Assessing nitrogen tipping points for harmful algal blooms in Peconic Estuary priority embayments, 2024 - 2027

Progress Report for Peconic Estuary Partnership, February 2025





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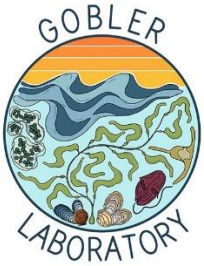


EXECUTIVE SUMMARY

While harmful algal blooms have been a serious issue for the Peconic Estuary for more than 40 years, the past decade has seen a series of first ever events for the estuary regarding HABs including fish kills, turtle kills, and shellfish bed closures due to elevated levels of biotoxin from HABs. While excessive nutrient loading if often cited as the primary cause of HABs, this subject has been grossly under studies in the Peconics. This project was designed to address this informational short-coming defining the spatial and temporal variability of the three distinct HABs in the Peconic Estuary. *Alexandrium catenella* and *Dinophysis acuminata* can causes of paralytic shellfish poisoning and diarrhetic shellfish poisoning, respectively, and are known to bloom during the months of March through May in the Peconic Estuary. Meanwhile, *Margalefinidium polykrikoides*, formerly *Cochlodinium*, is an ichthyotoxic dinoflagellate that has caused finfish and shellfish kills during summer. For this project, we monitored five Peconic Estuary. From 2022-2024, five locations in the Peconic Estuary (Meetinghouse Creek, Reeves Bay, Jockey Creek, Sag Harbor Cove, and Three Mile Harbor) were sampled as a time series from April through September. We sought to fully characterize the nutrient regime within each site, before, during, and after these HABs. We then performed incubation experiments with water from these sites to assess the impact of added and reduced nitrogen (N) and phosphorus (P) concentrations on HAB growth. During the study, there have been 'record-breaking' and 'first ever' HABs in the Peconic Estuary. For example, in 2023, blooms of *Alexandrium catenella* led the three distinct shellfish bed closures by the NYSDEC that included sites never closed before due to biotoxins and the largest PSP closure ever in the Peconic Estuary. In 2024, an intense *Dinophysis acuminata* bloom occurred in Reeves Bay with cell densities exceeding 50 million cells per liter and cell densities over one million cells per liter sustained for over a month. This was the second largest *Dinophysis acuminata* bloom ever recorded anywhere in the world. During experiments, we found that nutrient enrichment with N, and to a far lesser extent P, consistently increased total algal biomass within all sites. N was also found to specifically stimulate each of the individual HABs. In some cases, nitrogen reductions of 50% to 90% significantly reduced the intensity of these HABs, with reductions needed being both site and species specific. This project is ongoing, with further experiments to evaluate and replication of results required to generate confidence in managerial recommendations. Ultimately, this project will generate managerial recommendations on precise nutrient load reductions required to mitigate HABs within the Peconic Estuary.

BACKGROUND:

The Peconic Estuary has been plagued with harmful algal blooms (HABs) for decades. In 1985, brown tides caused by the pelagophyte, *Aureococcus anophagefferens* struck suddenly, recurred for three years, and caused the collapse the of $3M bay scallop fishery, as well as the destruction the eelgrass meadows (Gobler et al., 2005). While the final brown tide in the Peconic Estuary occurred at the end of the 20th century (Gobler and Sanudo-Wilhelmy, 2001), the 21st century has been a period of expansion and proliferation of HABs in the Peconic Estuary. In 2004, the first ever rust tide caused by *Cochlodinium polykrikoides* occurred across the Peconic Estuary (Gobler et al., 2008) and has since caused both fish kills and shellfish kills across the estuary (Kudela and Gobler, 2012; Li et al., 2012). While the first *Alexandrium* catenella bloom occurred in Northport in 2006 (Hattenrath et al., 2010), it was a decade later the most destructive *Alexandrium* bloom in the Peconics occurred, specifically in 2015. In May of that year, blooms occurred in multiple bays and tributaries across the western Peconics, leading to the closure of three shellfishing regions due to the presence of saxitoxin in shellfish and the threat of paralytic shellfish poisoning (PSP). During these blooms, hundreds of diamondback terrapin turtles died after consuming mussels contaminated with saxitoxin (Hattenrath-Lehmann et al., 2017). In the intervening years, there have been nearly 10 PSP closures in the Peconic Estuary within six locations (Sag Harbor Cove, James Creek, Deep Hole Creek, Terry Creek, Meetinghouse Creek, and Halls Creek). A final HAB of concern is caused by the dinoflagellate, *Dinophysis acuminata*, that synthesizes okadaic acid and causes diarrhetic shellfish poisoning (DSP). In 2011, the highest densities of *Dinophysis* ever recorded anywhere in the world (two million cells per liter) was quantified in Meetinghouse Creek (Hattenrath-Lehman et al., 2018). These three HABs recur annually across the Peconic Estuary with intensities and impacts varying year-to-year. Prior research has identified the ability of excessive nitrogen to promote and intensify these HABs (Hattenrath et al., 2010; Gobler et al., 2012; Hattenrath-Lehmann et al., 2015). Still, critical open questions regarding nitrogen and these HABs in the Peconic Estuary remain: Are the events similarly promoted by excessive nitrogen? What is the spatial and temporal variability of the nutrients promoting these events? What degree of nitrogen reduction is needed to lessen the intensity of these events? This project will aim to answer these questions.

Objectives:

1. Assess the temporal dynamics of nutrients and HABs within bloom prone regions of the Peconic Estuary.
2. Assess the ability of nitrogen and phosphorus to intensify HABs within bloom prone regions of the Peconic Estuary.
3. Asses the levels of nutrient load reduction needed to lessen the intensity of these HABs.

APPROACH:

Time series sampling of HABs and nutrients was performed at multiple locations across the Peconic Estuary from spring through fall, capturing the season succession of *Alexandrium*, *Dinophysis*, and *Cochlodinium*. Specifically, samples werecollected from: Sag Harbor, Three Mile Harbor, Jockey Creek, the Peconic River, Reeves Bay, and Meetinghouse Creek. During blooms of the HABs of interest, experiments were conducted. Bloom water was collected and transferred to two-liter polycarbonate bottles that were established in triplicate experimental treatments that include an unamended control, enrichment with nitrogen (ammonium), enrichment with phosphorus (orthophosphate) and enrichment with both elements. Parallel experimental bottles were established whereby nutrient levels are reduced by 25%, 50%, and 75% by mixing whole water with artificial seawater with no nutrients. To account for reductions in zooplankton grazing caused by dilution (Landry et al., 1995; Gobler et al., 2002), dilutions with nutrients added back to each dilution level will also be established. The concentrations of each HAB and nitrogenous nutrients and phosphorus were quantified at the start and end of each experiment. The functional relationship between HAB growth rates and nutrient levels were established. Thresholds of nutrient dilutions needed to cause low or negative growth rates were identified using linear regression models. The data generated from experiments regarding the level of nitrogen reduction required to lessen the intensity of HABs within distinct regions of the Peconic Estuary is being compared to management plans. This management end point can be used in conjunction with the Suffolk County Wastewater Subwatersheds Plan (2020) to identify the specific management actions that are most likely to achieve HAB mitigation.

RESULTS:

2022

Alexandrium

In 2022, *Alexandrium catenella* was monitored from 5-May-2022 to 22-June-2022. Jockey Creek had the most notable and highest bloom of all five sites in 2022 at a peak of 17,136 cells/L on 11-May-2022 (Fig. 1). Meetinghouse Creek did not have any *A. catenella* blooms throughout the whole sampling period (Fig. 1). Reeves Bay had one bloom on 9-May-2022 with a low density of 14 cells/L (Fig. 1). *A. catenella* in Sag Harbor Cove first appeared on 14 cells/L had the second highest bloom of the five sites at a peak of 756 cells/L on 16-May-2022 (Fig. 1). In Three Mile Harbor, *A. catenella* was consistent at 56 cells/L from 11-May-2022 to 23-May-2022 (Fig. 1).

Dinophysis

In 2022, *Dinophysis acuminata* was monitored simultaneously with *A. catenella* from 5-May-2022 to 22-June-2022. Jockey Creek had consistent high-density blooms over 1,000 cells/L. *D. acuminata* first appeared on 18-May-2022 at 5,838 cells/L (Fig. 2). Blooms were over 10,000 cells/L between 25-May-2022 to 6-June-2022 starting at 49,882 cells/L on 25-May-2022 (Fig. 2). The highest density bloom of *D. acuminata* in Jockey Creek was when it peaked at 171,500 cells/L on 1-June-2022 and was the highest amongst the five sites sampled (Fig. 2). The bloom went down to 91,000 cells/L on 6-June-2022 (Fig. 2). Meetinghouse Creek bloomed the second highest out of the five sites at its peak at 95,200 cells/L on 25-May-2022 (Fig. 2). Reeves Bay bloomed below 1,000 cells/L throughout the whole monitoring period with the peak on 30-May-2022 at 756 cells/L (Fig. 2). *D. acuminata* in Sag Harbor Cove bloomed consistently over 1,000 cells/L throughout the monitoring period except for the first day two days at 28 and 56 cells/L on 11-May-2022 and 16-May-2022, respectively (Fig. 2). *D. acuminata* peaked at 17,332 cells/L on 23-May-2022 (Fig. 2). There was a second peak of 5,012 cells/L on 13-June-2022 (Fig. 2). Three Mile Harbor had low density blooms below 1,000 cells/L with a peak on 7-June-2022 at 2,422 cells/L (Fig. 2).

Cochlodinium

In 2022, *Cochlodinium polykrikoides* was monitored from 5-July-2022 to 28-September-2022 and appeared at relatively low densities at all five sites. *C. polykrikoides* appeared only once on 12-July-2022 at 50 cells/mL (Fig. 3). Meetinghouse Creek had consistent blooms throughout September and had a peak on 13-September-2022 at 145 cells/mL (Fig. 3). Reeves Bay had the highest bloom density of the five sites at 500 cells/mL on the first day of monitoring on 6-July-2022 (Fig. 3). Sag Harbor Cove had more consistent blooms throughout the monitoring with the second highest density bloom of the five sites at 318 cells/mL on 18-July-2022 (Fig. 3). At Three Mile Harbor, *C. polykrikoides* appeared twice at 10 and 4 cells/mL on 11-July-2022 and 18-July-2022, respectively (Fig. 3).

2022 Experiments

In 2022, results from chlorophyll-*a* data showed nutrient addition experiments performed with Meetinghouse Creek bloom water had four experiments that were nitrogen limiting on 25-May-2022, 30-May-2022, 6-June-2022, and 22-June-2022 ($p>0.05$, Fig. 10), Two experiments were co-limiting between nitrogen and phosphorus on 9-May-2022 and 15-June-2022 ($p<0.05$, Fig. 10), and one that had no response on 18-May-2022 (Fig. 10). All seven nutrient addition experiments performed with Reeves Bay bloom water were nitrogen limiting ($p<0.05$, Fig. 11). Nutrient addition experiments performed with Sag Harbor Cove bloom were similar to Reeves Bay bloom water where all seven experiments were nitrogen limiting ($p<0.05$, Fig. 12). Three Mile Harbor bloom water nutrient addition experiments had similar results as Reeves Bay and

Sag Harbor Cove nutrient addition experiments where all seven were nitrogen limiting ($p<0.05$, Fig. 13). Nutrient addition experiments using Jockey Creek bloom water showed two nitrogen limitations on 11-May-2022 and 6-June-2022 ($p<0.05$, Fig. 14). Three experiments were phosphorus limiting on 18-May-2022, 1-June-2022, and 15-June-2022 ($p<0.05$, Fig. 14). Two experiments had no response on 25-May-2022 and 15-June-2022 (Fig. 14).

2023

Alexandrium

In 2023, *Alexandrium catenella* was monitored from 3-April-2023 to 26-June-2023. Jockey Creek had the highest density bloom of the five sites when it first appeared on 10-April-2023 at a peak bloom of 24,500 cells/L (Fig. 4). *A. catenella* sustained at over 1,000 cells/L the two weeks after that at 8,610 and 6,300 cells/L on 17-April-2023 and 24-April-2023, respectively. Meetinghouse Creek first bloomed on 12-April-2023 over 1,000 cells/L at 1,610 cells/L (Fig. 4). There were two sampling days that were over 100 cells/L on 19-April-2023 at 630 cells/L and 24-May-2023 at 238 cells/L (Fig. 4). Reeves Bay had the second highest bloom of the five sites at its peak at 23,800 cells/L (Fig. 4). *A. catenella* bloomed two more times in the next two weeks at 2,240 cells/L and 70 cells/L on 19-April-2023 and 26-April-2023, respectively (Fig. 4). *A. catenella* bloomed once in Sag Harbor Cove on 3-April-2023 at 224 cells/L (Fig. 4). Three Mile Harbor had a peak bloom over 1,000 cells/L on the first day at 3,444 cells/L on 3-April-2023 (Fig. 4). The rest of the monitoring density was below 100 cells/L on 24-April-2023, 1-May-2023, and 8-May-2023 at 140, 70, 70, cells/L, respectively (Fig. 4).

Three of these *Alexandrium* blooms were associated with the closure of shellfish beds in the Peconic Estuary due to elevated levels of saxitoxin in shellfish. On April 12, 2023, Meetinghouse Creek and Terry Creek were closed to shellfishing due to PSP. A week later, on April 20th, that closure expanded to include all of western Flanders Bay including Reeves Bay (Fig 4A). This was the first time this region had been closed due to PSP. On that same date (April 12th, 2023), Jockey Creek was closed to shellfishing due to PSP (Fig 4A).

Dinophysis

In 2023, *Dinophysis acuminata* was monitored from 3-April-2023 to 5-July-2023. In Jockey Creek, *D. acuminata* had the highest density bloom of the five sites on 15-May-2023 at 57,582 cells/L (Fig. 5). There was a second high density bloom over 10,000 cells/L on 30-May-2023 at 10,962 cells/L (Fig. 5). In Meetinghouse Creek, there was a bloom over 10,000 cells/L on 17-May-2023 at 10,262 cells/L (Fig. 5). On 24-May-2023, there was a bloom of 27,706 cells/L, which was the second highest bloom of the five sites (Fig. 5). Reeves Bay had its highest density bloom on 7-June-2023 at 7,182 cells/L (Fig. 5). There was another bloom over 1,000

cells/L a week prior to 2,856 cells/L on 31-May-2023 (Fig. 5). In Sag Harbor Cove, the peak bloom was on 22-May-2023 at 3,038 cells/L (Fig. 5). There was a second peak bloom on 5-June-2023 at 2,282 cells/L (Fig. 5). In Three Mile Harbor, the peak bloom was on 5-June-2023 at 7,056 cells/L (Fig. 5).

Cochlodinium

In 2023, *Cochlodinium polykrikoides* was monitored from 20-July-2023 to 21-September-2023 (Fig. 6). *C. polykrikoides* did not bloom throughout the monitoring period until the last day on 21-September-2023 at a very low density of 4 cells/mL (Fig 6). In Meetinghouse Creek, *C. polykrikoides* appeared once in July on 24-July-2023 at a low density of 15 cells/mL (Fig. 6). Throughout September there were low density blooms of 44, 65, and 35 cells/mL on 7-September-2023, 14-September-2023, and 21-September-2023, respectively. In Reeves Bay, *C. polykrikoides* appeared in very low densities sporadically throughout the monitoring period. On 20-July-2023, *C. polykrikoides* first appeared at 35 cells/mL and again a week later at 3 cells/mL on 27-July-2023 (Fig. 6). In August, *C. polykrikoides* was detected on 31-August-2023 at 20 cells/mL (Fig. 6). In September, it was detected at 8 and 4 cells/mL on 5-September-2023 and 11-September-2023, respectively (Fig. 6). *C. polykrikoides* in Sag Harbor Cove was detected sporadically and had the second highest bloom of the five sites on 19-September-2023 at 89 cells/mL (Fig. 6). Three Mile Harbor peaked on 31-July-2023 at 178 cells/mL, which was also the highest density bloom of the five sites (Fig. 6).

2023 Experiments

In 2023, Meetinghouse Creek *A. catenella* bloom water on 12-April-2023 cell density data showed that nutrient addition experiments were co-limiting ($p<0.05$, Fig. 15) and that 75% and 90% dilutions with artificial seawater were significantly lower density ($p<0.05$, Fig. 15). Similarly, an experiment using *D. acuminata* bloom water on 26-April-2023 also showed co-limitation ($p<0.05$, Fig. 16) in nutrient addition as well as significantly lower density in 75% and 90% dilutions with artificial seawater ($p<0.05$, Fig. 16). In an experiment on 15-Spetember-2023 using *C. polykrikoides* bloom water, nutrient addition experiment did not have a response, but the 90% dilution with artificial seawater was significant ($p<0.05$, Fig. 17). Reeves Bay *D. acuminata* bloom water experiment performed on 2-June-2023 showed no response in the nutrient addition experiment, but significance in both 75% and 90% dilution with artificial seawater ($p<0.05$, Fig. 18). Another Reeves Bay *D. acuminata* bloom water experiment performed on 9-June-2023 showed no response in the nutrient addition experiment, but significance in all three dilutions: 50%, 75%, and 90% ($p<0.05$, Fig. 19). Three Mile Harbor *D. acuminata* bloom water experiment performed on 1-June-2023 showed that there was nitrogen limiting in the nutrient addition experiment ($p<0.05$, Fig. 20), and the 75% and 90% dilution with artificial seawater

were significant ($p<0.05$, Fig. 20). *D. acuminata* bloom water experiment from Sag Harbor Cove on 7-June-2023 and 14-June-2023 both had the same results, showing nitrogen limitation ($p<0.05$, Fig. 21; Fig. 22), and that 75% and 90% dilution with artificial seawater were both significant ($p<0.05$, Fig. 21; Fig. 22). An experiment with *C. polykrikoides* bloom water from Sag Harbor Cove 20-Septmeber-2023 showed that it was co-limiting in the nutrient addition experiment, and significant when diluted by 75% and 90% with artificial seawater ($p<0.05$, Fig. 23). Another experiment with Jockey Creek *A. catenella* bloom water on 3-May-2023, showed that nutrient addition was co-limiting ($p<0.05$, Fig. 24), and that again 75% and 90% dilutions with artificial seawater were significant ($p<0.05$, Fig. 24). An experiment with *D. acuminata* bloom water on 1-June-2023 showed no response in the nutrient addition, but 75% and 90% dilutions with artificial seawater were significant ($p<0.05$, Fig. 25).

2024

Alexandrium

In 2024, *Alexandrium catenella* was monitored from 18-March-2024 to 24-June-2024. *A. catenella* in Jockey Creek was consistently blooming over 1,000 cells/L throughout the monitoring period except for one day on 13-May-2024 at 233 cells/L (Fig. 7). The peak bloom was on 24-April-2024 at 157,500 cells/L, which was also the highest density bloom of the five sites (Fig. 7). There was a second peak bloom on 22-May-2024 at 27,475 cells/L (Fig. 7). Meetinghouse Creek had the second highest bloom of the five sites on 29-May-2024 at its peak of 11,200 cells/L (Fig. 7). Reeves Bay had consistent high blooms first on 17-April-2024 at a peak of 8,867 cells/L and a week later on 24-April-2024 at 7,408 cells/L. The second peak was on 22-May-2024 at 1,750 cells/L (Fig. 7). Sag Harbor Cove had a peak bloom on 29-April-2024 at 1,108 cells/L (Fig. 7). There was a higher second bloom on 22-May-2024 at 6,125 cells/L (Fig. 7). Three Mile Harbor had a peak bloom on 22-May-2024 at 8,050 cells/L (Fig. 7).

Dinophysis

In 2024, *Dinophysis acuminata* was monitored from 18-March-2024 to 24-June-2024. In Jockey Creek, *D. acuminata* bloomed consistently over 1,000 cells/L from May through June (Fig. 8). The peak bloom was on 10-June-2024 at 395,500 cells/L, which was the second highest bloom of all five sites (Fig. 8). At Meetinghouse Creek, *D. acuminata* bloomed from May through mid-June and peaked on 29-May-2024 at 65,450 cells/L (Fig. 8). Reeves Bay had its most intense peak bloom on 4-June-2024 at 57,800,000 cells/L, which was the highest bloom of all five sites (Fig. 8). *Dinophysis acuminata* bloom occurred in Reeves Bay sustained cell densities over one million cells per liter sustained for over a month and was the second largest *Dinophysis acuminata* bloom ever recorded anywhere in the world. Sag Harbor Cove had its

peak on 28-May-2024 at 6,475 cells/L (Fig. 8). Three Mile Harbor had two peak blooms first on 28-May-2024 at 18,900 cells/L and the second on 10-June-2024 at 9,392 cells/L (Fig. 8).

Cochlodinium

In 2024, *Cochlodinium polykrikoides* was monitored from 3-July-2024 to 25-September-2024. Jockey Creek had the second highest bloom of the five sites on 24-July-2024 at 792 cells/mL (Fig. 9). Meetinghouse Creek had the highest bloom of the five sites on 18-July-2024 at 2500 cells/mL (Fig. 9). Reeves Bay bloomed over 100 cells/mL on 21-August-2024 at 625 cells/mL (Fig. 9). Sag Harbor Cove had one bloom on 26-August-2024 at 100 cells/mL (Fig. 9). Three Mile Harbor did not have any *C. polykrikoides* blooms throughout the whole monitoring period.

PRELIMINARY CONCLUSIONS AND CONTINUED WORK

During the study, there have been 'record-breaking' and 'first ever' HABs in the Peconic Estuary. For example, in 2023, blooms of *Alexandrium catenella* led the three distinct shellfish bed closures by the NYSDEC that included sites never closed before due to biotoxins and the largest PSP closure ever in the Peconic Estuary. In 2024, an intense *Dinophysis acuminata* bloom occurred in Reeves Bay with cell densities exceeding 50 million cells per liter and cell densities over one million cells per liter sustained for over a month. This was the second largest *Dinophysis acuminata* bloom ever recorded anywhere in the world. During experiments, we found that nutrient enrichment with N, and to a far lesser extent P, consistently increased total algal biomass within all sites. N was also found to specifically stimulate each of the individual HABs. In some cases, nitrogen reductions of 50% to 90% significantly reduced the intensity of these HABs, with reductions needed being both site and species specific. This project is ongoing, with further experiments to evaluate and replication of results required to generate confidence in managerial recommendations. Ultimately, this project will generate managerial recommendations on precise nutrient load reductions required to mitigate HABs within the Peconic Estuary. Future efforts will include evaluation of our 2024 experiments and 2025 monitoring and experiments which will commence in March.

Figures

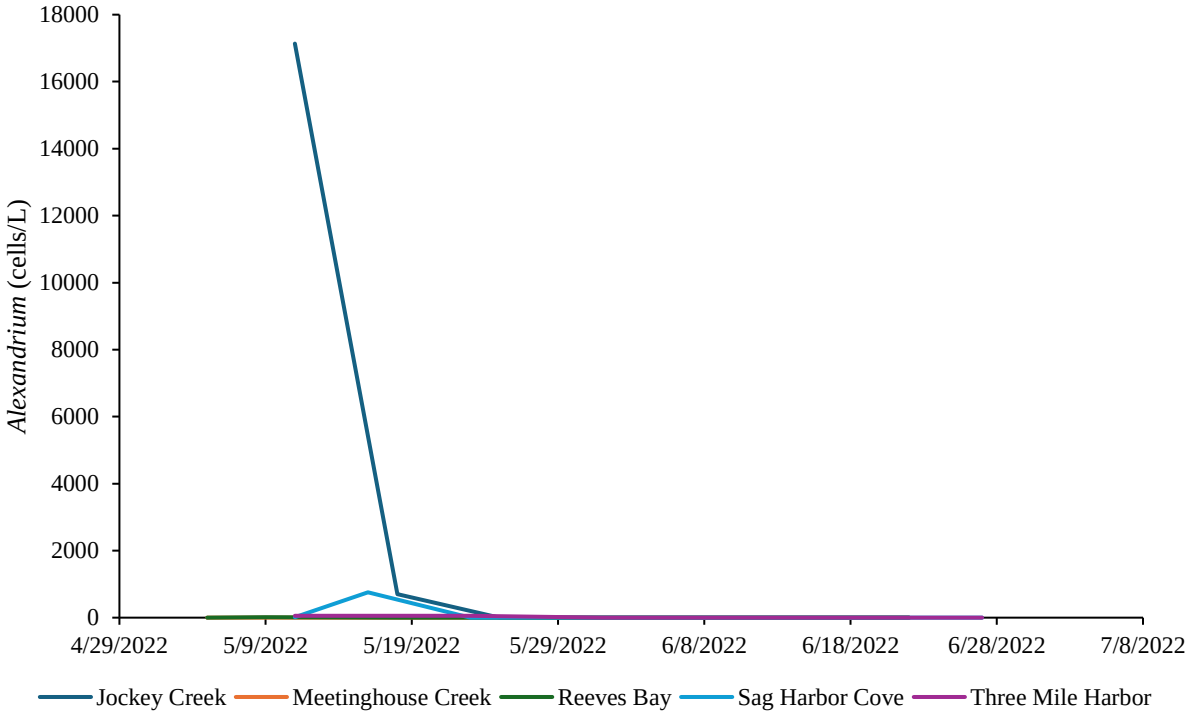


Figure 1. 2022 *Alexandrium* density times series.

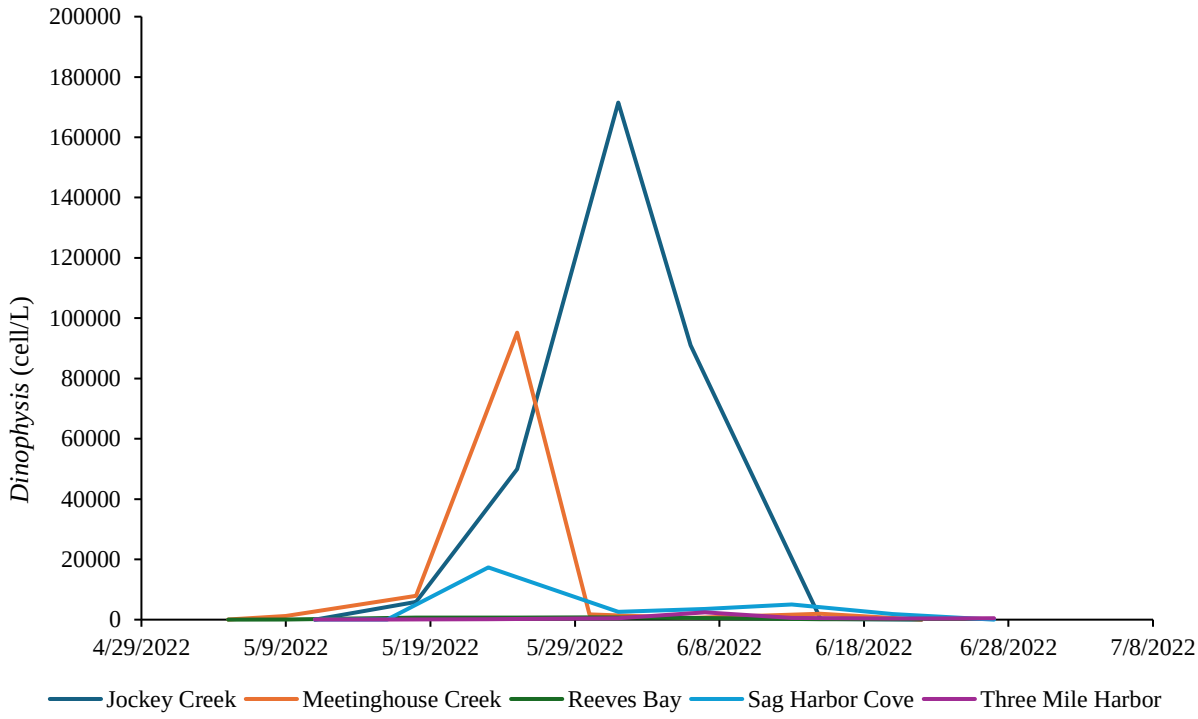


Figure 2. 2022 *Dinophysis* density times series.

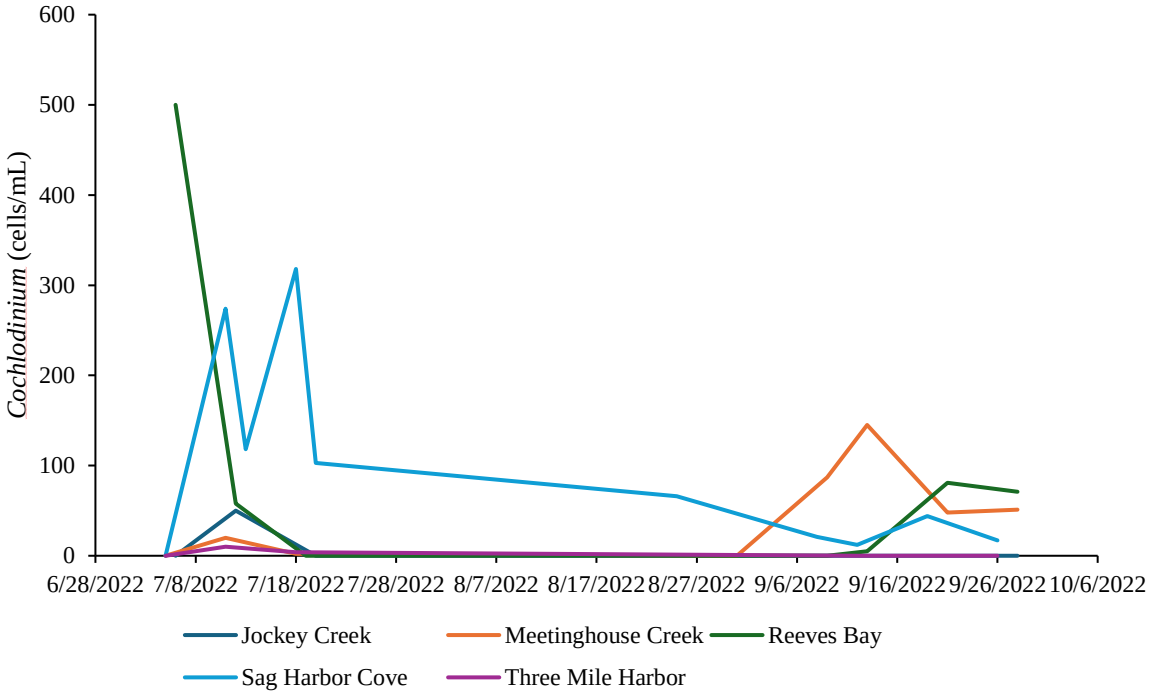


Figure 3. 2022 *Cochlodinium* density times series.

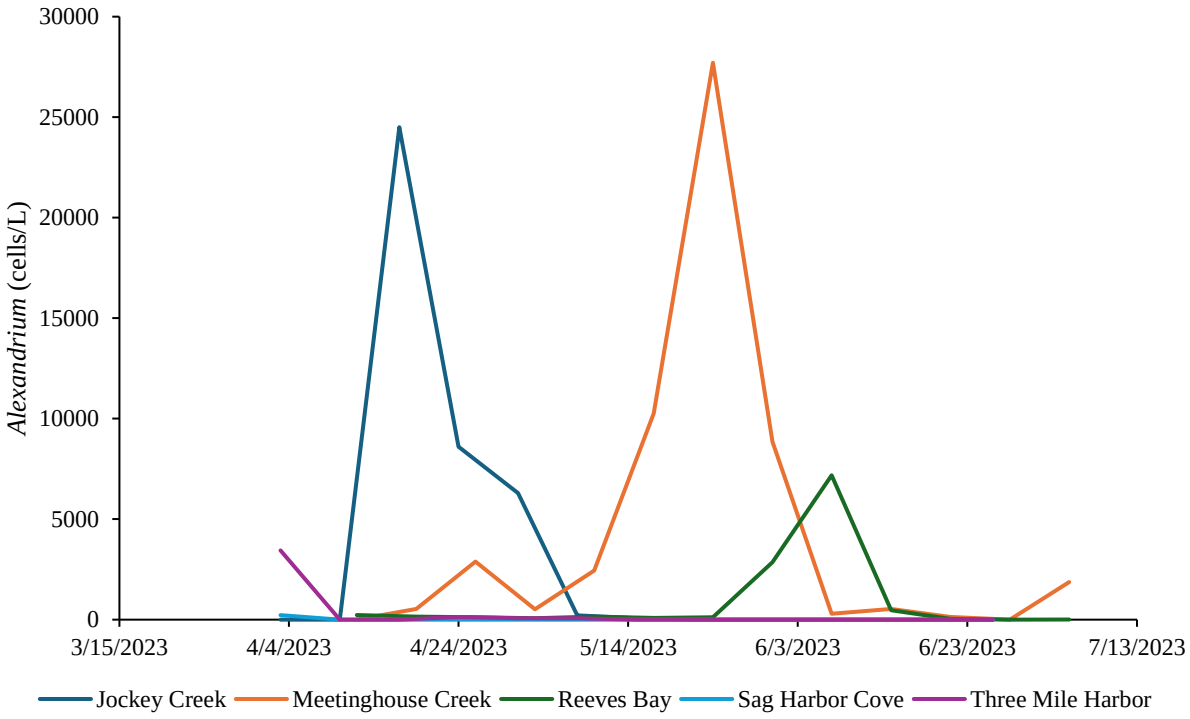
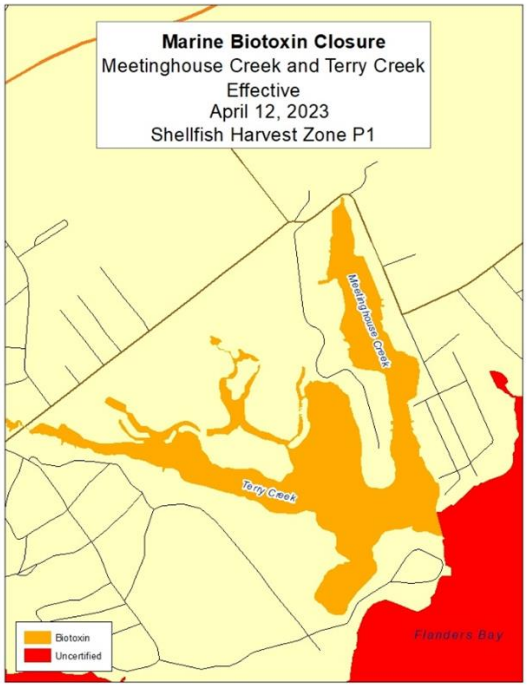
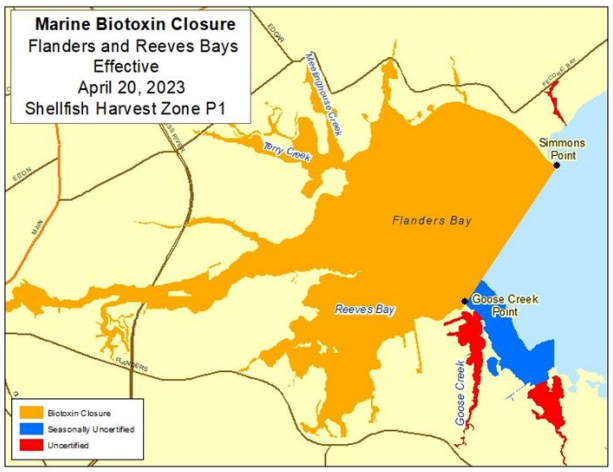
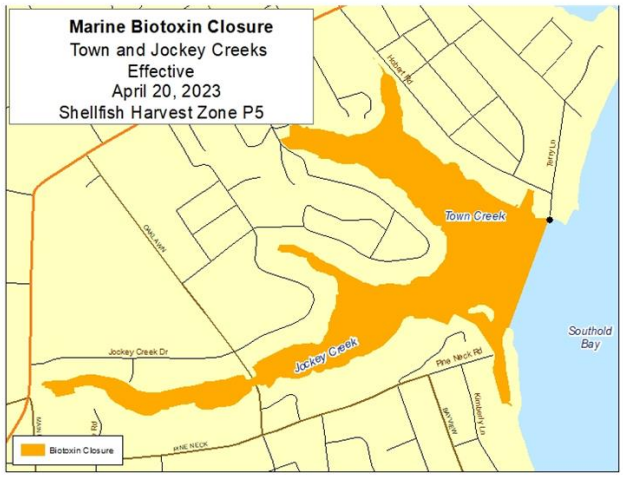


Figure 4. 2023 *Alexandrium* density times series.

Fig 4A. Three PSP biotoxin closures of shellfishing across the Peconic Estuary, April 2023







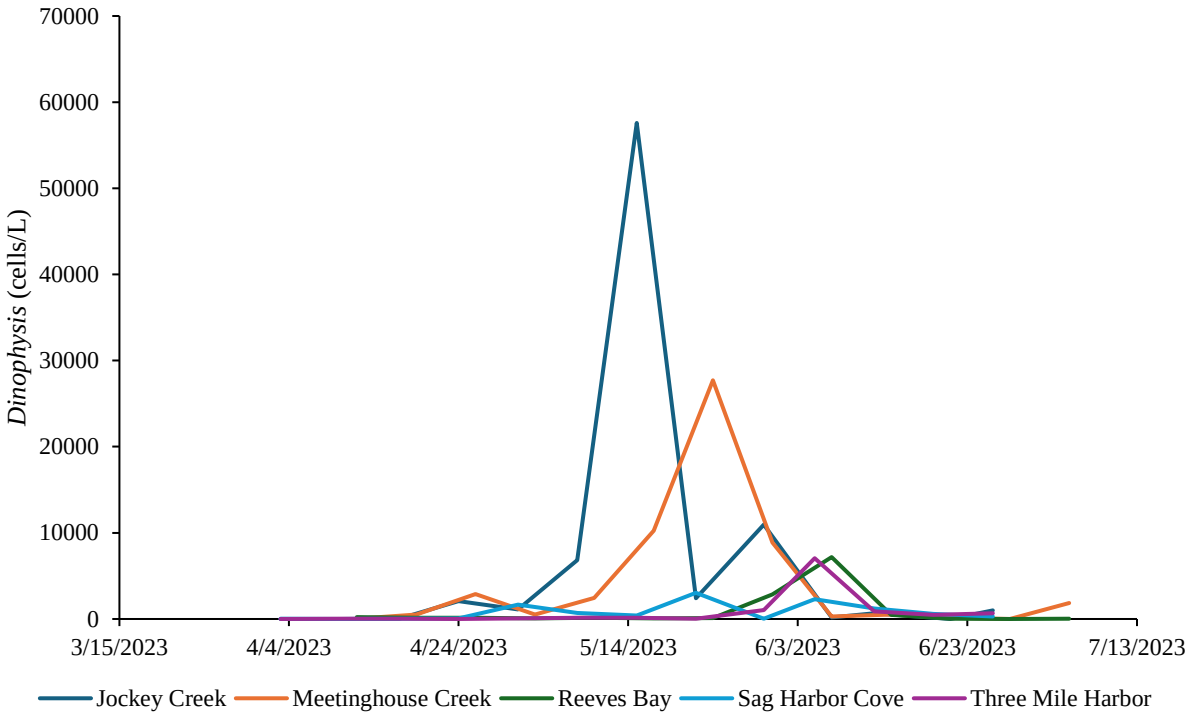


Figure 5. 2023 *Dinophysis* density times series.

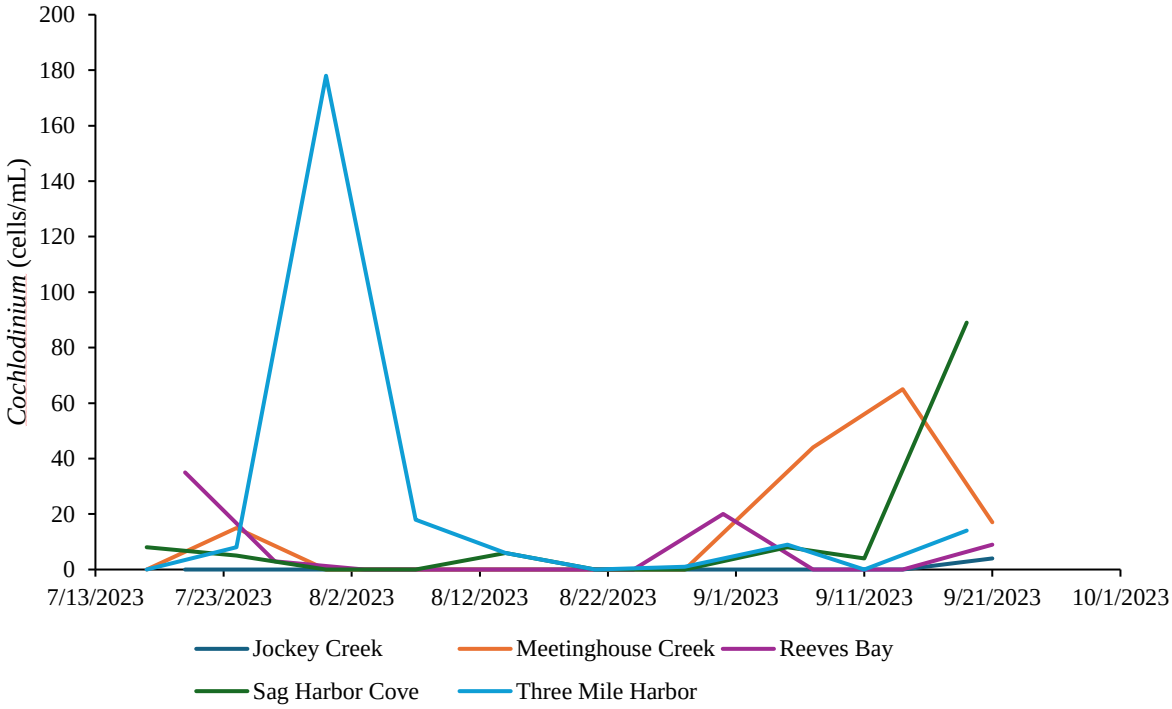


Figure 6. 2023 *Cochlodinium* density times series.

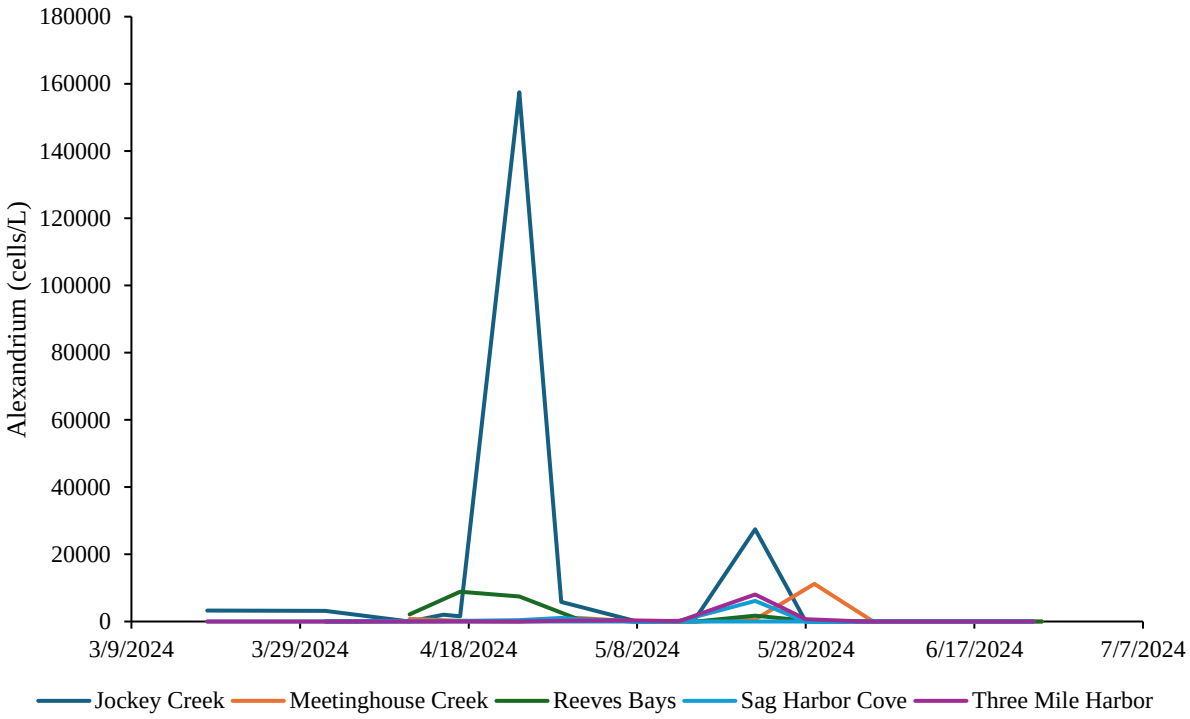


Figure 7. 2024 *Alexandrium* density times series.

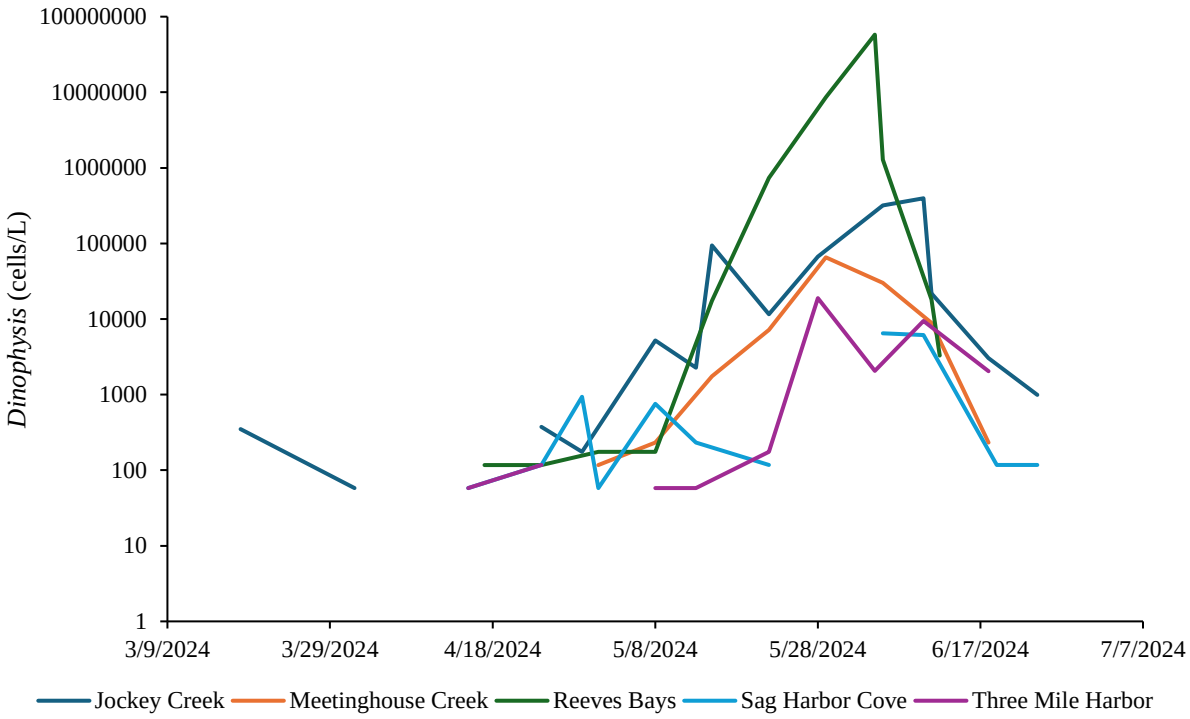


Figure 8. 2024 *Dinophysis* density times series.

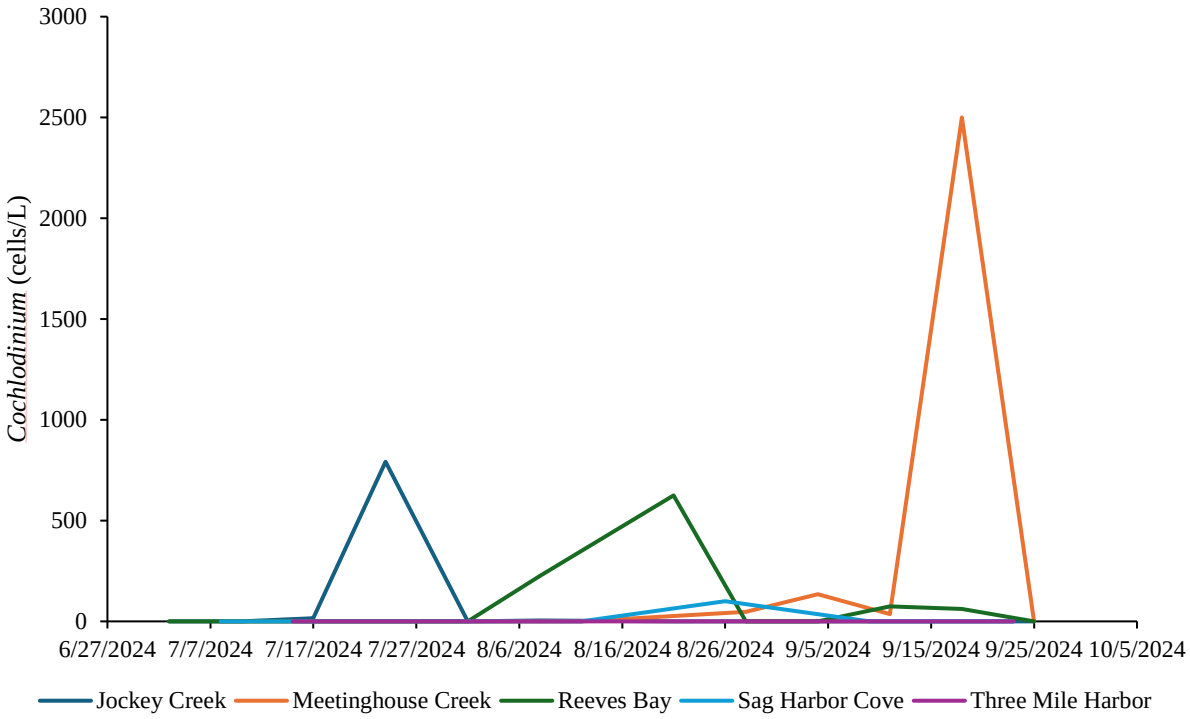


Figure 9. 2024 *Cochlodinium* density times series.

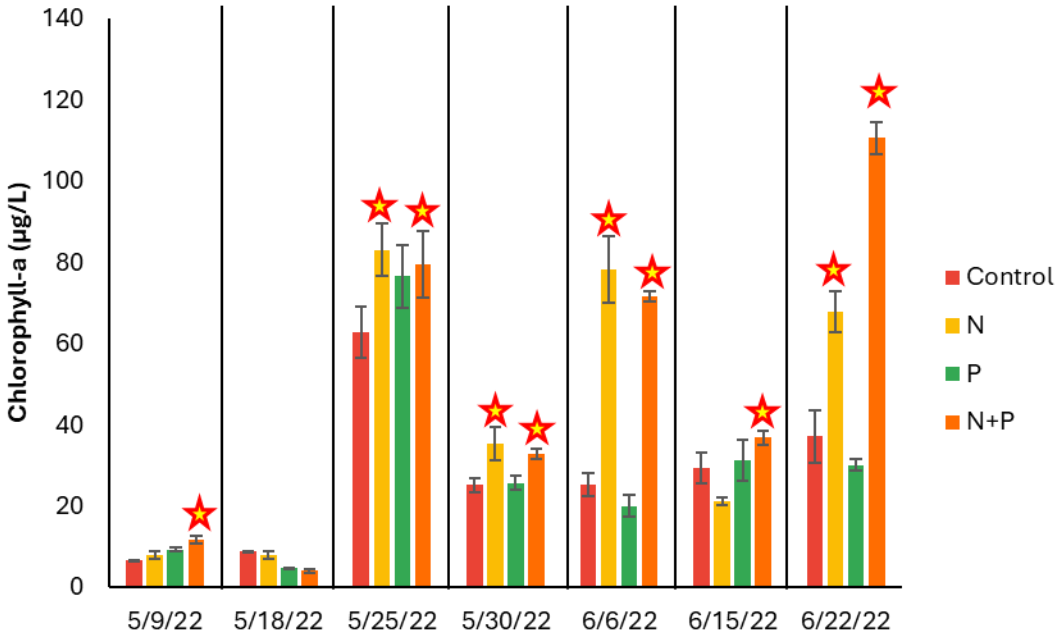


Figure 10. 2022 Meetinghouse Creek bloom water nutrient addition experiments. Stars represent significance.

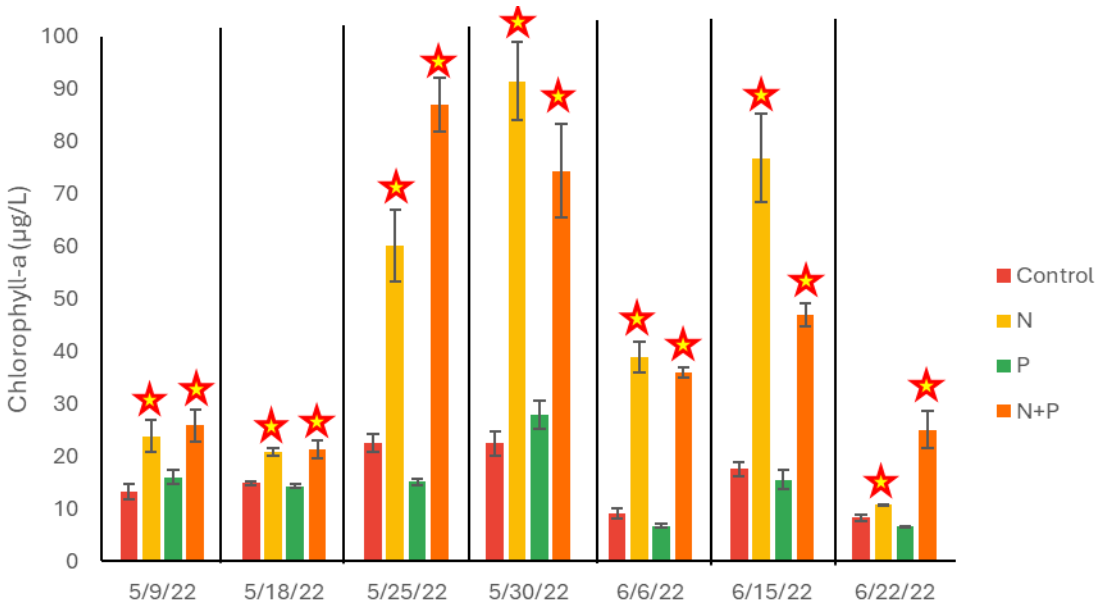


Figure 11. 2022 Reeves Bay bloom water nutrient addition experiments. Stars represent significance.

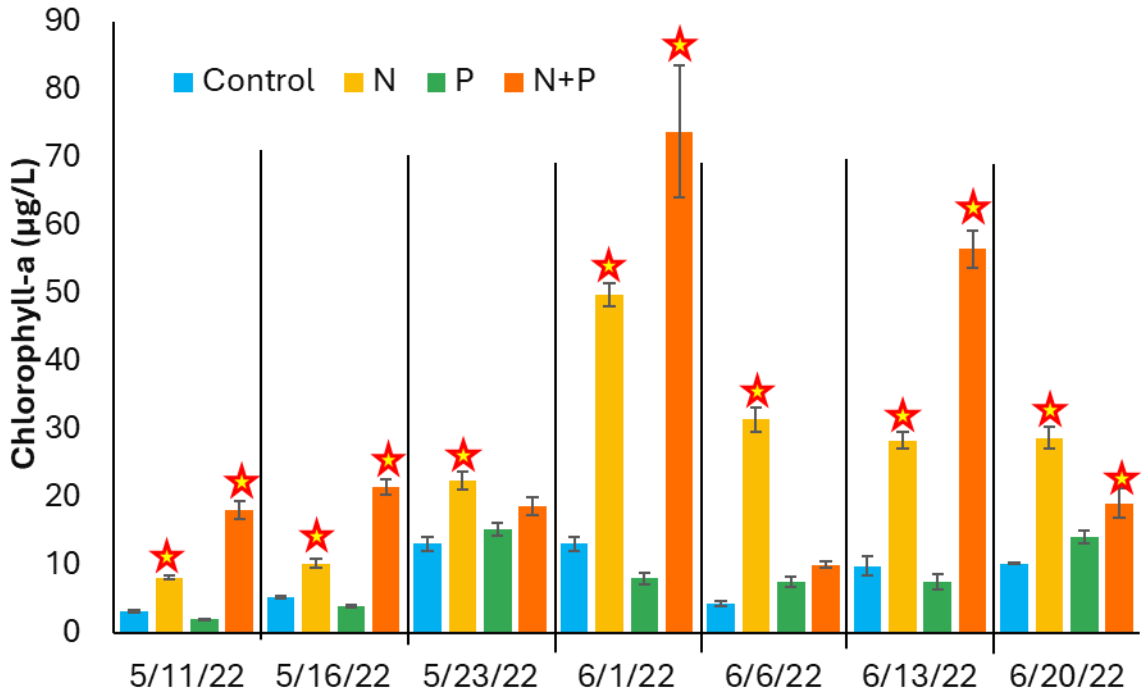


Figure 12. 2022 Sag Harbor Cove bloom water nutrient addition experiments. Stars represent significance.

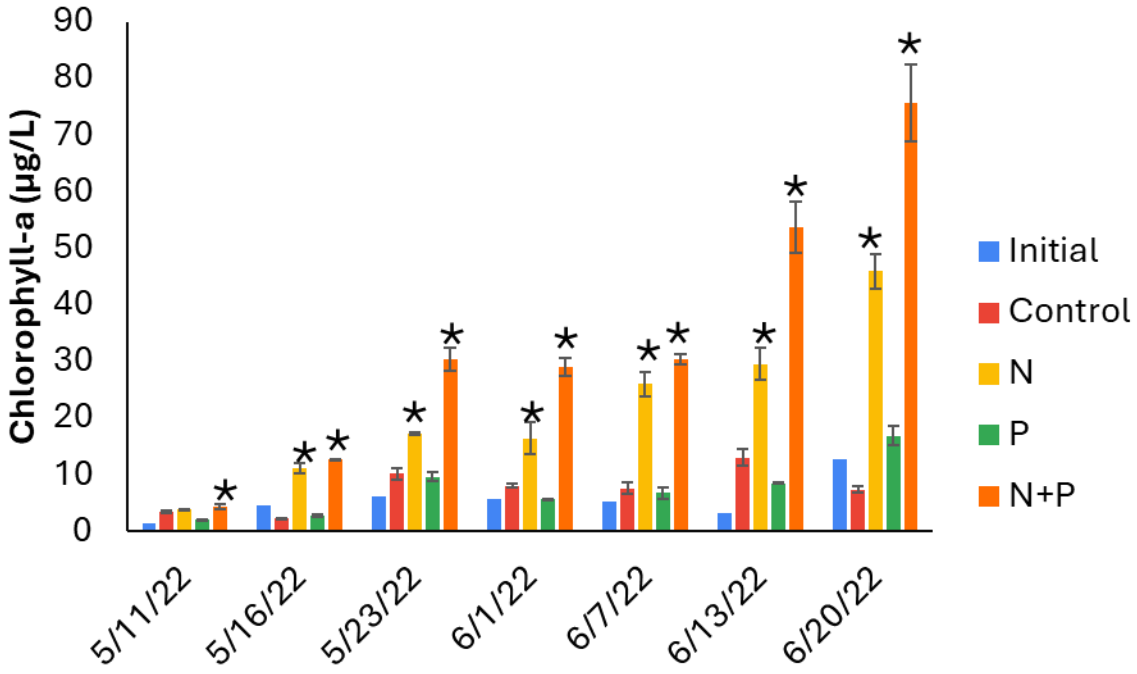


Figure 13. 2022 Three Mile Harbor water nutrient addition experiments. Stars represent significance.

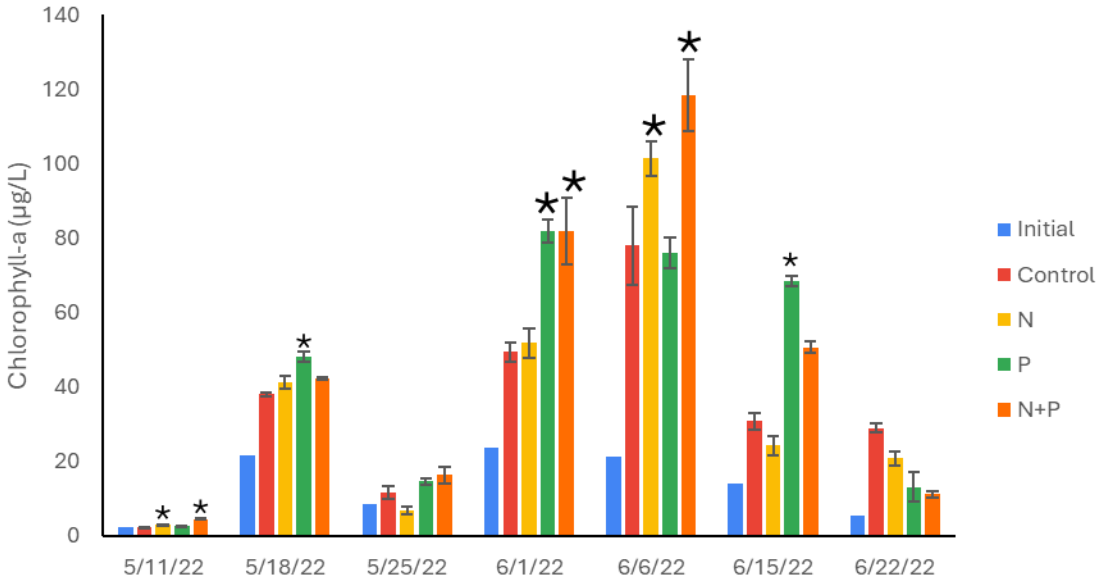


Figure 14. 2022 Jockey Creek water nutrient addition experiments. Stars represent significance.

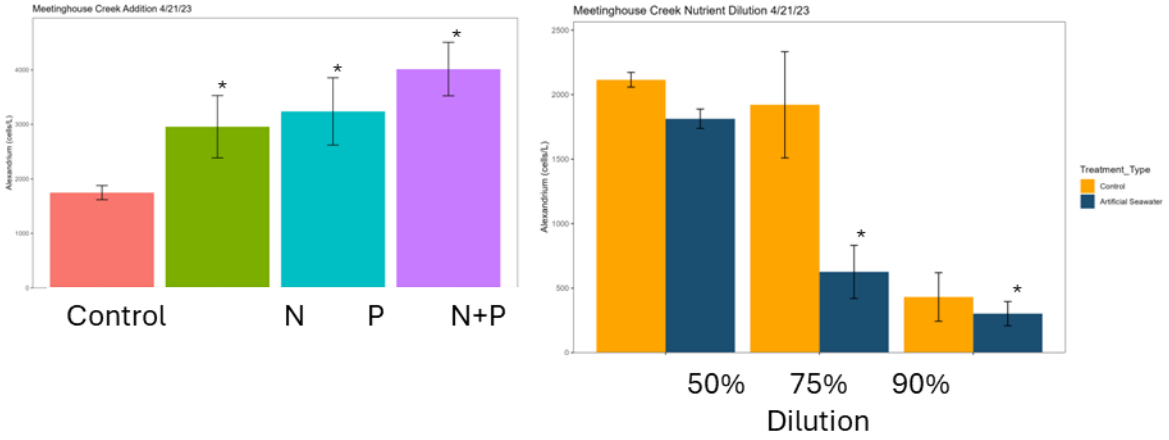


Figure 15. 2023 Meetinghouse Creek *Alexandrium* bloom water nutrient addition and dilution experiments. Stars represent significance.

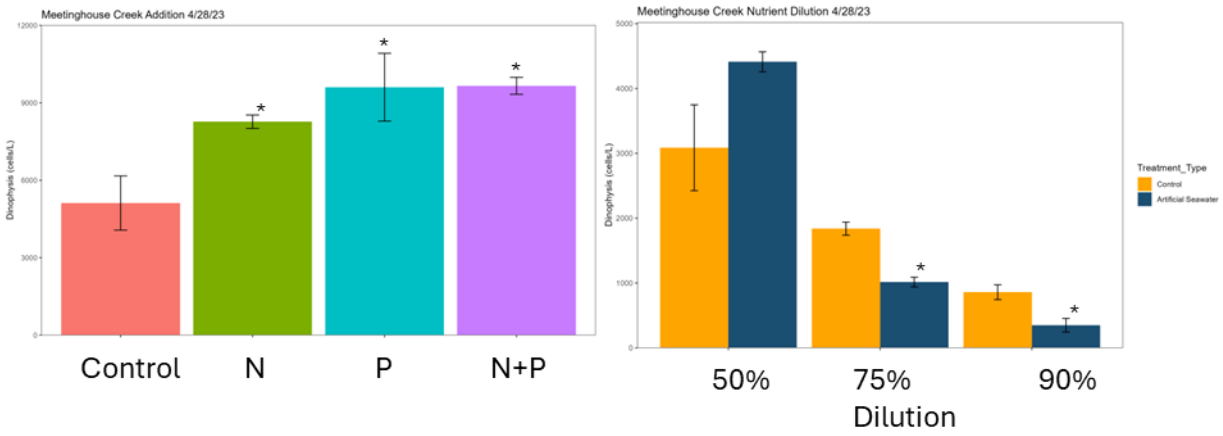


Figure 16. 2023 Meetinghouse Creek *Dinophysis* bloom water nutrient addition and dilution experiments. Stars represent significance.

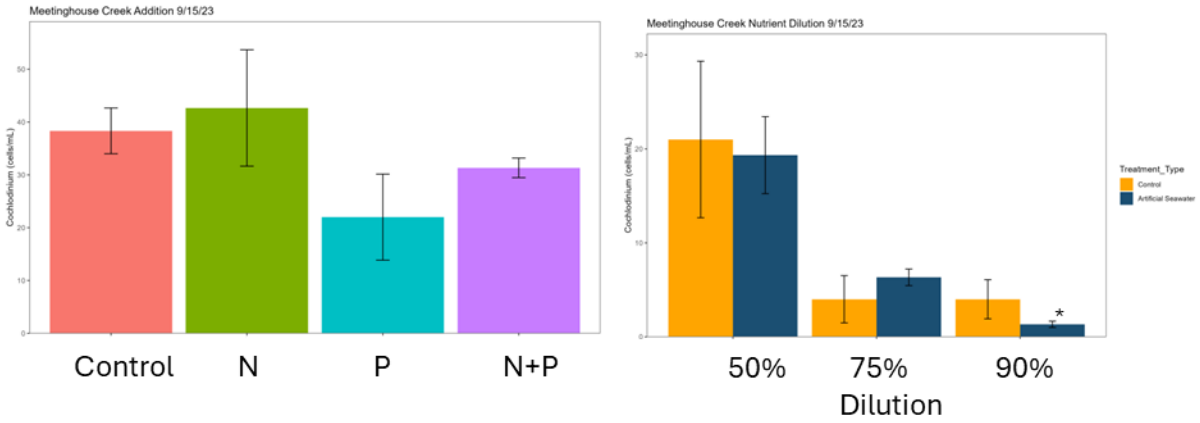


Figure 17. 2023 Meetinghouse Creek *Cochlodinium* bloom water nutrient addition and dilution experiments. Stars represent significance.

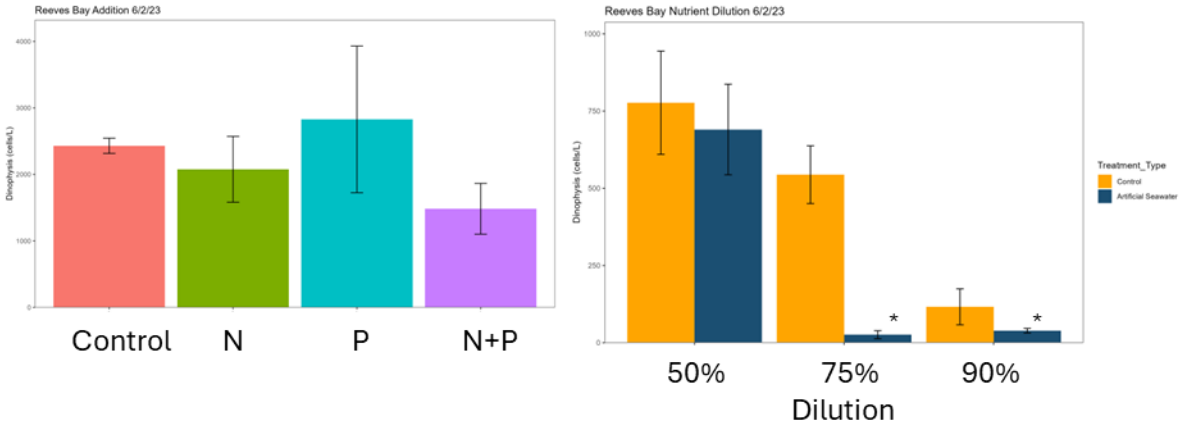


Figure 18. 2023 Reeves Bay *Dinophysis* bloom water nutrient addition and dilution experiments. Stars represent significance.

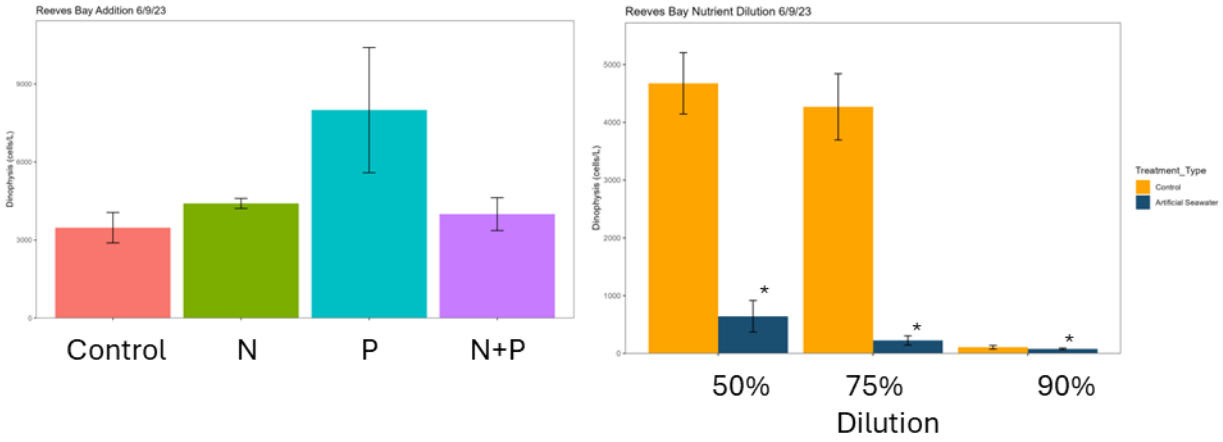


Figure 19. 2023 Reeves Bay *Dinophysis* bloom water nutrient addition and dilution experiments. Stars represent significance.

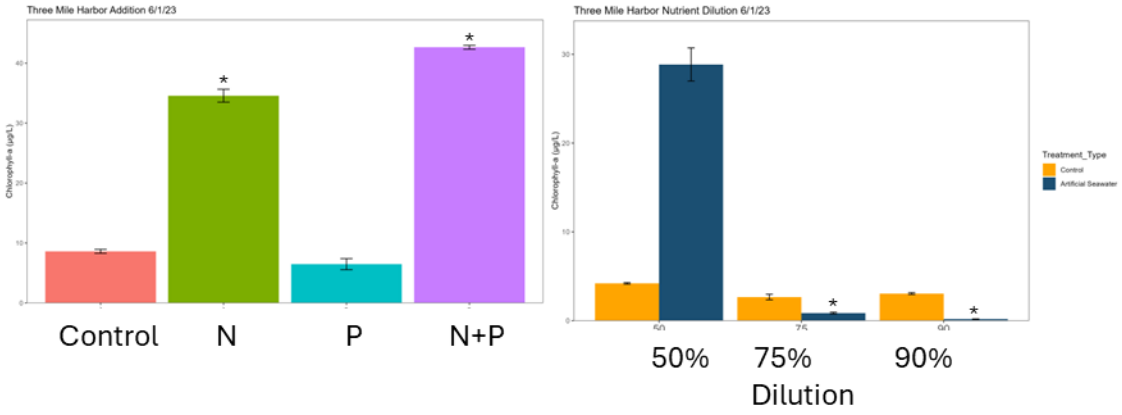


Figure 20. 2023 Three Mile Harbor *Dinophysis* bloom water nutrient addition and dilution experiments. Stars represent significance.

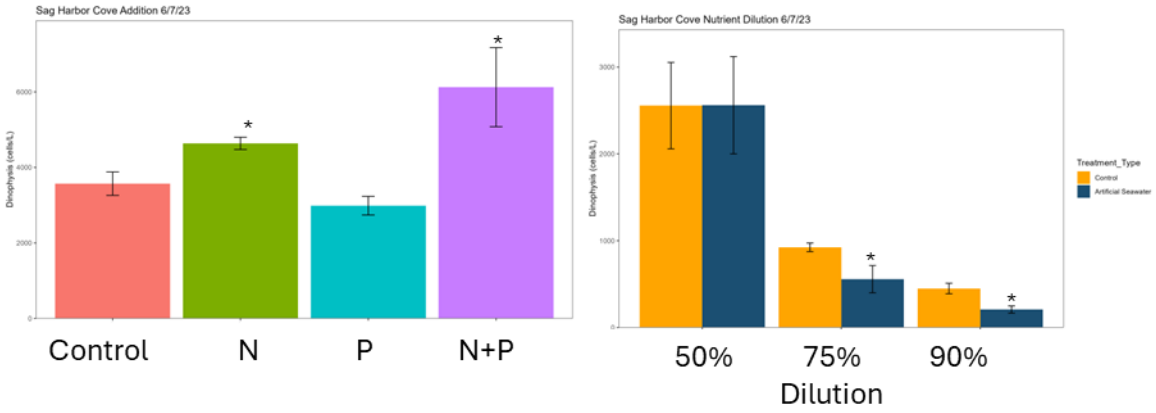


Figure 21. 2023 Sag Harbor Cove *Dinophysis* bloom water nutrient addition and dilution experiments. Stars represent significance.

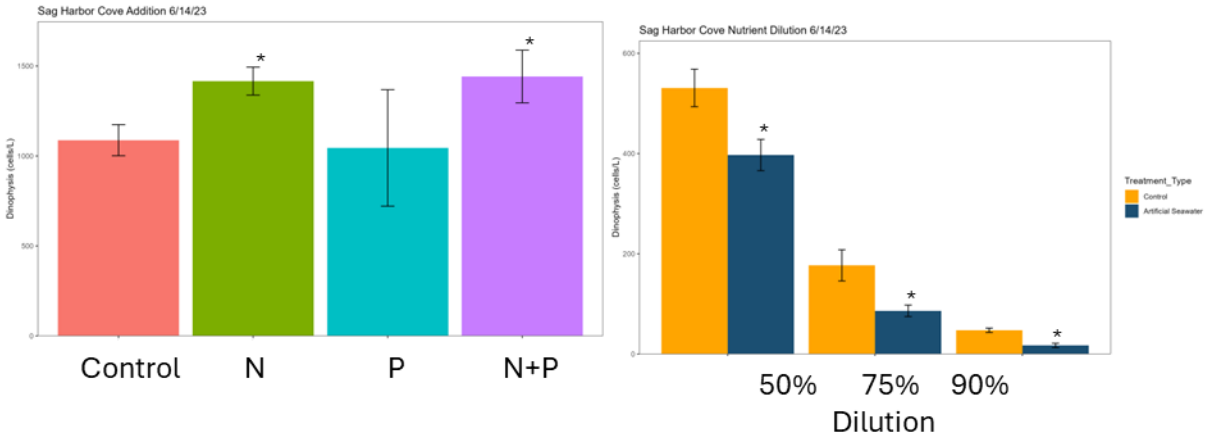


Figure 22. 2023 Sag Harbor Cove *Dinophysis* bloom water nutrient addition and dilution experiments. Stars represent significance.

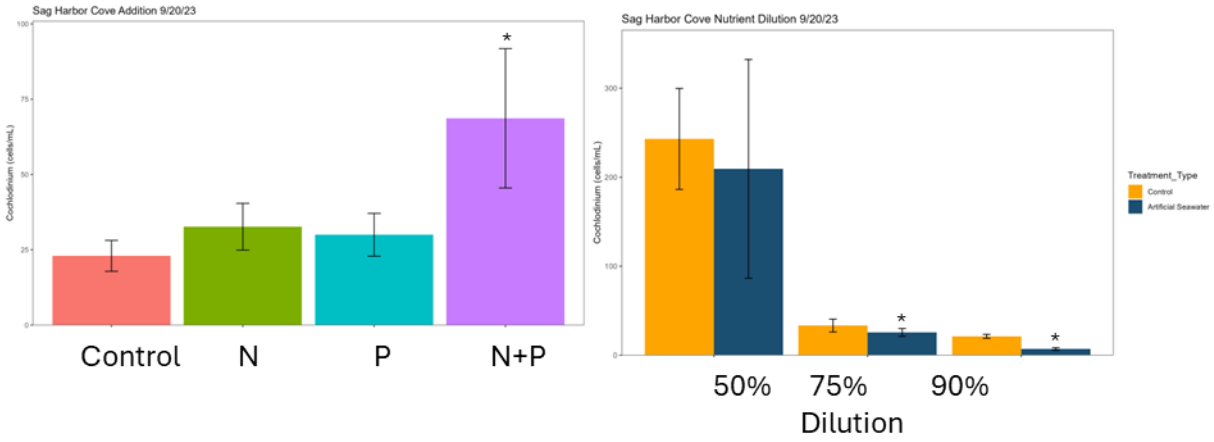


Figure 23. 2023 Sag Harbor Cove *Cochlodinium* bloom water nutrient addition and dilution experiments. Stars represent significance.

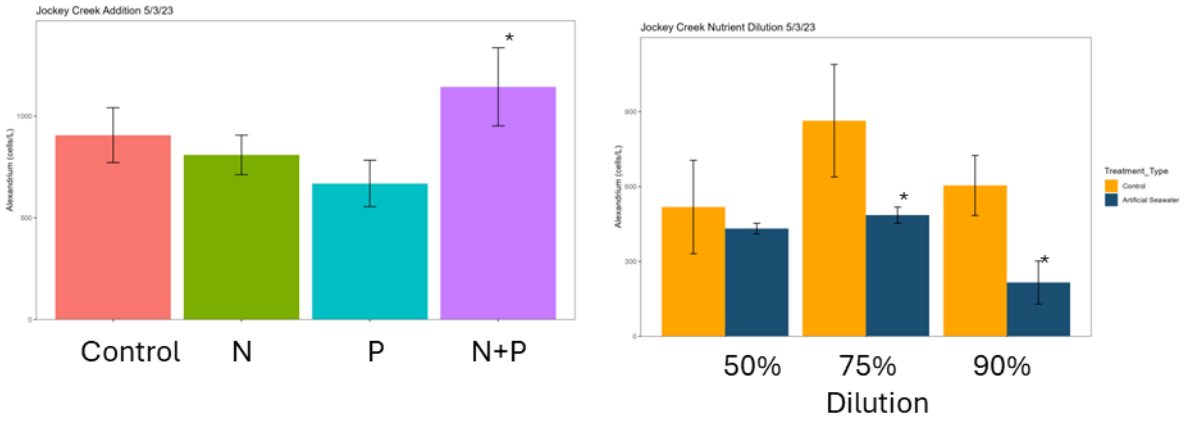


Figure 24. 2023 Jockey Creek *Alexandrium* bloom water nutrient addition and dilution experiments. Stars represent significance.

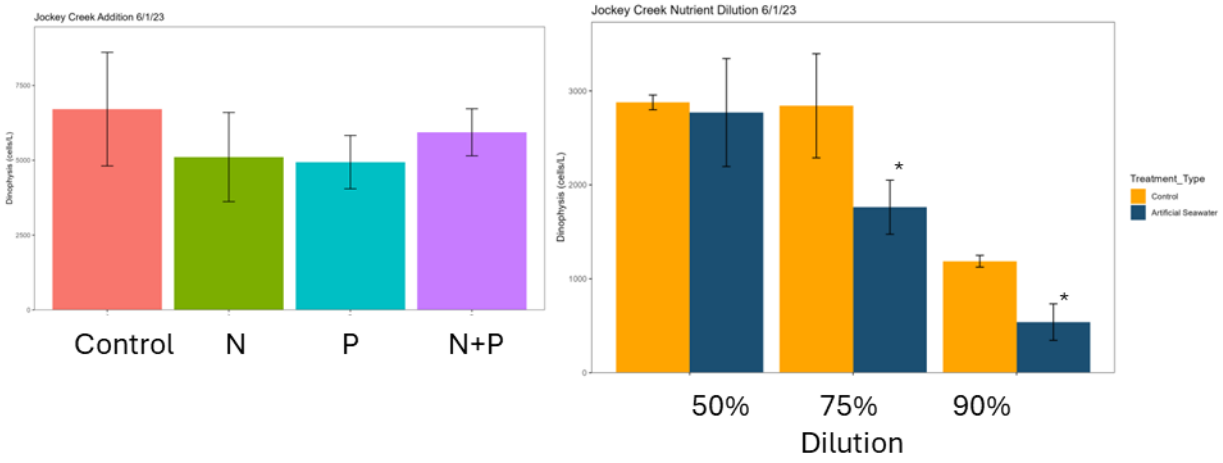


Figure 25. 2023 Jockey Creek *Alexandrium* bloom water nutrient addition and dilution experiments. Stars represent significance.