



Restoring aquatic food webs bottom-up

*Improving trophic transfer through lake
restoration project Marker Wadden*

Hui Jin

Propositions

1. Both humans and animals should benefit from restoration efforts.
(this thesis)
2. Habitat heterogeneity paves the way for biodiversity.
(this thesis)
3. Scientific publications should share ideas and not be used to judge the quality of its authors.
4. To do science is to be reasonable rather than to reach perfection.
5. Knowing when to adjust one's own expectations is the first step to achieve happiness.
6. Opening up to difference is a first step to creating harmony.

Propositions belonging to the thesis, entitled

Restoring aquatic food webs bottom-up: Improving trophic transfer through lake restoration project
Marker Wadden

Hui Jin

Wageningen, 13 December 2021

**Restoring aquatic food webs bottom-up:
Improving trophic transfer through lake
restoration project Marker Wadden**

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Restoring aquatic food webs bottom-up: Improving trophic transfer through lake restoration project

Marker Wadden

Hui Jin

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Chapter 1

General introduction

1.1 | Trophic transfer efficiency

Declines in higher trophic levels, such as fish and water birds, may indicate a problem at the base of the food web. Either the primary production may be low or it is poorly transferred to higher trophic levels. The transfer of production from lower to higher levels of a food web can be expressed by the trophic transfer efficiency. Trophic transfer efficiency (TTE) is defined as the total production ratio between adjacent trophic levels, which is originally described by Lindeman (1942). Low TTE indicates low transfer of production from a low trophic level to higher trophic levels, often resulting in high standing biomass at lower trophic levels. A high TTE indicates the opposite (Fig. 1.1). The trophic transfer efficiency, especially at lower levels of the food web such as the producer-consumer level, could fundamentally determine higher trophic levels (Ware and Thomson 2005, Dickman et al. 2008). Trophic transfer efficiency can be improved through various mechanisms, including enhanced edibility and nutrient content of food or greater foraging efficiency of consumers (Ersoy et al. 2017, McCauley et al. 2018, Kazama et al. 2021). That is to say, the quantity and quality of primary producers play a significant role in determining trophic transfer efficiency, which is fundamentally determined by the availability of light and nutrients (Hessen et al. 2002, 2013, Sterner and Elser 2002). Primary producer quantity (i.e. biomass) is determined by the absolute availabilities of both resources (Elser et al. 2007, Gruner et al. 2008), and typically increases with higher light and nutrient availability. Also the relative availability of both resources may affect primary producer biomass, as balanced input of two resources may support higher species diversity and thereby enhance resource use efficiencies and community productivity (Hillebrand et al. 2014). Moreover, the relative availabilities of light and nutrients determine primary producer elemental composition, and thereby their nutritional quality for higher trophic levels (Sterner et al. 1997, Sterner and Elser 2002). For lake ecosystems, a declined ecological status of higher trophic levels could be caused by a low transfer efficiency between phytoplankton and zooplankton (Filstrup et al. 2014a, Ger et al. 2016, Ersoy et al. 2017). This can be illustrated by the worldwide impacts of lake eutrophication. Eutrophication may lead to excessive phytoplankton biomass build-up, and often promotes cyanobacterial blooms (Schindler et al. 2016, Huisman et al. 2018). Despite the enhanced primary production, the poor nutritional quality and poor edibility of cyanobacteria limits trophic transfer of this primary production to higher trophic levels, which can lead to the collapse of the food web (Ger et al. 2014, 2016).

Although nutrient reduction has been widely used to address cyanobacteria related issues (Schindler et al. 2016, May et al. 2020, Spears et al. 2021a), which supposedly would increase food quality for higher trophic levels, these measures also unexpectedly resulted in declines of higher trophic levels due to declines in food availability (Jeppesen et al. 2005, N. John et al. 2005, Finger et al. 2007).

In this thesis, I study an innovative lake restoration approach which is based on a multiple-stressor intervention strategy, the Marker Wadden project in lake Markermeer, The Netherlands. The goal of Marker Wadden is to create a bird and fish paradise by stimulating the aquatic food web development bottom-up. My aim is to test whether the Marker Wadden will improve trophic transfer from phytoplankton to zooplankton, and thereby support higher trophic levels thus achieving the overall goal of the project.

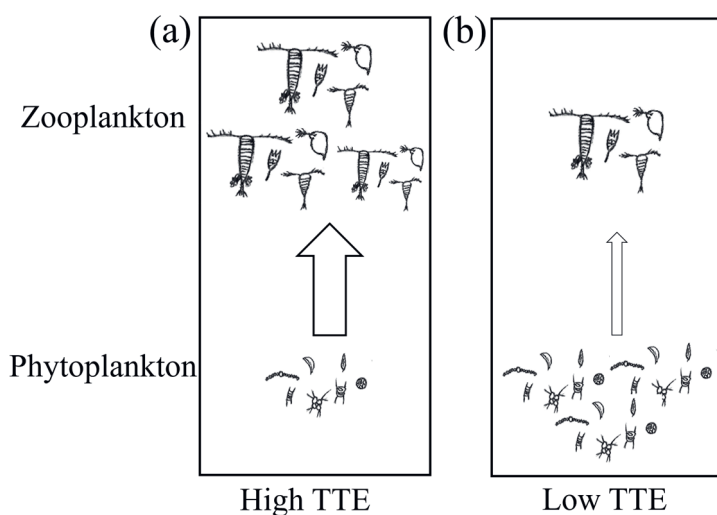


Figure 1.1. Schematic illustration of (a) high trophic transfer efficiency (TTE) and (b) low trophic transfer efficiency in an aquatic food web with two trophic levels. The thickness of the arrow indicates the amount of energy and nutrients transferred from the phytoplankton to zooplankton. The amount of phytoplankton and zooplankton, indicated by the number of symbols, represents the standing stock biomass of respectively the phytoplankton and zooplankton.

1.2 | Lake restoration

Many lake ecosystems worldwide are suffering from severe ecological degradation attributed to multiple anthropogenic stressors, including climate change, land-use intensification, eutrophication, acidification, water abstraction, morphological alteration, and invasive species (Smol 2019, Dudgeon 2019, Heino et al. 2021). Consequently, this leads to the loss of biodiversity and damage to ecosystem services provided by lakes.

To preserve and restore biodiversity and ecosystem services supported by lakes, ecological degradation through global change needs to be counteracted. One way to achieve this is through lake restoration projects (Søndergaard et al. 2007, May et al. 2020, Spears et al. 2021b). However, lake restoration is mainly done by single-stressor abatement approaches (Spears et al. 2021a). This can be exemplified by the restoration of eutrophicated lakes, eutrophication being considered as the most important cause of lake degradation worldwide (Smith and Schindler 2009, Downing 2014, Lüring and Mucci 2020). To combat eutrophication caused by excessive nutrient inputs, reduction of nutrient input has been widely applied (Schindler et al. 2016). This has been successful, and consequently, oligotrophication following nutrient loading mitigation measures became a frequently reported phenomenon in freshwater lakes worldwide (Finger et al. 2013, Sabel et al. 2020). Whereas this has led to successful water quality improvement, in many systems, an unintended decline of higher trophic level production, like zooplankton (Jeppesen et al. 2005, N. John et al. 2005) and fish (Finger et al. 2007), was observed simultaneously to this single-stressor abatement approach. Therefore, to improve lake ecological status and to maintain their ecosystem services nature-based multiple stressor management is needed (Heino et al. 2021, Spears et al. 2021a). Restoring natural littoral zones in human-altered lake shores may be such a nature-based approach to restore lake's ecological status.

1.3 | Littoral zones

Lake littoral zones, as interfaces between aquatic and terrestrial ecosystems, are among the most productive habitats on earth due to the input of nutrients from the land, the light available for primary production in shallow waters and the habitat heterogeneity (Strayer and Findlay 2010, Porst et al. 2019). They play significant

roles in the functioning of lake ecosystems. Littoral zones can directly function as habitat for different types of primary producers and consumers and serve as hot-spots of biodiversity by providing heterogeneity in physical structures due to co-occurrence of primary producers, i.e. submerged macrophytes, phytoplankton, periphyton and benthic algae (Fig. 1.2)(Amoros and Bornette 2002, Lewin et al. 2004, Toft et al. 2007, Strayer and Findlay 2010). A combination of light and nutrient availability determines which primary producers dominate (Scheffer 1990, Teixeira de Mello 2020). However, the presence of different types of primary producers and the physical structures they generate in turn could also mitigate environmental conditions, as they may reduce wave action and thereby alter light and nutrient availability in the water column by creating shelter against the wind (Jenkins et al. 2008, Strayer and Findlay 2010). A large littoral zone may reduce wind mixing and thereby decrease the turbidity and nutrient availability in the water column, which may facilitate submerged macrophyte establishment and growth. In turn, shifts in the dominant primary producer type may cascade to higher trophic levels, altering fish and bird community composition or biomass production. Especially the effect of shelter in the littoral zone is very important as wind has strong effects in shallow lakes, and affects which primary producers become dominant, which may cascade to higher trophic levels, altering fish and bird community composition or biomass production.

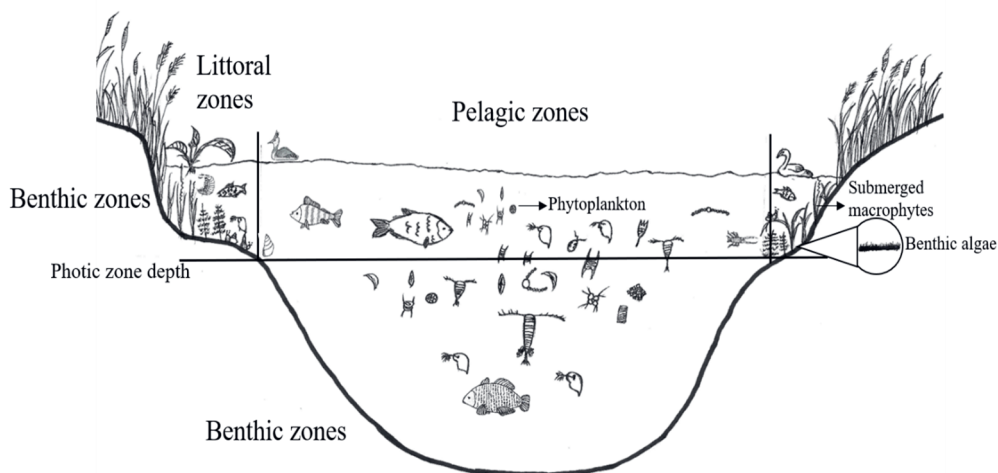


Figure 1.2. Schematic illustration of habitats in lakes. Littoral zones are nearshore, shallow habitats where water depth is above the photic zone depth. Photic zone depth is defined as the depth at which $\sim 1\%$ of the photosynthetically available radiation

(PAR) at the lake surface reaches. Benthic habitats are those associated with bottom substrate in lakes. Pelagic habitats are the open-water components of lakes. The figure is modified from Schindler and Scheuerell (2002).

1.4 | Wind effects on lake ecosystems, primary producers and trophic transfer

Shallow lake ecosystems are easily affected by wind (Janatian et al. 2020, Stockwell et al. 2020). These physical effects of wind can have strong implications for the composition and functioning of the aquatic food web (Fig. 1.3). Importantly, wind can determine the availability of light and nutrients through sediment resuspension processes (Fig. 1.3-a). Wind effects can determine which primary producers become dominant, and generally favors phytoplankton (Fig. 1.3b). Wind-induced turbulence may directly inhibit the establishment of macrophytes (Van Zuidam and Peeters 2015), through the forces it exerts on macrophytes and their propagules (Jupp and Spence 1977, Keddy 1983). Moreover, turbulence may also hinder the colonization of benthic algae due to instable sediment caused by sediment resuspension processes (Jorge and Beusekom 1995). As a result, wind can release phytoplankton from competition by other primary producers. Wind-induced high nutrient availability in the water column facilitates the growth of phytoplankton while it lowers light availability for the growth of macrophytes or benthic algae. Wind also affects secondary production through reduction of trophic transfer efficiency as wind-induced turbulence can modify both the invertebrate community (Fig. 1.3-cd) and the properties of the seston (suspended particulate matter, including phytoplankton). For instance, wind-induced turbulence may inhibit growth of large-sized zooplankton species whose body size exceeds the Kolmogorov length scale as they are more affected by eddy motion (Fig. 1.3-c) (Peters and 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 (Visser et al. 2009, G. -Tóth et al. 2011, Zhou et al. 2016). The dominance of small-sized zooplankton may potentially lower the trophic transfer efficiency as the zooplankton grazing capability is positively size-dependent (Hall et al. 1976). Moreover, wind induced turbulence may reduce invertebrates abundances (Fig. 1.3-d), such as gastropods as it increases gastropod mortality and/or cause dislodgement (Brown and Quinn 1988, Etter 1989). This may

lower the trophic transfer due to a simplified food web structure. Wind also can affect seston properties through sediment resuspension. Seston, i.e., suspended particulate matter, consists of allochthonous and autochthonous material and includes living algae, bacteria, and protozoa, as well as abiotic or dead material (Sterner et al. 1997). Wind-induced sediment resuspension can enhance inorganic suspended solid concentrations in the water (Fig. 1.3-a) and thereby may pose a constraint on herbivore (zooplankton) feeding, as suspended sediment could mechanically interfere with food intake or dilute gut content (Koenings et al. 1990, Kirk and Gilbert 1990). Many important ecosystem services, such as fish and bird production, are determined by the dominant primary producer and the transfer efficiency between primary producers and the herbivores, which are both affected by wind.

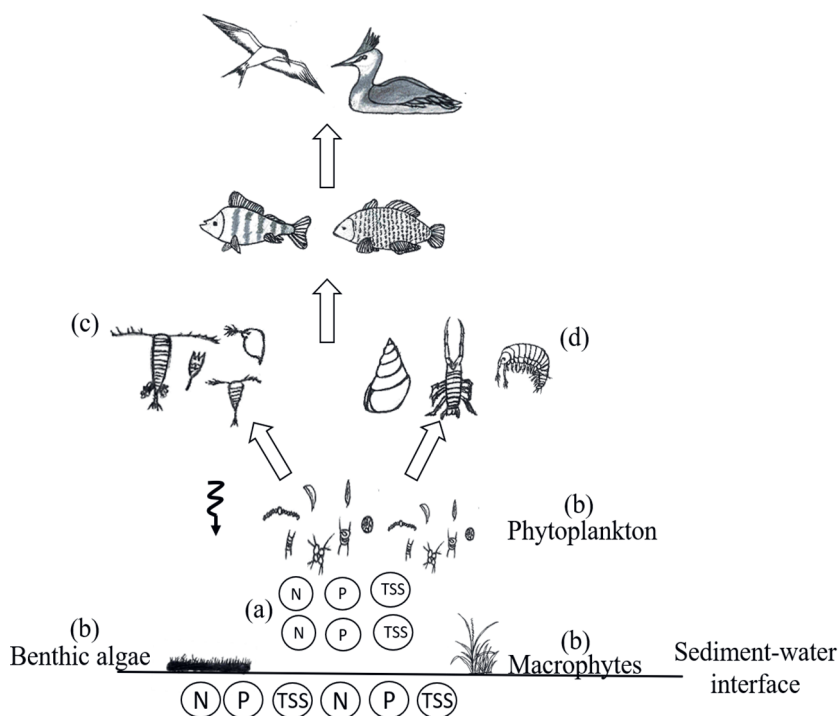


Figure 1.3. Schematic illustration of trophic transfer in a simplified aquatic food web in a shallow lake ecosystem. The arrows indicate the trophic transfer between adjacent trophic levels. This thesis focuses on how the base of the food web can be strengthened to increase trophic transfer to higher trophic levels. The interactions amongst the environment and the food web components a-d are central to this study. N represents nitrogen, P represents phosphorus, and TSS represents Total suspended solids.

1.5 | Restoration project Marker Wadden

As introduced above, declines of higher trophic levels – such as fish and birds – may indicate a problem at the base of the food web, either through a reduction in primary productivity or limited trophic transfer. This phenomenon has been observed in lake Markermeer. Covering an area of 680 km², lake Markermeer (52°32'23.4"N 5°13'56.4"E, the Netherlands) with a 3-5 m depth (mean depth 3.6) is among the largest shallow lakes in Western Europe. This freshwater lake with marine clay sediment used to be connected to the North Sea until the construction of the Afsluitdijk in 1932 (Fig. 1.4). In 1975, the newly formed lake was divided by the construction of the Houtribdijk, which created two lakes: lake Markermeer and lake IJsselmeer. After lake Markermeer was cut off from its marine nutrient supply, nutrient levels were relatively high because of input from surrounding lakes and influx of wastewater from surrounding municipalities, including the city of Amsterdam. During the 1980's the waste water effluent of Amsterdam and surrounding municipalities became disconnected from the lake, and the lake became less eutrophic following re-oligotrophication efforts (Van Riel et al. 2019). This is reflected in the decline of the nutrient concentrations in the water column over the last decades. This can be seen in the total phosphorus concentration (summer means) in the water column, which ranged between 0.20-0.25 mg/L in the first years after formation of the lake, then decreased to 0.01-0.07 mg/L during the period 1976-2002 and remained < 0.1 mg/L after 2002 (Van Riel et al. 2019). Furthermore, lake Markermeer became very turbid; since the original outlet of the lake towards the sea was blocked first by the Afsluitdijk and later by the Houtribdijk, the fine sediments in the lake cannot leave the lake anymore and are repeatedly resuspended by wind action, which can be seen from the turbid water (Fig. 1.4c – note the comparison with the more transparent water of IJsselmeer).

The effective reduction in nutrient loading, was followed by declines in phytoplankton biomass but also in the numbers of birds and fish (Fig. 1.5) (Noordhuis 2014).

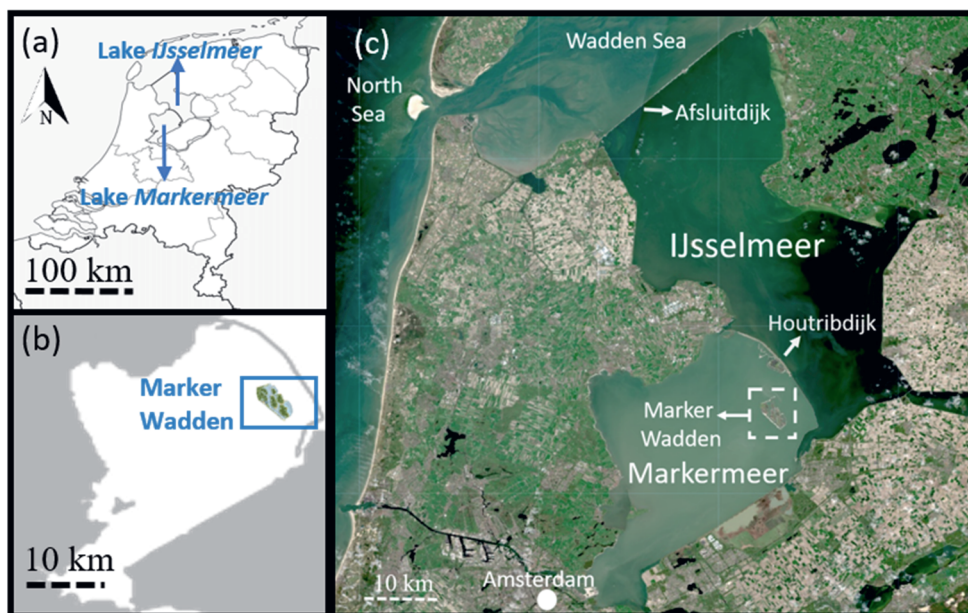


Figure 1.4. (a) map of the Netherlands; (b) map of lake Markermeer; (c) Sentinel-2 cloud free composite image from 15th March to 2nd June, 2021 (Satellietdataportaal 2021). Lake IJsselmeer and Markermeer in the center of the Netherlands. The lakes are part of a former estuary and now disconnected from marine influences by the Afsluitdijk since 1932. The Marker Wadden archipelago is built in lake Markermeer close to the Houtribdijk and emerged in 2016-2017.

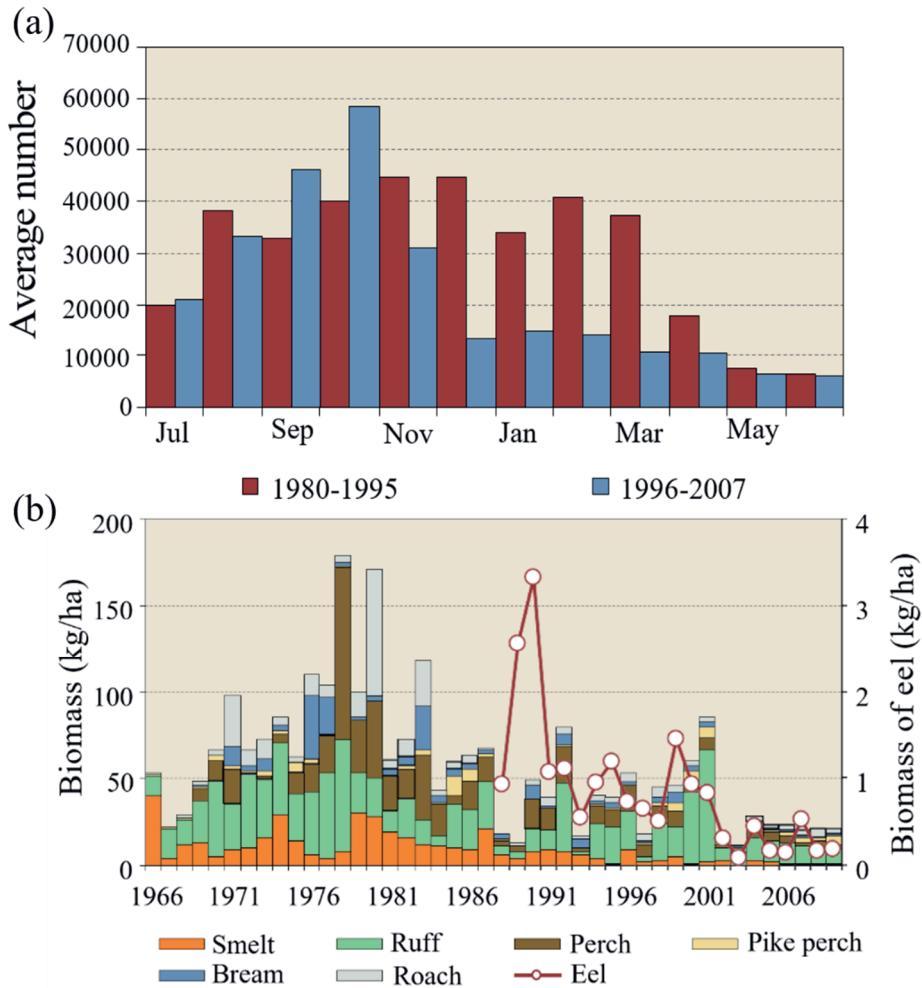


Figure 1.5. (a) The abundance of birds that use the open water of lake Markermeer for foraging during the year in the period 1980-1995 and 1996-2007. (b) Development of the fish stock in Markermeer based on surveys with a beam trawl (bar graph, left axis) and, for eel, electrified trawl (line, right axis). Figures from Noordhuis (2010).

The deteriorating ecological status of lake Markermeer has drawn much attention (Noordhuis 2010, 2014, Van Riel et al. 2019). To improve the ecological status of lake Markermeer, classical restoration methods are impossible, because the historical reference of the lake is marine, and after damming, the freshwater lake developed into a different ecosystem that has no true historical reference condition. Furthermore, classical restoration by for example removing the dikes is socio-

economically undesired due to the current economic and societal functions (flood protection, freshwater storage, water recreation, freshwater fisheries) that became important (Gulati and Van Donk 2002). Therefore, the Dutch Society for Nature Conservation ('Natuurmonumenten'), in cooperation with provincial and national authorities, proposed an innovative large-scale nature-based solution. It follows a rewilding approach by restoring natural processes as much as possible (Bakker and Svenning 2018), whereas it uses engineering to achieve this.

The restoration approach encompasses the building of a five-island archipelago from the lake's own soft-sediment – named 'Marker Wadden' – between 2016-2021. The project aims to increase the lake's primary production by creating gradual land-water transitions (i.e., littoral zones, Fig. 1, Fig. 1.6), heterogeneity in water depths, and decreasing turbidity by creating shelter against fine-sediment resuspension by wind – and thus introducing currently missing elements that are typical for more natural lakes. These elements are added, because the current declines of higher trophic levels (including birds and fish) in lake Markermeer may be caused by 1) negative wind effects, whereby wind causes high turbidity in the water leading to declines in primary productivity due to light limitation, 2) shortage of littoral zones and thereby habitat heterogeneity due to the lake's human-made shore lines of predominantly basalt and asphalt (Fig. 1.6a), and 3) low nutrient availability due to oligotrophication efforts and a lack of terrestrial inputs that reduce primary productivity and may cause food shortage for consumers (Van Riel et al. 2019).

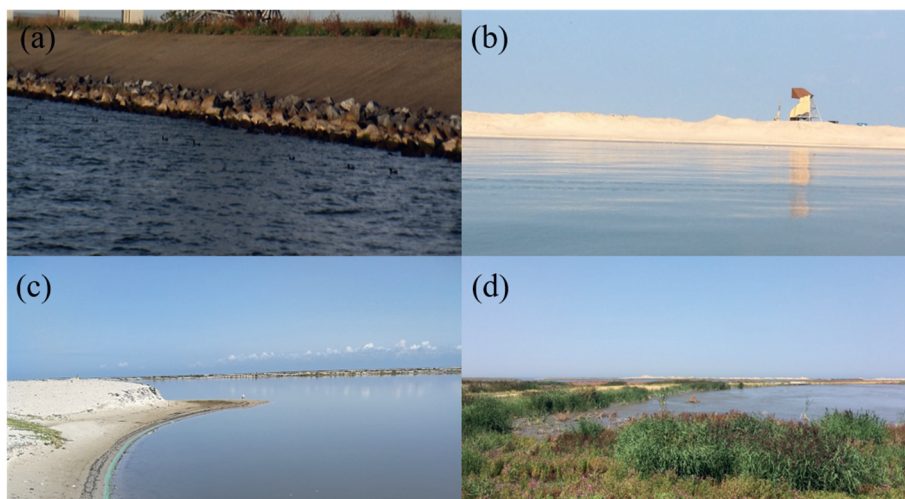


Figure 1.6. Diverse types of shore line in lake Markermeer. (a) Basalt and asphalt shore line without land-water transition area along lake Markermeer. This is the

dominant shoreline type along the lake. (b) Sand dune shore line on Marker Wadden on the exposed sites. (c) Sand dune shore inside Marker Wadden on the sheltered sites. (d) Soft mud shore line inside Marker Wadden on the sheltered sites.

1.6 | Objective and outline of the thesis

The goal of Marker Wadden is to create a bird paradise, for which the archipelago is expected to reverse these negative factors that are thought to cause the decline in birds and fish in lake Markermeer. In my thesis, my aim is to understand whether the Marker Wadden will improve trophic transfer from phytoplankton to zooplankton, and thereby support higher trophic levels thus achieving the overall goal of the lake restoration project.

In my thesis, I test the following overarching hypotheses:

- 1) Creating shelter against wind will increase trophic transfer between phytoplankton and zooplankton in shallow lakes by decreasing the suspended solids concentration;
- 2) Creating shelter against wind will increase trophic transfer by supporting habitat for more types of primary producers, which in turn can support a higher consumer diversity and biomass;
- 3) Creating littoral zones will increase nutrient availability coupled with improved light availability which increases primary producer quantity and quality, thereby stimulating the food web bottom-up and increasing trophic transfer.

To achieve these aims, I combined different approaches ranging from laboratory experiments and field mesocosm experiments to field monitoring.

Chapter 2 describes the large restoration project Marker Wadden in further detail. This project follows a rewilding approach while it uses engineering to achieve this. Marker Wadden is expected to enhance natural values in lake Markermeer without losing existing ecosystem services. In Chapter 2, I present the underlying ecological framework and first scientific results of this innovative on-going project.

In Chapter 3, I studied the relationships between wind-induced sediment resuspension and biomass build-up of phytoplankton and benthic algae, and the consequences for zooplankton biomass. To this end, I conducted a full-factorial sediment resuspension experiment in indoor microcosms using a no resuspension treatment and two levels of sediment resuspension across three water temperatures, as sheltered and shallow conditions may result in higher water temperatures. I hypothesized that shelter would facilitate benthic algae biomass build-up and enhance trophic transfer. The shelter effect could be amplified by the increased temperature.

In Chapter 4, I tested how shelter affects the relative dominance of primary producers and trophic transfer by performing a 2-month manipulative field mesocosm experiment in the shallow waters of Marker Wadden. I expected that reducing wind-induced turbulence would stimulate higher trophic level production in shallow lakes.

In Chapter 5, I evaluated whether Marker Wadden increases nutrient and light availability and thereby enhance the quantity and quality of primary producers. I conducted field monitoring to evaluate the resource availabilities (i.e. nutrients and light) inside Marker Wadden and outside Marker Wadden over a gradient of light and nutrient availabilities. I estimated the quality of primary producers from a stoichiometric viewpoint, i.e., the carbon:nutrients ratio. This also gave me the opportunity to test the light-nutrient hypothesis in an ecological restoration context. The light:nutrient hypothesis predicts how the balance between light and phosphorus availability affects phytoplankton stoichiometry and thereby their nutritional quality for higher trophic levels (Sterner et al. 1997).

In Chapter 6, I tested whether the modified quantity and quality of primary producers affects herbivores (zooplankton) biomass. I further analyzed zooplankton community composition and the quantity and quality of the edible fraction of the phytoplankton from the same field monitoring on which Chapter 5 is based.

In the final Chapter 7, I discuss the results presented in the thesis in the context of lake restoration and address the main aims of this thesis.



Chapter 2

Enhancing ecological integrity while preserving ecosystem services: constructing soft-sediment islands in a shallow lake

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Abstract

1. Ecosystems are increasingly managed to provide multiple benefits to humans, which often degrades their ecological integrity. This strongly applies to aquatic ecosystems, in which engineering can enhance flood protection, drinking water supply, fisheries and recreation. Although these activities typically increase ecosystem functionality to humans, they often impair key aspects of biodiversity and natural functioning.
2. Classical restoration of such degrading freshwater ecosystems can lead to societal opposition, if returning to a former ecosystem state affects previously acquired ecosystem services. Innovative nature-based solutions are therefore needed that enhance natural values in ecosystems, without affecting existing services.
3. We present a large-scale project aiming to increase the ecological integrity of a human-modified freshwater lake, while maintaining its services to humans. The freshwater lake Markermeer in the Netherlands was formed by closing off an estuary for flood protection. The ecological integrity of this lake diminished over time, likely because a declining primary productivity impaired biodiversity at higher trophic levels. This decline is associated with a lack of gradual land-water transitions, strong resuspension of fine sediments, a low nutrient availability and lack of dynamics typically to be expected in a natural temperate freshwater lake. Restoring the lake to its former marine state would conflict with current ecosystem services.
4. A nature-based solution was initiated in 2016, consisting of constructing a five-island archipelago from the lake's own soft-sediments called the "Marker Wadden". The project aims to increase the lake's primary production by creating gradual land-water transitions, more heterogeneity in water depths, and decreasing turbidity by creating shelter and deep sinks reducing fine-sediment resuspension by wind – thus introducing currently missing elements that are typical for natural lakes. We present the underlying ecological framework and first scientific results of this innovative on-going project.
5. Within four years, the Marker Wadden project shows how forward-looking sustainable development of lake ecosystems using a rewilding approach can enhance natural processes and attract birds and fish, without conflicting with existing ecosystem services. This inspires new directions for halting and reversing the degradation of other vital ecosystems worldwide.

Samenvatting (Dutch)

1. Economische ontwikkelingen gaan vaak ten koste van de ecologische integriteit van ecosystemen. Dit geldt zeker voor zoetwater-ecosystemen die worden ingericht ten behoeve van de waterveiligheid, drinkwatervoorziening, commerciële bevissing of recreatie. Maar wat voor mensen mogelijk een verbetering van de functionaliteit van een rivier of meer betekent, gaat vaak ten koste van de biodiversiteit en ruimte voor natuurlijke processen.
2. Herstel van beschadigde zoetwater-ecosystemen op klassieke wijze, namelijk het terugkeren naar de situatie van voor het menselijk ingrijpen, kan maatschappelijke weerstand oproepen als dit ten koste gaat van die eerder verworven ecosysteem diensten. Het vergt innovatieve oplossingen gericht op natuurlijke processen om de natuurwaarden te verhogen en tegelijkertijd de functionaliteit voor de mens ervan te behouden.
3. Deze nieuwe vorm van ecosysteemherstel is toegepast in een grootschalig project in het Nederlandse Markermeer. Het Markermeer is in 1975 kunstmatig ontstaan in het voormalig estuarium van De Zuiderzee door bedijking voor de waterveiligheid. De afgelopen decennia is de ecologische waarde van het Markermeer steeds verder achteruitgegaan, waarschijnlijk doordat de primaire productie afneemt, met consequenties voor het hele voedsel web. Deze afname van productiviteit wordt geassocieerd met een gebrek aan natuurlijke land-water overgangen, slecht doorzicht door continue opwerveling van grote hoeveelheden fijn slib, lage beschikbaarheid van voedingsstoffen en een gebrek aan natuurlijke dynamiek die past bij een natuurlijk gevormd ondiep zoetwatermeer. Klassiek herstel van de ecologische integriteit van het Markermeer via terugkeer naar de voormalige Zuiderzee is inmiddels onmogelijk omdat dit in strijd is met de huidige ecosysteemfuncties.
4. In 2016 is daarom begonnen met een innovatieve vorm van ecosysteemherstel: de bouw van een nieuwe archipel van vijf eilanden, de Marker Wadden. De eilanden hebben als doel de primaire productie van het Markermeer te stimuleren door het toevoegen van karakteristieke elementen van natuurlijke meren die op dit moment in het meer ontbreken. Dit zijn met name geleidelijke land-waterovergangen, variatie in waterdieptes en luwten tussen de eilanden waar het door de wind opwervende slib kan bezinken. Hier presenteren we de ecologische achtergrond en eerste wetenschappelijke

bevindingen van dit unieke en innovatieve project.

5. Binnen vier jaar laat het Marker Wadden-project zien hoe natuurontwikkeling volgens een rewilding benadering een stimulans kan geven aan natuurlijke processen. Vogels en vissen blijken het nieuwe gebied direct in gebruik te nemen, terwijl de ecosysteemfuncties voor de mens behouden zijn gebleven. Dit project kan dienen als voorbeeld van een nieuwe vorm van ecosysteemherstel, wat hard nodig is om de huidige achteruitgang van belangrijke ecosystemen wereldwijd ten goede te keren.

Key-words: ecosystem multifunctionality, forward-looking restoration, land-water connections, littoral zone, Marker Wadden, nature-based solution, novel ecosystems, rewilding

2.1 | Introduction

Human society strongly depends on vital functions and services of natural ecosystems (Zedler and Kercher 2005, IPBES 2019). These include food production, fisheries, recreation, drinking water supply, energy generation and carbon storage (Zedler and Kercher 2005, Clarkson et al. 2013). Consequently, ecosystems do not only have intrinsic natural and cultural values, but are increasingly requested to provide multiple functions simultaneously, including economic returns. This can lead to ecosystem degradation by overexploitation, pollution and habitat loss (Davidson 2014, WWF 2020). Many of the world's freshwater lakes, estuaries and wetlands have important functions for humans, but are also increasingly scarce, used and competed for (Schallenberg et al. 2013, Reynaud and Lanzaova 2017). Worldwide, many aquatic ecosystems are influenced by engineering for a specific, single service (for example damming a river to generate hydropower) that can strongly impair its ecological integrity. Engineering often homogenizes abiotic and biotic conditions, inhibits natural dynamics such as water level fluctuations, and leads to reductions in biodiversity, the trophic complexity and functional diversity at each trophic level (Gibbs 2000, Millennium Ecosystem Assessment 2005). Consequently, many aquatic ecosystems are currently in need of sustainable nature development strategies, because their ecological integrity has eroded as a result of a wide range of simultaneous demands and associated modifications (Davidson 2014).

Classical ecological restoration of freshwater ecosystems, which to a large degree has focussed on returning degraded ecosystems to their pre-human-use conditions, is often challenging (Higgs et al. 2014, 2018). Worldwide, many lakes are modified for flood protection, drinking water reservoirs, or to fulfil new, desired, ecosystem functions such as energy generation or recreation (Schallenberg et al. 2013, Reynaud and Lanzaova 2017). With classical restoration, where past modifications are undone, at least some of these new ecosystem functions to humans are unavoidably lost (Higgs et al. 2014). Furthermore, classical restoration projects that affect (part of) these desired functions mostly face complicated, long-term negotiations (Perring et al. 2015, Suding et al. 2015) – including about what should be the historical reference state of the ecosystem to return to (Higgs et al. 2014). To overcome such challenges, novel strategies for deteriorating ecosystems are needed that enhance their ecological integrity, while preserving their ecosystem services and socio-economic benefits (Gulati et al. 2008, Higgs et al. 2014, 2018, Corlett 2016, Martin 2017).

Here we present a forward-looking approach to enhance ecological integrity of the shallow lake Markermeer in the centre of the Netherlands, which is – like many freshwater lakes in the world – a human-created lake (Hogeboom et al. 2018). The large lake Markermeer was formed by the construction of two dikes and multiple land reclamations in a marine estuary, named the Zuiderzee (Fig. 2.1a, Fig. 2.1b). First, a 32-km long dike (named the Afsluitdijk) was completed in 1932, which turned the main tidal estuary of the river IJssel into a 357,000 ha freshwater lake over time. The new lake IJsselmeer, still fed with freshwater by the river IJssel, experienced a drastic change in salinity, food web composition and hydrology (Cremer et al. 2009). Second, land reclamation occurred in 1942 (60,000 ha) and between 1955-1968 (114,000 ha). Third, a 27-km long dike (named the Houtribdijk) was completed in 1975 and divided lake IJsselmeer into two lakes: a new almost land-locked lake Markermeer (70,000 ha) in the southwest with limited riverine input (river Eem, discharge of $10 \text{ m}^3 \text{ s}^{-1}$), and the drainage lake IJsselmeer (113,000 ha) in the northeast still fed by the river IJssel (discharge of $340 \text{ m}^3 \text{ s}^{-1}$, Fig. 1b, (Vijverberg et al. 2011), terminology *sensu* Heino et al. 2021). Both lakes developed distinct ecological values and started to provide many ecosystem services to humans, including recreation, drinking water supply, fishing and agriculture (Gulati and Van Donk 2002). However, the engineering activities did not automatically introduce elements such as gradual land-water transitions, heterogeneity in water depths or water level dynamics into these lakes that one would expect in well-functioning large lowland freshwater lakes formed by natural processes (Schindler and Scheuerell 2002).

Both lakes initially developed towards important ecosystems for piscivorous and benthic feeding waterbirds. Benthivorous water birds like the common pochard *Aythya ferina*, tufted duck *A. fuligula* and greater scaup *A. marila* profited from establishing populations of the non-native freshwater mussels zebra mussel *Dreissena polymorpha* and quagga mussel *D. rostriformis*. Piscivorous water birds like the great crested grebe *Podiceps cristatus*, smew *Mergellus albellus* and common merganser *Mergus merganser* started thriving on a rich stock of fish such as smelt *Osmerus eperlanus* as food source (Noordhuis 2014). However, over the last decades the ecological integrity of particularly lake Markermeer has been strongly declining (Lammens et al. 2008, Noordhuis 2014). Compared to the 1980's, numbers of many benthivorous and piscivorous bird species have halved, coinciding with a decrease of the smelt population to one-tenth of its biomass (de Graaf and Keller 2010, Noordhuis 2014). These decreases in the higher trophic levels of the food web were likely caused by multiple coinciding factors, including an increase in

turbidity and a decrease in primary productivity (Velde et al. 2010, Noordhuis 2014, Van Riel et al. 2019). This declining ecological integrity resulted in a long-standing societal wish for a nature-based solution to this problem, i.e., a solution addressing the societal challenge by working with and enhancing nature (Seddon et al. 2020). The goal was to improve the lake's ecological integrity by adding the structure and dynamics that are more typical for a natural freshwater lake at low altitudes (Heino et al. 2021), but without compromising the many ecosystem services it currently provides (Lammens et al. 2008).

Classical restoration of lake Markermeer is ecologically impossible, because the historical reference of the lake is marine, and after damming, the freshwater lake developed into a different ecosystem that has no true historical reference condition. Furthermore, classical restoration by for example removing the dikes is socio-economically undesired due to the current economic and societal functions (flood protection, freshwater storage, water recreation, freshwater fisheries) that became important (Gulati and Van Donk 2002). Therefore, the Dutch Society for Nature Conservation ('Natuurmonumenten'), in cooperation with provincial and national authorities, proposed an innovative large-scale nature-based solution. It follows a rewilding approach by restoring natural processes as much as possible, whereas it uses engineering to achieve this. This approach encompasses the building of a 700 ha archipelago consisting of five islands in the lake – named 'Marker Wadden' – between 2016-2020. Here we present the concept and first results of the Marker Wadden project, an ambitious, large-scale project in the Netherlands aimed at improving the ecological integrity of lake Markermeer, while maintaining the lake's current ecosystem functions and services.

2.2 | The Marker Wadden project

To reverse the decline of lake Markermeer's ecological integrity, the Marker Wadden project aims to enhance the food web bottom-up via nature-based solutions. The project therefore targets three factors that are currently missing in comparison to more natural lakes and are thought to limit primary production (Fig. 2.2). First, historically the marine estuary was a highly productive, nutrient-rich coastal system due to marine and riverine inputs (Fig. 2.2a). Nutrient levels that sustain primary production are currently low in the water column of the freshwater lake, due to closing off most marine and riverine inputs and retention of available nutrients in the iron-rich sediment. Second, the sediment of lake Markermeer consists of Pleistocene

sands covered with a 5 – 8 m layer of Holocene clays, silts and fine sands (Troelstra et al. 2018) covered with a layer of floating mud (Fig. 2.2b). This 0.1 - 0.2 m upper layer of floating mud consists of a fine fraction with a maximum settling velocity $<0.01 \text{ mm s}^{-1}$ and a slightly coarser fraction with a settling velocity between 0.5 and 4.0 mm s^{-1} , that is easily resuspended at wind speeds over 4 m s^{-1} (Vijverberg et al. 2011). While the floating mud was historically able to sink towards deeper areas of the larger estuary, the enclosed shallow water in lake Markermeer with a $>25 \text{ km}$ wind fetch length now suffers from continuous resuspension of this fine material (Fig. 2.2b). Lake Markermeer essentially became similar to a land-locked shallow lake with a long fetch length (Fig. 2.1a, Fig. 2.1b), leading to suspended sediment concentrations of easily 50 mg L^{-1} near the surface - increasing to well over 100 mg L^{-1} in case of very strong winds (Van Kessel et al. 2008, Vijverberg et al. 2011). Fine sediment resuspension reduces light availability for primary production in the water column and may hamper zooplankton feeding, thereby limiting the trophic transfer efficiency of phytoplankton to higher trophic levels (e.g. (G.-Tóth et al. 2011); (Penning et al. 2013); (de Lucas Pardo et al. 2015)). Third, basalt and asphalt dikes form homogeneous steep, hard shorelines – and the water level is stable, managed, and reversed (maximum variation 0.5-1.0 m, high in summer and low in winter). This offers limited space for ecological processes relying on land-water transitions and the littoral zone – such as reproduction by fish, nutrient cycling and the influx of carbon from terrestrial sources (Benson and Magnuson 1992, McGoff et al. 2013).

The Marker Wadden project aims to mitigate the negative effects of these aforementioned factors by constructing an archipelago of islands that add land-water connections, shelter, shallow and deeper waters to the lake (Fig. 2.1, Fig. 2.2c). These constructions aim to add previously missing habitat types and dynamics more typical of lowland natural freshwater lakes (Schindler and Scheuerell 2002, Heino et al. 2021) to this human-created lake. The construction of the archipelago started in 2016 by building stone dikes and sand dunes on the windward side (west) to provide shelter for subsequent constructions. On the leeward side of these strong structures, islands were constructed from sediment of lake Markermeer itself. These islands were constructed as ring dikes made of deeper Pleistocene sands, extracted from the lake bottom at depths ranging between 8 m and over 35 m deep. The areas within these ring dikes were subsequently predominantly filled – to levels above lake water level – with the fine clays and silts from the top 5 to 8 m of the lake bottom (Troelstra et al. 2018). Subsidence of the clays and silts to below the lake's water level (Temmink et al. 2021) resulted in marshlands with shallow water levels ($<1 \text{ m}$), which were partly reconnected to the lake water at the end of 2020. The constructed

islands add natural shorelines with gradual land-water transitions and waters between ~0.5 and 2 m deep to the lake, plus multiple sand excavations areas of over 35 m deep with their possible distinct own value (Fig. 2.2c). The construction procedure itself removed fine sediments from the lake, and the sheltered waters between the islands were expected to further stimulate settling of suspended sediments.

The construction of the islands also created a series of land-water connections, which would be typical for more natural freshwater lakes but were previously lacking in the Markermeer. These land-water connections were hypothesized to stimulate primary production by increasing runoff of nutrients from land to water. The shallow waters that develop between the islands would be more productive due to higher nutrient availability, quick warming in spring, and shelter from the wind, which reduces resuspension of the fine clays and silts. Hence, primary production was thought to increase, as this is no longer hampered by nutrients and light limitation (Schallenberg et al. 2013). Establishment of submerged macrophyte- and shoreline-vegetation could further help in trapping suspended solids (Barko and James 1998). These processes combined were hypothesized to positively affect the lake's food web via stimulation of primary production, providing habitat structure and increasing the efficiency of energy transfer to higher trophic levels - leading to higher functional diversity at all levels of the food web. The vision behind Marker Wadden is that it could induce highly productive conditions providing foraging and spawning and breeding habitat for higher trophic levels such as fish and waterbirds.

The Marker Wadden project also aimed to enhance the recreational function of the lake. The largest of the five newly constructed islands was therefore made accessible to the general public, whereas the other islands remain closed for the public (Natuurmonumenten 2013). On the largest island, the Dutch Society for Nature Conservation constructed a small settlement (Fig. 2.1c). This has been built off-grid using exclusively sustainable materials, and includes a small harbour, five holiday houses and a visitor centre. Moreover, they constructed a group accommodation and a field station for educational and research purposes, run a ferry to enable recreationists to visit the island, offer guided tours, and educate about nature. This is combined with dedicated regular communication about the project and the involvement of volunteers during all aspects of the project to ensure societal acceptance. The project therefore deliberately integrates recreation, nature education, innovation and research (Natuurmonumenten 2013).

2.3 | First observations on ecological integrity

Our first observations on ecological implications of the Marker Wadden project – even though it is still under development – suggest that nature is able to quickly profit from the newly created habitats (for a timeline see Fig. 2.3). The expected effects of the islands on primary production via reduction of suspended sediment concentrations followed by an increase in light levels in the water column have proven difficult to assess at this early phase of the project, in part because the building activities initially created sediment resuspension themselves. However, the construction of the archipelago included the creation of three basins of each 3-4 ha at an early building phase (late 2016, Fig. 2.1c). Each basin was a part of the lake that became surrounded by dikes – sheltering the water and separating it from the rest of the lake – but otherwise leaving it identical to the open lake water.

As a proof of concept of how shelter can affect the aquatic food web, we surveyed the development of these basins three years after their construction (on the 24th of May 2019) by comparing the sheltered basins to three locations in the open water close to the basins just off Marker Wadden. At three locations in the open water and in each of the basins we examined the aquatic food web by assessing (1) total chlorophyll-a concentrations in fresh water samples using a PHYTO-PAM phytoplankton analyser (Heinz Walz 91090 GmbH, Effeltrich, Germany), with the sum of the blue, green and brown channels as an indication of total phytoplankton concentrations ($\mu\text{g L}^{-1}$); (2) zooplankton densities by concentrating 30 L of water through a 80- μm zooplankton net into a 50 ml tube and fixating it with lugol's iodine, followed by counting zooplankton under a LEICA M125C stereo microscope; (3) macrophyte presence by dragging a 30-cm wide rake four times across 1 m of sediment, washing and drying the collected material at 60°C for 48 h, and weighing the dried material to the nearest 0.1 g; (4) sampling benthic macrofauna by grabbing a 15 × 15 cm sediment sample from the top 10 cm of the lake bottom, and estimating their dry weight based on identifications to species level and their known length-biomass relationships.

The sheltered conditions affected the food webs in the three basins within three years. Basin 1 moved towards a more phytoplankton-dominated state, with a zooplankton community consisting mostly of Copepoda and high densities of Annelida in the sediment (Fig. 2.4). Basins 2 and 3 moved towards much clearer conditions (Fig. 2.4b), with lower phytoplankton concentrations but large Cladocera visible by the naked eye (Fig. 2.4d). In these two basins three macrophyte species developed (Fig. 2.4f), and macrofauna became dominated by Arthropoda and

Mollusca instead of Annelida – including Chironomid larvae, freshwater snails and locally high densities of opossum shrimps *Neomysis* sp. (Fig. 2.4h). Although each basin developed differently, these early observations suggest that merely creating shelter in lake Markermeer has the potential to affect multiple trophic levels and their relations in the food web within three years. The observation that macrophytes can colonize the sheltered areas among the islands was confirmed in a larger-scale macrophyte survey on the Marker Wadden in 2020. Underwater vegetation was mapped in the shallow waters between the islands, which revealed the presence of low densities of eight submerged macrophytes and four Charophyte species. Dominant species were sago pondweed *Potamogeton pectinatus*, horned pondweed *Zannichellia palustris*, common stonewort *Chara vulgaris* and starry stonewort *Nitellopsis obtusa* (Scirpus Ecologisch Advies 2020). Before the project started, these species rarely occurred in the eastern part of the lake (Vonk et al. 2019), likely because the fine clay soil type combined with strong winds made this part of the lake less suitable for macrophyte establishment (Van Zuidam and Peeters 2015).

In the marshlands, vegetation developed on the land-water transition zones within one growing season. In the first year, marsh fleawort *Tephrosieris palustris* was the most dominant species, probably because it is a wind-dispersed, early pioneering plant that can easily establish in shallow water. Willows *Salix* sp. colonized and dominated the drier marshland zones. The aim of the project was to develop helophyte marshes rather than wet forests. Therefore, willows were actively removed and their germination prevented by water management until 2020, and rhizomes of common reed *Phragmites australis* and broadleaf cattail *Typha latifolia* were actively sown and protected against herbivores - as grazing pressure in aquatic systems can be high (Bakker et al. 2016a). Protection against avian herbivores (notably greylag geese *Anser anser*) at the establishment phase of the vegetation resulted in rapid development of a helophyte vegetation at the land-water transition zones (de Rijk and Dulfer 2020).

Surveys of higher trophic levels included assessments on what the new habitat could offer to fishes and birds. Fish were surveyed in 2018 and 2019, finding 19 different species – and including high larval densities in several of the new shallow habitat types. Dominant native species are common roach *Rutilus rutilus*, European perch *Perca fluviatilis* and Eurasian ruffe *Gymnocephalus cernua*, but also four typically pioneering non-native Gobidae can be found (Emmerik 2018, 2019). Numerous bird species use the islands, which is extensively monitored. Over 20,000 sand martins *Riparia riparia*, 3,000 northern shovelers *Spatula clypeata*, 1,000 pied avocets *Recurvirostra avosetta*, 1,000 black terns *Chlidonias niger* and hundreds of

little gulls *Hydrocoloeus minutus* colonized the islands within three years. For shovelers, black terns and common terns *Sterna hirundo* the islands harboured respectively >6%, 2% and 2% of the flyway population at a given moment in 2019 (van der Winden et al. 2019). For common ringed plover *Charadrius hiaticula* and common terns more than 10% of the national population was attracted to the new habitat. Many of the observed bird species had been present in much lower numbers and/or did not breed in such numbers for decades in the Netherlands. Rarer species such as greater flamingos *Phoenicopterus roseus* and Eurasian spoonbills *Platalea leucorodia* were also encountered, and nests were found of gull-billed terns *Gelochelidon nilotica* and long-tailed ducks *Clangula hyemalis* - two bird species that had not been breeding in the Netherlands for decades.

Overall, functional diversity seems to locally increase in many trophic layers and a shift may be on its way from a simplistic food web to a structurally more complex food web. This allows more coexistence of different trophic levels in the food web under the wider range of abiotic conditions. Natural processes are quickly taking advantage of the increased heterogeneity, land-water transitions and gradual shorelines typical of more natural temperate freshwater lakes. Even though the former estuarine conditions in this ecosystem did not return, the ecosystem seems to be developing towards a higher ecological integrity that might increase resilience to future perturbations (Carpenter and Cottingham 1997, Scheffer et al. 2001). Whether or not the Marker Wadden project is sufficient to change the downward trend in the lake completely remains to be determined.

2.4 | The Future of nature development

The 21st century requires nature-based solutions and thus new views on nature, sustainability, resilience, ecological restoration, rewilding and other forms of nature development. Initiatives for improving the ecological integrity of many human-impacted areas are often slowed down or stopped by societal resistance to give up existing benefits derived from ecosystems, or by a lack of vision on how a system should be developed. Here, we present a new perspective on nature development and rewilding ecosystems, in a situation where a return to a former ecosystem state was impossible due to the lack of historic reference, and strong societal adherence to existing (novel) benefits.

In the first four years since the start of the Marker Wadden project, the trends are positive. There are no signs that important functions of the lake such as flood

protection, freshwater storage or fisheries are negatively affected. With respect to recreation, the largest of the islands was opened for the general public in September 2018 – and welcomed over 20,000 visitors, 180 recreational charter vessels and 2,000 recreational ships for an overnight stay in the harbour in the year 2019 (Natuurmonumenten 2019). In 2019, the islands featured over 150 times in the regional and national news, which increased to over 250 times in 2020. It is too early to assess the how the project likely affects the many ecosystem services that the lake currently provides, but the first observations and responses from society are very positive.

The concept of a forward-looking approach to enhancing ecological integrity that we outline here can hopefully inspire other scientists and practitioners to design and initiate innovative solutions that do not collide with ecosystem multifunctionality. The Marker Wadden are designed with a dual function, aiming to facilitate human activities as well as increase ecological integrity and natural values of a deteriorating ecosystem. Although illustrated with an aquatic case-study, this new way of thinking may pave ways to enhance natural values in many types of human-made systems and counteract the loss of vital ecosystems globally. If given a chance, nature has great capacity to maintain ecological integrity while providing ecosystem functions to human societies.

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Conflict of interest

The co-authors RP and AB work for the non-profit nature conservation organisation that has been responsible for building the Marker Wadden (Natuurmonumenten). We declare no conflicts of interest.

Author's contribution

LB, HO and CL initiated the writing and HJ and AB contributed the data. After discussions with all authors about the concept design and interpretation, CL and RT wrote the first draft of the manuscript. All authors subsequently contributed to writing the final paper.

Data availability statement

Data available from the Dryad

DigitalRepository: <https://doi.org/10.5061/dryad.2v6wwpznx> (van Leeuwen et al 2021).

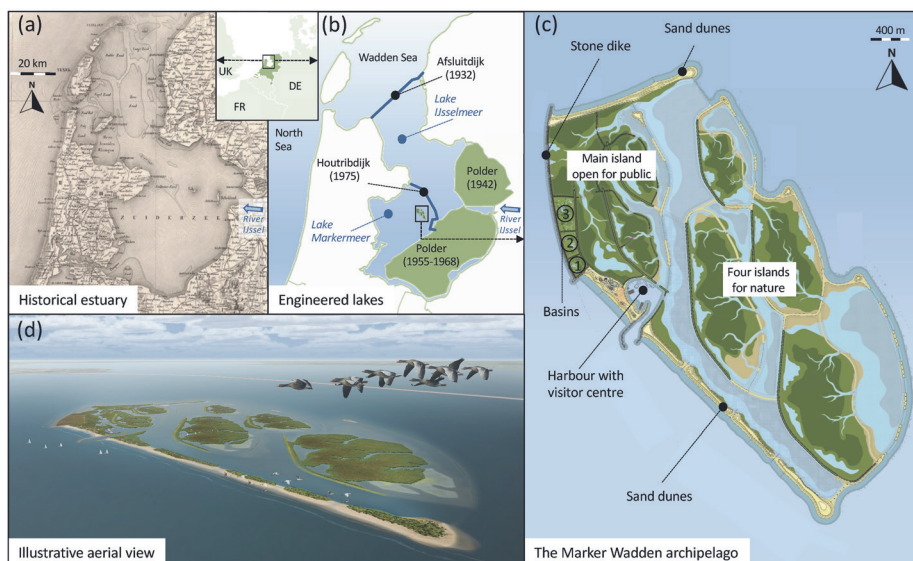


Figure 2.1: Overview of the location and structure of the Marker Wadden project. **(a)** The central marine estuary in the Netherlands in 1850 with its main inflow from the river IJssel. **(b)** After a series of catastrophic floods in the late 19th and early 20th century, several dikes were built to prevent flooding. The estuary was closed by a 32 km long dike (Afsluitdijk) in 1932, followed by several phases of land reclamation (polders), and finally the construction of a 27 km dike (Houtribdijk) in 1975. This created the 70,000 ha freshwater lake Markermeer in the southwest with limited riverine input, and the 113,000 ha lake IJsselmeer in the northeast still fed by the river IJssel. **(c)** To enhance ecological integrity of lake Markermeer without loss of existing ecosystem services, from 2016-2020 soft-sediment islands the “Marker Wadden” were built close to the Houtribdijk. Five islands were constructed – on the leeward side of stone dikes and sand dunes – by creating ring dikes from local deep Pleistocene sands (extracted from between 8 and 35 m deep in the lake’s sediment) that were subsequently mostly filled with fine clays and silts from the top 5-8 m of the lake’s sediment. In 2017, a harbour was constructed with stone dikes, and in 2018 a long-stretching sand dike was built in a southwest direction. This allowed the creation of more islands in the sheltered areas in subsequent years via sand dikes filled with fine clays and silts. Subsidence of the clays and silts to just below the water level results in marshlands with water levels <1 m, which were reconnected to the lake water late 2020. Only the main island is accessible to visitors via a small harbour with visitor centre. **(d)** The Marker Wadden illustrated as an aerial view. Image credits: (a) Kadaster, Apeldoorn, the Netherlands; (c) Boskalis, Capelle aan de IJssel, the Netherlands; (d) Bureau Vista, Amsterdam, the Netherlands.

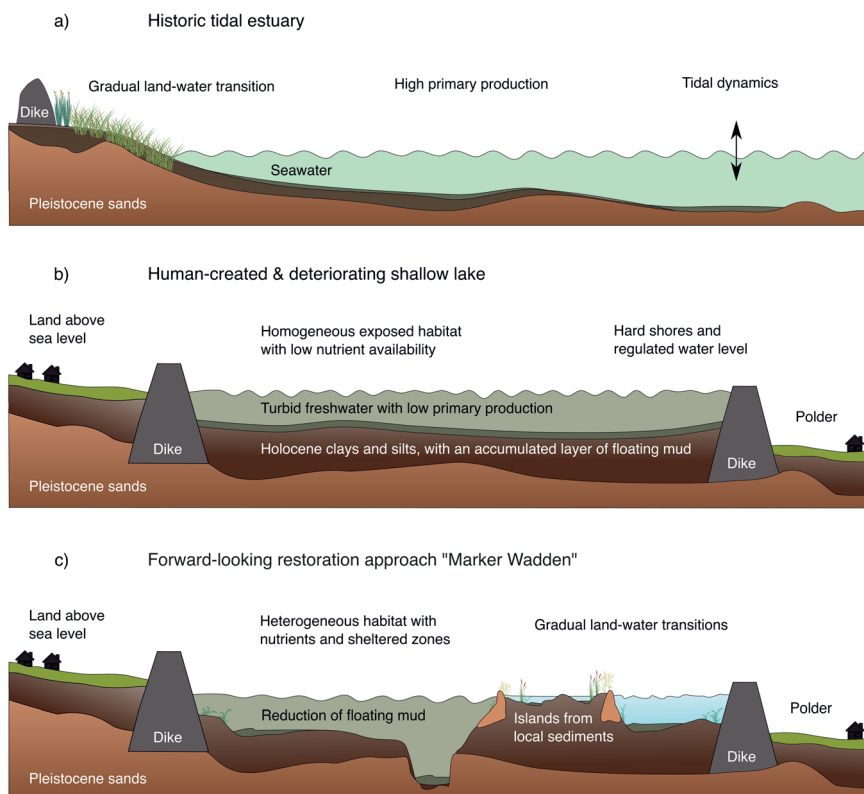


Figure 2.2: Schematic overview of the changes in the study area over the last century. **(a)** Before the 1930's, a highly productive tidal estuary was present with gradual land-water transitions. **(b)** In the twentieth century, basalt dike constructions created the homogeneous shallow freshwater lake Markermeer with stabilized water levels, which trapped high amounts of fine sediments (called “floating mud”) and lead to a high turbidity. A littoral zone was absent and primary production decreased. **(c)** Between 2016 and 2020, the Marker Wadden archipelago was constructed to add more heterogeneous habitat to the freshwater lake. The islands include soft shores with gradual land-water transitions that provide nutrients for primary production, and create sheltered areas where turbidity decreases due to a reduction of resuspension and accumulation of easily resuspended sediments in deeper areas.



Figure 2.3: Timeline of the construction of the islands showing their rapid development in aerial and corresponding ground pictures from selected representative locations for the different years since 2015. The first sand ring dikes appeared above the water level in the spring of 2016, followed by filling with clays and silts, and quickly expanding in surface area in 2017. In 2018, pioneering vegetation such as marsh fleawort *Tephroseris palustris* appeared, which expanded in 2019 to a surface cover of the islands of >25% by species such as willows, marsh fleawort and broadleaf cattail *T. latifolia* (Van der Winden 2019). In 2020, ring dikes were opened, the meanwhile vegetated marshlands were reconnected to the open water, and helophytes further developed on the land-water transitions. Aerial views were obtained from (Satellietdataportaal 2021); ground pictures by the authors.

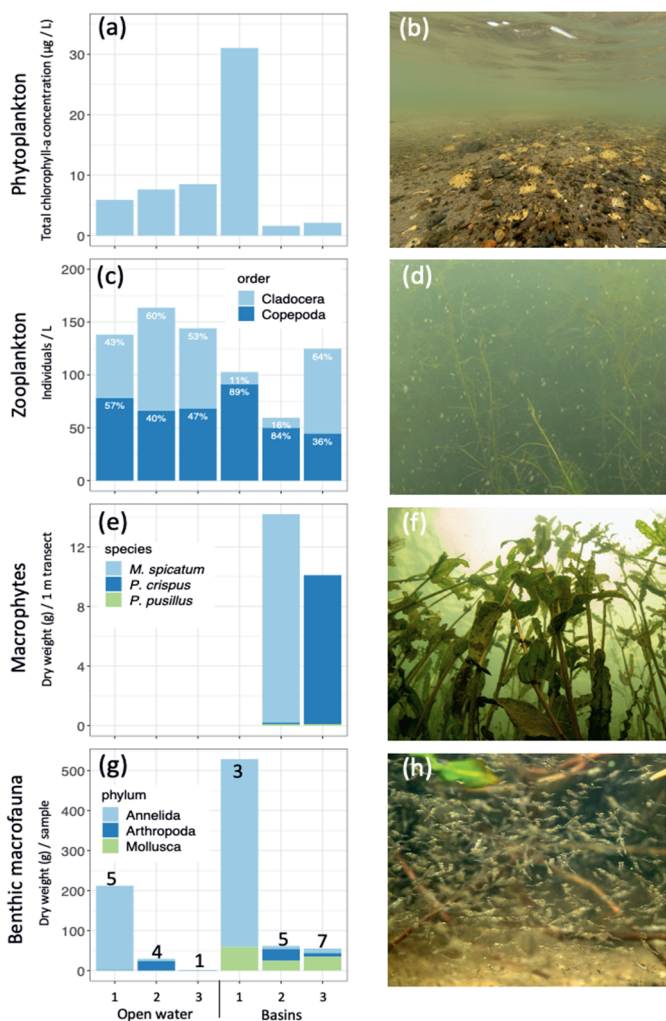


Figure 2.4:
Observed status of different trophic levels in the open water and their developments in the three sheltered basins after three years. **(a, b)** Phytoplankton (indicated by total chlorophyll-a concentrations) increased strongly in basin 1, but decreased in basin 2 and 3 where water became clearer. **(c, d)** Zooplankton communities in the open water consisted of similar numbers of Copepoda and Cladocera, but relative densities of both orders started

to shift in the basins – leading to high densities of large zooplankton in basins 2 and 3. **(e, f)** Macrophytes developed under the clear conditions of basins 2 and 3, including *Myriophyllum spicatum*, *Potamogeton crispus* and *Potamogeton pusillus*. **(g)** Macrofauna became more diverse in basins 2 and 3 with a shift towards more Arthropoda (including Chironomid larvae, opossum shrimps *Neomysis* sp.) and Mollusca (including the New Zealand mud snail *Potamopyrgus antipodarum* and European stream valvata *Valvata piscinalis*) and fewer Annelida (dominated by Tubificidae). The numbers above the columns in panel g indicate total species numbers. **(h)** Macrofauna in the basins included locally high densities of opossum shrimps. Photo credits: Arthur de Bruin.



Chapter 3

Impacts of sediment resuspension
on phytoplankton biomass production
and trophic transfer: implications for
shallow lake restoration

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Abstract

Wind-induced sediment resuspension in shallow lakes may enhance nutrient availability while reducing light availability for phytoplankton growth, thereby affecting the entire food-web. Lake restoration projects that reduce wind-induced resuspension are expected to enhance trophic transfer efficiencies, thereby improving food-web structure and functioning. Yet, reduced resuspension may also lead to lower nutrient concentrations in the water column, promote benthic algae development, reduce phytoplankton biomass production and thereby reduce secondary production by zooplankton. Lake Markermeer is a shallow delta lake in The Netherlands subject to wind-induced sediment resuspension. Restoration project Marker Wadden consists of newly built islands aiming to reduce sediment resuspension and promote higher trophic levels. Here, we tested the effects of reduced sediment resuspension on phytoplankton biomass build-up, benthic algae development, and zooplankton abundances at different temperatures in a 14-day indoor microcosm experiment. We used Marker Wadden sediment with three resuspension intensities combined with three temperatures, to also test effects of higher temperatures in shallow sheltered waters. Reduced sediment resuspension decreased nutrient concentrations and phytoplankton biomass build-up, while increasing light availability and enhancing benthic algae biomass development. Reduced sediment resuspension furthermore increased zooplankton biomass. Enhanced sediment resuspension and higher temperatures synergistically interacted, maintaining a high level of inorganic suspended solids. Our experimental results are in line with long-term seasonal observations from lake Markermeer. Our findings demonstrate that for shallow lakes suffering from wind effects, measures such as Marker Wadden aimed at reducing sediment resuspension can be effective in restoring secondary production and supporting higher trophic levels.

Keywords: benthic algae, food web, Marker Wadden, water temperature, zooplankton

3.1 | Introduction

Higher trophic levels depend on primary productivity and the transfer of nutrients and energy from the base of the food web up the food chain ('trophic transfer') (Lindeman, 1942; Burian et al., 2020). Hence, a decline in abundance of higher trophic levels – such as fish and birds – may indicate a problem at the base of the food web, either through a reduction in primary productivity or limited trophic transfer. In aquatic systems, generally, phytoplankton productivity increases with nutrient availability (Quinlan et al. 2021), provided that there is enough light available to sustain primary production (Edwards et al. 2016). As a result of increased primary production, zooplankton densities increase, if phytoplankton is edible and of good enough quality to sustain zooplankton production (Burian et al. 2020). However, this relationship becomes more complicated in water bodies that experience high turbidity from sediment resuspension. High amounts of suspended solids in the water column interfere with nutrient and light availability for phytoplankton production (Schallenberg and Burns 2004), which affects trophic transfer. Furthermore, trophic transfer may become impaired because zooplankton filter feeders may be hampered by the high concentrations of suspended sediment in the water column (Koenings et al. 1990, Kirk and Gilbert 1990).

Sediment resuspension can enhance release of nutrients bound to sediment particles (Tammeorg et al. 2013, Tang et al. 2020, Zhang et al. 2020), and make them available for phytoplankton. Under sheltered conditions, sediment may settle and more light becomes available for phytoplankton growth. However, under sheltered conditions, less nutrients are available in the water column, which may result in reduced phytoplankton biomass. In this situation, increased light availability may induce a shift in the dominant primary producers from phytoplankton to benthic algae (i.e. algae attached to the sediment surface) (Jäger and Diehl 2014), resulting in a further reduction of phytoplankton production due to nutrient competition. Benthic algae can directly take up nutrients from both the water column and the sediment (Spears et al. 2008, Zhang et al. 2014), and can reduce nutrient release rates from the sediment by oxidizing the sediment through their photosynthetic activity (Carlton and Wetzel 1988). Furthermore, benthic algae can stabilize the sediment surface through excretion of extra-cellular polymers (Paterson 1989) and mat formation (Dodds 2003), further reducing resuspension and thus becoming dominant over phytoplankton. Hence, sediment resuspension reduces light availability in the water column, reducing the prevalence of benthic algae, and increases nutrient availability which may result in a net positive effect on phytoplankton production.

Trophic transfer from phytoplankton to zooplankton is directly affected by sediment resuspension (Pécseli et al. 2014) and indirectly by nutrient availability (Hessen et al. 2013). Zooplankton, and filter feeders in general, are hampered by filtering water loaded with sediment as they have no ability to prevent ingesting the sediment, which limits their intake of phytoplankton and is energetically costly as they need to excrete the sediment (Kirk and Gilbert 1990, Penning et al. 2013). Furthermore, wind-driven sediment resuspension may cause problems for zooplankton due to physical effects that may damage them and can limit their filter feeding capacity (G. -Tóth et al. 2011, Zhou et al. 2016). Trophic transfer may thus be higher under sheltered conditions where the sediment settles. Nutrient availability indirectly affects trophic transfer as nutrient limitation in the water column may induce shifts in the phytoplankton community towards less edible algal species or towards phytoplankton of less nutritional value as it increases the phytoplankton stoichiometry, in particular the C:P and C:N ratios, depending on which nutrient becomes limiting (Sterner et al. 1998; Sterner and Elser 2002; Van de Waal et al. 2010).

As a result, the effect of sediment resuspension on trophic transfer remains uncertain, as it may promote trophic transfer indirectly by increasing nutrient availability leading to higher phytoplankton quantity (expressed as biomass) and quality (expressed as carbon:nutrient ratio), whereas it may directly reduce trophic transfer because zooplankton filter feeders may be hampered by the high concentrations of suspended sediment in the water column. Understanding the effect of sediment resuspension on trophic transfer will help revealing mechanisms that underlie declines of higher trophic levels in shallow lakes, and thereby support the development of lake restoration measures.

Lake Markermeer is a shallow (3-4 m depth) large delta lake (680 km²) in the Netherlands where the numbers of fish, benthivorous birds and piscivorous birds have been declining over the past decades (Noordhuis 2014). The decline of these higher trophic levels coincides with a strong reduction in external nutrient loading of the lake, reflected in a decline in total phosphorus concentrations in the water column and a concomitant decline in chlorophyll *a* concentrations (Fig. 1). This correlation suggests a limitation in primary productivity or inefficient transfer of primary productivity to higher trophic levels. An explanation for both these limitations can possibly be found in the resuspension of the lake's sediment. The sediment of lake Markermeer consists mainly of fine silts and clays that are easily resuspended by the wind (Troelstra et al. 2018). Because there is a general lack of sheltered areas, the lake remains turbid due to wind-induced sediment resuspension

(Kelderman et al. 2012a). To restore the food chain, and thereby the fish and bird populations in the lake, lake restoration project Marker Wadden has been initiated in 2016. The restoration project Marker Wadden consists of a newly constructed archipelago of five islands in the lake, which aims to create sheltered areas of varying depths in which primary production and filter feeding is no longer negatively affected by sediment resuspension. However, whether shelter leads to higher primary producer biomass, and whether this is transferred to higher trophic levels is not guaranteed as sediment resuspension, nutrient and light availability and zooplankton grazing efficiency interact with each other.

Here, we studied the relationships between resuspension and biomass build-up of phytoplankton and benthic algae, and the consequences for zooplankton biomass. To this end, we conducted a full-factorial sediment resuspension experiment in indoor microcosms using a no resuspension treatment and two levels of sediment resuspension across three water temperatures, as sheltered and shallow conditions may result in higher water temperatures. We hypothesized that (1) sediment resuspension increases turbidity and promotes the biomass build-up of phytoplankton through increased nutrient availability, while shelter (i.e. no resuspension) will facilitate benthic algae biomass build-up; (2) enhanced sediment resuspension limits trophic transfer, as zooplankton is damaged by the water movements causing resuspension and hampers its filter feeding, despite higher food availability; (3) increased water temperature promotes phytoplankton, benthic algae and zooplankton biomass build-up, but decreases food quality of phytoplankton for zooplankton; (4) enhanced sediment resuspension interacts synergistically with increasing temperature to promote phytoplankton biomass build-up, while further decreasing the benthic algae biomass build-up due to enhanced shading from phytoplankton.

To test our hypotheses, we measured the effect of sediment resuspension on biomass build-up of phytoplankton, benthic algae and zooplankton. Throughout the experiment we monitored concentrations of suspended matter (i.e. chlorophyll *a*, particulate organic carbon, nitrogen and phosphorus), phytoplankton species composition and stoichiometry, chlorophyll *a* at the sediment surface, concentrations of inorganic nutrients, light availability, and zooplankton biomass.

3.2 | Methods

3.2.1 Study system

Lake Markermeer is a 3–5 m deep (mean depth 3.6 m), 680 km² delta lake located in the center of The Netherlands (52°32'23.4"N 5°13'56.4"E). This freshwater lake with marine clay sediment used to be connected to the North Sea until the completion of a 30-km long dike (the Afsluitdijk) in 1932. In 1975, the newly formed lake was divided by the construction of another dike (the Houtribdijk), which created two lakes: lake Markermeer and lake IJsselmeer. After lake Markermeer was cut off from its marine nutrient supply, nutrient levels remained relatively high because of input from surrounding lakes and influx of wastewater from surrounding municipalities, including the city of Amsterdam. During the 1980's the waste water effluent of Amsterdam and surrounding municipalities became disconnected from the lake, and the lake became less eutrophic (Van Riel et al. 2019). This is reflected in the decline of the nutrient concentrations in the water column over the last decades (Fig. 3.1a). As the original outlet of the lake towards the sea is blocked first by the Afsluitdijk and later by the Houtribdijk, the fine sediments in the lake cannot leave the lake anymore and are repeatedly resuspended by wind action. Suspended solid concentrations in the lake ranged from 4.0 to 368.0 mg L⁻¹ from 1999-2016 (Fig. 3.1c). The temperature in the center of lake Markermeer fluctuates from 0-24.6 °C (Fig. S3.1b). The lake is a Natura2000 area under the bird directive and has experienced declines in benthic and fish eating birds over the last decades, as well as in fish abundance (Noordhuis 2014).

3.2.2 Experimental materials

Sediment was collected from lake Markermeer at the location of the Marker Wadden (52°35'17.0"N 5°22'00.5"E) on November 20, 2017, and stored in the dark at outdoor temperature for 94 days until use. One day before the experiment, water was collected from lake Markermeer (52°31'08.6"N 5°26'13.1"E). The initial concentrations of total nitrogen (TN) and total phosphorus (TP) in the sediment were 2.54 ± 0.04 mg g⁻¹ DW (dry weight, mean \pm SE, n=3) and 0.62 ± 0.01 mg g⁻¹ DW; and 157.08 ± 41.77 and 2.55 ± 0.20 μ mol L⁻¹ in the water, respectively. The sediment mainly consisted of fine silts (grain size less than 63 μ m), representing 84 ± 6 % (mean \pm SE, n=3) of the sediment (Fig. S3.2). Sediments and water were mixed (separately) prior to the experiment to ensure a homogeneous distribution of

organisms, which happened to occur in the collected water and sediment samples from the field, across the experimental units. The experiment consisted of 27 microcosms, which were cylindrical glass containers with an 18-cm inner-diameter and 48-cm height. Each microcosm was filled with a 5-cm layer of sediment, representing a sediment volume of 1.2 L, topped up with lake water of 40 cm depth, representing a volume of 10.2 L.

3.2.3 Experimental design

An experiment was conducted following a three-by-three factorial design with three resuspension intensities (No, Middle, High) and three temperatures (10, 20, 30°C). Each treatment included three replicates, leading to a total of 27 microcosms. To achieve three suspended solids ranges: 0~10, 10~30, 30~150 mg L⁻¹, which represented the natural range of suspended solids concentrations found in the lake (Fig. 3.1c) and functioned as No, Middle, and High resuspension treatments in our study, pilots were done to find out the right pump position to get those suspended solids range. The Middle and High resuspension treatments were achieved by an aquarium pump (EHEIM compact 300; EHEIM GmbH & Co. KG, Deizisau, Germany), positioned 6.5 and 20 cm below the water surface, respectively, while no pumps were installed in the No resuspension treatment. The final suspended solids concentrations achieved in our study are 0.7~1.5, 1.9~23, 27~157 mg L⁻¹ in the No resuspension, Middle resuspension, and High resuspension, respectively. The temperatures (10, 20°C) were chosen to represent the natural range of temperatures observed in lake Markermeer (Fig. S3.2b) and 30°C was chosen to represent the high temperature that occurs in the sheltered and shallow areas on Marker Wadden, where temperatures up to a maximum of 29.8 °C have been measured (June, 2018; H. Jin, unpublished data). All the microcosms were covered with a black plastic sheet on the sides to ensure that light only came from above and the microcosms could not influence each other. All the microcosms were put in temperature-controlled (10, 20, 30°C) aquaria (88×48.5×50 cm) with a 16h:8h light: dark cycle. During the experiment, tap water was added to each microcosm on a daily basis to compensate for losses caused by sampling or evaporation and to guarantee a stable water level. The experiment ran for 14 days; at the end of the experiment the physical parameters were measured and particulate organic carbon and nutrients, dissolved inorganic nutrients, and phytoplankton and zooplankton were sampled.

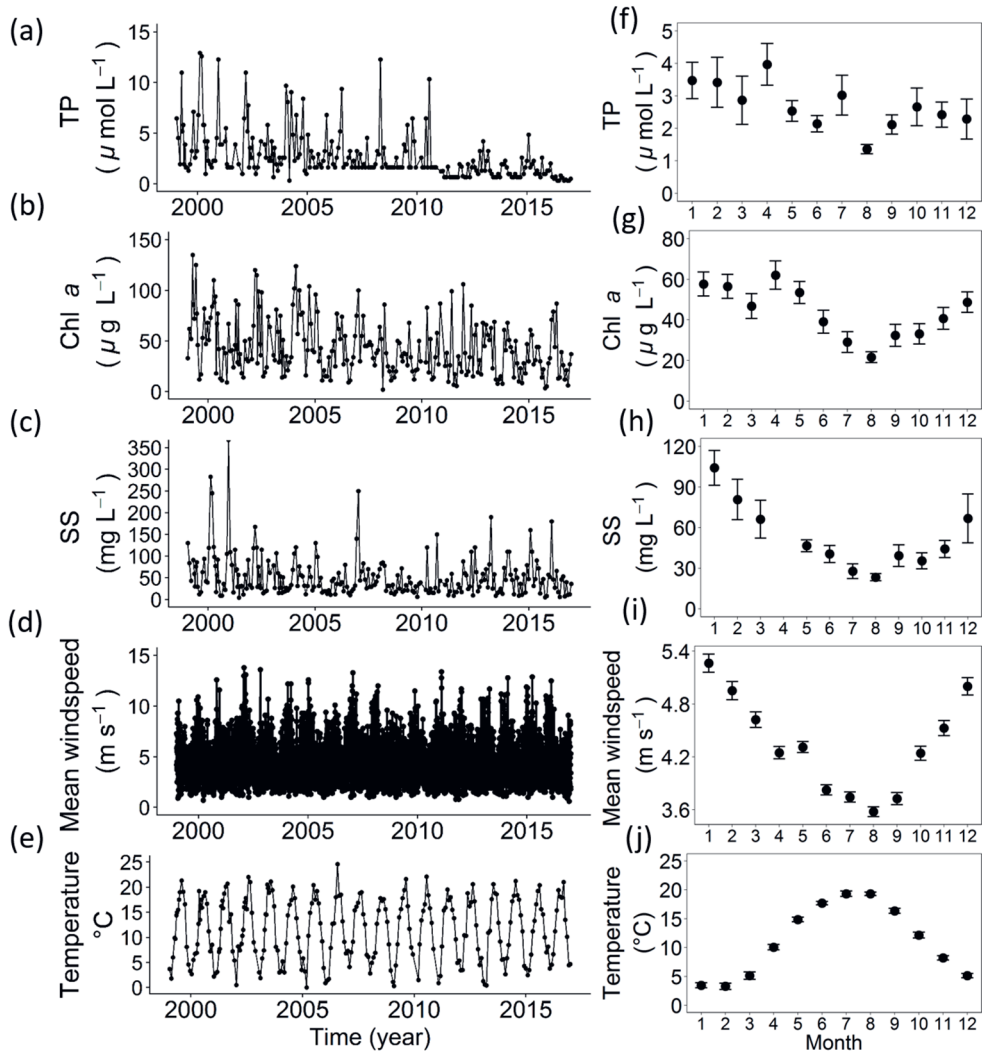


Fig. 3.1. The dynamics of (a) Total Phosphorus (TP), (b) chlorophyll *a* concentrations, (c) suspended solid concentrations (SS), (d) daily mean wind speeds from a nearby weather station in the city of Lelystad, (e) monthly water temperature, (f) monthly mean TP, (g) monthly mean Chl *a*, (h) monthly mean suspended solid concentration (SS), (i) monthly mean windspeed, and (j) monthly mean water temperature observed in lake Markermeer. TP, chlorophyll *a* and suspended solids were obtained from Rijkswaterstaat from their measurement station in the center of lake Markermeer from 1999 to 2016 based on monthly field surveys.

3.2.4 Physical measurements

Light intensity at the water surface and 20 cm below the water surface was measured with a LI-250A Light Meter (Biosciences, U.S.A). The mean light intensity in the entire water column and light intensity at the sediment surface (40 cm depth) were calculated following the method by Huisman et al. (2002); Lampert and Sommer (2007). The dissolved oxygen (DO) and pH were measured with an Oxi 323 probe (WTW 82326, Weilheim, Germany) and pH 330i probe (WTW 82326, Weilheim, Germany), respectively, in the center of the microcosm approximately 5 cm below the water surface. Subsequently, depth-integrated water samples (of 600 mL) were taken from the center of the microcosm with a sampling tube of 34.5 cm long and diameter of 4.1 cm. These water samples were used to determine the total suspended solids (TSS), inorganic suspended solids (ISS), seston elemental composition, dissolved inorganic nutrient concentrations, chlorophyll *a* concentrations and phytoplankton community composition.

TSS concentrations were determined by filtering 15-200 mL (adapted to the amount of suspended sediment) of the depth-integrated water sample over a pre-washed and pre-weighed GF/F filters (Whatman, Maidstone, UK), dried at 60°C overnight, and then weighed. Afterwards, filters were stored dry and dark in a desiccator for later assessment of seston elemental composition. To determine ISS concentrations, another 15-200 mL of depth-integrated water subsample was filtered over pre-combusted GF/F filters (Whatman, Maidstone, UK), then dried at 60°C overnight and weighed. These filters were combusted in a muffle furnace at 550°C for 2 hours, cooled in a desiccator, and afterwards weighed.

3.2.5 Chemical measurements

3.2.5.1 Seston elemental composition

For analysis of particulate organic carbon (C), nitrogen (N), and phosphorus (P), two subsamples were taken from the stored GF/F filters used for TSS determination. By means of a hole puncher, two circular subsamples with a diameter of 5.55 mm were taken (representing a total of about 15.4% of the filter). To determine the amounts of C and N, these pinched subsamples were folded into a tin cup (Elemental Microanalysis, Okehampton, UK) and analyzed for particulate C and N on a FLASH 2000 NC elemental analyzer (Brechtbuhler Incorporated, Interscience B.V., Breda, The Netherlands). To determine P contents, the remainder of the filter was combusted in a Pyrex glass tube at 550°C for 30 min. Subsequently, 5 mL of

persulfate (2.5%) was added and samples were autoclaved for 30 min at 121°C. Digested P (as PO_4^{3-}) was measured on a QuAAtro39 Auto-Analyzer (SEAL Analytical Ltd., Southampton, UK).

3.2.5.2 Dissolved nutrients

Dissolved inorganic nutrients were determined from the depth-integrated water samples, filtered over pre-washed GF/F filters (Whatman, Maidstone, UK), and the filtrate was stored at -20°C. Concentrations of dissolved nutrients (NH_4^+ , NO_3^- , NO_2^- , and PO_4^{3-}) of thawed samples were determined on a QuAAtro39 Auto-Analyzer (SEAL Analytical Ltd.).

3.2.6 Biological measurements

3.2.6.1 Chlorophyll *a* concentrations

Chlorophyll *a* (Chl *a*) in the water column was determined from filtered material retained after filtering 10-200 mL of the depth-integrated water subsamples on GF/F filters (Whatman, Maidstone, UK) and stored at -20°C. The Chl *a* samples were measured within one month after sampling. After thawing, the filters were extracted with 80 % ethanol in an 80°C water bath, thereafter a further filtration through Milipore Milles FG 0.2 μm membrane filters, Chl *a* concentrations were measured by High Performance Liquid Chromatography (HPLC, UltiMate 3000 (Thermo Scientific)) equipped with a Hypersil ODS column (25 cm, 5 μm , 4.6 \times 250 mm; Agilent) and a RF 2000 fluorescence detector (Dionex/Thermo Scientific).

3.2.6.2 Phytoplankton and zooplankton community composition

For phytoplankton community composition, a subsample of the depth-integrated water sample (50 mL) was fixed with alkaline Lugol's iodine solution and stored in the dark at room temperature. Microscopic determination of phytoplankton to genus level was performed in an inverted microscope (DMI4000B; Leica Microsystems CMS GmbH, Mannheim, Germany), counting up to 200 individuals or 100 fields of view using an Utermöhl counting chamber with a settling time of at least 12 hours.

Zooplankton were collected by filtering 1 L of depth-integrated samples (80- μm mesh size), after which the samples were preserved with 70% ethanol and stored at room temperature in the dark. The filtrate was gently returned to each microcosm to avoid sediment disturbance. Zooplankton specimens were counted using a stereomicroscope (LEICA M205C, Leica Microsystem, Wetzlar, Germany).

Rotifers and cladocerans were identified to genus level, whereas copepods were distinguished by order. Copepod nauplii were counted, but not distinguished taxonomically. Zooplankton biomass was estimated by taking the length of 30 individuals (if enough individuals were available) of all the genera and using published length-weight relationships (Dumont et al. 1975, Bottrell et al. 1976). The biomass of each genus was calculated by multiplying individual biomass with its density. The total zooplankton biomass was calculated by summing up all the biomass of the each genus.

3.2.6.3 *Periphyton and benthic algae biomass*

To assess periphyton biomass, a plastic strip (length \times width: 9.5 \times 2.0 cm) was attached vertically to the glass container wall just below the water surface. At the end of the experiment, the plastic strip was carefully removed from each mesocosm and placed in a plastic zip-lock bag for laboratory analysis of periphyton biomass. These samples were taken after the water samples, as described above, to avoid periphyton ending up in the water samples. The periphyton attached to the plastic strip was brushed off into a beaker with demi-water, then filtered through a GF/F filter (Whatman, Maidstone, UK) and subsequently analyzed as described before for determining Chl *a* in the water column.

To determine the biomass of benthic algae, after the water and periphyton samples were taken, a small transparent tube (diameter: 1.05 cm) was used to collect the upper 1 cm sediment. The collected sediment was stored at -20°C, and liquid chromatographically analyzed as described for determining Chl *a* in the water column.

3.2.7 *Statistical analyses*

Linear Mixed-Effect Models were used to analyze the effects of elevated temperature and resuspension on all the measured parameters, using the package nlme (Pinheiro et al. 2012) in R version 3.5.1 (R Core Team 2021). Following the randomized block design, aquarium (3 levels) and microcosm location within aquaria (3 levels) were included as nested random factors in all the models to account for the dependency structure in our experimental design. Residual plots were used to check for normality and homogeneity of variance by visual inspection. If variances were not normally distributed, dependent variables were ln, log2, log10 or square root transformed (as indicated in the results). Model selection was performed backwards based on AICc values starting from full models including the factors resuspension (3 levels: No, Middle and High) and temperature (modeled as a factor: 10, 20 and 30°C) and their

interaction. Models with the lowest AICc value were considered the best, and model averaging (function *model.avg* from MuMIn package) was applied if AICc values of the two best models differed less than 2.0 (Burnham and Anderson 2002).

3.3 | Results

3.3.1 Effects of the treatments on primary production, zooplankton and seston

The resuspension and temperature treatments both affected phytoplankton and benthic algae chlorophyll *a* concentrations (Fig. 3.2). Resuspension had positive effects on phytoplankton biomass and negative effects on benthic algae and this effect became stronger with increasing resuspension intensity (Fig. 3.2). Increased temperatures resulted in significantly lower phytoplankton and benthic algae biomass at 30°C compared to the lower temperatures.

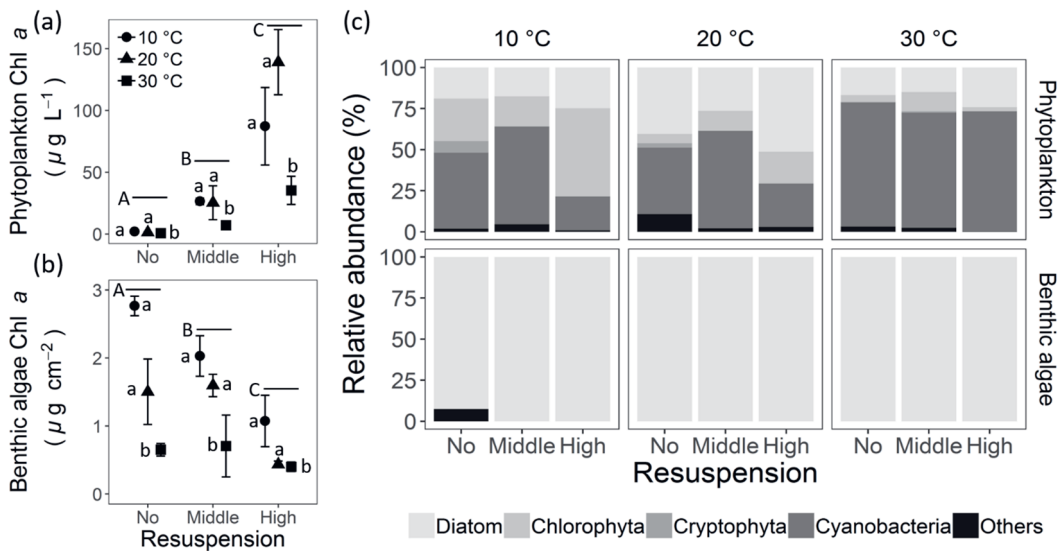


Fig. 3.2. Phytoplankton (a) and benthic algal (b) chlorophyll *a* concentrations, and their taxonomic composition (c) at three resuspension intensities (No, Middle, High) and three temperature scenarios (10°C, 20°C, 30°C). Values represent means \pm SE ($n=3$). The different uppercase letters with solid black line indicate significant differences among resuspension treatments. The different lowercase letters indicate

significant differences among temperature treatments (statistical details can be found in Table S2).

Resuspension and temperature both also affected the phytoplankton community composition (Fig. 3.2c). Overall, cyanobacteria dominated the phytoplankton community (i.e. *Chroococcus*, *Aphanocapsa* and *Oscillatoria*), particularly at the highest temperature with a mean contribution of 70-75%. At the intermediate temperature, a higher mean fraction of diatoms was found (26-51%), especially at high resuspension. At the lowest temperature, the mean fractions of diatoms (17-19%) and chlorophytes (18-25%) were similar for the low and intermediate resuspension treatments, while chlorophytes dominated at the highest resuspension level with a mean contribution of 53%. The benthic algal composition was 100% dominated by diatoms (i.e., *Sellaphora* and *Navicula*) across most treatments, only without resuspension at 10°C did other genera occur for up to 7% (Fig. 3.2c). The effect of resuspension on periphyton algae biomass depended on the temperature and was only significantly higher at the highest temperature under intermediate resuspension (Fig. 3.3).

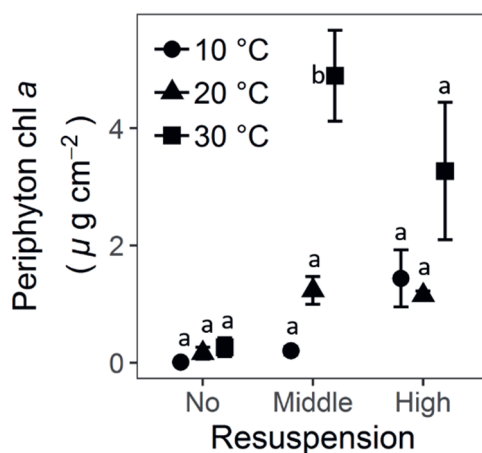


Fig. 3.3. Periphyton algae chlorophyll *a* concentrations at the end of the experiment at three resuspension intensities (No, Middle, High) and three temperature scenarios (10°C, 20°C, 30°C). Values represent means \pm SE ($n=3$). The different lowercase letters indicate significantly different periphyton concentrations across resuspension and temperature treatment combinations.

Resuspension significantly reduced zooplankton biomass, while no temperature effect was observed (Fig. 3.4a, Table S3.2). The zooplankton biomass in the middle and high resuspension treatments varied from 0 - 1.7 $\mu\text{g L}^{-1}$, whereas without resuspension this was 45.3 - 109.3 $\mu\text{g L}^{-1}$.

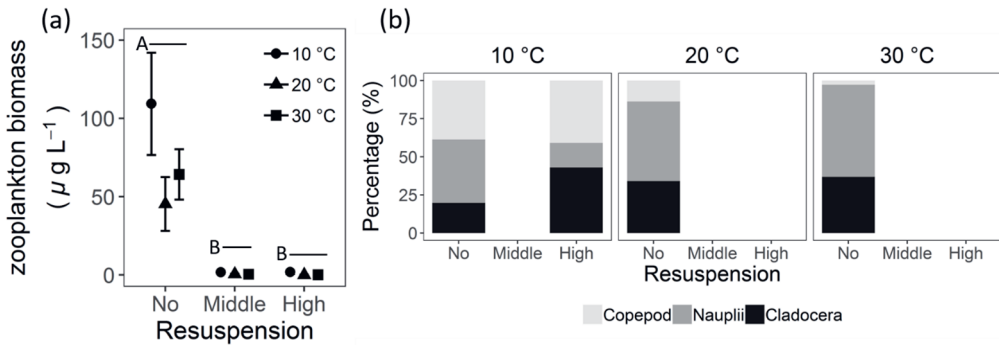


Fig. 3.4. Zooplankton biomass (a) and taxonomic composition (b) at the end of the experiment at three resuspension intensities (No, Middle, High) and three temperature scenarios (10°C, 20°C, 30°C). Values represent means \pm SE (n=3). The different uppercase letters with solid black line indicate significant differences among resuspension treatments.

Seven zooplankton taxa were recorded in all treatments across the entire experimental period, including five cladoceran genera (*Bosmina*, *Daphnia*, *Chydorus*, *Ceriodaphnia* and *Diaphanasoma*) and two copepod orders (Calanoida and Cyclopoida). Predominant zooplankton taxa at the end of the experiment under control resuspension were Copepoda, accounting for 80% (± 11), 66% (± 16) and 63% (± 18) of the total zooplankton biomass under the 10°C, 20°C, and 30°C temperature scenarios, respectively. The copepod adult biomass contribution decreased from 39 % (± 12) to 2.7 % (± 2) while the nauplii biomass contribution increased from 42 % (± 9) to 61 % (± 12) without resuspension when temperature increased from 10 °C to 30 °C (Fig. 3.4b, Table S3.2).

The seston C:P ratios showed large variation across treatments, with no clear trend across resuspension treatments (Fig. 3.5a). The C:N ratio increased significantly with increasing resuspension, whereas the effects of temperature were not significant (Fig. 3.5b, Table S3.2).

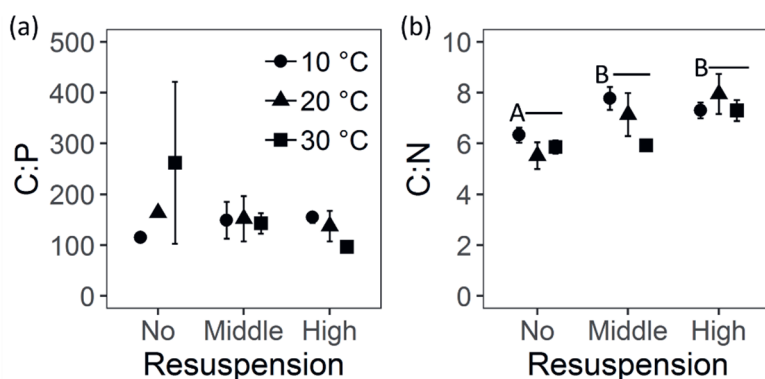


Fig. 3.5. Seston elemental composition with C:P (a) and C:N (b) molar ratios at the end of the experiment at three resuspension intensities (No, Middle, High) and three temperature scenarios (10°C, 20°C, 30°C). Values represent means \pm SE (n=3). The different uppercase letters with solid black line indicate significant differences among resuspension treatment.

3.3.2 Effects of the treatments on abiotic conditions

Resuspension increased the Total Suspended Solids concentration (TSS) and this effect increased with resuspension intensity, as targeted with the experimental set-up (Fig. 3.6a). The effect of resuspension on Inorganic Suspended Solids (ISS) present in the water column depended on the temperature; the ISS was higher at 20°C and 30°C than in all other treatments (Fig. 3.6b; Table S3.2). Resuspension strongly decreased the mean light intensity in the water column available for phytoplankton growth (Fig. 3.6c), as well as the mean light intensity at the sediment surface available for benthic algae (Fig. 3.6d). The light availability for phytoplankton and benthic algae was unaffected by temperature (Table S3.2).

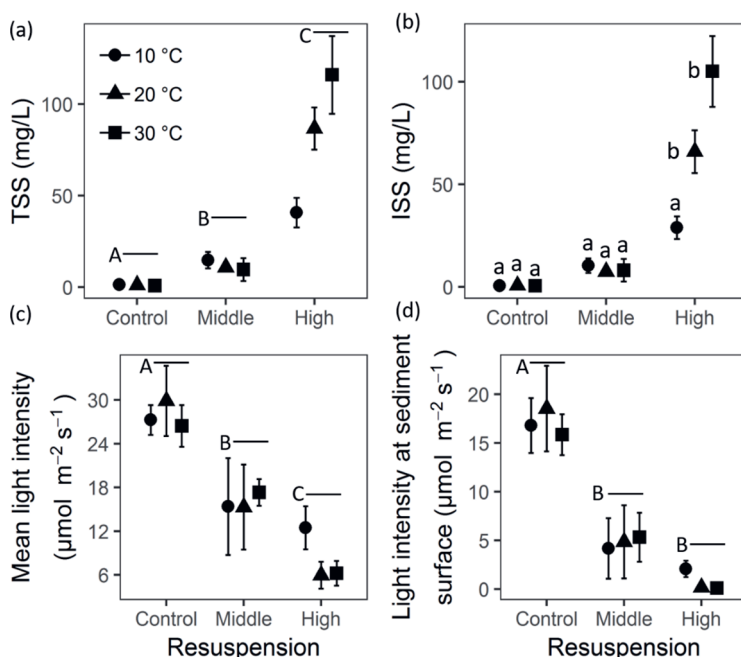


Fig. 3.6. The (a) total suspended solids (TSS), (b) inorganic suspended solids (ISS), (c) mean light intensity in the water column and (d) light intensity at sediment surface for each of the three resuspension intensities (No, Middle, High) and three temperature scenarios (10°C, 20°C, 30°C). Values represent means \pm SE ($n=3$). The different uppercase letters with solid black line indicate significant differences among resuspension treatments. The different lowercase letters indicate significant differences across all resuspension and temperature treatments.

Higher resuspension led to increased concentrations of particulate organic nitrogen (PON) (Fig. 3.7a) and particulate organic phosphorus (POP) (Fig. 3.7d), but decreased DIN (Fig. 3.7b). Both PON and POP reached their highest concentrations at the intermediate temperature under high resuspension. Dissolved inorganic phosphorus (DIP) concentrations (Fig. 3.7e) increased with rising temperatures. No clear effects of the treatments were found for total nitrogen concentrations (TN) (Fig. 3.7c). Total phosphorus (TP) increased significantly with both increasing resuspension and higher temperatures (Fig. 3.7f).

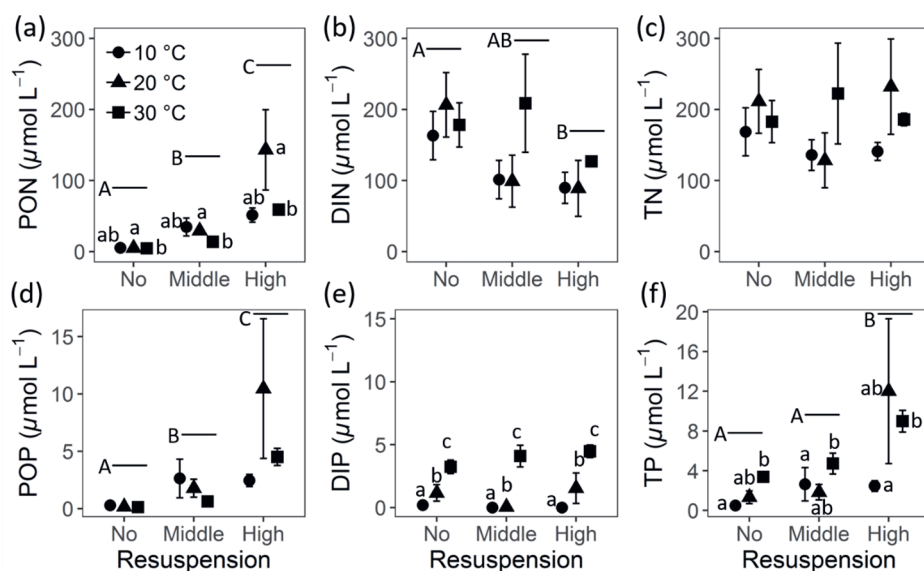


Fig 3.7. Particulate organic nitrogen (PON) (a), dissolved inorganic nitrogen (DIN) (b), Total nitrogen (TN) (c), particulate organic phosphorus (POP) (d), dissolved inorganic phosphorus (DIP) (e), and total phosphorus (TP) (f) at three resuspension intensities (No, Middle, High) and three temperature scenarios (10°C, 20°C, 30°C). Values represent means \pm SE (n=3). The different uppercase letters with solid blackline indicate significant differences among resuspension treatment. The different lowercase letters indicate significant differences among temperature treatments.

3.4 | Discussion

Our results demonstrate clear effects of sediment resuspension and temperature on phytoplankton and benthic algae biomass build-up, their stoichiometry and responses of zooplankton.

3.4.1 Effects of sediment resuspension

Following hypothesis 1, our results confirmed that sediment resuspension increases turbidity and promotes the biomass build-up of phytoplankton through increased nutrient availability, while under sheltered conditions (i.e. no resuspension) benthic

algae biomass builds up. This was partly attributed to strengthened bottom-up control, especially through phosphorus availability, as TP concentrations increased significantly with increasing resuspension. The phytoplankton biomass build-up increased despite the deteriorated light climate in the water column with stronger resuspension. This suggests that phytoplankton growth, at least in the low resuspension treatments, was not primarily limited by light. The enhanced phytoplankton biomass build-up with increased resuspension intensity is in line with observations in the field (Tammeorg et al. 2013, Tang et al. 2020) and in mesocosm experiments (Ding et al. 2017, Zhang et al. 2020), which also showed that sediment resuspension may support phytoplankton biomass build-up by enhancing nutrient availability. Furthermore, under the resuspension conditions, phytoplankton may be released from competition with benthic algae for nutrients as more nutrients are dissolved in the water. Benthic algae biomass was much higher without resuspension and strongly declined in the resuspension treatments, which was closely related to the decline in light availability at the sediment surface that, aside from physical disturbance of the sediment surface, presumably limited benthic algae biomass build-up (Hansson 1992, Fork et al. 2020).

Confirming hypothesis 2, we found that sediment resuspension limited zooplankton biomass build-up. This could have been a result of direct negative effects from the mixing that may have damaged the zooplankton. Indeed, continuous sediment resuspension may cause physical damage by abrasion and turbulent shear forces which may lead to decreases in zooplankton biomass (Peters and Marrasé 2000). Negative effects may also have occurred by the high concentrations of suspended sediment in the water hampering zooplankton filter feeding (Koenings et al. 1990, Kirk and Gilbert 1990). Moreover, zooplankton may have experienced negative effects of low food quality, as shown by the higher inorganic suspended solids concentration and higher seston C:N ratios with increased resuspension. The observed increase in seston C:N ratios are possibly caused by a higher contribution of resuspended sediment containing higher carbon to nitrogen ratios (i.e. molar ratios of 17 ± 0.3) as compared to the No resuspension treatment (i.e. molar ratios of 5.9 ± 0.4).

3.4.2 Effects of temperature

Our findings illustrate that increasing the temperature from 10°C to 30°C decreases phytoplankton and benthic algae biomass build-up, which contradicted our hypothesis 3. Although the TP concentration was significantly higher in the 30°C

compared to the 10°C treatment, phytoplankton biomass was significantly lower in the 30°C treatment than in the 10°C treatment. The increased TP may be attributed to the enhanced remineralization rates under higher temperature (Jensen and Andersen 1992), while decreased dissolved oxygen concentrations may have promoted phosphorus release from the sediment and resuspended matter (Table S3.3).

The benthic algae community in our study mainly consisted of diatoms, which have optimal growth temperatures that rarely exceed 25°C (Suzuki and Takahashi 1995, Mitrovic et al. 2010). As a result, the decline of benthic algae biomass in the 30°C treatment is likely a result of reduced performance of the diatoms. These benthic algae declines may also have stimulated nutrient release from the sediment (McKee et al. 2003). Although this may promote phytoplankton growth, the overall response of phytoplankton will depend also on the direct effect of high temperatures on prevailing species, which might be negative and determine the overall response in phytoplankton biomass.

In the phytoplankton community, both the diatom and chlorophyte abundance decreased in the 30°C treatment, while cyanobacteria became more dominant. Diatoms and chlorophytes contributed to up to $51 \pm 16\%$ and $53 \pm 11\%$ of the phytoplankton community at 10°C and 20°C treatments, which declined to a maximum contribution of $25 \pm 13\%$ in the 30°C treatment. This decrease in relative abundance of diatoms and chlorophytes may be attributed to their relatively low optimum growth temperatures, typically not exceeding 25-26°C (Suzuki and Takahashi 1995, McKee et al. 2003, Mitrovic et al. 2010), as compared to cyanobacteria with temperature growth optima of $>27^\circ\text{C}$ (Lüring et al. 2013). Thus, the highest temperature led to both overall declines in phytoplankton biomass, and caused a shift in phytoplankton community composition from dominance of diatoms or chlorophytes to cyanobacteria.

During the experiment, we found that the total zooplankton biomass showed a declining trend with increasing temperatures in the absence of resuspension, and a simultaneous shift from a population structure dominated by copepod adults to nauplii. According to the 'Metabolic Theory of Ecology' (Brown et al. 2004), faster metabolism at warmer temperatures may increase energy demands of organisms. Warming may consequently lead to higher feeding rates, which was shown for copepods feeding on phytoplankton (Garzke et al. 2015). In our study, however, the low phytoplankton biomass (indicated by Chl *a*, $0.6 - 2.7 \mu\text{g L}^{-1}$) in the absence of resuspension may not meet the food quantity demand of copepods. This food quantity shortage for copepods may further be exacerbated at higher temperatures as

phytoplankton biomass significantly decreased with increasing temperature. The shift in zooplankton community from dominance of copepod adults to nauplii may be attributed to enhanced hatching of copepods with higher temperatures. At the same time, the low food quantity do not support further development leading to an overall decline in zooplankton biomass.

3.4.3 The interaction of sediment resuspension and temperature effects on phytoplankton and benthic algae biomass build-up

We did not find support for hypothesis 4, in which we postulated that enhanced sediment resuspension would interact synergistically with increased temperature and thereby promote phytoplankton biomass build-up. We furthermore expected that benthic algae biomass build-up would decline due to enhanced shading from phytoplankton, with zooplankton unable to benefit due to resuspended sediments. While we found that enhanced sediment resuspension interacted synergistically with increased temperature, this did not lead to higher phytoplankton biomass, but it did lead to higher inorganic suspended solids concentrations in the warmest and most resuspended treatment. This may have resulted from a higher sediment water content due to the weakening of inter-particle bonds and/or the decreased viscosity of the pore water following the increased temperature (Grabowski et al. 2011), making the sediment more susceptible to resuspension (Neumeier et al. 2006, Nguyen et al. 2019). Furthermore, the decreased benthic algae biomass following the increased temperature suggests a weaker stabilizing effect produced by the biofilm, which also makes the sediment susceptible to resuspension (Sutherland et al. 1998). The enhanced sediment resuspension interacted synergistically with increased temperature to increase periphytic algae build-up; the periphyton biomass was highest in the intermediate and strongest resuspension treatments. It is conceivable that the periphyton benefitted from the temperature driven increase in P release from the sediment.

3.4.4 Wind-induced sediment resuspension in lake Markermeer

Lake Markermeer, with its large surface area and shallow depth, is very susceptible to wind-induced sediment resuspension (Kelderman et al. 2012a). The sediment

resuspension causes high turbidity in the water column, which is thought to be one of the main limitations for phytoplankton growth and thereby to constrain the productivity of the entire food web (Van Riel et al. 2019). Our experimental results, however, showed the reverse: we found that sediment resuspension enhanced phytoplankton biomass build-up, despite enhanced turbidity. This suggests that phytoplankton biomass build-up is mainly driven by nutrient availability, and increases when resuspension of sediments releases nutrients into the water. This is in line with the synchronized monthly dynamics of wind speed, suspended solids, and Chl *a* concentrations found in lake Markermeer (Fig. 3.1, Table S3.4). Here, higher wind speed in the winter half year coincides with the highest concentrations suspended solids, the lowest temperatures and the highest Chl *a* concentrations. The mechanism supporting this pattern has been ascribed to aggregate formation, where suspended sediment may form aggregates with phytoplankton that, in turn, obtain their nutrients from the sediment in this aggregate. Through this principle, sediment resuspension leads to benthification of the pelagic zone (Brinkmann et al. 2019).

Unfortunately, there is no zooplankton data over the same period in lake Markermeer. However, the low zooplankton biomass in our experiment coinciding with high phytoplankton availability suggests that resuspension of sediments may limit its trophic transfer to higher trophic levels. Taxa such as fish and fish-eating birds may not benefit from high phytoplankton availability if the transfer to zooplankton is inefficient. This low transfer efficiency between phytoplankton and zooplankton may be explained by reduced quality of the seston, indicated by the higher C:N ratio, suggesting a reduced nutritional value that may have limited zooplankton growth (Hessen et al. 2013). Moreover, the physical damage caused by turbulent mixing may also lead to lower zooplankton biomass. However, the reduced zooplankton may also have been a result of the experimental conditions. Under natural conditions, the effect of wind mixing on zooplankton may be mediated by the water depth, as zooplankton may actively migrate to deeper and more calm parts of the water column. However, this may have limited benefit for zooplankton in lake Markermeer, as wind can easily mix the entire water column due to its large surface and shallow water depth (Kelderman et al. 2012a).

We observed that sediment resuspension also negatively affected benthic algae biomass build-up. This suggests that light can be a limiting factor for benthic algae development in the open water area of lake Markermeer. Furthermore, the direct effect of wind induced resuspension could prevent benthic algae establishment. This limited opportunity for the benthic algal community to develop may, in turn, ultimately favor phytoplankton dominance.

3.4.5 Implications for lake restoration

The aim of lake restoration project Marker Wadden is to stimulate the aquatic food web by creating a sheltered archipelago and shallow areas of different depths which are expected to differ in sediment resuspension, temperature and resulting primary production and trophic transfer. Our results suggest that benthic algae will dominate the system under calm and sheltered conditions with low resuspension. Consequently, reaching a clear water state dominated by benthic algae might be feasible in case the archipelago will effectively reduce wind effects and thereby prevent resuspension. The improved light and reduced dissolved nutrient conditions following the recovery of benthic algae may ultimately pave the way for the re-establishment of submerged macrophytes (Vasconcelos et al. 2016, Hansson et al. 2020). Meanwhile, the enhanced zooplankton biomass under sheltered conditions may support higher trophic levels. Furthermore, the benthic algae can be grazed by macrofauna, such as gastropods, and in this way also contribute to the food web. In contrast, phytoplankton will dominate those habitats exposed to strong wind effects. Phytoplankton would maintain their dominance, as wind-induced sediment resuspension could improve nutrient availability for their growth while decrease competition from macrophytes or benthic algae by decreasing light availability or through the mechanic forces it exerts on macrophytes and their propagules, as well as early establishing benthic algal communities (Jupp and Spence 1977, Keddy 1983). As a result, the recolonization of both macrophytes and benthic algae will be limited. Our study suggests that for shallow lakes suffering from wind effects, measures aimed at reducing sediment resuspension such as Marker Wadden can be effective in restoring the trophic transfer between phytoplankton and zooplankton, thereby supporting higher trophic levels.

3.5 | Conclusion

Wind-induced sediment resuspension is a common phenomenon that has potentially contrasting effects on primary production and trophic transfer in shallow lakes. Our results demonstrate that sediment resuspension promoted nutrient availability and phytoplankton biomass build-up, while limiting light availability and benthic algae biomass development. However, despite promotion of higher phytoplankton

biomass, sediment resuspension decreased zooplankton biomass, thus limiting trophic transfer. Enhanced sediment resuspension and higher temperatures synergistically interacted, maintaining a high level of inorganic suspended solids and periphyton biomass. Our findings demonstrate that for shallow lakes suffering from wind effects, measures creating shelter by constructing islands, such as Marker Wadden, aimed at reducing sediment resuspension can be effective in restoring trophic transfer leading to higher secondary production which can support higher trophic levels.

Declaration of competing interest

The authors declare no conflicts of interest.

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Data availability statement

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

Appendix A. Supplementary data

Supporting tables

Table S3.1. Model selection results for effects of resuspension, temperature and their interaction on the parameters measured during the experiment. Model selection was performed backwards based on AICc values starting from the full models including the temperature x resuspension interaction. Models with the lowest AICc value were considered the best, and model averaging was applied if AICc values of the two best models differed less than 2.0. For each dependent variable the table indicates with a “+” which terms are included, the AICc values, delta AICc values to the next best model and the Akaike weight (as an indication of the relative importance of the model). Only best models are shown in the table.

Dependent variable	Resuspension	Temperature	Resuspension × Temperature	AICc	ΔAICc	Akaike weight
Phytoplankton chlorophyll- <i>a</i>	+	+		70.0	0.0	0.70
		+		71.6	1.6	0.31
Benthic algae chlorophyll- <i>a</i>	+	+		-26.8	0.0	0.97
Periphyton chlorophyll- <i>a</i>	+	+		45.6	0.0	0.61
	+	+	+	46.5	0.9	0.38
Total suspended solids	+			109.5	0.0	0.80
Inorganic suspended solids	+	+	+	110.7	0.0	0.52
	+			111.3	0.6	0.38
Organic suspended solids	+			69.5	0.0	0.62
	+	+		70.5	0.9	0.39
Mean light intensity	+			78.6	0.0	0.97
Light intensity at sediment surface	+			130.9	0.0	0.96
DIP		+		47.4	0.0	0.94
DIN	+			145.4	0.0	0.52
				146.3	0.9	0.34
DO		+		-0.7	0.0	0.92
Zooplankton biomass	+			104.3	0.0	0.62
	+	+		105.3	1.0	0.38
C:N ratio	+			85.9	0.0	0.83
C:P ratio				38.4	0.0	0.90
N:P ratio				46.6	0.0	0.76
Particulate organic carbon	+			79.6	0.0	0.57
	+	+		80.2	0.6	0.43
Particulate organic nitrogen	+			70.7	0.0	0.59
	+	+		71.5	0.8	0.41

Dependent variable	Resuspension	Temperature	Resuspension × Temperature	AICc	ΔAICc	Akaike weight
Particulate organic phosphorus	+			92.4	0.0	0.89
TN				135.8	0.0	0.81
TP	+	+		79.4	0.0	0.57
	+			80.2	0.8	0.39
Conductivity	+	+		-	0.0	0.97
				144.9		
pH				-	0.0	0.81
				152.6		
Total copepod adults	+	+	+	92.9	0.0	1.0
Total copepod nauplii	+	+		147.2	0.0	0.91
Total cladoceran	+			87.6	0.0	0.95
Phytoplankton density	+			589.3	0.0	0.95
Diatom relative abundance				107.2	0.0	0.57
	+			109.2	2.0	0.21
Chlorophyta relative abundance		+		116.3	0.0	0.85
Cryptophyta relative abundance	+			86.1	0.0	0.52
				86.6	0.5	0.42
Cyanobacteria relative abundance				138.5	0.0	0.78
Others relative abundance				155.2	0.0	0.44
	+			155.3	0.0	0.44
Benthic algae density				393.4	0.0	0.44
	+			394.7	1.3	0.23
		+		394.8	1.3	0.23

Table S3.2. Results of linear mixed-effects models exploring the effects of resuspension, temperature and their interaction on measured parameters. Model selection was based on the change of AICc-values due to removal of terms (Table S2). Parameter estimates and their significance are indicated for significant terms included in the final models, with estimates displayed for different contrasts as a result of running the models with different factor levels as intercepts. It is indicated in case data were transformed to meet model requirements. Significant *P*-values are indicated in bold.

Dependent variable	Transformation	Explanatory variable	Contrasts	Estimate	SE	Z	t	P-value
Phytoplankton chlorophyll <i>a</i>	Ln (x)	Resuspension	No-Middle	2.54	0.27	8.73		<0.001
			No-High	4.09	0.27	14.09		<0.001
			Middle-High	1.55	0.26	5.52		<0.001
		Temperature	10 °C-20 °C	-0.03	0.35	0.09		0.937
			10 °C-30 °C	-1.13	0.35	2.60		0.019
			20 °C-30 °C	-1.10	0.39	2.27		0.023
Benthic algae chlorophyll <i>a</i>	Ln (x+0.001)	Resuspension	No-Middle	-0.17	0.21		-0.78	0.445
			No-High	-0.91	0.21		-4.28	<0.001
			Middle-High	-0.74	0.21		-3.50	0.003
		Temperature	10 °C-20 °C	-0.57	0.28		-0.26	0.085
			10 °C-30 °C	-1.26	0.28		-4.58	0.004
			20 °C-30 °C	-0.69	0.28		-2.52	0.045
Periphyton chlorophyll <i>a</i>	Sqrt (x)	Resuspension	No-Middle	0.94	0.17	4.19		<0.001
			No-High	1.03	0.21	5.02		<0.001
			Middle-High	0.08	0.19	0.37		0.709
		Temperature	10 °C-20 °C	0.27	0.19	1.12		0.262
			10 °C-30 °C	0.88	0.19	3.54		<0.001
			20 °C-30 °C	0.64	0.20	2.59		0.010
		Resuspension×Temperature	No 10 °C-No 20 °C	0.24	0.24	0.97		0.989
			No 10 °C-No 30 °C	0.35	0.24	1.45		0.879
			No 20 °C-No 30 °C	0.12	0.24	0.48		1.000
			M 10 °C-M 20 °C	-0.66	0.24	-2.72		0.140
			M 10 °C-M 30 °C	-1.76	0.24	-7.24		<0.001
			M 20 °C-M 30 °C	-1.10	0.24	-4.52		<0.001
			H 10 °C-H 20 °C	0.10	0.24	0.40		1.000
			H 10 °C-H 30 °C	-0.57	0.24	-2.35		0.314
			H 20 °C-H 30 °C	-0.67	0.24	-2.74		0.133

Dependent variable	Transformation	Explanatory variable	Contrasts	Estimate	SE	Z	t	P-value
Total suspended solids	Sqrt (x)	Resuspension	No-Middle	2.20	0.68		3.23	0.005
			No-High	7.68	0.68		11.28	<0.001
			Middle-High	5.48	0.68		8.05	<0.001
Inorganic suspended solids	Sqrt (x)	Resuspension	No-Middle	2.36	0.80	2.68		0.007
			No-High	4.96	1.16	4.08		<0.001
			Middle-High	5.33	0.79	6.09		<0.001
		Temperature	10 °C-20 °C	0.12	0.80	0.12		0.905
			10 °C-30 °C	0.01	0.80	0.01		0.995
			20 °C-30 °C	-0.25	0.80	0.25		0.801
		Resuspension × Temperature	No 10 °C-No 20 °C	0.12	0.80	0.15		1.00
			No 10 °C-No 30 °C	0.01	0.80	0.01		1.00
			No 20 °C-No 30 °C	0.11	0.80	0.14		1.00
			M 10 °C-M 20 °C	0.40	0.80	0.51		1.00
Organic suspended solids	Sqrt (x)		M 10 °C-M 30 °C	0.65	0.80	0.82		1.00
			M 20 °C-M 30 °C	0.25	0.80	0.32		1.00
			H 10 °C-H 20 °C	-2.75	0.80	-3.45		0.017
			H 10 °C-H 30 °C	-4.87	0.80	-6.10		<0.01
			H 20 °C-H 30 °C	-2.11	0.80	-2.65		0.166
		Resuspension	No-Middle	0.93	0.33	4.60		<0.001
			No-High	2.88	0.33	4.98		<0.001
			Middle-High	1.95	0.33	5.52		<0.001
		Temperature	10 °C-20 °C	0.23	0.31	0.60		0.546
			10 °C-30 °C	-0.49	0.31	1.28		0.201
Mean light intensity	Sqrt (x)		20 °C-30 °C	-0.72	0.31	1.88		0.060
		Resuspension	No-Middle	-1.38	0.38		-3.59	<0.001
			No-High	-2.49	0.38		-6.48	0.002
Light intensity at sediment surface	Ln (x+0.001)		Middle-High	-0.11	0.38		-2.89	0.010
		Resuspension	No-Middle	-2.54	1.01	1.01	-2.51	0.023
			No-High	-4.65	1.01	1.01	-4.60	0.000
			Middle-High	-2.11	1.01		-2.09	0.053

Dependent variable	Transformation	Explanatory variable	Contrasts	Estimate	SE	Z	t	P-value
DIP	Log10 (x+0.001)	Temperature	10 °C -20 °C	1.89	0.46		4.11	0.006
			10 °C -30 °C	3.27	0.46		7.10	<0.001
			20 °C -30 °C	1.38	0.46		2.99	0.024
DIN	Sqrt (x)	Resuspension	No-Middle	-1.47	1.29		-1.14	0.271
			No-High	-2.85	1.29		-2.21	0.042
			Middle-High	-1.39	1.29		-1.08	0.297
DO	Sqrt (x)	Temperature	10 °C -20 °C	-0.33	0.09		-3.68	0.010
			10 °C -30 °C	-0.56	0.09		-6.34	<0.001
			20 °C -30 °C	-0.24	0.09		-2.66	0.038
Zooplankton biomass	Log10 (x+0.001)	Resuspension	No-Middle	-3.08	0.59	4.82		<0.001
			No-High	-3.52	0.59	5.51		<0.001
			Middle-High	-0.44	0.59	0.69		0.490
		Temperature	10 °C -20 °C	-1.28	0.57	1.80		0.072
			10 °C -30 °C	-1.21	0.57	1.80		0.088
			20 °C -30 °C	0.07	0.57	0.09		0.925
C:N ratio		Resuspension	No-Middle	1.04	0.44		2.36	0.031
			No-High	1.61	0.44		3.66	0.002
			Middle-High	0.57	0.44		1.29	0.213
Particulate organic carbon	Log2 (x)	Resuspension	No-Middle	2.53	0.36	6.42		<0.001
			No-High	4.30	0.36	10.89		<0.001
			Middle-High	1.76	0.36	4.48		<0.001
		Temperature	10 °C -20 °C	0.31	0.36	0.70		0.484
			10 °C -30 °C	-0.63	0.36	1.42		0.155
			20 °C -30 °C	-0.95	0.35	2.12		0.034
Particulate organic nitrogen	Log2 (x)	Resuspension	No-Middle	2.31	0.30	7.15		<0.001
			No-High	3.95	0.30	12.21		<0.001
			Middle-High	1.64	0.30	5.07		<0.001
		Temperature	10 °C -20 °C	0.39	0.32	0.98		0.328
			10 °C -30 °C	-0.47	0.32	1.17		0.242
			20 °C -30 °C	-0.86	0.32	2.15		0.032

Dependent variable	Transformation	Explanatory variable	Contrasts	Estimate	SE	Z	t	P-value
Particulate organic phosphorus	Log2 (x)	Resuspension	No-Middle	2.62	0.50		5.29	<0.001
			No-High	4.55	0.50		9.16	<0.001
TP			Middle-High	1.92	0.50		3.87	0.001
		Resuspension	No-Middle	0.44	0.36	1.15		0.249
			No-High	1.37	0.36	3.57		0.000
			Middle-High	0.93	0.36	2.42		0.015
		Temperature	10 °C-20 °C	0.61	0.35	1.39		0.165
			10 °C-30 °C	1.09	0.35	2.48		0.013
Conductivity	Log 10 (x)		20 °C-30 °C	0.48	0.35	1.10		0.27
		Resuspension	No-Middle	0.03	0.01		5.63	<0.001
			No-High	0.02	0.01		4.74	<0.001
			Middle-High	-0.004	0.01		-0.89	0.385
		Temperature	10 °C-20 °C	0.01	0.01		1.21	0.271
			10 °C-30 °C	0.04	0.01		4.79	0.003
			20 °C-30 °C	0.03	0.01		3.58	0.012
		Resuspension	No-Middle	-5.64	0.57		-9.92	<0.001
			No-High	-5.20	0.57		-9.15	<0.001
			Middle-High	-0.34	0.57		-0.60	0.561
Total copepod adults	Sqrt (x)	Temperature	10 °C-20 °C	-3.81	0.57		-6.65	0.001
			10 °C-30 °C	-4.84	0.57		-8.43	0.003
			20 °C-30 °C	-0.01	0.57		-0.02	0.985
		Resuspension×Temperature	No10 °C-No 20 °C	3.81	0.57	6.65		<0.001
			No 10 °C-No 30 °C	4.84	0.57	8.73		<0.001
			No 20 °C-No 30 °C	1.02	0.57	1.78		0.693
			M 10 °C-M 20 °C	0.01	0.57	0.02		1.000
			M 10 °C-M 30 °C	0.02	0.57	0.03		1.000
			M 20 °C-M 30 °C	0.01	0.57	0.02		1.000
			H 10 °C-H 20 °C	0.79	0.57	1.37		0.908
			H 10 °C-H 30 °C	0.79	0.57	1.37		0.908
			H 20 °C-H 30 °C	0.00	0.57	0.00		1.000

Dependent variable	Transformation	Explanatory variable	Contrasts	Estimate	SE	Z	t	P-value
Total copepod nauplii	Log ² (x)	Resuspension	No-Middle	-12.85	1.24		-10.39	<0.001
			No-High	-12.96	1.24		-10.48	<0.001
			Middle-High	-0.11	1.24		-0.09	0.932
		Temperature	10 °C -20 °C	-4.26	1.24		-3.45	0.014
			10 °C -30 °C	-3.98	1.24		-3.22	0.018
Total cladocerans	Sqrt (x)		20 °C -30 °C	0.28	1.24		0.23	0.826
		Resuspension	No-Middle	-3.94	0.44		-8.99	<0.001
			No-High	-4.07	0.44		-9.27	<0.001
Phytoplankton density	Ln (x)		Middle-High	-0.13	0.44		-0.29	0.773
		Resuspension	No-Middle	15684.63	4789		3.27	0.004
			No-High	17319.53	4789		3.28	0.002
			Middle-High	1634.91	4789		0.34	0.737
Diatom relative abundance	Log (x)	Resuspension	No-Middle	-0.94	1.01		-0.93	0.366
			No-High	0.80	1.01		0.79	0.441
			Middle-High	1.75	0.01		1.72	0.104
Chlorophyta relative abundance	Sqrt (x)	Temperature	10 °C -20 °C	-2.18	0.84		-2.60	0.041
			10 °C -30 °C	-3.56	0.84		-4.25	0.005
			20 °C -30 °C	-1.39	0.84		1.65	0.149
Cryptophyta relative abundance	Sqrt (x)	Resuspension	No-Middle	-0.84	0.43		-1.97	0.066
			No-High	-1.11	0.43		-2.57	0.021
			Middle-High	-0.26	0.43		-0.60	0.555
		Resuspension	No-Middle	-2.57	1.59		1.50	0.134
Others relative abundance	Ln (x+0.001)		No-High	-3.95	1.59		2.30	0.021
			Middle-High	-1.38	1.59		0.80	0.422
		Resuspension	No-Middle	-145.7	134	1.01	1.01	0.314
Benthic algae density	Sqrt (x)		No-High	-298.8	134	2.06		0.039
			Middle-High	-153.1	134	1.51		0.291
		Temperature	10 °C -20 °C	234.4	134	1.40		0.161
			10 °C -30 °C	275.8	134	1.65		0.099
			20 °C -30 °C	41.31	134	0.25		0.805

Table S3.3. Dissolved oxygen (DO), pH and Conductivity at the end of the experiment. Values represent means \pm SE (n=3). The different uppercase letters indicate significant differences among resuspension treatments. The different lowercase letters indicate significant differences among temperature treatments.

Parameter	Treatment	No	Middle	High
DO (mg L ⁻¹)	10 °C	11.63 \pm 1.17 ^a	9.69 \pm 1.39 ^a	10.38 \pm 0.62 ^a
	20 °C	8.52 \pm 0.89 ^b	8.56 \pm 1.08 ^b	8.55 \pm 1.08 ^b
	30 °C	7.48 \pm 0.51 ^c	7.85 \pm 0.03 ^c	6.39 \pm 1.53 ^c
pH	10 °C	8.53 \pm 0.18	8.27 \pm 0.18	8.54 \pm 0.17
	20 °C	8.26 \pm 0.17	8.30 \pm 0.20	8.29 \pm 0.35
	30 °C	8.25 \pm 0.13	8.52 \pm 0.04	8.10 \pm 0.34
Conductivity (μ S cm ⁻¹)	10 °C	902.67 \pm 12.06 ^{aA}	956 \pm 15.62 ^{aB}	961 \pm 8.89 ^{aB}
	20 °C	914.33 \pm 66.33 ^{aA}	998.33 \pm 16.86 ^{aB}	975.67 \pm 25.11 ^{aB}
	30 °C	1012.33 \pm 10.41 ^{bA}	1043.33 \pm 5.03 ^{bB}	1032.67 \pm 4.04 ^{bB}

Table S3.4. Pearson's coefficients among total phosphorus (TP), chlorophyll *a* (Chl *a*), suspended solids (SS) and water temperature from the center of lake Markermeer, and daily mean wind speed from Lelystad from 1999 to 2016 based on monthly surveys. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

		TP	Chl <i>a</i>	SS	Temperature	Mean windspeed
Yearly dynamics	TP	1				
	Chl <i>a</i>	0.46***	1			
	SS	0.53***	0.62***	1		
	Temperature	-0.14*	-0.36***	- 0.39***	1	
	Mean windspeed	0.30***	0.49***	0.65***	-0.33***	1
Monthly average	TP	1				
	Chl <i>a</i>	0.80*	1			
	SS	0.74	0.95***	1		
	Temperature	-0.56	-0.81**	- 0.87***	1	
	Mean windspeed	0.55	0.78**	0.95***	-0.85***	1

Supporting figures

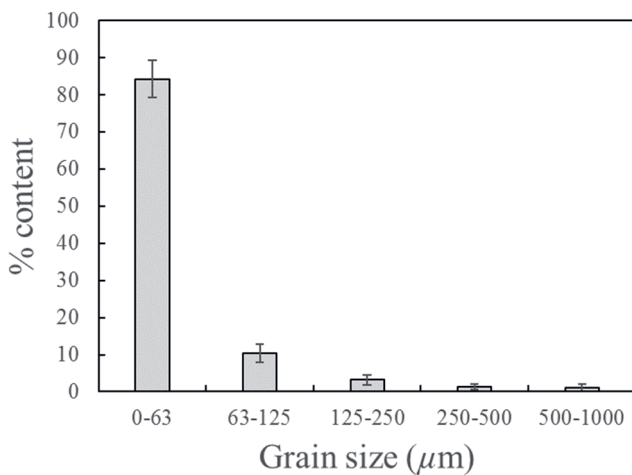


Fig. S3.1. The sediment grain size distribution. Values represent means \pm SE ($n=3$). Sediment samples were freeze-dried and sieved through a one mm sieve, sediment larger than one mm was weighed, while the remaining sediment grain size distribution was measured by laser diffraction on a Malvern Mastersizer 2000.

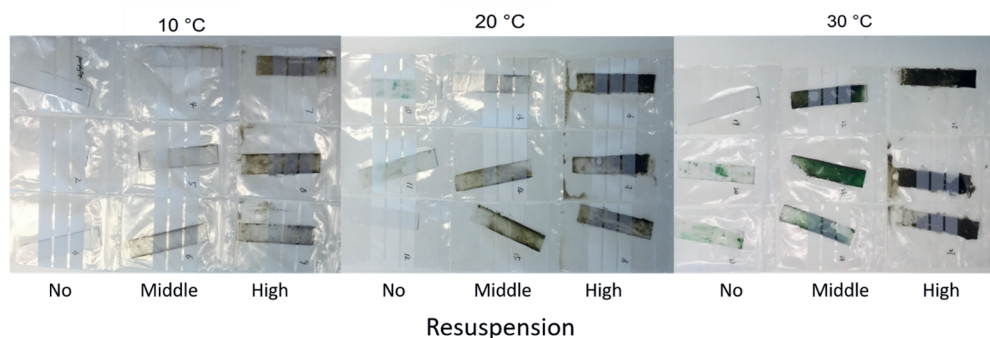


Fig. S3.2. Images showing periphyton algae at the end of experiment at three resuspension intensities (No, Middle, High) and three temperature scenarios (10°C, 20°C, 30°C). Each column with three strips represents the three replicates.

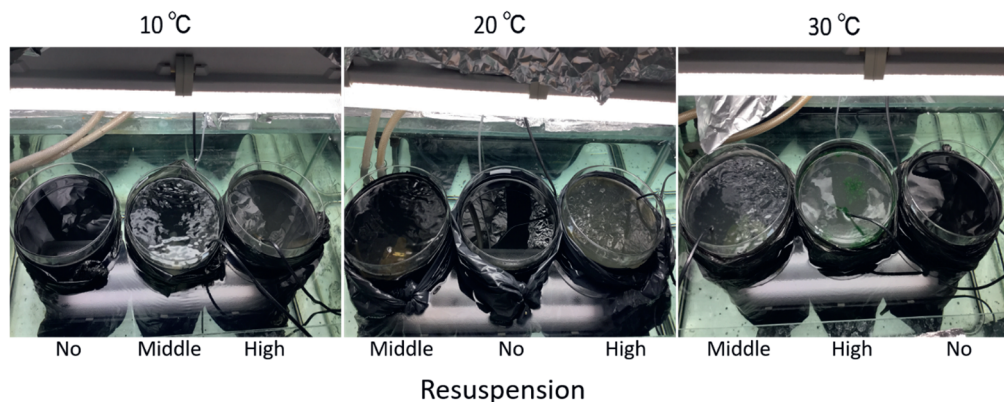


Fig. S3.3. Photographs of experimental design with three resuspension intensities (No, Middle, High) and three temperature scenarios (10°C, 20°C, 30°C). The microcosm locations in the aquarium were randomly distributed.



Chapter 4

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

Hui Jin, Casper H.A. van Leeuwen, Ralph J.M. Temmink, Elisabeth S. Bakker

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, for instance 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 due to wind-induced turbulence can potentially lead to declines of higher trophic levels in aquatic food webs, but is generally understudied.
2. Here, we focus on the impact of wind on aquatic primary producers and trophic transfer. We hypothesize 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 the Marker Wadden in lake Markermeer in the Netherlands. Lake Markermeer has experienced declining numbers of benthivorous and piscivorous birds over the last decades, as well as declines in fish. These declines have been related to wind-induced resuspension of the lake's fine sediments that potentially limits primary production as well as trophic transfer. The creation of the Marker Wadden archipelago in this lake is a large-scale restoration project that aims to add sheltered and more 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 between phytoplankton and zooplankton, 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 show that under unsheltered conditions phytoplankton was the dominant primary producer, while 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-times higher trophic transfer efficiency between phytoplankton and zooplankton under the sheltered conditions. Furthermore, under the sheltered conditions the Gastropoda density reached 746 individuals m^{-2} , while 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 gastropod densities and restoring trophic transfer 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.

4.1 | 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, i.e., the primary producers including macrophytes, benthic algae and phytoplankton. For example, macrophyte establishment may directly be inhibited because of stem breakage, uprooting, or limitations in establishment of their propagules (Jupp and Spence 1977, Keddy 1983, Schutten et al. 2005, Van Zuidam and Peeters 2015). In addition, benthic algae may be unable to colonize exposed habitat due to sediment resuspension and instable sediment (Jorge and Beusekom 1995). As such, wind-induced disturbances may favor phytoplankton dominance by releasing it from competition by other primary producers (Sand-Jensen and Borum 1991, Hansson et al. 2020). 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, while low light availability created by high phytoplankton abundance and suspended sediments inhibits or restricts the growth of submerged macrophytes or benthic algae (Jäger and Diehl 2014).

Wind-induced turbulence can also affect secondary producers in shallow aquatic ecosystems. Wind can modify the community of secondary producers (zooplankton) directly (Zhou et al. 2016, Ohman and Romagnan 2016) as well as indirectly by affecting the quantity and quality of their food (phytoplankton) (Cyr and Coman 2012, Durham et al. 2013, Tang et al. 2020). Direct effects are, for example, that wind-induced turbulence may inhibit growth of large-sized zooplankton species of which their body size exceeds the Kolmogorov length scale as they are more affected by eddy motion (Peters and 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 (Visser et al. 2009, G. -Tóth et al. 2011, 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 solids 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 (Koenings et al. 1990, Kirk and Gilbert 1990). As a result, wind-induced turbulence may potentially lower the trophic transfer efficiency between phytoplankton and zooplankton – defined as the total production ratio between adjacent trophic levels (Lindeman 1942) – due to 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 might subsequently lead to the decline of higher trophic production (Kazama et al. 2021, Barneche et al. 2021).

Reducing wind-induced turbulence may therefore be a suitable method to stimulate 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., at 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 (Zhang et al. 2020, Gao et al. 2021). Additionally, nutrient limitation may also decrease phytoplankton quality (in terms of carbon to nutrient ratio), because it potentially leads to higher carbon to nutrients ratios in primary producers (Sturner and Elser 2002, Ågren 2004). Furthermore, if submerged macrophytes or benthic algae establish under sheltered conditions, these will compete with phytoplankton for nutrients (Sand-Jensen and Borum 1991, Hansson et al. 2020), which may further strengthen nutrient limitation and decrease both phytoplankton biomass and its quality. As such, on the one hand, sheltered conditions seem favorable for larger zooplankton that can profit from easy feeding in a water column with little interference of suspended sediments (Kirk and 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 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 hypothesized that shelter would (1) 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; (2) enhance the trophic transfer efficiency between phytoplankton and zooplankton; (3) increase the abundance of benthic fauna grazing on benthic algae, periphyton and macrophytes.

4.2 | Methods

4.2.1 Study site

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 km² delta lake located in the center 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 et al. 2012a). Suspended solid concentrations in the lake ranged from 4.0 to 368.0 mg L⁻¹ from 1999–2016, with an annual average of 45 mg L⁻¹ (Kelderman et al. 2012a, 2012b).

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, with negative consequences for higher trophic levels in the food web (Van Riel et al. 2019).

To improve the ecological integrity of this lake, a large-scale restoration project called the “Marker Wadden” has been initiated in 2016 by the Dutch Society for Nature Conservation (“Natuurmonumenten”). Marker Wadden is a newly constructed archipelago of five islands spread across an area of about 1.000 ha in the northeastern part of Markermeer (52°35'02.8"N 5°21'55.5"E) (Fig. 4.1 A-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.

4.2.2 Experimental design

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 the Marker Wadden (Fig. 4.1). We used a randomized 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, and (3) an unsheltered control in the open water. This design allowed 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 (Fig 4.1).

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. Water depth ranged from 0.20-0.80 m across the cylinders. The field experiment started on the 24th of June 2019 and lasted until the 26th of August 2019. At the end of the experiment, all measurements, as described in detail the following

section, were conducted: physical parameters of the water column, suspended solids concentrations, seston elemental composition, nutrient concentrations in the water column, types of primary producers, the zooplankton community, and benthic fauna composition.

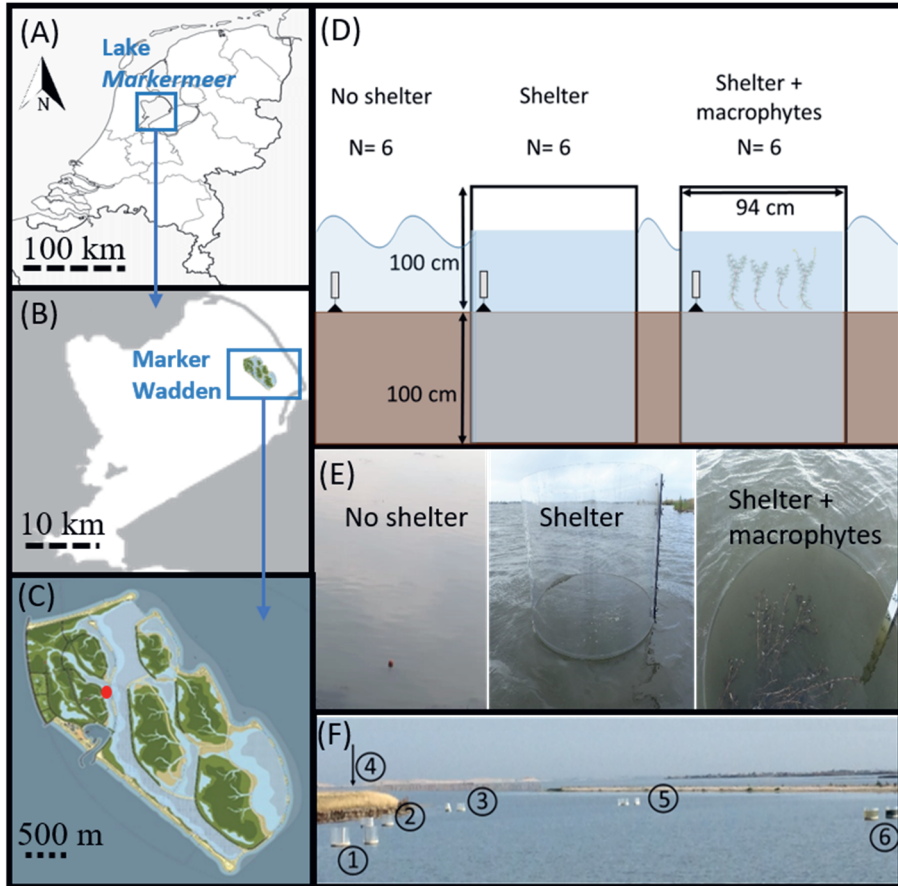


FIGURE 4.1 Location and design of the study. (A) The Netherlands. (B) Lake Markermeer. (C) Marker Wadden. The red dot indicates the location of the experiment. (D) Schematic overview of the experimental design, representing one block. The experiment consisted of six replicate blocks ($n=6$). The vertical strip in each treatment represents a plastic strip used to measure periphyton growth. (E) The experimental treatments in the field. (F) Overview of the location of the experimental blocks. Photo's: Liesbeth Bakker. Map of Marker Wadden: Boskalis.

4.2.3 Sampling and laboratory analyses

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, Bad Homburg, Germany). The vertical attenuation coefficient, K_d , was then calculated (Lampert and Sommer 2007). Light at the sediment surface was calculated based on the surface light intensity and the K_d (Lampert and Sommer 2007).

To determine total suspended solids (TSS), inorganic suspended solids (ISS), organic suspended solids (OSS), seston elemental composition, dissolved nutrients, chlorophyll *a* concentrations and zooplankton community composition, a depth-integrated water sample of 30 L volume was taken from the center of the mesocosm with a water sampler, which was then 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, Maidstone, UK), drying these filters at 60 °C overnight, and then reweighing them to determine their weight increase. After weighing, these filters were stored dark in a desiccator for subsequent seston elemental composition analysis (explained in the next section).

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

Seston elemental composition

To determine the quality of seston as food for zooplankton, in terms of carbon:nutrients ratios, we focused on the edible fraction (size < 30 μm) of the seston (Haney 1973, Cyr and Curtis 1999). 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, Maidstone, UK), dried at 60 °C overnight, and then reweighed. To determine C and 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, Okehampton, UK) and analyzed for particulate C and N on a FLASH 2000 NC elemental analyzer (Brechtbuhler Incorporated,

Interscience B.V., Breda, The Netherlands). The remainder of the GF/F filters were used to assess phosphorus contents, by combusting them in a Pyrex glass tube at 550°C for 30 min, adding 5 mL of persulfate (2.5%) to the glass tube, and autoclaving them for 30 min at 121°C. Digested P (as PO₄) was measured on a QuAatro39 Auto-Analyzer (SEAL Analytical Ltd., Southampton, UK).

Nutrients in the water

Dissolved inorganic nutrients were determined from water subsamples that were filtered using pre-washed GF/F filters (Whatman, Maidstone, UK). The filtrate was stored at -20°C before analyzes. Concentrations of dissolved nutrients (ammonium [NH₄⁺], nitrate [NO₃⁻], nitrite [NO₂⁻] and phosphate [PO₄³⁻]) in the filtrate were determined on a QuAatro39 Auto-Analyzer (Seal Analytical, Fareham, UK). Particulate organic nitrogen (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 analyzed 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, NH₄⁺, NO₃⁻, and NO₂⁻ concentrations, while the total phosphorus was calculated as the sum of the POP and PO₄³⁻ concentrations.

Chlorophyll a concentrations

The Chlorophyll *a* concentration (Chl *a*) in the water column was determined from filtered matter retained on a GF/F filters (Whatman, Maidstone, UK) after filtering a known volume of water subsamples. For logistic purposes the samples were stored at -20°C not more than one month. After thawing, the filters were extracted with 80% ethanol in an 80 °C water bath, and passed through Millipores 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), Waltham Massachusetts, United States) equipped with a Hypersil ODS column (25 cm, 5 µm, 4.6 ×250 mm; Agilent) and a RF 2000 fluorescence detector (Dionex/Thermo Scientific, Waltham Massachusetts, US). 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).

Zooplankton community composition

Crustacean zooplankton samples were collected by filtering 20 L of depth-integrated water samples through an 80- μ m mesh size net, while rotifer samples were collected by filtering 1 L of depth-integrated samples through a 30- μ m mesh size net. All samples were fixed with alkaline Lugol's iodine solution within an hour from collecting.

Zooplankton specimens were counted using a stereomicroscope (Leica M205C, Germany). 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 enough individuals to make this possible) of the most abundant genus and deriving biomass from published length-weight relationships (Dumont et al. 1975, Bottrell et al. 1976). Rotifera total biomass was estimated by using geometric formulas 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 $0.1 \times \text{wet weight}$ (*sensu* Doohan, 1973).

Macrophyte biomass and species composition

To determine submerged macrophyte biomass and species composition, all the plants that grew within the mesocosms were removed carefully with a rake on the final harvesting day (26-08-2019). 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.

Periphyton algae biomass

To measure the biomass of periphyton, one plastic strip (length \times width: 21.0 \times 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 (Fig. 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, Maidstone, UK). The residue was subsequently analyzed using the same method as for determining Chlorophyll *a* in the water column.

Benthic fauna composition

To quantify benthic fauna composition, we collected a sediment core with a 10 cm depth using a plastic tube ($\varnothing = 5.2$ cm) and analyzed 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 50 ml tubes with 70% ethanol. In the laboratory, all invertebrates from the sediment cores and attached to the macrophytes were identified to genus or species level.

Trophic transfer efficiency

To determine the trophic transfer efficiency (TTE) between phytoplankton and zooplankton, we used the zooplankton to phytoplankton biomass ratio in \log_{10} scale as a proxy (Gaedke and Straile 1994, Jennings et al. 2002, Yvon-Durocher et al. 2011, García-Comas et al. 2016). 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 and Straile 1994, Jennings et al. 2002, Yvon-Durocher et al. 2011, García-Comas et al. 2016).

4.2.4 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 randomized block design, block location (6 levels) was included as random factor in all 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 due to 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 analyze 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. 2012) in R version 3.5.1 (R Core Team 2021). All data are shown with their mean \pm Standard error (SE) and in all hypothesis testing procedures the significance level was pre-set at $\alpha = 0.05$ ($p < 0.05$).

4.3 | Results

4.3.1 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 (Fig. 4.2A, Table S4.1,S4.2). 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, although in the treatments with most macrophytes (Shelter + macrophytes) C:N ratios were highest (Fig. S4.1, Table S4.1). The edible fraction of phytoplankton was same among treatments (Table S4.1). The phytoplankton edible fractions were $75 \% \pm (11)$, $93 \% \pm (11)$, and $75 \% \pm (11)$ in the No shelter, Shelter, and Shelter + macrophytes treatments, respectively (Fig. S4.1).

Submerged macrophytes became the dominant primary producers in both shelter treatments and were not present in the no shelter treatment (Fig. 4.2B, Table S4.1,S4.2). 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 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 (Fig. 4.2B, Table S4.1,S4.2). Four submerged macrophyte species were recorded in all sheltered treatments, i.e. *Myriophyllum spicatum*,

Zannichellia palustris, *Potamogeton perfoliatus* and *Potamogeton pectinatus*, irrespective of the conditions at the onset of the experiment.

Periphyton algae chlorophyll *a* was 6-fold higher in the absence of shelter compared to both shelter treatments (Fig. 4.2C, Table S4.1,S4.2). 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 was generally much lower than the biomass of submerged macrophytes in both shelter treatments (comparing Fig. 4.2B and D). Benthic algae were equally present in all treatments, but at a generally low biomass (Fig. 2E).

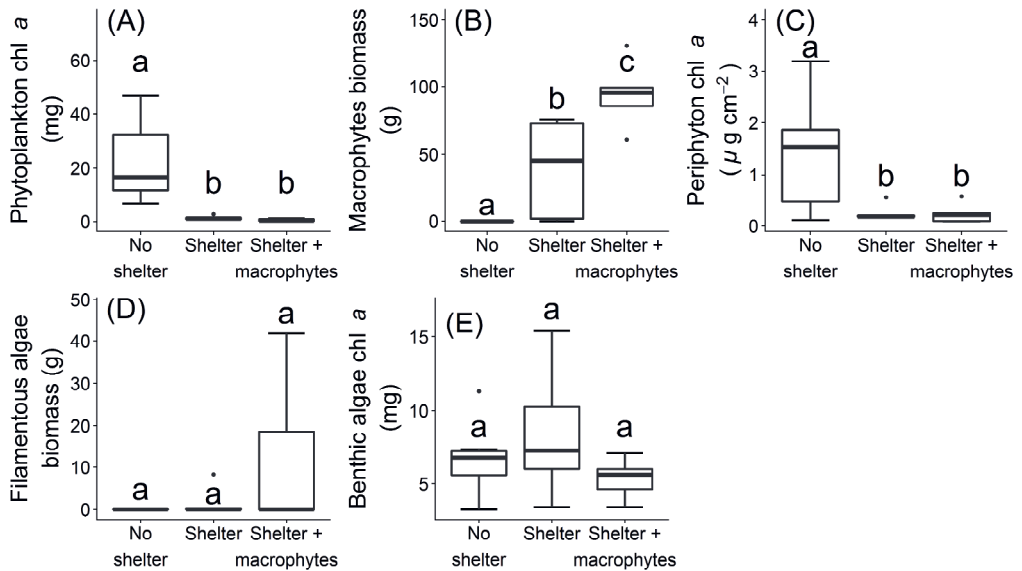


FIGURE 4.2 (A) Phytoplankton chl *a* (mg per plot), (B) macrophytes (g dry weight per plot), (C) periphyton chl *a* ($\mu\text{g cm}^{-2}$), (D) filamentous algae (g dry weight per plot), and (E) benthic algae chl *a* (mg per plot) in the treatments No shelter ($n=6$), Shelter ($n=5$), and shelter + macrophytes ($n=5$). Different lowercase letters indicate a significant difference among treatments. Boxplots show the median (middle line), quartiles (boxes), 1.5 times the interquartile range (IQR) (whiskers), and extreme values (dots). Dots outside the whiskers are extreme values.

4.3.2 Zooplankton

Total zooplankton biomass was similar among treatments (Fig. 4.3, Table S4.1,S4.2), but there were differences in the zooplankton community composition (Table S4.1,S4.2). Specifically, total copepod biomass in the shelter treatment was

significantly higher compared with the no shelter treatment, while macrophyte presence in the initial stage did not affect copepod biomass (Table S4.1,S4.2). No significant differences were found in total rotifer biomass, *Daphnia* biomass, nauplii biomass and biomass of small cladocerans among treatments (Table S4.1).

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 mainly consisted 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 mainly consisted of nauplii ($59\% \pm 9$) in the no shelter treatment, while copepods were dominant in the shelter ($42\% \pm 16$) and shelter + macrophytes ($42\% \pm 9$) treatments (Fig. 4.3). Small cladocerans contributed $11\% \pm 2$, $20\% \pm 14$ and $16\% \pm 8$, while *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.

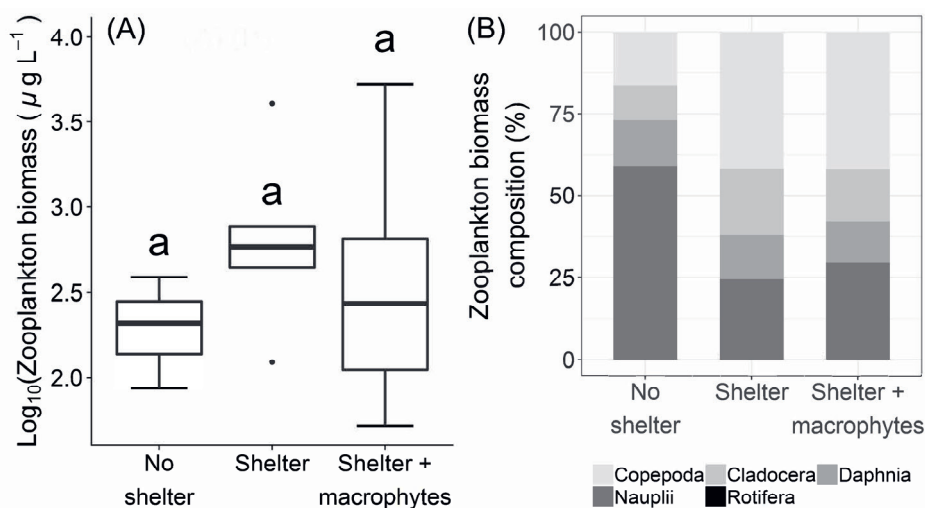


FIGURE 4.3 (A) Zooplankton biomass ($\mu\text{g L}^{-1}$), and (B) zooplankton biomass composition (%) in the treatments “No shelter” ($n=6$), “Shelter” ($n=5$), and “Shelter + macrophytes” ($n=5$). Different lowercase letters indicate a significant difference among treatments. Boxplots show the median (middle line), quartiles (boxes), 1.5 times the interquartile range (IQR) (whiskers), and extreme values (dots). Dots outside the whiskers are extreme values.

4.3.3 Shelter effect on trophic transfer efficiency

Shelter enhanced the trophic transfer efficiency between phytoplankton and zooplankton 5-fold, regardless of whether macrophytes were initially present or not, as indicated by the zooplankton biomass/chl *a* ratio (Fig. 4.4, Table S4.1,S4.2).

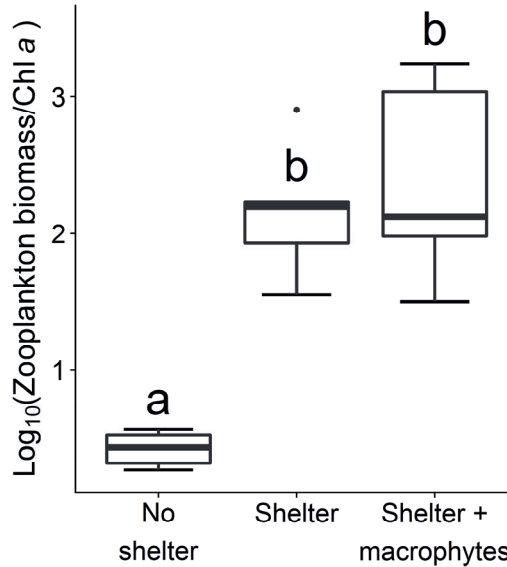


FIGURE 4.4 Trophic transfer efficiency (log10 ratio between the zooplankton biomass and phytoplankton biomass expressed as chlorophyll *a*) in the treatments “No shelter” (n=6), “Shelter” (n=5), and “Shelter + macrophytes” (n=5). Different lowercase letters indicate a significant difference among treatments. Boxplots show the median (middle line), quartiles (boxes), 1.5 times the interquartile range (IQR) (whiskers), and extreme values (dots). Dots outside the whiskers are extreme values.

4.3.4 Shelter effect on benthic fauna

Ten benthic animal 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 ind. m⁻² in the shelter treatment, while no Gastropoda were found under the no shelter treatment (Fig. 4.5, Table S4.1,S4.2). Macrophyte presence in the initial stage did not affect Gastropoda density (Fig. 4.5, Table S4.1,S4.2). The shelter treatment where macrophytes were present in the initial stage

harbored significantly larger Corophiidae densities, 46-fold more 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 ranging from 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 density in the cylinders varied from 0 – 4 and 0 – 9 ind. m⁻² in the shelter and shelter + macrophytes treatments, respectively.

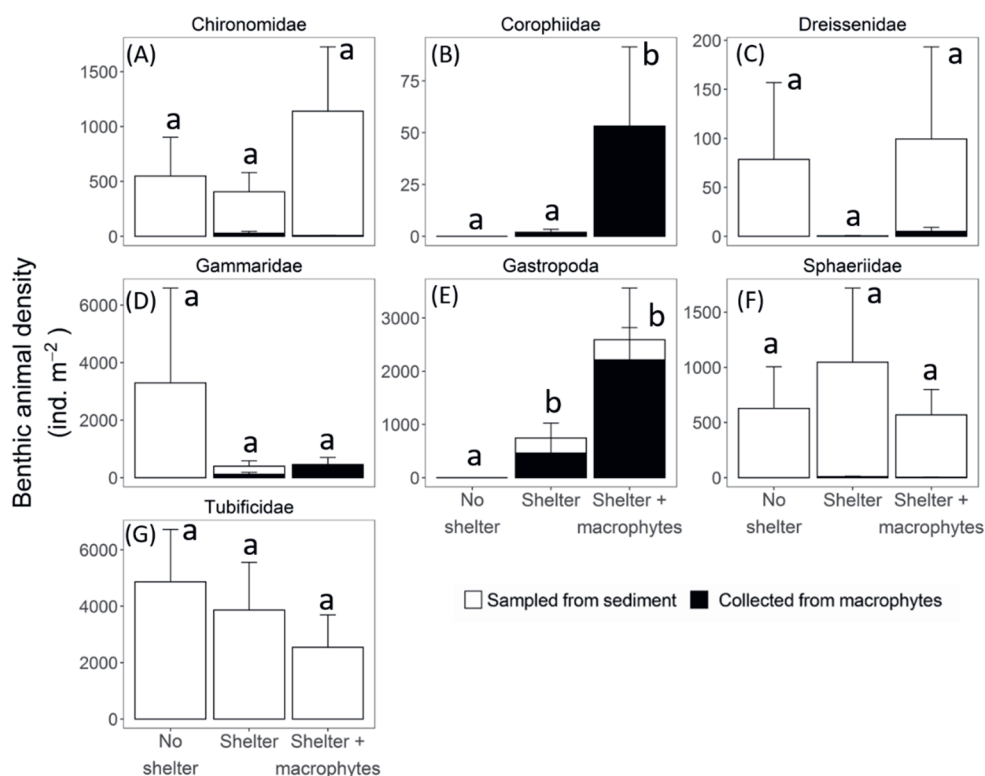


FIGURE 4.5 Benthic fauna composition (individuals m⁻²) in the treatments “No shelter” (n=6), “Shelter” (n=5), and “Shelter + macrophytes” (n=5) separately indicated in panels per family or in case of the Gastropoda for the whole class (panel c). The animals were either collected from the sediment (white bars) or from the macrophytes (black bars). Different lowercase letters indicate a significant difference among treatments.

4.3.5 Abiotic conditions

Shelter significantly decreased the total nitrogen concentration in the water column (TN), while total phosphorus (TP) in the water column was not affected by shelter (Fig. S4.2, Table S4.1,S4.2). Macrophyte presence at the initial stage did not affect TN or TP (Fig. S4.2, Table S4.1,S4.2). The presence of shelter reduced the dissolved inorganic nitrogen (DIN), particulate organic nitrogen (PON), and particulate organic phosphorus (POP) 38-, 7- and 5-fold, respectively (Fig. S4.2, Table S4.1,S4.2). Macrophyte presence in the initial stage significantly increased DIN concentrations 9-fold, whereas there was no significant effect of macrophyte presence in the initial stage on DIP, PON, and POP (Fig. S4.2, Table S4.1,S4.2).

Shelter facilitated the settlement of suspended solids and increased water transparency. Total suspended solids (TSS), inorganic suspended solids (ISS), and organic suspended solids (OSS) were 10-, 12-, and 6-fold lower in the shelter treatments than in the absence of shelter, respectively (Fig. S4.3, Table S4.1,S4.2). Shelter significantly decreased the vertical light attenuation coefficient (k_d). K_d was 2-fold lower in the shelter treatments than in the no shelter treatment (Fig. S4.3, Table S4.1). 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 (Fig. S4.3, Table S4.1,S4.2).

4.4 | 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 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 spontaneously developed, while they did not develop under unaltered conditions. At exposed sites, primary production was strongly dominated by phytoplankton, confirming hypothesis 1. However, the trophic transfer efficiency of the primary production by phytoplankton towards zooplankton was 5-fold higher under sheltered conditions (confirming hypothesis 2). Gastropoda densities

increased in response to shelter, confirming hypothesis 3. These findings suggest that for shallow lakes that are negatively affected by wind, measures aimed at ameliorating this stressor can be effective in facilitating macrophyte establishment, increasing trophic transfer and supplying more food resources for higher trophic levels.

4.4.1 Shelter effect on primary producers

Our results showed 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 was likely 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) were significantly lower, as well as nutrient availability in the water column (DIN, PON, POP, and TN), 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 (Phillips et al. 1978, Jones and Sayer 2003). Moreover, the high density of gastropods in the sheltered treatments may have further decreased the periphyton biomass through grazing (Bakker et al. 2013a).

Apart from these indirect effects, wind-induced turbulence can also directly affect macrophytes through the forces it exerts on macrophytes and their propagules (Jupp and Spence 1977, Keddy 1983, Van Zuidam and Peeters 2015). Shelter, which aims at reducing wind effects, could reduce the wave force which potentially prevents macrophyte damage, while it facilitates their anchorage (Schutten et al. 2005) and germination (Fonseca and Kenworthy 1987, Riis and Hawes 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 most likely have also reduced herbivory by birds (Bakker et al. 2013b, 2016b), such as mute swans *Cygnus olor* and Eurasian coots *Fulica atra* that are present on the Marker Wadden (pers. observations H. Jin).

Herbivorous waterbirds not only directly graze on macrophytes, but may also indirectly increase the shading effect by periphyton, which may causes the collapse of macrophytes (Hidding et al. 2016). However, the effects of herbivory in our study remain undetermined and warrant further study.

Although shelter significantly increased light availability by decreasing the vertical attenuation coefficient, 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 $255 \pm 108 \mu\text{mol m}^{-2} \text{s}^{-1}$, which was significantly higher than in the exposed plots (only $44 \pm 32 \mu\text{mol m}^{-2} \text{s}^{-1}$). As benthic algae growth is light-saturated at $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Hill et al. 2009), light was most likely 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 lead to lower benthic algae biomass through grazing (Yang et al. 2019).

4.4.2 Shelter effect on trophic transfer

Our results show that shelter enhanced the trophic transfer efficiency between phytoplankton and zooplankton, in agreement with hypothesis 2. This may partly have been caused 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 and 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 shows that Cyclopoida, *Daphnia*, and rotifers have a larger body size in the shelter treatments (Fig. S4.4). 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 carbon to nutrients ratio. Especially 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 and Downing 1985). Although the food quantity (indicated by the chlorophyll *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 inorganic suspended solids concentrations could mechanically interfere with food collection or dilute gut content (Koenings et al. 1990, Kirk and Gilbert 1990).

Fish predation may also inhibit the zooplankton biomass build-up by preferential feeding on *Daphnia* in the absence of shelter (Lemmens et al. 2018, Liu et al. 2020), potentially leading to decreased trophic transfer from phytoplankton to 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 amount of small fish and *Daphnia* biomass that are the most efficient grazers. However, we found no relationship between fish abundance and trophic transfer between phytoplankton and zooplankton (Table S3).

4.4.3 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 may also directly benefit from the calm conditions in the sheltered treatments as wind induced turbulence may increase their mortality and/or dislodgement (Brown and Quinn 1988, Etter 1989). 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 (Thomaz et al. 2008, Clemente et al. 2019).

4.4.4 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 from phytoplankton to zooplankton, and increase benthic fauna biomass. This knowledge can be applied in shallow lake management. For example, submerged macrophytes are often a prerequisite for high-quality shallow lake ecosystem services, including drinking water supply, fisheries production, and serving as hot-spots of biodiversity (Hilt et al. 2017, Hansson 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 (Jilbert et al. 2020, Abell et al. 2020). However, these efforts are counteracted or weakened due to the wind-induced sediment resuspension, 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.

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 food web bottom-up 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 (van Leeuwen et al 2021). Our experiments show that, provided that i) this new archipelago generates sufficient shelter and ii) that herbivory pressure by waterfowl is not too high (Bakker et al. 2013b, 2016b), 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 indirectly facilitated by shelter due to the enhanced trophic transfer efficiency between phytoplankton and zooplankton under more sheltered conditions, resulting in turn in high food availability for juvenile fish. 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 likely offers alternative pathways to stimulate higher trophic biodiversity (Karlsson et al. 2009).

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 (Malzahn et al. 2007, Dickman et al. 2008). In 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 due to the low trophic transfer efficiency (Ye et al. 2013). Altogether, the improved understanding of the effect of shelter on primary producers, trophic transfer, and benthic fauna provides important insights that can be used for more successful conservation and restoration of shallow lakes.

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Data availability statement

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

Author's contribution

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.

SUPPORTING INFORMATION

TABLE S4.1 Linear mixed-effect model results for the effects of the factor “treatment” with three levels (“No shelter”, “Shelter”, and “Shelter + macrophytes”) on each of the measured parameters. Bold numbers indicate a significance at the $\alpha = 0.05$ level.

Dependent variable	Transformation	Numerator d.f.	Denominator d.f.	<i>F</i>	<i>P</i>
Primary producers					
Macrophytes (g)	Sqrt (x)	2	8	22.9	<0.001
Phytoplankton Chl <i>a</i> (mg)	Sqrt (x)	2	8	40.1	<0.001
Periphyton Chl <i>a</i> ($\mu\text{g cm}^{-2}$)	Sqrt (x)	2	8	4.9	0.041
Benthic algae Chl <i>a</i> (mg)	Sqrt (x)	2	8	1.7	0.239
Filamentous algae (g)	Ln (x+0.001)	2	8	1.9	0.205
Zooplankton composition					
Total zooplankton biomass ($\mu\text{g L}^{-1}$)	Log 10 (x)	2	8	2.1	0.188
Total copepods biomass ($\mu\text{g L}^{-1}$)	Ln (x)	2	8	8.8	0.010
Total rotifer biomass ($\mu\text{g L}^{-1}$)	Ln (x+0.001)	2	8	0.4	0.689
Daphnia biomass ($\mu\text{g L}^{-1}$)	Ln (x+0.001)	2	8	3.5	0.081
Small cladocerans ($\mu\text{g L}^{-1}$)	Ln (x+0.001)	2	8	0.4	0.681
Nauplii biomass ($\mu\text{g L}^{-1}$)	Ln (x+0.001)	2	8	4.1	0.058
Trophic transfer efficiency	Log10 (x)	2	8	30.57	0.002
Benthic fauna composition					
Chironomidae (ind. m ⁻²)	Ln (x+0.001)	2	8	4.1	0.060
Tubificidae (ind. m ⁻²)	Sqrt (x)	2	8	0.8	0.490
Gastropoda (ind. m ⁻²)	Ln (x+0.001)	2	8	16.4	0.002
Gammaridae (ind. m ⁻²)	Ln (x+0.001)	2	8	4.4	0.050
Corophiidae (ind. m ⁻²)	Log10 (x+0.001)	2	8	8.8	0.010
Sphaeriidae (ind. m ⁻²)	Log10 (x+0.001)	2	8	1.6	0.252
Dreissenidae (ind. m ⁻²)	Log10 (x+0.001)	2	8	2.0	0.197
Seston property					
C:N (mol:mol)	Ln (x)	2	8	12.7	0.003
C:P (mol:mol)	Ln (x)	2	8	0.1	0.911
Edible fractions	Sqrt (x)	2	13	0.9	0.450
Nutrients concentration					
DIN ($\mu\text{mol L}^{-1}$)	Ln (x+0.001)	2	8	15.0	0.002
DIP ($\mu\text{mol L}^{-1}$)	Ln (x+0.001)	2	8	4.1	0.059
PON ($\mu\text{mol L}^{-1}$)	Ln (x)	2	8	49.6	<0.001
POP ($\mu\text{mol L}^{-1}$)	Ln (x)	2	8	28.9	0.002
TN ($\mu\text{mol L}^{-1}$)	Sqrt (x)	2	8	44.9	<0.001
TP ($\mu\text{mol L}^{-1}$)	Sqrt (x)	2	8	0.6	0.578
Suspended materials					
Inorganic suspended solids (mg L ⁻¹)	Sqrt (x)	2	8	71.7	<0.001

Dependent variable	Transformation	Numerator d.f.	Denominator d.f.	<i>F</i>	<i>P</i>
Organic suspended solids (mg L ⁻¹)	Sqrt (x)	2	8	112.9	<0.001
Total suspended solids (mg L ⁻¹)	Ln (x)	2	8	40.8	0.001
Light availability					
Attenuation coefficient	Ln (x)	2	8	5.8	0.028
Zooplankton body length					
Cyclopoida (μm)	Log10 (x)	2	461	31.1	<0.001
Calanoida (μm)	Log10 (x)	1	81	15.3	0.002
Small cladocerans (μm)	Ln (x)	2	598	2.0	0.139
Daphnia (μm)	Log10 (x)	2	206	26.3	<0.001
Nauplii (μm)	Log10 (x)	2	368	4.0	0.019
Rotifer (μm)	Sqrt (x)	2	538	13.2	<0.001

TABLE S4.2 Overview of effect of treatments on primary producers, trophic transfer efficiency, benthic animals composition, nutrients concentration in the water column, suspended materials, light availability, zooplankton composition, zooplankton body length, and seston property (mean \pm SE). The “NS”, “S”, and “SM” are short for No shelter, shelter, and shelter + macrophytes, respectively.

Dependent variable	No shelter	Shelter	Shelter + macrophytes	Transformation	Estimate	Contrasts	t	P
Primary producers								
Macrophytes (g)	0.0 \pm 0.0	39.2 \pm 16.5	94.4 \pm 11.3	Sqrt (x)	5.07	NS-S	3.55	0.008
					9.64	NS-SM	6.75	<0.001
					4.57	S-SM	3.07	0.015
Phytoplankton Chl <i>a</i> (mg)	22.5 \pm 6.4	1.4 \pm 0.3	0.6 \pm 0.2	Sqrt (x)	-3.03	NS-S	-7.15	<0.001
					-3.48	NS-SM	-8.19	<0.001
					-0.44	S-SM	-1.03	0.333
Periphyton Chl <i>a</i> ($\mu\text{g cm}^{-2}$)	1.4 \pm 0.5	0.3 \pm 0.1	0.2 \pm 0.1	Sqrt (x)	-0.58	NS-S	-2.62	0.031
					-0.60	NS-SM	-2.72	0.026
					-0.02	S-SM	-0.10	0.926
Zooplankton composition								
Total copepods biomass ($\mu\text{g L}^{-1}$)	32.4 \pm 5.7	293 \pm 101	378 \pm 285	Ln (x)	1.97	NS-S	3.92	0.004
					1.60	NS-SM	3.18	0.013
					-0.37	S-SM	-0.72	0.492
Trophic transfer efficiency	0.4 \pm 0.1	2.2 \pm 0.2	2.4 \pm 0.3	Log10 (x)	1.74	NS-S	6.27	<0.001
					1.95	NS-SM	7.04	<0.001
					0.21	S-SM	0.74	0.482
Seston property								
C:N (mol:mol)	11.3 \pm 0.3	15.3 \pm 2.2	24.7 \pm 5.0	Ln (x)	0.27	NS-S	1.87	0.099
					0.71	NS-SM	5.00	0.001
					0.45	S-SM	3.05	0.016
Benthic fauna composition								
Gastropoda (ind. m $^{-2}$)	0.0 \pm 0.0	746 \pm 316	2591 \pm 1354	Ln (x+0.001)	8.41	NS-S	3.61	0.007
					13.10	NS-SM	5.62	0.001
					4.70	S-SM	1.96	0.086
Corophiidae (ind. m $^{-2}$)	0.0 \pm 0.0	1.2 \pm 1.2	53.1 \pm 38.3	Log10 (x+0.001)	1.73	NS-S	0.84	0.427
					8.37	NS-SM	4.04	0.004
					6.64	S-SM	3.07	0.015

Dependent variable	No shelter	Shelter	Shelter + macrophytes	Transformation	Estimate	Contrasts	t	P
Nutrient concentrations								
DIN ($\mu\text{mol L}^{-1}$)	134 \pm 53.6	0.7 \pm 0.5	6.4 \pm 2.4	Ln (x+0.001)	-8.38	NS-S	-5.47	<0.001
					-4.39	NS-SM	-2.87	0.021
					3.99	S-SM	2.54	0.035
PON ($\mu\text{mol L}^{-1}$)	88.7 \pm 6.5	14.2 \pm 1.5	11.3 \pm 3.1	Ln (x)	-1.84	NS-S	-7.66	<0.001
					-2.20	NS-SM	-9.16	<0.001
					-0.36	S-SM	-1.43	0.188
POP ($\mu\text{mol L}^{-1}$)	7.1 \pm 0.4	1.2 \pm 0.1	1.4 \pm 0.4	Ln (x)	-1.77	NS-S	-6.40	<0.001
					-1.82	NS-SM	-6.58	<0.001
					-0.05	S-SM	-0.17	0.869
TN ($\mu\text{mol L}^{-1}$)	223 \pm 50.9	14.9 \pm 1.7	17.7 \pm 5.4	Sqrt (x)	-10.88	NS-S	-8.18	<0.001
					-10.74	NS-SM	-8.07	<0.001
					0.14	S-SM	0.11	0.919
Suspended materials								
Inorganic suspended solids (mg L^{-1})	93.3 \pm 10.0	7.4 \pm 1.7	7.8 \pm 3.4	Sqrt (x)	-6.98	NS-S	-10.14	<0.001
					-7.09	NS-SM	-10.30	<0.001
					-0.11	S-SM	-0.15	0.884
Organic suspended solids (mg L^{-1})	35.4 \pm 2.2	5.9 \pm 0.6	6.4 \pm 1.2	Sqrt (x)	-3.52	NS-S	-12.94	<0.001
					-3.46	NS-SM	-12.69	<0.001
					0.07	S-SM	0.24	0.820
Total suspended solids (mg L^{-1})	125 \pm 12.2	12.2 \pm 2.3	13.2 \pm 4.2	Ln (x)	-2.39	NS-S	-7.59	0.001
					-2.46	NS-SM	-7.81	0.001
					-0.07	S-SM	-0.21	0.838
Light availability								
Attenuation coefficient	11.8 \pm 1.1	6.2 \pm 2.6	10.4 \pm 2.8	Ln (x)	-1.04	NS-S	-3.29	0.011
					-0.26	NS-SM	-0.83	0.432
					0.78	S-SM	2.40	0.043
Zooplankton body length								
Cyclopoida (μm)	419 \pm 9.9	558 \pm 14.7	524 \pm 18.1	Log10 (x)	0.12	NS-S	7.73	<0.001
					0.08	NS-SM	5.23	<0.001
					-0.04	S-SM	-2.49	0.013
Calanoida (μm)	858 \pm 9.4	736 \pm 3.0	NA	Log10 (x)	-0.07	NS-S	-3.92	0.002
						NS-SM		
						S-SM		

Dependent variable	No shelter	Shelter	Shelter + macrophytes	Transformation	Estimate	Contrasts	t	P
Daphnia (μm)	769 \pm 21.3	938 \pm 19.1	1026 \pm 21.8	Log10 (x)	0.17	NS-S	5.73	<0.001
					0.18	NS-SM	6.22	<0.001
					0.01	S-SM	0.30	0.765
Nauplii (μm)	169 \pm 2.5	157 \pm 1.9	162 \pm 2.8	Log10 (x)	-0.03	NS-S	-2.26	0.025
					-0.02	NS-SM	-2.38	0.018
					0.01	S-SM	0.53	0.596
Rotifer (μm)	104 \pm 1.0	120 \pm 1.7	125 \pm 1.7	Sqrt (x)	0.86	NS-S	5.07	<0.001
					0.29	NS-SM	1.48	0.139
					-0.57	S-SM	-2.38	0.018

TABLE S4.3 Kendall's rank correlation tau between fish number and all the investigated parameters under the shelter and shelter + macrophytes treatment.

Category	Parameters	Fish	<i>P</i>
Primary producers	Macrophytes (g)	0.10	0.710
	Phytoplankton Chl <i>a</i> ($\mu\text{g L}^{-1}$)	-0.05	0.852
	Periphyton Chl <i>a</i> ($\mu\text{g cm}^{-2}$)	-0.05	0.852
	Benthic algae Chl <i>a</i> ($\mu\text{g cm}^{-2}$)	0.05	0.852
	Filamentous algae (g)	0.62	0.027
Zooplankton composition	Total zooplankton biomass ($\mu\text{g L}^{-1}$)	-0.19	0.456
	Total copepods biomass ($\mu\text{g L}^{-1}$)	0.00	1.00
	Total rotifer biomass ($\mu\text{g L}^{-1}$)	0.20	0.450
	Daphnia biomass ($\mu\text{g L}^{-1}$)	-0.60	0.038
	Small cladocerans ($\mu\text{g L}^{-1}$)	0.10	0.710
	Nauplii biomass ($\mu\text{g L}^{-1}$)	0.40	0.131
Trophic transfer efficiency	Zooplankton biomass/Chl <i>a</i>	-0.15	0.576
Benthic fauna composition	Chironomidae (ind. m^{-2})	0.15	0.576
	Tubificidae (ind. m^{-2})	0.12	0.640
	Gastropoda (ind. m^{-2})	0.17	0.513
	Gammaridea (ind. m^{-2})	-0.19	0.456
	Corophiidae (ind. m^{-2})	0.22	0.423
	Sphaeriidae (ind. m^{-2})	-0.18	0.509
	Dreissenidae (ind. m^{-2})	-0.03	0.916
Seston property	C:N (mol:mol)	-0.10	0.710
	C:P (mol:mol)	-0.53	0.041
Nutrients concentration	DIN ($\mu\text{mol L}^{-1}$)	0.60	0.027
	DIP ($\mu\text{mol L}^{-1}$)	0.36	0.195
	PON ($\mu\text{mol L}^{-1}$)	0.19	0.456
	POP ($\mu\text{mol L}^{-1}$)	0.63	0.015
	TN ($\mu\text{mol L}^{-1}$)	0.58	0.025
	TP ($\mu\text{mol L}^{-1}$)	0.48	0.063
Suspended materials	Inorganic suspended solids (mg L^{-1})	0.34	0.192
	Organic suspended solids (mg L^{-1})	0.53	0.040
	Total suspended solids (mg L^{-1})	0.44	0.094
Light availability	Attenuation coefficient	0.34	0.192

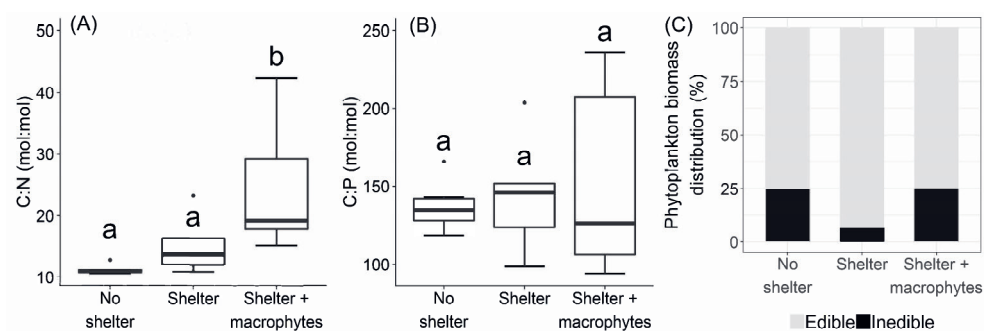


FIGURE S4.1 (A) Seston elemental composition with C:N (mol:mol), (B) C:P molar ratio (mol:mol), and phytoplankton biomass distribution (%) (C) in the treatments “No shelter” (n=6), “Shelter” (n=5), and “Shelter + macrophytes” (n=5). Different lowercase letters indicate a significant difference among treatments. Boxplots show the median (middle line), quartiles (boxes), 1.5 times the interquartile range (IQR) (whiskers), and extreme values (dots). Dots outside the whiskers are extreme values.

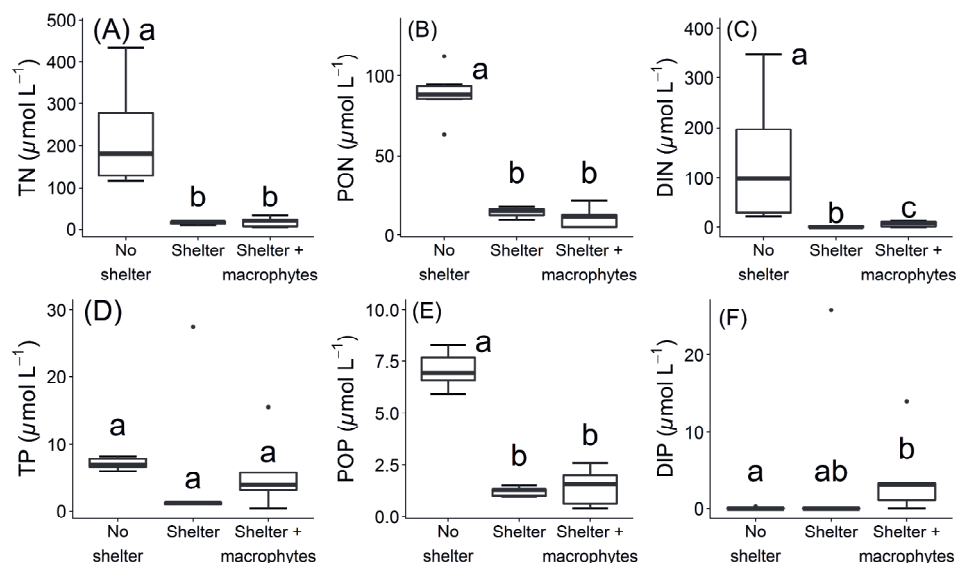


FIGURE S4.2 (A) Total nitrogen (TN, $\mu\text{mol L}^{-1}$), (B) particulate organic nitrogen (PON, $\mu\text{mol L}^{-1}$), (C) dissolved inorganic nitrogen (DIN, $\mu\text{mol L}^{-1}$), (D) total phosphorus (TP, $\mu\text{mol L}^{-1}$), (E) particulate organic phosphorus (POP, $\mu\text{mol L}^{-1}$), and (F) dissolved inorganic phosphorus (DIP, $\mu\text{mol L}^{-1}$) concentrations in the surface water 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 times the interquartile range (IQR) (whiskers), and extreme values (dots). Dots outside the whiskers are extreme values.

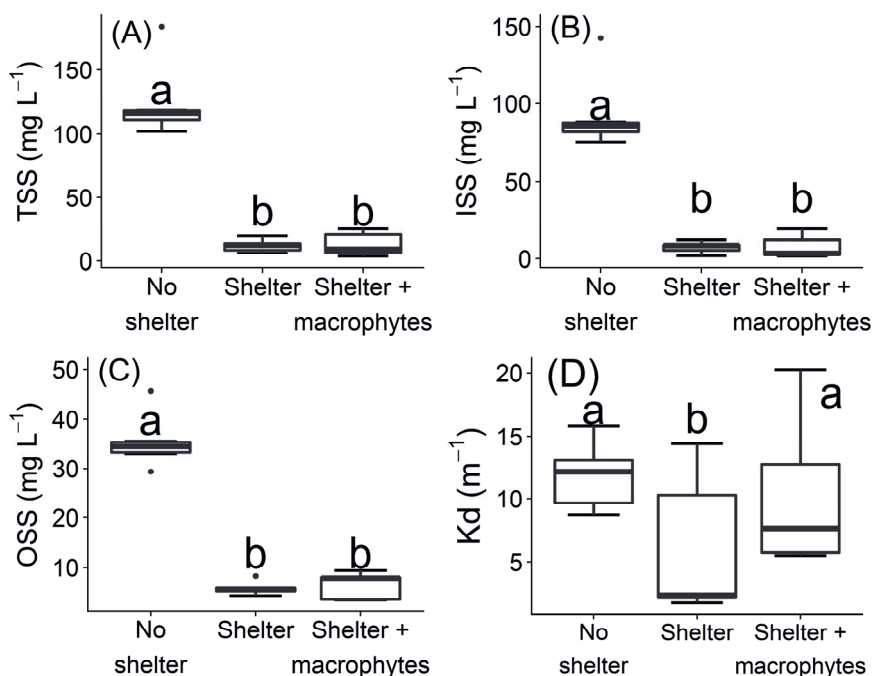


FIGURE S4.3 Total suspended solids (TSS, mg L⁻¹) (A), inorganic suspended solids (ISS, mg L⁻¹) (B), and organic suspended solids (OSS, mg L⁻¹) (C), and vertical attenuation coefficient (k_d , m⁻¹) in the treatments “No shelter” (n=6), “Shelter” (n=5), and “Shelter + macrophytes” (n=5). Different lowercase letters indicate a significant difference among treatments. Boxplots show the median (middle line), quartiles (boxes), 1.5 times the interquartile range (IQR) (whiskers), and extreme values (dots). Dots outside the whiskers are extreme values.

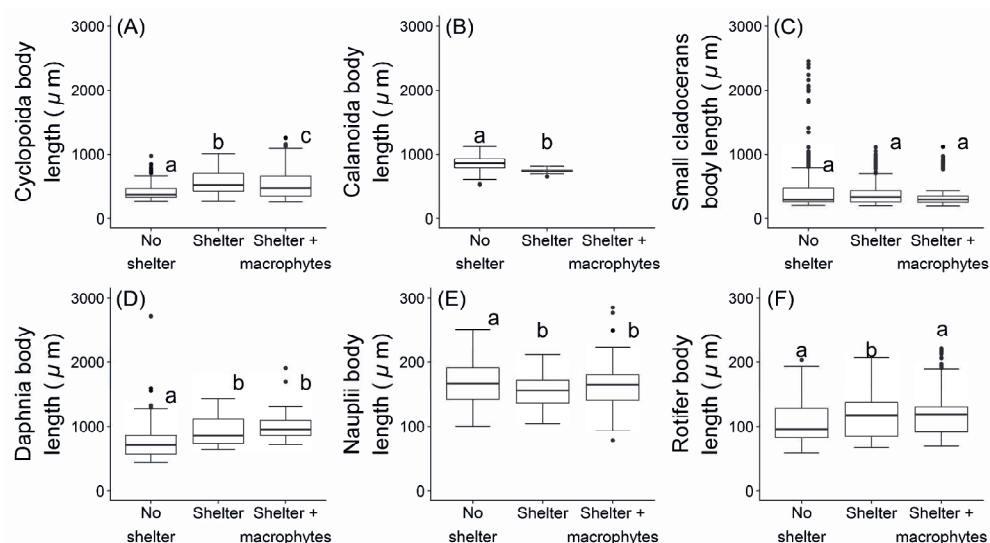


FIGURE S4.4 The body length of Cyclopoida (A), Calanoida (B), Cladocerans (C), Daphnia (D), Nauplii (E), and Rotifer (F) in the treatments “No shelter” (n=6), “Shelter” (n=5), and “Shelter + macrophytes” (n=5). Different lowercase letters indicate a significant difference among treatments. Boxplots show the median (middle line), quartiles (boxes), 1.5 times the interquartile range (IQR) (whiskers), and extreme values (dots). Dots outside the whiskers are extreme values.



Chapter 5

Optimizing phytoplankton quantity and quality for trophic transfer: extending the light-nutrient hypothesis for lake restoration

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Abstract

1. Higher trophic levels, such as fish and waterbirds in aquatic ecosystems, may decline when primary productivity and its transfer to higher trophic levels is limited. One way to restore the abundance of higher trophic levels is to strengthen the base of the food web by optimizing food quality and quantity. The light:nutrient hypothesis predicts how the balance between light and phosphorus availability affects phytoplankton stoichiometry and thereby their nutritional quality for higher trophic levels. However, it remains unclear how the balance between light and phosphorus affects phytoplankton quantity.
2. Here, we extended the light:nutrient hypothesis to mechanistically understand how changes in the availability of light relative to phosphorus affect primary producer quality (expressed as carbon:phosphorus (C:P) stoichiometry) as well as their quantity (expressed as chlorophyll-*a* concentration) in large-scale lake restoration project, “Marker Wadden”, in lake Markermeer, The Netherlands. Marker Wadden is a newly built archipelago aimed to increase the declining abundance of fish and waterbirds in this shallow lake by strengthening the food web from its base.
3. We found that phytoplankton C:P ratios increased upon an increasing availability of light relative to phosphorus, thereby decreasing its quality as food source, while phytoplankton biomass showed a unimodal relationship with the light:phosphorus ratio in the water across time and locations in Marker Wadden and the surrounding lake. In the Marker Wadden archipelago, phytoplankton quantity (biomass) and its quality (reverse of C:P ratio) were 1.8-fold and 2.7-fold higher, respectively, compared to the surrounding lake.
4. Synthesis and applications. Our results provide a mechanistic understanding of the role of light and phosphorus availability determining phytoplankton biomass and stoichiometry, and show that the light:nutrient hypothesis can provide a valuable framework to guide ecological restoration of aquatic ecosystems. To enhance the transfer of energy and matter to higher trophic levels in the food web (trophic transfer), a light:phosphorus ratio at which both quantity and quality of phytoplankton reach their optimum, as suggested by our extended light:nutrient hypothesis, might help steering

future lake restoration efforts aiming to improve the abundance of higher trophic levels, such as fish and waterbirds, in downgraded aquatic ecosystems.

5.1 | Introduction

Light and nutrients provide the energy and matter that enable food web production (Sterner et al. 1997; Elser et al. 2007; Gruner et al. 2008). The absolute availabilities of both resources in an ecosystem strongly determine primary producer biomass (Gruner et al. 2008, Campos-Silva et al. 2021), which typically increases with higher light and nutrient availability. In addition, the relative availabilities of light and nutrients can alter primary producer elemental composition, and thereby their nutritional value for higher trophic levels (Urabe and Sterner 1996, Sterner and Elser 2002). Specifically, increased light availability may lead to a higher carbon:nutrient stoichiometry in primary producers, whereas increased nutrient availability generally decreases this stoichiometry (Sterner & Elser, 2002; Hessen et al., 2013). The light:nutrient hypothesis integrates both responses, and postulates that primary producer carbon:phosphorus stoichiometry corresponds to the availability of light relative to phosphorus (Sterner et al. 1997).

These stoichiometric implications are important as the transfer efficiency of energy and nutrients from primary producers to higher trophic levels strongly depends on the nutritional value of primary producers (Burian et al. 2020), as regulated by the relative availabilities of light and nutrients. For example, higher light availabilities relative to phosphorus will lead to higher phytoplankton carbon:phosphorus (C:P) ratios that can form a stoichiometric bottleneck for herbivores, and lead to a decline in higher trophic level production (Dickman et al. 2008, Van de Waal et al. 2010). Besides food quality, however, the productivity of higher trophic levels additionally depends on food quantity (Marcarelli et al. 2011), which also varies with changes in the relative availability of light and nutrients. Here, we therefore extend the light:nutrient hypothesis to mechanistically understand how changes in the availability of light relative to phosphorus affect not only primary producer quality (i.e. carbon:phosphorus stoichiometry), but also their quantity (i.e. biomass). We expect phytoplankton biomass to be highest at intermediate light:phosphorus ratios, where supply by both resources balances the physiological requirements of the phytoplankton. To test this, we applied the light:nutrient hypothesis in a lake restoration project in lake Markermeer, and explore how changes in the relative light and phosphorus availabilities in response to restoration alter phytoplankton biomass and stoichiometry.

Covering an area of 680 km², Lake Markermeer (The Netherlands) is among the largest shallow lakes in Western Europe. Phytoplankton production in this lake is at present thought to be P limited (Van Riel et al. 2019, Brinkmann et al. 2019),

whereas the lake is also subject to strong wind-driven sediment resuspension leading to low light availabilities (Eleveld 2012, Kelderman et al. 2012a). The lake has experienced strong declines in the numbers of fish and benthivorous and piscivorous birds over the last decades (Noordhuis 2014). These declines have been associated with reduced phytoplankton production, and a limited trophic transfer to higher trophic levels. To improve the ecological integrity of this lake and increase the numbers of fish and birds, a large-scale ecosystem restoration project called the “Marker Wadden” started in 2016. This project involved the construction of a 700-ha archipelago of five islands in lake Markermeer, aiming to create sheltered areas where sediment can settle and light availability in the water column can increase (Fig. 5.1). The shorelines of the Marker Wadden archipelago connect water and land, which may lead to increased nutrient availability by run-off from the land, particularly within the archipelago. Such water-land connectivity is rare along the shores of lake Markermeer, where water and land are almost entirely disconnected by basalt dikes. As such, the restoration project is expected to simultaneously alter light and nutrient availability in the water column, hence affecting phytoplankton biomass production and its nutritional quality for higher trophic levels.

In this study, we assessed the impact of ecosystem restoration on nutrient and light availabilities in the Marker Wadden archipelago in comparison to the surrounding lake, and tested the consequences for phytoplankton biomass production and carbon:nutrient stoichiometry. We specifically hypothesized that (1a) phytoplankton biomass (expressed as the chlorophyll-*a* concentration in the water) increases with both light and phosphorus availability and is higher in the Marker Wadden archipelago than in the surrounding lake; (1b) shows an optimum at a particular light:phosphorus ratio. We further hypothesized that (2a) phytoplankton quality (expressed as the reverse of their carbon:phosphorus ratio) decreases with increasing light availability and increases with increasing phosphorus availability, and is higher in the Marker Wadden archipelago than in the surrounding lake; (2b) follows the light:nutrient hypothesis and decreases with increasing light:phosphorus ratios.

To test our hypotheses, we performed a field study at the Marker Wadden from May to December 2018. We measured chlorophyll-*a* concentrations, seston carbon:nutrients stoichiometry, nutrient concentrations in the water column, light availability in the mixed layer, and suspended solids concentrations at selected locations in and around the Marker Wadden archipelago representing a gradient in absolute and relative light and nutrient availabilities.

5.2 | Materials and methods

5.2.1 Study area

Lake Markermeer is a 3–5 m deep (mean depth 3.6 m), 680 km² delta lake located in the center of The Netherlands (Fig. 5.1). This freshwater lake is part of a former estuary that was disconnected from the sea in 1932 by damming and became a separate lake from lake IJsselmeer by the construction of a dam, the Houtribdijk, in 1975. The lake is a Natura2000 area under the European bird directive and has experienced declines in numbers of benthivorous and piscivorous birds over the last decades, as well as in fish abundance (Noordhuis 2014). Marker Wadden is a newly constructed archipelago of islands spread across an area of about 700 ha in the northeastern part of lake Markermeer (52°35'02.8"N 5°21'55.5"E), and was built in 2016-2017. These islands have been constructed from local lake sediments and aim to improve the ecological status of lake Markermeer. The archipelago consists of five islands protruding several meters above the water level and an underwater landscape with varied water depths and littoral zones (Fig. 5.1).

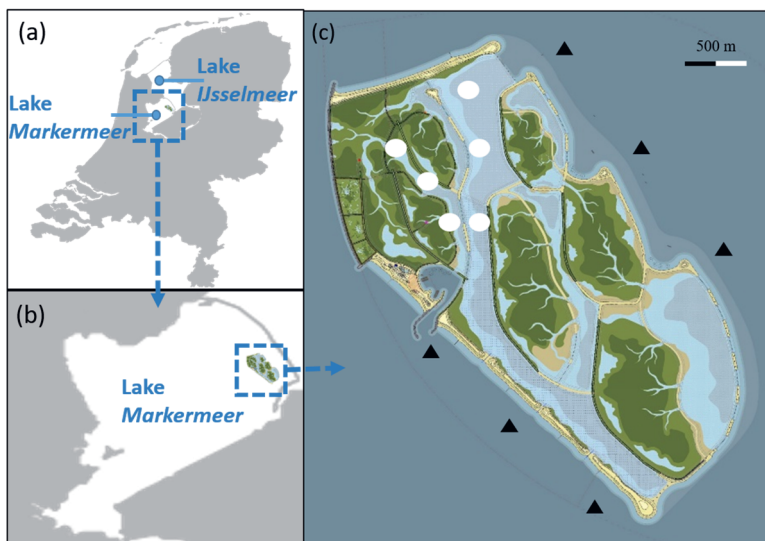


FIGURE 5.1 The Netherlands (a). Lake Markermeer (b). The Marker Wadden archipelago with the 12 sampling locations indicated (c). White circles indicate sampling points within the Marker Wadden archipelago. Black triangles indicate sampling points outside Marker Wadden. Credits: map of Marker Wadden: Boskalis.

5.2.2 Study design

We selected six sampling locations that represent the variation occurring within the Marker Wadden archipelago and six sampling locations in the open water surrounding the Marker Wadden (Fig. 5.1). The distance between the Marker Wadden shoreline and these sampling locations in the surrounding lake, outside of Marker Wadden, was about 200 meter. During the study no submerged macrophytes were present at the sampling locations. All the sampling locations on Marker Wadden are connected with the open water of the lake. We made a comparison between the surface waters within the Marker Wadden archipelago and the surrounding lake and used the range of light and nutrient availabilities across these habitats to test the light:nutrient hypothesis and its effect on phytoplankton biomass and carbon:phosphorus stoichiometry. For nutrients, we focus on phosphorus as the light:nutrient hypothesis postulates light:phosphorus relationships (Sterner et al. 1997). Furthermore, phytoplankton production in our study lake Markermeer is thought to be phosphorus limited (Van Riel et al. 2019, Brinkmann et al. 2019). However, we did include measurements of nitrogen availability in the water column and the seston carbon:nitrogen ratio in the comparison of the Marker Wadden archipelago with the surrounding lake and to assess the relative phosphorus and nitrogen availabilities in the water column.

5.2.3 Field sampling

All 12 locations were sampled every two weeks from the 17th of May to the 6th of December 2018. The deeper sampling points were sampled from a ship, whereas the shallow sampling points were sampled by carefully walking into the water from the shoreline, preventing disturbance of the sediment. The sampling protocol involved (1) measuring the water surface temperature with a handheld meter equipped with multiple sensors (Multi 350i, WTW, Germany) in the field; (2) measuring light intensity just below the water surface, at 50 cm depth and at 100 cm depth using a UW Quantum light sensor (LI-COR Environmental GmbH, Bad Homburg, Germany); (3) taking a depth-integrated water sample from three discrete water depths (i.e. near the top, middle and close to the bottom of the mixed layer; for the deeper sampling points with a 5 L LUWITEC water sampler). We took 15 L of water from each depth, then mixed this in a 45 L plastic tub (for very shallow sampling points, water was directly taken and mixed in the plastic tub). From this mixed 45-L sample, 1 liter water samples were taken for later analysis of chlorophyll-*a*

concentrations, suspended solids concentrations (total suspended solids (TSS), inorganic suspended solids (ISS), and organic suspended solids (OSS)), seston elemental composition (particulate C, N and P concentrations), dissolved inorganic nutrient concentrations (NH_4 , NO_3 , NO_2 , PO_4) and total nutrient concentrations (total nitrogen (TN), and phosphorus (TP)).

5.2.4 Laboratory analyses

Filtering 10-144 ml water subsamples (filtration volumes were dependent on the particle content of the water), the Chlorophyll-*a* concentration (Chl-*a*) in the water column was determined from filtered material retained on a GF/F filter (Whatman) which was first stored at -20°C . After thawing, the filters were extracted with 80% ethanol in a 80°C water bath, thereafter a further filtration through $0.2\ \mu\text{m}$ PTFE Membrane filter was performed and Chl-*a* concentrations were measured by High Performance Liquid Chromatography (HPLC, UltiMate 3000, Thermo Scientific, Waltham Massachusetts, United States) equipped with a Hypersil ODS column (25 cm, $5\ \mu\text{m}$, $4.6 \times 250\ \text{mm}$; Agilent, Santa Clara, US) and a RF 2000 fluorescence detector (Dionex/Thermo Scientific, Waltham Massachusetts, US).

To analyze the TSS concentrations in the water column, 15-122 ml water subsamples (filtration volumes were dependent on the particle content of the water) were filtered over pre-washed and pre-weighed GF/F filters (Whatman, Maidstone, United Kingdom), then dried at 60°C overnight and weighed. To determine the inorganic suspended solids concentration (ISS), 10-150 ml water subsamples were filtered over pre-ashed GF/F filters (Whatman, Maidstone, UK), then dried at 60°C overnight and weighed. These filters were then combusted in a muffle furnace at 550°C for 2 hours, brought to room temperature in a desiccator, and finally weighed to determine the ISS concentration. We calculated the organic suspended solids (OSS) by subtracting ISS from TSS.

For analysis of particulate organic carbon (C), nitrogen (N), and phosphorus (P), two circular subsamples (diameter 5.55 mm) were taken from each GF/F filter used for the TSS analysis. These subsamples were folded into a tin cup (Elemental Microanalysis, Okehampton, UK) and analyzed for particulate C and N on a FLASH 2000 NC elemental analyzer (Brechtbuhler Incorporated, Interscience B.V., Breda, The Netherlands). Digested P was measured (as PO_4) by combusting the remainder of the filter in a Pyrex glass tube at 550°C for 30 min. Subsequently, 5 mL of persulfate (2.5%) was added, and samples were autoclaved for 30 min at 121°C ,

before analysis on a QuAAtro39 Auto-Analyzer (SEAL Analytical Ltd., Southampton, UK). Total nitrogen and total phosphorus concentrations were calculated by summing up the dissolved and particulate nutrient concentrations.

Dissolved inorganic nutrients were determined from the filtrate of the water subsamples that were filtered over pre-washed GF/F filters (Whatman). The filtrate was stored at -20°C. After thawing, concentrations of dissolved nutrients (NH₄, NO₃, NO₂ and PO₄) were determined on a QuAAtro39 Auto-Analyzer (SEAL Analytical Ltd., Southampton, UK).

5.2.5 Data analysis

The mean light availability, expressed as a fraction of surface light, was calculated by the following formula (Riley 1957, Sterner et al. 1997):

$$I_m = \frac{1 - e^{K_d z_m}}{K_d z_m}$$

where z_m is the mixed depth. As the lake is shallow and subject to frequent winds, we assumed the z_m is equal to the water depth. K_d is the vertical attenuation coefficient, which is calculated by the following equation (Lampert and Sommer 2007):

$$K_d = \frac{\ln E_d(0) - \ln E_d(z)}{z}$$

in which $E_d(0)$ and $E_d(z)$ represent the light intensities at the surface and at depth z , respectively. In our study, z was measured at a water depth of 50 cm, except for the shallowest parts, where z represented the water depth (with a minimum of 8 cm).

To assess differences between the locations inside and outside of the Marker Wadden archipelago in all the measured parameters, we first averaged values per sampling location over the sampling season ($n=6$ inside, $n=6$ outside). We then confirmed normality of all parameters after natural log transformation using Shapiro-Wilks, and assessed homogeneity of variances using Levene's tests. We present statistical comparisons based on Welch's t-tests in case of unequal variances (all results were confirmed by non-parametric alternatives, not shown). All statistical analyses were conducted using R version 3.5.1 (R Core Team 2021).

To search for statistical descriptions of possible relationships between phytoplankton biomass (Chl-*a*) or seston quality (C:P ratio) as dependent variables, depending on either $\ln(\text{TP})$, $\ln(\text{mean light in the mixed layer})$ or $\ln(\text{TP:light ratio})$ as explanatory variables, we fitted linear as well as quadratic relationships to detect

possible positive, negative or unimodal relationships (i.e. an optimum). We fitted the relationships using the `nls`-function from the ‘stats’ package in R, and performed model selection among only the significant models based on Akaike Information Criteria (Akaike 1974). We presented the formulas that best describe these relationships as well as the R^2 -values of these models as indications of how much of the variation the models explained. We plotted the significant relationships that best described the data in the figures, including their respective formulas.

5.3 | Results

Nutrient concentrations in the water column (both TN and TP) were higher inside the Marker Wadden archipelago than outside the archipelago, whereas the mean light availability in the mixed layer did not statistically differ (Fig. 5.2, Table S5.1). TN, TP and mean light availability showed strong seasonal dynamics, with high TN concentrations inside the archipelago in autumn and high TP concentrations in summer and autumn.

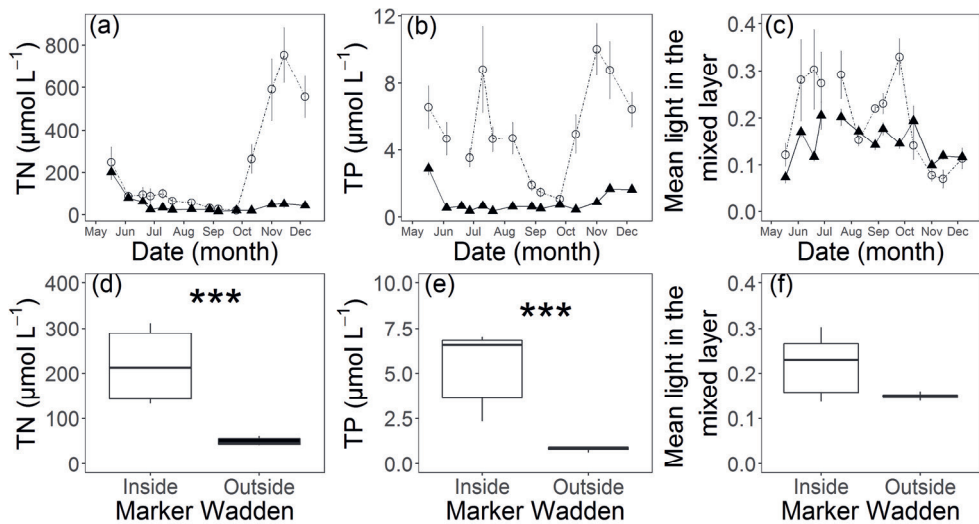


FIGURE 5.2 Seasonal variation in total nitrogen (TN) (a), total phosphorus (TP) (b), mean light in the mixed layer (c); mean TN (d), mean TP (e), and mean light in the mixed layer (f) inside (open circles) and outside (closed triangles) the Marker Wadden archipelago for the duration of the study. Values represent the means \pm SE ($n=6$). The asterisks indicate a significant difference at $P < 0.001$.

The phytoplankton biomass (expressed as chlorophyll-*a* concentration) was generally 1.8-fold higher at locations inside the Marker Wadden archipelago compared to those in the surrounding lake (Fig. 5.3, Table S5.1). The highest phytoplankton biomass inside the archipelago was found during summer.

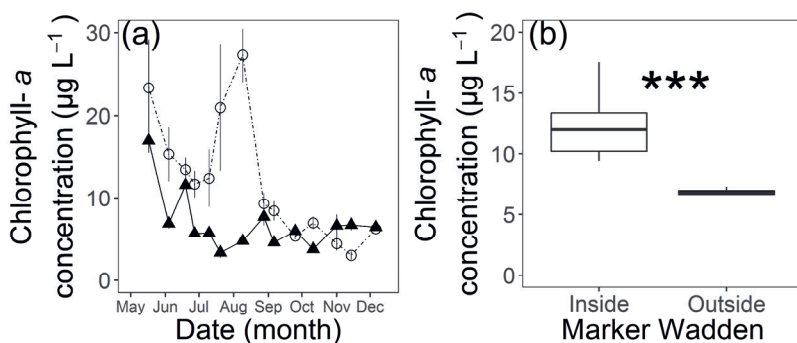


FIGURE 5.3 Bi-weekly phytoplankton biomass (as chlorophyll-*a*) (a), and mean phytoplankton biomass (b) over the year (May-December 2018) inside (open circles) and outside (closed triangles) the Marker Wadden archipelago. Values in panel A represent means \pm SE ($n=6$); the asterisks in panel B indicate a significant difference at $P < 0.001$.

Seston C:P ratios were low and stable inside the Marker Wadden archipelago for the entire duration of the sampling period, whereas seston C:P ratios showed a pronounced summer peak outside of the archipelago (Fig. 5.4a). Consequently, mean C:P ratios inside the archipelago were 2.7-fold lower compared to those in the surrounding lake (Fig. 5.4c). Seston C:N ratios were also lower (1.2-fold) at locations inside the Marker Wadden archipelago compared to outside, while the seasonal dynamics were less pronounced (Fig. 5.4b,d). Seston N:P ratios approximated the Redfield ratio across locations inside the Marker Wadden archipelago, suggesting balanced availability, while these ratios were 2.2-fold higher in the surrounding lake (Fig. S5.1), indicating P limitation.

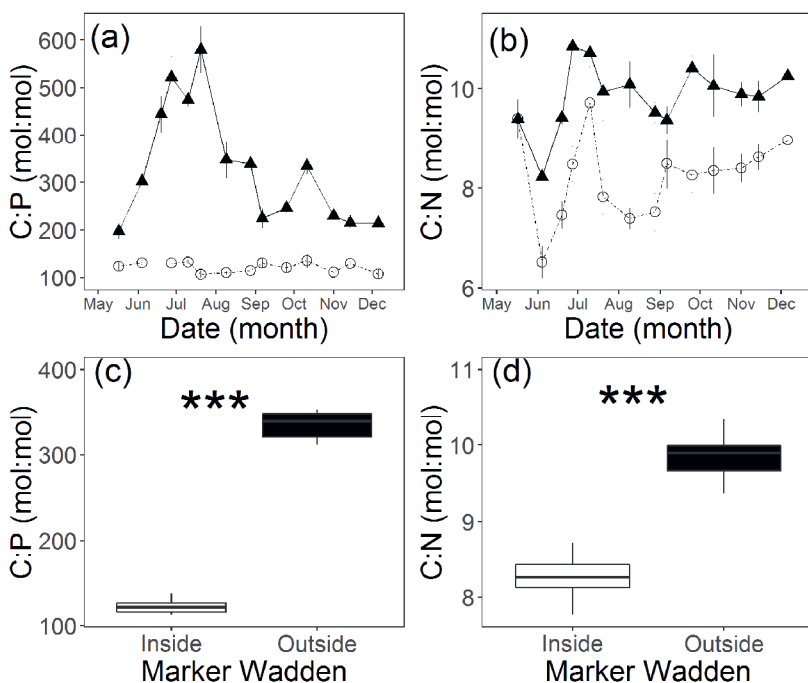


FIGURE 5.4 Seston elemental composition with C:P (a), C:N (b) molar ratios, mean C:P ratio (c), and mean C:N ratio (d) over the year (May–December 2018) inside (open circles) and outside (closed triangles) the Marker Wadden archipelago. Values represent the means \pm SE ($n=6$). The asterisks indicate a significant difference at $P < 0.001$.

Chlorophyll-*a* concentrations showed a unimodal relationship with TP and TN across locations (Fig. 5.5a, Fig. S5.2), while no significant relationship between phytoplankton and mean light in the mixed layer was found (Fig. 5.5b, Table S5.2). Phytoplankton biomass followed a unimodal relationship with the light:phosphorus ratio (Fig. 5.5c, Table S5.2). Seston C:P showed unimodal relationships with TP

(Fig. 5.5d), mean light in the mixed layer (Fig. 5.5e), and the light:phosphorus ratio (Fig. 5.5f, Table S5.2).

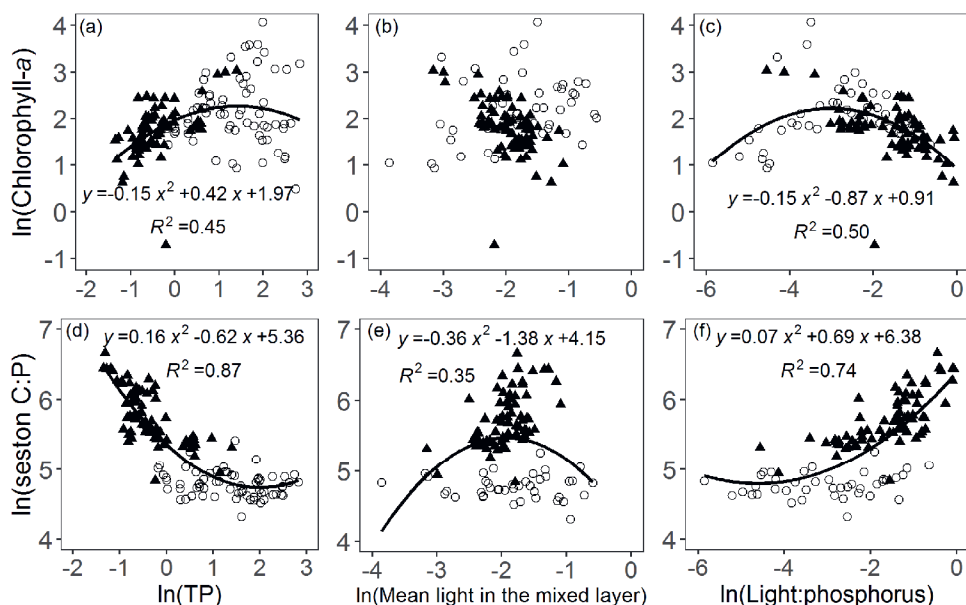


FIGURE 5.5 Effects of the total phosphorous concentration in the water column, mean light in the mixed layer and their ratio on phytoplankton biomass (panels a, b, c; expressed as chlorophyll-*a* concentrations) and phytoplankton quality (panels d, e, f; expressed as seston carbon:phosphorus ratios). Data are depicted for sampling locations inside (open circles) and outside (closed triangles) the Marker Wadden archipelago. Note that for all variables their natural logarithms are plotted, and solid lines (with corresponding formulas) indicate significant (at an alpha level of 0.05) statistical relationships fitted through all datapoints. Statistical details can be found in Table S2.

When analysed separately for the locations inside and outside of Marker Wadden, chlorophyll-*a* concentrations showed a unimodal relationship with TP, mean light in the mixed layer, and light:phosphorus ratio on both locations inside and outside of the archipelago (Fig. S5.3a-c, Fig. S5.4a-c, Table S5.2). No significant relationships between seston C:P ratio and TP (Fig. S5.3d) or mean light in the mixed layer (Fig. S5.3e) were found on locations inside the archipelago, whereas the seston C:P ratio showed a unimodal relationship with TP (Fig. S5.4d) and a linear relationship with mean light in the mixed layer (Fig. S5.4e) outside of Marker Wadden. A unimodal relationship between seston C:P ratio and light:phosphorus

ratio was found inside and outside Marker Wadden (Fig. S5.3f, Fig. S5.4f, Table S5.2).

The availability of light was regulated by the total suspended solids (TSS), inorganic suspended solids (ISS) and organic suspended solids (OSS), which showed strong seasonal dynamics (Fig. S5.5). Generally, TSS, ISS and OSS concentrations were higher inside than outside of the archipelago (Fig. S5.5, Table S5.1).

5.4 | Discussion

Our results demonstrated that the shallow waters inside the Marker Wadden archipelago contained higher nutrient availabilities than the surrounding lake and still sufficient light. This combination increased the quantity and quality of phytoplankton at the base of the aquatic food web, available for further transfer of energy to higher trophic levels. Phytoplankton quality was highest at low light:phosphorus ratios offered by the newly created archipelago, confirming the current light:nutrient hypothesis. We found that phytoplankton quantity was highest at intermediate light:phosphorus ratios, which provides a quantitative extension of the current hypothesis. This puts forward that manipulations of the ratio of light and phosphorus availabilities – following the light:nutrient hypothesis – can be used to increase primary productivity and quality to stimulate transfer to higher trophic levels in downgraded aquatic ecosystems and can be broadly applied in an ecosystem restoration context, on which we further elaborate below.

5.4.1 The light:nutrient hypothesis and phytoplankton biomass

Our results showed that phytoplankton biomass showed a unimodal relationship with TP and TN while no relationship between phytoplankton biomass and light availability was found, which partly supported hypothesis 1a. The unimodal relationship between phytoplankton and TP is consistent with previous studies, showing that phytoplankton and TP relationships are better described by nonlinear and sigmoidal models than log-linear models (Filstrup et al. 2014b, Quinlan et al. 2021). This unimodal relationship could be explained by the low P availability in the accelerating limb, indicating P limitation (Filstrup and Downing 2017), and/or limitation by N (Guildford and Hecky 2000), co-limitation between P and N

(Bracken et al. 2015), or limitation by light (Agusti et al. 1990) in the decelerating limb. In our study, we found that most of the locations in the surrounding lake, outside the Marker Wadden archipelago, grouped along the accelerating limb, which suggests that phytoplankton biomass in the lake was mainly P limited. This is also suggested by the seston N:P ratios outside Marker Wadden, which were generally much higher as compared to the Redfield ratio (i.e. and N:P of 16), suggesting that P may limit phytoplankton growth. The main driver controlling phytoplankton biomass inside the Marker Wadden archipelago is difficult to determine as the sampling points are distributed along the entire light:phosphorus gradient, and showed a unimodal relationship with both TP and light availability. Across the locations inside the Marker Wadden archipelago, the seston N:P ratio was close to 16, which suggests co-limitation of N and P and/or limitation by another factor.

Phytoplankton biomass showed a unimodal relationship with light availability as suggested by previous studies (Bergström and Karlsson 2019). We did not observe a relationship between phytoplankton biomass and light availability across all locations. However, when focussing on the locations inside the Marker Wadden archipelago, we found that phytoplankton biomass followed a unimodal relationship with light availability, while phytoplankton biomass showed a decreasing trend with increasing light availability outside of the archipelago. This suggests that nutrient availability may play a vital role in determining how phytoplankton biomass responds to increasing light availability, at low nutrient availability, phytoplankton growth is limited by nutrients, not light, whereas nutrient limitation may also inhibit the ability of phytoplankton to acclimate to increased light availability (Lewis et al. 2019).

Our findings demonstrate an optimum light and phosphorus availability for biomass build-up, where neither of them is limiting (i.e. an optimal resource ratio), or there is co-limitation. Indeed, we found that phytoplankton biomass showed a unimodal relationship with the ratio of light:phosphorus availability across locations, which supported hypothesis 1b. This unimodal relationship between phytoplankton biomass and light:phosphorus could be explained as follows. At low light:phosphorus, light presumably limits biomass build-up, and at a high light:phosphorus ratio, phosphorus will (primarily) limit biomass build-up. Phytoplankton biomass starts to decline when the light availability is relatively higher compared to phosphorus availability, which may be attributed to P limitation or co-limitation between P and N and possibly light inhibition.

Our results indicate a direct effect of relative light and phosphorus availabilities on phytoplankton biomass and reveal an optimum in the

light:phosphorus ratio for biomass. The existence of such an optimal resource ratio may further be strengthened by a higher phytoplankton diversity, exhibiting overall higher resource use efficiencies (Hillebrand et al. 2014). In contrast, an unbalanced availability of light and phosphorus may decrease phytoplankton diversity through enhanced competition (Cardinale et al. 2009). This in turn is expected to reduce overall resource use efficiencies of the phytoplankton community, which would also contribute to decreased phytoplankton biomass at lower and higher light:phosphorus ratios. While we did not assess phytoplankton diversity, our findings are in line with predicted relationships between phytoplankton biomass and resource ratios driven by their interaction with diversity.

5.4.2 The light:nutrient hypothesis and seston C:P ratio

Our results showed that the seston C:P ratio increased with an increasing light:phosphorus ratio as predicted by the light:nutrient hypothesis, which supported hypothesis 2a. We found that the seston C:P ratio response to TP and light availability varied by sampling locations. Specifically, seston C:P was negatively related to TP and positively related to light availability in the locations outside the Marker Wadden archipelago, as expected under P-limitation (Harpole et al. 2011). Inside Marker Wadden, no relationship between the seston C:P ratio and TP or light was found. Here, phosphorus availability was much higher than outside Marker Wadden, hence, P would not be limiting. This was further confirmed by the seston N:P ratio inside Marker Wadden, which slightly fluctuated around the Redfield ratio of 16 (Fig. S5.1). Therefore, inside Marker Wadden, high P and N concentrations were observed in the water which were at the Redfield ratio, suggesting that both high P and N availability were boosting production, given that enough light was available. As a result, the overall higher P and N concentrations explain a consistently low seston C:P and C:N ratio inside Marker Wadden irrespective of alterations in TP, TN and light availabilities.

The light:nutrient hypothesis has been tested and confirmed by laboratory experiments (Urabe & Sterner, 1996; Striebel et al., 2008) and field studies (Urabe et al., 2002; Hall et al., 2007). Our study provides new support for this hypothesis in a lake restoration context, which suggests that the light:nutrient hypothesis could be a valuable mechanistic framework to guide ecological restoration toward improved phytoplankton biomass and nutritional values.

5.4.3 Effects of ecosystem restoration

Ecosystem restoration resulted in higher TP and TN inside the Marker Wadden archipelago as compared to the surrounding lake. This higher nutrient availability was accompanied with higher phytoplankton biomass and lower seston C:P and C:N, which implies that both phytoplankton biomass and quality for higher trophic levels was improved by the restoration measures, confirming our hypothesis 1a and 2a. The increased TN and TP inside Marker Wadden may be attributed to the higher sediment resuspension rates as indicated by the higher TSS and ISS concentrations inside Marker Wadden, and the fact that the nutrient levels are very high in the lake sediment used for construction leading to higher mobilization and nutrient run-off from the shores (Temmink et al. 2021). The higher sediment resuspension rates inside Marker Wadden may well be attributed to the relatively lower water depth and small particles (i.e. over 50% of particles $<63 \mu\text{m}$; Fig. S7), which is more prone to be affected by wind despite the relatively sheltered conditions compared to the sampling points outside Marker Wadden.

Sediment resuspension may result in higher nutrient availability for phytoplankton growth, as has been demonstrated in lake Markermeer (Brinkmann et al. 2019). Furthermore, bioturbation induced by breeding birds, such as avocets and coots, and benthivorous fish, such as carp, may also have contributed to higher sediment resuspension and higher nutrient availability inside Marker Wadden (Vanni 2002). Following the sediment resuspension process, high TSS causes deteriorated light conditions indicated by a high light attenuation coefficient (Fig. S5.6), which potentially limits the growth of phytoplankton due to low light availability. However, the light availability for the phytoplankton is also mediated by the water depth. The water depth across locations inside the Marker Wadden archipelago ($1.2 \pm 1.0 \text{ m}$) was generally lower compared to the locations outside Marker Wadden ($4.3 \pm 0.2 \text{ m}$). This potentially compensated for the high light attenuation caused by the sediment resuspension process, resulting in a suitable light climate for phytoplankton biomass build-up.

Interestingly, we found that phytoplankton biomass showed an increasing trend inside Marker Wadden from late June to early August while it showed a decreasing trend outside of Marker Wadden (Fig. 5.3a). This corresponded with both a seasonal increase in light availability and temperature (Fig. 5.2c and Fig. S5.6c). The positive effect of temperature on the phytoplankton biomass production thus only occurred where the nutrients are abundant (hence, inside Marker Wadden), while a shortage of nutrient supply might result in a lack of response (as observed

outside Marker Wadden) or even detrimental temperature effects (Verbeek et al., 2018; Schulhof et al., 2019). Moreover, because organisms tend to be more sensitive to external factors in nutrient-poor environments (Finger et al. 2013), the increased light availability during this period may also pose a threat to phytoplankton biomass build-up outside Marker Wadden. Indeed, during the same period, the C:P ratio outside Marker Wadden showed a sharp increasing trend while it was stable across locations inside the Marker Wadden, which further confirms the nutrient shortage for phytoplankton growth, especially P, outside Marker Wadden.

5.4.5 Implications for lake management

Anthropogenic activities are changing the absolute and relative input of nutrients into freshwater ecosystems (Penuelas et al. 2020), thereby affecting the transfer of carbon and nutrients to higher trophic levels. Eutrophication may lead to excessive phytoplankton biomass build-up, and often promotes cyanobacterial blooms at very high P levels (Huisman et al. 2018). Despite the enhanced primary production, the poor nutritional quality and edibility of cyanobacteria can lead to the collapse of the food-web (Ger et al. 2016). To combat eutrophication, oligotrophication following nutrient mitigation measures is increasingly applied as a restoration approach in freshwater systems worldwide (Sabel et al. 2020). However, in many systems, an unintended decline of higher trophic production, like zooplankton (N. John et al. 2005) and fish (Finger et al. 2007), was observed to coincide with nutrient reduction. Nutrient reduction reduces phytoplankton primary production, which increases water transparency, increasing phytoplankton carbon:nutrient ratios. As a result, higher trophic organisms in lake ecosystems may suffer from both food quantity and quality shortage. Therefore, ideally, lake restoration measures are required to achieve both improved water quality and maintain higher trophic production. To achieve this, using the extended light:nutrient hypothesis to establish optimum light:phosphorus ratios, where both the phytoplankton quantity and quality are high, may guide future restoration efforts towards improved transfer of energy and matter in aquatic food webs, aiming to improve the abundance of higher trophic levels, such as fish and piscivorous and benthivorous waterbirds, in downgraded aquatic ecosystems.

Authors' contribution

HJ and ESB designed the experiment; HJ and ESB acquired the data, HJ, ESB, CVL and DBVDW performed the data analysis, and all authors contributed to data interpretation; HJ, ESB, DBVDW, and CVL wrote a first version of the manuscript, LL performed careful editing of versions of the manuscript, and all authors contributed to the final revision of the manuscript. Our research was discussed with local NGO (Natuurmonumenten) to seek feedback on the questions to be tackled and the approach to be considered. Meanwhile, efforts were made to provide suggestions for the management of the future development of Marker Wadden.

Data availability statement

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

Acknowledgements

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Supporting tables

Table S5.1 Results of Welch's t-tests exploring the difference between sampling locations inside the Marker Wadden and outside Marker Wadden on measured parameters. It is indicated in case data were transformed to meet model requirements. Significant *P*-values are indicated in bold.

Dependent variable	Transformation	Mean inside Marker Wadden	Mean outside Marker Wadden	<i>t</i>	df	<i>P</i> -value
TN	Ln	5.32	3.88	8.17	6.74	<0.001
TP	Ln	1.58	-0.17	7.99	5.91	<0.001
Mean light in the mixed layer	Ln	-1.57	-1.91	2.19	4.13	0.091
Chl- <i>a</i>	Ln	2.49	1.93	5.89	5.26	0.002
C:P ratio	Ln	4.81	5.81	-26.87	9.10	<0.001
C:N ratio	Ln	2.11	2.29	-8.27	9.82	<0.001
N:P ratio	Ln	2.69	3.52	-19.2	9.90	<0.001
TSS	Ln	4.80	3.00	7.38	5.21	<0.001
ISS	Ln	4.59	2.43	8.33	5.38	<0.001
OSS	Ln	3.13	2.16	4.92	5.58	0.003
<i>K_d</i>	Ln	1.92	0.60	7.58	4.10	0.001
Temperature	Ln	2.82	2.80	1.40	7.68	0.201

Table S5.2 Regression analyses of relationships based on linear and non-linear fitting models from all sampling locations, sampling locations in Marker Wadden, and sampling locations outside of Marker Wadden. Significant *P*-values are indicated in bold.

Sampling locations	Response variable	Dependent variable	Regression equation	R^2	<i>P</i>	AIC
All sampling location	Ln (Chl- <i>a</i>)	Ln(TP)	$0.23 x + 1.85$	0.38	<0.001	272.9
		Ln(TP)	$-0.15 x^2 + 0.42 x + 1.97$	0.45	<0.001	264.1
		Ln(Light)	$0.04 x + 2.02$	0.03	0.726	249.1
		Ln(Light)	$0.07 x^2 + 0.32x + 2.28$	0.07	0.450	250.6
		Ln(Light:TP)	$-0.12 x + 1.62$	0.25	0.007	209.0
		Ln(Light:TP)	$-0.14 x^2 - 0.87 x + 0.91$	0.51	<0.001	185.0
	Ln (C:P)	Ln(TP)	$-0.42 x + 5.49$	0.82	<0.001	91.7
		Ln(TP)	$0.16 x^2 - 0.62 x + 5.36$	0.87	<0.001	47.0
		Ln(Light)	$0.07 x + 5.50$	0.07	0.477	189.8
		Ln(Light)	$-0.36 x - 1.38 x + 4.15$	0.34	<0.001	178.4
		Ln(Light:TP)	$0.31 x + 6.04$	0.70	<0.001	114.3
		Ln(Light:TP)	$0.07 x + 0.69 x + 6.38$	0.74	<0.001	100.6
Sampling locations inside Marker Wadden	Ln (Chl- <i>a</i>)	Ln(TP)	$-0.06 x + 2.08$	0.07	0.570	150.7
		Ln(TP)	$-0.31 x - 0.86 x + 1.76$	0.28	0.021	147.5
		Ln(Light)	$0.29 x + 2.71$	0.33	0.022	101.8
		Ln(Light)	$-0.23 x - 0.63 x + 1.94$	0.40	0.004	100.6
		Ln(Light:TP)	$0.14 x + 2.49$	0.26	0.112	85.6
		Ln(Light:TP)	$-0.23 x - 1.30 x + 0.59$	0.62	<0.001	70.8
	Ln (C:P)	Ln(TP)	$-0.05 x + 4.86$	0.22	0.081	-32.9
		Ln(TP)	$0.02 x - 0.10 x + 4.88$	0.23	0.066	-31.2
		Ln(Light)	$-0.02 x + 4.74$	0.10	0.525	-21.8
		Ln(Light)	$0.02 x + 0.05 x + 4.80$	0.12	0.443	-20.0
		Ln(Light:TP)	$0.03 x + 4.87$	0.21	0.199	-23.2
		Ln(Light:TP)	$0.02 x + 0.18 x + 5.07$	0.31	0.047	-23.6
Sampling locations outside of Marker Wadden	Ln (Chl- <i>a</i>)	Ln(TP)	$0.46 x + 1.93$	0.51	<0.001	105.4
		Ln(TP)	$0.07 x + 0.48 x + 1.90$	0.51	<0.001	107.0
		Ln(Light)	$-0.81 x + 0.21$	0.54	<0.001	107.3
		Ln(Light)	$0.27 x + 0.31 x + 1.33$	0.55	<0.001	107.8
		Ln(Light:TP)	$-0.33x + 1.25$	0.54	<0.001	100.0
		Ln(Light:TP)	$0.03 x - 0.19 x + 1.34$	0.54	<0.001	101.4
	Ln (C:P)	Ln(TP)	$-0.47 x + 5.58$	0.72	<0.001	18.1
		Ln(TP)	$0.21 x - 0.42 x + 5.50$	0.76	<0.001	10.5
		Ln(Light)	$0.54 x + 6.76$	0.52	<0.001	44.6
		Ln(Light)	$0.09 x + 0.91 x + 7.12$	0.53	<0.001	46.3
		Ln(Light:TP)	$0.29 x + 6.17$	0.71	<0.001	16.3
		Ln(Light:TP)	$0.07 x + 0.58 x + 6.39$	0.75	<0.001	9.5

Supporting figures

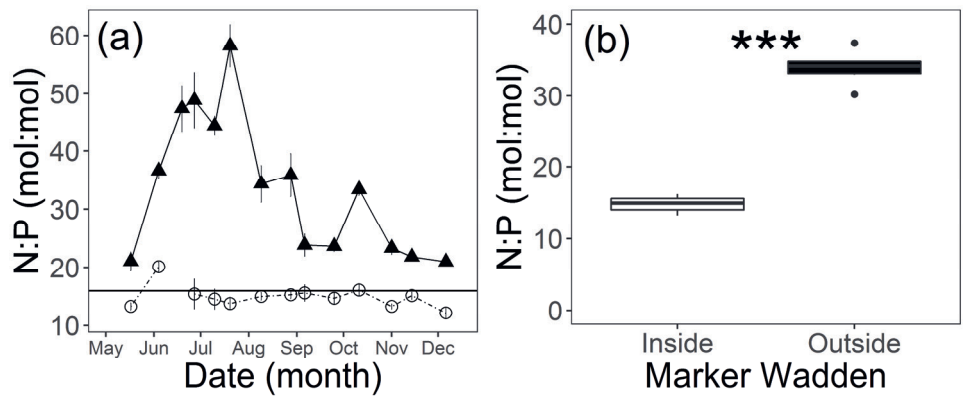


FIGURE S5.1 Seston N:P molar ratio (a), mean N:P ratio (b) over the year (May-December 2018) inside (open circles) and outside (closed triangles) the Marker Wadden archipelago. Values represent the means \pm SE (n=6). The solid line represents the Redfield ratio N:P =16, indicating the switchpoint between N and P limitation in aquatic systems, with >16 indicating limitation of P (Redfield 1958).

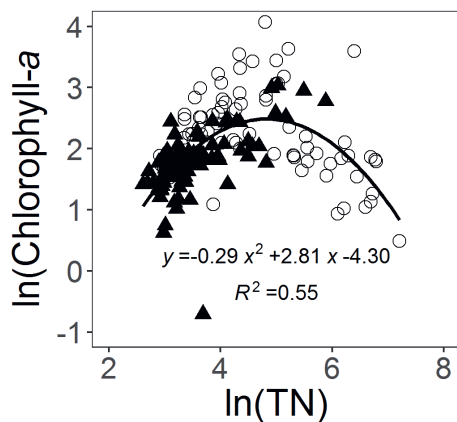


FIGURE S5.2 The relationship between phytoplankton biomass (\ln) and total nitrogen (\ln). The open circle represents the sampling locations inside Marker Wadden. The closed triangle represents the sampling locations outside Marker Wadden.

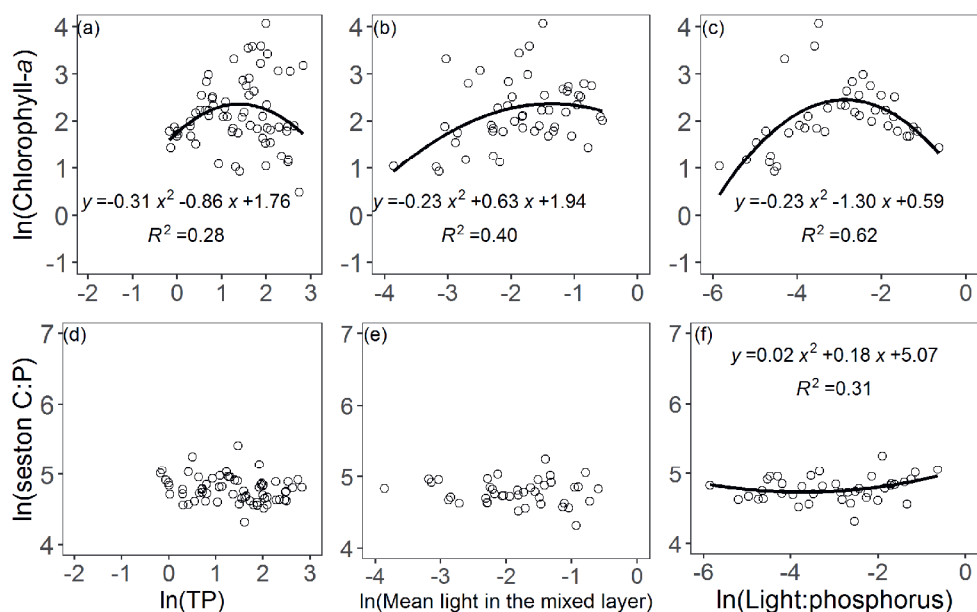


FIGURE S5.3 Effects of the total phosphorous concentration in the water column, mean light in the mixed layer and their ratio on phytoplankton biomass (panels a, b, c; expressed as chlorophyll-*a* concentrations) and phytoplankton quality (panels d, e, f; expressed as seston carbon:phosphorous ratios). Data are all from sampling locations inside the Marker Wadden archipelago. Note that for all variables their natural logarithms are plotted, and solid lines (with corresponding formulas) indicate significant (at an alpha level of 0.05) statistical relationships fitted through all datapoints.

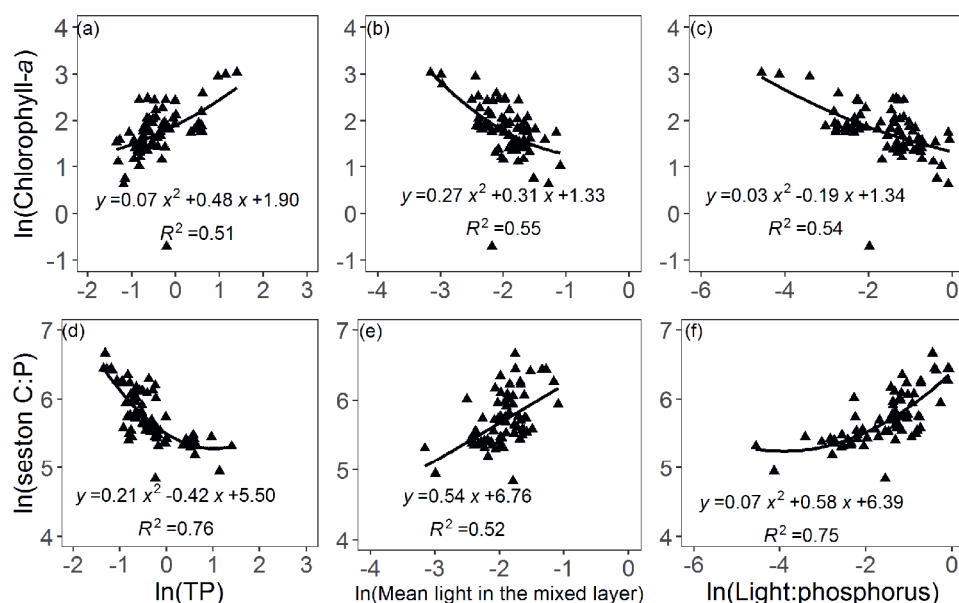


FIGURE S5.4 Effects of the total phosphorous concentration in the water column, mean light in the mixed layer and their ratio on phytoplankton biomass (panels a, b, c; expressed as chlorophyll-*a* concentrations) and phytoplankton quality (panels d, e, f; expressed as seston carbon:phosphorous ratio). Data are from sampling locations outside the Marker Wadden archipelago. Note that for all variables their natural logarithms are plotted, and solid lines (with corresponding formulas) indicate significant (at an alpha level of 0.05) statistical relationships fitted through all datapoints outside Marker Wadden.

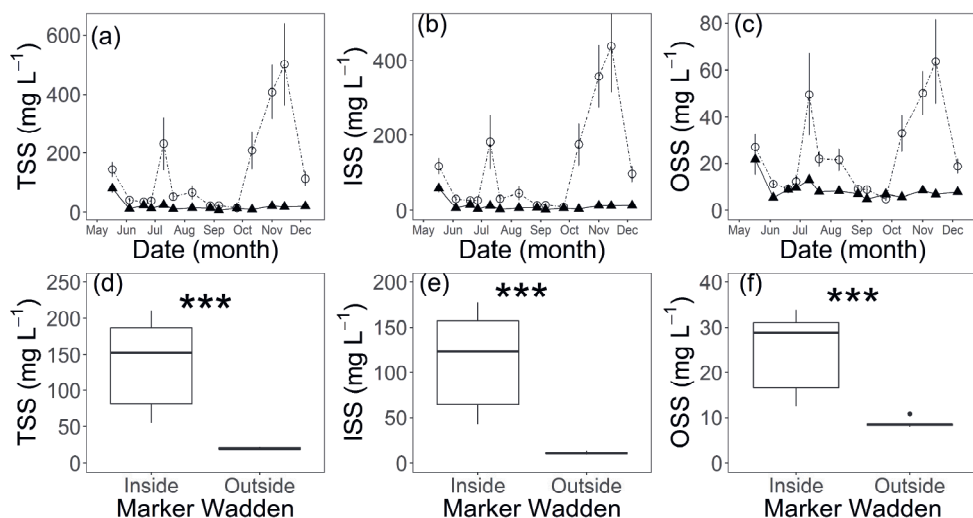


FIGURE S5.5 Total suspended solids (TSS) (a), inorganic suspended solids (ISS) (b), organic suspended solids (c) dynamics, mean TSS (d), mean ISS (e), and mean OSS (f) inside (open circles) and outside (closed triangles) the Marker Wadden archipelago across the duration of the study. Values represent the means \pm SE (n=6). The asterisks indicate a significant difference at $P < 0.001$.

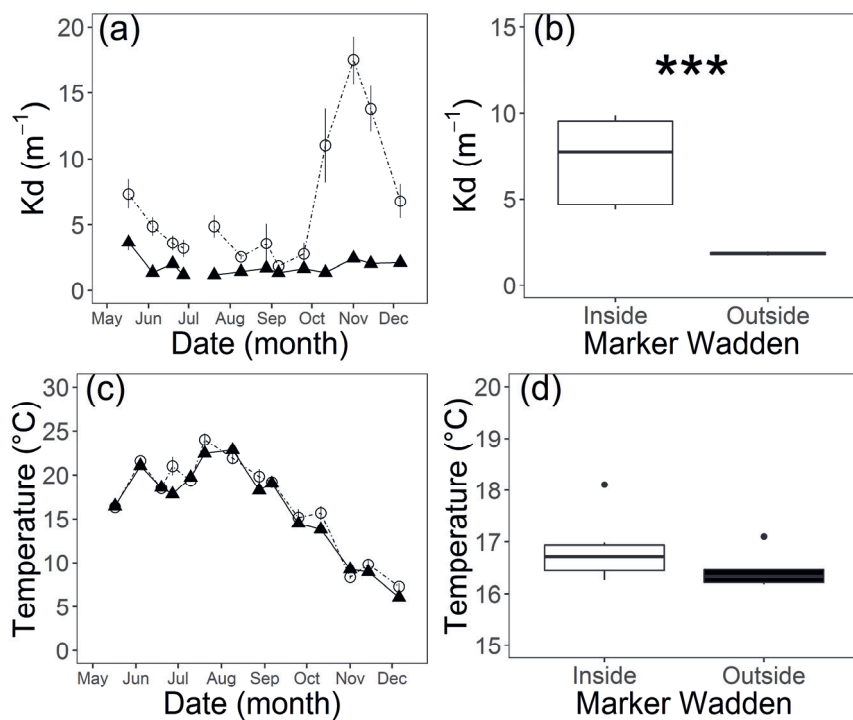


FIGURE S5.6 Light vertical attenuation coefficient (K_d) (a), mean K_d (b), surface water temperature (c) and mean temperature (d) inside (open circles) and outside (closed triangles) Marker Wadden across the duration of the study. Values represent the means \pm SE ($n=6$). The asterisks indicate a significant difference at $P < 0.001$.

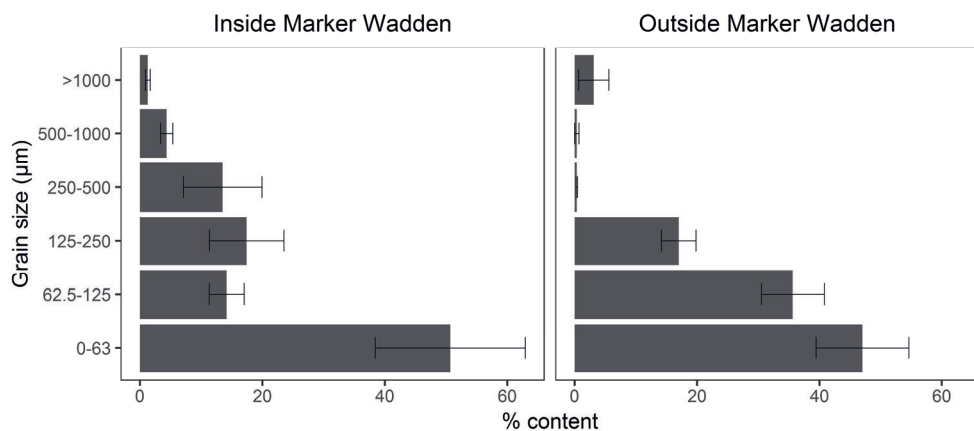


FIGURE S5.7 The sediment grain size distribution. Values represent means \pm SE ($n=6$). Sediment samples were freeze-dried and sieved through a one mm sieve, sediment larger than one mm was weighed, while the remaining sediment grain size distribution was measured by laser diffraction on a Malvern Mastersizer 2000 (McCave et al. 1986).



Chapter 6

The relative availability of light and phosphorus affect phytoplankton biomass and quality with cascading effects on higher trophic levels

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Elisabeth S. Bakker

Abstract

The trophic transfer of energy and matter from primary producers to higher trophic levels is a fundamental aspect of food web functioning. The amount of energy and matter that can transfer to higher trophic levels, especially the herbivores, depends on the quantity and quality of primary producers, which is fundamentally determined by the availability of light and nutrients. This suggests that the abundance of the herbivore community may also vary predictably with environmental light and nutrient availability. Here, we applied the light:nutrient hypothesis to assess how changes in the relative availabilities of light and phosphorus affect higher trophic levels in a large-scale lake restoration project, the “Marker Wadden” (the Netherlands). Marker Wadden is a newly built archipelago aimed to increase the abundance of fish and waterbirds which have been declining for decades in lake Markermeer by strengthening the food web from its base. We focused on the edible phytoplankton size fraction (i.e. $<30\ \mu\text{m}$), and determined consequent shifts in food quantity and quality as well as zooplankton biomass along a gradient of light:nutrient availabilities. We found that both the quantity (as indicated by the chlorophyll-*a* concentrations) and quality (as indicated by the phosphor:carbon (P:C) ratio) of the edible phytoplankton fraction showed a unimodal function with an optimum at intermediate and lowest light:total phosphorous (TP) ratios in the water column, respectively. We also found that the total zooplankton biomass showed an optimum at intermediate light:TP ratios and thereby largely followed phytoplankton biomass. Moreover, we found that different zooplankton taxa exhibited specific optima along the light:TP gradient. Specifically, copepod biomass was highest at low light:TP ratios, while cladocerans peaked at intermediate and rotifers at high light:TP ratios. This is likely driven by their differences in nutritional demands as well as feeding strategy. These results demonstrate that the relative availability of light and phosphorus affect phytoplankton biomass and quality, and that these effects cascade to higher trophic levels.

6.1 | Introduction

The trophic transfer of energy and matter from primary producers to higher trophic levels is a fundamental aspect of food web functioning (Lindeman 1942), influencing food-chain length (Frost et al. 2006), productivity (McCauley et al. 2018) and ecosystem services such as fisheries yields (Chassot et al. 2010, Finstad et al. 2014). The amount of energy and matter that can transfer to higher trophic levels depends on the quantity and quality of primary producers, which is fundamentally determined by the availability of light and nutrients (Hessen et al. 2002, 2013, Sterner and Elser 2002). Primary producer quantity (i.e. biomass) is determined by the absolute availabilities of both resources (Elser et al. 2007, Gruner et al. 2008), and typically increases with higher light and nutrient availability. Also the relative availability of both resources may affect primary producer biomass, as balanced input of two resources may support higher species diversity and thereby enhance resource use efficiencies and community productivity (Hillebrand et al. 2014). Moreover, the relative availabilities of light and nutrients determine primary producer elemental composition, and thereby their nutritional quality for higher trophic levels (Sterner et al. 1997, Sterner and Elser 2002). Specifically, the primary producer carbon:phosphorus (C:P) stoichiometry is expected to increase with a higher availability of light relative to phosphorus, following the light:nutrient hypothesis (Sterner et al. 1997). Through the impact on quantity and quality of primary producers, the absolute and relative availabilities of light and nutrients also determine primary producer-herbivore interactions (Hillebrand et al. 2009). High phytoplankton C:P ratios, for example caused by an increase in the availability of light relative to phosphorus, can form a stoichiometric bottleneck for zooplankton and lead to reduced growth and reproduction (Sterner et al. 1998, Dickman et al. 2008, Hessen et al. 2013). This suggests that the abundance of the herbivore community may also vary predictably with environmental light and nutrient availability.

Zooplankton taxa such as copepods, cladocerans, and rotifers have different nutrient requirements. While, cladocerans and rotifers generally have relatively high phosphorus demands and are therefore more prone to phosphorus limitation, copepods tend to have lower phosphorus demands and may become more easily nitrogen limited (Andersen and Hessen 1991, Rothhaupt 1995, Schulz and Sterner 1999). Besides, the feeding strategy of zooplankton also varies with taxa. For instance, most cladocerans are herbivorous species, while for copepods there are herbivorous, planktivorous and omnivorous species (Hart and Bychek 2011). Such

differences in feeding strategies may determine how species respond to changes in food quality and quantity. Filter feeders such as *Daphnia*, for example, have a limited potential to select for higher quality food, making them more susceptible to lowered food quality irrespective of the availability of food (Boersma and Kreutzer 2002). Copepods exhibit diverse feeding strategies and may selectively feed on the most abundant and/or highest quality food (Wootton 2017). Rather than on autotrophs, they may preferentially feed on animal prey with a stable and lower carbon:nutrient ratio (i.e., cladocerans and/or rotifers) than on algal food with flexible and mostly higher carbon:nutrient ratios (Van de Waal et al. 2010), as has been observed in other aquatic omnivores (Dorenbosch and Bakker 2011, Zhang et al. 2018). As a result, Copepods may be prone to be regulated by food quality and only consume phytoplankton with low carbon:nutrient ratios (e.g., Zhang et al. 2018).

In earlier work, we extended the light:nutrient hypothesis to explain not only the variation in phytoplankton C:P ratios, but also primary producer biomass along natural gradients in light and phosphorus availabilities (Chapter 5). We confirmed the light:nutrient hypothesis, showing that total phytoplankton C:P ratios closely followed the light:total phosphorus availability in the water. Moreover, we demonstrated that total phytoplankton biomass was highest at intermediate light:phosphorus ratios, where biomass production is neither limited by light or phosphorus (Chapter 5; Fig. 6.1a). Here, we applied the extended light:nutrient hypothesis to assess how changes in the relative availabilities of light and phosphorus affect higher trophic levels. To this end, we focused on the edible phytoplankton size fraction (i.e. $<30\ \mu\text{m}$), and determined consequent shifts in food quantity and quality as well as zooplankton biomass along a gradient of light:nutrient availabilities. We hypothesized zooplankton biomass to 1a) follow edible phytoplankton biomass given food quantity is the main determinant (Fig. 6.1b; dark orange), 1b) follow edible phytoplankton biomass but with higher biomass when food quality is high due to the complementary effect of higher food quality (Fig. 6.1b; light orange), and 2) show distinct optima across taxonomic groups driven by food quantity, quality or feeding strategy (Fig. 6.1c).

To test our hypotheses, we performed a field study at the Marker Wadden from May to December 2018. The Marker Wadden is an artificial archipelago in the eutrophic shallow lake Markermeer, constructed to provide bird and fish habitat, and improve water quality (van Leeuwen et al. in press; Chapter 5). We measured chlorophyll-*a* concentrations, seston nutrient:carbon stoichiometry, nutrient concentrations in the water column, light availability in the mixed layer in and around the Marker Wadden

archipelago, representing a gradient in absolute and relative light and nutrient availabilities, and tested their relationships with the biomass and composition of major zooplankton groups.

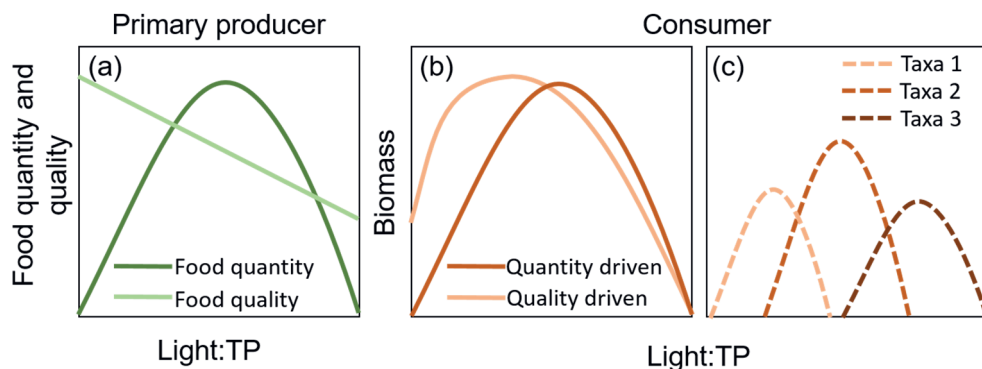


Figure 6.1. Conceptual overview of the extended light:nutrient hypothesis showing the relationships between food quantity (siston Chl-*a*, dark green) and quality (P/C ratio, light green) (a), and anticipated changes in zooplankton biomass(b). If food quantity drives zooplankton biomass production, zooplankton biomass production follows the food quantity dynamics (b, dark orange); If both food quantity and quality drive zooplankton production, the zooplankton biomass production will not very low at the low light:TP ends and peak at lower light:TP where light may potentially limit phytoplankton biomass, which may be attributed to the compensation effect of high food quality (b, light orange), and differential responses of zooplankton taxa (c).

6.2 | Methods

6.2.1 Study site

Covering an area of 680 km², Lake Markermeer (the Netherlands) is among the largest shallow lakes in Western Europe. The lake is a Natura2000 area under the European bird directive and has experienced declines in benthivorous and piscivorous birds over the last decades, as well as in fish abundance (Noordhuis 2014). To improve the ecological integrity of this lake and increase the numbers of fish and birds, a large-scale ecosystem restoration project called the “Marker

Wadden” started in 2016. This project aimed to construct an archipelago of islands spread across an area of about 700 ha in the northeastern part of Lake Markermeer (52°35'02.8"N 5°21'55.5"E). The archipelago consists of five islands protruding several meters above the water level and an underwater landscape with varied water depths and littoral zones.

6.2.2 Field sampling

We chose 12 sampling locations, with six distributed within the Marker Wadden archipelago and six distributed outside the Marker Wadden archipelago, to represent a gradient in absolute and relative light and nutrient availabilities. All 12 locations were sampled every two weeks from the 17th of May to the 6th of December 2018 (see also Chapter 5). Before the depth-integrated water samples were taken from each sampling location, light intensity just below the water surface, below the water surface at 50 cm and 100 cm depth were measured using a UW Quantum light sensor (LI-COR Environmental GmbH, Bad Homburg, Germany). A depth-integrated water sample was taken from three discrete water depths (i.e. near the top, middle and close to the bottom of the mixed layer) with a 5 L LUWITEC water sampler. 15 L water was collected from each depth, then mixed in a 45 L plastic tub. After that, water samples were taken from the tub for later analysis of chlorophyll-*a* concentrations, nutrient concentrations (TP), seston elemental composition (P:C and N:C ratio), and zooplankton community composition and biomass. In this study, we used the edible part (size fraction < 30 µm) of the chlorophyll-*a* concentrations and seston carbon:nutrient ratio as a proxy of food quantity and quality for zooplankton (Haney 1973, Cyr and Curtis 1999), respectively. The edible food quantity and quality were measured by sieving the water subsamples through 30 µm mesh, and then processing the samples as we describe below.

6.2.3 Laboratory analyses

Chlorophyll-a concentrations

To determine the chlorophyll-*a* concentrations, 10-144 mL water subsamples (filtration volumes were dependent on the particle content of the water) were filtered on GF/F filters (Whatman, Maidstone, U.K.) and stored at -20°C. After thawing, the filters were extracted with 80% ethanol in an 80°C water bath, thereafter a further filtration through 0.2 µm PTFE Membrane filter was performed and chl-*a* concentrations were measured by High Performance Liquid Chromatography

(HPLC, UltiMate 3000, Thermo Scientific, Waltham Massachusetts, United States). Chlorophyll-*a* concentrations were also measured by means of chlorophyll-*a* fluorescence. Chlorophyll-*a* fluorescence was measured on a Phyto-PAM (Heinz Walz GmbH, Effeltrich, Germany), using a 0.2 µm filtered water subsamples for background correction. Linear regression of the HPLC chl-*a* data versus Phyto-PAM data confirmed a significant relationship ($y=0.25x + 3.02$, $R^2=0.60$, $n=171$, Fig. S6.1) that was used to calculate chlorophyll-*a* concentrations from the fluorescence signal.

Seston elemental composition

To determine the food quality in terms of nutrient:carbon ratio, we here focused on the edible fraction (size fraction < 30 µm) of the seston (Haney 1973, Cyr and Curtis 1999). Data on the total seston fraction was obtained from earlier work (Chapter 5). 10-110 mL water subsamples were filtered over a pre-washed and pre-weighed GF/F (Whatman, Maidstone, UK), dried at 60°C overnight, and then weighed. To determine C and N concentrations of the seston, we extracted two disk of 5.55 mm diameter of the dried whatman filters using a hole puncher. The two disk were thereafter folded together into a tin cup (Elemental Microanalysis, Okehampton, UK) and analyzed for particulate C and N on a FLASH 2000 NC elemental analyzer (Brechtbuhler Incorporated, Interscience B.V., Breda, The Netherlands). The remainder of the filter was combusted in a Pyrex glass tube at 550°C for 30 min. Subsequently, we added 5 mL of persulfate (2.5%) to the glass tube, after which the samples were autoclaved for 30 min at 121°C. Digested P (as PO_4^{3-}) was measured on a QuAAtro39 Auto-Analyzer (SEAL Analytical Ltd., Southampton, UK).

Zooplankton biomass

Crustacean samples were collected by filtering 30 L of depth-integrated water samples through an 80-µm mesh size net, while rotifer samples were collected by filtering 1 L of depth-integrated samples through a 30-µm mesh size net, after which the samples were fixed with alkaline Lugol's iodine solution in the field.

Zooplankton specimens were counted using a stereomicroscope (Leica M205C, Germany). Rotifers and cladocerans were determined to genus level, whereas copepods were divided in two main groups (Calanoida and Cyclopoida). Copepod *nauplii* were counted, but not distinguished taxonomically. The cladoceran and copepod biomasses were estimated after measuring 30 individuals (provided there were enough individuals to allow this) of each genus and using published length-weight relationships (Dumont et al. 1975, Bottrell et al. 1976). The total rotifer

biomass was estimated by extracting empirical individual dry weight from the literature (Dumont et al. 1975, Bottrell et al. 1976, Ejsmont-Karabin 1998), then multiplied by the density.

6.2.4 Data analysis

To test for the relationships between phytoplankton biomass (chl-*a*), seston quality (P:C ratio), total zooplankton biomass, and biomass of different zooplankton taxa, with $\ln(\text{TP})$, $\ln(\text{mean light in the mixed layer})$ and $\ln(\text{light:TP ratio})$ as explanatory variables, we fitted linear as well as quadratic models assessing possible positive, negative or unimodal functions (i.e. an optimum). We fitted the models using the `nls`-function from the 'stats' package in R, and performed model selection among only the significant models based on Akaike Information Criteria (Akaike 1974). We only presented the functions that best describe these relationships.

To assess differences between the locations inside and outside of the Marker Wadden archipelago in edible phytoplankton biomass, seston elemental composition, total zooplankton biomass, and the biomass of different zooplankton taxa, we first averaged values per sampling location over the sampling season ($n=6$ inside, $n=6$ outside). We then confirmed normality of all parameters after natural log transformation using Shapiro-Wilks, and assessed homogeneity of variances using Levene's tests. We present statistical comparisons based on Welch's *t*-tests in case of unequal variances (all results were confirmed by non-parametric alternatives, not shown). All statistical analyses were conducted using R version 3.5.1 (R Core Team 2021).

To compare how phytoplankton quantity (i.e chl-*a*) and quality (P:C ratio), total zooplankton biomass, and biomasses of different zooplankton taxa (copepods, cladocerans, and rotifers) response to the gradient of $\ln(\text{light:TP})$, data mentioned before was normalized by divided their maximum value.

6.3 | Results

The edible phytoplankton biomass (expressed as chlorophyll-*a* concentration) increased with increasing TP, while it showed a unimodal function with light and light:TP ratios (Fig. 6.2 a,b,c; Table S6.1). Similar to phytoplankton quantity, the quality of the edible phytoplankton size fraction (expressed as the P:C ratio)

increased with TP following a unimodal function (Fig. 6.2d). Total zooplankton biomass largely followed the patterns in phytoplankton quantity and quality, with a unimodal function with TP, light, and light:TP ratios (Fig. 6.2 g,h,i; Table S6.1).

Part of the variation in light:nutrient ratios and the consequent food quality, quantity and thereby zooplankton biomass was driven by the differences between sampling locations inside and outside the Marker Wadden archipelago. For example, the edible phytoplankton biomass was generally 1.9-fold higher at locations inside the Marker Wadden archipelago compared to those outside (Fig. S6.2, Table S6.3). Similarly, the quality of the edible phytoplankton fraction P:C and N:C ratios were generally 2.2-fold and 1.1-fold higher at locations inside the Marker Wadden archipelago compared with those outside of the Marker Wadden archipelago (Fig. S6.3, Table S6.3), respectively. Total zooplankton biomass was generally 3.9-fold higher at locations inside the Marker Wadden archipelago compared to those outside of the Marker Wadden archipelago (Fig. S6.4, Table S6.3).

The various zooplankton taxonomic groups showed distinct responses to the absolute and relative light and nutrient availabilities. Specifically, copepods biomass increased with increasing TP and decreased with light:TP ratios while it showed a unimodal function with light (Fig. 6.3, Table S6.2). Cladocerans and rotifer biomasses showed a unimodal function with TP and light:TP ratios (Fig. 6.3 d,f,g,i, Table S6.2). Rotifer biomass showed a unimodal function with light while no relationship between cladoceran biomass and light was been found (Fig. 6.3 e,h, Table S6.2). Total copepods, cladocerans, and rotifers biomasses were generally 5.8-, 2.7-, and 3.1-fold higher at locations inside the Marker Wadden archipelago compared to those outside of the Marker Wadden archipelago (Fig. S6.5, Table S6.3), respectively.

Edible phytoplankton biomass, phytoplankton quality, total zooplankton biomass and different zooplankton taxa (copepods, cladocerans, and rotifers) reach their maxima or minima at different values of light availability, TP, and light:TP ratio (Table S6.4).

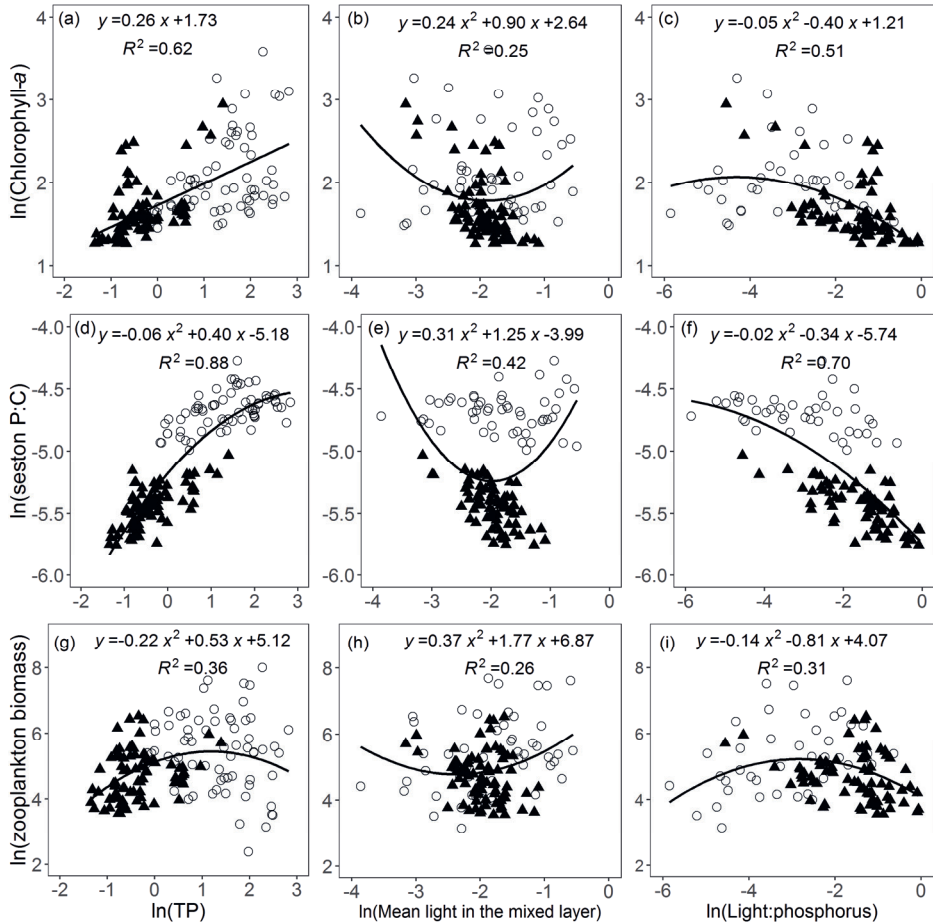


Figure 6.2. Relationship between edible phytoplankton biomass and the total phosphorus concentration in the water column (a), mean light in the mixed layer (b) and their ratio (c); Relationship between edible phytoplankton quality (expressed as seston phosphorus:carbon ratio) and the total phosphorus concentration in the water column (d), mean light in the mixed layer (e) and their ratio (f); Relationship between total zooplankton biomass and the total phosphorus concentration in the water column (g), mean light in the mixed layer (h) and their ratio (i). Data are depicted for sampling locations inside (open circles) and outside (closed triangles) the Marker Wadden archipelago. Note that for all variables their natural logarithms are plotted, and solid lines (with corresponding formulas) indicate significant (at an alpha level of 0.05) statistical relationships fitted through all datapoints.

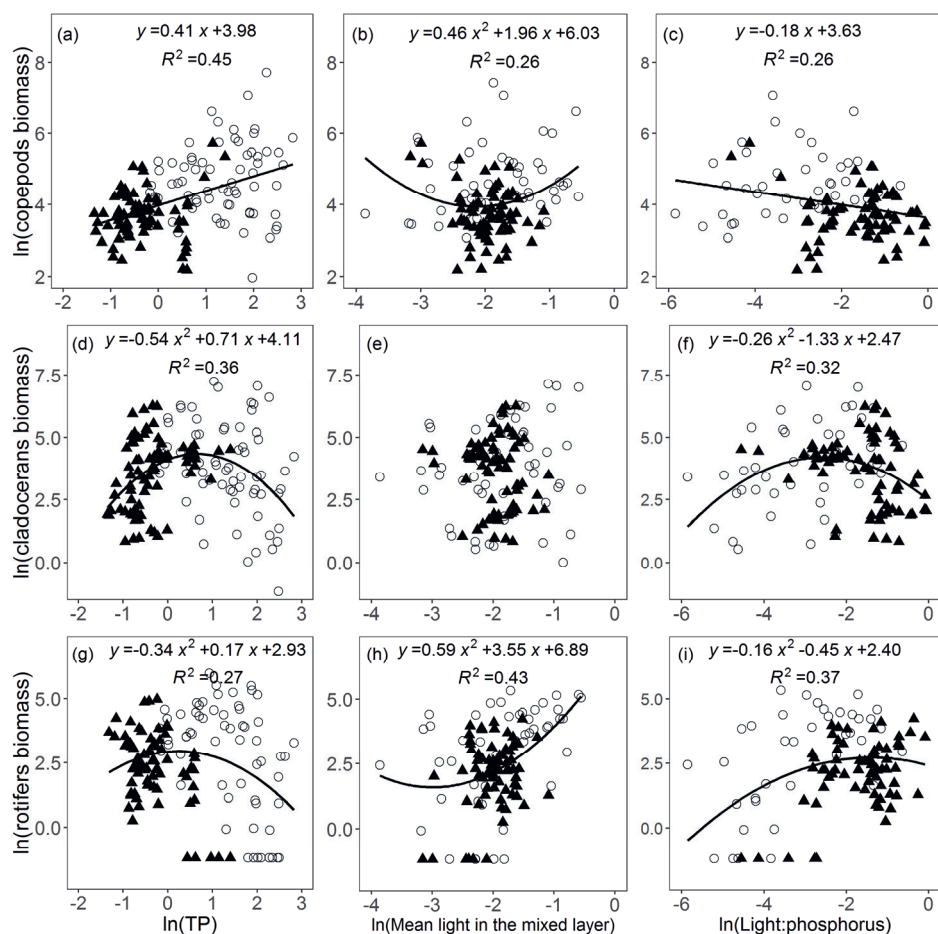


Figure 6.3. Relationship between copepods biomass and the total phosphorus concentration in the water column (a), mean light in the mixed layer (b) and their ratio (c); Relationship between cladocerans biomass and the total phosphorus concentration in the water column (d), mean light in the mixed layer (e) and their ratio (f); Relationship between rotifers biomass and the total phosphorus concentration in the water column (g), mean light in the mixed layer (h) and their ratio (i). Data are depicted for sampling locations inside (open circles) and outside (closed triangles) the Marker Wadden archipelago. Note that for all variables their natural logarithms are plotted, and solid lines (with corresponding formulas) indicate significant (at an alpha level of 0.05) statistical relationships fitted through all datapoints.

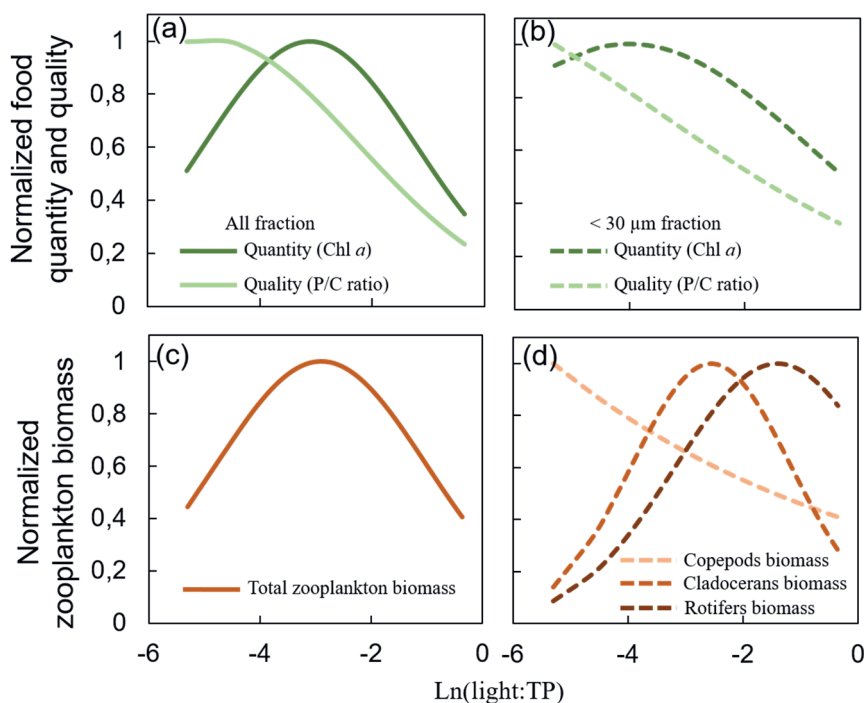


Figure 6.4. Normalized relationship between all fraction food quantity (Chl-*a*, solid dark green line), food quality (P/C ratio, solid light green line) and $\ln(\text{light:TP})$ (data was obtained from Chapter 5) (a); Normalized relationship between edible food quantity (Chl-*a*, dash dark green line), food quality (P/C ratio, dash light green line) and $\ln(\text{light:TP})$; Normalized relationship between total zooplankton biomass and $\ln(\text{light:TP})$; Normalized relationship between different zooplankton taxa and $\ln(\text{light:TP})$ (d).

6.5 | Discussion

We found that both the quantity (as indicated by the chlorophyll-*a* concentrations) and quality (as indicated by the P:C ratio) of the edible phytoplankton fraction showed a unimodal function with an optimum at intermediate and lowest light:TP ratios, respectively. Also the total zooplankton biomass showed an optimum at intermediate light:TP ratios and thereby largely followed phytoplankton biomass, thus supporting hypothesis 1a. In line with hypothesis 2, the different zooplankton

taxa exhibited specific optima along the light:TP gradient. Specifically, copepod biomass was highest at low light:TP ratios, while cladocerans peaked at intermediate and rotifers at high light:TP ratios. These results demonstrate that the relative availability of light and phosphorus affect phytoplankton biomass and quality, and that these effects cascade to higher trophic levels. Interestingly, taxonomic groups show differential responses that may possibly depend on their elemental demands and feeding strategy.

6.5.1 Effects of light:TP availability on primary producers quantity and quality

Phytoplankton quantity showed a unimodal relationship along a light:TP gradient, with a maximum at light:TP with a value of -4.0 on a ln scale. This optimum may result from intermediate resource ratios where light and phosphorus are either non-limiting or co-limiting, with potential light limitation at lower light:TP ratios and phosphorus limitation at higher light:TP ratios. In addition, intermediate resource ratios may also enhance phytoplankton diversity that will support community resource use efficiencies and may ultimately lead to higher biomass production (Cardinale et al. 2009, Mazancourt and Schwartz 2010). Interestingly, the smaller phytoplankton fraction (i.e. <30 μm) could attain a higher quantity both at low and high light:TP ratios compared to the whole fraction (Fig. 4b). This may be attributed to the high light and phosphorus use efficiency of small phytoplankton at low and high light:TP, respectively (Litchman et al. 2007, Finkel et al. 2010). For example, small phytoplankton experience less self-shading through a packaging effect of pigments as compared to larger species (Kirk 1975, Malerba et al. 2018), and smaller species have higher surface-to-volume ratios enhancing their nutrient uptake affinity (Litchman et al. 2007, Fiksen et al. 2013). Therefore, the smaller phytoplankton fraction could maintain relatively higher standing biomass at light or phosphorus availabilities that are potentially limiting for larger sized phytoplankton. Besides, at low light:TP ratios, small sized phytoplankton may profit from the high copepod biomass. Copepods may preferentially feed on large phytoplankton particles (Sommer et al. 2001), thereby releasing smaller sized phytoplankton from competition.

6.5.2 Effects of light:TP ratio on zooplankton biomass at a community level

Total zooplankton biomass followed the phytoplankton biomass of the total fraction, showing a unimodal function with light:TP availability with an optimum in the same range of phytoplankton, thereby supporting our hypothesis 1a. At both the lowest and highest light:TP ratios, total zooplankton biomass build-up is presumably limited by the phytoplankton biomass. At high light:TP ratios, zooplankton biomass may furthermore be limited by the low food quality. In contrast to our hypothesis 1b, the higher food quality at low light:TP ratios could apparently not compensate for the lower food quantity, as we did not see the anticipated higher zooplankton biomass at the low light:TP ends and peak earlier at lower light:TP where light may potentially limit phytoplankton biomass. Intermediate light:TP conditions seem to result in optimal conditions for zooplankton, with the highest food quantity and intermediate food quality. In our study, total zooplankton biomass mainly consists of copepods and cladocerans (Fig. S6.5). The edible seston C:N ratios vary between 6.8 ± 0.3 - 10.0 ± 0.4 , which are lower than the threshold ratios of copepods (7.3 - 11.5) (Anderson et al. 2021), suggesting copepods growth is limited by food quantity. Besides, the edible seston C:P ratios vary between 92.1 ± 3.9 - 279.6 ± 8.1 , which are lower than the threshold of *Daphnia* (i.e., 150 - 385 , depends on the species) (Urabe and Watanabe 1992, Shimizu and Urabe 2008, Khatkhat et al. 2018), indicating cladocerans growth may not be limited by food quality, especially since other cladocerans, such as *Bosmina* and *Chydorus*, have even lower P demands compared to *Daphnia* (Moody and Wilkinson 2019). While food quality was therefore presumably not limiting, it is unclear from our results to what extent food quantity played a role in determining overall zooplankton biomass.

Furthermore, at low light:TP ratios, high POC concentrations may be attributed to the sediment resuspension process. On one hand, it could directly increase organic carbon concentrations in the water due to the high organic carbon content in the sediment. On the other hand, the high sediment composition in the seston may facilitate bacteria production by providing substrate and carbon sources when phytoplankton biomass build-up is limited by the light (Fig. S6.6). Although some zooplankton can directly consume bacteria, most zooplankton are inefficient bacterial grazers (Vaqué and Pace 1992, Faithfull et al. 2011). Besides, bacteria are generally considered to be poor food quality, as they lack sterols and essential fatty acids required by zooplankton for production (Brett and Müller-Navarra 1997, Martin-Creuzburg et al. 2011). Consequently, the high edible POC availability at

low light:TP ratios may not necessarily promote the zooplankton biomass build-up as found in our study.

6.5.3 Effects of light:TP ratio on zooplankton biomass at a taxa level

The various zooplankton taxonomic groups showed differential responses to the light:TP gradient. Copepod biomass decreased with light:TP ratios, while cladocerans peaked at intermediate and rotifers at high light:TP ratios. These differences among zooplankton taxa responses to light:TP ratios may be attributed to the essential differences in body nutrient content (Sterner et al. 1997). Copepods have relatively high N and low P demand for their development (Sterner and Schulz 1998, Elser and Urabe 1999), therefore their biomass build-up may less be regulated by food quality (as indicated by the edible seston P:C ratios). However, we found that copepod biomass closely followed the food quality dynamics, rather than that of food quantity. This may result from their preference for animal prey with relative stable carbon:nutrient ratios. In contrast, cladocerans and rotifers generally have a high P demand (Sterner and Elser 2002), which suggests their biomass build-up may be more regulated by food quality. However, we found that both cladocerans and rotifers followed the phytoplankton biomass dynamics closer than the phytoplankton quality and peaked at intermediate and high light:TP ratios, respectively. The observation that cladocerans biomass peaked at lower light:TP ratio compared to rotifers may be attributed to their higher nutrient demands (Sterner et al. 1997). The peak growth rates of herbivores that have high phosphorus demands should occur at lower light:phosphorus ratios than those of herbivores that have lower phosphorus demands (Sterner and Schulz 1998, Hill et al. 2010, Sikora et al. 2016), thereby reaching their highest biomass production at a lower light:phosphorus ratio.

The difference in responses among zooplankton taxa to light:TP ratios may also be driven by exploitative competition (Hill et al. 2010). Copepods can vary in feeding strategy with herbivorous, planktivorous and omnivorous species (Hart and Bychek 2011). This makes them as a group superior competitors for food compared to cladocerans and rotifers. Thus, at low light:TP when primary production is low, they may adaptively feed on other zooplankton taxa (i.e. cladocerans and/or rotifers) (Wootton 2017). With the declining copepod biomass following increases in light:TP ratios, cladocerans and rotifers may be released from predation pressure. For cladocerans and rotifers, both taxa could be classified as filter feeder, and their feeding ability is expected to depend on body size according to the size-efficiency

hypothesis (Brooks and Dodson 1965, Hall et al. 1976, Gianuca et al. 2016). This indicates that large-bodied cladocerans are better food competitors than small-bodied rotifers, which may explain why they have a maximum biomass at lower light:TP ratios. With further increases in light:TP ratios, cladoceran biomass build-up may become limited by the low food quantity and quality. While this may also limit rotifer biomass build-up, it seems so to a lesser extent, and food quantity and quality are apparently sufficiently high to maintain some rotifer biomass.

Differences in zooplankton biomass may also be linked to differences in sampling locations. We observed that copepod, cladoceran, and rotifer biomass was generally higher at locations inside the Marker Wadden archipelago compared to those outside of the Marker Wadden archipelago. This may be attributed to the higher food quantity (as indicated by the edible phytoplankton biomass, Fig. S6.1) and better quality (as indicated by the edible seston P:C and N:C ratios, Fig. S6.2) inside the Marker Wadden archipelago compared with those outside of the Marker Wadden archipelago. The improved food quantity and quality may be attributed to enhanced nutrients availability within the archipelago due to sediment resuspension (Chapter 5). Besides, zooplankton at the locations inside the Marker Wadden archipelago may also benefit from the reduced wind-induced turbulence, which may enhanced zooplankton food detection or capture, or directly prevent body damage (Peters and Marrasé 2000, G. -Tóth et al. 2011), compared to the conditions outside of the Marker Wadden archipelago. Furthermore, those newly created habitat inside the Marker Wadden may harbor less fish in its initial stage, resulting higher zooplankton biomass inside the Marker Wadden compared with those outside of Marker Wadden archipelago due to low fish predation pressures (Hessen et al. 2006, Carpenter et al. 2016).

In conclusion, our study shows that consumer biomass at the community level mainly related to primary producer quantity, while predominant consumer taxa respond differentially to a combination of primary producer quantity and quality. This is likely driven by their differences in nutritional demands as well as feeding strategy. This indicates that the relative availability of light and nutrients could fundamentally determine primary producer quantity and quality, and that such shifts in resource ratios will alter zooplankton biomass and species composition.

Supporting information

Supporting tables

Table S6.1 Regression analyses of relationships based on linear and non-linear fitting models from all sampling locations. Significant *P*-values are indicated in bold.

Response variable	Dependent variable	Regression equation	R^2	<i>P</i>	AIC
Ln(Chl- <i>a</i>)	Ln(TP)	$0.26 x + 1.73$	0.62	<0.001	128.3
	Ln(TP)	$0.0004 x^2 + 0.26 x + 1.73$	0.62	<0.001	130.3
	Ln(Light)	$-0.04 x + 1.78$	0.05	0.610	190.9
	Ln(Light)	$0.24 x^2 + 0.90 x + 2.64$	0.25	0.004	184.7
	Ln(Light:TP)	$-0.16 x + 1.44$	0.47	<0.001	104.4
	Ln(Light:TP)	$-0.05 x^2 - 0.40 x + 1.21$	0.51	<0.001	100.0
Ln(POC)	Ln(TP)	$0.58 x + 5.01$	0.86	<0.001	130.5
	Ln(TP)	$0.19 x^2 + 0.33 x + 4.86$	0.91	<0.001	77.6
	Ln(Light)	$-0.52 x + 4.17$	0.45	<0.001	226.5
	Ln(Light)	$0.37 x^2 + 0.94 x + 5.50$	0.54	<0.001	213.3
	Ln(Light:TP)	$-0.45 x + 4.17$	0.87	<0.001	76.0
	Ln(Light:TP)	$0.08 x^2 - 0.05 x + 4.55$	0.89	<0.001	53.1
Ln(P:C)	Ln(TP)	$0.32 x - 5.23$	0.86	<0.001	-36.4
	Ln(TP)	$-0.06 x^2 + 0.40 x - 5.18$	0.88	<0.001	-50.4
	Ln(Light)	$0.005 x - 5.13$	0.01	0.942	131.6
	Ln(Light)	$0.31 x^2 + 1.25 x - 3.99$	0.42	<0.001	109.3
	Ln(Light:TP)	$-0.21 x - 5.62$	0.69	<0.001	38.5
	Ln(Light:TP)	$-0.02 x^2 - 0.34 x - 5.74$	0.70	<0.001	37.5
Ln(total zooplankton biomass)	Ln(TP)	$0.25 x + 4.94$	0.27	0.001	409.7
	Ln(TP)	$-0.22 x^2 + 0.53 x + 5.12$	0.36	<0.001	402.7
	Ln(Light)	$0.28 x + 5.51$	0.17	0.064	354.7
	Ln(Light)	$0.37 x^2 + 1.77 x + 6.87$	0.26	0.003	351.1
	Ln(Light:TP)	$-0.07 x^2 + 4.78$	0.09	0.321	309.0
	Ln(Light:TP)	$-0.14 x^2 - 0.81 x + 4.07$	0.31	<0.001	300.8

Table S6.2 Regression analyses of relationships based on linear and non-linear fitting models from all sampling locations for different zooplankton taxa. Significant *P*-values are indicated in bold.

Response variable	Dependent variable	Regression equation	R^2	<i>P</i>	AIC
Ln(copepods biomass)	Ln(TP)	$0.41 x + 3.98$	0.45	<0.001	381.6
	Ln(TP)	$-0.03 x^2 + 0.45 x + 0.001$	0.45	<0.001	383.4
	Ln(Light)	$0.13 x + 4.36$	0.08	0.378	351.7
	Ln(Light)	$0.46 x^2 + 1.96 x + 6.03$	0.26	0.002	345.0
	Ln(Light:TP)	$-0.18 x + 3.63$	0.26	0.005	293.4
	Ln(Light:TP)	$-0.05 x^2 - 0.46 x + 3.37$	0.28	<0.001	293.8
Ln(cladocerans biomass)	Ln(TP)	$0.02 x + 3.67$	0.02	0.855	555.7
	Ln(TP)	$-0.54 x^2 + 0.71 x + 4.11$	0.36	<0.001	538.1
	Ln(Light)	$0.13 x + 3.91$	0.05	0.601	486.1
	Ln(Light)	$0.13 x^2 + 0.63 x + 4.36$	0.06	0.486	487.9
	Ln(Light:TP)	$0.01 x^2 + 3.75$	0.01	0.945	423.0
	Ln(Light:TP)	$-0.26 x^2 - 1.33 x + 2.47$	0.32	0.001	412.7
Ln(rotifers biomass + 0.3)	Ln(TP)	$-0.30 x + 2.68$	0.19	0.031	538.1
	Ln(TP)	$-0.34 x^2 + 0.17 x + 2.93$	0.27	0.001	534.4
	Ln(Light)	$1.16 x + 4.68$	0.39	<0.001	438.2
	Ln(Light)	$0.59 x^2 + 3.55 x + 6.89$	0.43	<0.001	435.2
	Ln(Light:TP)	$0.41 x + 3.27$	0.33	0.001	390.8
	Ln(Light:TP)	$-0.16 x^2 - 0.45 x + 2.40$	0.37	<0.001	389.0

Table S6.3 Results of t-test exploring the difference between sampling locations inside the Marker Wadden and outside Marker Wadden on measured parameters. It is indicated in case data were transformed to meet model requirements. Significant *P*-values are indicated in bold.

Dependent variable	Transformation	Mean inside Marker Wadden	Mean outside Marker Wadden	<i>t</i>	df	<i>P</i> -value
Chl- <i>a</i>	Ln	2.36	1.75	6.34	5.97	<0.001
P:C ratio	Ln	-4.66	-5.42	19.9 6	7.46	<0.001
N:C ratio	Ln	-2.06	-2.17	6.37	9.83	<0.001
Total zooplankton biomass	Ln	6.25	4.99	5.88	6.09	0.001
Total cladocerans biomass	Ln	5.23	4.30	4.26	7.27	0.003
Total copepods biomass	Ln	5.56	3.97	5.87	5.61	0.001
Total rotifers biomass	Ln	4.07	2.98	6.70	7.51	<0.001

Table S6.4. Edible phytoplankton biomass (expressed as chlorophyll-*a* concentration), edible phytoplankton quality (expressed as the P:C ratio), total zooplankton biomass, different zooplankton taxa reach their maxima/minima at different scale of light, TP, and light:TP.

Parameters	status	Predictor	Ln scale	No transformation
Ln(Chl- <i>a</i>)	Minima	Light	-1.9	0.15
	Maxima	Light:TP	-4.0	0.02
Ln(P:C ratio)	Maxima	TP	3.3	27.11
	Minima	Light	-2.0	0.14
	Maxima	Light:TP	-8.5	0.0002
Ln(zooplankton biomass)	Maxima	TP	1.2	3.32
	Minima	Light	-2.4	0.09
	Maxima	Light:TP	-2.9	0.06
Ln(copepods biomass)	Minima	Light	-2.1	0.12
Ln(cladocerans biomass)	Maxima	TP	0.7	2.01
	Maxima	Light:TP	-2.6	0.07
Ln(rotifers biomass)	Maxima	TP	0.3	1.35
	Minima	Light	-3	0.05
	Maxima	Light:TP	-0.4	0.67

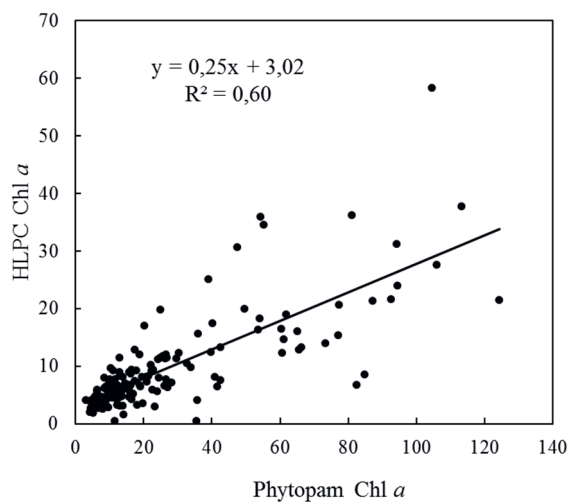


Figure S6.1. Linear regression of the HPLC Chl-*a* data versus Phyto-PAM data.

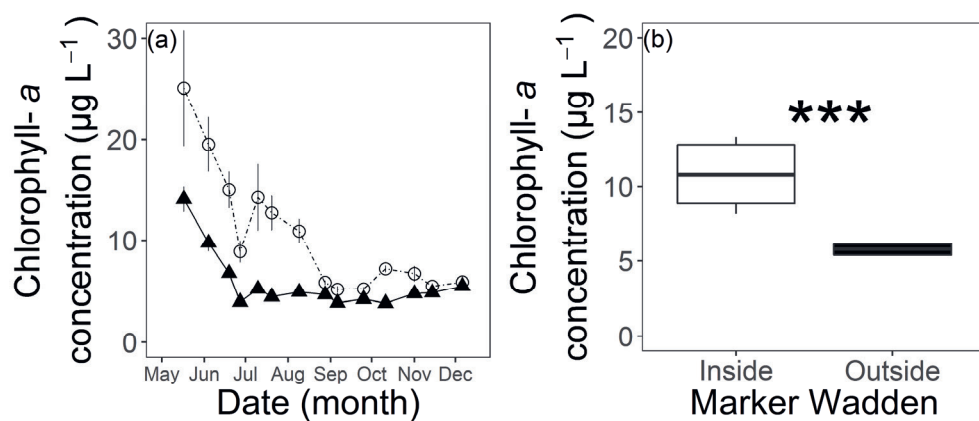


Figure S6.2. Seasonal variation in edible phytoplankton biomass (Chlorophyll-*a*) (a) and mean phytoplankton biomass (b) inside (open circles) and outside (closed triangles) the Marker Wadden archipelago for the duration of the study. Values represent the means \pm SE ($n=6$). *** represents $P < 0.001$.

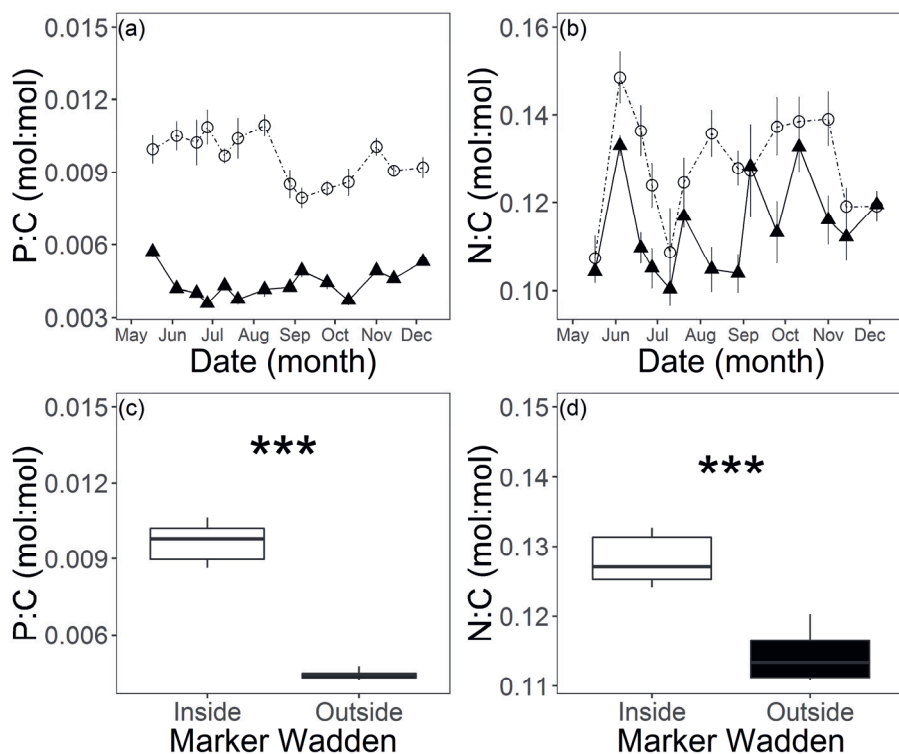


Figure S6.3. Seasonal variation in seston quality P:C ratio (a), N:C ratio (b), mean P:C ratio (c) and mean N:C ratio (d) inside (open circles) and outside (closed triangles) the Marker Wadden archipelago for the duration of the study. Values represent the means \pm SE ($n=6$). *** represents $P < 0.001$.

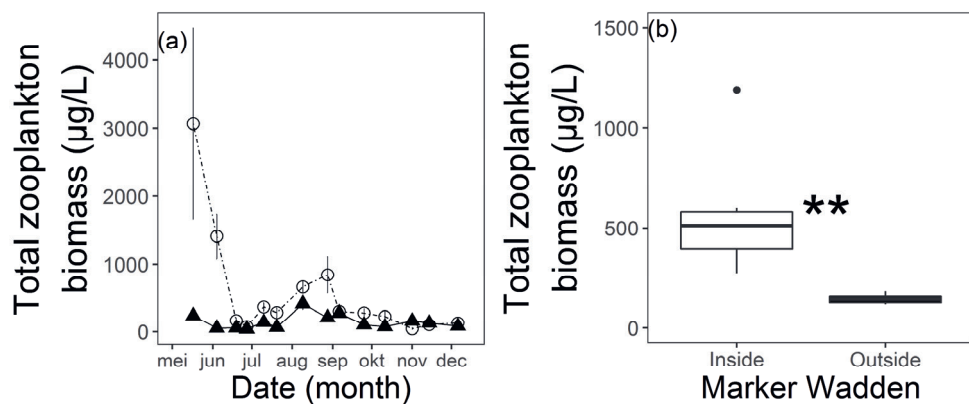


Figure S6.4. Seasonal variation in total zooplankton biomass (a) and mean zooplankton biomass (b) inside (open circles) and outside (closed triangles) the Marker Wadden archipelago for the duration of the study. Values represent the means \pm SE ($n=6$). ** represents $P < 0.01$.

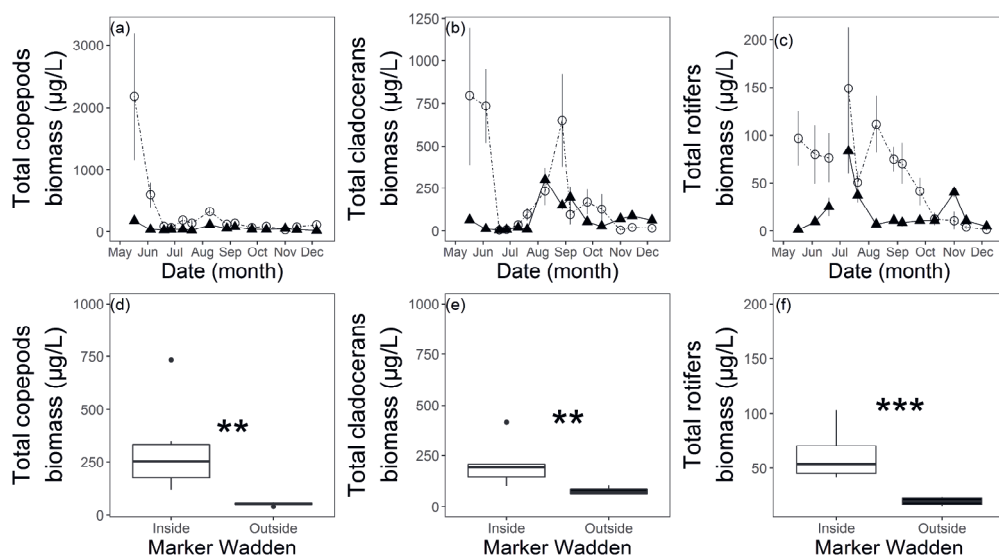


Figure S6.5. Seasonal variation in total copepods biomass (a), total cladocerans biomass (b), total rotifer biomass (c); mean total copepods biomass (d), mean total cladocerans biomass (e), and total rotifer biomass (f) inside (open circles) and outside (closed triangles) the Marker Wadden archipelago for the duration of the study. Values represent the means \pm SE ($n=6$). ** represents $P < 0.01$. *** represents $P < 0.001$.

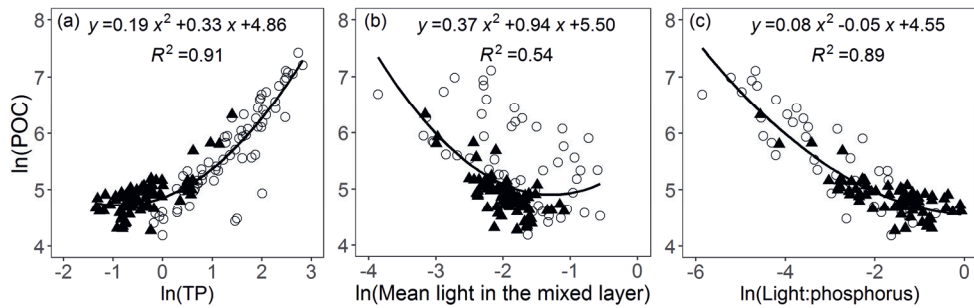


Figure S6.6. Relationship between particulate organic carbon concentrations and the total phosphorus concentration in the water column (a), mean light in the mixed layer (b) and their ratio (c). Data are depicted for sampling locations inside (open circles) and outside (closed triangles) the Marker Wadden archipelago. Note that for all variables their natural logarithms are plotted, and solid lines (with corresponding formulas) indicate significant (at an alpha level of 0.05) statistical relationships fitted through all datapoints.



Chapter 7

General discussion

Shallow lake ecosystems are the dominant types of lakes worldwide (Downing et al. 2006), and provide many important ecosystem services such as drinking water supply and food provisioning (Delpla et al. 2009, Qin et al. 2010). However, lake ecosystems are suffering from severe ecological degradation attributed to multiple anthropogenic stressors, such as climate change, land-use intensification, eutrophication, acidification, water abstraction, morphological alterations, and invasive species (Smol 2019, Dudgeon 2019, Heino et al. 2021). To counteract the degradation of lake ecosystems, great efforts have been done worldwide, mainly by means of single-stressor abatement approaches (Spears et al. 2021a). In particular, nutrient load reduction is a frequently applied restoration measure in aquatic ecosystems (Schindler et al. 2016). While it has been proven successful in reducing phytoplankton biomass and cyanobacterial blooms in many cases, nutrient reductions can also cause unintended declines of higher trophic production (such as fish and water birds) (Finger et al. 2007, Van Riel et al. 2019). Hence, the desired goals of single-stressor abatement approaches could be counteracted by unintended side effects. The potential effects of other key factors in lake ecosystems, such as wind-induced sediment resuspension, hydromorphological modifications and pollution, can have confounding effects during restoration measures but are often overlooked in shallow lake restoration efforts (Carrick et al. 1993, Bachmann et al. 1999, Tammeorg et al. 2013, EEA 2018). Therefore, nature-based multiple stressor management is needed to improve lake ecological status and to maintain their ecosystem services (Spears et al. 2021a).

In this thesis, I studied an innovative lake restoration approach which is based on such a multiple-stressor intervention strategy: the Marker Wadden project in lake Markermeer, The Netherlands. Marker Wadden is a 1000-ha man-made archipelago consisting of five islands with natural shorelines and sheltered waters, aiming to stimulate the development of a littoral zone that is currently largely lacking due to the presence of basalt dikes surrounding most of lake Markermeer (Chapter 2). The goal of Marker Wadden is to create a bird and fish paradise by stimulating the aquatic food web development bottom-up. In my thesis, my aim is to understand whether the Marker Wadden can support higher trophic levels via bottom-up development of the food web and an increase in trophic transfer, thereby achieving the overall goal of the restoration project. In my thesis, I tested the following overarching hypotheses:

- 1) Creating shelter against wind will increase trophic transfer between phytoplankton and zooplankton in shallow lakes by decreasing the suspended solids concentration;

- 2) Creating shelter against wind will increase trophic transfer by supporting habitat for more types of primary producers, which in turn can support a higher consumer diversity and biomass;
- 3) Creating littoral zones will increase nutrient availability coupled with improved light availability which increases primary producer quantity and quality, thereby stimulating the food web bottom-up and increasing trophic transfer.

In my thesis, I combined different approaches ranging from laboratory experiments and field mesocosm experiments to field monitoring to test these hypotheses. Based on the results from all different chapters, I will discuss my findings in a broader context. First, I will discuss the effects of shelter in shallow lakes with a focus on trophic transfer. Second, I will place my findings in the context of future lake restoration and management.

7.1 Shelter effects on trophic transfer

The trophic transfer of energy and matter from primary producers to higher trophic levels is a fundamental aspect of food web functioning (Lindeman 1942) and an important aspects of the Marker Wadden restoration project. Trophic transfer influences many ecological attributes such as the food-chain length (Frost et al. 2006) and productivity (McCauley et al. 2018). This implies that restoration measures targeting trophic transfer can be powerful approaches, with consequences for the ecological integrity of aquatic systems as well as the ecosystem services they can provide (such as fisheries yields, Chassot et al., 2010; Finstad et al., 2014). In shallow lakes that are lacking shelter, wind-induced resuspension of lake sediments can hamper this important process of trophic transfer to higher trophic levels, and lead to declines in higher trophic levels such as observed in lake Markermeer. Lake Markermeer is strongly affected by the wind due to its overall shallowness and large surface areas with long fetch lengths (Kelderman et al. 2012a). Due to the wind, suspended solid concentrations in the lake ranged from 4 to 368 mg L⁻¹ from 1999-2016, with an annual average of 45 mg L⁻¹ (Kelderman et al. 2012a, 2012b). These high suspended solids concentrations in the water column are assumed to limit primary production and trophic transfer, with negative consequences for higher trophic levels in the food web (Van Riel et al. 2019). Marker Wadden is expected to

reduce this negative effect caused by wind-induced mixing. To achieve this goal, the Marker Wadden archipelago is built with stone dikes and sand dunes on the windward side (west) to provide shelter, but open structures on the east side where sediment can settle in calm shallow waters. This is aimed to stimulate primary production and enhance trophic transfer on the lee side of those structures, where light availability is expected to increase due to lower concentrations of suspended solids.

7.1.1 Shelter can reduce the suspended solids concentration

High amounts of suspended solids in the water column interfere with nutrient and light availability for phytoplankton production (Schallenberg and Burns 2004), and can lower the food quantity available for transfer to higher trophic levels. Furthermore, trophic transfer itself may become impaired because zooplankton filter feeders may be hampered by high concentrations of suspended sediments in the water column (Koenings et al. 1990, Kirk and Gilbert 1990). Therefore, shelter could increase trophic transfer by reducing the suspended solids concentration. Indeed, this is confirmed by our lab experiment (Chapter 3) and mesocosm field experiment (Chapter 4), where the results showed that reduced mixing of the water column reduced suspended solid concentrations in the water column, facilitated zooplankton biomass build-up (Chapter 3) and shelter enhanced trophic transfer efficiency between phytoplankton and zooplankton (Chapter 4). Although zooplankton may benefit from the sediment resuspension process due to higher food availability from increased benthic algae and microorganism abundances following the sediment resuspension process (Schallenberg and Burns 2004) and decreased overall mortality caused by visually hunting fish as a result of increased turbidity (Vinyard and O'Brien 1976), these positive effects may be countered, at least partially, by the negative effects caused by sediment resuspension. These negative effects are mechanical interference with food intake (Levine et al. 2005), decreased food assimilation (Arruda et al. 1983) and making the zooplankton individuals heavier (Zurek 1983). Our results suggest that the positive effects caused by sediment resuspension are overridden by the negative effects. However, differences among lakes, such as in water depth and wind fetch, may eventually determine how zooplankton respond to sediment resuspension, and thereby the trophic transfer efficiency between phytoplankton and zooplankton.

7.1.2 Shelter effects on the diversity of primary producers

The littoral zone on Marker Wadden was expected to increase trophic transfer by supporting habitat for more types of primary producers, which in turn can support a higher consumer diversity and biomass. Our results confirmed the arrival of more types of primary producers in response to the creation of Marker Wadden (Fig. 7.1; personal observations C.H.A. van Leeuwen, 2021). More than just providing shelter, I also found that shelter had significant effects on the interaction among different types of primary producers by changing physical, chemical, and biological conditions in the water column. Specifically, the provisioning of shelter favored benthic algae (Chapter 3) and submerged macrophytes (Chapter 4). The dominance of these primary producers under sheltered conditions may be attributed to several factors. First, more light may have become available deeper in the water column following the settlement of the suspended solids, which is line with former research (Hansson, 1992; Fork et al., 2020). Second, benthic algae and macrophytes may be released from competition with phytoplankton for nutrients, because more nutrients remain stored in the sediment. These nutrients are only accessible for benthic algae or macrophytes, providing a relative advantage over phytoplankton. Third, shelter may directly facilitate the colonization of benthic algae or macrophytes as it may prevent them from wind induced shear stress and physical disturbance of the sediment (Jupp and Spence 1977, Keddy 1983, Schutten et al. 2005, Van Zuidam and Peeters 2015).

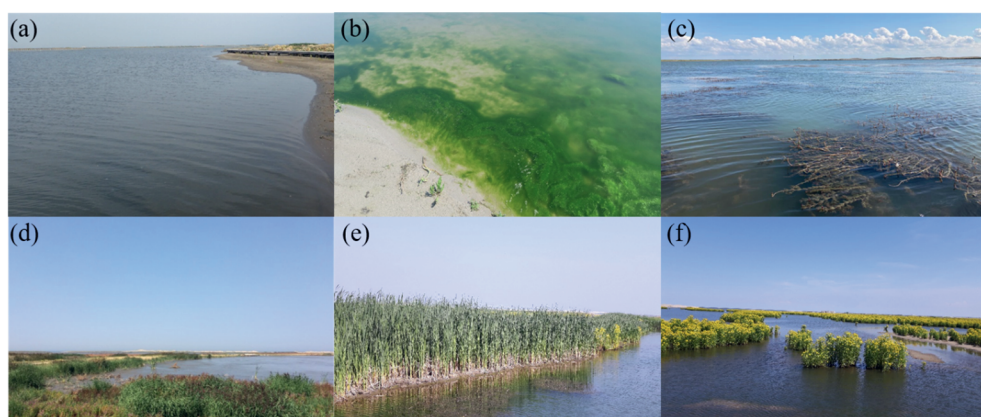


Figure 7.1. Littoral zone with different types of primary producers: (a) phytoplankton, (b) benthic algae, (c) submerged macrophytes *Myriophyllum*

spicatum, (d) Common reed *Phragmites australis*, (e) Broadleaf *Typha latifolia*, (f) Marsh fleawort *Tephrosia palustris* inside of Marker Wadden.

7.1.3 Improving quantity and quality of primary producers for herbivores by increasing nutrients and light

The littoral zones on the leeside of Marker Wadden were hypothesized to stimulate primary production for several reasons. One important assumption was that the gradual land-water transitions offered by the islands would increase runoff of nutrients from land to water. This is confirmed by our 2018 field study, where we showed that the nutrient concentrations at the leeside inside Marker Wadden were higher as compared to the locations outside Marker Wadden (Chapter 5). Moreover, we also expected lower suspended solid concentrations within the Marker Wadden archipelago because of more shelter. Yet, we found higher suspended solids concentrations on locations inside of Marker Wadden (the sheltered sites) compared to those outside of Marker Wadden (the exposed sites), while we did not observe a significant difference in light availability among these sites (Chapter 5). These observations contradict our expectations, and are not in line with our lab (Chapter 3) and field experimental results (Chapter 4) and the basin survey (Chapter 2, two of the basins), where we showed that shelter significantly reduced the suspended solids concentration in the water column. The higher sediment resuspension rates inside Marker Wadden may well be attributed to the relatively lower water depth and small particles (i.e. over 50% of particles <63 µm), which are more prone to be affected by wind despite the relatively sheltered conditions compared to the sampling points outside Marker Wadden (exposed sites). Besides, bioturbation induced by breeding birds, such as avocets and coots, and benthivorous fish, such as carp, may also have contributed to the higher sediment resuspension inside Marker Wadden (Vanni, 2002; van Altena et al., 2016). I note, however, that our field survey was conducted in 2018, which is the third year of the project and during this year extensive engineering work was performed at the Marker Wadden. The engineering work caused frequent disturbances of the sediment, which may have masked the sheltering effect of the Marker Wadden. Therefore, I expect that the shelter effects of Marker Wadden will strengthen and become visible over time after the engineering related disturbances stop. Indeed, during calm days in 2021, the water inside Marker Wadden already showed very high transparency, with visibility over one meter into the water column (personal observations, C.H.A. van Leeuwen, 2021). After the

engineering part of the Marker Wadden project is completed further field studies are possible. By monitoring the light availability and suspended solids concentration inside and outside Marker Wadden, it is possible to assess whether Marker Wadden contribute to the settlement of suspended solids and thereby the improvement of light availability.

Despite the possible influence of the engineering work on nutrient availabilities, I do expect that runoff from the land may increase the nutrient availability in the water column over time. With the development of emergent vegetation, the amount of organic material that decomposes or flushes into the water will increase. Furthermore, the amount of birds that the islands attract may import nutrients from elsewhere that may end up in the water column eventually. However, based on my results, it is hard to estimate how much nutrients in the water column are derived from runoff. Yet, I expect that the importance of the contribution of the runoff from the land to the overall nutrient availability in the water column will increase over time as the sediment within the littoral zones becomes more stable and solid due to the development of benthic algae and submerged macrophyte communities and thus nutrient release from suspended sediment will decline. The contribution of run-off relative to sediment resuspension and atmospheric deposition, may be assessed in future studies, for example by using stable isotope tracers, which may now become possible as the engineering stage of the first islands is completed.

Following the enhanced nutrient availabilities, I found that phytoplankton quantity and quality as food for herbivores on locations inside Marker Wadden were higher compared to those outside of Marker Wadden (Chapter 5). The enhanced phytoplankton quantity and quality increased zooplankton biomass (Chapter 6). Following the increased zooplankton biomass, high fish densities can be expected to develop. The presence of several species of fish was confirmed by surveys in 2018 and 2019, which showed that 19 different species used the newly created littoral zones (Van Emmerik and de Laak 2019, Van Emmerik 2020). The higher phytoplankton and zooplankton biomass, and the observation of the presence of fish suggests that the shelter provided by Marker Wadden could increase trophic transfer efficiency by improving the quantity and quality of primary producers. Future fish surveys should establish to what extent the Marker Wadden contributes to fish stocks, also taking into account the foraging by birds.

7.1.4 Increasing food web complexity

In the previous sections, I confirmed that shelter can increase trophic transfer by 1) reducing suspended solids concentrations (Fig. 7.2b①), 2) supporting diverse types of primary producers (Fig. 7.2b②), and 3) improving the quantity and quality of primary producers through nutrient and light enhancement (Fig. 7.2b③). Besides these three main mechanisms, in Chapter 4, I found that shelter also facilitated invertebrates such as gastropods. The high gastropod density in the sheltered treatments may be attributed to high food availability. I have shown that benthic algae (Chapter 3) or macrophytes (Chapter 4) were the dominant primary producers under sheltered conditions, which both could be grazed by gastropods (Schuler et al. 2020, Chen et al. 2020, Liu et al. 2021). Moreover, higher macrophyte biomass under the sheltered conditions can not only serve as food and thereby directly benefit gastropods, but can also function as substrate to support periphyton growth, further provisioning food for gastropods (Ferguson et al. 2021). Furthermore, the gastropods may also directly benefit from the calm conditions in the sheltered treatments as wind induced turbulence may increase their mortality and/or dislodgement (Brown and Quinn 1988, Etter 1989). These findings suggest that shelter may result in higher food web complexity (Fig. 7.2b④), offering alternative pathways that together may stimulate higher trophic levels, from zooplankton and macrofauna all the way up to fish and waterbirds.

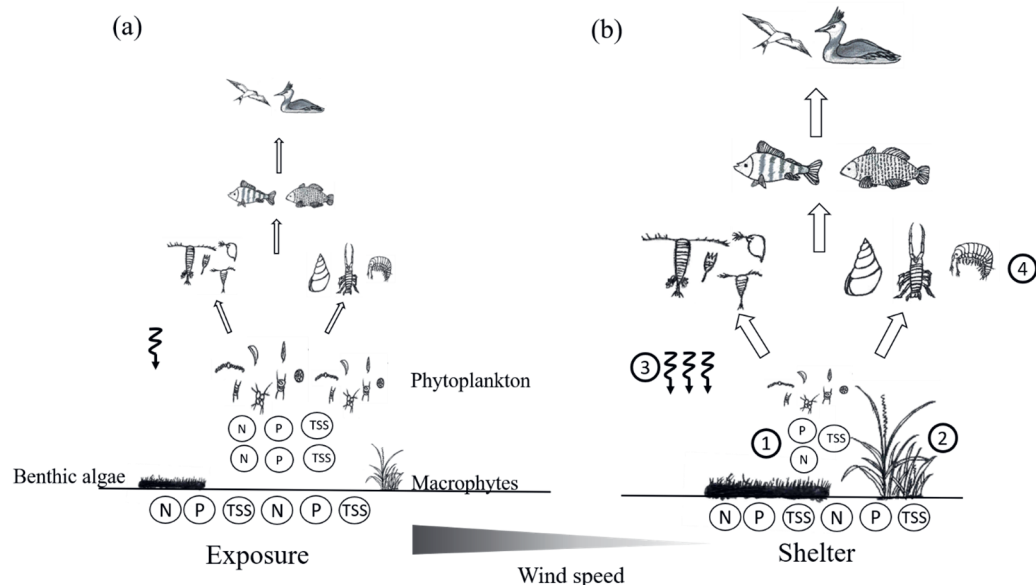


Figure 7.2. Schematic illustration of how shelter affects trophic transfer in a simplified aquatic food web in shallow lake ecosystem. The arrows indicate the trophic transfer between adjacent trophic levels while the width of the arrows indicates the strength of the trophic transfer efficiency. N represents nitrogen, P represents phosphorus, and TSS represents Total suspended solids. ① indicates the reduced Total suspended solids. ② increased diverse types of primary producers. ③ indicates the increased light availability. ④ increased invertebrate biomass.

7.1.5 Towards optimal levels of shelter

The mechanisms demonstrated above are the result of interactions among physical habitats, wind and water depth, resulting in a gradient of turbulence inside Marker Wadden. In marine systems, productivity has often been shown to follow a dome-shaped relationship with turbulence (Fig. 7.3a). That is to say, a little turbulence stimulates production, but too much has a negative effect (Visser and Stips 2002). Taking phytoplankton as an example, increased turbulence can mix more nutrients into the well-lit surface layer (the euphotic zone) stimulating production, but when the turbulence is too strong, plankton cells may be mixed out of the euphotic zone, resulting in reduced phytoplankton production. Such alterations in primary production due to turbulence could travel up the food web and affect productivity at

higher trophic levels. Moreover, turbulence may directly affect organisms from higher trophic levels. For example, at moderate turbulence, zooplankton may increase the rates at which they encounter their prey (Rothschild and Osborn 1988), thereby increasing zooplankton production, while strong turbulence may impair food detection or capture, or directly lead to body damage of zooplankton (Visser et al. 2009, G. -Tóth et al. 2011, Zhou et al. 2016), leading to decreased zooplankton production (Fig. 7.3a).

In line with these earlier studies, I observed different responses of organisms at different trophic levels to turbulence in my study on freshwater ecosystems. I found that phytoplankton biomass decreased with reduced turbulence while benthic algae and submerged macrophytes biomass increased due to the modified light and nutrient availabilities. Furthermore, reduced turbulence also enhanced the trophic transfer efficiency between phytoplankton and zooplankton (Chapter 4) by enhancing zooplankton biomass production (Chapter 3), and favoring the large-sized zooplankton (Chapter 4). This is further confirmed by the field study where I show that zooplankton biomass production was significantly higher at locations inside the Marker Wadden archipelago (i.e. the sheltered sites with low turbulence) compared with those outside of the Marker Wadden archipelago (i.e. the exposed sites with high turbulence) (Chapter 6). Besides, low turbulence also facilitated invertebrate biomass, especially the Gastropoda, offering alternative pathways to stimulate higher trophic levels besides the phytoplankton-zooplankton interaction (Chapter 4). Although these results only reflect results from the accelerating limb of the dome-shape relationship between turbulence and productivity found in the ocean, due to the limitation of the data set, I do think a similar dome-shaped response of primary, secondary and tertiary (fish) production to turbulence as observed in marine systems may apply to shallow lakes as well (Fig. 7.3b).

These relationships may be tested by incorporating data from lake Markermeer and different locations of the Marker Wadden, creating a gradient in turbulence as physical and biological components are differentially regulated by wind. In this productivity-turbulence dome-shaped relationship I suggest for the shallow lakes, both the pelagic habitat (solid line) and benthic habitat (dashed line) are included (fig. 7.3b). For primary producers, the pelagic primary producers and benthic primary producers respond to turbulence differently. Pelagic primary producer biomass will follow the dome-shaped relationship from the marine system, which is

expected to increase with turbulence due to the increased nutrient availability under the optimum turbulence, and decrease with further increasing turbulence due to light limitation and flocculation by forming phytoplankton-sediment aggregates, that sink to the lake bottom (e.g. Brinkmann et al., 2019). Subsequently, this would cause declines in zooplankton production. In contrast, benthic primary producers can derive nutrients from the non-suspended sediments at the lake bottom and thus can maintain their biomass at low turbulence as well as sustain invertebrate populations (Fig. 7.3b, the dashed line). Increasing turbulence eventually causes disappearance of benthic primary producers through light limitation by sediment resuspension or dislodging. This suggests that shelter, which aims to reduce the turbulence, favors the development of the benthic food web over the pelagic food web. The general food web development in the whole lake, however, is hard to predict due to the coupling of different habitats through the littoral zone, e.g. the benthic and pelagic habitat. This suggests that further restoration efforts should not only focus on the pelagic habitat, as benthic habitats also play an important role in the functioning of lake ecosystems. Furthermore, for shallow lakes that suffer from wind-induced turbulence, measures aiming to reduce wind-induced turbulence and diversifying the underwater habitats, such as more littoral zones in Marker Wadden, could be a successful strategy to recover higher trophic level production.

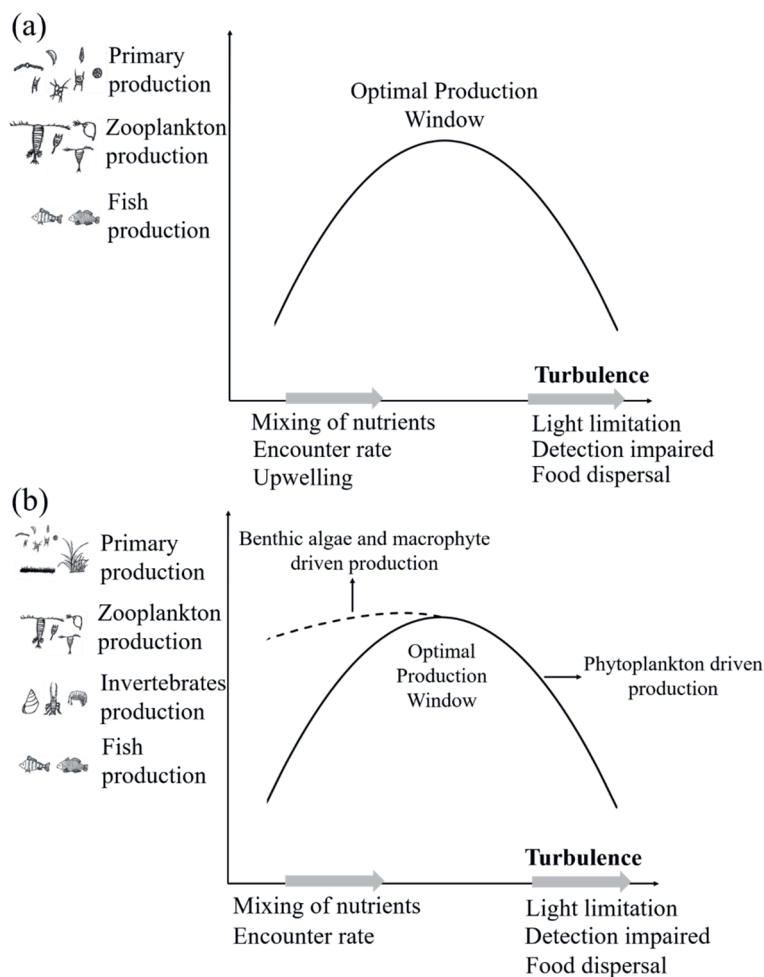


Figure. 7.3 The dome-shaped response of primary, secondary and tertiary production to turbulence in aquatic systems. (a) Pelagic, phytoplankton driven production in marine systems in relation to turbulence, modified from Visser and Stips (2002). (b) The extended dome-shaped response of primary, secondary and tertiary production in shallow freshwater systems to turbulence, including the phytoplankton-driven production (solid line) and the benthic primary producer-driven production (dashed line) in response to turbulence.

7. 2 Future management

7. 2.1 Marker Wadden

The climate is changing at an unprecedented rate due to anthropogenic activities, resulting in rising global mean temperatures and increased frequency of extreme climate events such as storms (Young et al. 2011, IPCC 2014). These changes are affecting many components of the aquatic ecosystem, including primary producers (Woodward et al. 2010, Walther et al. 2002). My results showed that sediment resuspension enhanced phytoplankton biomass build-up while it inhibited benthic algae biomass production. The enhanced phytoplankton biomass, however, may not necessarily promote growth at higher trophic levels, as zooplankton biomass production could not profit (Chapter 3). This suggests that if the exposed sites with shallow depth on the Marker Wadden will increasingly suffer from wind effects in the future, those sites may remain dominated by phytoplankton due to the strengthened bottom-up and the weakened top-down effects under turbulent conditions. Furthermore, I also observed that sediment resuspension could interact with rising temperature to maintain higher inorganic suspended solids concentrations and periphyton biomass (Chapter 3), which both inhibit the recovery of the macrophytes due to shading effects (Chapter 3,4). This suggests that the exposed sites with shallow water depth on Marker Wadden may also be dominated by phytoplankton. In contrast, macrophytes could become the dominant primary producers on the sheltered sites inside Marker Wadden. These results combined suggest that a shelter gradient provided by heterogenous habitats on Marker Wadden can support diverse types of primary producers and thereby a higher diversity of primary consumers. This highlights the importance of maintaining habitat heterogeneity on Marker Wadden.

7. 2.2 Shallow lakes

7. 2.2.1 Shelter creation

Submerged macrophytes are often a prerequisite for providing shallow lake ecosystem services, including drinking water supply, fisheries production, and hot-

spots of biodiversity (Hilt et al. 2017, Hansson et al. 2020, Janssen et al. 2020). Therefore, substantial efforts have been made globally to shift systems with a phytoplankton-dominated turbid state to a macrophyte-dominated clear water state by reducing external nutrient loading (Jilbert et al. 2020, Abell et al. 2020). However, these efforts are counteracted or weakened due to the wind-induced sediment resuspension, especially for shallow lakes (Tammeorg et al. 2013, Tang et al. 2020). My 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 from phytoplankton to zooplankton, and increase benthic fauna biomass. This suggests that in these cases the creation of shelter to reduce negative effects of wind could facilitate a shift in primary producers from phytoplankton to macrophyte dominance. Despite the local increase in nutrients at sheltered sites, it led to the development of macrophytes. This highlights the importance of habitat structure in shifting from a turbid to clear water state. These effects, however, are quite local, and future monitoring of the water in and outside Marker Wadden will reveal to what extent such a restoration project will contribute to improved water quality in the lake.

7. 2.2.2 Achieving optimum light:TP

Anthropogenic activities are changing the absolute and relative input of nutrients into freshwater ecosystems (Falkowski et al., 2000; Carpenter et al., 2011; Penuelas et al., 2020), thereby altering the dominant primary producer and affecting the transfer of carbon and nutrients to higher trophic levels (Van de Waal et al. 2010). Eutrophication may lead to excessive phytoplankton biomass build-up, and often promotes cyanobacteria to be the dominant primary producer (Schindler et al., 2016; Huisman et al., 2018). Despite the enhanced primary production, the poor nutritional quality and edibility of cyanobacteria can lead to the collapse of the food-web (Ger et al. 2014, 2016). To combat eutrophication, oligotrophication following nutrient mitigation measures is increasingly applied as a restoration approach in freshwater systems worldwide (Finger et al. 2013, Sabel et al. 2020). However, in many systems, an unintended decline of higher trophic production, like zooplankton (Jeppesen et al. 2005, N. John et al. 2005) and fish (Finger et al. 2007), was observed simultaneously to nutrient reduction. Moreover, this declining trend may become even more severe in the future with global warming. For example, increased temperatures drive thermal stratification and cause shoaling of the mixed layer,

which can reduce nutrient inputs from the deeper waters while increasing average light availability (Woolway et al. 2020). Combined with ongoing nutrient reduction measures, climate warming may lead to a higher light:nutrient ratio in lake ecosystems (Fig. 7.4 red shadow).

My results showed that high light to nutrient inputs could decrease both phytoplankton biomass and their nutritional quality (Chapter 5), and have cascading effects on higher trophic level organism production (Chapter 6). That is to say, higher trophic level organisms in lake ecosystems may suffer from both food quantity reduction and quality deterioration with warming, potentially resulting in the loss of many important ecosystem services provided by lake ecosystems, such as the fish production. Therefore, lake restoration measures are required to achieve both improved water quality while also maintaining sufficient production of higher trophic levels. Thus, establishing optimum light:phosphorus ratios for given systems, where both the phytoplankton quantity and quality are high (Fig. 7.4 grey shadow), may guide future restoration efforts towards improved transfer of energy and matter in aquatic food webs.

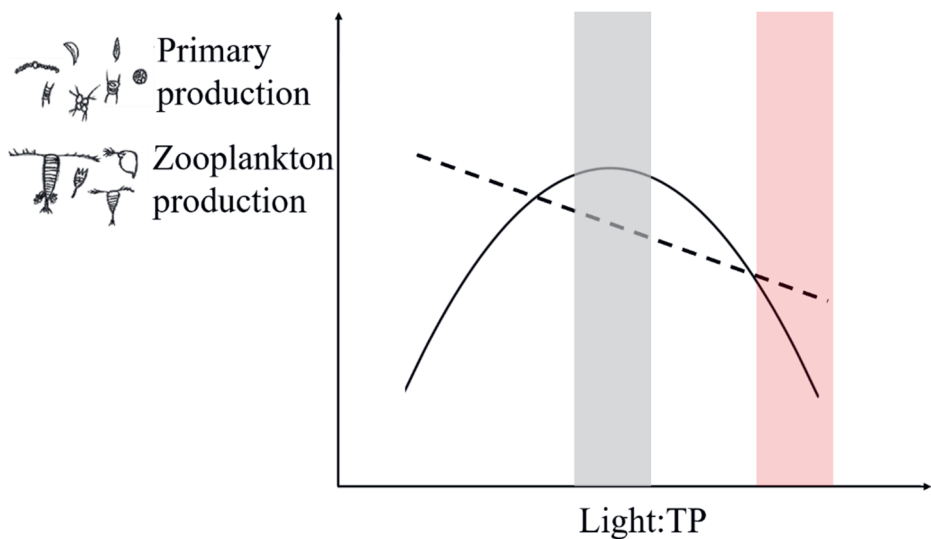


Figure 7.4. The effect of the light:total phosphorus ratio on primary production and zooplankton production (solid line) and phytoplankton quality (dashed line). The red shadow indicates a future scenario caused by warming and nutrient reduction. The grey shadow indicates the optimum.

Closing remarks

Overall, my findings show that the creation of a littoral zone by restoring land-water connections in the Marker Wadden project can be considered as a form of nature-based multiple stressor management that increases shelter, nutrient availability and habitat heterogeneity providing a higher diversity in primary producers. This results in improved trophic transfer between phytoplankton-zooplankton as well as increased abundance of invertebrates as an alternative food source, which together could facilitate the recovery of higher trophic organisms, in particular fish and water birds. As such, Marker Wadden, as a forward-looking approach enhancing ecological integrity while maintaining ecosystem services, can provide a new direction for our future restoration efforts.



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Summary (English)

Lakes are important freshwater ecosystems and although they only cover ~3% of the Earth's surface, they provide a substantial number of ecosystem services. These include drinking water supply, fisheries production and they serve as hot-spots of biodiversity. Many lake ecosystems worldwide are suffering from severe ecological degradation attributed to multiple anthropogenic stressors, including climate change, land-use intensification, eutrophication, acidification, water abstraction, morphological alteration, and invasive species. Consequently, this leads to the loss of biodiversity and damage to ecosystem services provided by lakes. To preserve and restore biodiversity and ecosystem services supported by lakes, ecological degradation through global change needs to be counteracted. One way to achieve this is through lake restoration projects. To date, lake restoration is often based on single-stressor abatement approaches, in particular nutrient loading reduction. While this has been often shown to successfully improve water quality, it also may cause unintended declines of higher trophic production, such as fish and water birds. Besides, the desired goals of single-stressor abatement approaches could be counteracted by other factors, such as wind-induced sediment resuspension that may lead to enhanced internal nutrient loading, specifically for the shallow lakes. Therefore, nature-based multiple stressor management is needed to both improve lakes' ecological status and maintain their ecosystem services.

In this thesis, I study the effectivity of an innovative lake restoration approach which is based on such a multiple-stressor intervention strategy, the Marker Wadden project in lake Markermeer, The Netherlands. Marker Wadden is a 1000-ha man-made archipelago consisting of five islands with natural shorelines and lagoons, aiming to stimulate the development of a wind protected littoral zone that is currently largely lacking due to basalt dikes surrounding lake Markermeer (Chapter 2). The goal of Marker Wadden is to create a bird and fish paradise by stimulating the aquatic food web development bottom-up. In my thesis, my aim is to understand whether the Marker Wadden will improve trophic transfer from phytoplankton to zooplankton, and thereby support higher trophic levels, thus achieving the overall goal of the project. Specifically, I tested the following overarching hypotheses:

- 1) Creating shelter against wind will increase trophic transfer between phytoplankton and zooplankton in shallow lakes by decreasing the suspended solids concentration;
- 2) Creating shelter against wind will increase trophic transfer by supporting habitat for more types of primary producers, which in turn can support a higher consumer diversity and biomass;

- 3) Creating littoral zones will increase nutrient availability coupled with improved light availability which increases primary producer quantity and quality, thereby stimulating the food web bottom-up and increasing trophic transfer.

To achieve this, I combined different approaches ranging from laboratory experiments and field mesocosm experiments to field monitoring.

My results showed that reducing water turbulence reduced suspended solid concentrations in the water column and facilitated zooplankton biomass build-up in an indoor microcosm experiment (Chapter 3). Similarly, providing shelter reduced suspended solid concentrations and enhanced trophic transfer efficiency between phytoplankton and zooplankton in a mesocosm field experiment (Chapter 4). These results suggest that shelter provided by Marker Wadden can enhance trophic transfer between phytoplankton and zooplankton if Marker Wadden reduces wind-induced turbulence, which I show decreases the suspended solids concentration. Reduced wind-induced turbulence may protect zooplankton from shear forces, especially the large body sized ones. Furthermore, reduced mixing may release zooplankton from feeding interference with suspended solids as this may mechanically complicate food collection or dilute gut content. In contrast, I found higher suspended solid concentrations on locations within the Marker Wadden compared to those outside the Marker Wadden, even though these locations that were in between the islands can be considered sheltered (Chapter 5). These unexpected higher suspended solids concentrations may be due to the initial development phase of Marker Wadden, where construction work could still have affected sediment resuspension. Indeed, in three separate large basins, which were disconnected from those locations affected by construction work, sediment settled and large amounts of zooplankton were found in two of the basins (Chapter 2).

In the indoor microcosm (Chapter 3) and field mesocosm (Chapter 4) experiment I also tested the effects of water turbulence and shelter, or the absence of turbulence, on the dominance of different types of primary producers. The results showed that decreased turbulence (Chapter 3) and shelter (Chapter 4) had significant effects on the interaction among different types of primary producers by changing physical, chemical, and biological conditions in the water column. Specifically, decreased water turbulence favored benthic algae (Chapter 3) and shelter favored submerged macrophytes (Chapter 4) to be the dominant primary producer. These results suggest that diverse types of primary producers could colonize on Marker Wadden as a

gradient of shelter has been provided. On Marker Wadden, in two of three large separate sheltered basins, submerged macrophytes established and became locally abundant (Chapter 2). Furthermore, I show that shelter also facilitated the abundance of invertebrates, such as Gastropoda (Chapter 2 and 4), which suggests that shelter may result in higher food web complexity, offering alternative pathways to stimulate higher trophic levels.

I applied the light:nutrient hypothesis in the restoration context of Marker Wadden and found that nutrient availabilities were significantly higher on sheltered locations within Marker Wadden compared to those outside of Marker Wadden (Chapter 5). These increased nutrients availability improved the quantity and quality (expressed as carbon:nutrient stoichiometry) of the phytoplankton, thereby supporting higher zooplankton biomass on sheltered locations inside Marker Wadden compared to outside Marker Wadden (Chapter 6). However, I did not find higher light availability in the sheltered areas of Marker Wadden, because suspended solids concentrations in the water column were higher at locations in Marker Wadden as compared to those outside of Marker Wadden. Interestingly, my findings reveal an optimum light:nutrient ratio at which phytoplankton quantity is highest, which provides a quantitative extension of the current light:nutrient hypothesis (Chapter 5). The observed unimodal relationship between phytoplankton biomass and the light:phosphorus ratio could be explained as follows: at low light:phosphorus ratios, phytoplankton biomass build-up is limited by light, while at a high light:phosphorus ratio it is limited by phosphorus, or a co-limitation of phosphorus and nitrogen. These changes in quantity and quality of primary producers (Chapter 5) may also cascade to higher trophic levels. Indeed, I demonstrated that total zooplankton biomass showed also an optimum at intermediate light:TP ratios, and thereby largely followed phytoplankton biomass (Chapter 6). The relationship can be explained by limited food availability for zooplankton at both the lowest and highest light:TP ratios. At high light:TP ratios, zooplankton biomass may furthermore be limited by the low food quality. However, I also found that different zooplankton taxa exhibited specific optima along the light:TP gradient. Specifically, copepod biomass was highest at low light:TP ratios, while cladocerans peaked at intermediate and rotifers at high light:TP ratios. This is likely driven by their differences in nutritional demands as well as feeding strategy where some groups may exclusively forage on phytoplankton while other groups may inclusively forage on phytoplankton, zooplankton, and bacteria (Chapter 6).

Overall, I conclude that the creation of a littoral zone by restoring land-water connections in the Marker Wadden project can be considered as a form of nature-based multiple stressor management, increasing shelter, nutrient availability and habitat heterogeneity in the form of dominance by multiple primary producers. This results in improved trophic transfer between phytoplankton-zooplankton as well as increased abundance of invertebrates as an alternative food source. Together, this may facilitate the recovery of higher trophic organisms, in particular fish and water birds. As such, Marker Wadden, as a forward-looking approach to enhancing ecological integrity while maintaining ecosystem services, can provide a new direction for our future lake restoration efforts.

Summary

(Nederlands)

Meren zijn belangrijke zoetwaterecosystemen. Hoewel ze slechts ~3% van het aardoppervlak beslaan, leveren ze een substantiële hoeveelheid ecosysteem diensten, waaronder de levering van drinkwater en vis voor visserij, en het zijn hotspots van biodiversiteit. Wereldwijd hebben veel zoetwater ecosystemen te maken met een ernstige achteruitgang van de ecologische toestand, wat toe te schrijven is aan diverse door de mens veroorzaakte stress factoren, waaronder klimaatverandering, intensivering van landgebruik, verzuring, wateronttrekking, aanpassing van de morfologie en de aanwezigheid van invasieve soorten. Dit leidt tot biodiversiteitsverlies en een aantasting van de ecosysteemdiensten die meren leveren. Om de biodiversiteit en de ecosysteem diensten te behouden en te herstellen moet de ecologische achteruitgang, veroorzaakt door deze stress factoren, tegengegaan worden. Het herstellen van meren is een manier om dit te bereiken. Tot nu toe is het herstellen van meren vaak gebaseerd op het aanpakken van één stress factor, met name het verminderen van de nutriënten belasting. Hoewel dit vaak succesvol is gebleken om de waterkwaliteit te verbeteren, kan het tegelijkertijd leiden tot een onbedoelde afname van hogere trofische niveaus, zoals vissen en watervogels. Daarnaast kan het gewenste doel door het aanpakken van één stress factor tegengegaan worden door andere stress factoren, zoals het opwervelen van sediment door windwerking, dat kan leiden tot verhoogde interne nutriënten belasting, vooral in ondiepe meren. Daarom is het nodig om over te gaan tot het aanpakken van meerdere stress factoren tegelijk, volgens op de natuur gebaseerde maatregelen, om de ecologische toestand van meren te verbeteren en daarbij hun ecosysteem diensten te behouden.

In dit proefschrift bestudeer ik de effectiviteit van een innovatieve benadering voor het herstel van meren, die gebaseerd is op zo'n multi-stressor interventie strategie, het Marker Wadden project in het Markermeer in Nederland. Marker Wadden is een door mensen gemaakte archipel van 1000 hectare, die bestaat uit vijf eilanden met natuurlijke oevers en ondiepe lagunes. Het project richt zich op het stimuleren van de ontwikkeling van een beschutte oeverzone, die momenteel grotendeels ontbreekt in het Markermeer systeem doordat basalt dijken het Markermeer omringen (Hoofdstuk 2). Het doel van Marker Wadden is om een vis- en vogel paradijs te creëren door het aquatische voedsel web van onderaf te stimuleren. In mijn proefschrift bestudeer ik of Marker Wadden de overdracht van voedsel in de voedselketen (*trophic transfer*) van algen naar dierlijk plankton verbeteren, en daarbij de hogere trofische niveaus ondersteunen, en dus de hoofddoelstelling van het Marker Wadden project bereiken. Ik test specifiek de volgende overkoepelende hypothesen:

1. Het creëren van beschutting zal de *trophic transfer* van fytoplankton naar zoöplankton in ondiepe meren verhogen door een reductie van de concentratie zwevend sediment in de waterkolom;
2. Het creëren van luwte zal de *trophic transfer* verhogen door het bieden van habitat aan verschillende typen primaire producenten, die vervolgens een grotere diversiteit en biomassa van consumenten kunnen herbergen;
3. De aanleg van oeverzones zal de nutriëntenbeschikbaarheid verhogen samen met de lichtbeschikbaarheid onder water, wat de kwantiteit en kwaliteit van de primaire productie verhoogt, waarbij het voedsel web van onderaf gestimuleerd wordt en de *trophic transfer* verhoogd wordt.

Om dit te bereiken heb ik verschillende methoden gecombineerd, variërend van lab experimenten en mesocosm experimenten in het veld tot veld monitoring.

Mijn resultaten laten zien dat het reduceren van turbulentie in de waterlaag de hoeveelheid zwevend sediment in de waterkolom verlaagde en de zoöplankton biomassa verhoogde in een lab experiment in microcosms (Hoofdstuk 3). Een experiment in het veld met mesocosms liet een vergelijkbaar resultaat zien: het bieden van beschutting verminderde de hoeveelheid zwevend sediment in de waterkolom en verhoogde de efficiëntie van *trophic transfer* tussen fytoplankton en zoöplankton (Hoofdstuk 4). Deze resultaten suggereren dat de luwte die ontstaan is door Marker Wadden, de *trophic transfer* van fytoplankton naar zoöplankton kan verhogen, als Marker Wadden inderdaad de turbulentie, veroorzaakt door windwerking, kan reduceren, waarvan ik heb laten zien dat dit leidt tot een kleinere hoeveelheid zwevend sediment in de waterkolom. Een vermindering van de turbulentie in de waterlaag, veroorzaakt door windwerking, kan zoöplankton beschermen tegen fysische schuifkrachten veroorzaakt door turbulentie, met name het grotere zoöplankton. Bovendien kan verminderde menging van de waterkolom ervoor zorgen dat zoöplankton minder te lijden heeft van interferentie met sediment deeltjes tijdens het foerageren, aangezien deze deeltjes het moeilijker maken om voedsel te verzamelen en zij het fytoplankton in de maag verdunnen. Tegen de verwachting in, vond ik echter hogere concentraties zwevende sediment deeltjes in de waterkolom op locaties tussen de eilanden van Marker Wadden, ten opzichte van locaties buiten Marker Wadden, terwijl de locaties tussen de eilanden van Marker Wadden als beschut kunnen worden beschouwd (Hoofdstuk 5). Deze onverwachte hogere concentraties zwevend sediment in de waterkolom zouden het gevolg kunnen

zijn van de initiële ontwikkelingsfase van Marker Wadden, waar bouwwerkzaamheden aan de eilanden de opwerveling van het sediment in de waterlaag beïnvloedt kan hebben. Het was inderdaad zo dat in drie afgesloten bassins op Marker Wadden, die niet in verbinding stonden met de locaties die door bouwwerkzaamheden beïnvloed werden, het sediment bezonk en grote hoeveelheden zoöplankton werden waargenomen in twee van de drie bassins (Hoofdstuk 2).

Ik heb in de lab microcosm (Hoofdstuk 3) en veld mesocosm (Hoofdstuk 4) experimenten ook het effect getest van turbulentie in de waterkolom en beschutting, oftewel de afwezigheid van turbulentie, op de dominantie van verschillende typen primaire producenten. De resultaten laten zien dat verminderde turbulentie (Hoofdstuk 3) en beschutting (Hoofdstuk 4) significante effecten hadden op de interactie tussen de verschillende typen primaire producenten door verandering van de fysische, chemische en biologische condities in de waterkolom. Verminderde turbulentie leidde tot dominantie van bentische algen, die matten vormen op het sediment (Hoofdstuk 3), terwijl ondergedoken waterplanten dominant werden bij beschutting (Hoofdstuk 4). Deze resultaten suggereren dat verschillende typen primaire producenten Marker Wadden kunnen koloniseren, aangezien hier een gradiënt in beschutting wordt geboden. Op Marker Wadden, in twee van de drie afgescheiden, beschutte, bassins vestigden zich ondergedoken waterplanten, die lokaal erg talrijk werden (Hoofdstuk 2). Verder laat ik zien dat beschutting de hoeveelheid zoetwaterslakken (Gastropoda) bevorderde (Hoofdstuk 2 en 4), wat suggereert dat beschutting kan resulteren in een grotere complexiteit van het voedsel web, hetgeen alternatieve routes biedt om hogere trofische niveaus te stimuleren.

Ik heb de licht:nutriënten hypothese toegepast in de context van het ecosysteem herstel door Marker Wadden en vond dat de nutriënten beschikbaarheid in de waterkolom significant hoger was op locaties binnen Marker Wadden, vergeleken met locaties buiten Marker Wadden (Hoofdstuk 5). Deze verhoogde nutriënten beschikbaarheid verbeterde de kwantiteit en kwaliteit (uitgedrukt als koolstof:nutriënten ratio (stoichiometrie)) van het fytoplankton. Hierbij werd ook een hogere zoöplankton biomassa bereikt op beschutte locaties binnen Marker Wadden vergeleken met locaties buiten Marker Wadden (Hoofdstuk 6). Ik vond echter geen hogere licht beschikbaarheid onder water in de beschutte delen van Marker Wadden, omdat de hoeveelheid zwevend sediment in de waterkolom hoger was op locaties binnen Marker Wadden dan daarbuiten. Interessant is dat mijn onderzoek laat zien dat er een optimum is in de licht:nutriënten ratio in de waterkolom waarbij de fytoplankton kwantiteit het hoogste is. Dit betekent dat de

huidige licht:nutriënten hypothese uitgebreid kan worden met een kwantitatieve component, aangezien deze hypothese van origine alleen een optimum voorspelde voor fytoplankton kwaliteit (Hoofdstuk 5). De waargenomen unimodale relatie tussen fytoplankton biomassa en de licht:fosfor ratio in de waterkolom kan als volgt verklaard worden: bij lage licht:fosfor ratio's is de ontwikkeling van fytoplankton biomassa gelimiteerd door licht beschikbaarheid, terwijl deze bij een hoge licht:fosfor ratio gelimiteerd is door de beschikbaarheid van fosfor, of een co-limitatie optreedt van fosfor en stikstof. Deze veranderingen in kwantiteit en kwaliteit van primaire producenten (Hoofdstuk 5) kunnen doorwerken op de hogere trofische niveaus. Inderdaad kon ik laten zien dat de totale zoöplankton biomassa ook een optimum had bij intermediaire licht:fosfor ratio's in de waterkolom, en daarbij grotendeels de fytoplankton biomassa volgde (Hoofdstuk 6). Deze relatie kan verklaard worden door gelimiteerde voedselbeschikbaarheid voor zoöplankton bij zowel de laagste als hoogste licht:fosfor ratio's. Bij hoge licht:fosfor ratio's kan de zoöplankton biomassa bovendien gelimiteerd zijn door lage voedselkwaliteit. Ik vond echter ook dat verschillende zoöplankton taxa specifieke optima lieten zien langs de gradiënt van licht:fosfor ratio's in de waterkolom. De biomassa van roeipootkreeftjes (Copepoda) was het hoogste bij lage licht:fosfor ratio's, terwijl watervlooien (Cladocera) piekten bij intermediaire licht:fosfor ratio's en raderdieren (Rotifera) bij hoge licht:fosfor ratio's. Deze patronen worden waarschijnlijk veroorzaakt door verschillen in de nutriënten behoefte en de foerageer strategieën, waarbij sommige taxa exclusief op fytoplankton foerageren, terwijl andere taxa zowel op fytoplankton, zoöplankton en bacteriën kunnen foerageren (Hoofdstuk 6). Samenvattend concludeer ik dat de aanleg van een oeverzone door het herstel van land-water verbindingen in het Marker Wadden project beschouwd kan worden als een vorm van een multi-stressor aanpak, gebaseerd op natuurlijke principes, die de beschutting en nutriënten beschikbaarheid verhoogt en habitat heterogeniteit creëert in de vorm van dominantie door meerdere typen primaire producenten (vrijzevende algen, bentische algen en ondergedoken waterplanten). Dit resulteert in een verbeterde *trophic transfer* tussen fytoplankton en zoöplankton en verhoogt de talrijkheid van andere ongewervelden als een alternatieve voedselbron. Samen kan dit het herstel van hogere trofische niveaus bevorderen, met name vissen en watervogels. Als zodanig kan Marker Wadden, als een toekomstgerichte benadering om de ecologische integriteit te herstellen waarbij ecosysteem diensten behouden blijven, een nieuwe richting bieden voor onze toekomstige inspanningen om meren te herstellen.

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About the Author

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Hui Jin was born on 5 June 1990 in Yuxi, China. He grew up in a small village. After finishing high school in 2009, he started studying Environmental Engineering at South-central University for Nationalities. Here, he gained knowledge about municipal wastewater treatment. After the internship at the Nanjing Institute of Geography & Limnology, he realized natural lakes and ecological restoration is what he fons most. After finishing his bachelor's study in 2013. He worked as a research assistant at the Nanjing Institute of Geography & Limnology, where he developed stronger interests in lake ecosystems. Then he started his joint training master program at Jiangnan University and Nanjing Institute of Geography & Limnology in 2014, supervised by associate professor Gui-Jun Yang and researcher Kuan-Yi Li. During his master's, he studied the effects of benthic animals (mainly *Corbicula fluminea* and *Limnodrilus hoffmeisteri*) on nutrient recycling in the water. In 2017, he obtained financial support from China Scholarship Council (CSC) to continue his PhD study at the Netherlands Institute of Ecology (NIOO-KNAW) and at Wildlife Ecology and Conservation Group, at Wageningen University. Hui's research was based on a large lake restoration project- Marker Wadden, where he studied how Marker Wadden improves trophic transfer.

Publications

Publications

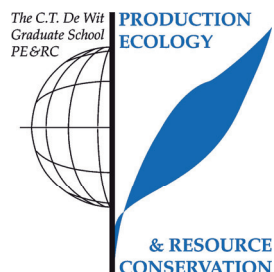
Van Leeuwen, C.H.A., Temmink, R.J.M., **Jin, H.**, Kahlert, Y., Robroek, B.J.M., Berg, M.P., *et al.* (2021). Enhancing ecological integrity while preserving ecosystem services: Constructing soft-sediment islands in a shallow lake. *Ecological Solutions and Evidence*, 2, e12098.

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PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)



Review of literature (6 ECTS)

- Effects of benthic animals on nutrient cycling in the water column (2017)

Writing of project proposal (4.5 ECTS)

- How trophic transfer efficiency varies among habitats with different primary producers in ecological restoration project Marker Wadden

Post-graduate courses (3.8 ECTS)

- Aquatic ecology; PE&RC / SENSE / RSEE (2018)
- Linking community and ecosystem dynamics; PE&RC / SENSE / RSEE (2018)

Competence strengthening / skills courses (2.1 ECTS)

- Workshop: science communication: what's your strategy?; NIOO (2019)
- Scientific writing course; Wageningen in'to Languages (2021)

Scientific integrity/ethics in science activities (0.3 ECTS)

- Scientific integrity workshop; NIOO (2019)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.2 ECTS)

- Preventing the end of the world-how science can save our planet (2017)
- Biodiversity: reflecting on the past to transform the future (2021)
- PE&RC Last years weekend (2021)

Discussion groups / local seminars or scientific meetings (8.8 ECTS)

- NIOO Seminars (2017-2021)
- Symposia Centre for Wetland Ecology (CWE) (2018)
- Marker Wadden yearly science meeting (2018)
- NIOO Research day (2019)
- Marker Wadden nature in production meeting with Natuurmonumenten (2019)
- Rewilding Europe online symposium (2020)
- Netherlands Annual Ecology Meeting (NAEM) (2021)

International symposia, workshops and conferences (7.3 ECTS)

- Netherlands Annual Ecology Meeting; poster presentation; Lunteren (2018)
- Netherlands Annual Ecology Meeting; oral presentation; Lunteren (2019)
- Netherlands Annual Ecology Meeting; oral presentation; Lunteren (2020)

- The 10th International Shallow Lakes conference; oral presentation; online (2021)

Societally relevant exposure (0.3 ECTS)

- NIOO Open day for the public; poster presentation about my PhD work and explaining my work and the work of NIOO to the general public

Lecturing / supervision of practical's / tutorials (0.6 ECTS)

- Aquatic ecology practical (2018)

Colophon

The research presented in this thesis was conducted at the department of Aquatic Ecology at the Netherlands Institute of Ecology (NIOO-KNAW) and at the Wildlife Ecology and Conservation Group at Wageningen University.

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This is NIOO Thesis 188

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