Modelling the transport of sloughed *Cladophora* in the nearshore zone of Lake Michigan

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Abstract

The invasion of dreissenid mussels has profoundly altered benthic physical environments and whole-lake nutrient cycling in the Great Lakes over the past several decades. The resurgence of the filamentous green alga *Cladophora* appears to be one of the consequences of this invasion. Sloughed *Cladophora* deteriorates water quality, fouls recreational beaches, and may contribute to outbreaks of avian botulism, which have been especially severe in the Sleeping Bear Dunes National Lakeshore (SLBE) region of Lake Michigan. To help determine the fate of sloughed *Cladophora*, a Lagrangian particle trajectory model was developed to track the transport of *Cladophora* fragments in the nearshore zone based upon a physical transport-mixing model. The model results demonstrate that the primary deposition sites of sloughed *Cladophora* within the SLBE region are mid-depth sites not far away from their initial growth area. Because of high algae production in the nearshore waters and limited exchange between the inner and outer bay, the shoreline beach of Platte Bay appears to be particularly vulnerable to fouling, with overall three times as many accumulated particles as those along the Sleeping Bear Bay and Good Harbor Bay. The results of this model may be used to guide regional environmental management initiatives and provide insights into the mechanisms responsible for avian botulism outbreaks. This model may also inform the development of whole-lake ecosystem models that account for nearshore-offshore interactions.

Keywords: *Cladophora*, ecosystem health, numerical modelling, Lake Michigan, national lakeshore, hydrodynamics.

Introduction

Cladophora is a filamentous green alga that has frequently grown at nuisance levels in the nearshore zone of the Laurentian Great Lakes since the 1950s as a result of lake-wide eutrophication (Auer et al., 2010; Higgins et al., 2005a). This alga primarily grows on hard substrate in the nearshore zone (<30 m depth) where its growth may be limited by light and/or nutrients (Dayton et al., 2014; Bootsma et al., 2015; Gill et al., 2018). Recent studies in Lake Erie revealed a surprisingly high-coverage as much as 40% of the nearshore benthic area during productive seasons (Brooks et al., 2015). The implementation of phosphorus management programs during the late 1970s successfully led to significant reductions of *Cladophora* biomass in the Great Lakes (Bootsma and Liao, 2013; Chapra and Sonzogni, 1979). However, the establishment of dense populations of dreissenid mussels in the Great Lakes has altered physical and biogeochemical conditions in such a way as to favor *Cladophora* growth, despite the declines in phosphorus loading that have been achieved over the past five decades. Nearshore waters have become clearer, due to plankton reductions resulting from mussel grazing, resulting in higher depth-specific growth rates of benthic algae, and extension of the depth range over which benthic algae can grow (Auer et al., 2010). Hecky et al. (2004) suggested that dreissenid grazing would result in more efficient retention of phosphorus in the nearshore zone, and radionuclide tracer studies support this hypothesis, showing that nearshore dreissenids rely heavily on plankton transported from the pelagic to the nearshore (Waples et al., 2017). Recycling of nutrients in this food source by nearshore dreissenids results in a supply of dissolved phosphorus that is directly available to benthic algae growing adjacent to dreissenids (Bootsma and Liao 2013; Dayton et al. 2014). Creation of hard benthic substrate in the form of dreissenid shells may also provide greater benthic surface areas on which *Cladophora* can grow (Higgins et al., 2008). As a result of these various factors, *Cladophora* biomass is now comparable to that during the peak eutrophication period (Bootsma et al., 2004; Tomlinson et al., 2010).

The resurgence of *Cladophora* has had numerous ecological and economic effects. A significant portion of sloughed *Cladophora* is ultimately stranded on shore, where it negatively affects aesthetic conditions, tourism, and the value of lakeshore property (Kuczynski et al., 2016; Lenzi et al., 2015). Stranded *Cladophora* can also facilitate the persistence of enteric bacteria and other human pathogens, resulting in health risks (Chun et al., 2017; Przybyla-Kelly et al., 2013). Within the lake, bacterial decomposition of decaying mats of *Cladophora* can result in near-bottom hypoxic and anoxic conditions (Tyner, 2013), which will alter the abundance and composition of benthic invertebrates and may promote the growth of the bacterium *Clostridium botulinum* and the production of the botulism neurotoxin (Chun et al., 2013; Mathai et al., 2019), which has resulted in the deaths of thousands of birds in the Sleeping Bear Dunes National Lakeshore region in some years (Chun et al., 2013; Princé et al., 2017). Hence, an understanding of the mechanisms regulating the sloughing, transport, and deposition of *Cladophora* may improve our understanding of the conditions that lead to avian botulism outbreaks, and our ability to predict these outbreaks.

Numerical models are useful tools to reproduce the spatiotemporal dynamics of the lake-wide ecosystem, and to explore the underlying mechanisms that control these dynamics. A number of modelling studies have been conducted in the Great Lakes to explore a variety of physical, biological and ecological processes, including mass transport (Bai et al., 2013; Beletsky et al., 2013), nutrient cycling (Chen et al., 2002), and invasive dreissenid impacts (Rowe et al., 2017; Shen et al., 2018). Several models have been used simulate *Cladophora* growth and biomass, which is primarily driven by solar radiation, water temperature, and soluble reactive phosphorus (Higgins et al., 2005b; Tomlinson et al., 2010; Auer et al., 2021). Higgins et al. (2005b) simulated *Cladophora* sloughing as a function of wave-induced shear stress, which was modified by Malkin et al. (2008) to include “catastrophic detachment” under conditions of high winds, high waves, and high *Cladophora* biomass. By comparison, the transport and fate of *Cladophora* after sloughing has received little attention, despite the fact that these processes likely play a critical role in determining the impacts of excessive *Cladophora* growth on human activities and important ecosystem processes such as nutrient and energy transport (e.g., Turschak et al., 2014), oxygen consumption, and the growth of potentially toxic bacteria.

In this study, we constructed a 3-D hydrodynamic model of Lake Michigan to reproduce multiple physical processes. Simulation results were validated against empirical observations. A Lagrangian particle trajectory model was embedded in the whole-lake model to track the transport of detached *Cladophora* mats within the Sleeping Bear Dunes National Lakeshore area based upon the physical model outputs. Our goal was to identify potential hotspots where sloughed *Cladophora* mats are likely to accumulate within the lake, and to identify the pathways between *Cladophora* sloughing and stranding along the shoreline beaches. A longer-term goal is to incorporate this *Cladophora* transport model into a broader whole-lake-wide physical-biogeochemical model to better understand nearshore-offshore interactions.

Materials and Methods

Study Site

Sleeping Bear Dunes National Lakeshore (SLBE) is located along the northwest coast of Michigan's lower peninsula (Fig. 1a). It is the second most-visited of the Great Lakes national parks with more than a million visitors per year. The coastal region of the national lakeshore is characterized by a complex bathymetry covering a wide range of depths from 5 m to 150 m (Fig. 1b). The lake bottom is a mix of hard (rocky) and soft (sand, silt) substrate. Hard substrate is densely covered with quagga mussels, and at depths less than ~15 m hard substrate is also covered with dense benthic algal growth from late May until September/October. Mussel and benthic algae abundance, along with other environmental variables, have been monitored at a long-term research site in Good Harbor Bay since 2010, where the substrate is primarily rocky. Mean mussel density at this site is 4,000 to 5,000/m^2, and benthic algal biomass, which is dominated by *Cladophora* for most of the summer, usually peaks at between 100 and 200 g dry weight per m^2. Fouling of local beaches with sloughed *Cladophora* is common on both the mainland and islands, primarily from mid-summer to fall, and these decomposing algae may promote the growth of *Clostridium botulinum* (Byappanahalli and Whitman, 2009). Bird deaths due to avian botulism are especially frequent in this part of Lake Michigan (Chipault et al., 2015).

Hydrodynamic Model

The hydrodynamic circulation and mixing model used in this study is the Finite Volume Community Ocean Model (FVCOM). The model has been adapted and used for the Great Lakes, and has been shown to reliably reproduce regional and lake-wide physical dynamics at various time scales (Anderson et al., 2015; Rowe et al., 2016; Xue et al., 2015). The horizontal unstructured mesh in this study contains 3301 nodes and 6242 triangle elements, with higher resolution in the nearshore (~1.2 km between nodes on average) compared with the offshore (~3.5 km, Fig.1). A sigma coordinate was used in the vertical direction (30 layers) with higher resolution approaching the surface and bottom to better resolve mixing processes near the boundaries. Other model configurations include a roughness height of 0.5 mm for a logarithmic bottom boundary layer, 2.5 level Mellor-Yamada turbulence closure scheme for vertical mixing, and the formulation of Smagorinsky for horizontal diffusion. The background diffusivity and viscosity were set at 1×10^{-6} m^2 s^{-1}. The model boundary was closed at the Straits of Mackinac which connects Lake Michigan and Lake Huron. Surrounding tributaries were not included as they are expected to have a negligible effect on whole-lake circulation. In this study, we hindcasted the hydrodynamic conditions for 2013. Lake-wide simulations were initiated on March 1st with a spatially uniform water temperature of 4.0 °C, and were run for 9 months until the end of November. The first 30 days are considered as model spin-up to obtain a hot-start with ambient flow, water temperature and surface elevations. A mode split technique, which separates vertical integration equations from vertical structure equations, was applied within FVCOM for better computing efficiency. The time step of the external mode (integrated equations) was set to 10 s to avoid advective instability according to the Courant-Friedrich Levy (CFL) criterion, and the split number was set to 10, which represents a time step of 100 s for the internal mode (structure equations).

Lagrangian Particle Trajectory Model

We constructed a 3-D Lagrangian particle trajectory model following the procedures described by Beletsky et al. (2007) based on a new Matlab platform featured with flexible postprocess and explicit visualization. The advection of particles was determined as:

$$\frac{dx}{dt} = u(x,y,z), \quad \frac{dy}{dt} = v(x,y,z), \quad \frac{dz}{dt} = w(x,y,z)$$

(1)

where *x*, *y*, *z* are the positions of the particle, and *u*, *v*, *w* are the velocity components. A higher resolution unstructured mesh (~100m, Fig.1b) for the SLBE lakeshore region was nested into the large lake-wide mesh to precisely track the motions of *Cladophora* 'particles'. The velocity components with higher spatiotemporal resolutions for the SLBE lakeshore area were linearly interpolated from the whole-lake FVCOM outputs. The motion of particles due to physical advection was updated by integrating Eq.1 using an explicit fourth-order Runge-Kutta scheme with a time step of 300 s (5 min). Turbulence eddy diffusivity induced vertical mixing movement was calculated using the random walking scheme from Huret et al. (2007),

$$z(t+\delta t) = z(t) + w_b \delta t + K'\big(z(t)\big)\delta t + R\sqrt{\frac{2K(\tilde{z})\delta t}{\sigma^2}} \quad (2)$$

in which, δt is the vertical random walk time step (set as 10 s), w_b is the sinking velocity, K is the vertical diffusivity, K' is the diffusivity gradient, R is a random variable from a distribution with zero mean and standard deviation of σ, and $\tilde{z} = z + 0.5K'\delta t.$ Particle transport across the surface and bottom boundaries was not permitted, and the *Cladophora* particles were assumed to stay at the shoreline if they reached the lake-land boundary. The sinking velocity was set as 10 m day^{-1} according to Rowe et al. (2016). The current speed of resuspension threshold for deposited particles was set as 2 cm s^{-1} according to the laboratory experiments (Flindt et al., 2007).

The Lagrangian particle trajectory model was run for 3 months from June to August, 2013 to track the transport of sloughed *Cladophora* from a simplified perspective. 200 particles were initially released at the shallow nearshore area (<10 m) along the shoreline and islands at the beginning of June (Fig. 2), and an extra of 200 particles were released every 5 days assuming a constant sloughing rate until the end of summer when growth slows. Released particles were all initially distributed at the middle position of the water column.

Model Forcing and Field Data

The bathymetry of Lake Michigan including the SLBE coastal area was obtained from the NOAA National Geophysical Data Center (https://www.ngdc.noaa.gov/mgg/greatlakes/michigan.html) with ~2 km resolution for open lake and ~400 m for nearshore waters. The bathymetry data was interpolated into the mesh grids based on a natural neighbor interpolation algorithm for further model setup. The hydrodynamic model FVCOM was forced by surface heat radiation flux and air-sea momentum as driven by meteorological conditions including wind speed at a height of 10 m, short wave radiation, relative humidity, cloud cover and air temperature following the methods from Beletsky and Schwab (2001). These meteorological data were directly downloaded from the North American Regional Reanalysis (NARR) database which is a 32-km-resolution and 3-hr interval dataset (psl.noaa.gov/data/gridded/data.narr.monolevel.html) and is derived from the NCEP meteorological model with assimilation of observational data from variable sources including remoting sensing and the Great Lakes buoy data. Surface water temperature of Lake Michigan was obtained from the Great Lakes Surface Environmental Analysis (coastwatch.glerl.noaa.gov/glsea) based on satellite observations.

Field measurements were conducted at the Good Harbor Bay in 2013 to collect a time series of *Cladophora* biomass. A bottom-mounted Acoustic Doppler Current Profiler (ADCP, 250 kHz) was deployed at a 10m-depth site of Good Harbor Bay (*Cladophora* producing site, Fig. 2) from June to October, 2013 to collect the vertical profiles of the current velocity at one-hour intervals with 1-meter vertical resolution. We also installed a camera with a vertical measuring stick planted in a 20m-depth site for field view (*Cladophora* depositional aera, Fig. 2), allowing us to monitor the thickness of the depositional bed over time (Fig. 3). While the time lapse imagery does not allow for quantitative measurements of biomass as accurate as those derived from grab samples, it allows for semi-quantitative measurements at high temporal resolution (hourly daytime images), which allows for the identification of major sloughing, resuspension, and depositional events.

Results and Discussion

Physical results

Simulated surface water temperatures in the SLBE nearshore region agreed reasonably well with satellite observations, with an average root mean square error (RMSE) of 0.6 °C over the year (Fig. 4). Seasonal dynamics of surface water temperature were captured well, characterized by a gradual increase from early spring to a maximum in late July/early August, and a gradual decrease through autumn. The model was able to capture the observed dramatic temperature decline in mid-August, although it slightly overestimated the magnitude of the decline. Discrepancies between simulations and observations in spring and early summer are likely the result of the assumed spatially uniform initial conditions with barely one-month spin-up.

The eastern (u) and northern (v) velocity components from the ADCP mounted at the bottom of 10m-depth site (Fig. 2) were used to validate the near-bottom current simulations. Comparison results indicated a satisfying performance of the physical model in reproducing the current speed, particularly after late July (Fig. 4). In general, an average benthic current speed of 1.4 cm s^{-1} was recorded by the ADCP over the summer, while the model predicted a slightly higher value of 1.6 cm s^{-1}. The standard deviations of current variations, which are likely due to basin scale waves, were 0.84 cm s^{-1} from model simulation, and 0.73 cm s^{-1} from field observations. Compared to our previous simulations at a deeper, open-water site (55m, Shen et al., 2020), it is more challenging to reproduce the hydrodynamic environment at shallow nearshore regions such as the area we focused on in this study, where complex bathymetry and shoreline structure, and proximity to large islands, likely result in current dynamics that are highly variable spatially and temporally.

Trajectory results

The sloughed *Cladophora* particles were released from the productive shallow areas during the growing seasons, and their trajectory as determined by physical advection and resuspension were predicted without algae aggregation and biological degradation considered. The particle model indicated that only a small portion of particles was transported out of the SLBE region (Fig. 5), implying the impacts of sloughed *Cladophora* on nutrient cycling, energy flow, and shoreline conditions are largely confined at a regional/local scale. The trajectory simulation results suggested that the majority of sloughed *Cladophora*, if not washed up on the shoreline or beach, quickly deposited at nearby sites after sloughing because of the sinking process (Fig. 5). Those *Cladophora* particles depositing at the shallow nearshore sites could be easily resuspended to the water column due to relatively strong near bottom currents. Differently, drifting *Cladophora* particles generally could not be resuspended to the water column when they finally deposited to the mid-depth region (with a depth between 20–50 m) unless significant upwelling and storm events occur. The mechanisms driving *Cladophora* deposition are complex, and multiple factors including wind, temperature, geomorphology and hydrodynamics may affect the deposition process. When and where *Cladophora* deposition will occur, though attracted substantial attentions due to its ecosystem consequences, is still difficult to predict and have been less reported till now. Observations along the shoreline of Lake Michigan suggest that much drifting *Cladophora* finally ends up on beaches (Riley et al., 2015).

We counted the *Cladophora* particles deposited at the bottom of the 20m-depth site (Fig. 2) within a radius of 500 m between June and August, and compared the count to the thickness of the depositional mat recorded by the underwater time-lapse camera. It should be noted that the number of particles counted within the specified area only qualitatively represent the predictions of the thickness of *Cladophora* mats. The variability and temporal trend of bottom particle numbers at the observation site were quite consistent with the dynamics of the benthic mat (Fig. 6). The camera recorded an increasing trend of 30 cm thickness per month, with shorter term deposition and resuspension events. The trajectory model also predicted an increasing deposition during the growing season with abundant sloughed *Cladophora*, and the model successfully captured the rapid deposition immediately followed by resuspension and export in early August. Compared with the mat thickness recorded by the camera in summer, the model generally predicted a relatively smooth increasing trend with less fluctuations, possibly resulting from the simplifying assumptions of no community aggregation or biological degradation, which would accelerate deposition and enhance decaying, respectively.

The particle model applied a cohesive shoreline boundary configuration instead of a reflective one, with the objective of assessing the potential for accumulation of detached *Cladophora* along the shore. The trajectory model results demonstrated that the quantity of particles attached along the shoreline displayed substantial variability (Fig. 6). In general, the shoreline beaches adjacent to the shallow productive area are much more vulnerable to *Cladophora* fouling with an overall large number of particles accumulated in summer. The shoreline with high fouling risk is the Platte Bay area, which is adjacent to a large area of submerged aquatic vegetation, which becomes trapped in the bay by the prevailing northward alongshore current in summer (Fig. 6). By comparison, simulated shoreline fouling in Sleeping Bear Bay and Good Harbor Bay were more moderate. Though the summer-time northward currents would favor the accumulation of local *Cladophora* particles, the benthic algal biomass density near these two bay areas was comparably lower (Fig. 5), which reduced the releasing of *Cladophora* particles and the potential washing up onto the shorelines.

Model limitations and future work

In our Lagrangian trajectory model, the detached benthic algae were treated as passive particles in the aquatic environments to track their transport and deposition sites. The model is simplified in that it ignores certain important physical and biological processes including aggregation, decaying and decomposition, which inevitably will result in discrepancies between observed and simulated results. For example, a fixed sinking velocity and resuspension threshold were applied in our model. However, these values can be expected to vary with the size of algal aggregations after detaching. To account for the biological and physical aggregation, size-dependent sinking rates were generally applied to model their advection transport (Ackleh and Fitzpatrick, 1997). Laboratory experimental results showed relatively higher resuspension thresholds for large-size macroalgae compared with small species (Flindt et al., 2007). As expected, model sensitivity scenarios indicated the distance between detachments sites and depositional sites becomes smaller if higher sinking velocities and resuspension thresholds are used. Similarly, a constant releasing rate of particles at the shallow nearshore regions was applied, and the spatiotemporal dynamics of the benthic sloughing influenced by the variabilities of biomass distributions and bottom shear stress had not been fully considered. In our study, initiation of sloughed *Cladophora* was hypothetically from the very shallow sites where photosynthesis of these benthic algae is possible. The accuracy of initial distributions could be improved with more in situ data and remote sensing images. Some success in using optical parameters to identify in situ density of submerged aquatic vegetation has been achieved in the Great Lakes (Shuchman et al., 2013; Brooks et al., 2015). Meanwhile, dynamics of *Cladophora* growth has been successfully simulated in the Great Lakes through comparisons to abundant field observations (Auer et al., 2010; Higgins et al., 2005a). These biological models, if coupled with the hydrodynamic models (e.g., FVCOM) to better represent the spatiotemporal dynamics of *Cladophora* biomass at different depths, could provide more accurate and dynamic *Cladophora* sloughing rates to the trajectory transport model in this study. *Cladophora* decomposition will be important to account for, in part because the decomposition process may determine the location and timing of botulism toxin production, and also because it will determine the long-term fate of sloughed *Cladophora*. For example, if significant amounts of sloughed *Cladophora* remain intact late into the fall, when the lake becomes isothermal and storm events promote deep mixing and horizontal transport, then a significant portion of the *Cladophora* that has been deposited close to its original sloughing location may ultimately be transported further offshore, possibly contributing energy to the offshore food web (Turschak et al., 2014).

While prediction of the timing and magnitude of shoreline stranding and in-lake depositional events can be improved with model refinement, the results of this study help to determine the spatial scale over which *Cladophora* sloughing, transport and deposition can be expected to occur on time scales of weeks to months. This has important implications for critical in-lake processes such as energy transport, nutrient dynamics, oxygen dynamics, and avian botulism outbreaks. Coupled hydrodynamic-biogeochemical models have been established and used to investigate nutrient cycling in the Great Lakes (Rowe et al., 2017; Shen et al., 2020). Meanwhile, existing *Cladophora* (or submerged aquatic vegetation) models appear to reliably simulate the direct response of their growth and mortality to the nearshore temperature, light and phosphate levels (Tomlinson et al., 2010). These existing model studies make it possible to establish a much broader hydrodynamic-biogeochemical-Cladophora coupled model, in which, the interactions between the physical, biogeochemical and vegetation parts could all be simulated in a short time step, and the parameter configuration and forcing driver of each sub-module could be updated quickly. For example, the temperature and nutrient concentrations from the hydrodynamic-biogeochemical module could drive the *Cladophora* module. Meanwhile, the biomass density of these benthic algae could be used dynamically to better represent the bottom roughness and wave-current interaction scheme for the hydrodynamic model (Aleynik et al., 2016). The development of such model could improve the accuracy of simulations in their biomass dynamics, transport, response to external nutrient loading management as well as the potential ecosystem risks at a lake-wide scale.

Management implications

The trajectory model indicates that, on the time scale of weeks to months, most of the sloughed *Cladophora* within the SLBE region does not transport to the offshore, generally settling at nearby mid-depth sites where benthic shear stress is weak. Hence the anoxic conditions required for *C. botulinum* growth are more likely to occur at these mid-depth sites. Meanwhile, the shoreline beach of the Platte Bay is more vulnerable to fouling by sloughed *Cladophora* according to the model results, and special attention needs to be paid in this area to maintain ecosystem health and recreational function. The SLBE region is an avian botulism hotspot in Lake Michigan (Chipault et al., 2015; Chun et al., 2013), and if *Cladophora* sloughing and decomposition is indeed a factor promoting the production of the botulism toxin, the results presented here suggest that the unique set of features of this region, including plentiful hard, shallow substrate, high areal concentrations of benthic algae, and complex bathymetry that promotes the retention of sloughed algae, may explain why the region has this distinction.

The depth averaged circulation along the SLBE shoreline in summer is traditionally northward under the seasonal southwest winds (Beletsky and Schwab, 2001), and this prevailing current prevents large portions of detached *Cladophora* from moving out of the local bay area, leaving it to either be deposited at mid-depth sites or stranded on the shore. These findings underscore the potential impact of localized *Cladophora* management actions on *Cladophora* deposition in beach and nearshore waters at SLBE. The growth of *Cladophora* in the Great Lakes is basically limited by light, temperature and phosphate (Tomlinson et al., 2010). Favorable *Cladophora* growing conditions, including increased water clarity and light availability are likely to persist for some time due to widespread dreissenid mussel colonization in the broader lake. Nutrient limitation (phosphorus in specific) remains the most viable way to restrict *Cladophora* growth and related fouling of nearshore and beach environments. The phosphorus loading management since 1970s have successfully leaded to lake-wide *Cladophora* biomass reduction, though the invasive benthic mussels reduced the efficiency of such actions (Bootsma et al., 2015). In the more recent Great Lakes Water Quality Protocol of 2012, developing phosphorus loading targets is recognized a key step to a healthy lake ecosystem, particularly for the nearshore waters. Though invasive mussels were supposed to be associated with the resurgence of benthic *Cladophora*, recent invasive mussel control experiments on Good Harbor Reef resulted in shifts in benthic algal communities and biomass, and may provide an alternative technique for managing localized growth and deposition of *Cladophora* in the future (LimnoTech, 2020).

Conclusions

In this study, we applied a hydrodynamic and particle trajectory model to simulate the transport of sloughed *Cladophora* in the SLBE area. The hydrodynamic model well reproduced the physical features in the study area, including a relatively small RMSE of 0.6 °C between simulated and observed surface water temperature, and comparable near-bottom current speeds (1.6 vs 1.4 cm s^{-1}). The trajectory model qualitatively predicted the thickness dynamics of depositional mats, with temporal patterns fairly consistent with those recorded by the time lapse camera (~30 cm thickness increase per month). Our model results revealed that the sloughed *Cladophora* generally deposited at nearby mid-depth regions (20-50 m) after detached from their growing sites. The southern shoreline beaches, particularly around the Platte Bay, was demonstrated vulnerable to the fouling of decayed *Cladophora*. Our study is a first trial to simulate the trajectory of detached *Cladophora*, and could inform the regional ecosystem management.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

This material is based upon work supported by the Wisconsin Sea Grant under Project No. R/HEC-17 and R/HEC-36, the National Science Foundation under Grant No. 1658390, and the U.S. EPA Great Lakes Restoration Initiative, via a cooperative agreement with the National Park Service.

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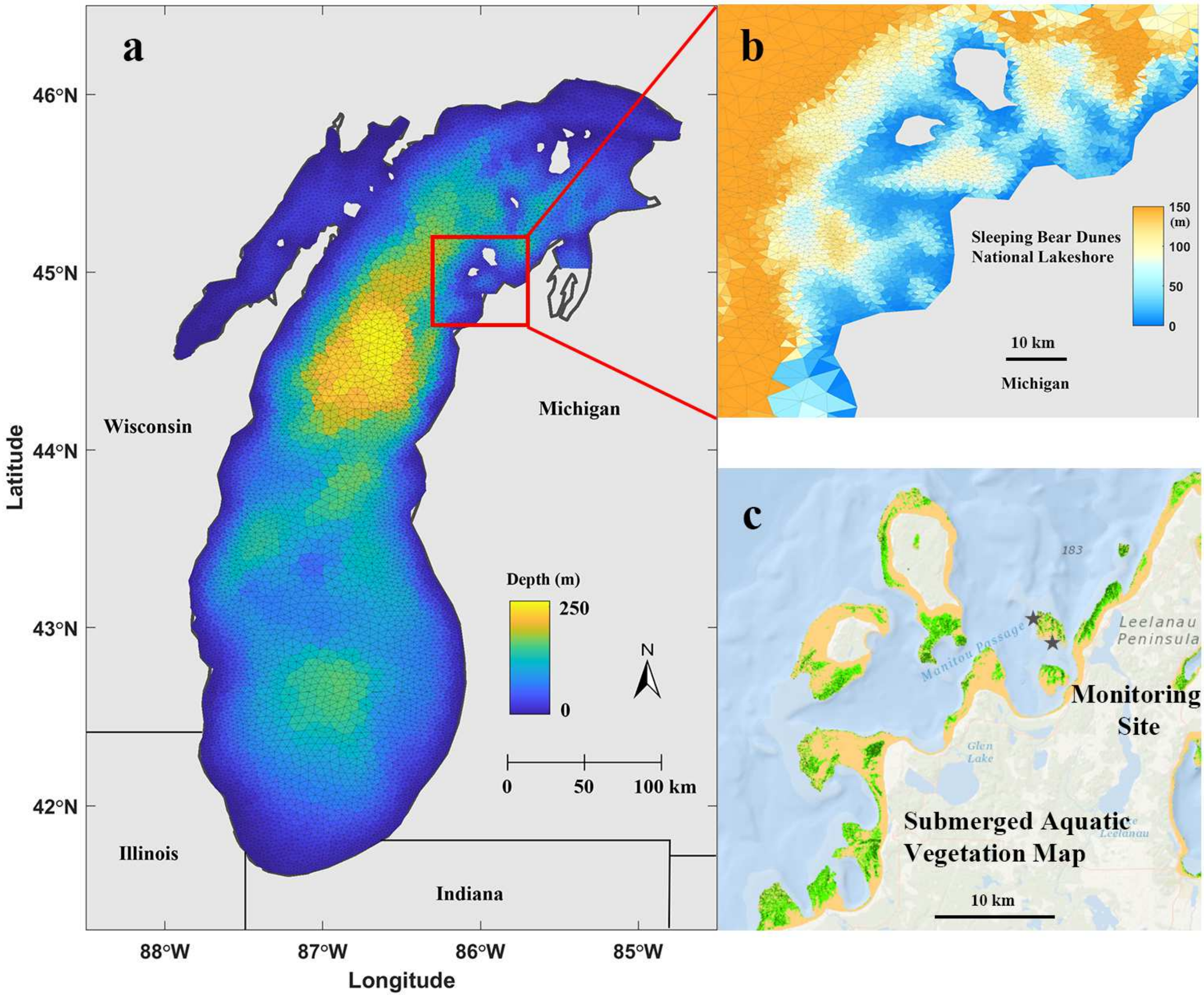


Fig. 1 (**a**) Bathymetry and model mesh grids of Lake Michigan. (**b**) The nested high-resolution grids at the Sleeping Bear Dunes National Lakeshore area (**c**) Submerged aquatic vegetation distribution within the region, as determined with satellite imagery (Brooks et al., 2015).

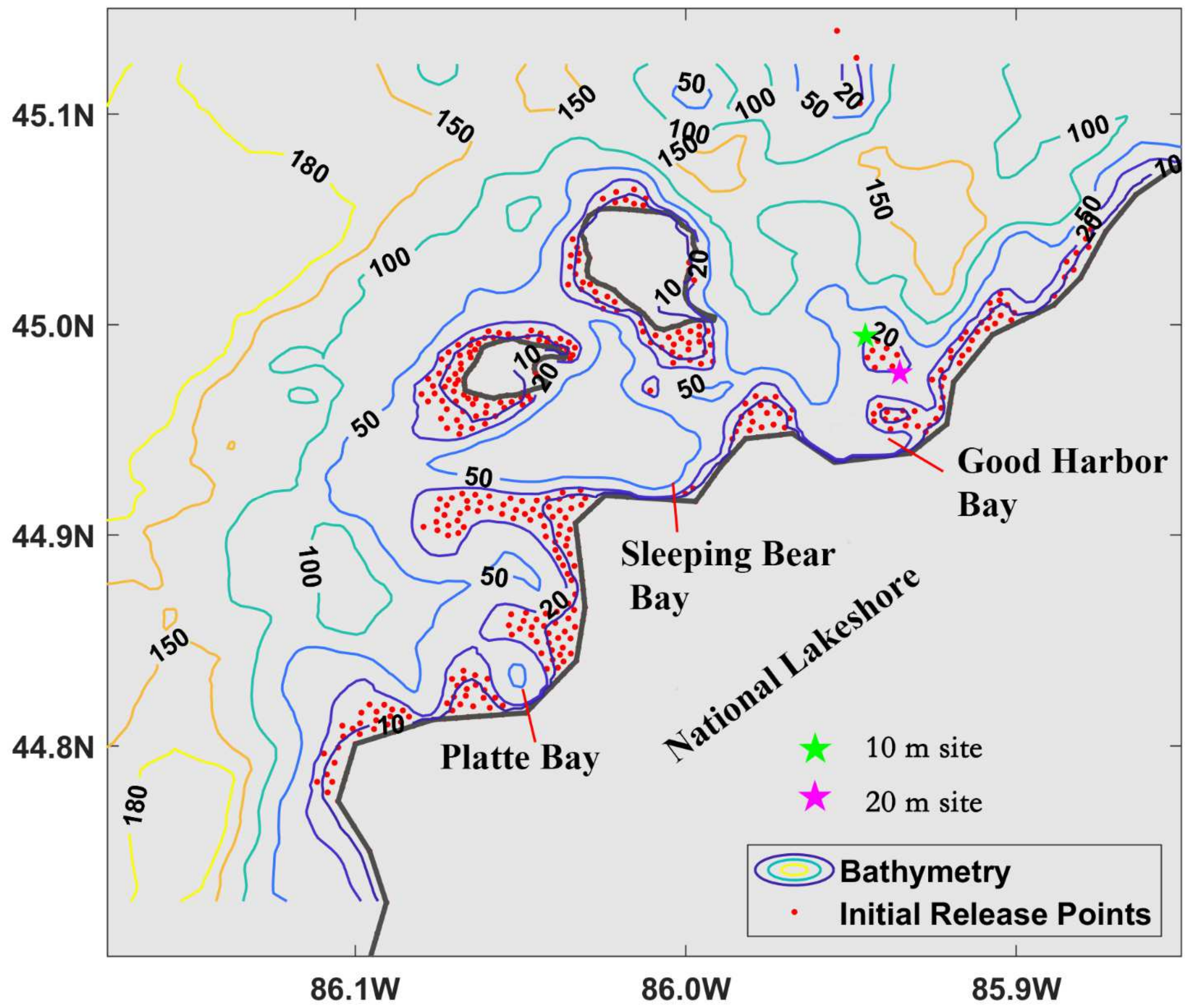


Fig. 2 Detailed bathymetry map of the study area. Red dots represent the growth and detaching sites of *Cladophora*, pink star represents the 20 m field observational site, and green star represents the 10 m site.

Fig. 3 Time lapse images of bed thickness at the Good Harbor Bay depositional site (20m depth). The vertical measuring stick is used to record the thickness of the deposition mats. Left: June 10. Right: August 10.

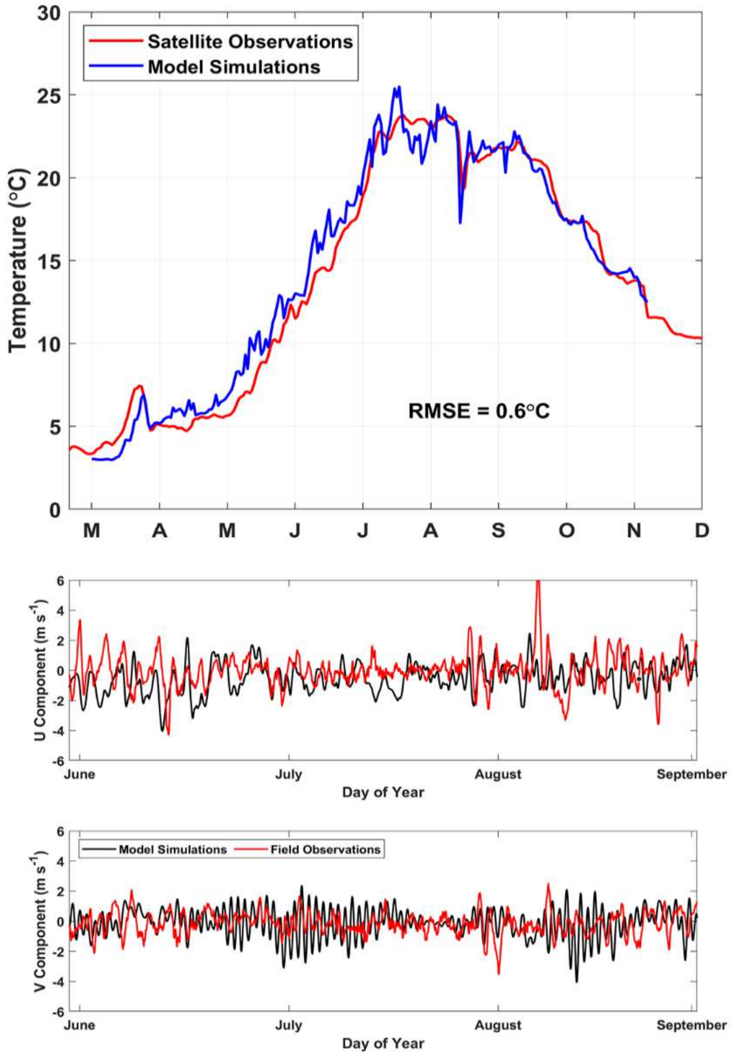


Fig. 4. (up) Comparisons of simulated and satellite-derived surface water temperatures in the SLBE Good Harbor Bay region. (bottom) Comparisons of simulated and measured (ADCP) northern and eastern near-bottom current velocity components at the Good Harbor Bay site (10m-depth site).

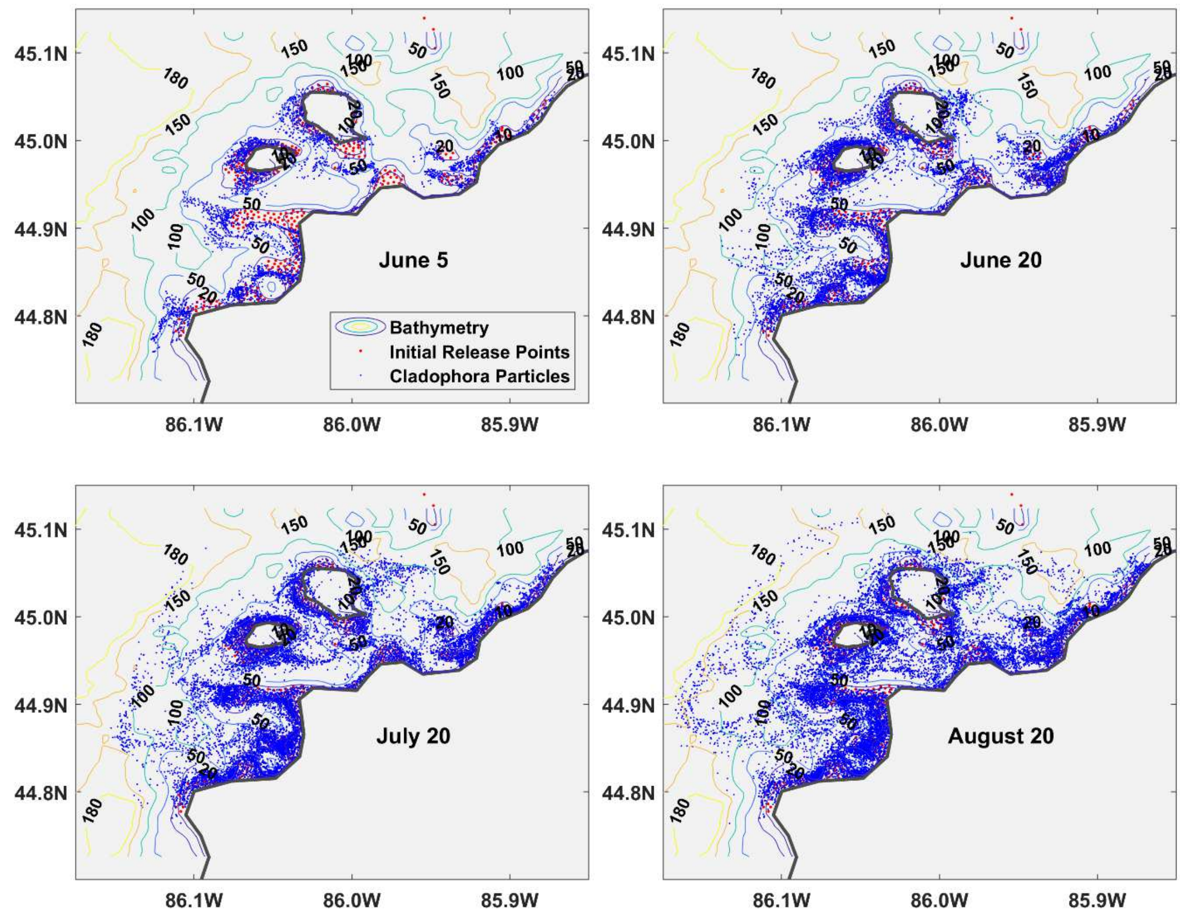


Fig. 5 Simulated distribution maps of detached *Cladophora* particles within the national lakeshore in June 5th, June 20th, July 20th and August 20th.

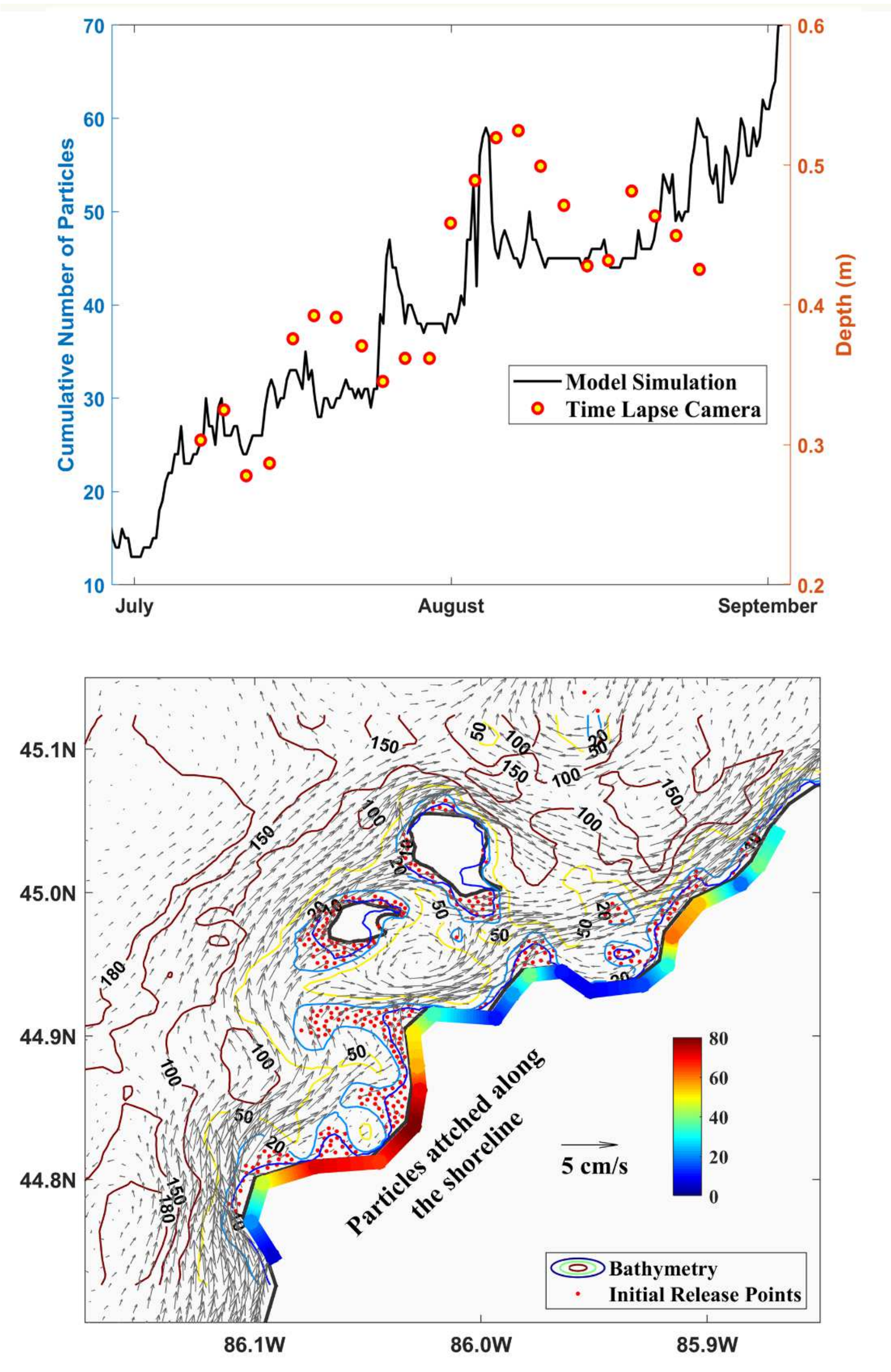
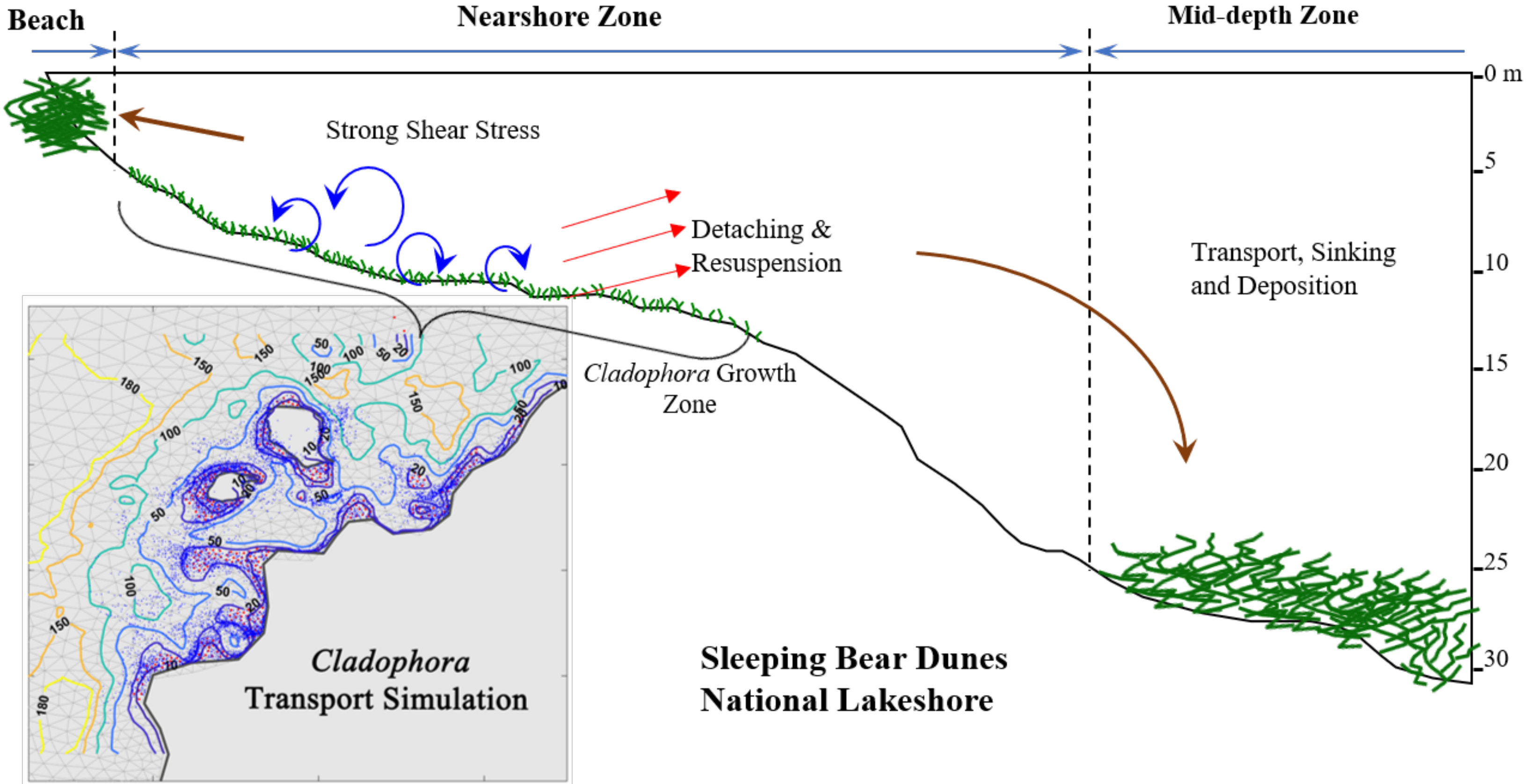


Fig. 6. (up) Comparisons between counted particles from model simulations and deposition mats thickness recorded by the underwater camera. (bottom) Depth averaged currents of the study area in summer and accumulated particles along the shoreline beaches.



Beach
Nearshore Zone
Mid-depth Zone
0 m
5
10
15
20
25
30
Strong Shear Stress
Detaching &
Resuspension
Transport, Sinking
and Deposition
Cladophora Growth
Zone
Cladophora
Transport Simulation
Sleeping Bear Dunes
National Lakeshore