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Exploring the Relationship between Dreissenids and the Deep Chlorophyll Layer in the Laurentian Great Lakes

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Exploring the Relationship between Dreissenids and the Deep Chlorophyll Layer in the Laurentian Great Lakes

By Lara Hargrave

An Abstract of a Thesis
In
Great Lakes Environmental Science

Submitted in Partial Fulfillment
Of the Requirements for the Degree of
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State University of New York
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Abstract of Thesis

In the Laurentian Great Lakes, two invasive bivalves *Dreissena polymorpha* and *Dreissena rostriformis bugensis* have induced a number of changes, including increased water transparency, alterations in nutrient cycling, decreased chlorophyll concentrations, and changes in phytoplankton community composition and structure. These changes are likely to have implications for the deep chlorophyll layer (DCL), a feature characterized by phototrophic organisms reaching abundance at light levels far below ideal for photosynthesis. Though the impacts of *D. polymorpha* and *D. r. bugensis* in the Great Lakes have been studied for at least the last three decades, little is known about how these ecosystem engineers affect the features of the DCL, such as the depth at which it forms, the magnitude of space it occupies, and the concentration of chlorophyll it contains. I set out to explore the impacts of dreissenid biomass on these deep chlorophyll layer features and the relationships between dreissenid presence and variables that may impact or be impacted by their presence or by the presence of the deep chlorophyll layer, including water transparency, specific conductance, dissolved oxygen concentrations, photosynthetically active radiation, and chlorophyll-a fluorescence. I found that in some cases, increased dreissenid biomass was associated with decreased concentrations of total integrated chlorophyll in the deep chlorophyll layer, but no significant relationships between dreissenids and deep chlorophyll layer depth or thickness were observed. Consistently, water transparency was higher in the presence of dreissenids; significant relationships between dreissenid presence and specific conductance and dissolved oxygen concentrations were inconsistent but when they occurred, dreissenid presence was associated with greater dissolved oxygen concentrations and specific conductance, and lower chlorophyll fluorescence. DCLs can contribute significantly to overall primary productivity; understanding the impact of dreissenids

on the deep chlorophyll layer—a feature which occurs commonly in most Great Lakes during summer stratification--is likely to increase in importance as the lakes shift towards increasing oligotrophy.

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Literature Review: The Relationship between Dreissenids and the Deep Chlorophyll Layer in the Laurentian Great Lakes

By creating a connection to the Atlantic Ocean, and allowing for increased shipping activity, the St. Lawrence Seaway opened the Laurentian Great Lakes up to serial invasions. Since 1960, every ~28 weeks a new invasive species has been discovered in the Great Lakes, which is the highest rate of invasion ever reported for a freshwater system (Ricciardi, 2006). 65% of invasions reported since the St. Lawrence Seaway opened in 1959 have arisen from the release of ballast water, with a considerable portion of these invaders originating from the Ponto-Caspian (10% between 1960-1988, 69% between 1994-2003; Ricciardi, 2006). Notable among these Ponto-Caspian invaders arriving via ballast water is *Dreissena polymorpha* and its fellow ballast water invader and congener from the Dnieper-Bug Liman, *Dreissena rostriformis bugensis*.

Dreissena polymorpha and *D. r. bugensis* are notorious and aggressive freshwater invaders and ecosystem engineers capable of causing extensive environmental and economic impacts in the waterbodies they invade (Karatayev and Burlakova, 2022a, Karatayev et al., 2002). Likely arising in part due to these considerable consequences, there have been over 4,000 scientific publications pertaining to *D. polymorpha* and/or *D. r. bugensis* since 1771 (Karatayev and Burlakova, 2022a). Though the impacts of *D. polymorpha* and *D. r. bugensis* in the Great Lakes have been studied for at least the last three decades (Karatayev and Burlakova, 2022b), much of the relationship between dreissenids and the deep chlorophyll layer (DCL) remains mysterious. Dreissenids have been attributed to increases in water transparency (Mayer et al., 2014; Leach, 1993; Barbiero et al., 2006a), declines in total chlorophyll concentrations (Howell

et al., 1996; Pothoven and Fahnenstiel, 2013), and changes in nutrient cycling (Higgins, 2014; Schaller and Planer-Friedrich, 2017; Arnott and Vanni, 2011) which may in turn affect the structure, formation, and location of the DCL. Other parameters, such as the concentration of dissolved oxygen (Caraco et al., 2000) and specific conductance (Sherman et al., 2013) may also impact or be impacted by dreissenids and the DCL.

The systemic impacts of invasive dreissenids and the degree to which they are experienced by a waterbody are dependent on the time since initial invasion, attributes of the waterbody (water mixing rates, morphometry, trophic status) where the organisms are found, and which species are present and how abundant they are (Burlakova et al., 2006; Karatayev et al., 2015). *Dreissena polymorpha* and *D. r. bugensis* were first detected in the North America in Lake Erie in 1988 (though they were likely present in 1986 or 1987; Carlton, 2008; Hebert et al., 1989) and 1989 (Mills et al., 1993), respectively. *Dreissena polymorpha* was first found in Lakes Huron, Michigan, and Ontario in 1989 (reviewed in Karatayev et al., 2021a). In 1990, *D. r. bugensis* was first reported in Lake Ontario and would be found seven years later (in 1997) in Lakes Huron (reviewed in Karatayev et al., 2021a) and Michigan (Nalepa et al., 2001). While dreissenids have been detected in Lake Superior, they may not yet be as well-established in these relatively unproductive, calcium and nutrient poor waters (Vanderploeg et al., 2002).

Environmental Attributes Influencing Dreissenid Impacts

Environmental attributes impact dreissenid establishment and abundance, and by doing so they also influence the magnitude and timing of dreissenid impacts. Water mixing rates play a role in the movement of veligers (Reid et al., 2010; Kerfoot et al., 2008) and the availability of phytoplankton for adult dreissenids, which are mostly sedentary (Reed-Andersen et al., 2000). Currents moving at 9 cm/s appear to allow for ideal clearance rates for shallow water dreissenids,

possibly due to algae replenishment at the boundary layer (Ackermann, 1999). Lake morphometry often controls invasion dynamics and the long-term magnitude of dreissenid impacts on primary production (Karatayev et al., 2021a). In shallow waters or shallow lakes, dreissenids tend to achieve their highest densities shortly after colonizing an area and then experience population declines (Karatayev et al., 2021a). It tends to take longer for dreissenids to reach peak densities at intermediate depths (30-50m), after which these populations decline, though to a lesser degree than in shallower waters (Karatayev et al., 2021a). In the deepest depths of the Great Lakes (>90m), *D. r. bugensis* densities appear to continue to increase (Karatayev et al., 2021a). Deep, thermally stratified lakes are likely to experience significantly (~4x) less decline in primary production than shallower, non-stratified lakes because more mussel biomass is required to filter the same amount of water in deep areas of the lakes and stratification precludes dreissenids below the thermocline to access phytoplankton in the epilimnion (Karatayev et al., 2021a). *Dreissena polymorpha* were able to spread deeper in mesotrophic lakes than in eutrophic lakes, possibly due to higher water clarity, lower siltation, and deeper macrophyte growth in mesotrophic environment (Burlakova et al., 2006). Trophic status is related to morphometry and may have an impact on dreissenid carrying capacity (Burlakova et al., 2006; Karatayev et al., 2021a) and the degree to which dreissenids impact water clarity (Qualls et al., 2007).

The Role of Species Type

Though *D. polymorpha* and *D. r. bugensis* belong to the same genus, they differ in their physical characteristics, population dynamics, and within-lake distributions; the latter two of which fluctuate based in part on time elapsed since initial invasion (Burlakova et al., 2006; Karatayev et al., 2015). With its ability to withstand lower food availability, adhere to soft

substrate, and withstand, feed, and reproduce at lower temperatures, *D. r. bugensis* can be found in more regions of a waterbody than *D. polymorpha*, including the profundal zone (Orlova et al., 2005; Karatayev et al., 2011; Karatayev et al., 2021a, Roe and MacIsaac, 1997; reviewed in Karatayev et al., 2015). *Dreissena r. bugensis* have a substantial competitive advantage by being able to devote more energy to growth and reproduction and less to metabolic maintenance than *D. polymorpha* (Stoeckmann, 2003). *Dreissena r. bugensis*' ability to occupy a larger habitat may allow them to colonize and filter a greater volume of water, causing them to have a larger magnitude of impact on the waterbody. However, the thermocline separates *D. r. bugensis* in the profundal zone from the epilimnion seasonally, potentially limiting their impact (reviewed in Karatayev et al., 2015). However, *D. polymorpha* may maintain their populations in shallow regions where both species coexist, in part due to their ability to withstand greater wave action (Karatayev et al., 2015). The impacts of *D. polymorpha* and *D. r. bugensis* become more challenging to predict after the initial stages of invasion are over and there is a greater likelihood of indirect impacts (Karatayev et al., 2015). The time necessary for a system to experience the greatest impacts of *D. r. bugensis* is longer than for *D. polymorpha* because *D. r. bugensis* require more time to reach their maximum population size (Karatayev et al., 2011). Populations of both *D. polymorpha* and *D. r. bugensis* may not stabilize over time (Karatayev et al., 2014). Once the sufficient time has passed—typically 9 years or more—*D. r. bugensis* density can surpass and replace *D. polymorpha* in waterbodies where both species coexist (Karatayev et al., 2015), however, *D. polymorpha* and *D. r. bugensis* abundance can vary widely both spatially and temporally (Burlakova et al., 2006; Nalepa et al., 2010; Karatayev et al., 2011, Karatayev et al., 2015). Although *D. polymorpha* and *D. r. bugensis* have similar ecological impacts in shallow areas of the Great Lakes, their impacts are different on deep waters in the Great Lakes (reviewed

in Karatayev and Burlakova, 2022b). *Dreissena polymorpha* are restricted to the nearshore and are unable to affect the offshore or the entire waterbody of a deep lake to the same degree as *D. r. bugensis* (reviewed in Karatayev and Burlakova, 2022b).

The Impacts of Dreissenid Invasion

Aggregations of dreissenids are capable of connecting the benthic and pelagic portions of the water column by removing inorganic and organic materials from the pelagic zone as they filter and redistribute these materials to the benthos in the form of feces and pseudofeces (Karatayev et al., 2002). This creates a feedback between the benthic and pelagic zones that did not exist prior to dreissenid arrival (Karatayev et al., 2002). Through benthic-pelagic coupling and substantial planktivory, dreissenids can bring about changes in food webs (Woodruff et al., 2021), including changes in the community composition (Fishman et al., 2010; Bastviken et al., 1998) and structure of phytoplankton (Barbiero et al., 2006b). Consequently, changes in the plankton community will likely impact the DCL.

Dreissenids' substantive feeding and filtration processes can increase water transparency (*Dreissena polymorpha*, Fahnenstiel et al., 1995; Caraco et al., 1997). By removing appreciable amounts of seston from the water column dreissenids are able to increase photic depth (Karatayev et al., 2002; Kissman et al., 2010). *Dreissena polymorpha* aggregations were able to filter an amount equal to twice the volume of water in Lake St. Clair daily (Hebert et al., 1991) and when food is abundant, individuals can consume and assimilate as much as 40% of their body carbon daily (Vanderploeg et al., 2001). With increased water transparency, macrophyte abundance and coverage may increase as well (Mayer et al., 2014); macrophytes consume nutrients and interfere with water mixing, reducing the nutrient availability for phytoplankton (Karatayev and Burlakova, 2022a). Dense dreissenid aggregations may also alter water mixing

by creating 3-D structure where none previously existed, or by covering area where sediment and surface interchange, which may affect waterbody specific conductance. By increasing the area available for photosynthesis, increased photic depth may impact dissolved oxygen concentrations (by increasing the area available for photosynthesis, though this may be offset by dreissenid respiration), photosynthetically active radiation (PAR), and chlorophyll concentrations, which may in turn affect the DCL.

The Deep Chlorophyll Layer Defined

During periods of stratification, photosynthetic organisms can reach abundance far below light levels ideal for photosynthesis (at least below the 5% level—Moll and Stoermer, 1982; Fee, 1976), forming a deep chlorophyll layer (DCL) or deep chlorophyll maximum (DCM) (Leach et al., 2018). DCMs and DCLs are common features in both freshwater and marine stratified environments (Scofield et al., 2017), occurring in all the Great Lakes (Scofield et al., 2020). With the exception of Lake Erie, DCMs and DCLs occur regularly in the Great Lakes during summer stratification (Bramburger and Reavie, 2016). Stratification is requisite for a stable DCL or DCM because mixing precludes subsurface phototroph accumulation (Reynolds, 1994; Fee, 1976).

Despite the terminology's reference to "deep", DCMs and DCLs need not occur at great depths, so long as they are subsurface (Cullen, 2015). Often the term "DCM" is used to describe a subsurface maximum chlorophyll-a concentration but may not be the greatest chlorophyll concentration present vertically in the water column (Camacho, 2006; Cullen., 2015; Bramburger and Reavie, 2016), in which case DCL or subsurface chlorophyll maximum layer (SCML) may be a more suitable descriptor (Camacho, 2006; Cullen., 2015). The terms "DCM" and "DCL" will both be used throughout this review, based on the literature cited. Though the DCMs and

DCLs vary slightly in their definition, the processes that form and maintain DCMs and DCLs appear to be identical (Camacho, 2006).

The Formation of Deep Chlorophyll Layers

Photoacclimation and production at depth are often attributed as key drivers of DCM formation in oligotrophic and mesotrophic environments, though the processes responsible for the extent and depth of DCMs can differ greatly between systems due to biological and physical variation within each system (Scofield et al., 2020). Photoacclimation is an adaptation in which phytoplankton raise or lower chlorophyll concentrations in their cells, based on the amount of available light—with greater concentrations of chlorophyll corresponding with low-light settings and lower concentrations of chlorophyll corresponding with high-light settings (Scofield et al., 2020). Chlorophyll-a concentrations are often used as a proxy for phytoplankton biomass; however, this may be a misleading metric if photoacclimation is prevalent. Photoacclimation can cause a DCM to occur, but does not account for the deep biomass maxima that is coincident with some DCMs (Moeller et al., 2019). Other processes that may form or contribute to the formation of a DCM include phototrophs settling along the pycnocline, significant variation in grazing pressure between the upper and lower portions of a stratified waterbody, and metalimnion blooms resulting from algae and protozoan interactions (reviewed in Camacho, 2006; Cullen, 1982; Moeller et al., 2019).

In oligotrophic and mesotrophic environments, nutrient availability is usually higher in the metalimnion and upper hypolimnion (Fee, 1976), and when the euphotic zone exceeds the mixing depth, phototroph growth may occur at depth (reviewed in Camacho, 2006). Non-motile phototrophs may accumulate where the buoyancy of their cells matches that of the surrounding water (Keifer et al., 1972). Sustained stratification allows phototrophs adapted to survive in the

metalimnion and upper hypolimnion to accumulate in this area that may not support their competitors or predators (Camacho, 2006). The physical and chemical gradients in light, water density, oxygen, and nutrients associated with a stable, stratified water column govern the vertical distribution of phototrophs—phototroph communities become stratified based on their ability to withstand these gradients and may form a DCM in the process (Camacho and Vincente, 1998; Camacho et al., 2000; Gervais, 2001; Gervais et al., 2003). Therefore, DCMs and DCLs often occur in proximity to vertical gradients, such as the thermocline, pycnocline, or nutricline (Camacho and Vincente, 1998; reviewed in Cullen, 2015; Camacho, 2006). Great Lakes DCLs, particularly in Lake Ontario and Lake Erie, tend to have lower pHs than the epilimnion and the surrounding water column (Bramburger and Reavie, 2016). Symbiotically-linked heterotrophic protists and algae may form a DCM by blooming in the metalimnion (Camacho, 2006). All of the mechanisms described above may work in concert to form a DCM (Camacho, 2006).

Drivers of DCM formation are impacted by nutrient availability, water clarity, and lake productivity—all of which often correspond with trophic status (Scofield et al., 2020). Trophic status, along with waterbody size and water transparency, can be used to make predictions about the structure of a DCM (Moll and Stoermer, 1982; Scofield et al., 2020). Light attenuation supersedes thermal stratification in importance when predicting DCM depth, while lake size is the greatest predictor of DCM thickness, with bigger lakes tending to have thicker DCMs (Leach et al., 2018). In contrast, Reinl et al. (2020) found that in Lake Superior, surface temperature was the best predictor of DCM concentration and DCL thickness, with warmer waters having less concentrated, thinner DCLs—though lake size was not considered in this study. Lake Superior is the largest Great Lake by surface area, and is followed by (in order of decreasing surface area) Lake Huron, Lake Michigan, Lake Erie, and Lake Ontario

(<https://www.glerl.noaa.gov/education/ourlakes/lakes.html>). With increasing oligotrophy, DCMs should be deeper, thicker, and less productive (Scofield et al., 2020). Decreased nutrient loading and dreissenid invasion has caused the Great Lakes to shift towards oligotrophy over the past few decades (Dove and Chapra, 2015). The Great Lakes are currently thought to range in trophic status from ultra-oligotrophic Lakes Superior and Huron, ultra-oligotrophic to oligotrophic Michigan, oligotrophic Ontario, and oligotrophic to eutrophic Erie (Scofield et al., 2020).

Productivity and the Deep Chlorophyll Layer

The extent to which the DCL contributes to overall productivity is dependent on the trophic status of the waterbody and the relative importance of the processes that form the DCL (Scofield et al., 2017). The DCL can account for a significant portion of a waterbody's primary (Moll et al., 1984) and secondary productivity (Twiss et al., 2012); up to 60% of Lake Michigan's areal primary productivity (Moll et al., 1984). Dreissenids may have altered lake productivity by bringing about changes in water transparency and nutrient cycling, which likely directly or indirectly impacted the drivers of DCM formation. Productivity may become increasingly important with several of the Great Lakes experiencing dreissenid-induced oligotrophication. However, in some systems, benthic productivity increased enough to compensate for dreissenid-induced declines in phytoplankton productivity, so primary productivity does not always majorly fluctuate (*D. polymorpha*, Fahnenstiel et al., 1995).

Photic Depth: Dreissenids and the Deep Chlorophyll Layer

Increased photic depth may lead to the DCL forming deeper and occupying a greater area of the water column due to the increased area available for photosynthesis, although this may be counterbalanced by dreissenid consumption of suspended phototrophs between 0.4 and 750 mm in size (as found for *D. polymorpha*; Roditi et al., 1996; Ten Winkel and Davids, 1982) and

macrophyte-induced decreases in nutrient availability (Karatayev and Burlakova, 2022a), which may lead to declines in chlorophyll concentrations within the DCL. Declines in chlorophyll-a in the water column have been associated with dreissenids (Nicholls, 2001).

Nutrient Cycling and Chlorophyll: Dreissenids and the Deep Chlorophyll Layer

Decreases in chlorophyll concentrations, as well as changes in DCL depth, may also be promoted through dreissenid-induced changes in nutrient availability and cycling. Organic consumption and inorganic deposition through fecal and pseudofecal matter by large aggregations of dreissenids elevates the rate of sedimentation (at times, by several orders of magnitude), increases the concentration of organic material present in the sediment, and ultimately changes nutrient cycling (*D. polymorpha*, Karatayev et al., 2002). Nutrient loading can affect phytoplankton and zooplankton biomass (Dillon and Rigler, 1974; Schindler, 1974) thus may impact the DCL. Phosphorus is a limiting nutrient for productivity in the Great Lakes and *D. r. bugensis* now contain almost as much phosphorus in their shells and tissues as the whole water column they reside in (Li et al., 2021). The main driver of phosphorous cycling (in all Great Lakes except Superior) is now *D. r. bugensis* (Li et al., 2021). Sediments devoid of mussels undergo phosphorous exchange with the water column orders of magnitude more slowly than those colonized by *D. r. bugensis* in the four of the five Great Lakes invaded by dreissenids (excluding Lake Superior, Li et al., 2021). Chlorophyll production in lakes is a function of phosphorous concentrations (in hypereutrophic systems, nitrogen is a co-driver, Liang et al., 2020), thus chlorophyll concentrations in the DCL are likely to be impacted by changes in phosphorus availability and cycling. Already, dreissenids have been attributed to erratic alterations in phosphorus and chlorophyll-a concentrations (Mellina et al., 1995; Li et al., 2021) and decreased chlorophyll-a per unit total phosphorus (Hall et al., 2003). When dreissenid

densities are very high or invaded lakes are shallow, dreissenids are capable of decoupling the relationship between chlorophyll-a and nutrients and give rise to a decline in the average size of algal cells (*D. polymorpha*, Mellina et al., 1995). Chlorophyll and phosphorus can become decoupled in very shallow waters or in waters with very high densities of dreissenids when the rate of dreissenid grazing exceeds that of phytoplankton growth, as a result of phytoplankton declining without nutrient depletion (Mellina et al., 1995).

Phytoplankton biomass has decreased in multiple systems occupied by dreissenids (Vanderploeg et al., 2010; Barbiero et al., 2006b; Nicholls, 2001) along with declines in algal biovolume (Idrisi et al., 2001). Declines in chlorophyll concentrations within the DCL will likely arise from declines in phototroph populations and productivity due to dreissenid consumption of phototrophs and decreased nutrient availability. Phytoplankton productivity has decreased by over 36% in inner Saginaw Bay since dreissenids have invaded--though benthic productivity increased enough that primary productivity was not appreciably affected (*D. polymorpha*, Fahnenstiel et al., 1995). As dreissenids ingest sediment particles, the anoxic environment of their intestinal organs may release iron-bound phosphorous with their feces (Hecky, 2004), increasing primary productivity by changing the iron-bound phosphorus into a soluble form that phytoplankton can utilize (Carpenter et al., 1992). If this occurs, it will likely happen near the bottom, promoting benthic algae and periphyton.

Dreissenid-induced reductions in total phosphorous concentrations induced oligotrophication in the Great Lakes (reviewed in Karatayev and Burlakova, 2022a) and the magnitude of how much a DCL contributes to a waterbody's overall productivity is partially dependent on trophic status (Scofield et al., 2017). DCLs in Lakes Michigan and Ontario had

elevated nitrates and nitrites, relative to the epilimnion (Bramburger and Reavie, 2016).

Decreased nutrient availability may also impact the rate and depth at which phototroph settle at neutral buoyancy depth because sinking is slower in areas richer in nutrients (Davey & Heaney, 1989; Jackson et al., 1990; Karpowics and Ejsmont-Karabin, 2017). Settling can also impact cell size and species—in some species, heavier individuals appear to be more buoyant while in other species, heavier individuals are more susceptible to sinking (Bramburger and Reavie, 2016).

Dreissenids may impact species presence and abundance directly through selective feeding or indirectly through altering nutrient cycling and nutrient availability.

Specific Conductance: Dreissenids and the Deep Chlorophyll Layer

Dreissenids may further impact the DCL by altering water chemistry, including possibly altering specific conductance and dissolved oxygen concentrations. Specific conductance is often predominately determined by natural characteristics of a waterbody, such as soil, geology, hydrology, and climate (Bachmann et al., 2013) and indirectly measures dissolved ion concentration within a solution (U.S. Geological Survey, 2019). Specific conductance can also be used to infer where terrestrial or riverine nutrients influxes occur, though it does not measure nutrients directly (Yurista and Kelly, 2007).

While specific conductance can be a reliable predictor of dreissenid colonization (dreissenids are unable to occupy areas where the specific conductance $< 244 \pm 3.7$ mS/cm, Sherman et al., 2013), little is known about how dreissenids may impact specific conductance. Dreissenids may possibly alter the geophysical exchange processes associated with sediment-water column interface through the buildup of their shells in the benthic boundary layer (Turner, 2010), which could impact specific conductance by altering deposition and gas exchange. Systems with high levels of calcium carbonate are especially prone to dreissenid shell

accumulations persisting on sediments (Strayer and Malcom, 2007). Specific conductance may decrease in areas surrounding *Dreissena* because calcium, which contributes to specific conductance, is used by dreissenids for growth and reproduction (*D. polymorpha*, reviewed in Cohen and Weinstein, 2001) and makes up a considerable portion of their shells-- *D. polymorpha* shells can be 40% calcium by weight (Secor et al., 1993). Sufficient levels of calcium are the requisite for dreissenid presence (Karatayev et al., 1997; Vanderploeg et al., 2002). Calcium concentrations in offshore Lake Ontario waters have been lessened by around 4-5 mg/L since dreissenid invasion (Barbiero et al., 2006a). Calcium ions in the water column contribute to specific conductance, thus, if the concentration of calcium in the water column decreases, specific conductance is likely to also decrease. Dreissenids also sequester other elements, such as arsenic, carbon, calcium, copper, iron, magnesium, aluminum, and vanadium, that may contribute to specific conductance (reviewed in Karatayev and Burlakova, 2022a). Furthermore, strong correlations between soluble reactive phosphorus, of which dreissenids alter the cycling of, and specific conductance have been observed (Celik, 2013). Phosphorus can impact chlorophyll-a concentrations and water transparency (Filstrup and Downing, 2017), which can affect the DCL and dissolved oxygen concentrations (because increased water transparency can lead to increased photosynthesis, which produces oxygen). Finally, some zooplankton are predators of phytoplankton, and zooplankton biomass in Lake Superior were found to be a function of a number of variables, including specific conductance (Yurista and Kelly, 2007).

Dissolved Oxygen: Dreissenids and the Deep Chlorophyll Layer

Dissolved oxygen concentrations can impact and be impacted by dreissenids. The oxygen usage of dreissenids is temperature dependent (Aldridge et al., 1995), thus may depend on the location of dreissenids in the water column during stratification when the DCL is likely to be

formed. Dissolved oxygen was observed to be higher in the DCL than in the epilimnion in all the Great Lakes except Erie, which exhibited no difference (Bramburger and Reavie, 2016). Empty dreissenid shells can lead to increased oxygen consumption in the benthos, possibly from decomposing organic matter on the shell surface or through increased surface area available for deposition and biofilm growth (Turner, 2010). Dreissenids may decrease the amount of oxygen available through respiration and consumption of phototrophs, but may increase the amount of oxygen available by increasing the amount of habitat available for photosynthesis. In addition to respiration, dreissenid deposition and decomposition of feces and pseudofeces consume oxygen and oxygen consumption was observed to be twice as great on river sediments where dreissenids were present (Turner 2010). Dreissenids are unable to occupy areas where dissolved oxygen concentrations are too low (1.8-2.4 mg/l for *D. polymorpha*, 1.5 mg/l for *D. r. bugensis* at 20°C, reviewed in Karatayev et al., 2007).

Dreissena polymorpha and *D. r. bugensis* have been associated with changes in nutrient cycling and nutrient availability (Higgins, 2014; Schaller and Planer-Friedrich, 2017; Arnott and Vanni, 2011), trophic status (Dove and Chapra, 2015; Karatayev and Burlakova, 2022a) water transparency (Leach, 1993; Barbiero et al., 2006a), phytoplankton community composition (Fishman et al., 2010) and structure (Barbiero et al., 2006b), declines in chlorophyll-a (Fahnenstiel et al., 1995; Caraco et al., 1997) and phytoplankton productivity in the Great Lakes (Li et al., 2021; Liang et al., 2020). These changes may directly or indirectly impact the DCL. Despite this, to our knowledge, dreissenid biomass and density have not been linked to the features of the DCL, such as DCL depth, DCL thickness, and integrated chlorophyll-a concentrations. Similarly, there is little theoretical or experimental literature about the impacts dreissenids may have on specific conductance. I suspected specific conductance will be lower in

areas where dreissenid biomass and density are high due to dreissenid-induced changes in geophysical processes between the sediment and water column, nutrient cycling, and nutrient requirements. I predicted that dissolved oxygen concentrations will be lower where dreissenids are present due to their respiration activities. I predicted chlorophyll fluorescence (RFU), which can be used as a proxy for phytoplankton biomass (Richert et al., 2019) and to detect the DCL (Xu et al., 2019), to be lower in areas where dreissenids are present since dreissenids have been attributed to the declines in water column chlorophyll concentrations (Howell et al., 1996; Pothoven and Fahnenstiel, 2013) and diminished phytoplankton biovolume (Barbiero et al., 2006b). I predicted photosynthetically active radiation (PAR), the portion of electromagnetic radiation green plants can utilize for photosynthesis (Möftus et al., 2013), will increase with dreissenid presence due to dreissenid-induced changes in photic depth. I anticipated that with greater dreissenid biomass and density, DCLs will be deeper, occupy an increased amount of space vertically in the water column, and be less concentrated in chlorophyll-a.

I explored the relationship between the presence of dreissenids and dissolved oxygen concentrations, PAR, chlorophyll fluorescence (RFU), specific conductance, and water transparency, which are parameters that could impact or be impacted by the DCL, with the expectations that areas with dreissenid presence would have increased water transparency, PAR, and RFU, and decreased specific conductance and dissolved oxygen concentrations due to the feeding, filtration, and respiration processes of dreissenids.

Methods

The Great Lakes National Program Office (GLNPO) of the US Environmental Protection Agency (EPA) collected information on water quality parameters and dreissenid biomass in the Great Lakes within the Biological Monitoring Program's Long-Term Monitoring in all of the

Great Lakes (LTM, <https://www.epa.gov/great-lakes-monitoring>) during summer surveys conducted in August 2012-2018 and in September 2017 during the Lake Huron Cooperative Science and Monitoring Initiative (CSMI, <https://www.epa.gov/great-lakes-monitoring/cooperative-science-and-monitoring-initiative-csmi>) benthic surveys. Samples were collected and treated as described by Bayba et al. (2022). 129 stations were sampled during the 2017 CSMI Lake Huron sampling (Karatayev et al., 2020). There were 9 benthic LTM stations in Lake Erie in 2012 and 10 in 2013, 2016, and 2018. In 2012 and 2013, Lake Huron had 10 benthic LTM stations and 9 in 2016 and 2018. In 2012, 2013, 2016, and 2018, Lake Michigan had 16 LTM benthic stations. In 2012, 2016, and 2018, Lake Ontario had 9 benthic LTM stations and 10 in 2013.

Environmental parameters were measured using a conductivity/temperature/depth (CTD) probe and sensors attached to a Rosette sampling device. The measured parameters included dissolved oxygen (mg/L), chlorophyll fluorescence (RFU), beam transmission (used as a measure of water transparency), and specific conductance ($\mu\text{S}/\text{cm}$). I extracted measurements for each parameter for values occurring at 1 meter above the sediment using a version “CTD Data Extraction.R” (<https://github.com/hannahbarkley/occ/>, 2019), which I modified to specify our parameters of interest (depth, specific conductance, PAR, beam transmission, relative fluorescence units (RFU), and oxygen. There were not enough sites with dreissenids in Lake Erie and no sites with dreissenids in the main basin of Lake Superior to include in analysis (see Table 1). Only one station out of 43 sampled did not have dreissenids present in the 2018 Lake Ontario CSMI survey, thus it could not be used in our presence-absence analysis.

To see whether sites with dreissenids differed significantly than those without dreissenids, I used the non-parametric Mann-Whitney U Test (Mann & Whitney, 1947;

Wilcoxon, 1945) on datasets broken down by depth zones for each year for each lake when sample size permitted. Long-term monitoring data from Lakes Huron, Michigan, and Ontario were pooled and analyzed in aggregate because sample sizes were limited and these lakes have similar habitats (Table 1, Table 2; please note that only the datasets listed in Table 2 were used in the present-absence analysis). Considering that Great Lakes benthic macroinvertebrate taxa richness and density generally decrease with increasing depth with an apparent change in community composition occurring at around approximately 70 m depth (Cook and Johnson, 1974; Burlakova et al., 2018), long-term monitoring data from Lakes Huron, Michigan, and Ontario were analyzed at depths of over 70 meters and depths less than or equal to 70 meters. Following accepted depth categories for Lake Huron (Karatayev et al., 2020), I analyzed the larger 2017 Lake Huron CSMI dataset by the following depth zones: 0-30 m, 31-50 m, 51-90 m, and 91 m or more. Because data were mostly non-normally distributed or had heterogeneous variance and could not be successfully transformed, I used the non-parametric Mann-Whitney U Test (Mann & Whitney, 1947; Wilcoxon, 1945) to compare sites with and without *Dreissena*. The sampling stations used in CSMI and long-term monitoring cruises in Lake Huron are not the same. The more spatially explicit 2017 CSMI Lake Huron dataset was examined by depth-zone for significant relationships between presence/absence of *Dreissena* and beam transmission, oxygen, and conductivity.

For 1996-2017 water chemistry LTM data I back-calculated biomass for sites that did not have biomass data but had density data using *Dreissena* average weight values found in Hrycik et al. (in prep). This provided an additional 24 sites in Lake Huron, 29 sites in Lake Michigan, and 58 sites in Lake Ontario. Next, I ran a breakpoint analyses for each dataset to see whether a consistent threshold in biomass (expressed in total wet weight, TWW, g m^{-2}) of *Dreissena*

existed for each response variable (specific conductance [$\mu\text{S}/\text{cm}$], water transparency [as measured by beam transmission] chlorophyll fluorescence ([relative fluorescence units; RFU], and dissolved oxygen [mg/L]) across datasets. This regression excluded biomass values of 0.

To account for measurements being taken from the same sites annually for DCM characteristics, I ran a mixed model where station was treated as a random effect and the natural log of dreissenid biomass was treated as a fixed effect. Slopes and intercepts were allowed to vary. I ran the model for each response variable: total integrated chlorophyll in the DCM ($\mu\text{g}/\text{dm}^2$), DCM depth (m), DCM thickness (m), and Secchi depth (m). DCM depth is the depth at which the peak of the DCM occurred. DCM thickness is the difference between the start depth and end depth of the DCM depth. Total chlorophyll was integrated over the full depth range between the start and end depth of the DCM. Secchi depth was estimated and was determined by back-calculating K_{par} , in which $K = 1.07/(\text{Secchi Depth, m}) + 0.05$. This model was run on Lakes Huron, Michigan, and Ontario LTM data individually. The mixed model was run again in a dataset combining Lakes Huron, Michigan, and Ontario LTM data. All analyses were performed in the statistical software R (R version 4.1.2). The lme4 and tidyverse libraries were used for modeling, ggplot and cowplot were used for data visualization, and sjstats was used to extract statistical information from the model. Secchi depth data was extracted from the Great Lakes Environmental Database (GLENDa) via the U.S. EPA central data exchange website (<https://cdx.epa.gov/>). DCM data was collected using the algorithm described in Xu (et al., 2019) by Scofield (2018, et al., 2020).

Results

Presence-Absence Analysis: Long-term Monitoring Data

Beam transmission, which was used as a measure of water transparency (Thomson and Jerome, 1973), was significantly higher in areas where dreissenids were present in a subset of datasets (there were a total of 10 datasets, only 5 of which exhibited significant results; all of the datasets with significant results showed increased water transparency where dreissenids were present Table 3; Figure 1 and Figure 2). Where relationships with chlorophyll (RFU) were significant, mean chlorophyll was lower (2012 Lake Huron, Michigan, and Ontario combined LTM, less than 70m in depth) in sites with *Dreissena* (Table 3; Figure 3). All other tested parameters (PAR, dissolved oxygen, and specific conductance) were not significantly different with and without the presence of dreissenids in the LTM datasets.

Presence-Absence Analysis: 2017 CSMI Lake Huron Data

Sites with *Dreissena* had significantly higher water transparency than sites where dreissenids were absent in the following depth zones: 31-50m ($p = 0.009$), 51 - 90m ($p = 0.029$), and >91m ($p = 0.030$) (Table 3; Figures 4, 5, and 6). Significant relationships between dreissenids and specific conductance, dissolved oxygen concentrations, chlorophyll fluorescence (RFU), and PAR did not occur consistently, where dreissenids were present. A significant relationship between dissolved oxygen concentrations and dreissenids was only observed at the 31-50m depth zone ($p = 0.026$), with mean oxygen higher in sites with *Dreissena* than sites without (Table 3; Figure 7); in all other cases there were no differences in oxygen concentration between sites with and without *Dreissena*. Significantly higher ($p = 0.011$) specific conductivity was also found at sites with dreissenids within the 31-50m depth zone (Table 3; Figure 8). Mean PAR was higher in sites with dreissenids in the 51-90m depth interval ($p = 0.025$, Table 3,

Figure 9). No significant relationships between the presence of dreissenids and fluorescence (RFU) were observed in all depth zones, and no significant relationships were found in the shallowest region (< 30m) of Lake Huron.

Biomass Analysis:

I regressed dreissenid biomass against each variable in each dataset to see whether a consistent threshold of *Dreissena* biomass (TWW, g m⁻²) existed to induce a significant response in tested variables (Table 4). There was a wide range of biomass breakpoints associated with each parameter: for specific conductance the biomass ranged from 0.03955 to 1684 g m⁻², for beam transmission: 1.292 - 2245, for RFU: 2.617 to 2154, and for dissolved oxygen: from 3.577 to 2931 g m⁻². Therefore, our results (Table 4) suggested that no consistent threshold of *Dreissena* biomass exists to consistently induce changes in water quality parameters.

Mixed model results showed some significant relationships between dreissenid biomass and total integrated chlorophyll. Additionally, a significant relationship between dreissenid biomass and Secchi depth was detected in the mixed model. Nearly all of the results from the mixed model were singular (15 out of 16), suggesting that the model may be overfitted. Significant relationships between dreissenid biomass and total integrated chlorophyll in the DCM were observed in Lake Ontario (p = 0.024, Table 5, Figure 10) and Lake Michigan (p = 0.003, Table 6, Figure 11), where total integrated chlorophyll decreased with increasing dreissenid biomass. A significant relationship between dreissenid biomass and Secchi depth was observed in Lake Huron whereupon Secchi depth increased with increasing dreissenid biomass (Table 7, Figure 12).

Discussion

Presence-Absence Analysis

We explored the relationship between the presence of dreissenids and dissolved oxygen concentrations, PAR, chlorophyll fluorescence (RFU), specific conductance, and water transparency, which are parameters that could impact or be impacted by the DCL. It was expected that areas where dreissenids are present would have increased water transparency, PAR, and chlorophyll fluorescence (RFU), and decreased specific conductance and dissolved oxygen concentrations due to dreissenid feeding, filtration, and respiration. Some of our hypotheses were supported; we observed increased water transparency in areas where dreissenids were present. However, contrary to our expectations, there was an increase in specific conductance and dissolved oxygen concentrations in the presence of dreissenids. Chlorophyll fluorescence (RFU) declined in the presence of *Dreissena* and PAR increased.

Important considerations salient to all of my results include that at some sites dreissenids may be absent because study parameters may not sustain dreissenid mussel populations. This analysis is representative of a snapshot in time taken when the lakes were likely to be stratified, and dreissenids have a postulated ability to intercept resources from other areas of the water body. Stratification can impact levels and spatial distribution of dissolved oxygen concentrations, nutrients, phytoplankton. Furthermore, the epilimnion can experience seasonal nutrient depletion (Camacho, 2006; Moll et al., 1984). Some effects of dreissenids may be indirect and remote, due to the suspected ability of dreissenids' to pull in resources from other areas of the waterbody, potentially masking impacts (Hecky et al., 2004; Vanderploeg et al. 2010). The nearshore phosphorus shunt hypothesis proposes that *Dreissena* are capable of intercepting nutrients from non-point resources and advected offshore waters in the nearshore, creating a nutrient decline or

deficit in offshore areas (Hecky et al. 2004). There is some indication that nearshore shunt may also occur at mid-depth levels, causing carbon and phosphorus sinks at mid-depth levels corresponding with high densities of *Dreissena* (Vanderploeg et al. 2010), and recently an offshore sink was proposed due to the movement of dreissenids deeper into the lakes (Karatayev et al., 2021b).

A significant relationship between PAR and the presence of dreissenids occurred in the 51-90 m depth zone while significant relationships between the presence of dreissenids and water transparency occurred in some datasets. The remainder of significant relationships in the presence-absence analysis occurred only between 31-50 m in depth (CSMI) or at less than 70 m depth range (LTM). This corresponds with the mid-2000s shift in lakes Huron, Michigan, and Ontario where dreissenid population density transferred from the nearshore to mid-depth levels between 30-50m as *D. r. bugensis* replaced *D. polymorpha* (Karatayev et al., 2022b). These are also the areas where *D. r. bugensis* forms the highest density and biomass in lakes Huron, Michigan, and Ontario (Karatayev et al., 2021). In some datasets, observed increases in dissolved oxygen concentrations and PAR at locations where dreissenids are present may be associated with increased photic depth, as observed by the positive relationship between the presence of dreissenids and water transparency, allowing for increased photosynthesis. In another dataset, however, dreissenid presence was also associated with decreased chlorophyll fluorescence (RFU), which could be due to dreissenid consumption of phytoplankton. It is possible that these seemingly contradictory findings occurred because in some cases, increased photosynthesis by periphyton growing on dreissenid shells may compensate for decreases in phytoplankton abundance. Thus, active benthic photosynthesis was registered from 10 to 40 m in Lake Ontario (Katona, 2021). Brothers et al. (2016) estimated that benthic contribution to ecosystem primary

productivity have a significant proportion (53% in Lake Huron, 23% in Lake Michigan, and 22% in Lake Ontario) of whole-lake production. Thus, the large declines (5–45%) in phytoplankton production in the Great Lakes from the 1970s to 2000s may be substantially compensated by benthic primary productivity, which increased by up to 190%. It is also possible that dreissenids increased dissolved oxygen concentrations through filtering excess organic matter and increasing water mixing (Yu and Culver, 2000).

Elevated dissolved oxygen concentrations and higher specific conductance in areas where dreissenids are present may also be simply due to dreissenids only being found in areas that meet their resource requirements (Karatayev et al., 2017; Sherman et al., 2013). Dreissenids are so sensitive to hypoxia and have an expected lifespan of over three years, that dreissenid presence may be used as a means for mapping the magnitude of frequency of hypoxic events in freshwater (Karatayev et al., 2018; Burlakova et al.; 2022b).

Given the calcium requirements of dreissenids (Barbiero et al., 2006; Secor et al., 1993), it was surprising that specific conductance was slightly higher in sites with *Dreissena* than without. In general, specific conductance in Lakes Huron, Michigan, and Ontario has been changing. Over the last 40 years, specific conductance has been increasing in Lakes Huron and Michigan but declining in Lake Ontario (Chapra et al., 2012). Lake Ontario experienced a decline in calcium concentrations prior to the first detection of dreissenids (Chapra et al., 2012). It is possible that a confounding effect is contributing to the observed relationship between dreissenids and specific conductance.

Dreissena and the DCL

We examined the relationship between dreissenid biomass and the DCL, anticipating that in areas of high dreissenid biomass DCLs would be deeper, occupy a greater area of the water

column vertically, and be less concentrated in chlorophyll-a. Some of our hypotheses were supported; we observed increased Secchi depth and decreased total integrated chlorophyll in the DCM where dreissenid biomass was high. No significant relationships between dreissenid biomass and DCM depth and DCM thickness were observed. There are a number of factors that may account for these results.

There were no apparent thresholds upon which dreissenids induced a significant response in test variables (specific conductance, beam transmission, chlorophyll fluorescence (RFU), and dissolved oxygen). There may be a threshold that we did not detect because we used linear regression and dreissenid impacts may be nonlinear in nature (Karatayev et al., 2002), or because dreissenid populations in these lakes are decades old and have already colonized most of the bottom areas (Karatayev et al., 2021), or it could be due to variation within or between individual lakes. Some invasive species exhibit non-linear behavior, whereupon after a threshold of invasive species abundance is attained, increases in abundance have a greater impact on community characteristics e.g. species richness (Panetta and Gooden, 2017). The impacts of invasive dreissenids and the degree to which they manifest are dependent on the morphology, turnover rates, water mixing rates of the waterbody where the organisms are found (Karatayev et al., 2015). The magnitude of dreissenid-induced impacts may depend on dreissenid population density, which in turn is dependent on the amount of time elapsed since the initial invasion, the amount of substrate available, and the trophic status and morphometry of the waterbody (Burlakova et al., 2006). The strongest impacts of dreissenids are observed within the first decade of invasion, after which their impacts may stabilize or the system may revert closer to pre-invasion conditions (Karatayev et al., 2021b; reviewed in Karatayev et al., 2022a). It has been over two decades since dreissenids have invaded lakes Huron, Michigan and three decades

since invasion of Lake Ontario (Griffiths et al., 1991; Nalepa et al., 2001; Nalepa, 2010), and they now have multiple predators (Liebig and Vanderploeg, 1995; Lederer et al., 2006). The lack of apparent consistent thresholds could also be due to the inherent chemical, physical, and subsequent biological variation between and even within individual lakes—which may also contribute to the lack of significant relationships observed between dreissenids and DCM depth and DCM thickness.

The Great Lakes vary seasonally and annually, partially due to inherent physical processes (e.g. upwelling, stratification), and anthropogenic activity (e.g. nutrient loading, dredging). Differences in phytoplankton assemblages may also vary temporally, though summer DCL assemblages in the Great Lakes partially contained algae from the spring isothermal period (Bramburger and Reavie, 2016). The samples from each dataset are representative of the conditions of a station during a short snapshot of time and may not capture the big picture or be reflective of the relationship between dreissenids and parameters in general, because the impacts of dreissenids are subject to change over time.

The lack of significant relationships between DCM depth and DCM thickness and dreissenid biomass could be due to dreissenids feeding selectively, giving rise to changes in phytoplankton community structure (Barbiero et al., 2006b) and composition (Fishman et al., 2010). The species that are not fed upon or are rejected, may be less likely to form a DCM or there may be so few that they are unable to form a DCM. If the remaining species exhibit photoacclimation or photoacclimate to a greater degree than pre-dreissenid communities, results may be obfuscated. Furthermore, dreissenid reduction of suspended particulate may cause particles that remain to sink more quickly, impacting DCLs formed by algal cells settling. Remote effects may contribute to the absence of a relationship between DCM depth and DCM

thickness. Dreissenid-induced changes in photic depth and nutrient cycling, could also be responsible—nutrient availability may now play a bigger role than light availability in DCL formation. The seasonal timing of sampling and the time elapsed since dreissenid invasion may also play a role in the location of the DCL. The DCLs can change significantly over the course of stratification (Fahnenstiel and Scavia 1987) and can also be impacted by physical perturbances, like seiches (Barbiero and Tuchman, 2001; Moll and Stoermer 1982, Moll et al., 1984). Qualls (et al., 2007) observed that in Lower Green Bay, Secchi depth increased post-dreissenid invasion but reverted to normal levels after a few years. It could also be the relationship between DCM depth and dreissenids that has stabilized over time; the lakes have changed significantly since dreissenid invasion, with reductions in chlorophyll a being particularly relevant and drastic (Qualls et al., 2007; Barbiero et al., 2006b; Nicholls, 2001).

The association between high dreissenid biomass and low total integrated chlorophyll in the DCM in some of the datasets may be due to dreissenid feeding, decreased nutrient availability, and/or dreissenid-induced changes in nutrient cycling (Karatayev and Burlakova, 2022a; Karatayev et al., 2002). Dreissenids may directly or indirectly decrease nutrient availability by uptaking nutrients themselves or promoting greater macrophyte coverage (through increasing photic depth), which use nutrients, possibly at the expense of suspended phototrophs. In some systems, chlorophyll in the DCL is dependent on phosphorus (Liang et al., 2020) and dreissenids have been implicated in bringing about changes in phosphorus cycling and chlorophyll production (*Dreissena polymorpha*, Mellina et al., 1995) as well as in decreasing total water column chlorophyll through grazing (Idrisi et al., 2001). The relationship between chlorophyll-a and nutrients has broken down and been decoupled when high dreissenid densities occurred or the invaded system was shallow, leading to smaller average algal cell size

(*Dreissena polymorpha*, Mellina et al., 1995). Decreased phytoplankton biomass (Leach, 1993, Caraco et al., 1997), algal biovolume (Idrisi et al., 2001), and phytoplankton productivity have been attributed to dreissenid invasion.

Conclusion

This work furthers our understanding of the direct and indirect impacts of dreissenids on the DCL. Notably, we have observed increased water transparency and decreased total integrated chlorophyll in the DCM when dreissenid biomass was high, but no significant relationships between dreissenid biomass and DCM depth and DCM thickness. Further work, ideally with more frequent sampling is needed to understand the dynamic relationship between dreissenids and the DCL. The presence of dreissenids was consistently associated with increased water transparency and sometimes (though inconsistently) associated with decreased chlorophyll fluorescence and elevated specific conductance, dissolved oxygen concentrations, and PAR.

DCMs are an essential puzzle piece in understanding a system's health and productivity, with alterations in DCMs having consequences for food webs, primary production, and nutrient cycling (Leach et al., 2018). While dreissenids have been linked to changes in phototroph communities (Fishman et al., 2010; Bastviken et al., 1998; Barbiero et al., 2006b), observed alterations in phototroph species trait assemblages in Great Lakes DCLs may also be due to climate-change induced changes in the physical features in lake stratification (Bramburger and Reavie, 2016). Understanding the relationship between dreissenids and the DCL is an important element for understanding the past and future of our Great Lakes.

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Tables and Figures

Table 1. Sample sizes for each benthic LTM dataset. Present and absent indicates the number of stations where *Dreissena* were present or absent, respectively, in benthic samples. Datasets that were of insufficient size (less than 3 present or less than 3 absent) for analysis are indicated with an *. Due to low sample size, no LTM datasets were analyzed individually for the presence-absence analysis.

Year	Lake	Sample Size	
		Present	Absent
2012	Erie*	8	1
	Huron	4	6
	Michigan	13	3
	Ontario*	7	2
	Superior*	0	11
2013	Erie*	8	2
	Huron	7	3
	Michigan	13	3
	Ontario*	10	0
	Superior*	0	11
2016	Erie*	8	2
	Huron	6	3
	Michigan	13	3
	Ontario*	8	1
	Superior*	0	11
2018	Erie*	8	2
	Huron*	8	1
	Michigan*	14	2
	Ontario*	9	0
	Superior*	0	11

Table 2: Sample sizes for each dataset used in the presence-absence analysis. Present and absent indicates the number of stations where *Dreissena* were present or absent, respectively, in benthic samples. Datasets that were of insufficient size (less than 3 present or less than 3 absent) for analysis are indicated with an *.

Dataset	Depth Zone	Sample Size	
		Present	Absent
2012 Huron, Michigan, Ontario LTM	<70m	13	4
	>70m	11	7
2013 Huron, Michigan, Ontario LTM	<70m*	17	1
	>70m	13	5
2016 Huron, Michigan, Ontario LTM	<70m	12	3
	>70m	15	4
2018 Huron, Michigan, Ontario LTM	<70m*	15	0
	>70m	16	3
2017 Lake Huron CSMI	0-30m	18	8
	31-50m	27	5
	51-90m	26	14
	90+m	6	5

Table 3: Averages (\pm standard error, SE) of parameters that exhibited significant differences in the presence of dreissenids. Present and absent indicates *Dreissena* were present or absent.

Datasets with Significant Results	Significant Results	Means	
		Present	Absent
2012 Huron, Michigan, and Ontario, <70 m	Beam transmission (p = 0.045)	92.473 \pm 0.80	86.245 \pm 4.29
	RFU (p = 0.015)	0.3275 \pm 0.047	0.8842 \pm 0.25
2013 Huron, Michigan, and Ontario, >70m	Beam transmission (p = 0.059)	97.398 \pm 0.65	96.131 \pm 0.51
2017 Lake Huron 31-50m	Oxygen (p = 0.026)	11.775 \pm 0.12	9.791 \pm 0.76
	Specific Conductance (p = 0.011)	0.134 \pm 0.0013	0.126 \pm 0.0021
	Beam transmission (p = 0.009)	97.186 \pm 0.29	94.016 \pm 1.49
2017 Lake Huron 51 - 90m	Beam transmission (p= 0.029)	98.747 \pm 0.10	97.753 \pm 0.43
	PAR (p=0.021)	0.8307 \pm 0.23	0.2480 \pm 0.19
2017 Huron 91m+	Beam Transmission (p = 0.030)	99.0143 \pm 0.25	97.646 \pm 0.47

Table 4: Biomass (Total Wet Weight, g m⁻²) of dreissenids at which a breakpoint in data series for each parameter was found. NBE indicates that no breakpoint was estimated.

Erie		2012	2013	2016	2018
All depth zones	Specific Conductance	678.1	10.62	509.3	34.25
	Beam Transmission	37.89	536.1	1216	1287
	RFU	14.18	536.1	543	1379
	Oxygen	35.35	3.577	194.8	1432
Huron, Michigan, & Ontario Combined					
		2012	2013	2016	2018
< 70m	Specific Conductance	0.03955	NBE	491.8	1684
	Beam Transmission	2253	17.5	1916	0.008
	RFU	1621	9.917	2154	NBE
	Oxygen	2931	15.82	1224	1241
> 70m	Specific Conductance	2.878	310.5	NBE	NBE
	Beam Attenuation	24.43	665.5	58.31	5.257
	RFU	2.617	18.47	56.24	621.5
	Oxygen	6.555	1077	NBE	455.9

Table 5: Mixed model results for Lake Ontario total integrated chlorophyll in the DCM ($\mu\text{g}/\text{dm}^2$). The columns (from left to right) indicate the predictor, estimates for that predictor, confidence intervals, and p-values. The rows underneath (from top to bottom) describe the residual variance (σ^2), the between-group variance in stations (τ_{00}), variance between stations and the natural log of dreissenid biomass (τ_{11}), intraclass correlation (ρ_{01}), the number of stations, the number of observations, and marginal R^2 / conditional R^2 .

Effect of Dressed Biomass on Total Integrated Chlorophyll in Lake Ontario			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	60.35	44.77 – 75.93	<0.001
	-3.20	-5.95 – -0.45	0.024
Random Effects			
σ^2	531.47		
τ_{00} station_tidy	35.62		
τ_{11} station_tidy.NLB	0.64		
ρ_{01} station_tidy	-1.00		
$N_{\text{station_tidy}}$	7		
Observations	44		
Marginal R^2 / Conditional R^2	0.127 / NA		

Table 6 : Mixed model results for Lake Michigan total integrated chlorophyll in the DCM ($\mu\text{g}/\text{dm}^2$). The columns (from left to right) indicate the predictor, estimates for that predictor, confidence intervals, and p-values. The rows underneath (from top to bottom) describe the residual variance (σ^2), the between-group variance in stations (τ_{00}), variance between stations and the natural log of dreissenid biomass (τ_{11}), intraclass correlation (ρ_{01}), the number of stations, the number of observations, and marginal R^2 / conditional R^2 .

Effect of Dreissenid Biomass on Total Integrated Chlorophyll in Lake Michigan			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	60.39	39.67 – 81.11	<0.001
	-4.64	-7.67 – -1.62	0.003
Random Effects			
σ^2	244.71		
τ_{00} station_tidy	376.95		
τ_{11} station_tidy.NLB	8.84		
ρ_{01} station_tidy	-1.00		
$N_{\text{station_tidy}}$	6		
Observations	52		
Marginal R^2 / Conditional R^2	0.404 / NA		

Table 7: Mixed model results for Lakes Huron Secchi depth (m). The columns (from left to right) indicate the predictor, estimates for that predictor, confidence intervals, and p-values. The rows underneath (from top to bottom) describe the residual variance (σ^2), the between-group variance in stations (τ_{00}), variance between stations and the natural log of dreissenid biomass (τ_{11}), intraclass correlation (ρ_{01}), the number of stations, the number of observations, and marginal R^2 / conditional R^2 .

Effect of Dressenid Biomass on Secchi Depth in Lake Huron			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	15.25	9.89 – 20.60	<0.001
	1.50	0.10 – 2.89	0.037
Random Effects			
σ^2	32.37		
τ_{00} station_tidy	15.93		
τ_{11} station_tidy.NLB	0.83		
ρ_{01} station_tidy	1.00		
N station_tidy	6		
Observations	22		
Marginal R^2 / Conditional R^2	0.400 / NA		

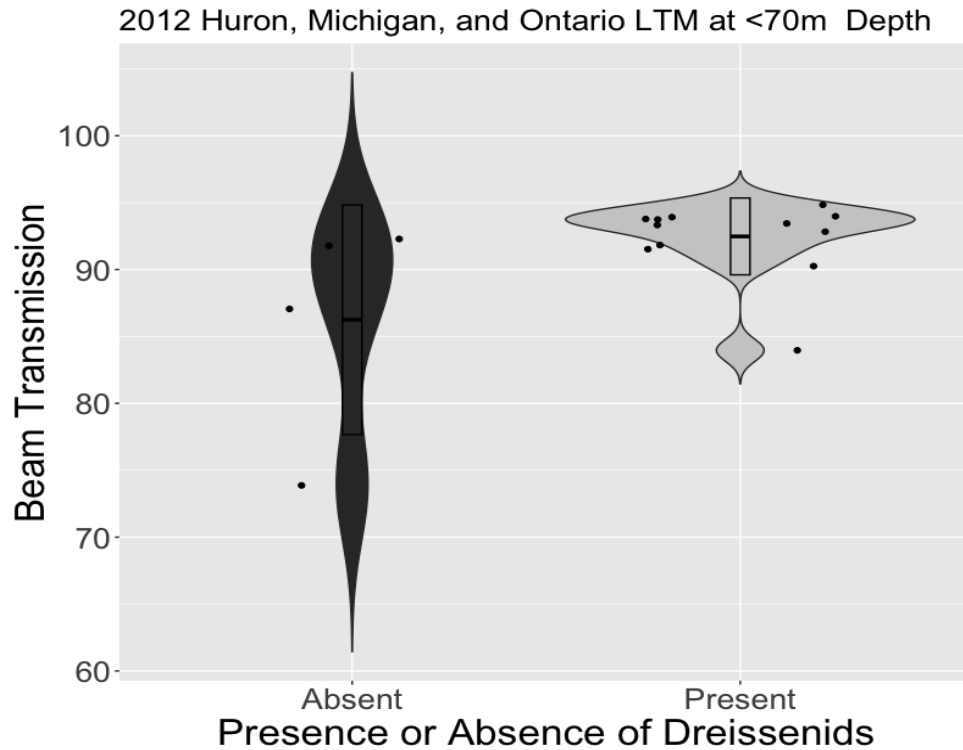


Figure 1: Violin plot comparing sites with and without dreissenids for datasets with significant results in the presence-absence analysis, in this case LTM Beam Transmission in 2012 Lakes Huron, Michigan, and Ontario combined at <70 m depth. The shape of each plot illustrates the data density. The middle line in the rectangle within each plot is the mean of the data and the horizontal edges that enclose the rectangle are located at one standard deviation away from the mean.

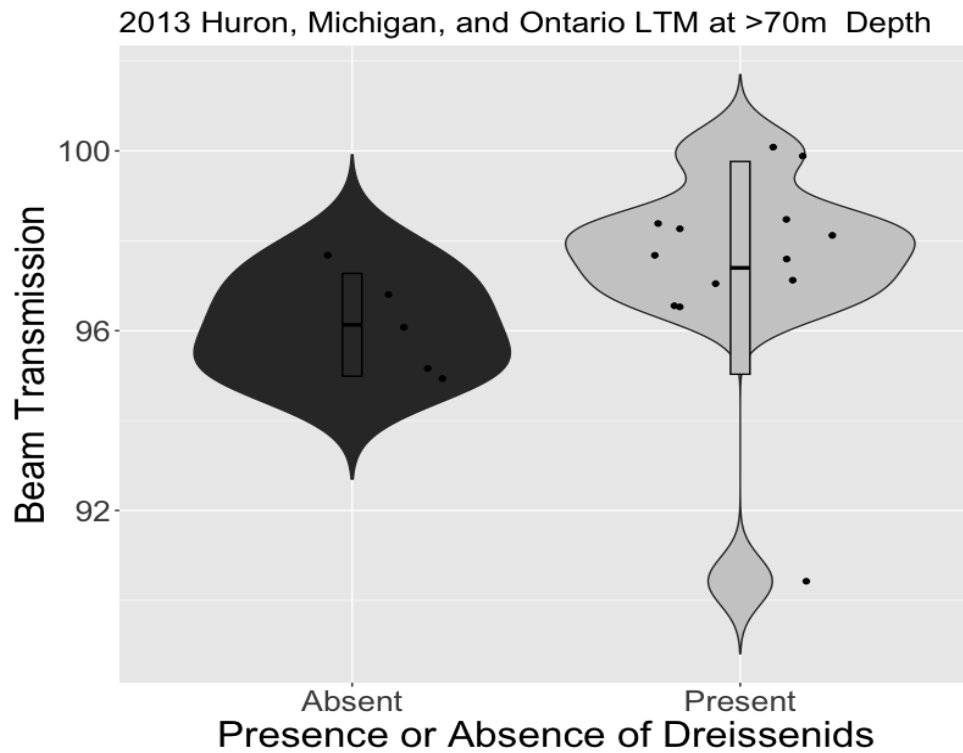


Figure 2: Violin plot comparing sites with and without dreissenids for datasets with significant results in the presence-absence analysis, in this case LTM Beam Transmission in 2013 Lakes Huron, Michigan, and Ontario combined at >70 m depth. The shape of each plot illustrates the data density. The middle line in the rectangle within each plot is the mean of the data and the horizontal edges that enclose the rectangle are located at one standard deviation away from the mean.

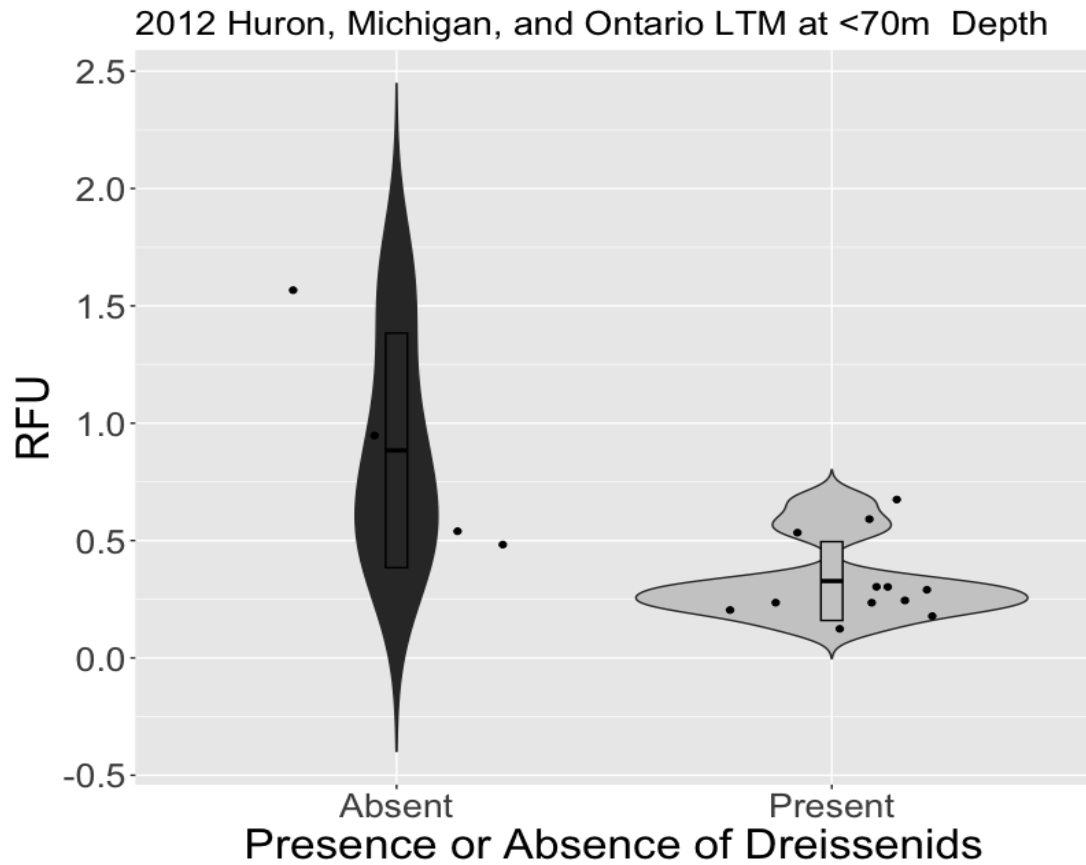


Figure 3: Violin plot comparing sites with and without dreissenids for datasets with significant results in the presence-absence analysis, in this case LTM Chlorophyll Fluorescence (RFU) in 2012 Lakes Huron, Michigan, and Ontario combined at <70 m depth. The shape of each plot illustrates the data density. The middle line in the rectangle within each plot is the mean of the data and the horizontal edges that enclose the rectangle are located at one standard deviation away from the mean.

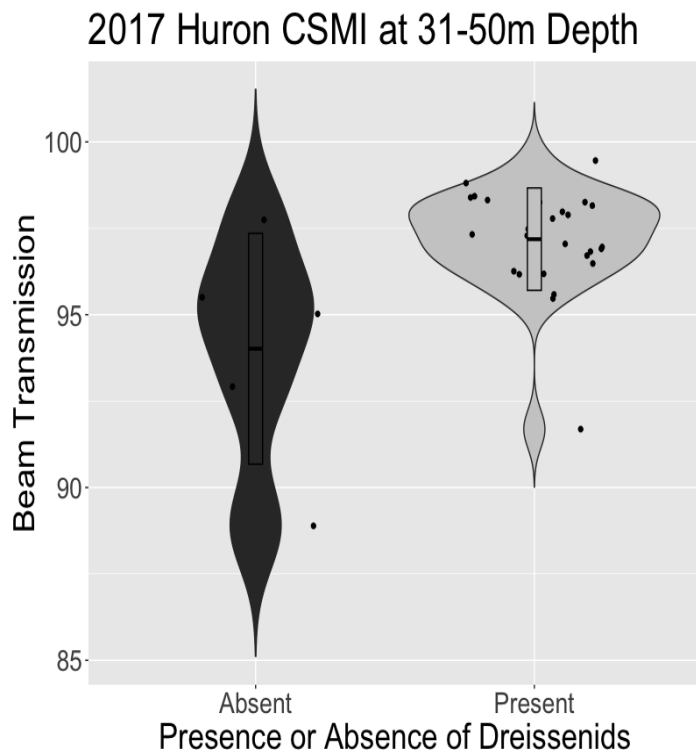


Figure 4: Violin plot comparing sites with and without dreissenids for datasets with significant results in the presence-absence analysis, in this case CSMI Beam Transmission in 2017 Huron at 31-50m depth. The shape of each plot illustrates the data density. The middle line in the rectangle within each plot is the mean of the data and the horizontal edges that enclose the rectangle are located at one standard deviation away from the mean.

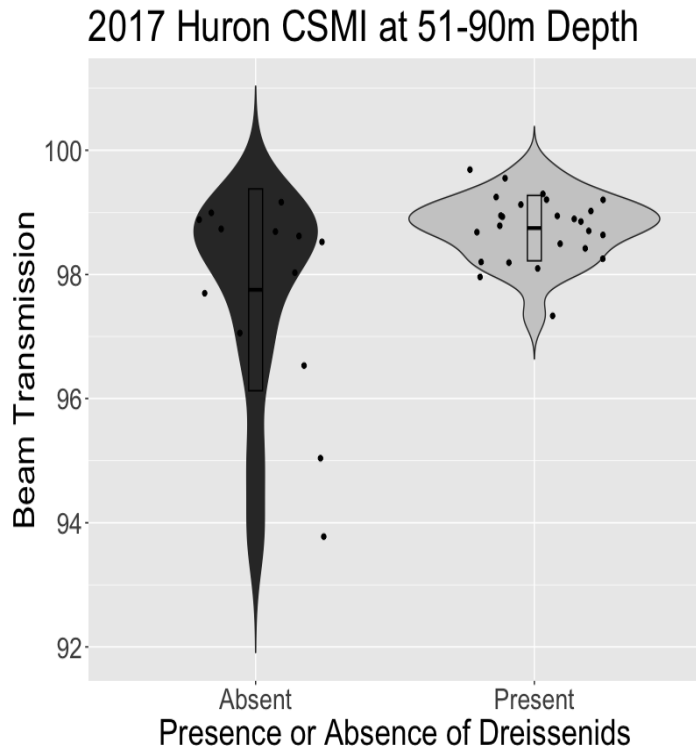


Figure 5: Violin plot comparing sites with and without dreissenids for datasets with significant results in the presence-absence analysis, in this case Beam Transmission in 2017 Huron at 51-90m depth. The shape of each plot illustrates the data density. The middle line in the rectangle within each plot is the mean of the data and the horizontal edges that enclose the rectangle are located at one standard deviation away from the mean.

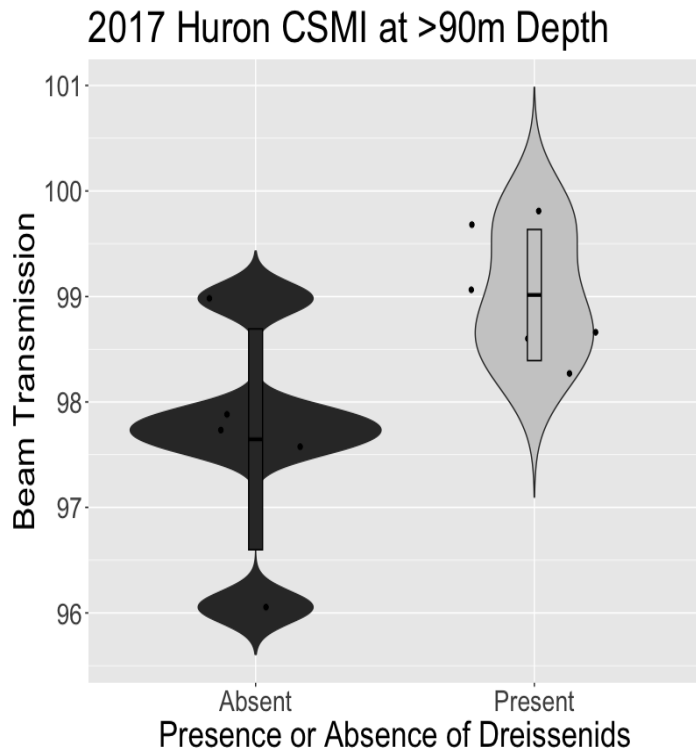


Figure 6: Violin plot comparing sites with and without dreissenids for datasets with significant results in the presence-absence analysis, in this case Beam Transmission in 2017 Huron at >90m depth. The shape of each plot illustrates the data density. The middle line in the rectangle within each plot is the mean of the data and the horizontal edges that enclose the rectangle are located at one standard deviation away from the mean.

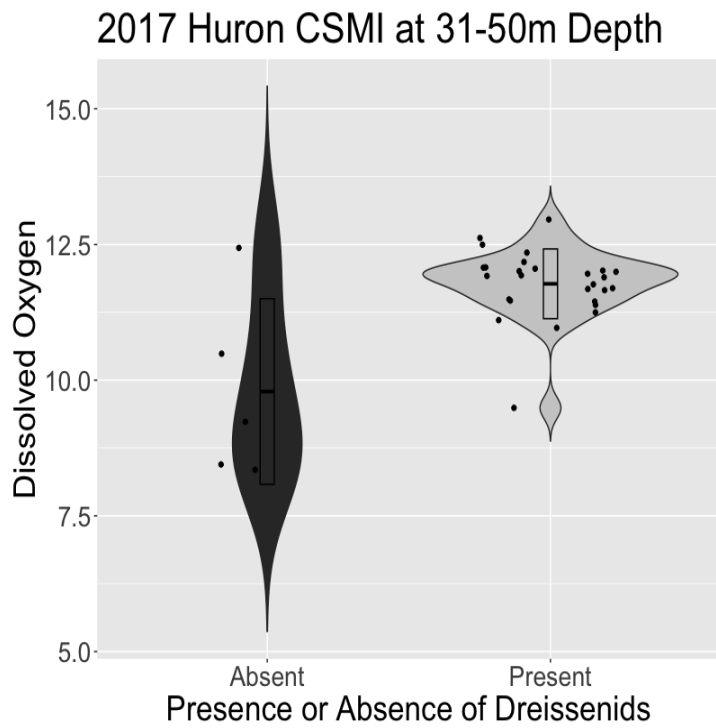


Figure 7: Violin plot comparing sites with and without dreissenids for datasets with significant results in the presence-absence analysis, in this case Dissolved Oxygen (mg/L) in 2017 Huron at 31-50m depth. The shape of each plot illustrates the data density. The middle line in the rectangle within each plot is the mean of the data and the horizontal edges that enclose the rectangle are located at one standard deviation away from the mean.

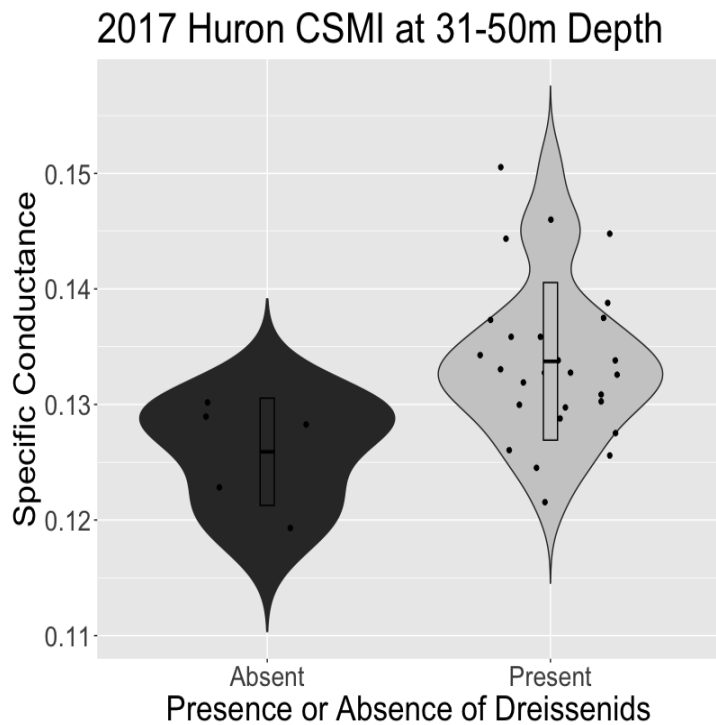


Figure 8: Violin plot comparing sites with and without dreissenids for datasets with significant results in the presence-absence analysis, in this case Specific Conductance ($\mu\text{S}/\text{cm}$) in 2017 Huron at 31-50m depth. The shape of each plot illustrates the data density. The middle line in the rectangle within each plot is the mean of the data and the horizontal edges that enclose the rectangle are located at one standard deviation away from the mean.

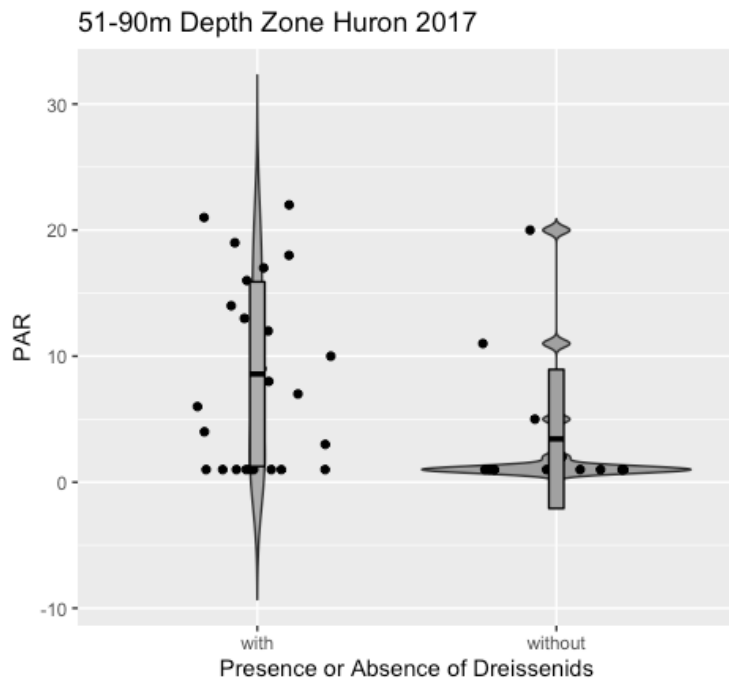


Figure 9: Violin plot comparing sites with and without dreissenids for datasets with significant results in the presence-absence analysis, in this case PAR in 2017 Huron at 51-90m depth. The shape of each plot illustrates the data density. The middle line in the rectangle within each plot is the mean of the data and the horizontal edges that enclose the rectangle are located at one standard deviation away from the mean.

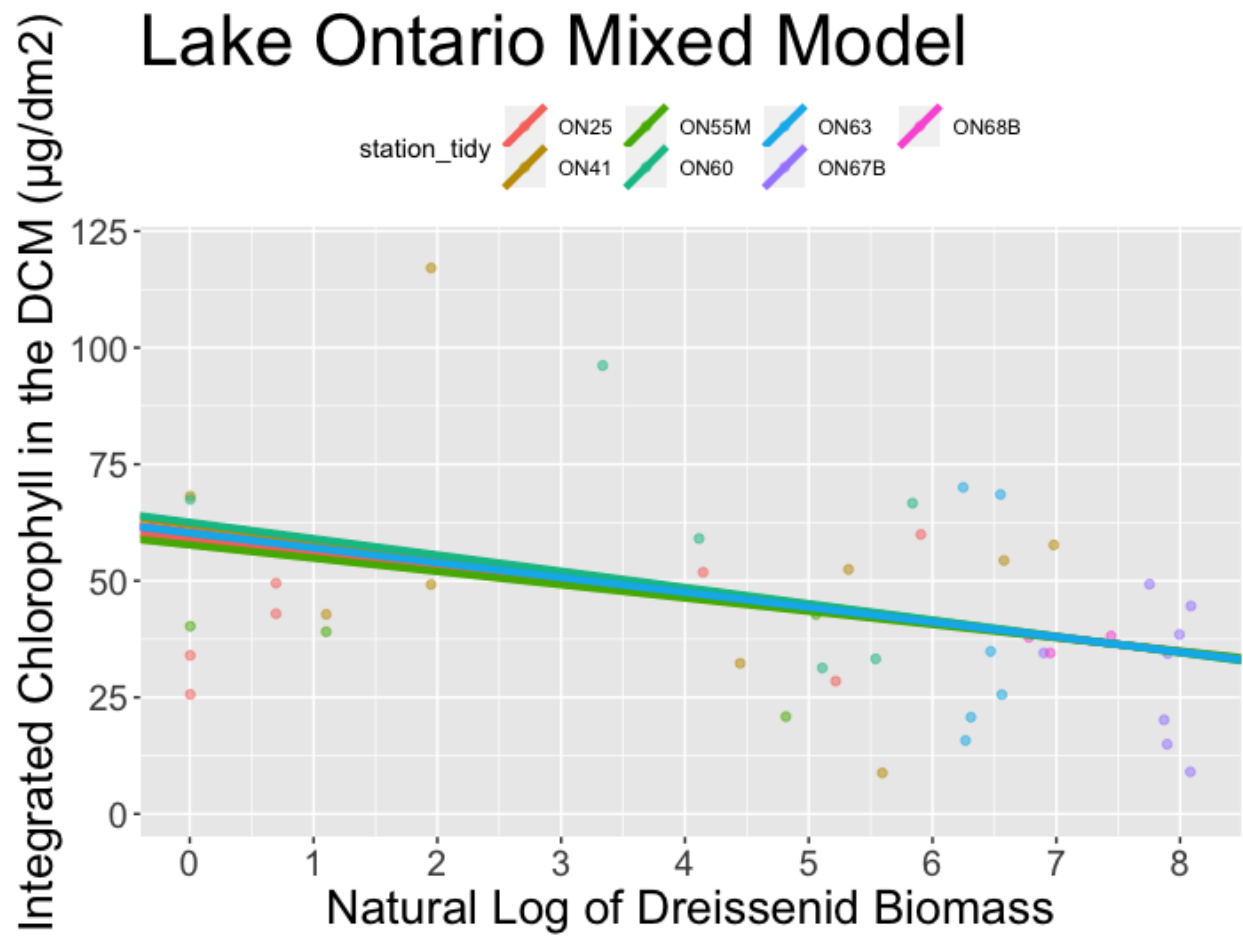


Figure 10: Mixed model results for Lake Ontario total integrated chlorophyll in the DCM ($\mu\text{g}/\text{dm}^2$).

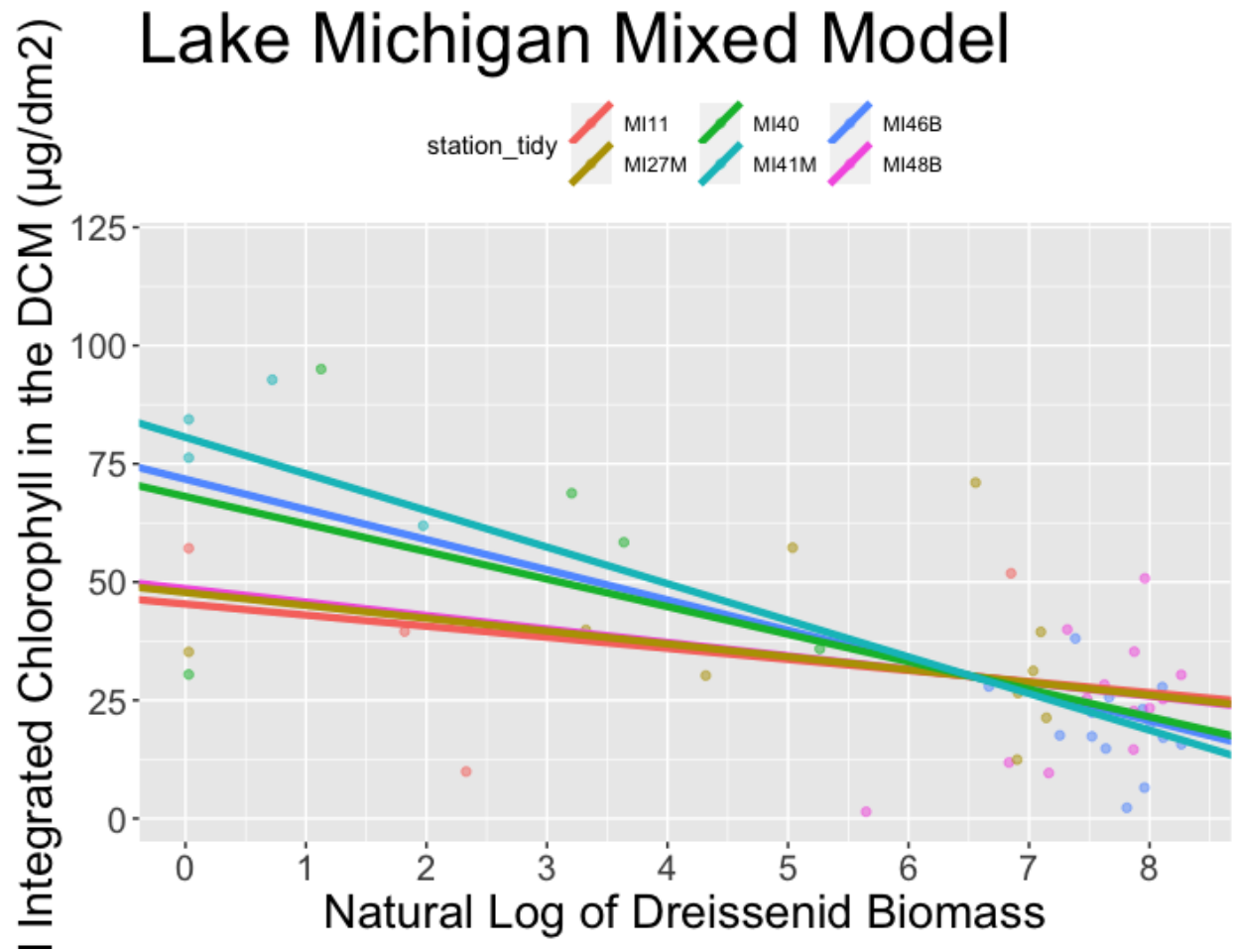


Figure 11: Mixed model results for Lake Michigan total integrated chlorophyll in the DCM ($\mu\text{g}/\text{dm}^2$).

Lake Huron Mixed Model

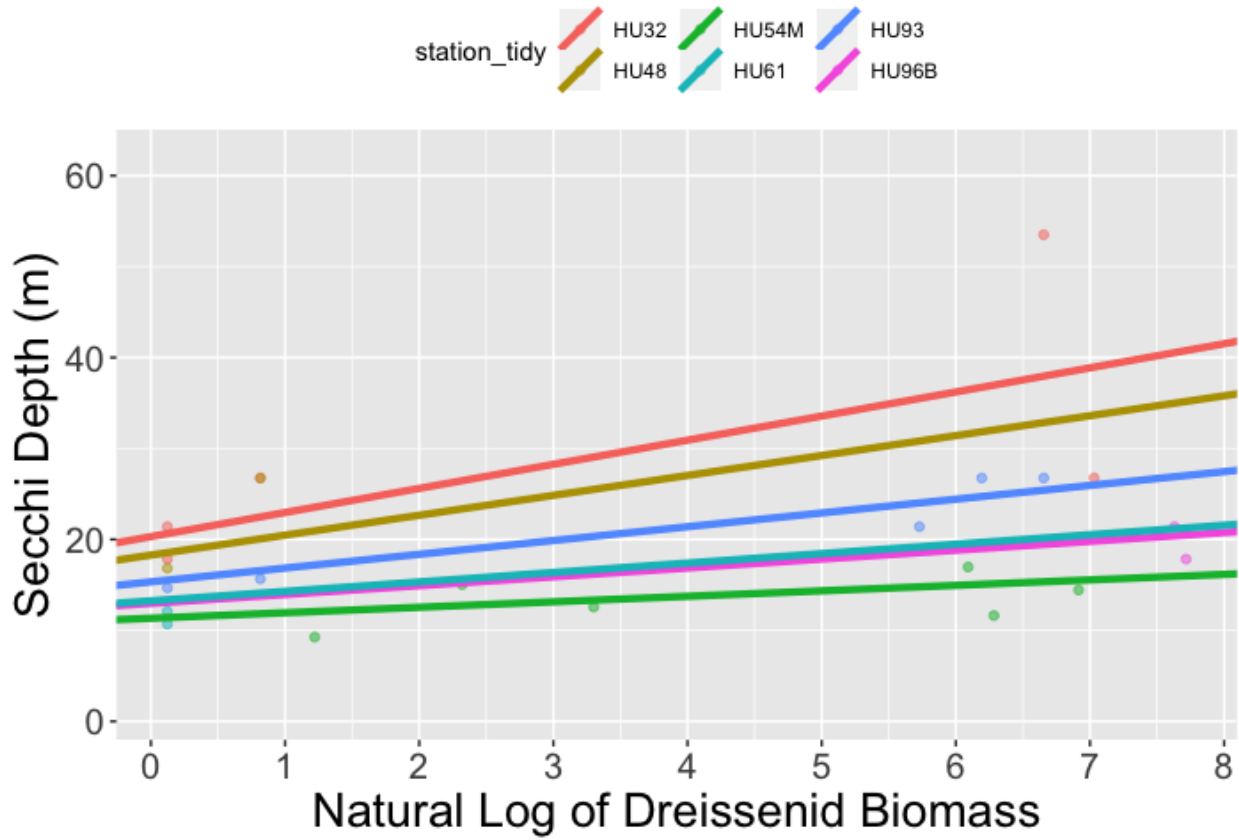


Figure 12: Mixed model results for Lake Huron Secchi depth (m).