Charles University

Faculty of Science

Study programme: Biology

Branch of study: Ecological and Evolutionary Biology

Dispersal of microscopic algae: the role of human introductions.

Johanna Weber

Dispersal of microscopic algae: the role of human introductions.

Šíření mikroskopických řas: význam antropogenních introdukcí.

Bachelor´s thesis

Supervisor: Mgr. Jana Kulichová, Ph.D.

Prague, 2024

Acknowledgements

I would like to thank my supervisor for her kind advice and my friends and family for their support and patience.

Prohlášení:

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu, Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

Praha, 7. 8. 2024 Johanna Weber

Abstract

The topic of microalgae dispersal is fairly recent, because of past assumptions of them having a cosmopolitan distribution. While some microalgae do show a cosmopolitan distribution, many have geographic restrictions and are absent from parts of the world. Microalgae dispersal is mostly passive, naturally they get transported by currents in water, in the air, on animals and in their gut. This thesis examines the role of human mediated dispersal of microalgae, mostly on the example of diatoms. Main vectors of anthropological dispersal are ballast water transport, aquaculture introductions or the direct transport on equipment. Ways to determine non-native species are described and prominent diatom introductions are mentioned. Possible prevention methods to new introductions are explored along with current guidelines and their effectivity.

Keywords

diatoms, vectors of anthropogenic transport, non-native species, ballast water, biogeography

Abstrakt

Téma šíření mikroskopických druhů řas je poměrně nové, jelikož byla v minulosti předpokládána jejich kosmopolita. Některé mikroskopické řasy se kosmopolitně vyskytují, na mnohé ale působí geografické bariéry a v některých částech světa se nevyskytují. Šíření mikroskopických řas je převážně pasivní, přirozeně se šíří s vodními proudy, ve vzduchu, na těle zvířat a skrz jejich trávicí soustavu. Tato práce zkoumá roli antropogenních introdukcí mikroskopických druhů řas, převážně na příkladu rozsivek. Hlavními vektory antropogenního šíření jsou přenosy v balastní vodě, introdukce spojené s akvakulturou, nebo přímý transport na vybavení. V práci jsou popsané způsoby, jak poznat nepůvodní druhy a jsou zmíněny významné introdukce rozsivek. Dále se práce zabývá možnostmi pro zabránění nových introdukcí a také aktuálními opatřeními a jejich efektivitou.

Klíčová slova

rozsivky, vektory lidského transportu, nepůvodní druhy, balastní voda, biogeografie

.

Table of Contents

1 Introduction 1

1.1 Biogeography 1

1.2 Biogeography of protists and other microorganisms 1

1.3 Everything is everywhere hypothesis 1

1.4 Natural dispersal of microalgae 2

2 Diatoms as an example of microscopic algae 6

2.1 Defining diatoms 6

3 Human mediated dispersal 7

3.1 How can an introduction be confirmed? 7

3.2 Ballast water 8

3.3 Introductions with aquaculture 11

3.4 Direct transport on material 13

4 Discussion 15

Bibliography 18

Appendix 26

1 Introduction

Human activity has been changing the environment for centuries and is the cause of many introductions of organisms, including microalgae. New introductions change biographical patterns, alter local ecosystems and can also have an effect on economy (Ricciardi & MacIsaac, 2022).

1.1 Biogeography

Biogeography is an interdisciplinary science combining biology and geography (Briggs, 1995). This field of study was first explored in the 18th century by Alfred Russel Wallace, who noticed natural barriers between species, such as rivers or mountains. (Biogeography: Wallace and Wegener, n.d.) With the discovery of plate tectonics (by Alfred Wegener, 1915) this area of interest became more complex, because it now had to consider paleontology. Species used to be recognized mostly by morphological structures, but in past decades, molecular biology and genetics are playing a significant role, often revealing seemingly closely related species to be very distant relatives instead (Fontaneto & Hortal, 2012).

1.2 Biogeography of protists and other microorganisms

The first observations which lead to the idea of a possible geographical distribution of organisms were made about larger animals and plants, mostly because of their vast differences between habitats. Microbes didn't show an obvious variation, compared to the larger organisms, which made them less interesting for biogeography (Fontaneto & Hortal, 2012). Before the regular use of molecular biology, taxa were determined based on their morphology. Sometimes if species were too similar, they were wrongly labelled as the same species. This was one of the reasons that lead to the belief in the "Everything is everywhere" hypothesis (EIE) (Foissner, 2006).

1.3 Everything is everywhere hypothesis

The EIE, with the full title being "everything is everywhere, but the environment selects" was first noted at beginning of the 20th century by Beijerinck (1913), then later conceptualized by Baas Becking, in 1934. It states that microbes do not a have local distribution - they are cosmopolitan and only spread noticeably in favourable conditions. Their small size and abundance enable them to have ubiquitous dispersal (Finlay & Fenchel, 2004), while this was originally stated for microbes smaller than 1 mm, this was also believed for microalgae (Finlay

et al., 2002). Modern advocates for the EIE are Fenchel and Finley, who released multiple articles supporting it (Finlay et al., 2002, 2004; Finlay & Fenchel, 2004).

Their work received a lot of criticism (e. g. De Wit & Bouvier, 2006; Foissner, 2006; Bass & Boenigk, 2011; Fontaneto & Hortal, 2012), but is still referenced in papers on microalgae dispersal (i. e. Vanormelingen et al., 2009; Spaulding et al., 2010). One of the main critics is Foissner (2006), who denies the EIE being a hypothesis – more a metaphor by Beijernick in 1913, because a hypothesis should be, by definition, falsifiable. Because of the small size of microbes and unresearched areas, we cannot deny it. Moreover, he states that Finley's research doesn't consider the not yet discovered and described taxa, with the protist's diversity expecting to be sized bigger. The main argument for the global distribution of protists is their small size (Finlay & Fenchel, 2004) – but many lichens, mosses and higher plants have seeds/spores of a similar size and they don't show a cosmopolitan distribution.

Foissner (2006) offers a counterpart – the moderate endemicity model. According to it, there are some microbes with a cosmopolitan distribution, but not all of them. It is also important to mention that the moderate endemicity model still assumes most microbes have a cosmopolitan distribution (Foissner, 2006).

This thesis will assume the position that microorganisms (and therefore microalgae) are not all cosmopolitan.

1.4 Natural dispersal of microalgae

Microalgae are a polyphyletic group of single-celled organisms that photosynthesize (Tesson et al., 2016), with species from the eukaryotic supergroups Archaeplastida, SAR and Excavata and the prokaryotic Cyanobacteria (Heimann & Huerlimann, 2015). There are many means of dispersal for microalgae. Most of their transport is passive, active dispersal is of minor significance[1] (Kristiansen, 1996). Passive dispersal is with vectors that are either physical (water or wind) or biological (animal mediated dispersal). Populations can migrate as live individuals or via spores (Incagnone et al., 2015), which can spread through:

[1] Microalgae are able to move across surfaces or through the water column, diatoms and desmids for example can glide along stones and other material (Domozych & Domozych, 2008; Mann et al., 2016). Although this movement is very slow, they might be able to colonize new water habitats, if they are close enough (Messikommer, 1943). When compared to passive dispersal methods, their active movement has almost no significance.

1. Water

As most microalgae are aquatic organisms, they are regularly transported through streams and currents, floating freely or stuck to debris, such as wood, stones or other material. This way, they spread in streams or rivers. Marine species transport through the ocean the same way (Kristiansen, 1996; Sharma & Rai, 2010). Microalgae in single bodies of water or ephemeral ponds have to depend on other vectors to colonize new habitats, for example on water birds or air dispersal (Incagnone et al., 2015).

2. Air

The occurrence of airborne microalgae has been confirmed in multiple habitats, from Antarctica (Marshall & Chalmers, 1997) to tropical spaces (Sherwood et al., 2020).

Air dispersal consists of multiple steps (Figure 1), the microalgae first have to get into the air; this can happen by wind picking up dust particles or water drops ejecting from water surfaces. After the transport itself, the microalgae have to settle back on the ground – either by rainfall or as dry depositions (Tesson et al., 2016). The presence of microalgae in the air does not have to lead to a successful colonization. They get into harsh conditions, so they often get damaged. During transport they are faced with dehydration, UV stress or low temperatures (Souffreau et al., 2013; Chiu et al., 2020). Due to the high desiccation stress tolerance, terrestrial microalgae seem to be more successful with air mediated dispersal (Sharma et al., 2007).

Some airborne microalgae are considered a health risk for humans, as they can be allergens (Schlichting, 1974; Jain & Gupta, 1998; Tesson et al., 2016), contaminate water bodies (Schlichting, 1974), or cause disease. One example is the dinoflagellate *Karenia bravis,* which causes massive blooms[2] in Florida (Flewelling et al., 2005). Because of the fragile nature of its cells, when they get ejected into the air, they get damaged and harmful toxins get released (Kirkpatrick et al., 2004). These toxins can lead to respiratory diseases when inhaled or neurotoxic shellfish poisoning when ingesting contaminated shellfish (Kirkpatrick et al., 2004; Sharma et al., 2007). Microalgae can also grow on buildings, changing their appearance (Sherwood et al., 2020). Therefore, most research focuses on the presence of microalgae in the

[2] Algal blooms are events of massive cell growth (Mann et al., 2016). When a species is considered harmful, these events are called harmful algal blooms (Murray & Hallegraeff, 2018).

air, which taxa and how abundant they are (e. g. Schlichting Jr., 1969; Marshall & Chalmers, 1997) or on the seasonality of their presence (e. g. Sherwood et al., 2020).

Research of airborne microalgae is difficult, because of technical limitations – it's difficult to sample airborne microalgae, as their concentrations in the air are low. Furthermore, the air environment is difficult to simulate (Tesson et al., 2016). The success rate, of how well they colonize new habitats through this vector is difficult to measure.

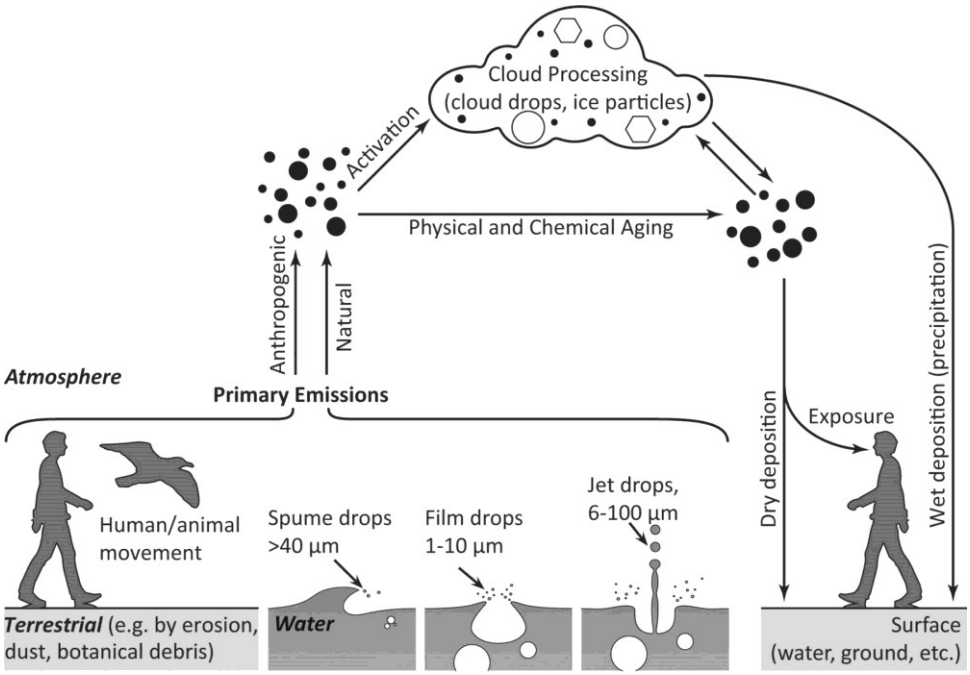

Figure 1: The process of air dispersal of microalgae, from primary emissions to final deposition. (Pöschl, 2005 modified by Tesson et al., 2016)

3. With other organisms

The most common animal vector (especially for longer distances) is transport by waterbirds (Kristiansen, 1996). Microalgae can travel in the gut of waterbirds; this process is then called endozoochory. In this instance, microalgae have to survive passing through the birds' digestive tract (Atkinson, 1972; Tesson et al., 2018). If they succeed, they can colonize the new habitat. Another way of transport, called epizoochory, is to attach to their feathers and feet (Manning et al., 2021) and then be transported to a new location. During this process they undergo harsh conditions, such as strong wind, lack of humidity and air pressure. This transport can be studied by sampling microalgae from waterbirds, but it is difficult to determine when the microalgae attached and therefore how far they have travelled (Manning et al., 2021). The resistance to

these conditions can be studied experimentally (e. g. Souffreau et al., 2013; Manning et al., 2021).

Other animals that can serve as a vector are Odonata and amphibians (Cochak et al., 2024), Coleoptera (Milliger et al., 1971), fish (also endozoochory) (Kristiansen, 1996) or mammals like the mink (Leone et al., 2014). Additionally, there are diatoms living on whales (Nemoto, 1956) or sea turtles (Van de Vijver et al., 2020) - this could also be viewed as a vector.

4. With anthropological influence

Humans have greatly altered natural distribution means. A common man induced vector is ship transport (Klein et al., 2010). Microalgae can be part of ballast water, or attached to the ship, in the ballast tank or as fouling on the ship itself. Additionally, microalgae can disperse with introductions of animals/plant for purposes of aquaculture (Murray & Hallegraeff, 2018; Mann, 2022). Furthermore, a factor to consider is climate change and pollution. People alter local habitats making them more vulnerable to new invaders (Stachowicz et al., 2002).

It is important to note that dispersal always consists of a combination of these vectors (Cochak et al., 2024). After initial anthropological introduction, microalgae can disperse naturally, in the ways mentioned above (Leone et al., 2014).

The aim of this thesis is to determine how relevant human mediated transport is for the dispersal microalgae, what new introductions it causes and if there are any ways to prevent these introductions.

2 Diatoms as an example of microscopic algae

Microalgae are a polyphyletic group, consisting of Cyanobacteria, Stramenopils and green algae, therefore their characteristics are quite different. To explore the topic of man-induced dispersal, I will focus on diatoms as an example.

2.1 Defining diatoms

Diatoms, also called Bacillariophyta, are a group of microscopical algae, belonging to the SAR clade, specifically the Stramenopiles (Adl et al., 2012). They are unicellular organisms that sometimes form colonies. This group of algae lives in aquatic habitats, both marine and freshwater, with some species also living terrestrially, e. g. in soil (Mann et al., 2016).

Their cell walls form a silica-based shell called a *frustule*, which consists of a glass-like material, made of SiO_2. This inorganic material allows this group to fossilize easily and creates diatomite (also called diatomaceous earth), a sedimentary rock often used for industrial purposes (Dobrosielska et al., 2022). The fossilized frustules allow the usage of diatoms in paleontology, as stratigraphic markers or for the study of diatom evolution. The oldest fossils date back to the late Cretaceous, but they are estimated to be older – distributed around the world during the early Cretaceous already (Harwood & Gersonde, 1990).

Reproduction occurs both sexually and vegetatively. During asexual reproduction, cells divide and then split into daughter cells, each inherits one valve of the frustule. The cell wall is then synthesized as the smaller valve, over time, this makes the daughter cells smaller and smaller (Kaczmarska et al., 2013). To combat the shrinking population, sexual reproduction occurs. This leads to a size variation in the cells within a population, thus while determining a species, multiple specimen must be observed.

Diatoms are mostly aquatic species, living in marine and freshwater habitats, but they can also be found in soil. Some diatoms also live as endosymbionts, in Dinoflagellates or Foraminifera. The aquatic species are either part of the plankton or benthos. Planktonic species float in the water column, occasionally sinking to the ground. Benthic diatoms grow attached to different surfaces, they can grow on rocks, plants, sand, but even on animals, algae or other diatoms (Mann et al., 2016). To combat harsh conditions diatoms can form resting stages, these are mostly found in centric diatoms (Souffreau et al., 2013).

3 Human mediated dispersal

The biogeography of diatoms is still being questioned on whether they have a non-cosmopolitan distribution (Sharma & Rai, 2010). Because of their size, it is much harder to monitor microalgae introductions when compared to larger organisms. Species recognition relies on microscopy, therefore, unlike with birds or higher plants, there is less of an option for help from the general public. This makes it difficult to claim a species was newly introduced (Vanormelingen et al., 2009). Only after extensive research and ruling out natural vectors can an introduction be labelled as human-mediated. (Harper, 1994).

3.1 How can an introduction be confirmed?

There are a few options of how to determine if a species is non-indigenous. One is comparing previous research of the diatom community (like water column and benthic sampling) with the current state and checking if the species has been previously mentioned (S. Spaulding et al., 2010). Here it can be assumed that for example a large species or one with a significant shape would have to have been noticed before (Saber et al., 2022). This however, relies on a good record of local species (Mann, 2022). Therefore, a more reliant method is paleolimnological sampling, where diatoms can be found in sediment cores, because of their silica-based frustules (Spaulding et al., 2010).[3] When a species is missing from these records, it is considered a new introduction (Harper, 1994).

An interesting aspect is that the presence of the diatom in sediment sometimes reveals that the species invaded many years before the first live specimen are noticed. For example, in the Great Lakes, the species *Stephanodiscus binderanus* was found in sediments in Lake Michigan from 1938, however, the first records of it were 17 years later, in 1955 when it was recorded in the St. Lawrance River (Mills et al., 1993). This proves that after an initial release, introductions often stay unnoticed, especially if specimen are of small size and rarely abundant (Mann, 2022).

With insufficient records, false claims can be made of a species not being indigenous. Another obstacle is the false identification of species. It can happen that a diatom considered non-indigenous has just been formerly known under a different name (Gómez, 2008). Thus, it is important to research possible synonyms for the studied species (Mann, 2022).

[3] When diatom cells die, they sink to the bottom of lakes/rivers/the ocean they live in. At the same time, sediment accumulates and creates layers. These sediments can get sampled with core tubes and after the core is pulled out of the sediments, it can be analysed (Glew et al., 2001). The layers then get assigned dates and based on these changes in the diatom community can be analysed (Mann et al., 2016).

3.2 Ballast water

Ballast water is assumed to be the most common vector for man mediated dispersal (Zhang & Dickman, 1999; Klein et al., 2010). It is used as a stabilizing element for ships. Before the use of water, stone, gravel or other solid material was used – in the past that was a dispersal vector for plants (Reichard, 1997) or insects (Sailer, 1983). Handling water as ballast is easier, so it is the only ballast used nowadays. When a ship is not carrying any cargo ballast is necessary for the journey. The ships take on water at a starting port and after loading on new cargo the water is released at a new location (Locke et al., 1993). Some ships travel with no ballast on board if they are fully loaded. During transport, ships often release and take on water after loading on more cargo, or for technical purposes during the journey. This way, the water discharged can come from multiple locations (Holeck et al., 2004; Gollasch & David, 2020). While releasing the water, many organisms get released into the water at a new location (Mills et al., 1993).

The first mentions of diatoms being transported with ballast water date back to the early 1900s, with the diatom *Odontella sinensis* reported in the North Sea. This diatom, originally known from the Indo-Pacific, was supposedly discovered in Europe for the first time in 1903 by Ostenfeld (1908) as cited in Hallegraeff & Bolch (1992). However, this introduction has since been questioned (Gómez, 2008; Gómez & Souissi, 2010). Other ballast water introductions include marine species *Pseudo-nitzschia seriata, Chaetoceros peruvianus* and *Cerataulina pelagica* transported from the Black Sea to the Caspian Sea (Pautova et al., 2022) or the multiple freshwater diatoms transported into the Great Lakes (Table 1 in appendix).

Diatoms can be found in the ballast water itself, or in sediments that are at the bottom of the ballast tanks (Hallegraeff & Bolch, 1992). They have to survive periods of time without sunlight and temperature changes (Dickman & Zhang, 1999; Lavoie et al., 1999). Because of these stressors, the mortality rate is higher the longer the journey is (Lavoie et al., 1999). Experiments sampling the ballast water on cargo ships (e. g. Hallegraeff & Bolch, 1992; Dickman & Zhang, 1999; Zhang & Dickman, 1999; Burkholder et al., 2007; Klein et al., 2010; Cheniti et al., 2018) have shown that species travelling within the tanks are quite diverse, containing both planktonic and benthic species (Hallegraeff & Bolch, 1992; Villac et al., 2013), freshwater, brackish and marine types.

Most studies focus on sampling the ballast water itself, the sediments at the bottom of ballast tanks however, can be a refuge for many species (Villac et al., 2013). During ballast water

release some sediment (and also residual water) often stays in the tanks (Dickman & Zhang, 1999), meaning that the longer ships go without cleaning out the tanks, the more sediment accumulates (Villac et al., 2013).

Possible introductions of diatoms being transported in ballast water are either marine species living in ports, or freshwater/brackish ones. Ballast water introductions can be of species from different continents, but also can happen inland, for example within a lake system (Mills et al., 1993).

3.2.1 Regulations

Because of the many introductions related to ballast water, different methods that could prevent them are being studied. One of these methods (for oceanic shipping) is the practice of ballast water exchange (BWE). If a ship is carrying any ballast water, it must empty its tanks in the open ocean and then refill them. This way, the brackish or even freshwater gets exchanged in the tanks (Gollasch & David, 2020).

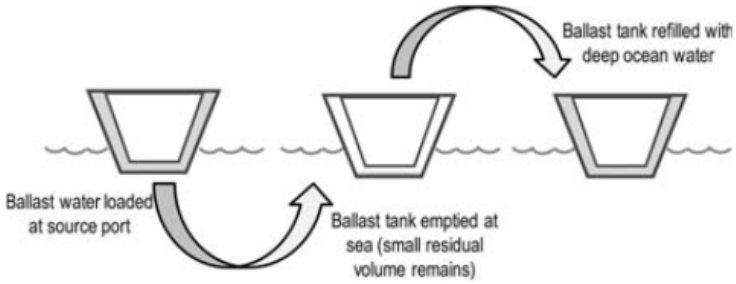

Figure 2: The process of ballast water exchange (Bailey, 2015)

When first established, it was expected that the brackish or freshwater organisms in the ballast tanks would be released into the open ocean where they would die, because of the high salinity and individuals that stayed in the tanks would get killed by the saline water taken in (Ricciardi & MacIsaac, 2022). Many cells however, stay in the ballast tanks even after water exchange and survive the new salinity levels (Klein et al., 2010). As mentioned before, the tanks also contain sediment, which gets rarely released form the tanks. In the sediments, diatoms can survive the BWE (Villac et al., 2013). The effectivity of the exchange also depends on the type of ship, older tanks release less water and more residual water then stays in the tanks (Dickman & Zhang, 1999). This was the case in a study by Dickman & Zhang (1999), where BWE lowered the mean number of cells (diatoms and dinoflagellates) on board only by

48%. Klein et al. (2010) and Zhang & Dickman (1999) report a success rate of 87%. Another aspect to consider is the uptake of marine species living in the open ocean with the exchanged water, some seem to survive habitats with lower salinity, so they could be a problem in the future (Klein et al., 2010).

To combat introductions some countries have made BWE mandatory, when entering their ports. An example of such regulations are the United States and Canada, as they try to regulate the number of introductions in the Great Lakes.[4] Currently around 182 non-indigenous species have been reported in the Great Lakes since 1940 (Ricciardi, 2006), among them are 17 diatom species (Table 1) (Mills et al., 1993; Edlund et al., 2000). In 1959, the modern St. Lawrance Seaway (a larger canal enabling more and larger ships to enter) opened and 65% of the introductions that have been reported since then are due to ballast water (Ricciardi & MacIsaac, 2022). Because of invasive species like the Zebra mussel (*Dreissena polymorpha*) effort has been made to lower the number of introductions. The US and Canadian government have put out multiple guidelines for ballast water, the first being a requirement for ships carrying ballast on board (BOB) to perform BWE (Guard, 1993). This however, was only mandatory for BOB ships and those not carrying ballast water (NOBOB) could enter freely. After offloading cargo NOBOB ships pumped in new water from the lakes, this was partly mixed with the residual water stuck in the tanks (Locke et al., 1993; Ricciardi, 2006). Since diatoms can survive for long periods of time in the sediments or residual water of the tanks, even taking on water makes them a threat. The implementation of the new regulations did not result in a decline of newly introduced species[5] (Ricciardi & MacIsaac, 2022).

This example shows that while BWE is not ineffective in reducing the number of transported organisms (for example the temperature difference between the water in the tanks and in the open ocean makes the survival of warm water species less likely (Dickman & Zhang, 1999), it doesn't seem to be enough to prevent new introductions. This leads to the study of other possible treatments, for example heating of the ballast tanks with waste heat from engines (Hallegraeff, 2015). The ballast tanks would be heated up to 40° C for multiple hours/days,

[4] The Great Lakes consist of a series of lakes (Lake Superior, Lake Michigan, Lake Huron, Lake Erie and Lake Ontario) on the US Canadian border, connected to the Atlantic Ocean through the Saint Lawrance River. This freshwater complex has many ports used to on- and offload cargo, which leads to a large number of introductions (Holeck et al., 2004; Ricciardi, 2006).

[5] The mean rate of new introductions went from 1.0 species per year (1960 to 1988) to 1.2 species year^{-1} (1993 – 2006) (Ricciardi, 2006)

killing the cells or cysts of microalgae (Rigby et al., 2004). This would however require constructional changes to ships.

Another possibility of ballast water treatment (BWT) would be filtration, which can be done with filters of different sizes. This method proved to be a good first treatment (meaning that other treatments would have to follow) for the removal of microalgae, as many remain present after filtration (Cangelosi et al., 2007). Other BWTs include UV irradiation or the dosing of biocides (Murray & Hallegraeff, 2018). A way of prevention would be not refilling ballast during times of harmful algal blooms (Murray & Hallegraeff, 2018); this would however require monitoring of bloom events by local algologists, which the article does not mention. Most of these methods are quite expensive and have not shown promising results. However, a successful method of preventing more introductions seems to have been found in the Great Lakes. In 2006 and 2008 their BWE laws were updated and a new treatment became mandatory – flushing the water tanks with salt water upon arrival into the lakes (Government of Canada, 2021). This way, freshwater organisms are faced with osmotic stress and low nutrient water, leading to their death (Ricciardi & MacIsaac, 2022). This seems to be a successful method, because in the last years, the introductions have gone from 2.0 to 0.31 new species per year (Ricciardi & MacIsaac, 2022). These were studies done on all aquatic organisms, so it is possible that a new diatom introduction has just gone unnoticed. Unfortunately, due to the nature of this method it cannot be used for marine species.

Probably the most effective method is a combination of BWE and BWT. It is also important to mention the risks of BWE in areas where the transported diatoms could be invasive.

3.3 Introductions with aquaculture

In some cases, diatoms get co-introduced along with other animals or plants, especially with fish, that are either intentionally released or escape captivity (Harper, 1994; Alverson et al., 2021). During the introduction of grey mullets in the Caspian Sea, water from the Black Sea was used to transport these fish. It is assumed that this way the diatom *Pseudosolenia calcar-avis* was introduced accidentally (Kostianoy & Kosarev, 2005; Karpinsky, 2010). The species was identified in 1934 and within a year it spread in the Caspian Sea and dominated the biomass of phytoplankton - it usually reached more than 80% even up to 99% (of total phytoplankton biomass in g/m^3) in some cases (Zenkevich, 1963; Karpinsky, 2010). Similarly to the release of grey mullets, salmon (and other fish) were released in New Zealand in the 1800s. These releases are most likely the vector of introduction for the diatom *Asterionella formosa*. This

species is common in New Zealand fresh water; however, it cannot be found in core samples older than from 1880 (Harper, 1994). It also was not present in samples from Australia and other near countries making dispersal by birds very unlikely.

While *P. calcar-avis* quickly became a dominant part of the local flora, some diatoms stay unnoticed several years after their introduction. *Discostella asterocostata* is also assumed to be introduced by fish, namely Asian carp. It was first noticed in 2010, but sediment core sampling revealed that it has been in the US since the 1980s (Alverson et al., 2021). Asian carp species were released in the US since the 1970s and share native habitats with this diatom (Figure 3) therefore a joined introduction is likely. Compared to other studies mentioned, this approach is different, because native locations of the fish are considered whereas the other fish introductions are not based on proper research. Another recent introduction, the diatom *Licmophora normaniana,* was found in a mineral spring in the Siwa oasis. This diatom had not been seen in previous studies on the species in the pond and is therefore assumed to be a non-indigenous species. The assumed vector of introduction is with fish that locals release for farming (Saber et al., 2022).

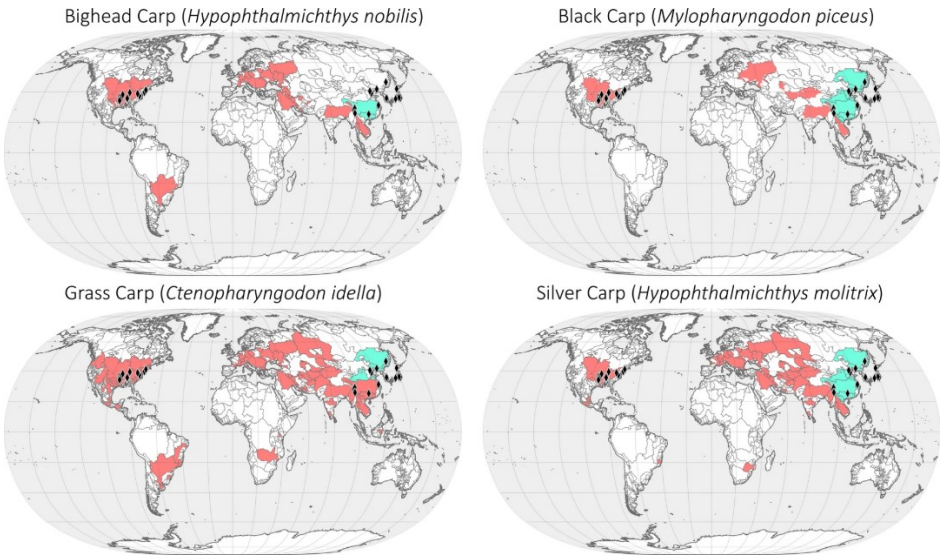

Figure 3: The distribution of 4 species of Asian carp and the diatom Discostella asterocostata*. Native ranges of the carps are in teal and non-native orange. Diamonds represent occurances of* D. asterocostata*. The areas overlap in their native and introduced regions* (Alverson et al., 2021)

3.4 Direct transport on material

Especially after a primary introduction in a new area, diatoms can travel on sports or research equipment. This is seen as one of the vectors for the spread of *Didymosphenia geminata* across locations in New Zealand. This diatom is seen as an invasive species in New Zealand since its discovery in 2004. Because of the specific shape and large size of this species, it is assumed to be newly introduced, as it could not have been overlooked in past samples in New Zealand (Kilroy & Unwin, 2011). Another factor speaking for *D. geminata* not being native is the similarity between genomes of samples from New Zealand and the US. If it had been present in the past, there would be some variations (Kilroy & Novis, 2018). While the vector of its introduction is unclear, it most likely was human mediated. Natural vectors that can be considered for its spread, are birds or air dispersal, however experimental results show that it would not survive a passage through bird guts (Kilroy et al., 2006).

This benthic diatom produces extracellular stalks used to attach to substrate it grows on. These stalks can grow multiple centimetres long and divide along with the diatom cells, creating a dense cover on streambeds, often several kilometres long (Spaulding & Elwell, 2007). Apart from its ecological impact the blooms lower the visual appeal of rivers, resulting in the decrease of angling and therefore negatively affect local economy (Kilroy et al., 2009). After its initial appearance in 2004 *D. geminata* spread through New Zealand's South Island and by 2007 it was present in most of the rivers (Kilroy & Unwin, 2011). While natural vectors have also played a role in spreading the species, human vectors are responsible for this rapid spread. Among these are anglers, kayaking, motorboats or livestock living close to streams with a *D. geminata* presence (Kilroy & Unwin, 2011). To combat the spread of *D. geminata* New Zealand started to evaluate imported goods at the border and also started the "Check, Clean and Dry" campaign (Champion, 2018). The campaign is a guide for people on how to clean their clothes or equipment when entering the water bodies, depending on the type and frequency of use different guidelines apply (Ministry for Primary Industries, 2024). These measures could also prevent further spreading of another invasive New Zealand diatom - *Lindavia intermedia.* This freshwater species produces so called lake snow, which are aggregates of mucilage. The snow accumulates on fishing lines and clogs filters, but it is not noticeable at the surface (Novis et al., 2017). It is not clear, how this diatom invaded, but genetically it is identical to specimen from Lake Youngs (US), suggesting a link to North America (Novis et al., 2017).

Introductions are not just due to recreational use, biologists can also be a vector of spreading phytoplankton, for example via plankton nets. Wejnerowski et al. (2022) surveyed biologists on methods how they clean their plankton nets between samples. Most of them wash them with distilled/tap water and leave them to dry, but their research showed that many organisms survive this method. For this reason, disinfection by ethanol is recommended.

Even floating plastic has been colonized by diatoms (Masó et al., 2003, 2016; Prabowo et al., 2023) on pieces in benthic and pelagic habitats. Mostly epiphytic (epilithic and epizoic) species adhere to the material (Reisser et al., 2014). In studies done in the Mediterranean (Masó et al., 2016), in Indonesian waters (Prabowo et al., 2023), Australian waters (Reisser et al., 2014), the North Pacific Gyre (Carson et al., 2013) and in the North Atlantic (Zettler et al., 2013), diatoms were either the most abundant or one of the most abundant species found on the plastic (along with Dinoflagellates and bacteria).

4 Discussion

When determining whether microalgae have been spread by human activity, their natural dispersal options should always be considered. Proper research on whether a species is not indigenous is also needed, consisting of evaluating past records and new sampling. A helpful tool can be comparing genetic information of the newly found species with specimen from native, or other introduced locations. Species that were separated geographically showed genetical differences. This method was used on *Lindavia intermedia* when it was discovered in New Zealand and it was genetically identical to strains from the US (Novis et al., 2017), which suggests an introduction from North America.

Ballast water transport is the most common vector for human mediated dispersal of microalgae. Diatoms can survive long periods of time in the dark (Klein et al., 2010) and their ability to reproduce asexually enables them to colonize new habitats quickly (Lavoie et al., 1999). Similarly to other environmental issues, international agreements are needed to manage these introductions. When it comes to ballast water transport, it is difficult to come to an agreement between all parties. Cargo gets transported around the world and specific laws are needed to ensure less introductions. International agreements include the Ballast Water Management convention (BWM) of 2004, implemented in 2017 negotiated by the United Nations International Maritime Organization. The BMW is certainly a step in the right direction, but its regulations are not sufficient in preventing further introductions. Cost is an important factor as well, because unless effective treatment methods of ballast water are made accessible, they won't be put in use. Therefore, more research must be done on these methods. The only treatment that showed promising results so far is salt water flushing, which is however only effective in preventing the introduction of fresh water species. Dispersal in ballast water can be traced by going through records of ships' voyages and ballast tanks can be sampled to assess which species survive transport.

Out of the four aquaculture introductions mentioned in this thesis only one compared native distribution of the fish which were probably the vector with distribution of the found diatom (Alverson et al., 2021). Other introductions known so far have been mostly based on assumptions about possible cotransport of diatoms with larger organisms. This makes preventing aquaculture introductions complicated along with the demand to expand fish farming. One possible measure is control of the entry of diatom species that are not native to an area (or country). This is already the case in NZ and Canada. Species that are not seen as

native cannot enter. While strict restrictions and policies can prevent new introductions, there is a risk of illegal import (Champion, 2018) becoming of larger impact, as has happened in NZ.

Further issues are possible harmful variants to native species present. After massive blooms of *Didymosphenia geminata* in Vancouver Island and later New Zealand, some researchers believe there might be multiple genetic variants of *D. geminata* – those causing these nuisance blooms and harmless ones (Bothwell et al., 2009). If the harmless variant of a species is already present in local flora, the potentially harmful variant could be imported without any restrictions. A less researched dispersal vector is the spread of diatoms between water bodies by activity like angling or swimming (Murray & Hallegraeff, 2018). Proper cleaning of equipment (like the New Zealand - Check, Clean, Dry) can lower the chance of spreading the introduced species further. But even after an initial human mediated introduction the human vector is eliminated completely, microalgae can be dispersed by natural vectors (and vice versa).

More research should focus on regular sampling from multiple habitats: benthic substrates, water column and sediments. With sufficient records new introductions can be noticed faster, as the appearance of *Licmophora normaniana* in a spring in Egypt (Saber et al., 2022), which solely rely on records of past samples of a location. Sediment core sampling should be used to determine a new introduction, especially if the aim is to find out when the introduction occurred. Klein et al. (2010) sampled ballast water and then compared the species found in the water with local diatom flora. Thanks to such research, potential risks can be assessed before introductions occur. In other work (not focused on microalgae however) Ricciardi & Rasmussen (1998) suggest forming lists of possible invaders based on: 1. their past invasive behaviour; 2. their donor region – if there have been invasions from it before, new ones are more likely; 3. similarity in habitat and 4. if they are known to be transported by human activity (i. e. ballast water). After determining potential invaders, research should be focused on determnening their ecology in the native region. Knowledge of a species' ecology can make control sampling easier, because researchers know where to look and can note which habitats might be endangered (Mann, 2022). Limitation of new introductions is easier for isolated regions, like New Zealand, because it is fairly easy to monitor what gets inside the country.

It is very difficult to estimate the total number of diatom introductions by humans. Most of those mentioned were of large species or those with a specific shape, species of a smaller size and small populations can be overlooked (Pautova et al., 2022). Furthermore, often when new species are noticed, their introduction is rarely managed and usually less researched, unless it

is causing problems. An example of this is the focus on *D. geminata* in New Zealand compared to another invasive diatom *Lindavia intermedia* that also produces mucilage forming blooms, however on a smaller scale. Apart from human mediated transport, changes to the environment can alter natural distribution and therefore affect microalgae dispersal. Successful prevention of further human mediated introductions (regardless of vector) depends on the cooperation of scientists, local authorities and the whole of society.

Bibliography

Adl, S. M., Simpson, A. G. B., Lane, C. E., Lukeš, J., Bass, D., Bowser, S. S., Brown, M. W., Burki, F., Dunthorn, M., Hampl, V., Heiss, A., Hoppenrath, M., Lara, E., Gall, L. Le, Lynn, D. H., McManus, H., Mitchell, E. A. D., Mozley-Stanridge, S. E., Parfrey, L. W., … Spiegel, F. W. (2012). The Revised Classification of Eukaryotes. *Journal of Eukaryotic Microbiology*, *59*(5), 429–514. https://doi.org/10.1111/J.1550-7408.2012.00644.X

Alverson, A. J., Chafin, T. K., Jones, K. A., Manoylov, K. M., Johnson, H., Julius, M. L., Nakov, T., Ruck, E. C., Theriot, E. C., & Yeager, K. M. (2021). Microbial biogeography through the lens of exotic species: the recent introduction and spread of the freshwater diatom *Discostella asterocostata* in the United States. *Biological Invasions*, *23*, 2191–2204.

Atkinson, K. M. (1972). Birds as transporters of algae. *British Phycological Journal*, *7*(3), 319–321. https://doi.org/10.1080/00071617200650331

Bailey, S. (2015). An overview of thirty years of research on ballast water as a vector for aquatic invasive species to freshwater and marine environments. *Aquatic Ecosystem Health and Management*, *18*, 261–268. https://doi.org/10.1080/14634988.2015.1027129

Bass, D., & Boenigk, J. (2011). Everything is everywhere: A twenty-first century de-/reconstruction with respect to protists. *Biogeography of Microscopic Organisms: Is Everything Small Everywhere?*, 88–110. https://doi.org/10.1017/CBO9780511974878.007

Beijerinck, M. W. (1913). De infusies en de ontdekking der backteriën. Jaarboek van de Koninklijke Akademie voor Wetenschappen. *Müllerm Amsterdam*.

Briggs, J. C. (1995). *Global biogeography*. Elsevier.

Burkholder, J. M., Hallegraeff, G. M., Melia, G., Cohen, A., Bowers, H. A., Oldach, D. W., Parrow, M. W., Sullivan, M. J., Zimba, P. V, Allen, E. H., Kinder, C. A., & Mallin, M. A. (2007). Phytoplankton and bacterial assemblages in ballast water of U.S. military ships as a function of port of origin, voyage time, and ocean exchange practices. *Harmful Algae*, *6*(4), 486–518. https://doi.org/https://doi.org/10.1016/j.hal.2006.11.006

Cangelosi, A., Mays, N., Balcer, M., Reavie, E., Reid, D., Sturtevant, R., & Gao, X. (2007). The response of zooplankton and phytoplankton from the North American Great Lakes to filtration. *Harmful Algae*, *6*, 547–566. https://doi.org/10.1016/j.hal.2006.11.005

Carson, H. S., Nerheim, M. S., Carroll, K. A., & Eriksen, M. (2013). The plastic-associated microorganisms of the North Pacific Gyre. *Marine Pollution Bulletin*, *75*(1), 126–132. https://doi.org/https://doi.org/10.1016/j.marpolbul.2013.07.054

Champion, P. D. (2018). Knowledge to action on aquatic invasive species: Island biosecurity–the New Zealand and South Pacific story. *Management of Biological Invasions*, *9*(4), 383.

Cheniti, R., Rochon, A., & Frihi, H. (2018). Ship traffic and the introduction of diatoms and dinoflagellates via ballast water in the port of Annaba, Algeria. *Journal of Sea Research*, *133*, 154–165. https://doi.org/https://doi.org/10.1016/j.seares.2017.07.008

Chiu, C.-S., Chiu, P.-H., Yong, T. C., Tsai, H.-P., Soong, K., Huang, H.-E., & Chen, C.-N. N. (2020). Mechanisms protect airborne green microalgae during long distance dispersal. *Scientific Reports*, *10*(1), 13984. https://doi.org/10.1038/s41598-020-71004-y

Cochak, C., Zanon, F. M., Pineda, A., Lansac-Tôha, F. M., Jati, S., & Velho, L. F. M. (2024). Beta diversity of freshwater algal communities: influence of different dispersal mechanisms. *Aquatic Sciences*, *86*(2), 26. https://doi.org/10.1007/s00027-023-01040-z

De Wit, R., & Bouvier, T. (2006). 'Everything is everywhere, but, the environment selects'; what did Baas Becking and Beijerinck really say? *Environmental Microbiology*, *8*(4), 755–758. https://doi.org/https://doi.org/10.1111/j.1462-2920.2006.01017.x

Dickman, M., & Zhang, F. (1999). Mid-ocean exchange of container vessel ballast water. 2: Effects of vessel type in the transport of diatoms and dinoflagellates from Manzanillo, Mexico, to Hong Kong, China. *Marine Ecology-Progress Series - MAR ECOL-PROGR SER*, *176*, 253–262. https://doi.org/10.3354/meps176253

Dobrosielska, M., Dobrucka, R., Brzakalski, D., Frydrych, M., Kozera, P., Wieczorek, M., Jałbrzykowski, M., Kurzydłowski, K. J., & Przekop, R. E. (2022). Influence of Diatomaceous Earth Particle Size on Mechanical Properties of PLA/Diatomaceous Earth Composites. *Materials*, *15*(10). https://doi.org/10.3390/MA15103607/S1

Domozych, D. S., & Domozych, C. R. (2008). Desmids and Biofilms of Freshwater Wetlands: Development and Microarchitecture. *Microbial Ecology*, *55*(1), 81–93. https://doi.org/10.1007/s00248-007-9253-y

Edlund, M., Taylor, C., & Schelske, C. (2000). *Thalassiosira baltica* (Grunow) Ostenfeld (Bacillariophyta), a new exotic species in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 610–615. https://doi.org/10.1139/cjfas-57-3-610

Finlay, B. J., Esteban, G. F., & Fenchel, T. (2004). Protist Diversity is Different? *Protist*, *155*(1), 15–22. https://www.proquest.com/scholarly-journals/protist-diversity-is-different/docview/207944061/se-2?accountid=8179

Finlay, B. J., & Fenchel, T. (2004). Cosmopolitan metapopulations of free-living microbial eukaryotes. *Protist*, *155*(2), 237–244. https://doi.org/10.1078/143446104774199619

Finlay, B. J., Monaghan, E. B., & Maberly, S. C. (2002). Hypothesis: The Rate and Scale of Dispersal of Freshwater Diatom Species is a Function of their Global Abundance. *Protist*, *153*(3), 261–273. https://doi.org/https://doi.org/10.1078/1434-4610-00103

Flewelling, L. J., Naar, J. P., Abbott, J. P., Baden, D. G., Barros, N. B., Bossart, G. D., Bottein, M.-Y. D., Hammond, D. G., Haubold, E. M., Heil, C. A., Henry, M. S., Jacocks, H. M., Leighfield, T. A., Pierce, R. H., Pitchford, T. D., Rommel, S. A., Scott, P. S., Steidinger, K. A., Truby, E. W., … Landsberg, J. H. (2005). Red tides and marine mammal mortalities. *Nature*, *435*(7043), 755–756. https://doi.org/10.1038/nature435755a

Foissner, W. (2006). Biogeography and Dispersal of Microorganisms: A Review Emphasizing Protists. *Acta Protozool.*, *45(2)*, 111–136.

Fontaneto, D., & Hortal, J. (2012). *Microbial biogeography: is everything small everywhere?* (pp. 87–98).

Glew, J. R., Smol, J. P., & Last, W. M. (2001). Sediment core collection and extrusion. *Tracking Environmental Change Using Lake Sediments: Basin Analysis, Coring, and Chronological Techniques*, 73–105.

Gollasch, S., & David, M. (2020). Ballast Water. In S. de Mora, T. Fileman, & T. Vance (Eds.), *Environmental Impact of Ships* (pp. 96–111). Cambridge University Press. https://doi.org/DOI: 10.1017/9781108381598.006

Gómez, F. (2008). Phytoplankton invasions: Comments on the validity of categorizing the non-indigenous dinoflagellates and diatoms in European Seas. *Marine Pollution Bulletin*, *56*(4), 620–628. https://doi.org/https://doi.org/10.1016/j.marpolbul.2007.12.014

Gómez, F., & Souissi, S. (2010). The diatoms *Odontella sinensis, Coscinodiscus wailesii* and *Thalassiosira punctigera* in the European Atlantic: recent introductions or overlooked in the past? *Fresenius Environmental Bulletin*, *19*.

Government of Canada. (2021). Ballast Water Regulations: SOR/2021-120. In *Canada Gazette*.

Guard, U. S. C. (1993). Ballast water management for vessels entering the Great Lakes. *Code of Federal Regulations*.

Hallegraeff, G., & Bolch, C. (1992). Transport of Diatom and Dinoflagellate Resting Spores in Ships' Ballast Water: Implications for Plankton Biogeography and Aquaculture. *Journal of Plankton Research - J PLANKTON RES*, *14*, 1067–1084. https://doi.org/10.1093/plankt/14.8.1067

Hallegraeff, G. M. (2015). Transport of harmful marine microalgae via ship's ballast water: Management and mitigation with special reference to the Arabian Gulf region. *Aquatic Ecosystem Health & Management*, *18*(3), 290–298. https://doi.org/10.1080/14634988.2015.1027138

Harper, M. (1994). Did Europeans introduce *Asterionella formosa* Hassall to New Zealand? *Proceedings of the 11th International Diatom Symposium*, 479–484.

Harwood, D. M., & Gersonde, R. (1990). Lower Cretaceous diatoms from ODP Leg 113 Site 693 (Weddell Sea). Part 2: resting spores, chrysophycean cysts, an endoskeletal dinoflagellate, and notes on the origin of diatoms. In *Proc., scientific results, ODP, Leg 113, Weddell Sea, Antarctica*.

Heimann, K., & Huerlimann, R. (2015). Chapter 3 - Microalgal Classification: Major Classes and Genera of Commercial Microalgal Species. In S.-K. Kim (Ed.), *Handbook of Marine Microalgae* (pp. 25–41). Academic Press. https://doi.org/https://doi.org/10.1016/B978-0-12-800776-1.00003-0

Holeck, K., MILLS, E., MacIsaac, H., DOCHODA, M., Colautti, R., & Ricciardi, A. (2004). Bridging Troubled Waters: Biological Invasions, Transoceanic Shipping, and the Laurentian Great Lakes. *Bioscience*, *54*. https://doi.org/10.1641/0006-3568(2004)054[0919:BTWBIT]2.0.CO;2

Incagnone, G., Marrone, F., Barone, R., Robba, L., & Naselli-Flores, L. (2015). How do freshwater organisms cross the “dry ocean”? A review on passive dispersal and colonization processes with a special focus on temporary ponds. *Hydrobiologia*, *750*(1), 103–123. https://doi.org/10.1007/s10750-014-2110-3

Jain, A., & Gupta, M. (1998). Role of air borne bioparticles with special reference to algal components. *Perspectives in Environment.(Ed. Agarwal, SK, Kaushik, JP, Koul, KK and Jain, AK)*, 93–105.

Kaczmarska, I., Poulíčková, A., Sato, S., Edlund, M. B., Idei, M., Watanabe, T., & Mann, D. G. (2013). Proposals for a terminology for diatom sexual reproduction, auxospores and resting stages. *Diatom Research*, *28*(3), 263–294. https://doi.org/10.1080/0269249X.2013.791344

Karpinsky, M. G. (2010). *Pseudosolenia calcar-avis* (Bacillariophyta, Centrophyceae) in the Caspian Sea. *Russian Journal of Biological Invasions*, *1*(2), 81–86. https://doi.org/10.1134/S2075111710020050

Kilroy, C., Lagerstedt, A., Davey, A., & Robinson, K. (2006). Studies on the survivability of the invasive diatom *Didymosphenia geminata* under a range of environmental and chemical conditions. *Report by National Institute of Water & Atmospheric Research, New Zealand*.

Kilroy, C., Larned, S. T., & Biggs, B. J. F. (2009). The non-indigenous diatom *Didymosphenia geminata* alters benthic communities in New Zealand rivers. *Freshwater Biology*, *54*(9), 1990–2002. https://doi.org/https://doi.org/10.1111/j.1365-2427.2009.02247.x

Kilroy, C., & Novis, P. (2018). Is *Didymosphenia geminata* an introduced species in New Zealand? Evidence from trends in water chemistry, and chloroplast DNA. *Ecology and Evolution*, *8*(2), 904–919. https://doi.org/https://doi.org/10.1002/ece3.3572

Kilroy, C., & Unwin, M. (2011). The arrival and spread of the bloom-forming, freshwater diatom, *Didymosphenia geminata*, in New Zealand. *Aquatic Invasions*, *6*. https://doi.org/10.3391/ai.2011.6.3.02

Kirkpatrick, B., Fleming, L. E., Squicciarini, D., Backer, L. C., Clark, R., Abraham, W., Benson, J., Cheng, Y. S., Johnson, D., Pierce, R., Zaias, J., Bossart, G. D., & Baden, D. G. (2004). Literature review of Florida red tide: implications for human health effects. *Harmful Algae*, *3*(2), 99–115. https://doi.org/https://doi.org/10.1016/j.hal.2003.08.005

Klein, G., MacIntosh, K., Kaczmarska, I., & Ehrman, J. M. (2010). Diatom survivorship in ballast water during trans-Pacific crossings. *Biological Invasions*, *12*(5), 1031–1044. https://doi.org/10.1007/s10530-009-9520-6

Kostianoy, A. G., & Kosarev, A. N. (2005). *The Caspian Sea environment* (Vol. 5). Springer Science & Business Media.

Kristiansen, J. (1996). Dispersal of freshwater algae — a review. In J. Kristiansen (Ed.), *Biogeography of Freshwater Algae: Proceedings of the Workshop on Biogeography of Freshwater Algae, held during the Fifth International Phycological Congress, Qingdao, China, June 1994* (pp. 151–157). Springer Netherlands. https://doi.org/10.1007/978-94-017-0908-8_15

Lavoie, D. M., Smith, L., & Ruiz, G. (1999). The Potential for Intracoastal Transfer of Non-indigenous Species in the Ballast Water of Ships. *Estuarine, Coastal and Shelf Science*, *48*, 551–564. https://doi.org/10.1006/ecss.1999.0467

Leone, P. B., Cerda, J., Sala, S., & Reid, B. (2014). Mink (*Neovison vison*) as a natural vector in the dispersal of the diatom *Didymosphenia geminata*. *Diatom Research*, *29*(3), 259–266. https://doi.org/10.1080/0269249X.2014.890957

Locke, A., Reid, D. M., van Leeuwen, H. C., Sprules, W. G., & Carlton, J. T. (1993). Ballast Water Exchange as a Means of Controlling Dispersal of Freshwater Organisms by Ships. *Canadian Journal of Fisheries and Aquatic Sciences*, *50*(10), 2086–2093. https://doi.org/10.1139/f93-232

Mann, D. (2022). Determining geographical range and alien status in diatoms: three instructive case histories of species newly recorded in the British Isles, including a non-native marine species from the Pacific, *Diademoides luxuriosa*. *Diatom Research*, 1–29. https://doi.org/10.1080/0269249X.2022.2078428

Mann, D. G., Crawford, R. M., & Round, F. E. (2016). Bacillariophyta. *Handbook of the Protists*, 1–62. https://doi.org/10.1007/978-3-319-32669-6_29-1

Manning, F. S., Curtis, P. J., Walker, I. R., & Pither, J. (2021). Potential long-distance dispersal of freshwater diatoms adhering to waterfowl plumage. *Freshwater Biology*, *66*(6), 1136–1148. https://doi.org/https://doi.org/10.1111/fwb.13706

Marshall, W. A., & Chalmers, M. O. (1997). Airborne dispersal of antarctic terrestrial algae and cyanobacteria. *Ecography*, *20*(6), 585–594. https://doi.org/https://doi.org/10.1111/j.1600-0587.1997.tb00427.x

Masó, M., Alos, J., Juan, S., & Demestre, M. (2016). Microfouling communities from pelagic and benthic marine plastic debris sampled across Mediterranean coastal waters. *Scientia Marina*, *80*, 117–127. https://doi.org/10.3989/scimar.04281.10A

Masó, M., Garcés, E., Pagès, F., & Camp, J. (2003). Drifting plastic debris as a potential vector for dispersing Harmful Algal Bloom (HAB) species. *Scientia Marina*, *67*.

Messikommer, E. (1943). Untersuchungen über die passive Verbreitung der Algen. *Zeitschrift Für Hydrologie*, *9*(3), 310–316. https://doi.org/10.1007/BF02486103

Milliger, L. E., Stewart, K. W., & Silvey, J. K. G. (1971). The Passive Dispersal of Viable Algae, Protozoans, and Fungi by Aquatic and Terrestrial Coleoptera1. *Annals of the Entomological Society of America*, *64*(1), 36–45. https://doi.org/10.1093/aesa/64.1.36

Mills, E. L., Leach, J. H., Carlton, J. T., & Secor, C. L. (1993). Exotic Species in the Great Lakes: A History of Biotic Crises and Anthropogenic Introductions. *Journal of Great*

Lakes Research, *19*(1), 1–54. https://doi.org/https://doi.org/10.1016/S0380-1330(93)71197-1

Ministry for Primary Industries. (2024, February 2). *Check, Clean, Dry: preventing didymo and other pests*.

Murray, S., & Hallegraeff, G. (2018). Harmful Algae Introductions: Vectors of Transfer, Mitigation, and Management. In *Harmful Algal Blooms* (pp. 493–506). https://doi.org/https://doi.org/10.1002/9781118994672.ch13

Nemoto, T. (1956). On the diatoms on the skin film of whales in the northern pacific. *Sci. Rep.*, *11*, 99–132.

Novis, P., Mitchell, C., & Podolyan, A. (2017). *Lindavia intermedia*, the causative organism of New Zealand lake snow: relationships between New Zealand, North American and European populations according to molecular and morphological data. *Lincoln, NZ: Landcare Research*.

Novis, P., Schallenberg, M., Saulnier-Talbot, É., Kilroy, C., & Reid, M. (2017). The diatom *Lindavia intermedia* identified as the producer of nuisance pelagic mucilage in lakes. *New Zealand Journal of Botany*, *55*(4), 479–495. https://doi.org/10.1080/0028825X.2017.1377263

Ostenfeld, C. J. (1908). On the immigration of *Biddluphia sinensis* Grev. and its occurrence in the North Sea during 1903-1907. *Meddelelser Fra Kommissionen Fur Danmarks Fiskeri-Og Havundersogelser. Serie Plankton*, *1*, 44.

Pautova, L. A., Kravchishina, M. D., Silkin, V. A., Klyuvitkin, A. A., Artemiev, V. A., Vazyulya, S. V, & Burenkov, V. I. (2022). Alien Diatom Species of the Autumn Phytoplankton in the Caspian Sea: Their Role in the Formation of the Total Biomass and the Distribution along the Salinity Gradient. *Russian Journal of Biological Invasions*, *13*(3), 325–337. https://doi.org/10.1134/S2075111722030134

Pöschl, U. (2005). Atmospheric Aerosols: Composition, Transformation, Climate and Health Effects. *Angewandte Chemie International Edition*, *44*(46), 7520–7540. https://doi.org/https://doi.org/10.1002/anie.200501122

Prabowo, D., Noerdjito, D., Purbani, D., & Ragamustari, S. (2023). Unwanted hitchhikers: The potential dispersal of harmful marine microalgae via plastic garbage and debris in Indonesian waters. *AIP Conference Proceedings*, *2972*, 70001. https://doi.org/10.1063/5.0182790

Reichard, S. E. (1997). Prevention of Invasive Plant Introductions on National and Local Levels. In J. O. Luken & J. W. Thieret (Eds.), *Assessment and Management of Plant Invasions* (pp. 215–227). Springer New York. https://doi.org/10.1007/978-1-4612-1926-2_16

Reisser, J., Shaw, J., Hallegraeff, G., Proietti, M., Barnes, D. K. A., Thums, M., Wilcox, C., Hardesty, B. D., & Pattiaratchi, C. (2014). Millimeter-Sized Marine Plastics: A New Pelagic Habitat for Microorganisms and Invertebrates. *PLOS ONE*, *9*(6), e100289-. https://doi.org/10.1371/journal.pone.0100289

Ricciardi, A. (2006). Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Diversity and Distributions*, *12*(4), 425–433. https://doi.org/10.1111/j.1366-9516.2006.00262.x

Ricciardi, A., & MacIsaac, H. (2022). Vector control reduces the rate of species invasion in the world's largest freshwater ecosystem. *Conservation Letters*, *15*. https://doi.org/10.1111/conl.12866

Rigby, G., Hallegraeff, G., & Taylor, A. (2004). Ballast water heating offers a superior treatment option. *Journal of Marine Environmental Engineering*, *7*, 217–230.

Saber, A. A., Borrini, A., Saber, H., El-Sheekh, M., Gontcharov, A. A., & Cantonati, M. (2022). A marine invasive benthic diatom species [*Licmophora normaniana* (Greville) Wahrer, 1985] in an inland oasis mineral spring in Egypt. *BIOINVASIONS RECORDS*, *11*(1), 13–22. https://doi.org/10.3391/BIR.2022.11.1.02

Sailer, R. I. (1983). History of insect introductions. *Exotic Plant Pests and North American Agriculture*, 15–38.

Schlichting, H. E. (1974). Ejection of microalgae into the air via bursting bubbles. *Journal of Allergy and Clinical Immunology*, *53*(3), 185–188. https://doi.org/https://doi.org/10.1016/0091-6749(74)90006-2

Schlichting Jr., H. E. (1969). The Importance Of Airborne Algae and Protozoa. *Journal of the Air Pollution Control Association*, *19*(12), 946–951. https://doi.org/10.1080/00022470.1969.10469362

Sharma, N. K., & Rai, A. K. (2010). Biodiversity and biogeography of microalgae: progress and pitfalls. *Environmental Reviews*, *19*(NA), 1–15. https://doi.org/10.1139/a10-020

Sharma, N. K., Rai, A. K., Singh, S., & Brown Jr., R. M. (2007). AIRBORNE ALGAE: THEIR PRESENT STATUS AND RELEVANCE. *Journal of Phycology*, *43*(4), 615–627. https://doi.org/https://doi.org/10.1111/j.1529-8817.2007.00373.x

Sherwood, A. R., Wade, R. M., & Conklin, K. Y. (2020). Seasonality of tropical airborne algae: a 16-month study based on high-throughput sequencing in the Hawaiian Islands. *Grana*, *59*(5), 354–365. https://doi.org/10.1080/00173134.2020.1738541

Souffreau, C., Vanormelingen, P., Sabbe, K., & Vyverman, W. (2013). Tolerance of resting cells of freshwater and terrestrial benthic diatoms to experimental desiccation and freezing is habitat-dependent. *Phycologia*, *52*(3), 246–255. https://doi.org/10.2216/12-087.1

Spaulding, S. A., & Elwell, E. (2007). *Increase in nuisance blooms and geographic expansion of the freshwater diatom Didymosphenia geminata*. US Geological Survey.

Spaulding, S., Kilroy, C., & Edlund, M. (2010). Diatoms as non-native species. *The Diatoms: Applications for the Environmental and Earth Sciences, Second Edition*, 560–569. https://doi.org/10.1017/CBO9780511763175.033

Stachowicz, J. J., Terwin, J. R., Whitlatch, R. B., & Osman, R. W. (2002). Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species

invasions. *Proceedings of the National Academy of Sciences*, *99*(24), 15497–15500. https://doi.org/10.1073/pnas.242437499

Tesson, S. V. M., Skjøth, C. A., Šantl-Temkiv, T., & Löndahl, J. (2016). Airborne Microalgae: Insights, Opportunities, and Challenges. *Applied and Environmental Microbiology*, *82*(7), 1978–1991. https://doi.org/10.1128/AEM.03333-15

Tesson, S. V. M., Weißbach, A., Kremp, A., Lindström, Å., & Rengefors, K. (2018). The potential for dispersal of microalgal resting cysts by migratory birds. *Journal of Phycology*, *54*(4), 518–528. https://doi.org/https://doi.org/10.1111/jpy.12756

Van de Vijver, B., Robert, K., Majewska, R., Frankovich, T. A., Panagopoulou, A., & Bosak, S. (2020). Geographical variation in the diatom communities associated with loggerhead sea turtles (*Caretta caretta*). *PLOS ONE*, *15*(7), e0236513-. https://doi.org/10.1371/journal.pone.0236513

Vanormelingen, P., Verleyen, E., & Vyverman, W. (2009). The diversity and distribution of diatoms: from cosmopolitanism to narrow endemism. In W. Foissner & D. L. Hawksworth (Eds.), *Protist Diversity and Geographical Distribution* (pp. 159–171). Springer Netherlands. https://doi.org/10.1007/978-90-481-2801-3_12

Villac, M. C., Kaczmarska, I., & Ehrman, J. M. (2013). The diversity of diatom assemblages in ships' ballast sediments: colonization and propagule pressure on Canadian ports. *Journal of Plankton Research*, *35*(6), 1267–1282. https://doi.org/10.1093/plankt/fbt090

Wejnerowski, Ł., Aykut, T. O., Pełechata, A., Rybak, M., Dulić, T., Meriluoto, J., & Dziuba, M. K. (2022). Plankton hitch-hikers on naturalists' instruments as silent intruders of aquatic ecosystems: current risks and possible prevention. *NeoBiota*, *73*, 193–219. https://doi.org/10.3897/neobiota.73.82636

Zenkevich, L. A. (Lev A. (1963). *Biology of the seas of the U.S.S.R*. Interscience Publishers. https://www.biodiversitylibrary.org/item/28854

Zettler, E. R., Mincer, T. J., & Amaral-Zettler, L. A. (2013). Life in the "Plastisphere": Microbial Communities on Plastic Marine Debris. *Environmental Science & Technology*, *47*(13), 7137–7146. https://doi.org/10.1021/es401288x

Zhang, F., & Dickman, M. (1999). Mid-ocean exchange of container vessel ballast water. 1: Seasonal factors affecting the transport of harmful diatoms and dinoflagellates. *Marine Ecology-Progress Series - MAR ECOL-PROGR SER*, *176*, 243–251. https://doi.org/10.3354/meps176243

Appendix

Table 1: Diatoms assumed to be introduced by humans, their year of introduction, type of introduction (BW= ballast water, AQ = aquaculture, "?" = not yet certain) along with the source

Name	Year of introduction (if unknown, year of discovery)	Assumed vector	Source
THE GREAT LAKES			
Thalassiosira baltica	1988	BW	(Edlund et al., 2000)
Actioncyclus normanii fo. *subsalsa*	1938	BW	(Mills et al., 1993)
Biddulphia laevis	1978	BW	(Mills et al., 1993)
Cyclotella aromus	1964	BW	(Mills et al., 1993)
Chaetoceros hohnii	1978	BW	(Mills et al., 1993)
Skeletonema potamos	1963	BW	(Mills et al., 1993)
Skeletonema subsalsum	1973	BW	(Mills et al., 1993)
Stephanodiscus binderanus	1938	BW	(Mills et al., 1993)
Stephanodiscus subtilis	1946	BW	(Mills et al., 1993)
Thalassiosira guillardii	1973	BW	(Mills et al., 1993)
Thalassiosira lacustris	<1978	BW	(Mills et al., 1993)
Thalassiosira pseudonana	1973	BW	(Mills et al., 1993)
Thalassiosira weissflogii	1962	BW	(Mills et al., 1993)
Diatoma ehrenbergii	1930s	BW	(Mills et al., 1993)
Cyclotella cryptica	1964	BW	(Mills et al., 1993)
Cyclotella pseudostelligera	1946	BW	(Mills et al., 1993)
Cyclotella woltereki	1964	BW	(Mills et al., 1993)
SIWA OASIS EGYPT			
Licmophora normaniana	2021 (?)	AQ	(Saber et al., 2022)

CASPIAN SEA			
Pseudosolenia calcar-avis	1934	AQ	(Karpinsky, 2010)
Cerataulina pelagica	2002	BW	(Kostianoy & Kosarev, 2005; Pautova et al., 2022)
Chaetoceros pendulus	2004	?	(Karpinsky, 2010)
Tropidoneis lepidoptera	2004	?	(Karpinsky, 2010)
Chaetoceros peruvianus	2007	BW	(Karpinsky, 2010; Pautova et al., 2022)
Pseudo-nitzschia seriata	1990	BW	(Kostianoy & Kosarev, 2005; Pautova et al., 2022)
NEW ZEALAND			
Asterionella Formosa	1810	AQ	(Harper, 1994)
Didymosphenia geminata	2004	?	(Kilroy et al., 2006)
Lindavia intermedia	2002	?	(Novis, Schallenberg, et al., 2017)
COAST OF ENGLAND			
Diademoides luxuriosa	2014	?	(Mann, 2022)
UNITED STATES OF AMERICA			
Discostella asterocostata	1980s	AQ	(Alverson et al., 2021)