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UNIVERSITY OF HELSINKI

# Exploring the environmental drivers of invasive moss animal *Pectinatella magnifica* statoblast dispersal in Kokemäenjoki watercourse

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Master's thesis

Author:
Sara Virkki

Supervisors:
Leena Nurminen
Kirsi Kuoppamäki

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Helsinki

HELSINGIN YLIOPISTO

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| Tekijä - Författare – Author<br>Sara Virkki | | |
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Tiivistelmä - Referat - Abstract

Akvaattiset vieraslajit uhkaavat kotoperäisiä lajeja, sekä vesiekosysteemejä ja niiden toimintaa. Pohjois-Amerikasta kotoisin oleva hyytelösammaleläin (*Pectinatella magnifica*) (Leidy 1851) on yhdyskuntana elävä sammaleläin, joka on viime vuosikymmenten aikana levinnyt Eurooppaan ja Aasiaan. Laji havaittiin Suomessa ensimmäisen kerran vuonna 2006 Saimaan kanavassa, minkä jälkeen se on levinnyt myös Kokemäenjoen vesistöön. Laji leviää pääasiassa vapaasti kelluvien ja talvehtivien statoplastien avulla, mutta leviämiseen vaikuttavat tekijät ovat edelleen huonosti tunnettuja. Tämän pro gradu -tutkielman tavoitteena on selvittää *P. magnifican* statoplastien runsauden ajallista ja paikallista vaihtelua sekä statoplastien ja lajin leviämiseen vaikuttavia tekijöitä. Leviämisprosessien taustalla olevien tekijöiden ymmärtäminen luo perustan tehokkaammille vieraslajin seuranta- ja hallintamenetelmille.

Statoplastien passiiviseen keräämiseen käytettiin inkubaatiolevyjä, joita pidettiin vedessä 24–30 päivän ajan kymmenellä eri näytteenottopisteellä Kokemäenjoen vesistössä vuoden 2024 kesän ja syksyn aikana. Statoplastien runsauteen vaikuttavien tekijöiden selvittämiseen käytettiin yleistettyä lineaarista sekamallia (GLMM). Lisäksi tutkielmassa verrattiin fysikaaliskemiallisia ominaisuuksia permutationaalista monimuuttuja-analyysiä (PERMANOVA) käyttäen järvien välillä, joissa hyytelösammaleläintä esiintyi ja joissa sitä ei esiintynyt.

Tulokset osoittivat, että järven pyyhkäisymatka, etäisyys merkittävistä venesatamista sekä etäisyys alueen ensimmäisestä lajin leviämiskohteesta vaikuttivat kaikki merkitsevästi ja negatiivisesti statoplastien havaintomääriin. Lisäksi vuodenajalla oli merkitsevä vaikutus näiden tekijöiden vaikutuksen voimakkuuteen. Lukuun ottamatta etäisyyttä alueen ensimmäisestä hyytelösammaleläimen esiintymästä, negatiiviset vaikutukset olivat muuttujilla voimakkaampia syksyllä kuin kesällä. Tulokset viittaavat siihen, että vuodenaika vaikuttaa statoplastien välityksellä tapahtuvaan leviämisprosessiin. Mallien ennusteiden mukaan suojaisilla alueilla, jotka sijaitsevat lähellä alkuperäistä leviämiskohdetta sekä veneilyliikennettä, esiintyy todennäköisesti enemmän statoplasteja, ja statoplasteja esiintyy runsaammin laajemmalla alueella kesäaikaan. Vesistöjen Fysikaalis-kemiallisissa ominaisuuksien ei havaittu vaikuttavan lajin esiintymiseen.



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Tiivistelmä - Referat – Abstract

Invasive species pose a threat to native aquatic species and ecosystems. The magnificent bryozoan (*Pectinatella magnifica*) (Leidy 1851) is a colonial sessile bryozoan native to North America, that has been spreading throughout Europe and Asia over past decades. Observed for the first time in Finland in 2006 at the Saimaa canal, the species has since spread to Kokemäenjoki watercourse. The species spreads mainly by free-floating overwintering survival pods known as statoblasts, yet the detailed dynamics and factors affecting species dispersal are still largely unknown. This master's thesis aims to fill knowledge gaps about the spatiotemporal variation of *P. magnifica* statoblast abundance and seeks to find environmental factors contributing to the species dispersal dynamics. Understanding drivers behind dispersal pressures creates a foundation for developing better monitoring and managing practices for this invasive species.

Incubation plates were used to passively collect statoblast for 24-30 days in 10 different sites during summer and fall of 2024 in Kokemäenjoki watercourse. Generalized mixed effects modeling (GLMM) was used to determine factors affecting statoblast abundance, and to predict possible statoblast abundance across a larger area. In addition, permutational multivariate analysis of variance (PERMANOVA) was used to compare physicochemical profiles of local lakes with and without *P. magnifica,* to determine if occurrence of species is affected by water quality parameters

Results showed that lake fetch, distance from major boating ports and distance from initial invasion all had a statistically significant negative effect on statoblast accumulation rates, with season significantly affecting the strength of these effects. Excluding distance from origin, negative effects were stronger in fall than in summer, indicating that dispersal via statoblasts is not a static process, but dynamic. Model predictions indicate that low-fetch areas closer to initial invasion and near boating traffic are likely to have higher amounts of statoblasts present in the water column, and statoblasts are present in a larger area during summer. No significant difference was found in the physicochemical profiles between invaded and non-invaded lakes, which is supported by earlier results.



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invasive species, *Pectinatella magnifica*, statoblasts, dispersal

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## Abbreviations

TP = Total phosphorus
TN = Total nitrogen
DO = Dissolved oxygen
SDI = Shoreline development index
DFO = Distance from origin
DCP = Distance to closest port
GLMM = Generalized linear mixed effects model
AIC = Akaike's information criterion
XPS = Extruded polystyrene
PCoA = Principal coordinates analysis
PERMANOVA = Permutational analysis of variance
LB = Lempäälä beach
LBP = Lempäälä boating pier
VP = Vaihmala pier
KP = Kärjenniemi pier
SGP = Sointula guest pier
KC = Kyhkysenniemi cape
LSB = Lehijärvi swimming beach
IB = Idänpää beach
AS = Alajärvi slipway
TB = Tervaniemi beach

Table of Contents

1. INTRODUCTION ..... 1
1.1 Invasive species ..... 1
1.2 Overview of *P. magnifica* ..... 1
1.3 Life cycle of *P. magnifica* ..... 3
1.4 Ecological significance ..... 5
1.5 Global spread of *P. magnifica* ..... 6
1.6 Occurrence in Kokemäenjoki- water system ..... 6
1.7 Aim of the study and research questions ..... 8
2. MATERIALS AND METHODS ..... 10
2.1 Study site and area ..... 10
2.2 Incubation plates ..... 11
2.3 Statoblast density modelling ..... 12
2.3.1 Model variables ..... 13
2.3.2 Model validation and overfitting assessment ..... 14
2.4 Statoblast density prediction ..... 14
2.5 Lake differences in physical and chemical traits ..... 15
3. RESULTS ..... 16
3.1 Statoblast accumulation rate ..... 16
3.2 Statoblast accumulation rate by sampling device components ..... 16
3.3 Variables affecting statoblast accumulation rate ..... 17
3.4 *P. magnifica* dispersal pressure ..... 20
3.5 Physicochemical differences between lakes ..... 21
4. DISCUSSION ..... 23
4.1 Spatiotemporal differences in statoblast abundance ..... 23
4.2 Sampling device component performance ..... 23
4.3 Physical drivers of statoblast dispersal ..... 24
4.4 Seasonal dynamics ..... 26
4.5 Spatial distribution of dispersal pressure ..... 27
4.6 Physicochemical differences between study lakes ..... 28
4.7 Limitations ..... 28
4.8 Future research and implications ..... 30
5. CONCLUSIONS ..... 31
6. ACKNOWLEDGMENTS ..... 32
7. REFERENCES ..... 33

# 1 Introduction

## 1.1 Invasive species

Invasive species pose major threats to natural ecosystems. Most invasive species are introduced to their non-native range due to human activity, and the amount of invasive species is expected to increase due to global warming (Hulme et al., 2024). Invasive aquatic species can displace native species, alter biodiversity function (Zhu et al., 2006), introduce diseases or parasites (Costello et al., 2021) and cause substantial economic loss via biofouling (Nakano & Strayer, 2014). One such species is the magnificent bryozoan (*Pectinatella magnifica*). *P. magnifica* was first described by Leidy in 1851 in Philadelphia, PA, USA (C. M. Brooks, 1929) and it is considered to be native to eastern North America, although it has since then been observed throughout the continent (Ricciardi & Reiswig, 1994), and around the globe (Balounová et al., 2011). *P. magnifica* has not yet been classified as a harmful invasive species in Finland, but the impacts of the species remain still poorly understood (Vuorio et al. 2019).

## 1.2 Overview of *P. magnifica*

*P. magnifica* is a freshwater bryozoan belonging to the phylum Bryozoa, class Phylactolaemata and family Pectinatellidae (Wood 2001). Bryozoans are sessile, aquatic invertebrates characterized by modular growth, where individuals known as zooids function collectively as a colony (Wood, 2001). Species in the class Phylactolaemata occur only in freshwater environments and are distinguished by their ability to produce asexual survival pods known as statoblasts (Wood 2001). *P. magnifica* is the largest freshwater bryozoan (Wilcox, 1906) and a colony can grow up to 65 cm in diameter and weigh up to tens of kilograms (Joo et al., 1992; Kollar et al., 2016). Large colonies are formed by smaller rosette-like colonies that consist of 12-18 individual zooids (C. M. Brooks, 1929). Each zooid is made of a chitinous protective body wall and a polypide, which contains the organ system of the animal (Wood, 2005; Wood & Okamura, 2005). The mouth of the polypide is surrounded by a ring of ciliated tentacles, called a lophophore, which is used to filter food such as phytoplankton and bacteria from the surrounding water (C. M. Brooks, 1929; Wood, 2001, 2019). Zooids only appear on the surface of the colony, where food can be filtered (Henchman & Davenport, 1913), and secrete a gelatinous mass, which makes up the center of the colony (Kang & An, 2015). As the gelatinous center grows, so does surface-area for the zooids, which allows for colony growth by asexual budding (Henchman & Davenport, 1913).

Colonies grow most often as spherical attached to substrate from the core or as a gel-like coating directly on substrate (Kang & An, 2015), and sometimes as free-floating (C. M. Brooks, 1929). The

sessile colonies grow most commonly attached to submerged branches, reeds, roots or bare substrate (C. M. Brooks, 1929; Joo et al., 1992; Kang & An, 2015; Starunova et al., 2021), as well as human built structures like piers, and boating or fishing gear (Wang et al., 2017; Vuorio et al., 2018). Colonies are most abundant in the littoral zone, where water is warm, shallow and growing substrate is available, but have been reported even in depths of 3 m (Okamura & Hatton-Ellis, 1995; Starunova et al., 2021).

*P. magnifica* is found in a wide range of freshwater habitats, including both lotic and lentic systems, and appears to require moderate water movement (Wood, 2001). Although most commonly associated with slow-flowing waters (Szekeres et al., 2013), *P. magnifica* has also been recorded in lotic environments with water current velocities of up to 15.5 cm $s^{-1}$, demonstrating a tolerance for moderate flow conditions (Jo et al., 2014). Wood and Okamura (2005) hypothesize that strong water flow may damage the structures of individual zooids. Turbidity appears to play a complex and somewhat debated role in habitat suitability. Cooper and Burris (1984) reported that *P. magnifica* is averse to highly turbid waters, suggesting that excessive suspended sediments may interfere with feeding efficiency or colony stability, yet ambient water flow is thought to also increase feeding and growth rates (Wood & Okamura, 2005).

Temperature is considered to be the most important growth-limiting factor for *P. magnifica* colonies. According to multiple authors, colonies begin growing when water temperature reaches a temperature of 15-20°C, and zooids hatch and grow faster in warmer water (Brown, 1933; Dendy, 1963; Wood, 2005; Balounová et al., 2011; Ježková et al., 2018). Growth halts when temperatures drop below 20°C during growing season (Balounová et al., 2011) and most colonies are reported to regress and disintegrate when water temperature reaches below 15°C for a maintained period of time (Brown, 1933). Smaller colonies with immature statoblasts are reported to tolerate lower temperatures, and zooids have been reported to tolerate a temperature of 10°C (C. M. Brooks, 1929; Brown, 1933).

Nutrient availability is one of the most common lake chemistry parameters limiting and enabling species spread and abundance (Wetzel, 2001), but doesn't seem to be the driving factor behind *P. magnifica* invasions. *P. magnifica* has been observed in various different water systems ranging from oligotrophic (Šetlíková et al., 2013) to eutrophic (Musil et al., 2018) indicating a tolerance for a wide range of nutrient and thus, food availability. Wilcox (1906) describes the species to occur in clean and pure ponds and reservoirs, whereas Wood (2001) states that the species occurrence is linked to eutrophication.

Total phosphorus (TP) and total nitrogen (TN) concentrations in lakes and rivers with *P. magnifica* occurrences range from 0.005 to 0.38 mg $L^{-1}$ and 1.6 to 2.1 mg $L^{-1}$ respectively (Rodriguez &

Vergon, 2002; Šetlíková et al., 2013; Jo et al., 2014). According to Musil et al. (2018), species occurrence is positively linked to nitrate nitrogen ($NO_3 - N$) but negatively correlated with ammonium nitrogen ($NH_4 - N$). Although commonly considered a species of eutrophic waters, *P. magnifica* seems to avoid hypertrophic waters (Šetlíková et al., 2013; Musil et al., 2018).
Other chemical and biological parameters such as chlorophyll-a, alkalinity, dissolved oxygen (DO), pH and conductivity have also been considered as limiting environmental variables. *P. magnifica* is considered to be a species preferring alkaline waters, with pH of 8 (Ricciardi & Reiswig, 1994; Ko et al., 2019), but it has also been reported to occur in waters with a pH ranging from 6.0 to 6.8 (Joo et al., 1992; Šetlíková et al., 2013), and Everitt (1975) considered the species to prefer lower pH (< 7.1). It has been reported in water systems with a pH of 7.07 to 9.5 (Cooper & Burris, 1984; Balounová et al., 2011) and 7.05-9.93 (Ko et al., 2019) demonstrating a tolerance for a high variety of pH values. Conductivity in lakes with *P. magnifica* present, range from 50 µS $cm^{-1}$ (Balounová et al., 2013) to 530 µS $cm^{-1}$ (Rodriguez & Vergon, 2002). Chlorophyll-a levels range from 1 µg $L^{-1}$ to in South Korea (Jo et al., 2014), 36 µg $L^{-1}$ in Finland (Vuorio et al., 2018) and 0,77 to 43,5 µg $L^{-1}$ in France (Rodriguez & Vergon, 2002). Musil et al. (2018) found that DO saturation, pH and conductivity had a significant negative correlation with the incidence of the species, but chlorophyll-a did not.

## 1.3 Life cycle of *P. magnifica*

*Pectinatella magnifica* can reproduce both sexually and asexually (Ingold et al., 1984). Asexual reproduction of the species occurs by the release of survival pods called statoblasts, or by the budding of new zooids from the midventral wall of parental zooids (Ingold et al., 1984; Wood, 2001). The statoblasts of *P. magnifica* are circular or ovoid, around 1mm in diameter and radially surrounded by anchor-like hooks (Figure 1) (Davenport, 1900; C. M. Brooks, 1929; Kang & An, 2015). When released from the colony, statoblasts are covered by a thin layer of slime, which prevents the statoblasts from clinging to the colony (C. M. Brooks, 1929). The statoblast floats due to air-filled cells and makes distribution via water currents viable (C. M. Brooks, 1929; Wood, 2001). Once the covering slime has decayed, the hooks may attach to growing substrates such as aquatic plants and branches (C. M. Brooks, 1929). *P. magnifica* produces statoblasts throughout the growing season, but the majority of statoblasts are released during fall, when temperatures decrease and colonies degrade (Brown, 1933; Okamura & Hatton-Ellis, 1995; Wood, 2001). Most of the statoblasts will germinate after an overwintering period due to long maturation time (Brown, 1933; Bushnell & Rao, 1974; Okamura & Hatton-Ellis, 1995). Once attached, fully developed, and water temperatures have reached an appropriate temperature the statoblast opens and a single zooid called

ancestrula emerges, beginning the growth of a new colony (Okamura & Hatton-Ellis, 1995; Wood, 2001).

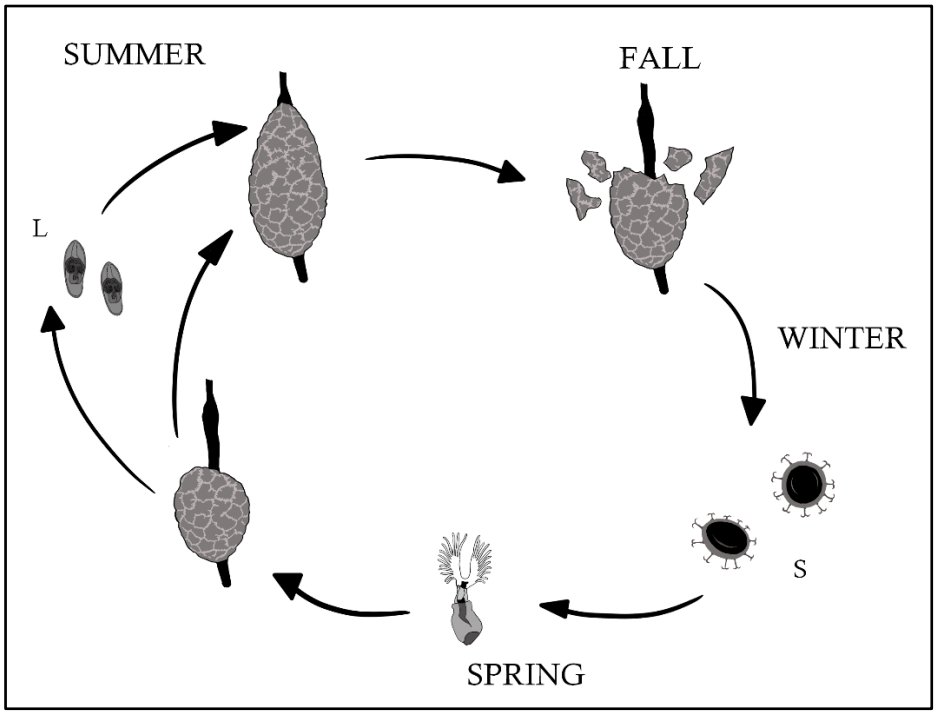



Figure 1. Annual life cycle of *P. magnifica*. L= Larvae, S= Statoblast. Asexual reproduction during the year produces overwintering statoblasts that germinate in the spring. Colony growth begins from a single zooid emerging from a germinated statoblast. Sexual reproduction during spring results in larval forms, that attach to suitable substrate within 24 hours. Colonies begin disintegrating during fall, releasing significant amounts of statoblasts.

Sexual reproduction in *P. magnifica* occurs early during the growing season for a short time period (Wood, 2001). Each individual zooid is a hermaphrodite, and fertilization of the egg happens within the zooid (Brown, 1933). Once fertilized, the larvae is kept within the zooid, before it is fully developed and released into surrounding water (Brown, 1933; Wood, 2001). Larvae of species belonging to the Phylactolaemate class are made of a ciliated outer mantle, with one to four fully formed zooids inside (Wood, 2001). *P. magnifica* larvae are free-swimming for a short time, and usually attach to a potential growing substrate within 1 to 24 hours (Brown, 1933; Wood, 2001). In the early stages of colony growth either from asexual or sexual origins, colonies are mobile (Wilcox, 1906). The gelatinous matrix of a colony is soft and malleable during early growth stages, which allows the colony to move around as individual zooids expand and contract (Wilcox, 1906). Young colonies grow rapidly as water temperatures rise, and in a few weeks colonies may reach a weight of 2 to 5 kg (Wood, 2001; Kang & An, 2015). *P. magnifica* colonies in the early stages of growth go through divisions, which indicates that multiple colonies close by may in fact originate from the same statoblast or larvae, instead of multiple (Wilcox, 1906). At the end of the growing season when water temperatures drop, colony growth stops, as statoblast production intensifies

(Wood, 2001). Colonies then disintegrate and release the rest of the statoblasts within the colony matrix (Brown, 1933; Wood, 2001). In an experiment by Brown (1933) a large colony with 850 $cm^2$ surface area released approximately 90,000 statoblasts.

## 1.4 Ecological significance

Ecological interactions between *Pectinatella magnifica* and the surrounding environment have for the most part been unexplored in Europe and especially in the boreal zone. Some mentions of species interactions exist, but an assessment of the species overall effect on an ecosystem has not been assessed even in its' native distribution area in North America.

Bryozoans feed on floating particles such as green algae, cyanobacteria, protozoans, rotifers, detritus and bacteria (Wood, 2019). Despite going through the digestive tract of *P. magnifica* ingested algal cells remained intact and unaltered, and cells found in fecal pellets were indistinguishable from those residing in surrounding waters, suggesting that despite ingesting algae and rotifers, the majority of their ingested diet consists of bacteria and related detritus (Wood, 2019). As *P. magnifica* colonies do not fully digest all algae, the fecal pellets they produce play a role in feeding benthic animals in a lake ecosystem, such as oligochaetes, microcrustaceans, water mites and immature insects (Wood, 2019).

The colony matrix of *P. magnifica* has been found to host a variety of microscopic algae and bacteria (Balounová et al., 2011; Šetlíková et al., 2013; Vlková et al., 2015), which have been found to affect surrounding waters (Šubrtová Salmonová et al., 2020). In addition to algae, Dendy and Sublette (1959) report that within the colony of *P. magnifica* resides chironomid larvae. In addition to chironomids, trichopteran larvae, snails, oribatid mites, flatworms and spongefly larvae have been observed to prey upon or reside in freshwater bryozoans (Cooper & Burris, 1984; Ricciardi & Reiswig, 1994; Okamura & Hatton-Ellis, 1995). Wood (2019) suggests that benthic animals reside within the colonies to feed on fecal pellets rather than the colony itself, while earlier literature hypothesized that perhaps invertebrates such as chironomids find shelter in holes in the colony (Wood, 2001).

Competition between bryozoans or *P. magnifica* and other filter-feeders has not been studied in its native range nor invaded range in Eurasia. However, fast growing robust colonies have been reported to cause lethal damage to different freshwater mussels such as *Cristaria plicata* (Wang et al., 2017) in China and *Dreissena polymorpha* (Ricciardi & Reiswig, 1994) in North America, due to the jelly-like colony preventing gas exchange and normal feeding (Ricciardi & Reiswig, 1994; Wang et al., 2017).

In their native range, statoblasts of bryozoans are often found in the stomachs of the bluegill (*Lepomis macrochirus*) and other fish (Dendy, 1963). Statoblasts have also been found to pass unharmed through waterfowl and fish guts (Brown, 1933), though it is unclear if their occurrence is by accident or if statoblasts were present as a result of intentional feeding on colonies.

## 1.5 Global spread of *P. magnifica*

The rapid spread of *P. magnifica* can be partly attributed to its ability to reproduce asexually through the release of statoblast survival pods (Davenport, 1900; Brown, 1933). *P. magnifica* has rapidly spread throughout Europe and Asia, with first occurrences in Europe reported in 1883 in Germany (Kraepelin, 1887; Zimmer, 1905) and 1972 in Japan (Mawatari, 1973). Since then, *P. magnifica* invasions have been reported in Austria (Schwaha & Bauder, 2021), Czech Republic (Šetlíková et al., 2013), Romania (NĂSTASE, et al. 2017), Serbia (Zorić et al., 2015), Bulgaria (Todorov et al., 2020), France (Rodriguez & Vergon, 2002), Poland (Kamiński, 1984), Hungary (Szekeres et al., 2013), Ukraine (Aleksandrov et al., 2014), Russia (Starunova et al., 2021), South Korea (Seo, 1998; Jo et al., 2014) and China (Wang et al., 2017). In Finland mass occurrences of *P. magnifica* were first reported in 2014 in the Vuoksi watercourse, and the first confirmed records of the species were made in 2006 close to the inlet to the Saimaa Canal (Vuorio et al., 2018).
In addition to statoblasts spreading due to natural water flow, waterfowl migration, improperly cleaned fishing equipment and distribution by fish metabolism are possible ways of statoblast dispersal in upstream or unconnected waterbodies (Rodriguez & Vergon, 2002; Balounová et al., 2013).

## 1.6 Occurrence in Kokemäenjoki- water system

First observations of *P. magnifica* in Kokemäenjoki water system were made in 2016 in Lake Kirkkojärvi, Lempäälä (Finnish Biodiversity Information Facility (FinBIF), 2026). This observation indicates that the species can spread between unconnected water systems. Since 2016 the species has been spreading to surrounding lakes, and although initially species spread happened downstream, it has also traversed upstream to Hämeenlinna area (Figure 2). Most observations have been made in Pyhäjärvi-Kirkkojärvi area and Hiidenjoki-Hattulanselkä, south of Hämeenlinna. Despite being in between these two hotspots, Vanajanselkä in Lake Vanajavesi has had no verifiable observations of the species up until 2024 (FinBIF, 2026).

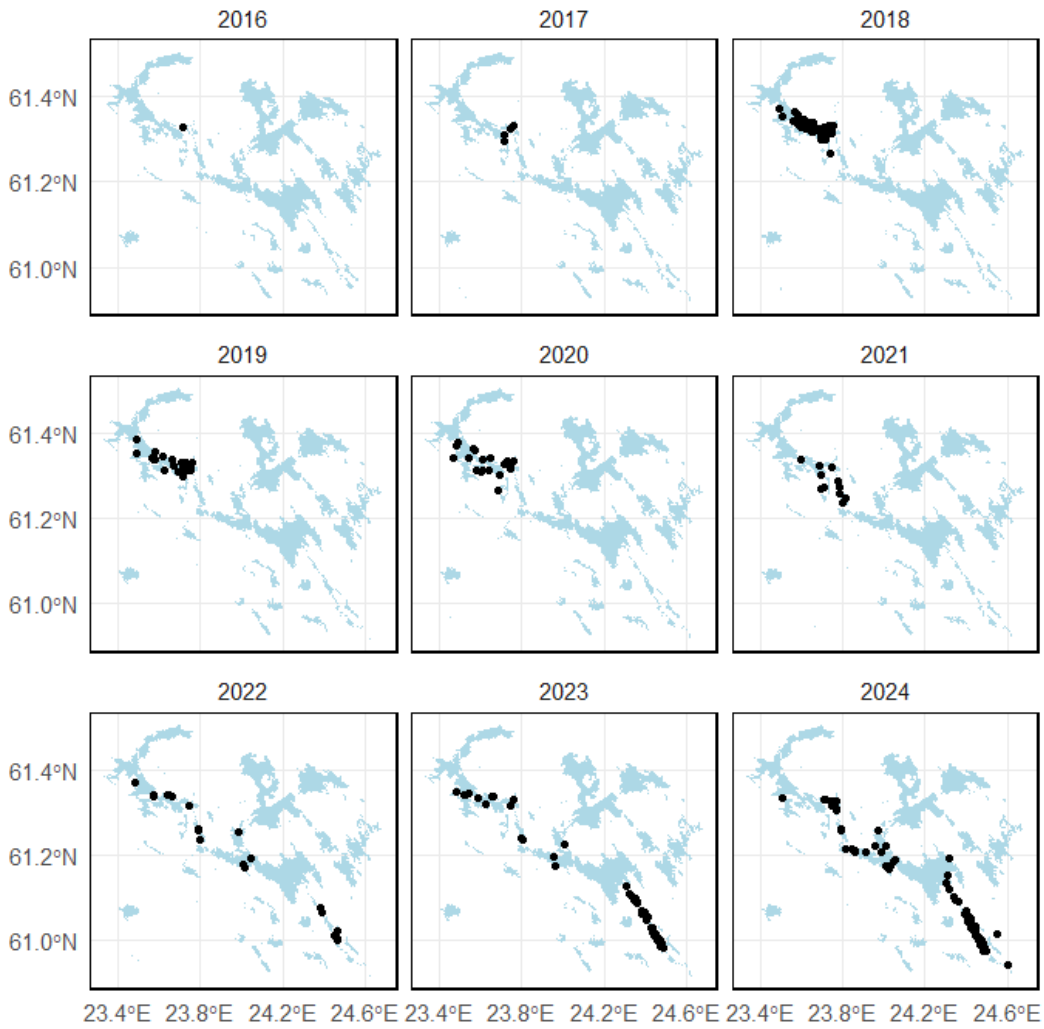



Figure 2. Spatial distribution of confirmed citizen observations of P. magnifica from 2016 to 2024. Panels represent individual years, showing the progressive expansion of observations across the study area. Data obtained from the Finnish Biodiversity Information Facility (FinBIF, 2026).

The dispersal dynamics behind the initial introduction of the species to Lempäälä have not been studied or reported. The main pathways of spread in the area, and Finland in general, are still unclear. Possible pathways include human activities such as swimming, boating, fishing, construction, international and national shipping, as well as dispersal via aquatic fauna such as fish and waterfowl (Rodriguez & Vergon, 2002; Balounová et al., 2013; Vuorio et al., 2018). Species spread downstream is likely due to natural water movement that carries floating statoblasts to new environments. The dispersal dynamics of produced statoblasts is an important factor in species spread and invasion potential.

## 1.7 Aim of the study and research questions

*P. magnifica* has established populations across Europe, with its Finnish range rapidly expanding in recent decades. Despite its growing presence, the ecological consequences of the spread of the species remain understudied. This gap is critical, given that bryozoans restructure aquatic food webs through filter feeding, competition, and nutrient cycling (Brown, 1933; Wang et al., 2017; Wood, 2019). Freshwater ecosystems are among the most vulnerable to biological invasions, as introduced filter feeders can rapidly alter nutrient cycling, phytoplankton communities, and the availability of food resources for other organisms (Dendy, 1963; Vlková et al., 2015; Wood, 2019). Understanding the invasion dynamics of *P. magnifica* is therefore both an ecological and a management priority, especially before the species reaches remaining unaffected lake systems.

A key obstacle to managing the spread of *P. magnifica* is that questions about its dispersal pathways remain unresolved. The species spreads primarily via statoblasts, yet statoblast abundance dynamics in natural water bodies has rarely been quantified. Existing literature on the water quality preferences and dispersal pathways of the species is scarce and often contradictory (Szekeres et al., 2013; Jo et al., 2014; Musil et al., 2018), with much resting on speculation (Rodriguez & Vergon, 2002; Vuorio et al., 2018; Starunova et al., 2021). In particular, the relative roles of passive hydrological transport, boating activity and waterfowl movement in enabling spread have not been specified. This limits the capacity to predict invasion risk, identify priority monitoring targets or design effective management.

Physical characteristics of water bodies are likely to play an important role in governing statoblast dispersal (da Silva et al., 2026), yet their influence has not been thoroughly examined. Fetch is the unobstructed distance over which wind can act on a water surface, and determines wave energy and surface mixing, which in turn influence the transport of buoyant propagules such as statoblasts (Zhang & Chen, 2023). Similarly, proximity to boating infrastructure such as marinas and guest piers may facilitate human-mediated dispersal, as statoblasts might adhere to boat hulls and equipment (Rodriguez & Vergon, 2002). Proximity to the initial invasion site may further structure abundance gradients if dispersal is limited by distance (Brown, 1933). Substrate type and time since first observation likely affect the establishment of colonies on a spatiotemporal scale. Quantifying the relative importance of these factors and how they interact across seasons is essential for building predictive models of the spread.

In addition, understanding whether *P. magnifica* exhibits preferences for particular physicochemical conditions could reveal which lake types are most susceptible to colonization. Water quality parameters including nutrient concentrations, pH, oxygen concentrations and conductivity are known to shape the distribution of many aquatic invertebrates (Elo et al., 2018; Banerjee et al.,

2022), yet their association with *P. magnifica* remains unclear and contradictory (Musil et al., 2018). Resolving this is important both for understanding the species' ecological niche and for identifying lakes at risk based on their water chemistry profiles.

This study addresses these gaps by combining statoblast monitoring using an incubation plate method that, to the best of my knowledge, has previously only been used by Ko et al. (2021), spatiotemporal abundance modeling and multivariate analysis of lake physicochemical and biological characteristics. Together, these approaches allow us to progress from qualitative descriptions of spread toward quantitative predictions of invasion pressure, and to evaluate which currently unaffected water bodies face the greatest risk of future colonization. Research questions and hypotheses are as follows:

**RQ1**: Are there temporal or spatial differences in the accumulation rate of *P. magnifica* statoblasts?

H1: Statoblast accumulation rates differ between locations and seasons and are higher in fall after colonies break apart.

**RQ2**: Are there differences in statoblast accumulation rate between different materials in sampling devices?

H2: Rough, complex surfaces allow for increased attachment of statoblasts, leading to a higher number of accumulated statoblasts compared to smooth surfaces.

**RQ3**: How do physical and environmental features such as season, fetch, distance from the initial invasion, distance from boating traffic, surrounding substrate type and invasion stage influence statoblast accumulation rates?

H3: Accumulation rates are higher during fall in low-fetch areas closer to initial invasion and boating traffic as well as in vegetated or built environments, compared to rocky shores.

**RQ4**: Which areas within the study area face the highest expected statoblast dispersal pressure, and does this vary between seasons?

H4: Low-fetch areas close to boating traffic and initial invasion are under greater statoblast dispersal pressure. Overall dispersal pressure is higher during fall when colonies break down.

**RQ5**: Do lake physicochemical characteristics such as pH, nutrient concentrations, conductivity, turbidity and color differ between lakes with *P. magnifica* and reference lakes without the species?

H5: Physicochemical characteristics do not differ between lakes with the species and those without.

# 2 Materials and methods

## 2.1 Study site and area

The project and study area encompasses the lakes and other water bodies surrounding Lake Vanajavesi. Lakes in the area are mostly in moderate ecological condition although some such as Äimäjärvi are considered to be in poor condition, while others, including Alajärvi, are classified as being in good condition (Aroviita et al., 2025; Finnish Environment Institute (SYKE), 2026). Locations for initial sampling sites, where *P. magnifica* was known to be present, were Lempäälä beach (LB) in Kirkkojärvi, Lempäälä boating pier (LBP) and Vaihmala pier (VP) in Hiidenselkä and Kärjenniemi pier (KP) in Kärjenniemenselkä, while Sointula guest pier (SGP) in Mallasvesi acted as a kind of reference, since no observations of *P. magnifica* colonies had been made in Mallasvesi (Figure. 3A). Additional reference sampling sites where *P. magnifica* had not yet been observed include Kyhkysenniemi cape (KC) in Äimäjärvi, Lehijärvi swimming beach (LSB) in Lehijärvi, Tervaniemi beach (TB) and Alajärvi slipway (AS) in Alajärvi, and Idänpää beach (IB) in Katumajärvi (Figure 3A).

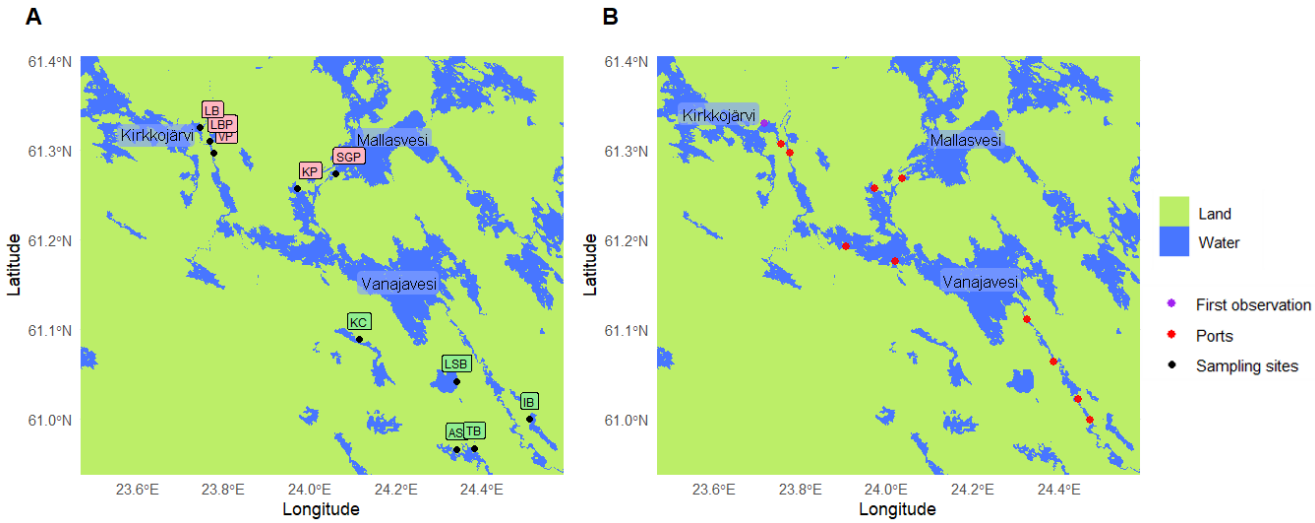



Figure 3. A. Study site with sampling points. Red labels indicate sites where *P. magnifica* statoblasts were found, and green those with no *P. magnifica* statoblasts. B. Study site with major ports and the first observation of the species in the study area.

The connected waterbodies from Hämeenlinna to Tampere, make up a popular boating and cruising route which has been in continuous commercial use since 1949 by Suomen Hopealinjat Oy (Väkiparta, 2014). Multiple stops of the route as well as other major boating ports are located within the study area (Figure 3B). Though the area consists of many smaller slipways and piers, the ports chosen for this study were local cruising ship Hopealinjat stops, as well as Valkeakoski port, as it is a major boating pathway to the northeastern lakes of the system such as Mallasvesi and

Pälkänevesi. Kärjenniemi dock, operated by Hopealinjat was also chosen. Despite not being an official stop for the cruises, it is used for the maintenance of ships, including Hopealinjat cruise ships.

## 2.2 Incubation plates

Extruded polystyrene (XPS) incubation plates were used to collect statoblasts from the water column (Figure 4A). Plates were modeled after Ko et al. (2021) with dimensions of 15x15x5cm. Plates were pierced through the middle and tied to bricks using a 1.5 m long and 4 mm wide polyurethane twine. Incubation plates were then left in place for multiple weeks to catch possible floating statoblasts. This method was chosen for statoblast monitoring due to having a higher detection sensitivity than other common methods such as water filtering (Ko et al., 2021). The sampling devices were divided into two components for analysis, panel and string, to compare how effective different materials were in capturing statoblasts. Statoblast observations with incubation plates were done twice in 2024: first in the summer 27.6.-26.7. and later in fall 22.10.-14.11. to test the variability in statoblast accumulation rate and occurrence on a temporal scale. The summertime period was chosen to represent the statoblast abundance during growing season and fall to capture the abundance of statoblasts after colony degradation and statoblast release.

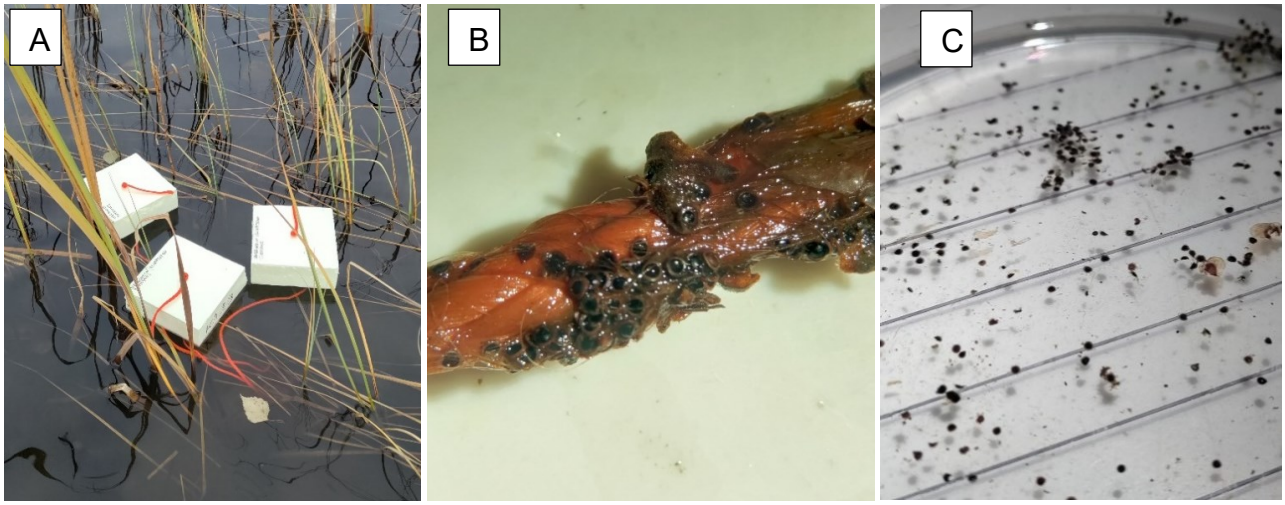



Figure 4. A. Sampling devices consisting of panel and string component deployed in a study lake in fall. B. Statoblasts attached to the string component of a collected sampling device. C. P. magnifica statoblasts collected from a sampling device into petri-dish.

In the first sampling period, 30 plates were placed for 34 days in four different locations in lakes with *P. magnifica* present and one location without *P. magnifica*. In study sites KP and SGP, 9 plates were set up in 3 sets of 3 in differing environments. In LBP and VP 4 plates were put in 2 sets of 2 and in LSB 4 plates in one spot. Sets within a sampling site were placed in areas with different surrounding substrates such as vegetation, rocky shoreline, or built environment such as

piers. The number of plates and sets varied between sites due to a limited amount of sampling devices, accessibility of terrain and variability of surrounding substrate in the sampling site. After the incubation 27 out of 30 plates were retrieved, with VP missing 1 plate and SGP 2 plates. Water temperature at the littoral zone during removal was 21-23 °C.

For the second sampling period sampling in SGP, KP and LB was done as before, but in LBP and VP sampling was done with 2 sets of 3 plates, as more sampling devices were available. In addition to the previous sampling sites, 5 different sampling points were chosen in lakes with no prior *P. magnifica* observations but with the risk of invasion, given the connection to Vanajavesi watercourse, with the goal to find out whether *P. magnifica* had spread to those lakes or not. In KC and AS 3 sets of 3 plates were placed in areas of differing substrates, and in TB, LSB, and IB 2 sets of 3 plates were deployed. For the second sampling period plates were left in sampling sites for 24 days to avoid sampling structures getting caught in forming lake ice. Water temperature during removal was 4.3-5.5 °C.

Sampling devices were carefully collected and packed individually to avoid cross-contamination and analyzed in the laboratory. Statoblasts were counted separately for string (Figure 4B) and panel components, picked onto a petri dish (Figure 4C), and species identification was done using a stereomicroscope, as statoblasts of *P. magnifica* and another moss animal *Cristatella mucedo*, native in Finland, are visually similar, and accurate identification often requires magnification. Samples were stored in a cooled room to prevent statoblasts from germinating before analysis. Abundance data was compiled in Excel for data analysis.

## 2.3 Statoblast accumulation rate modeling

All statistical analyses were performed in R (version 4.5.1; R Core Team, 2025). Relationship between statoblast accumulation rate and environmental variables as well as the accumulation rate between sampling device components were examined using two different generalized linear mixed effects model (GLMM) using glmmTMB (M. E. Brooks et al., 2017). Since statoblast density was calculated from count data (species per sampling device/component), and amounts varied from very low (0) to high (600+), a negative binomial distribution was used. Sampling effort was used as offset in model 1 that did not differentiate between sampling methods, and alongside area in model 2, where methods were separated. Sampling site was used as a random effect, to account for 2-4 pseudo replicates per sampling site. For the method-separated model surface area of each component was also used as an offset. Initial predictor variables for both models included season, fetch, method, substrate type and dispersal potential. Season was tested as both an additive variable as well as an interactive variable in both models.

### 2.3.1 Model variables

Dispersal potential was calculated in two different ways: colonization stage, which was years since first observation in the sampled lake (ranging from 0-10), and distance, which was distance from origin (DFO), where the first ever observation from the project area was made (ranging from 230-18000 km). Since these two variables describe the invasion process and were expected to be correlated, their relationship was examined prior to modeling. Colonization stage and DFO showed high correlation ($r = -0.90$), indicating that they do describe the same spatial gradient of spread. To determine which proxy provided greater explanatory power, two GLMMs with identical structures were fitted, differing only in the dispersal proxy used. Model comparison based on Akaike's Information Criterion (AIC), showed lower AIC values for the DFO model, which also reduced unexplained variation among sampling points and provided greater spatial resolution. Thus, DFO was selected as the primary proxy for dispersal in following analyses.

Distance to closest major port (DCP) was chosen as a variable to account for boating traffic and human activity, which is a likely vector of upstream dispersal of the species. DCP varied only by tens of meters among subsites within a site (32-115 m) but ranged from half a kilometer to several kilometers among sites. Therefore, distance from major ports was interpreted as a between-site proxy for proximity to boating traffic, rather than a within-site explanatory variable.

Fetch was calculated in R using different geoinformatics packages. Initial lake and island polygon data was extracted from OpenStreetMap using packages osmdata (Mark Padgham et al., 2017), and sf (Pebesma, 2025). Data was then rasterized using terra (Hijmans, 2025), and fetch calculated with fetchr package (Watters, 2025). Resolution of the fetch raster was set at 0.0002°, which equals to around 13m x 13m cells in the study latitude (~ 60°N). This resolution was chosen to capture shoreline complexity and small-scale spatial variation, to gain accurate fetch estimation. Maximum wind distance was set at 16 km to ensure that all potential wind paths across the lake surface were fully captured. Fetch distances were calculated as the mean uninterrupted water distance across major and minor directions, resulting in a directionally averaged measure of wind exposure.

Substrate type was initially considered as a predictor but comparisons between models showed that fetch and substrate explained overlapping variation. The two variables did not exhibit any collinearity, but models including fetch showed lower AIC values than comparable models including substrate, indicating better performance. In addition, fetch provides a continuous quantitative measure of water movements, whereas substrate represents a categorical habitat description that is partly driven by wave action and wind exposure. Based on the model

comparisons and the biological connections between fetch and substrate type, substrate was left out of the final models.

### 2.3.2 Model validation and overfitting assessment

Potential overfitting and model generalizability was evaluated by using leave-one-sampling-point-out cross-validation. For each of the 10 sampling points, the negative binomial mixed model was refit excluding that point and used to predict counts at the site left out using population-level predictions (random effects excluded). Predictive performance was quantified using the summed log-likelihood of left out observations. Model adequacy was also evaluated using DHARMa (Hartig, 2024) simulation-based residual diagnostics, including tests of residual uniformity, dispersion, zero inflation, outliers, and quantile deviations in residuals vs. fitted values.

## 2.4 Statoblast density prediction

Statoblast densities were predicted in a spatial context with fitted models using ggeffects (Lüdecke, 2018). Model predictors were calculated in R onto different sets of raster data, which were then used to calculate predictions on a final raster. The gridded predictor surfaces showed clear and contrasting spatial gradients across the study area at the 13 × 13 m cell resolution (Figure 5).

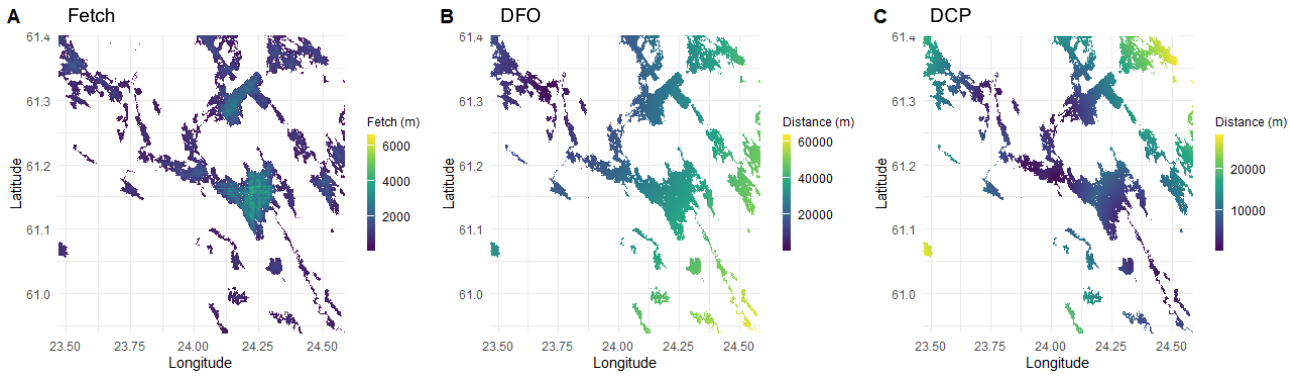



Figure 5. Spatial distribution of environmental predictor variables used in the analysis: (A) fetch, (B) distance from origin (DFO), and (C) distance to closest port (DCP). Color gradients represent increasing values (m) across the study area.

Fetch (Figure 5A) ranged from low values across most cells (dark purple) to localized areas of higher exposure (blue–green), reaching approximately 6000 m in the highest-exposure patches. In contrast, DFO (Figure 5B) exhibited the broadest spatial range, increasing to roughly 60,000 m and forming a large-scale gradient across the map extent. DCP (Figure 5C) showed a distinct spatial pattern with values up to approximately 25,000 m, separating areas that are relatively close to major ports (dark purple) from more isolated areas (green–yellow). Together, these rasters quantify fine-

scale spatial heterogeneity in the three model covariates and provide the spatially continuous inputs required to generate cell-by-cell predictions of expected abundance from the fitted models.

## 2.5 Lake differences in physical and water quality traits

Permutational Multivariate Analysis of Variance (PERMANOVA) from R package vegan (Oksanen et al., 2025) was used to compare differences in physicochemical parameters between two sets of 4 waterbodies: initial study lakes with confirmed *P. magnifica* colony observations and reference lakes without *P. magnifica*. Euclidean distance metric was chosen, as water quality parameters used are continuous. Parameters used in the PERMANOVA included: total phosphorus (TP), total nitrogen (TN), chlorophyll a (Chl-a), dissolved oxygen (DO), turbidity, color, conductivity, shoreline development index (SDI) and DFO (Table 1). Water quality parameters (TP, TN, chl-a, DO, pH, turbidity, color and conductivity) were retrieved from Hertta database (Finnish Environment Institute (SYKE), 2026). Used values were average from summer and early fall samplings (July - September) for the latest 5 years of measurements (2024-2019). Summer and early fall data were chosen to represent the conditions during colony growth. Data from the chosen period was not found for three lakes, thus it was supplemented by samplings from earlier years up until 2009. SDI and DFO in the study area were calculated in QGIS (QGIS Development Team, 2026). Dissimilarity between lakes was visualized using a PCoA ordination.

Table 1. Physicochemical variables of sampled lakes. Data averaged from June-September samples from 2024-2019 with few exceptions. Data from Hertta database (2026). * Years 2023,2020, 2017, 2014, 2009. ** Years 2024, 2021, 2018, 2015, 2012. *** Years 2023, 2020, 2018, 2017, 2014.

| Lake | Presence | TP µg $L^{-1}$ | TN µg $L^{-1}$ | Chl-a µg $L^{-1}$ | pH | DO mg $L^{-1}$ | Turbidity FNU | Colour mg $L^{-1}$ Pt | Conductivity mS $m^{-1}$ | SDI | DFO km |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Kirkkojärvi | Yes | 26.6 | 528.0 | 9.1 | 7.3 | 7.1 | 7.4 | 31.2 | 9.5 | 2.5 | 0.9 |
| Hiidenvuolle | Yes | 20.2 | 498.0 | 11.4 | 7.3 | 7.6 | 38.7 | 30.2 | 9.3 | 4.1 | 3.2 |
| Mallasvesi | No | 9.8 | 336.0 | 3.8 | 7.3 | 8.6 | 1.3 | 15.4 | 7.5 | 5.0 | 23.2 |
| Kärjenniemenselkä | Yes | 13.8 | 364.0 | 9.1 | 7.4 | 8.5 | 2.3 | 17.8 | 7.6 | 10.8 | 16.1 |
| Lehijärvi* | No | 25.4 | 527.8 | 11.4 | 8.0 | 9.1 | 2.8 | 19.8 | 19.0 | 1.5 | 44.0 |
| Alajärvi | No | 14.4 | 484.0 | 7.8 | 7.3 | 7.9 | 2.2 | 54.4 | 7.7 | 4.8 | 52.4 |
| Äimäjärvi** | No | 42.4 | 682.0 | 30.2 | 7.9 | 8.6 | 6.9 | 34.2 | 11.2 | 3.8 | 35.2 |
| Katumajärvi*** | No | 16.8 | 428.0 | 3.9 | 7.5 | 8.7 | 1.1 | 21.0 | 12.2 | 2.7 | 57.4 |

# 3 Results

## 3.1 Statoblast accumulation rate

Statoblasts were found in all initial study sites where devices were deployed during summer and fall, and statoblast accumulation rates pooled across sampling device components varied between sites and seasons (Figure 6). Relative statoblast accumulation rates (statoblasts $m^{-2}$ $d^{-1}$) across sites ranged from 0.9 to 271 during summer sampling period, and from 0 to 285 during fall sampling period. Summer accumulation rates were generally higher than fall rates at most sites, with particularly high mean values (mean ± SD) recorded at VP (223 ± 44), LBP (116 ± 45) and LB (106 ± 30). KP and SGP had consistently lower summer accumulation rates with averages of 8.4 ± 5.9 and 1.16 ± 0.8, respectively. VP maintained high fall values (162 ± 94), while LBP (21 ± 13) and LB (1.89 ± 1.3) had much lower rates in fall. KP (7.1 ± 6.4) and SGP (0.2 ± 0.2) maintained low rates during fall. No *P. magnifica* statoblasts were found in the sampling devices from reference lakes, which were only sampled in fall. *C. mucedo* statoblasts were found in both reference lakes as well as initial study sites.

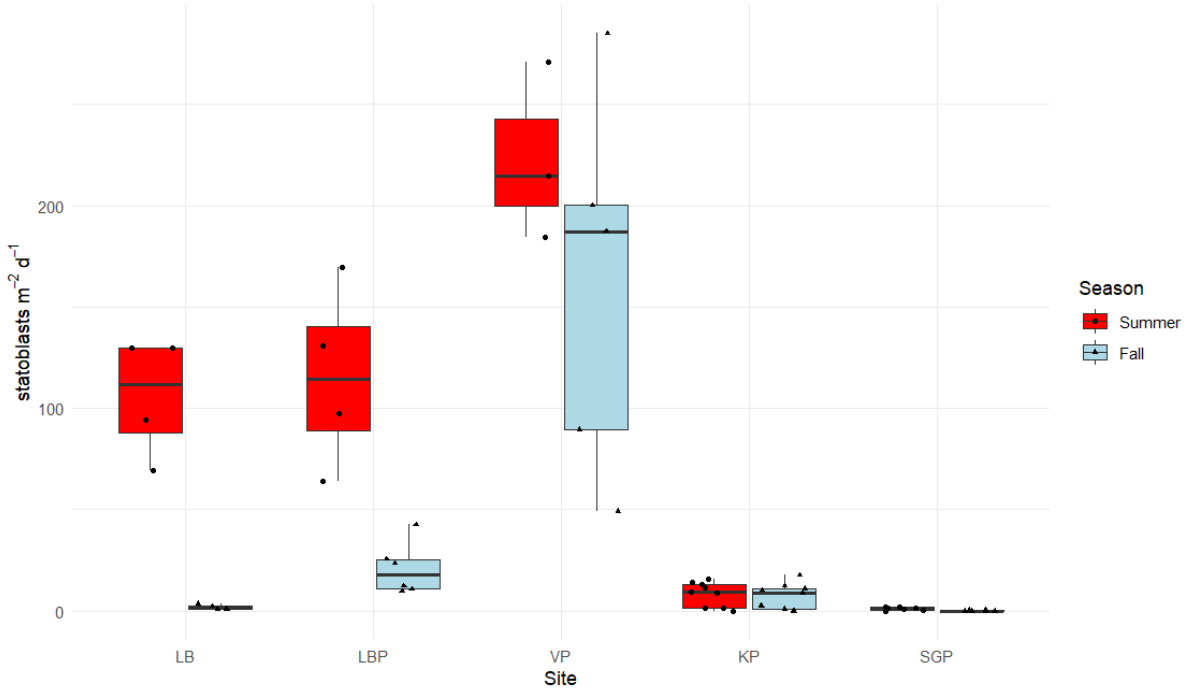



Figure 6. Comparison of accumulation rates (statoblasts $m^{-2}$ $d^{-1}$) across sites for summer and fall. Boxplots show the median and interquartile range, with whiskers showing range and points representing individual observations.

## 3.2 Statoblast accumulation rate by sampling device components

Statoblast accumulation rates varied by different sampling device components. For most sites, string components had a higher accumulation rate than the panel component, especially during summer (Figure 7). Accumulation rates are reported as mean ± SD (statoblasts $m^{-2}$ $d^{-1}$). At LB, string

components yielded higher accumulation rates than panels in both seasons, particularly in summer (242 ± 49 vs. 72 ± 49). In fall values were much lower, but the string component still retained a higher accumulation rate (6.1 ± 4.9 vs. 0.8 ± 0.7). At LBP, summer sampling resulted in similar differences between string and panel (228 ± 178 vs 87 ± 32), whereas fall values were quite similar between methods (22 ± 11 vs 21 ± 15). At VP, string components exhibited a higher accumulation rate in summer and fall (378 ± 224 and 206 ± 172), compared to panels (184 ± 27 and 151 ± 78). In contrast to other sites KP showed smaller differences between methods. Summer rates ranged from 12.8 ± 10.5 (string) to 7.3 ± 6.6 (panel), while fall rates were slightly lower for strings (4.4 ± 5.8) than panels (7.8 ± 7.1). At SGP accumulation rates were low across all seasons and methods. Summer string components showed higher values (4.2 ± 3.1) than panels (0.4 ± 0.3), while both methods produced near zero values in fall.

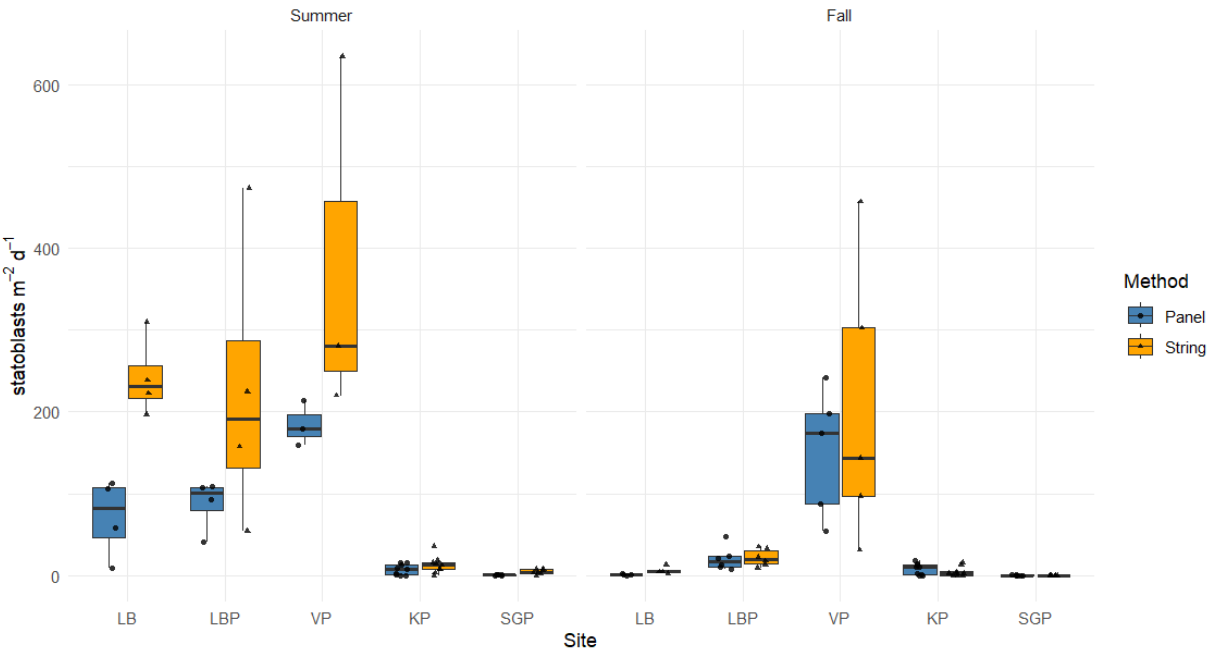



Figure 7. Comparison of accumulation rates (statoblasts $m^{-2}$ $d^{-1}$) between sampling device components (panel and string) across sampling sites for summer and fall. Boxplots show median, interquartile range, and data spread, with individual observations overlaid.

## 3.3 Variables affecting statoblast accumulation rate

Final variables for the method aggregated model included season, fetch, DFO and DCP. Model selection and testing favored the season-interaction model (AIC 483.5) compared to an additive model (AIC 509.5), with a likelihood-ratio test confirming the difference ($\chi^2 = 31.96$, df = 3, p = $5.35 \times 10^{-7}$). Clear variation between sampling points was detected in baseline summed counts (random-intercept variance =0.205, SD = 0.452). Cross-validation and residual diagnostics

indicated generally good model performance with no evidence of overfitting or major violations of model assumptions.

In fall all distance-related predictors were negatively associated with statoblast counts and significant: fetch ($\beta = -0.0126 \pm 0.00203$, $p < 0.001$), DCP ($\beta = -0.00249 \pm 0.000433$, $p < 0.001$), and DFO ($\beta = -0.000128 \pm 0.0000310$, $p < 0.001$) (Figure 8). This corresponds with a 71.6% decline in counts per 100 m increase in fetch, a 22% decline per 100 m increase in distance to closest port, and a 1.3% decline per 100 m increase in distance from first observation. Summer vs Fall effect was not significant ($\beta = -0.251 \pm 0.542$, p=0.64), but Summer had a significant effect on all three slopes (Figure 8). The negative effects of both fetch and distance from major port were weaker in summer; 37.5% and 9.4% decline per 100 m respectively, meanwhile distance from first observation had a stronger negative effect: 2.36% decrease per 100 m.

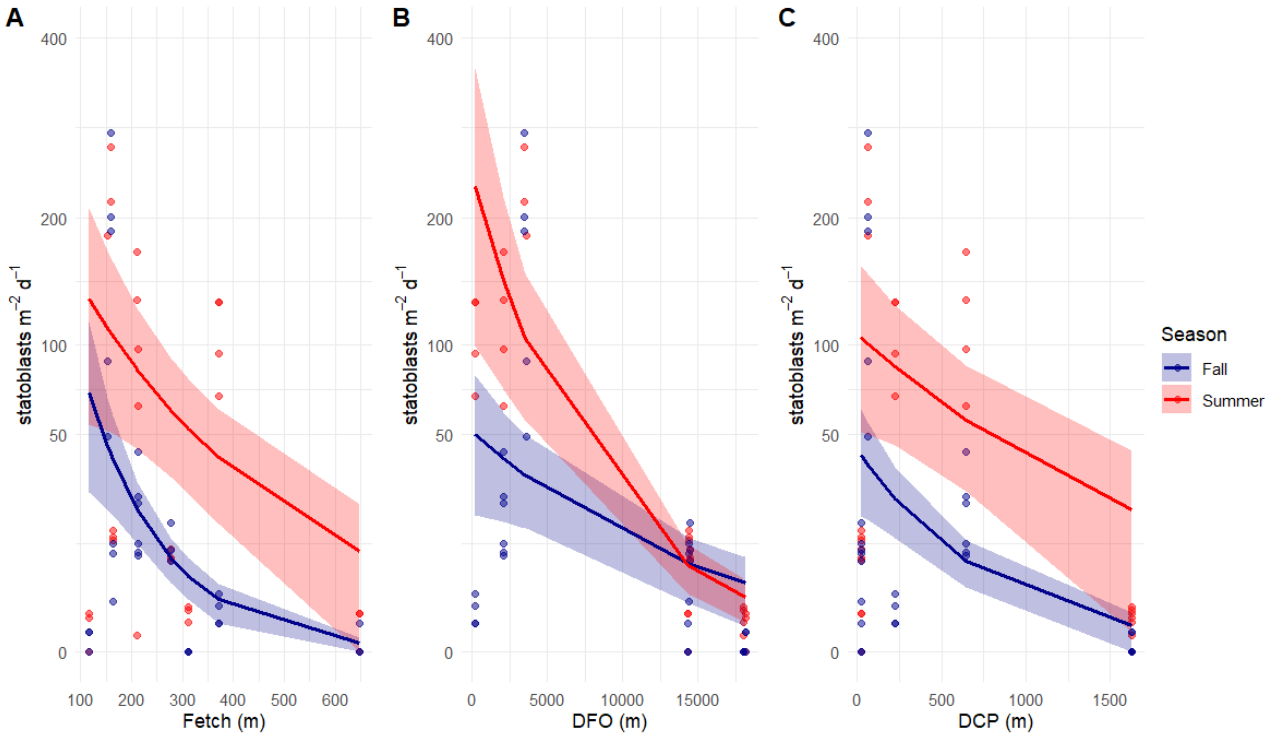



Figure 8. Relationships between statoblast accumulation rates (statoblasts $m^{-2}$ $d^{-1}$) and environmental variables on a square root scaled y axis: (A) fetch (m), (B) Distance from origin (DFO) (m), and (C) Distance to closest port (DCP) (m). Points represent observations, and lines show fitted trends for summer and fall with shaded confidence intervals.

Final variables for the method-segregated model included season, fetch, DFO and DCP. As with the method-aggregated model, selection and testing favored season-interaction model (AIC 825.7) instead of the additive model with same variables (AIC 858.3). The model showed substantial variability in baseline counts between sampling points (random-intercept variance = 0.215;

SD=0.464). Cross-validation and residual diagnostics indicated generally good model performance, with no evidence of overfitting or major violations of model assumptions.

All distance-related predictors were significantly negatively associated with statoblast accumulation rates (Figure 9) in fall: fetch ($\beta$ = -0.0121 ± 0.00204, $p < 0.001$), DCP ($\beta$ = -0.00243 ± 0.000442, $p<0.001$), DFO ($\beta$ = -0.0001345 ± 0.0000318, $p<0.001$). Expressed as rate ratios these correspond to declines in accumulation rate of approximately 11.4 per 10 m increase in fetch, 24% per 100 m increase in distance to closest port, and 13% decline per 100 m increase in distance from first observation. The main effect of Summer vs. Fall was not significant ($\beta$ = -0.171 ± 0.545, $p = 0.754$), but season significantly altered the slopes of all three predictors. The negative effects of fetch and distance to closest port were weaker in summer; 4.2% decline per 10 m increase in fetch and 9% decline per 100 m increase in distance from ports. The negative effect of distance from origin was stronger in summer, 24% decrease per 100 m. Method also had a significant effect on accumulation rate. Rates were higher in string component than in panel ($\beta$= 0.647 ± 0.154, $p < 0.001$) which corresponds to an estimate of 1.91 times higher expected accumulation rate.

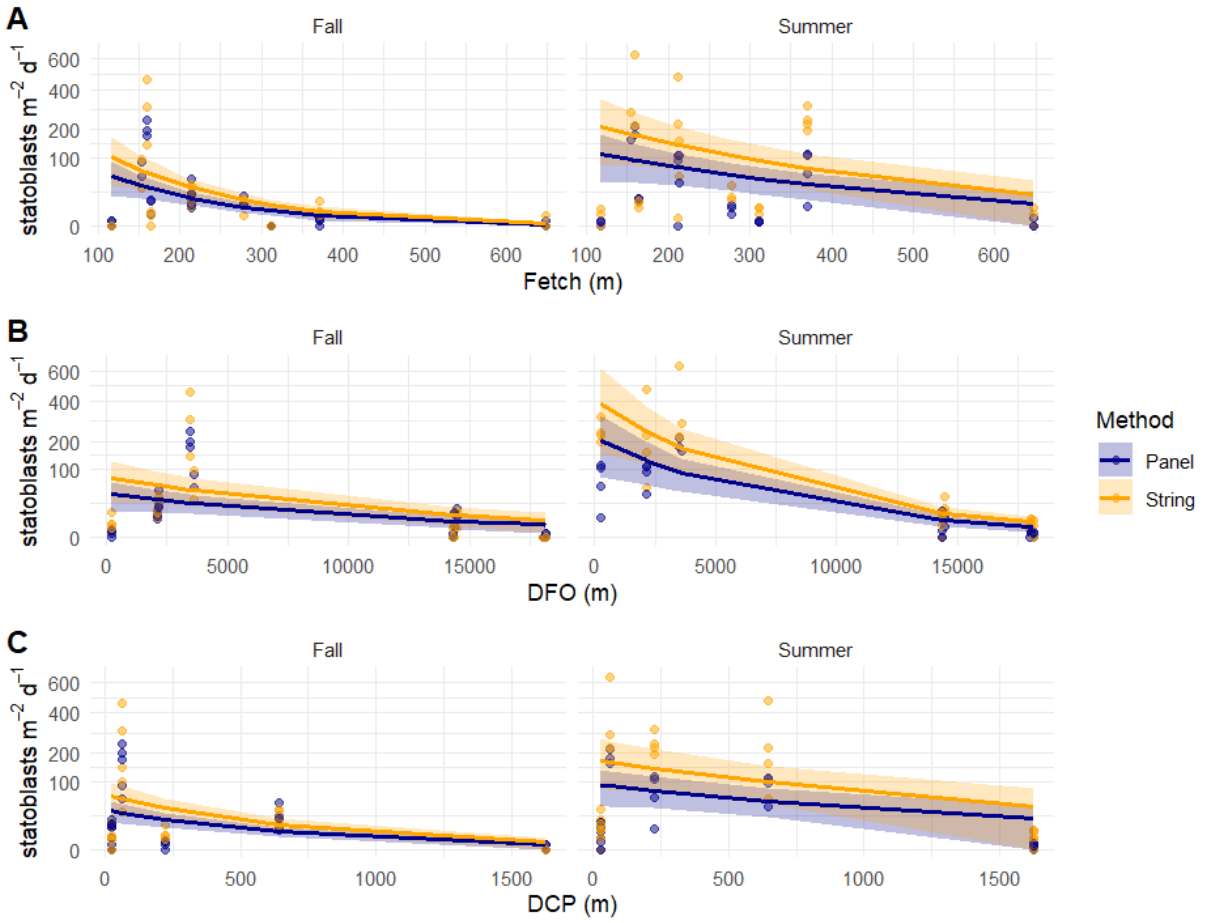



Figure 9. Relationships between statoblast accumulation rates (statoblasts $m^{-2}$ $d^{-1}$) and environmental variables: (A) fetch, (B) distance from origin, and (C) distance to closest port. Data are shown separately for fall and summer on a square root transformed y axis, with points representing individual samples and lines showing fitted trends for each sampling method (panel and string) with confidence intervals.

## 3.4 *P. magnifica* dispersal pressure

Predicted statoblast accumulation rates differed between seasons and revealed clear spatial patterns of dispersal pressure across the study area (Figure 10). Across both seasons, the most distinct hotspot was consistently located in the Lempäälä channel. This area is characterized by low fetch and proximity to two major ports as well as the first recorded occurrence of the species. A second distinct hotspot was observed in the narrow channel connecting Kärjenniemenselkä to Mallasvesi, in the vicinity of the Valkeakoski guest pier and boat dock. In addition, predicted statoblast values exceeding 1 statoblast $m^{-2}$ 7 $d^{-1}$ were present in the southeastern parts of Lake Vanajavesi, including the Hattulanselkä region, despite its distance from the first recorded observation point.

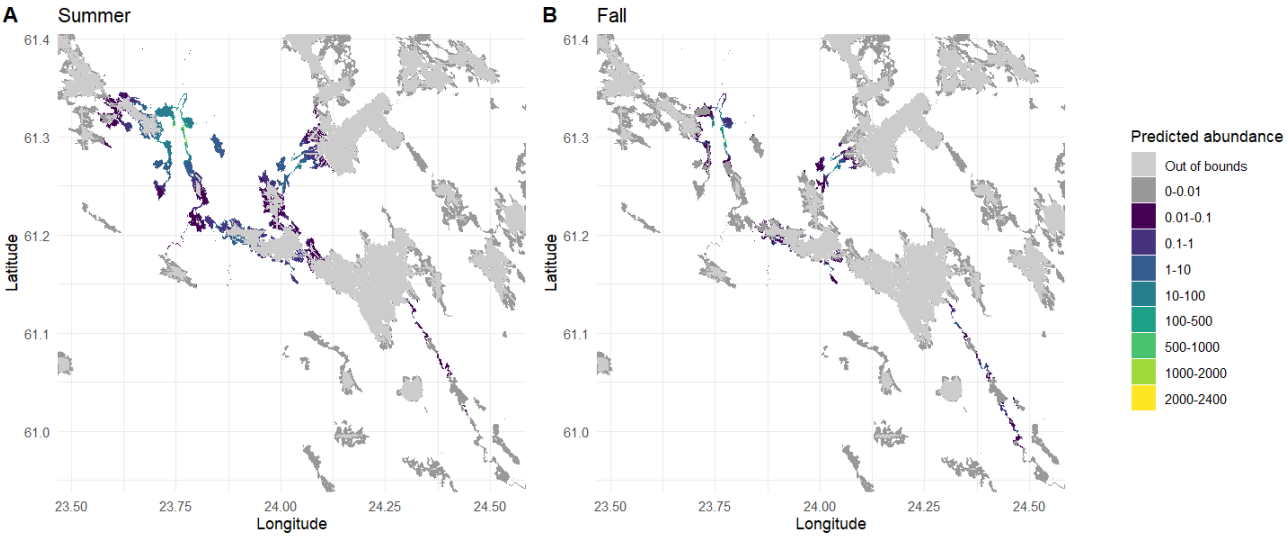



Figure 10. Model-predicted spatial distribution of statoblast abundance for summer (A) and fall (B). Predicted values are grouped into abundance classes (statoblasts $m^{-2}$ 7 $d^{-1}$), with grey areas indicating locations outside the modeled fetch range. Dark blue colors indicate probable invasion front, whereas light green and yellow values represent possible current hotspots.

Most of the modeled water surface area within the bounds fell within the lowest rate class. In fall this pattern was stronger, and 90.5% of the surface area was classified within the lowest rate class, compared to 70.1% in summer (Table 2). In accordance, summer predictions were distributed across a wider range of classes. Areas with the highest predicted statoblast accumulation rates were rare in both seasons, comprising less than 0.1% of the total surface area. In fall, less than 1% of surface area had predicted values of over 10 statoblasts caught $m^{-2}$ 7 $d^{-1}$, whereas in summer areas with the same amount of predicted abundance represented around 5%. Areas with moderate amounts of statoblasts predicted (1-10) accounted for 7.5% and 1.2% of total area in summer and fall respectively.

Summer predictions showed a spatially broader extent of non-zero values compared to fall, although most of these values were low and fell within the lowest rate classes (Table 2). Elevated

statoblast abundances surrounding identified hotspots extended over longer distances, especially in the northwestern parts of Lake Vanajavesi, where predicted abundance reached values higher by orders of magnitude than in fall. In fall, non-zero predictions covered a smaller spatial extent. However, in the southeastern region of Lake Vanajavesi, predicted abundances in the surrounding areas of Hattulanselkä, were higher in fall compared to summer (Figure 10), despite total predicted abundances being greater in summer and distributed over a larger area (Table 2).

Table 2. Comparison of model-predicted statoblast accumulation rate categories (ind. $m^{-2}$ 7 $d^{-1}$) between summer and fall, including percentage area and spatial extent ($km^2$) for each accumulation rate class. Higher rate values indicate higher risk of dispersal and invasion.

| Summer | | | Fall | | |
|---|---|---|---|---|---|
| Accumulation rate | Percentage (%) | Area ($km^2$) | Accumulation rate | Percentage (%) | Area ($km^2$) |
| 0-0.01 | 70.1 | 46.1 | 0-0.01 | 90.5 | 59.5 |
| 0.01-0.1 | 9.4 | 6.2 | 0.01-0.1 | 4.5 | 2.9 |
| 0.1-1 | 8.1 | 5.3 | 0.1-1 | 3.0 | 2.0 |
| 1-10 | 7.5 | 4.9 | 1-10 | 1.2 | 0.8 |
| 10-100 | 3.8 | 2.5 | 10-100 | 0.6 | 0.4 |
| 100-500 | 0.8 | 0.5 | 100-500 | 0.2 | 0.2 |
| 500-1000 | 0.3 | 0.2 | 500-1000 | 0.03 | 0.04 |
| 1000-2000 | 0.1 | 0.004 | 1000-2000 | 0.01 | 0.01 |
| 2000-2400 | 0.002 | 0.001 | 2000-2400 | 0.001 | 0.001 |

## 3.5 Physicochemical differences between lakes

PERMANOVA showed no significant differences between study lakes with *P. magnifica* and reference sites when conducted with only water quality variables with this sample size (n = 8) ($R^2$ = 0.14, pseudo-F = 0.98, p = 0. 41). A test for homogeneity of multivariate dispersion indicated no significant difference between groups (PERMDISP: F = 0.45, p = 0.53), confirming that the PERMANOVA result was not influenced by unequal group variances. When DFO and SDI were included in the analysis, the p value decreased to 0.21. Based on the used permutation tests several lake chemistry variables were significantly associated with PCoA ordination structure when DFO and SDI were included ($p < 0.05$) (Figure 11). Such variables were TP (p = 0.002), TN (p = 0.002), chl-a (p = 0.009), pH (p = 0.016), DO (p = 0.013) and conductivity (p = 0.036). These variables were generally aligned along the main axis of variation in the ordination space, which explained 40,0% of the variation (Figure 11). In contrast color, turbidity, SDI and DFO were not significantly

associated with ordination structure ($p > 0.2$). Based on the PCoA ordination (Figure 12) that visualizes the dissimilarity between lakes based on the variables tested with PERMANOVA, there is no clear separation between lakes with *P. magnifica* colonies and those without.

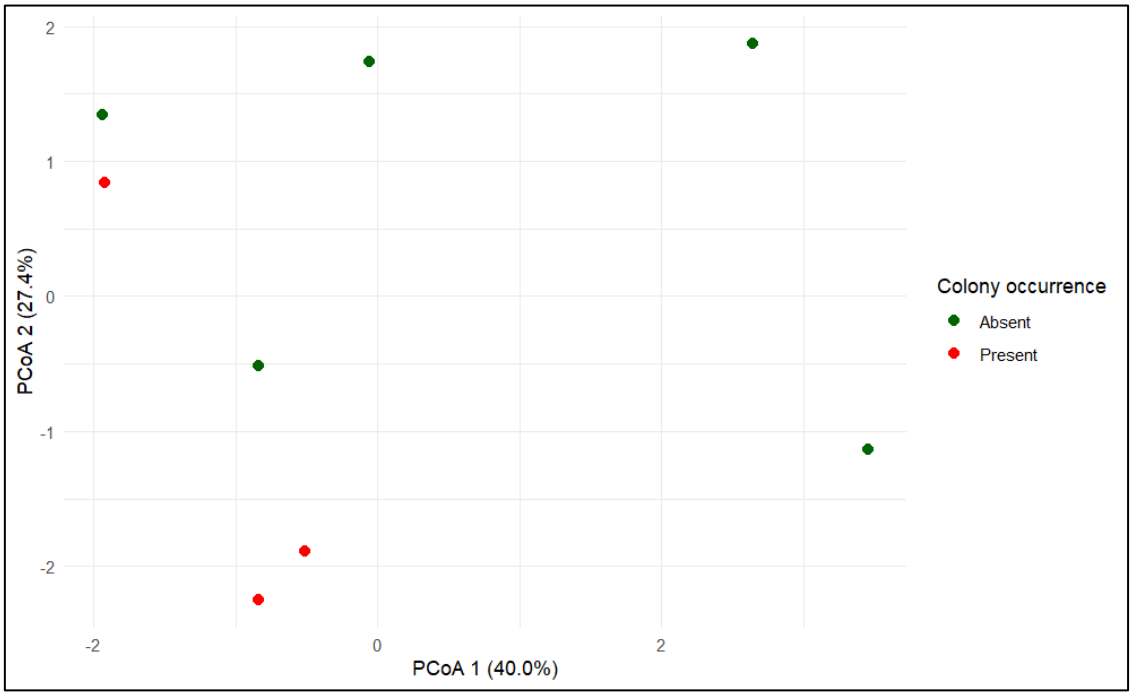



Figure 11. Principal coordinates analysis (PCoA) of lakes with confirmed *P. magnifica* colonies and those without, based on water quality variables, SDI and DFO. Axes represent the first two principal coordinates, explaining 40.0 % (PCoA1) and 27.4 % (PCoA2) of the variation in water quality and physical trait profiles between study lakes.

# 4 Discussion

## 4.1 Spatiotemporal differences in statoblast abundance

Collecting accumulated statoblasts on incubation plates worked not only as a detection method and as a proxy for species occurrence but also captured the structure of species dispersal dynamics between seasons. Despite dispersal pathways of *P. magnifica* being largely speculative in existing literature (Rodriguez & Vergon, 2002; Vuorio et al., 2018; Starunova et al., 2021), statoblast abundance in this study followed clear and consistent spatial and seasonal patterns, suggesting that physical characteristics of the water body are significant and quantifiable drivers of dispersal dynamics for *P. magnifica*. Statoblast accumulation rate differed spatially, which was in alignment with the first hypothesis. Hotspots for statoblast accumulation were local and focused in sheltered areas near human activity and invasion front. These patterns show that statoblast accumulation rate is a meaningful and useful component in predicting species spread. Statoblast accumulation rate was also hypothesized to be higher in fall due to increased statoblast output after colony disintegration. In fall, sampling was done after temperatures had decreased to 4-5 °C, and thus, colonies had obviously broken. Contrary to the hypothesis, statoblast accumulation rate was generally lower in fall than in summer in many sites. However, season was not a significant predictor of overall abundance in the GLMM, suggesting that seasonal differences were not consistent across the study area. Instead, results indicated that the influence of spatial variables varied between seasons.

## 4.2 Sampling device component performance

String components of the sampling device captured statoblasts at nearly twice the rate of panel components. This pattern was observed across most sites and in both seasons, supporting the second hypothesis that rougher and more complex surfaces allow for higher statoblast accumulation. This suggests that the texture of the string material provides a more effective surface for statoblast capture than the flat panel surface. Thus, future monitoring efforts using a similar method should not ignore the statoblasts caught in the string component of the sampling device. Adding other textured materials or prioritizing the string component could improve detection sensitivity, especially in areas where statoblast abundances are predicted to be low, such as the invasion front. Furthermore, as rougher surfaces are more likely to capture free-floating statoblasts, transporting such materials from one lake to another, should be done with extra caution, to avoid statoblast transport. Overall, in addition to providing knowledge about the presence or absence of *P. magnifica* (Ko et al., 2021), incubation plates as a method also captured important dispersal structures.

## 4.3 Physical drivers of statoblast dispersal

The third hypothesis expected statoblast accumulation rates to be higher in low-fetch areas closer to initial invasion and boating traffic, as well as in vegetated or built environments, compared to rocky shores. This hypothesis was partly supported by the results, as fetch and both distance variables had a negative effect on statoblast accumulation rates. However, different substrates could not be assessed independently from fetch and were ultimately left out of the final model. The physical factors structuring statoblast abundance align with what is known about the species' habitat preferences (Szekeres et al., 2013; Starunova et al., 2021) and statoblast biology (C. M. Brooks, 1929; Brown, 1933) and help explain distributional patterns observed in the Kokemäenjoki water system, including the scarcity of confirmed observations in Lake Vanajavesi.

The association between low fetch and high statoblast abundance is consistent with the species' documented preference for sheltered, slow-flowing environments (Szekeres et al., 2013). Sheltered areas showed higher statoblast abundance, than areas with higher fetch and more wave action. As statoblasts float and primarily disperse by water movements, it is therefore expected that floating statoblasts would end up getting packed into sheltered bays where water flow is slower and wave action lower (Szekeres et al., 2013; Starunova et al., 2021). These areas often have more abundant macrophyte vegetation due to lower wave action and a more settled sediment (Van Zuidam & Peeters, 2015), providing ample growing substrate for *P. magnifica* colonies that are often present in macrophyte stalks (Brown, 1933; Moravcová et al., 2025). In this study, macrophyte species of each location were not recorded, but some variation between sites with vegetation might be explained by vegetation type, specifically leaf complexity. Serrated, fine and complex leaves are more likely to retain hooked statoblasts, than large leaves with smooth edges (Smyth & Reynolds, 1995).

Higher statoblast abundance in sheltered areas is also supported by the lack of confirmed citizen observations in Lake Vanajavesi, noted as an anomaly given its location between two established hotspots. Lake Vanajavesi has a low SDI and the highest fetch values of lakes in the study area. Although citizen observations do not reflect the actual distribution of the species as they are dependent on human presence, the coast of Lake Vanajavesi is far from uninhabited, with hundreds of summer cottages surrounding the lake. This suggests that the lack of observations is not simply due to the lack of citizen presence. A shoreline susceptible to continuous wave action caused by long distances of undisturbed wind travel is likely not a suitable environment for the species, as strong waves dislodge settled colonies and disturb statoblast attachment, which can also explain the lack of observations in Lake Vanajavesi. Greater fetch also increases wave-induced resuspension and transport near the shoreline, which can relocate particles such as statoblasts to deeper

environments (Tammeorg et al., 2013), where conditions do not support colony development. The negative effect of fetch varied between seasons, being weaker in summer than in fall.

Statoblast abundance and accumulation rates were highest near already-established populations, which was expected. Existing populations suggest that environmental conditions are sufficient for species occurrence and reproduction (Okamura et al., 2019). Established colonies act as a continuous source of statoblasts, contributing to the observed decline in abundance with increasing distance from established populations (Karlson, 1992; Moravcová et al., 2025).

The significant negative effect of distance from the first recorded observation on statoblast accumulation rates provides empirical support for what has previously been inferred. The strength of this relationship varied between seasons, with a stronger negative effect in summer than in fall. Although floating statoblasts have been observed to drift a distance of 800 m (Brown, 1933), distances much longer than that seem unlikely, especially upstream, without assistance from waterfowl, fish or human activity. The decline in statoblast abundance with increasing distance from the origin observed in this study is consistent with this previously observed constraint. This suggests that the spread of *P. magnifica* to distant upstream locations after 2020, as documented in citizen observation data (Finnish Biodiversity Information Facility (FinBIF), 2026), is unlikely to occur through passive water movement alone. Probable dispersal pathways to such distances are human-mediated or other faunal vectors proposed in existing literature (Rodriguez & Vergon, 2002; Balounová et al., 2013; Vuorio et al., 2018).

The negative effect of distance from major boating ports on statoblast accumulation rates provides support for boating traffic as a dispersal vector in the study area. This dispersal pathway for bryozoans has been proposed in earlier literature (Rodriguez & Vergon, 2002; Balounová et al., 2013), and even observed in the US (Kipp et al., 2010), but has not been demonstrated in Finland or Europe. Major ports represent points where statoblasts can be introduced to new lakes and waterways or transported upstream via boat hulls, anchor ropes or improperly cleaned equipment. The cruising route connecting the majority of major ports in the study area represents a probable corridor for human-mediated dispersal (Rodriguez & Vergon, 2002; Vuorio et al., 2018). It links the initial invasion site in Lempäälä to upstream distant water bodies where the species has been observed more recently, such as Hattulanselkä in Hämeenlinna (Figure 2). The significant effect of port proximity, combined with the distance-limited nature of passive dispersal established above, suggests that boating traffic is not merely a possible vector but a likely driver of upstream spread in this system, which should be considered when planning preventative actions for further spread. Similarly with distance from origin, the strength of this effect varied between seasons, with a weaker negative effect observed in summer than in fall.

## 4.4 Seasonal dynamics

Statoblast production intensifies in fall as colony growth ceases and colonies begin to degrade, with the majority of statoblasts overwintering before germination in early summer (Brown, 1933; Aleksandrov et al., 2014; Starunova et al., 2021). This biological cycle provides a basis for expecting not only seasonal differences in accumulation rates but also differences in what those accumulation rates represent ecologically. Higher accumulation rates were hypothesized for fall, although no specific predictions were made regarding the effect of season on the relationships between environmental predictors and statoblast accumulation. Yet how these seasonal patterns interact with physical predictors of dispersal have rarely been quantified. Although there was no significant effect of season on overall abundance, the interaction terms between season and the tested predictors indicate that there are differences in the strength of relationships between predictors and abundance between summer and fall. The negative effects of fetch and distance from closest port were weaker in summer, compared to fall. In contrast, the negative effect of distance from first observation was stronger in summer, suggesting that the effects of spatial variables are not static, but varies seasonally, and statoblast abundances are not distributed across the study area in an identical manner in summer and fall.

It is important to note that statoblasts caught during summer are most likely a mixture of new statoblasts and statoblasts that were produced during the previous growing season, as statoblast production occurs after colony formation. Statoblasts produced in the previous fall are likely to resurface in littoral zones due to spring turnover and the increased turbidity caused by wind after ice cover loss (Karlson, 1992). In the summer of 2024, water temperatures were warm during the start of the sampling (> 20 °C), but it is unlikely that colonies that had started growing that season would have produced all of the statoblasts that were collected within a month. Thus, seasonal differences in statoblast accumulation rates as well as differences in the strength of explanatory variables may be due to differences between years, rather than seasons. Regardless of whether summer statoblasts originate from the current or previous growing season, the differences in spatial distribution between seasons reflect genuine variation in dispersal dynamics. The abundances observed in the summer are most representative of areas where colonies are likely to grow during the sampling period, whereas abundances observed in the fall, are likely to represent the active dispersal phase. Importantly, these results suggest that similar average abundances between seasons do not imply identical spatial patterns, nor the same phases of dispersal processes.

Another possible interpretation of seasonal differences in explanatory variable strengths is differences in prevailing wind directions during seasons, which were not tested in this study. The stronger negative effect of distance from origin during summer suggests that wind conditions may

not have been favorable for long-distance statoblast transport compared to fall. Alternatively, the pattern may reflect a shifting invasion front and differences in life cycle stage. If the species has been establishing new upstream populations in recent years or during the sampled growing season, summer statoblast abundance may disproportionately reflect previous establishment processes (Brown, 1933) and depletion of overwintered propagules. In contrast, statoblasts captured in fall represent those produced by colonies established from last season's propagules further from the origin. These seasonal patterns may suggest that dispersal dynamics of *P. magnifica* can shift between phases of establishment and active spread across the growing season, though disentangling these processes would require monitoring at a higher temporal resolution than was possible in this study.

## 4.5 Spatial distribution of dispersal pressure

Predicted statoblast dispersal pressure was highest in low-fetch areas, and near major ports. These results support the fourth hypothesis. Predictions identified the narrow channel near Valkeakoski, and Lempäälä channel as invasion front hotspots across both seasons. High dispersal potential was also predicted to be close to the initial invasion. However, in addition to areas close to the initial invasion site of the species, statoblast accumulation rate predictions suggest elevated dispersal pressure in Hattulanselkä, Hämeenlinna, especially in fall. This finding was contrary to the fourth hypothesis, since Hämeenlinna is located far from the initial invasion site. Hattulanselkä was not sampled in this study, but citizens have been reporting occurrences of *P. magnifica* colonies in the area since 2022 (FinBIF, 2026). The stronger fall predictions in this area are likely related to the season-dependent effects of spatial variables identified in modeling. Prior to this study, no observations of *P. magnifica* colonies had been made in Mallasvesi. Statoblast rate predictions suggest high dispersal pressure on the southern parts of the lake, where it connects to Lake Vanajavesi. Interestingly, in the summer of 2025, first confirmed observations of *P. magnifica* colonies were made in Mallasvesi, in the southern areas of high predicted accumulation rate (FinBIF, 2026), supporting the accuracy of the predictions.

The spatial prediction output provides a practical foundation for interpreting invasion pressure across the study area and highlights specific locations where monitoring should be focused. Lakes and waterways with complex and sheltered shorelines should be considered at elevated risk and prioritized in monitoring planning, as these areas consistently showed the highest statoblast abundance and therefore the greatest risk of new colony establishment. Early detection in these areas, as well as other narrow waterways near invasion front, could allow management responses

before populations reach the densities at which colonies become difficult to eradicate (Rodriguez & Vergon, 2002).

These predictions would benefit from sampling at higher spatial and temporal resolution such as sampling during the whole open water season to better characterize statoblast dynamics. Incorporating wind direction as a covariate would further strengthen the modelling framework, and yearly monitoring would shed light on the influence of previous growing seasons on early summer statoblast abundances.

## 4.6 Physicochemical differences between study lakes

As hypothesized, physicochemical factors did not differ between lakes with and without *P. magnifica*, which is consistent with previously documented occurrence of the species in a wide range of conditions (Everitt, 1975; Balounová et al., 2013; Musil et al., 2018). As described in existing literature, *P. magnifica* has been observed to occur across water systems ranging from oligotrophic to eutrophic, as well as broad ranges of pH and conductivity. This indicates that there is no single chemical parameter that acts as a clear threshold for occurrence.

Although several water chemistry variables related to nutrient availability were significantly associated with ordination structure, their importance should be interpreted as a general trophic gradient rather than as independent predictors. Variables related to productivity are often collinear, and with a small sample size of only eight lakes, the statistical power to distinguish their individual contributions is low. The association with a higher trophic state may still be ecologically meaningful. Productive lakes are likely to offer greater food availability for filter-feeding colonies than those with lower production (Dendy, 1963). This may not determine the presence or absence of the species, but can influence growth rates, colony size or statoblast production.

This raises the possibility that physicochemical conditions, despite not acting as barriers to invasion, may influence the rate at which a lake is colonized once statoblasts arrive. More productive lakes may support faster colony growth and earlier statoblast production, accelerating the establishment of self-sustaining populations. If this is the case, trophic state could be a meaningful predictor for invasion severity rather than invasion risk and should be explored further in future studies.

## 4.7 Limitations

The PERMANOVA results should be interpreted with caution due to several methodological and conceptual limitations. First, the number of lakes included in the analysis was limited, reducing statistical power and increasing sensitivity to the inclusion or exclusion of variables. This sensitivity was observed in the loss of statistical significance when distance from DFO was removed from the

PERMANOVA distance matrix. Second, PERMANOVA assesses group separation in multivariate space but does not identify causal mechanisms. Significant differences reflect associations rather than drivers of invasion. In this study, nutrient-related variables were significantly correlated with ordination structure, but their importance should be viewed collectively as a general trophic gradient rather than as independent predictors due to probable collinearity. Finally, because PERMANOVA tests only for differences in group centroids, it cannot detect nonlinear responses. For these reasons, the PERMANOVA analysis is best interpreted as a complementary, exploratory assessment that provides environmental context for invasion patterns, not as a standalone explanatory model.

Overall diagnostics suggested an acceptable fit of the GLMM model, with no evidence of zero inflation or excessive outliers. However, the DHARMa residual-fitted quantile test for the method aggregated model was significant and driven by the upper quantile. This indicates that the model is less accurate when predicting higher fitted values, and they should be interpreted cautiously. Upper quantile deviation often reflects remaining structure in the data, that is not accounted for by the model, such as mild nonlinearity in predictor effects, or missing predictors that become important at higher abundance levels (Hartig, 2026). At the same time, the inclusion of a random intercept for sampling point revealed notable variability among sites. This indicates that there are likely other environmental factors affecting the abundance, that were not measured in this study, such as microhabitats, or flow rates, which have been proven to affect aquatic invertebrates (Son et al., 2021) even in small spatial scale.

It is important to note that these spatial predictions based on the GLMM do not represent direct measurements, but expectations based on the fitted model. Accuracy of predictions is dependent on how well the model performs in capturing the relationships between predictors and statoblast abundance, and whether covariate values in raster cells fall within the training range of the model. In this study, areas with higher fetch than what was included in sampled data, was excluded from predictions. However, both DFO and DCP were kept to assess distribution potential at the invasion front, as well as the effects of boat traffic via ports. It should be noted that predictions on areas that are outside of the distances in these two predictors used in model training, are extrapolations. They are based on the observed relationships in lower values, and thus, dynamics relating to longer distances may actually vary from model predictions to some extent. In addition, the predictions are based on relationships observed at a limited number of sampling points during two sampling periods, and should be interpreted as indicative rather than precise.

For the purposes of this study, which focuses on identifying broad spatial patterns and relationships rather than making precise predictions at individual locations, the model can still be considered

sufficient. The main conclusions regarding the direction and significance of predictor effects are unlikely to be substantially affected by model limitations. However, the presence of quantile deviations highlights an opportunity for future work to refine the model by exploring nonlinear relationships or incorporating additional predictors such as wind direction. Despite the limitations, the spatial prediction output provides an important base for interpreting abundance distribution across the study area and highlights specific locations where invasion pressure is higher, and species monitoring should be focused.

## 4.8 Future research and implications

Understanding the dispersal dynamics of *P. magnifica* is necessary for assessing its ecological impacts, which currently remain understudied, especially in European boreal lake systems. Given how little is known about the ecological impacts of *P. magnifica* in boreal systems, future work should move beyond dispersal dynamics toward quantifying the species' effects on native communities, nutrient cycling and water quality in invaded Finnish lakes.

The species has been shown to have the potential to alter aquatic food webs through filter-feeding, nutrient cycling and hosting bacteria and invertebrates (Dendy, 1963; Ricciardi & Reiswig, 1994; Šetlíková et al., 2013; Kim et al., 2019; Wood, 2019). These interactions have not yet been explored in invaded Finnish waters, which makes assessments of the species' impact difficult. Identifying the physical drivers of statoblast dispersal and areas of highest invasion pressure provides a foundation for future ecological impact assessments. Without understanding the species' dispersal dynamics, the evaluation of its impact on ecosystems remains underdeveloped.

# 5 Conclusions

This thesis set out to explore the drivers of *P. magnifica* statoblast dispersal in the Kokemäenjoki water system, reveal areas where dispersal pressure is high, evaluate physicochemical differences in invaded and uninvaded lakes in the area, and assess the suitability of incubation panels as a method for sampling and monitoring *P. magnifica* statoblasts, and thus, the occurrence of the species.

Statoblast monitoring by passive incubation plates proved to be a sensitive and efficient way for detecting *P. magnifica* statoblasts and provided insight into interesting dynamics related to the timing, and dispersion of statoblasts. These dynamics would have been difficult to observe through traditional visual colony surveys, especially in large lakes and waterways.

This research has uncovered that lake fetch, distance from initial invasion, human boating activity and season have an impact on the dispersal dynamics and accumulation rates. In contrast, lake physicochemical profiles between invaded and non-invaded lakes did not differ significantly and cannot be used in predicting the risk of *P. magnifica* invasion, in line with earlier studies.

All analyses except for water quality parameter PERMANOVA have been done on statoblast counts and, based on the biology and life history of the species results, can be applied as predictive indicators of future spread of *P. magnifica*.

Overall, this thesis highlights some of the more complex dynamics of *P. magnifica* statoblast dispersal and abundance and contributes to the limited amount of knowledge on the dispersal ecology of this species. The distribution dynamics of *P. magnifica* have rarely been quantified, and earlier studies have been more speculative and based on qualitative, rather than quantitative results. Despite its globally increasing distribution, and given the conspicuous size and appearance, *P. magnifica* still remains surprisingly understudied, and the impact of its occurrence in invaded lakes has not been sufficiently explored. Further research is needed to evaluate long-term impacts of the species on aquatic ecosystems and mechanisms driving its continued and efficient expansion.

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DECLARATION OF GENERATIVE AI USE

Microsoft 365 CoPilot (GPT-5) was used in troubleshooting R code used in plotting and handling raster and polygon datasets.

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