The Influence of Macrophytes on Aquatic Microclimate

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Makrofyters påverkan på akvatiskt mikroklimat
1. Sammanfattning


1. Abstract

How terrestrial vegetation influences microclimate and what effects this has on associated ecosystems is well studied, but it is less known if and how aquatic macrophytes affect their microclimate. In this study I therefore aim to investigate the question of how aquatic macrophytes influence their microclimate, and how these effects in turn may affect associated aquatic organisms and ecosystems. This was done by conducting a literature search and review of relevant scientific articles. I found that aquatic macrophytes influence microclimate in several ways. First, their photosynthetic activity can affect water and sediment chemistry by changing carbon and oxygen levels, which also influences pH. Secondly, local temperature can also be influenced by macrophytes through shading and heat retention, which in turn also can affect water movement via density differences. Third, aquatic macrophytes can affect light levels in the water column, both negatively through shading, and positively by reduction of particles in the water. I conclude that aquatic macrophytes do influence microclimate. This influence can change the local environment, thus also affecting associated organisms and ecosystems. These conclusions are important for future research of aquatic environments when looking at challenges such as climate change and maintaining and protecting biodiversity and whole ecosystems.
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2. Introduction

2.1 Background
Changes in climate, i.e. long-term weather patterns (National Geographic Society, 2022), affects ecosystems all over the world (Scheffers et al., 2016). These changes occur because of changes in the variables which influence large-scale climate, including temperature, wind, humidity, precipitation, and atmospheric pressure (National Geographic Society, 2022), which in turn can occur with changes in solar radiation levels reaching Earth and changes in the Earth’s orbit (MSFC, 2015). However, if you look at a smaller scale, the local climate of habitats may not always reflect the large-scale macroclimate fluctuations (De Frenne et al., 2019, 2021; Woodson et al., 2019). These local variations in climate are called microclimates (National Geographic Society, 2022). The variables affecting microclimate conditions are traditionally seen as temperature, solar radiation, humidity, wind speed, and pressure (Rotach & Calanca, 2003), which in an aquatic environment could be translated to water temperature, solar radiation, water composition or chemistry, water movement speed, and pressure. Microclimates can also be greatly influenced by topography, including vegetation, lakes, and even cities (National Geographic Society, 2022), causing local variations in abiotic factors such as temperature and carbon dioxide levels (De Frenne et al., 2019, 2021; Woodson et al., 2019). The definition of microclimate does, however, also depend on what scale you want to look at. A microclimate can range from being several hundred kilometers to only a few centimeters, depending on the question being addressed (Mislank & Helmuth, 2008). In both terrestrial and aquatic environments, microclimates may play an important role as refuges for species affected by global warming as they may be able to buffer extreme temperatures (De Frenne et al., 2019, 2021; Woodson et al., 2019).

Terrestrial plants, especially forests, affect their microclimate in several ways (De Frenne et al., 2019, 2021). Forest canopies in different environments all over the world can strongly affect direct sunlight and wind speeds under the canopy, which in turn have effects on in-canopy temperature and humidity (De Frenne et al., 2021). With increasing density of a forest canopy comes a decrease in wind speeds which can affect the temperature within the canopy (De Frenne et al., 2021). The effects forest canopies have on temperature can be seen as a buffering effect. High macroclimate temperatures are cooler below a canopy and low temperatures are higher, meaning forests reduce temperature extremes (De Frenne et al., 2019). High temperatures are lowered under forest canopies by an average of 4.1°C globally (De Frenne et al., 2019) under forest canopies as a result of absorption or reflection of incoming solar radiation, for example during clear sunny days (De Frenne et al., 2021). Contrasting, low temperatures for example during the night, are on average 1°C higher inside than outside forests (De Frenne et al., 2019), mainly because of heat retention under the canopy (De Frenne et al., 2021). These effects are present in different environments all over the world, from tropical to boreal systems (De Frenne et al., 2019, 2021), and does not seem to differ depending on the type of dominant tree species (De Frenne et al., 2019).

Microclimate has been shown to have important effects on ecosystems, for example on biodiversity, species distribution and climate change (De Frenne et al., 2021). These effects have been well studied in terrestrial environments where the buffering of rising temperatures from global warming in forests can act as a refugia for organisms (De Frenne et al., 2021). The microclimate under forest canopies may thus give organisms time to adapt to climate change. Microclimate can also affect individual, population, and species distribution (De Frenne et al., 2021). For example, if temperatures become too high outside a
forest, it may cause an organism to seek refuge in a forest where the climate is different, thereby changing its distribution (De Frenne et al., 2021).

Climate change also affects marine environments (Cavole et al., 2016). Ocean climate change is already impacting marine organisms in a number of ways, mainly because of rising temperatures and ocean acidification, but also because of declining ocean oxygen levels and changes of ocean circulation (Poloczanska et al., 2016). The effects climate change has on marine organisms includes, to mention a few, distribution changes, reduction in body size, and declining calcification rates, which in turn affects species abundance and population growth (Poloczanska et al., 2016). Ocean warming is slower than warming of terrestrial environments, but in marine environments the pace of climate change is greater than on land (Burrows et al., 2011). In this case that means that geographic shifts of some organisms over time and shifts in seasonal timing of temperatures are faster in ocean environments, i.e. the effects of global warming are faster in the ocean compared to land, but the actual warming itself is slower (Burrows et al., 2011) This makes ocean environments just as important to study in regard to for example biodiversity. The responses of marine environments to climate change can vary locally which creates marine microclimates (Woodson et al., 2019). Similarly to terrestrial microclimates, these marine microclimates have the potential to work as refuges for marine organisms (Woodson et al., 2019). However, the effects of vegetation specifically, on microclimate and what consequences these effects have on associated organisms and ecosystems, is to my knowledge less known in aquatic environments, especially when looking at effects on water temperature. In this study I therefore aim to review how and to what extent aquatic macrophytes affect their microclimate.

2.2 Aims and research question

My research question is: How do aquatic macrophytes influence their microclimate? Therefore, the aim of this study is to review what effects macrophytes have on their local aquatic environment, i.e., their microclimate. I will review effects on local water chemistry, such as pH, oxygen, and carbon dioxide levels, as well as effects on light, temperature, and water movement. I will also look at and discuss how these macrophyte-effects on aquatic microclimate may affect other associated organisms and ecosystems.

3. Methods

To answer my research question, I conducted a literature search for relevant scientific articles about aquatic microclimate, and how macrophytes affect different aspects of aquatic microclimate. From these articles I have done a literature review. The literature search was done exclusively in the database ISI Web of Science, meaning all articles used in this study have been peer-reviewed. I used different combinations of search words and phrases such as “aquatic microclimate”, “macrophyte”, “macroalgae”, “macrophyte effects”, “temperature” and “canopy” and chose articles with relevant titles and abstracts. I also looked at the found articles references to broaden the search in finding even more literature on the subject.
4. Results

4.1 Effects of macrophytes on local water chemistry

One of the main effects macrophytes have on their microclimate is changes in the surrounding water chemistry due to photosynthesis (Anthony et al., 2011; Axelsson et al., 1995; Beer et al., 2006; Frankignoulle & Distèche, 1984; Unsworth et al., 2012). Photosynthetic processes by macrophytes affect CO₂ and oxygen levels, as CO₂ is taken up and oxygen is produced. The uptake of CO₂ from the water can in turn affect pH levels, i.e. the H⁺ concentrations, in the surrounding water (Millero, 2007). The pH of seawater mainly depends on the equilibrium of CO₂ between the atmosphere and the water, but also on the equilibrium of the carbonate systems (Millero, 2007). Macrophytes can shift these equilibriums by taking up CO₂ and bicarbonate (Beer, 1989), which increases the pH. Some macrophytes may also increase the pH by transporting OH⁻ to the water (Beer, 1989). The production of oxygen from rooted macrophytes can also affect the chemistry of the sediments where they grow (Burdige & Zimmerman, 2002; Kemp & Murray, 1986; Sand-Jensen et al., 1982). Increased oxygen levels in the sediments can potentially decrease hypoxic conditions (Kemp & Murray, 1986; Sand-Jensen et al., 1982) as well as causing changes in alkalinity (Burdige & Zimmerman, 2002).

Several studies have shown effects on pH by macrophytes. One study using the three Mediterranean seagrass species Posidonia oceanica, Cymodocea nodosa and Zostera noltii showed a daily variation of pH above, within and under the seagrass canopies (Invers et al., 1997). They found that pH levels were highest during the day, and also higher above the canopies compared to at the bottom underneath them. Another study done of the shores of east Africa using the three seagrasses Halophila ovalis, Cymodocea rotundata and Thalassia hemprichii measured an increase of pH from 8.1 (pH of normal seawater) to a peak during the day at 8.5, 8.8 and 9.2 for each species respectively (Beer et al., 2006). A third study done in marine waters in Zanzibar also showed that seagrass meadows can increase the pH of surrounding water as an effect of photosynthetic activity (Semsei et al., 2009). Their results showed an increase of water pH from between 8.3-8.4 to up to 8.6-8.9 when seagrass was present. An analysis done using data on seagrass meadows in the Indo-Pacific also indicates that the presence of seagrass can increase the pH of up to 0.38 units, compared to water where seagrass is absent (Unsworth et al., 2012). Lastly, a fifth study done in the Mediterranean using the seagrass P. oceanica showed slightly higher pH levels in the water closer to the seagrass bed at 8 meters depth, than at the water surface (Frankignoulle & Distèche, 1984).

Another effect of the photosynthetic processes of macrophytes is effects on carbonate levels. One study done in a freshwater lake in Poland has shown that carbonate levels correlated to the biomass of the group of macrophytes called charophytes (Pukacz et al., 2014). They found that a greater biomass correlated to higher carbonate levels in the water (Pukacz et al., 2014). This is the result of these macrophytes’ ability to produce carbonates in the form of calcium carbonate encrustations (Pukacz et al., 2014). Other macrophytes have also been shown to affect carbonates in the sediment. Seagrass can, according to one study, affect the alkalinity of marine sediments by transporting oxygen into the sediment which drives aerobic respiration (Burdige & Zimmerman, 2002). This will increase the dissolution of carbonates which in turn increases the total alkalinity of the sediments, meaning they get a higher buffering capacity against changes in pH (Burdige & Zimmerman, 2002).
Macrophytes can, as mentioned above, transport oxygen into sediments (Burdige & Zimmerman, 2002). This has also been studied with regards to aspects other than alkalinity. One study measuring oxygen release from 8 different rooted macrophyte species from different habitats (marine, freshwater lake and stream) showed that macrophytes can transport oxygen into sediment through their roots, at different rates depending on species and light exposure (Sand-Jensen et al., 1982). The transport of oxygen to sediments has the ability to oxidize potentially toxic metabolites such as sulphide (Kemp & Murray, 1986; Sand-Jensen et al., 1982), while also increasing the nutrient availability for the macrophytes (Sand-Jensen et al., 1982). The transport of oxygen from macrophytes does not only happen from roots into sediments, it also occurs from stem and leaves into the water (Kemp & Murray, 1986; Sand-Jensen et al., 1982). How much of the oxygen that is released from the roots compared to stem and leaves varies between macrophyte species (Sand-Jensen et al., 1982). For example the marine seagrass Zostera marina had 1% of oxygen release from its roots, while the stream living species Potamogeton pectinatus had 3-4% and the freshwater species Lobelia dortmanna had 100% of its oxygen release from the root (Sand-Jensen et al., 1982).

4.2 Effects of macrophytes on light
Adding to the effects of macrophytes on microclimate is the direct effect they have on light penetration. The effects on light can be negative as a result of shading. One study done in coastal waters off of Western Australia using the kelp Ecklonia radiata showed how light levels decrease below canopy with increasing canopy density (Wernberg et al., 2005). The light was reduced by up to almost 99% in dense canopies compared to open water (Wernberg et al., 2005). There are also other studies showing that macrophyte canopies reduce how much light reaches below canopy depth, compared to if there would have been an absence of macrophytes (Critchley et al., 1990; Kennelly, 1989; Strong et al., 2006). The reductions in light are explained as a result of blocking or absorption of light by the macrophytes (Critchley et al., 1990; Strong et al., 2006). S. muticum canopies have been shown to reduce light levels reaching below the canopy by up to 97% (Critchley et al., 1990; Strong et al., 2006) while S. latissima canopies can reduce the light by up to 95% (Strong et al., 2006). The net effects of macrophytes on light penetration can, however, also be positive. Macrophytes affect near bottom water movement negatively which indirectly also can affect light penetration positively. By reducing near-bottom water movement and waves, the resuspension of sediment particles is reduced, making the water column more clear which lets more light through (Hansen & Reidenbach, 2012). Also, the amount of sediment particles being suspended in the water has been shown to decrease with seagrass canopy density (Carr et al., 2010), and the time sediment particles remain in the water column after for example a large wave has passed, also decreases with higher seagrass canopy density (Carr et al., 2010). Macrophytes can also affect light penetration indirectly by trapping particles and nutrients from the water column, again increasing the water clarity (Carr et al., 2010; Maxwell et al., 2017). Finally, when seagrass beds are present more nutrients are taken up from the water, reducing the possibility for phytoplankton to grow, also making the water more clear and allowing more light into the water column (Maxwell et al., 2017).

4.3 Effects of macrophytes on local temperature
Macrophytes also have effects on other aspects of microclimate besides water chemistry and light. Local temperatures, both in the water column and in the sediment, can be affected by macrophytes (Critchley et al., 1990; Dale & Gillespie, 1977; Gilson & Davies, 2020; Strong et al., 2006; Willis et al., 2017). Studies
done in temperate saline waters using the macrophyte *Sargassum muticum* show that temperatures are different under and within canopies compared to unvegetated areas (Critchley et al., 1990; Strong et al., 2006). One study done in the saline Lake Grevelingen in the Netherlands showed that surface water temperatures above a canopy of *S. muticum* was 2.7°C warmer than surface water with no canopy (Critchley et al., 1990). The same study also showed that temperatures within the canopy was higher than in open water, but also that the water below the canopy was considerably cooler than water outside the canopy. Another study also using *S. muticum* as well as *Saccharina latissima* (previously known as *Laminaria saccharina*) showed similar results with higher temperatures within canopies of both species, compared to unvegetated waters. (Strong et al., 2006). Below *S. muticum* canopies, close to the sediment, the temperature was lower than water close to the sediment of unvegetated areas. However, below *S. latissima* canopies the temperature was the same as unvegetated areas (Strong et al., 2006). The warmer surface water is explained to be a result of surface water exchange being reduced by the high density of the canopy (Strong et al., 2006). Additionally, the warmer surface water could also be the result of the *S. muticum* canopies colour and morphology as the dark colour absorbs a lot of light and the standing morphology allows it to reach the surface water completely (Strong et al., 2006). The cooler water under canopies is explained as a result of shading (Critchley et al., 1990; Strong et al., 2006).

Several studies using other macrophytes, both freshwater and marine, have also shown similar results, where temperatures are affected by macrophytes due to shading or solar radiation (Coombes et al., 2013; Dale & Gillespie, 1977; Michael & John, 1994; Willis et al., 2017). One study showed that with a larger macrophyte biomass the temperatures near the bottom were lower, while surface temperatures were higher (Dale & Gillespie, 1977) This stratification of temperature was explained to be a result of an increase in shading with a higher macrophyte biomass, meaning less solar radiation penetrating the water column (Dale & Gillespie, 1977). They also mention this effect to be reinforced by the macrophytes ability to reduce water movement, which is also why the surface water is warmed up (Dale & Gillespie, 1977). The study also stated that macrophytes can convert radiation energy to heat, warming the surrounding water (Dale & Gillespie, 1977). Another study done in the marine waters of south-west England showed that the macroalgae *Fucus* spp. can lower the temperature maxima and range with 25% and 56% respectively, compared to areas without seaweed (Coombes et al., 2013). Another study using the floating freshwater macrophytes *Lemna* sp. and *Azolla* sp. also showed lower water temperatures below the macrophytes, as a result of shading (Michael & John, 1994). Lastly, a forth done in a stream could correlate increased macrophyte biomass to a decrease in surface water temperature below the macrophytes (Willis et al., 2017). Their results showed that an increase in biomass lead to a decrease in solar radiation reaching the water, which in turn reduced stream heating, temperature maxima and temperature variability.

In addition to the effect macrophytes have on local water temperatures, they can also affect sediment temperatures (Gilson & Davies, 2020). One study used the marine macrophyte *Ascophyllum nodosum*, which normally grows on hard substrates but can also grow within soft substrates using emerging rocks and other hard surfaces as holdfasts (Gilson & Davies, 2020). They wanted to extend knowledge on how macroalgae canopies affect soft sediments, as much of previous research had been done focusing on hard substrates. It was shown that temperature extremes were reduced in the sediment below canopies, compared to open sediment areas (Gilson & Davies, 2020). During the colder months of December and January the sediment temperatures below the canopy were around 2°C higher, while they were around 2-4°C lower in the warmer months of March and May (Gilson & Davies, 2020). They suggest the warming effect in the colder months to be the effect of the canopy acting as a buffer, protecting the underlying...
sediments from the cooler ambient temperatures and thereby warming it (Gilson & Davies, 2020). The cooling effect in the warmer months are explained as a result of shading from the macroalgae canopy (Gilson & Davies, 2020).

A few of the above referenced studies show results indicating that macrophytes create a thermal stratification in the water column, with higher surface temperatures and lower below-canopy temperatures (Critchley et al., 1990; Dale & Gillespie, 1977; Strong et al., 2006) This phenomenon has also been studied in more detail, where results show that thermal stratification occurs when macrophytes occupy at least 50% of the water column height (Vilas et al., 2017). The greatest observed difference in temperature between surface water and sediment bed was 10°C (Vilas et al., 2017). Thermal stratifications with similar temperature differences have also been recorded with temperature differences of 7.1°C (Dale & Gillespie, 1977), 9.2°C (Critchley et al., 1990), and 2°C and 13°C depending on macrophyte species (Strong et al., 2006).

4.4 Effects on water movement

Surface water, just above macrophytes, can have a higher temperature compared to open water surface water (Critchley et al., 1990; Dale & Gillespie, 1977; Strong et al., 2006; Vilas et al., 2017). But also, the surface water may be cooled by emergent macrophytes, like reed, that grow out of the water column to shade it (Lövstedt & Bengtsson, 2008). The difference in temperature between an area with macrophytes and an open water area can cause local water currents (Lövstedt & Bengtsson, 2008; Michael & John, 1994). Surface water currents directed towards reed vegetation of speeds between 0.1-2.3 cm/s have been observed and measured (Lövstedt & Bengtsson, 2008). These currents occurred because of temperature differences of 0.5-1.2°C between warmer, open water and cooler, vegetated areas as a result of shading from the vegetation (Lövstedt & Bengtsson, 2008). The currents were also determined to not be affected by wind speed, but are what the authors call density-driven currents (Lövstedt & Bengtsson, 2008). Similar results have been shown looking at temperature differences under floating macrophytes, where surface water flows from illuminated open water towards the cooler shaded area (Michael & John, 1994). This is also the result of density differences as the cooler water sinks and gets replaced by the warmer surface water.

The water exchange, both horizontal and vertical, has been shown to be substantially reduced by macrophytes (Vilas et al., 2017). When the canopies reach the water surface, horizontal water exchange between the surface water above canopy and open water can be reduced as the water gets more or less trapped in the canopy (Vilas et al., 2017). Vertical water movement can also be reduced by the thermal stratification caused by macrophyte canopies growing tall enough (Vilas et al., 2017). As explained in section 4.3 the surface water above a macrophyte canopy can be warmed up at the same time as the water under the canopy is cooled. This causes a thermal stratification, i.e. a thermocline, which can reduce vertical water exchange because of density differences (Vilas et al., 2017). Seagrass beds have also been shown to reduce near-bottom water movement by 70-90%, as well as reducing high frequency wave velocities by 20% compared to unvegetated areas (Hansen & Reidenbach, 2012). Macrophytes can also decrease flow velocity of streams, with an increase depending on macrophyte biomass (Willis et al., 2017). Results of up to an 111% decrease in flow velocity has been shown when the macrophyte biomass increased with 264% from winter to late summer (Willis et al., 2017). One study however, has also shown no conclusive effect on water movement by macrophyte canopies, in that case using the kelp *Ecklonia radiata* of western coastal waters in Australia as the study species (Wernberg et al., 2005)
5. Discussion

5.1 Discussion of main results

Overviewing the results, it is clear aquatic macrophytes do indeed influence their microclimate. The different aspects of microclimate affected can be hard to single out as many of them seem to be connected and affect each other. For example, the effects on light from shading can affect the water and sediment temperature. Further, the negative effects on water movement from macrophytes can affect sediment resuspension, in turn affecting water clarity, bringing us back to the starting effect, which could possibly also influence water temperature (Fig. 1). Looking at this, there seems to be some sort of feedback loop mechanisms happening where many of the aspects of the microclimate associated with macrophytes flow, come together and also goes back to influence the macrophyte itself. Similar feedback loops have been seen in previous studies, looking at feedback mechanisms in seagrass ecosystems, but with the basis of how seagrass density is affected (Maxwell et al., 2017).

Figure 1. Conceptual model of mechanisms influencing macrophyte microclimate, including knock on effects and feedback mechanisms. The light blue field shows effects in the water column, and the light brown field shows effect in the sediment. Blue arrows indicate positive effects and red arrows indicate negative effects. The effects on temperature are indicated both as negative and positive as they can depend on ambient water temperature varying with seasons. The dashed lined arrows indicate potential effects.
5.1.1 Water chemistry effects

The effect macrophytes have on pH has the potential to be both positive and negative for surrounding organisms and ecosystems. From the literature review it is clear that macrophytes have a positive effect on pH. Potentially the increase in pH from macrophytes could help control or buffer ocean acidification, which is a growing problem with continued CO₂ emissions (Caldeira & Wickett, 2003). A higher pH may also affect other organisms positively, especially calcifying and shell-forming organisms. An increase in pH also means an increase in carbonate ions which calcifying and shell-forming organisms are dependent on (Kleypas et al., 2006). The effects macrophytes have on pH may thus increase the calcification rates of other organisms. This has also been shown in other studies, both locally close to macrophytes (Semesi et al., 2009), and in habitats downstream from macrophytes (Anthony et al., 2011; Unsworth et al., 2012). In addition the production of carbonates from certain macrophytes (Pukacz et al., 2014) could possibly further support this positive effect on calcification rates. Important to note is, however, that an increase in pH can have negative effects as well as a too high pH can be toxic and impair macrophyte growth: a negative feedback mechanism (Fig. 1) (Beer et al., 2006).

The other main influence macrophytes have on the aspects of microclimate concerning water chemistry is on oxygen. This aspect of microclimate is essential for all respirating organisms meaning macrophytes play an important role in aquatic ecosystems. The oxygen production from macrophytes has the potential to help systems in or of risk of hypoxia as macrophytes, as mentioned in the results, can pump oxygen into sediments through their roots (Burdige & Zimmerman, 2002). Increasing the oxygen in sediments is important as hypoxic and anoxic zones is a growing problem in aquatic environments (Diaz & Rosenberg, 2008) An indirect effect of this on microclimate is the increase in sediment alkalinity from carbonate dissolution via aerobic respiration (Burdige & Zimmerman, 2002). This can potentially further help the local system with buffering against ocean acidification.

The hypoxic conditions of many aquatic environments can also create toxic environments. Under aerobic conditions release of hydrogen sulphide may occur, which has toxic properties (Folmer et al., 2012). However, this process may be controlled and reversed with the help of the macrophytes themselves. There are certain symbionts living on bivalves which have the ability to oxidise hydrogen sulphide (van der Heide et al., 2012). As mentioned in section 4.1, macrophytes can release oxygen from their roots, this oxygen is utilised by the sulphide oxidising symbionts making the sediments less toxic.

5.1.2 Effects on light

My results show both positive and negative effects on light from macrophytes. On one hand they directly decrease the light reaching the bottom by shading (Critchley et al., 1990; Kennelly, 1989; Strong et al., 2006; Wernberg et al., 2005). But on the other hand, they can also indirectly increase how much light penetrates the water column by decreasing the amount of resuspended sediment particles and nutrients in the water (Carr et al., 2010; Hansen & Reidenbach, 2012; Maxwell et al., 2017). However, these two types of effects on light most likely influence different parts of the microclimate. I would assume shading to mostly affect the microclimate below a macrophyte canopy, while the clearing of the water column probably affects below-canopy microclimate as well as above-canopy microclimate.

Clearer waters and more light penetration throughout the water column can give macrophytes the right conditions to be able to grow at greater depths (Carr et al., 2010). Therefore, macrophytes themselves may influence their own distribution by affecting microclimate: a positive feedback mechanism (Fig. 1).
The trapping of nutrients and sediment particles by macrophytes could have the potential to affect water temperature as well. The reasoning for this I derive in the main mechanism suggested by Maxwell et al. (2017), which suggests that seagrass traps nutrients and sediment particles which increases light penetration. My thoughts continuing from this is that an increase in light potentially could increase temperature in and just above the macrophyte canopy. In an already warming macroclimate even higher microclimate temperatures may affect the macrophyte itself, as well as surrounding organisms and ecosystems, negatively.

Furthermore, the shading effect may also affect other organisms associated with macrophytes. Light-sensitive species can probably benefit from the shading, while understory primary producers are negatively affected. Overall, there is a possibility that these effects therefore could affect other organisms’ distribution, a phenomenon also seen in terrestrial vegetation (De Frenne et al., 2021).

5.1.3 Effects on water temperature

There are several studies showing temperature effects, both in the water column and in the sediment. The way these effects are produced by macrophytes seems to vary. Some of the studies mention shading as the main cause of a lowering effect on temperature (Coombes et al., 2013; Critchley et al., 1990; Dale & Gillespie, 1977; Michael & John, 1994; Strong et al., 2006; Willis et al., 2017), other studies have also seen warming effects and explain this as a result of absorption of solar radiation (Strong et al., 2006) or conversion of radiation energy to heat (Dale & Gillespie, 1977). Interestingly, only one study had a result of a higher temperature below macrophyte canopy (Gilson & Davies, 2020). This different result could be because of that study being partly done during a colder season than other studies, but maybe also because it uses a species not used in any of the other studies. The warming below the canopy can perhaps also be explained by similar mechanisms seen for microclimate under terrestrial vegetation. Under forest canopies ambient temperature minimums are higher because of heat retention (De Frenne et al., 2021). My hypothesis is that this mechanism could be the same for aquatic macrophytes, where the canopy works as a sort of insulating layer. All studies, but one, that I have found all seem to have conducted their experiments only during parts of the year when the temperatures are relatively high, or in climates with high temperatures. This could have effects on the results as vegetation, at least terrestrial, seems to have a warming effect on under-canopy microclimate only when the ambient temperatures are low enough. Because of the partly missing information about warming effects of macrophytes during cool ambient temperatures, I suggest more future research on how under-canopy temperatures are affected by macrophytes during both high and low ambient temperatures.

Another interesting finding is that macrophyte height compared to the depth of the water column seems to affect how substantial the effect on temperature is. A taller canopy seems to affect the temperature more, causing more significant thermal stratification (Vilas et al., 2017). This thermal stratification can also affect oxygen conditions, as the mixing of water is reduced with a stronger stratification. In that case, macrophytes could also indirectly contribute to hypoxia or anoxia instead of limiting it as mentioned before. The thermal stratification caused by shading and reduced water movement could therefore cause a negative feedback mechanism to the macrophyte and associated organisms (Fig. 1), which is also suggested by another study (Vilas et al., 2017). The surface water currents created by temperature differences because of macrophytes could potentially counter this stratification by mixing of the water. But to my knowledge these surface currents can probably only mix the top parts of the water column and may not affect the hypoxic bottom parts.
5.1.4 Variation between macrophyte species

At least one of the studies reviewed in the results have shown a difference between species in effects on microclimate (Strong et al., 2006). The difference shown concerns light absorption and under-canopy temperature between S. muticum and S. latissima, where a higher light absorption and lower under-canopy temperature was seen with S. muticum (Strong et al., 2006). This difference is probably due to the different morphologies of the two species, as S. latissima has a lower standing biomass making it less acceptable to absorption of light at the water surface, as well as reducing its shading effect. A difference in morphology might therefore give a difference in thermal stratification. Supporting this theory are results showing that thermal stratification depends on macrophyte canopy height in relation to water column depth (Vilas et al., 2017).

Adding to the variation of effects seen between species is the effects of plant density on pH. Differences in rates of pH increase and how much a macrophyte can increase the pH have been found (Beer et al., 2006). The rate of pH increase due to photosynthesis is largely dependent on the density of the macrophyte plants (Beer et al., 2006). Therefore, it seems like macrophytes with different morphologies affecting density should affect pH to different degrees. This knowledge could perhaps be important for example for future efforts in trying to decrease ocean acidification efficiently. Another difference which could be important for future conservation efforts is how different species affect oxygen levels. Some species have a far greater release of oxygen from the root than others (Sand-Jensen et al., 1982), which perhaps could be key knowledge trying to restore hypoxic or anoxic sediments. Overall, it seems like it is not the species per se that makes the difference. More likely is that macrophytes with different traits can influence microclimate differently, both within and between species. This can also be seen when looking at how macrophytes affect different aspects of their ecosystems (Su et al., 2019). For example, plant height can affect water clarity and water chlorophyl levels in different ways (Su et al., 2019).

For this study I chose to use both marine and freshwater studies. This decision was made on the basis that marine and freshwater studies can give complementary data, which at least one other review article also has concluded (Madsen et al., 2001) and also to overall get more data for the results. In future studies it therefore could be interesting to look at marine and freshwater macrophytes separately. Some differences have already been shown when it comes to oxygen release from rooted macrophytes (Sand-Jensen et al., 1982). I believe at least some of the effects on microclimate would differ between marine and freshwater environments, especially the effects on water chemistry. However, some effects may not differ at all, for example effects on water movement may be more dependent on macrophyte morphology than salinity. It may also be interesting to look at different habitats separately, for example tropical vs temperate, as well as comparing different species. What could be interesting about this is that there may be a difference in how macrophytes of certain types influence their microclimate, as indicated in this study. Looking at for example marine and freshwater species separately could give more knowledge about how for example different traits may influence microclimate differently. Separating them could in that case rule out the habitat or salinity as a factor influencing possible differences, giving more focus to the actual traits of the macrophytes.

5.2 Similarities and dissimilarities to effects of terrestrial vegetation

Looking at my results there are some similarities between effects of terrestrial vegetation and aquatic macrophytes on microclimate. Firstly, both terrestrial and aquatic vegetation seem to have similar effects on temperature. High temperatures are clearly reduced below canopies in both terrestrial and aquatic
environments. The same can probably be said for low temperatures, which are increased under terrestrial canopies, and have been shown to be higher under aquatic canopies in at least one study (Gilson & Davies, 2020). Related to the effect on temperature is the effects on medium movement, i.e., wind and waves, and the effects on light. Both terrestrial and aquatic vegetation seems to reduce the movement of its surrounding medium (air and water), as well as reducing under-canopy light by shading and absorption of solar radiation. As both trees and aquatic macrophytes are primary producers having photosynthetic activity, they both also influence carbon dioxide and oxygen levels. However, there may also be some dissimilarities. For aquatic vegetation there seems to be more of a species or morphological aspect involved, which affects how different aquatic macrophytes influence microclimate. This can, according to some studies, also be seen in terrestrial vegetation, where differences in traits such as canopy height and leaf area density can influence how and how much microclimate is affected (Jucker et al., 2018; Landsberg & Gower, 1997). However, another study reviewing forest canopy effects on temperature have shown that factors such as tree type and height may not impact how much below-canopy temperatures are affected (de Frenne 2019). As there are contradicting results regarding this possible dissimilarity between aquatic and terrestrial vegetation, more studies are needed in both fields to confirm how different morphologies and traits of vegetation affects microclimate in different ways.

5.3 Importance for associated ecosystems

The microclimates provided by macrophytes are also important for other associated organisms. Some organisms are, for example, sensitive to light and heat and therefore depend on the shading effects of macrophytes to survive (Burnaford, 2004). This seeking of protection seems to be related to the level of abiotic stress experienced by the organism seeking refuge (Burnaford, 2004). With rising temperatures this could thus increase the importance of the effects of macrophytes on microclimate. Macrophyte canopies could also provide some sort of protection from other stressors such as wave exposure, as macrophytes can reduce water movement (Hansen & Reidenbach, 2012).

Furthermore, macrophytes have also been shown to provide some sort of protection from heat waves to some corals, protecting them from bleaching (Smith et al., 2022). This could indicate that the effects macrophytes have on their microclimate could be important to buffer climate change, as they lower temperature extremes, and to provide refuge for temperature sensitive organisms. Another sort of protecting mechanism of macrophytes on corals among other organisms, is how they can increase pH and calcification rates. The effects macrophytes have on pH may enhance the resilience of calcifying organisms to ocean acidification which could be of importance as ocean acidification is a growing problem (Unsworth et al., 2012). This effect may also be of importance when constructing for example marine protected areas as macrophytes also has a downstream effect on pH and calcification (Anthony et al., 2011; Unsworth et al., 2012).

Distribution of organisms could also be affected by microclimate. Effects of terrestrial vegetation on microclimate has been suggested to influence the distribution of organisms (De Frenne et al., 2021) and this has been shown in aquatic environments as well (Burnaford, 2004). As organisms seek refuge from stressors in microclimates of macrophytes, individual, population and species distribution could be influenced.
5.4 Importance for macroclimate

The influence of aquatic macrophytes on microclimate could be important in trying to counteract a number of environmental threats seen today. As mentioned in section 5.1.5, the effect macrophytes have on microclimate seems to be able to decrease effects of ocean acidification and hypoxia or anoxia. Another big environmental problem today is climate change and global warming. When assessing the effects that climate change has on the environment, macroclimate data is usually used (De Frenne et al., 2021). This could give a misleading picture of what conditions organisms and even whole ecosystems experience as this kind of data do not take microclimate into account, which studies done on terrestrial environments have also reported (De Frenne et al., 2021). As I have shown in this review microclimate can evidently deviate from macroclimate. It is therefore important to also take this into account, not only in terrestrial forests but in aquatic environments as well, when predicting and trying to better understand how biodiversity and function of ecosystems associated with macrophytes will cope with changing climate.

The microclimates that aquatic macrophytes provide could work as refuges for other aquatic organisms, especially when looking at temperature. Other studies have shown that in marine environments climate change can create locally different marine microclimates (Woodson et al., 2019). The implication of my review looks to point to the same conclusion where microclimates associated with macrophytes can be different from unvegetated areas. With the effects macrophytes have on local water and sediment temperature one may speculate that aquatic macrophytes could work well as thermal refugia for other organisms in today’s changing climate. With similar ideas suggested for forest environments to work as thermal refugia (De Frenne et al., 2021), macrophytes could potentially work as some sort of buffering environment to climate change where organisms could avoid extreme heat events or even have the time to adapt to the global climate changes. Even though the microclimates of macrophytes could work as refuges for other organisms, marine microclimates are as of now not considered when constructing marine protected areas (Woodson et al., 2019).

However, it is also important to note that aquatic macrophytes themselves are also affected by climate change in several ways (Duarte et al., 2018). They are affected directly by the rising temperatures, as well as other indirect effects of global warming such as ocean acidification (Duarte et al., 2018). Not only could this have effects on their influence on microclimate, but it could also lead to a loss of many aquatic macrophytes, which in turn could decrease the chances of them being used as refuges by other organisms too.
6. Conclusions

To answer my research question, microclimate is influenced by aquatic macrophytes in several ways. The water chemistry, including pH, carbonates, CO$_2$, and oxygen levels is affected, as well as light, temperature, and water movement. These effects can relate to each other, influence the macrophyte itself via feedback mechanisms, and also directly or indirectly influence associated organisms and ecosystems.

This review shows that the effects of macrophytes on microclimate can be important for associated organisms and ecosystems in the changing macroclimate we see today. I therefore suggest that microclimate should also be considered when looking at climate change effects on ecosystems, and that it should also be considered in marine and aquatic conservation efforts.

In this review I have been trying to look at different aspects of microclimate separately, which has been proven hard. What is clear is that the different effects macrophytes have on microclimate in turn also affect one another in several ways, creating knock-on effects as well as feedback mechanisms. For future research it could therefore be interesting to try and look at these knock-on effects and feedbacks within the boundary of microclimate. As this review looks at all aquatic macrophytes at once and since different species have been shown to have different influence on microclimate, additionally I think it could also be important to look at different types of macrophytes separately when it comes to microclimate.

The potential of macrophytes to work as thermal refuges or “buffering environments” to climate change is also something I think is worth doing more research on in the future. As climate change is a global problem threatening ecosystems all over the world in different environments, having habitats which could buffer these effects could be essential.

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8. References


