996), which can help in improving the efficiency of shallow lake restoration practices. However, it should be noted that our experiment ran for 2 months, which may be an insufficient duration for a shallow lake to reach a stable state that often is determined by seasonal processes (Hargeby et al., 2004). In that light, our experiment demonstrates that shelter can facilitate macrophytes in becoming the dominant primary producer.

Our study site was located in lake Markermeer, which is a typical example of a shallow lake in which eutrophication has been halted, but a macrophyte-dominated state has not been reached. The aim of lake restoration project Marker Wadden is to stimulate the base of the food web by creating sheltered and heterogeneous habitats. By doing so, it is expected that it will facilitate various primary producers that stimulate the development of the food web in the lake to benefit the higher trophic levels, including fish and water birds (Hansson et al., 2010; van Leeuwen et al., 2021). Our experiments show that, provided that (a) this new archipelago generates sufficient shelter and (b) that herbivory pressure by waterfowl is not too high (Bakker, Sarneel, et al., 2013; Bakker et al., 2016), the benthic aquatic ecosystem of the Marker Wadden that is protected by the archipelago may become dominated by submerged macrophytes over time. Simultaneously, the recovery of higher trophic levels, such as juvenile fish and breeding birds relying on these fish as a food source, might be facilitated indirectly by shelter as a result of the enhanced trophic transfer efficiency between phytoplankton and zooplankton under more sheltered conditions, resulting in turn in high food availability for juvenile fish (Hargeby et al., 1994, 2005). Moreover, the recovery of the benthic fauna under sheltered conditions could increase food web complexity at a larger – Marker Wadden – scale. The creation of shelter thus most probably offers alternative pathways to stimulate

higher trophic biodiversity (Karlsson et al., 2009). Although the low levels of wind disturbance inside our experimental set-ups will be difficult to achieve in the real world, submerged macrophytes (i.e., *Chara globularis* and *Potamogeton pusillus*) have colonised the shallow areas close to the lee side (western shore) of lake Markermeer (Van Zuidam & Peeters, 2015). This suggests that lower degrees of shelter already may provide opportunities for macrophytes to establish in this system. Moreover, *Chara* sp. and *P. pusillus* occurred less at locations with small wave forces and reached their optimum occurrence at intermediate wave forces, potentially as a result of the shading effect of the periphyton and grazing by birds in the most sheltered conditions (Van Zuidam & Peeters, 2015). These results suggest that establishing a macrophyte-dominated state is possible in this large lake in somewhat sheltered, but not completely sheltered, conditions.

Under sheltered conditions, the enhanced trophic transfer efficiency between phytoplankton and zooplankton and the increase in benthic fauna biomass may further facilitate the recovery of higher trophic organisms, and stimulate ecosystem services such as fisheries production (Dickman et al., 2008; Malzahn et al., 2007). By contrast, our results suggest that the enhanced primary production of phytoplankton biomass as a consequence of wind-induced turbulence may not necessarily promote the higher trophic levels as a consequence of the low trophic transfer efficiency (Ye et al., 2013). Altogether, the improved understanding of the effect of shelter on primary producers, trophic transfer efficiency and benthic fauna provides important insights that can be used for more successful conservation and restoration of shallow lakes.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

HJ, ESB and CVL designed the experiment; HJ and ESB acquired the data, HJ, ESB and CVL performed the data analysis, and all authors contributed to data interpretation; HJ, ESB and CVL wrote a first version of the manuscript; RJMT performed careful editing of versions of the manuscript; and all authors contributed to the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Data will be archived online on DataDryad (http://datadryad.org/) upon publication.

ORCID

Hui Jin [ID] https://orcid.org/0000-0002-6325-031X

Casper H. A. van Leeuwen [ID] https://orcid.org/0000-0003-2833-7775

Ralph J. M. Temmink [ID] https://orcid.org/0000-0001-9467-9875

Elisabeth S. Bakker [ID] https://orcid.org/0000-0002-5900-9136

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