The effect of lower pH on phytoplankton growth in the Galapagos Archipelago

Trina Litchendorf

University of Washington

School of Oceanography

Box 357940

Seattle, WA 98195-7940

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Acknowledgements

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Non-technical Summary

Climate change is not the only issue facing us as a result of the ever-increasing levels of carbon dioxide introduced to the atmosphere by the burning of fossil fuels. Because the oceans absorb up to half of the annual output of CO_2, the oceans are acidifying. Already average ocean pH has dropped 0.1 units over the last 100 years to its current level of 8.1 and models suggest that ocean pH could further drop by up to 0.7 units within the next 300 years. This research focused on the effect of lower pH on marine phytoplankton in water samples taken from two locations around the Galapagos Islands. Water samples were incubated onboard for three days at three different pH levels: 8, 7 and 6. Iron was added to half of all the samples to determine the effect iron might have on phytoplankton growth at each pH level. After the incubation period, the samples were then filtered through three different-sized filters to determine the size distribution of phytoplankton and chlorophyll concentration, as well as the effect of pH change on each. I hypothesized that water samples collected from a region of presumed high iron and another from a region of low iron would have different starting assemblages of phytoplankton, which might respond then differently to changes in pH and iron addition. The results showed that marine phytoplankton are sensitive to pH and that different phytoplankton populations respond differently to shifts in pH.

Abstract

The oceanic uptake of antropogenically-produced CO_2 is predicted to continue to lower ocean pH in the future. As a result, iron will become more soluble. Both the lower pH and greater availability of iron could cause shifts in phytoplankton assemblages. To examine this, a series of shipboard incubation experiments were conducted at three different pH levels, ambient (approximately 8), 7 and 6, using water collected from a region of presumed low iron/low productivity, and a region of presumed high iron/high productivity from around the Galapagos Archipelago. Additional iron, in the form of $FeCl_3$, was added to half the samples at each pH level. Samples were incubated onboard at near in situ temperature for three days then size fractionated through 20-μm, 2-μm and 0.7-μm filters to determine chlorophyll *a* biomass and phytoplankton response to pH change and iron addition. Phytoplankton smaller than 20 μm dominated at both stations initially. After incubation at ambient pH, phytoplankton greater than 20 μm dominated in samples with and without added iron at both stations. Station 1 total chlorophyll concentrations were greater for the samples without added iron than those with added iron, though the difference was not statistically significant. Greater growth at ambient pH was observed at Station 2 than at Station 1, with concentrations of 13.8 μg L^{-1} and 9.9 μg L^{-1} for samples with and without added iron, respectively. Station 1, at pH of 7, showed no growth in contrast to Station 2 which exhibited increased growth at pH 7. For both stations a pH of 6 was too extreme resulting in the death of virtually all phytoplankton regardless of iron addition.

Introduction

The burning of fossil fuels has resulted in elevated levels of carbon dioxide in the atmosphere. The oceans absorb half of the annual output of CO_2, thus mitigating the rate of climate change (Hardy 2003). But the hydrolysis of CO_2 leads to a decrease in pH; already ocean pH has dropped by 0.1 units since pre-industrial times to its current value of approximately 8.1 (Orr et al. 2005). Modeling experiments suggest that ocean pH may be reduced by a further 0.7 units over the next 300 years assuming a scenario where CO_2 emission rates continue to increase until 2100 then begin to decrease as fossil fuel resources are diminished (Caldeira and Wickett 2003).

The acidification of the oceans as a result of CO_2 uptake is predicted to have deleterious effects on calcifying organisms such as corals and some phytoplankton species, for example the cocolithophorids (Orr et al. 2005). Very few studies, however, have examined the effect of pH on marine phytoplankton more generally. A recent review by Hinga (2002) found only 21 such studies and all of these studies focused only on coastal marine phytoplankton species. In these studies, phytoplankton were found to grow over a wide range of pH with some species being more tolerant of pH shifts while others were sensitive to changes of just 0.1 units (Fig. 1). This suggests that shifting pH may affect not only calcifying phytoplankton species but others as well. This has the potential to change the overall distribution of species at the base of the food web. Shifts in phytoplankton growth rates and community composition could impact not only marine life but also terrestrial life that depend on the oceans as a source of food.

Numerous studies have been conducted in the equatorial Pacific examining the effects of iron on phytoplankton growth and primary productivity. Iron enrichment experiments have supported the hypothesis that iron limitation in high-nutrient, low-chlorophyll (HNLC) regions

may limit phytoplankton growth (Martin et al. 1994, Gordon et al. 1998, Lindley and Barber 1998). The Galapagos Islands lie in the pathway of the Equatorial Undercurrent (EUC) and it is the upwelling of the EUC that creates the iron-rich environment that usually supports greater phytoplankton growth to the west of the islands (Gordon et al. 1997). The availability of iron for primary production is limited by the solubility of Fe(III) in seawater. At decreasing pH levels, the solubility of Fe(III) increases (Fig. 2) (Millero 1998, Liu and Millero 2002). Future acidification of the oceans could therefore potentially make iron more available to phytoplankton, which in turn could increase growth rates, assuming the effect of pH is not deleterious to the phytoplankton.

This research project examined the size-fractionated phytoplankton response to pH change. Picoplankton and nanoplankton (the ultraplankton) are known to dominate HNLC areas while diatoms and other normally rare taxa in HNLC regions (the microplankton) are known to dominate blooms following iron addition (Lindley and Barber 1998). I hypothesized that water collected from the region of presumed low iron would contain species assemblages of phytoplankton shifted to smaller sized compared to samples collected from the region of presumed high iron and that these different starting assemblages may respond differently to changes in pH and iron addition

Methods

Samples were collected from the *R/V Thomas G. Thompson* during the 12 – 20 January 2006 Galapagos Archipelago cruise. Water samples were collected from two sites (Fig. 3): Station 1 was selected as a region of presumed low productivity south of Isabela Island at 1°09’00” S, 91°00’00” W and Station 2, at 0°37’00” S, 91°19’00” W, was selected as a region of

presumed high iron and high productivity in Elizabeth Bay based on known upwelling of the EUC (Palacios 2002) and satellite imagery in Feldman et al. (1984).

Water samples were collected with a CTD rosette from the chlorophyll maximum as determined by the CTD fluorometer. Station 1 samples were collected from a depth of 24 meters on 13 February 2006 and Station 2 samples were collected from a depth of 18 meters on 14 February 2006. To minimize the presence of meso-zooplankton grazers, the water was discharged from the CTD Niskin bottles through a 209-μm Nitex mesh filter. Samples were collected from the CTD into five 10-liter carboys and one 20-liter carboy, all of which had been acid-washed prior to filling.

The pH of the seawater samples was lowered using 10% hydrochloric acid (HCl). For Station 1, initial pH was measured at 7.98 and 3.0 ml of 10% HCl was added to two of the 10-L carboys to achieve a final pH of 7.08; 11.5 ml was added to two other 10-L carboys to achieve a final pH of 6.04. The 20-L and remaining 10-L carboy were left at ambient pH. For Station 2, initial pH was measured at 7.85 and 2.8 ml of 10% HCl was added to two 10-L carboys to achieve a final pH of 7.05 and 11.1 ml was added to two of the other 10-L carboys to achieve a final pH of 6.03. One ml of a 20 μM $FeCl_3$ solution, in which ethylendiamintetraacetic acid (EDTA) had been added at a 1:1 ratio to $FeCl_3$ in order to complex the Fe ions, was then added to one 10-L carboy for each of the three pH levels to achieve a final concentration of 2 nM. A 2 nM concentration was selected to ensure the iron-amended samples exceeded naturally occurring levels based on a concentration of 1.3 nM measured in the upwelling area west of Isabela Island by Martin et al. (1994).

After pH and iron adjustment, water samples were decanted from the carboys into clear 2-L, acid-washed Nalgene bottles as follows: for each of the three pH levels there were three

bottles without Fe addition and three with Fe added. The samples at ambient pH provided a control for phytoplankton response to lower pH, while the samples with added Fe allowed for an estimation of phytoplankton response to increased Fe for a given pH. Three 250 ml samples from the 20-L carboy were analyzed at this time to determine an initial chlorophyll concentration prior to the start of the incubations.

After pH and iron adjustment, the samples were then incubated shipboard for 72 hours in flow-through incubators with a constant flow of seawater to maintain an ambient temperature. The incubators were also shrouded with mesh netting to reduce the ambient light by 50% to approximate light levels at the sampled depth in the water column. Upon completion of the 72-hour incubation the sample bottles were brought inside the lab and covered with black plastic while awaiting analysis. A final pH reading was taken of each sample prior to filtration and averaged for each pH and iron amendment. From each sample bottle, 250 ml was filtered successively through 20-µm, 2-µm and 0.7-µm filters. Each filter was then placed in an individual centrifuge tube and 10 ml of 90% acetone were added. Chlorophyll was extracted by placing the tubes in an ice water bath within a sonicator set at 120 Watts for 7 minutes to disrupt the cells and release their chlorophyll. Samples were refrigerated until analysis 24 hours later at which time they were placed in a centrifuge and spun for 10 minutes at 5000 rpm. Samples were then allowed to come to room temperature in darkness prior to chlorophyll and phaeopigment concentration analysis.

The fluorescence of each sample was measured by decanting an aliquot into a clean cuvette, which was then placed in a Turner TD900 fluorometer. If it was necessary to dilute a sample because of chlorophyll concentrations that exceeded the fluorometer's range, 6.3 ml of 90% acetone was placed in a cuvette with 0.7 ml of the sample extract to achieve a dilution factor of

10:1. After the initial reading, the sample was then acidified with 0.15 ml of HCl to release phaeopigments and the fluorescence again recorded. The chlorophyll and phaeophytin concentrations were calculated using the formula described by Lorenzen (1966).

$$[Chl\ a]\left(\mu g / L\right) = K\left(\frac{F_m}{F_m - 1}\right)\left(F_o - F_a\right)\frac{E_x}{V_F}D_F$$

$$[Phaeopigment]\left(\mu g / L\right) = K\left(\frac{F_m}{F_m - 1}\right)\left(F_m F_a - F_0\right)\frac{E_x}{V_F}D_F$$

where K (= 0.15112) is the calibration response factor, F_m (= 2.091) is the chlorophyll *a* acidification coefficient, F_0 is the fluorescence prior to acidification, F_a is the fluorescence after acidification, E_x is the sample extraction volume (L), V_F is the sample filtration volume (L), and D_F is the dilution factor. Final chlorophyll concentrations were calculated by averaging the size-fractionated results of each of the three sample bottles for a given pH and iron amendment; standard deviations were calculated for each average.

Results

Final averaged pH measurements and standard deviations for the sample bottles and overall change in pH are shown in Table 1. Station 1 samples were similar at each pH for both the iron amended and unamended samples, and showed an average increase of 0.07 – 0.13 units. At Station 2, the ambient samples, with an initial pH of 7.85, showed the greatest change with an increase of 0.59 and 0.29 units for the samples with and without added iron, respectively.

Individual size fractionated contributions and total chlorophyll *a* measurements for both

stations can be found in Table 2. At Station 1, initial time-zero total chlorophyll measurements were 1.08 μg L^{-1} ± 0.08. After the incubation period, at pH 8, the unamended samples had a greater total chlorophyll concentration than the samples with added iron. Total chlorophyll concentrations for samples without added iron were 5.6 μg L^{-1} ± 0.90 while they were 4.3 μg L^{-1} ± 1.98 for the samples with added iron. In both cases, phytoplankton larger than 20 μm dominated. Final total chlorophyll concentrations at pH 7 declined slightly in unamended samples but did not change much from initial values in iron treatments. At pH 6 in both cases, there were very low chlorophyll concentrations for both samples regardless of iron addition (Fig. 4).

At Station 2, time-zero total chlorophyll measurements were 0.97 μg L^{-1} ± 0.37. The pH 8 samples both showed significant growth over the initial samples with final, total chlorophyll concentrations of 9.9 μg L^{-1} ± 3.15 for the unamended samples and 13.8 μg L^{-1} ± 0.51 for the amended samples. As with the Station 1 samples, phytoplankton larger than 20 μm dominated. At pH 7, there was also an increase in total chlorophyll *a* concentration with 3.9 μg L^{-1} ± 2.00 measured for the unamended samples and 7.8 μg L^{-1} ± 1.98 measured for the samples with added iron. As with Station 1, pH 6 showed negligible chlorophyll for both the amended and unamended samples (Fig. 5).

The change in total chlorophyll concentration from initial concentration measurements is shown in figure 6 for each station location. At Station 1 for a pH of 8, the greater change occurred within the samples that did not have added iron with little to no change at a pH of 7 and a negative change in chlorophyll concentration at pH 6. The greatest growth for the incubation experiments occurred at Station 2 at pH 8, with the iron amended samples showing the greatest growth. In contrast to Station 1, the samples at pH 7 did show an increase in chlorophyll, with

greater growth occurring in the iron-amended samples. As with Station 1, pH of 6 showed a loss in chlorophyll concentration.

Discussion

Initial samples from both locations were dominated by small phytoplankton as is usually expected from a region of low iron. Station 2, however, was selected as a region of presumed high iron where large phytoplankton were expected to dominate. The station locations were selected based on circulation patterns around the islands and known upwelling of the EUC (Palacios, 2002) and satellite images in Feldman et al. (1984). Satellite data on the days of the sample collections were obscured by cloud cover; however, examination of satellite imagery taken on 11 January 2006 (Fig. 1A), two days before Station 1 was sampled, show low chlorophyll concentrations at Station 1 as is generally expected in low iron regimes. On 13 January 2006 (Fig. 7B) the day before Station 2 was sampled, low chlorophyll concentrations are also observed in Elizabeth Bay. Though low pigment does not necessarily correlate with low iron it is possible that concentrations were low as a result of low iron due to a previous bloom and subsequent grazing may have reduced the numbers of large phytoplankton down to the levels initially measured at Station 2.

The change in pH measured at the end of the incubation period can be attributed to the uptake of CO_2 by the phytoplankton in a closed system that is unable to equilibrate with the atmosphere (Hinga 2002). The magnitude of the change in pH is a reflection of the amount of photosynthesis that occurred during the incubation.

After the incubation period, phytoplankton greater than 20 μm dominated in samples from both locations in samples with and without iron. This suggests either that the samples may

have been contaminated with iron during collection, giving larger species an advantage, or that the increased light levels on the deck favored diatom growth. Perhaps most likely is that the 209-μm Nitex mesh filter used during the sample collection filtered out the larger grazers but left smaller ones behind to graze down the smaller phytoplankton.

Though the unammended samples at Station 1 and pH 8 had greater chlorophyll concentrations than the samples with added iron, the difference did not appear to be statistically significant, suggesting that iron was not a limiting factor. Since it was not possible to collect samples in such a way as to completely avoid iron contamination, or determine the starting levels of iron in the samples, it is conceivable that the samples that were meant to be without iron were accidentally contaminated. At Station 2, the increase in growth rates in the samples with added iron at pH 8 and 7 suggest that this location was iron-limited at the time of sampling.

At Station 1 the phytoplankton species were especially sensitive to pH change, since little to no growth occurred at pH 7. Also, there was a near-complete die-off of all phytoplankton at pH 6. However at Station 2, the starting assemblage of phytoplankton was more tolerant to pH changes, with growth more than tripling in the samples with no added iron and an approximate seven-fold increase in samples with added iron at pH 7. As for Station 1, a pH of 6 was too extreme, resulting in the death of the phytoplankton. The tolerance to lower pH by phytoplankton at Station 2 suggests that the disparity of final chlorophyll concentrations between stations 1 and 2 may be a reflection of the differences in species composition at the two locations, considering that the initial concentrations at both locations were essentially equal. Both the large and the smaller phytoplankton from this location exhibited a greater growth rate and tolerance for pH shift than the phytoplankton found at Station 1. Investigations by Snow (2006) on phytoplankton species composition in the region around Station 2 found that the

diatoms *Psuedo-nitshia / Nitzschia* and *Citoserous* were most abundant; however, there were no identifications made in the region around Station 1 in that study. It most likely that the increases seen at pH 8 for both stations in the greater than 20 μm size fraction can be attributed to diatoms.

Conclusion

This study demonstrated that different open-ocean phytoplankton populations respond differently to pH change. A pH of 6 was clearly too acidic for any of the phytoplankton while some species apparently were better able to tolerate a pH of 7. Though phytoplankton species were not identified within this study, this suggests an area for further investigation. Though the effect of pH on iron solubility in these pH experiments was not determined, the results of Station 2 demonstrate that the addition of iron had a measurable effect on phytoplankton growth at both a pH of 8 and 7. It is likely that the effect of any small increase in iron solubility as a result of lower pH is dwarfed by the negative effect of lower pH on phytoplankton growth.

Table 1.

Final averaged pH measurements and standard deviations taken after the incubation period and the change in pH from initial measurements.

	pH 8 no Fe	pH 8 with Fe	pH 7 no Fe	pH 7 with Fe	pH 6 no Fe	pH 6 with Fe
Station 1	8.05 ± 0.04	7.99 ± 0.03	7.17 ± 0.02	7.17 ± 0.01	6.16 ± 0.01	6.15 ± 0.01
Δ pH	0.07	0.01	0.10	0.10	0.13	0.12
Station 2	8.14 ± 0.07	8.43 ± 0.06	7.26 ± 0.06	7.39 ± 0.09	6.23 ± 0.01	6.18 ± 0.04
Δ pH	0.29	0.58	0.21	0.34	0.20	0.15

Table 2.

Chlorophyll concentration averages, in μg L^{-1}, showing sized-fractionated contributions, total chlorophyll measurements and standard deviations for sample averages for Stations 1 (St1) and 2 (St2).

St1 Size fraction	T_o	pH 8 no Fe	pH 7 no Fe	pH 6 no Fe
> 20 μm	0.08 ± 0.01	3.71 ± 0.81	0.07 ± 0.36	0.004 ± 0.001
20 μm to 2 μm	0.46 ± 0.03	1.11 ± 0.36	0.36 ± 0.21	0.012 ± 0.002
2 μm to 0.7 μm	0.54 ± 0.07	0.73 ± 0.16	0.36 ± 0.20	0.012 ± 0.004
Total	1.08 ± 0.08	5.55 ± 0.90	0.79 ± 0.46	0.028 ± 0.006

St1 Size fraction	T_o	pH 8 with Fe	pH 7 with Fe	pH 6 with Fe
> 20 μm	0.08 ± 0.01	2.68 ± 1.91	0.06 ± 0.01	0.004 ± 0.001
20 μm to 2 μm	0.46 ± 0.03	1.15 ± 0.47	0.65 ± 0.23	0.013 ± 0.005
2 μm to 0.7 μm	0.54 ± 0.07	0.45 ± 0.21	0.40 ± 0.23	0.005 ± 0.012
Total	1.08 ± 0.08	4.28 ± 1.98	1.11 ± 0.33	0.022 ± 0.013

St2 Size fraction	T_o	pH 8 no Fe	pH 7 no Fe	pH 6 no Fe
> 20 μm	0.19 ± 0.01	8.34 ± 3.14	1.62 ± 1.34	0.013 ± 0.008
20 μm to 2 μm	0.35 ± 0.03	1.00 ± 0.23	1.01 ± 0.55	0.035 ± 0.008
2 μm to 0.7 μm	0.43 ± 0.02	0.53 ± 0.24	1.24 ± 1.38	0.057 ± 0.002
Total	0.97 ± 0.04	9.87 ± 3.15	3.87 ± 2.00	0.105 ± 0.011

St2 Size fraction	T_o	pH 8 with Fe	pH 7 with Fe	pH 6 with Fe
> 20 μm	0.19 ± 0.01	12.49 ± 0.49	4.39 ± 1.84	0.014 ± 0.014
20 μm to 2 μm	0.35 ± 0.03	0.69 ± 0.06	2.18 ± 0.48	0.032 ± 0.007
2 μm to 0.7 μm	0.43 ± 0.02	0.64 ± 0.13	1.21 ± 0.35	0.039 ± 0.014
Total	0.97 ± 0.04	13.82 ± 0.51	7.78 ± 1.93	0.085 ± 0.021

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Figure Captions

Figure 1. The effect of pH on growth rates for 40 different species of marine phytoplankton. Bars represent the range of pH for maximum growth rate, growth, substrate uptake, production or photosynthesis/respiration ratio for each species. An * indicates there was no data below that pH so maxima may extend below that value. Data was compiled from 17 different studies. From Hinga (2002).

Figure 2. The solubility of Fe(III) in seawater (S = 36) as a function of pH at various temperatures. From Liu and Millero (2002).

Figure 3. Location of the two sampling sites. Station 1 is at 1°09'00" S, 91°00' 00" W. Station 2 is at 0°37'00" S, 91°19'00" W.

Figure 4. Size-fractionated chlorophyll for Station 1 incubation experiments samples A.) without and B.) with added iron. Error bars represent the standard deviation of averages samples.

Figure 5. Size-fractionated chlorophyll for Station 2 incubation experiments samples A.) without and B.) with added iron. Error bars represent the standard deviation of averages samples.

Figure 6.

Figure 7. SeaWiFS satellite images of chlorophyll concentration around the Galapagos Islands during the time of the research cruise. Red areas indicate areas of high chlorophyll concentration

and blue indicates regions of low chlorophyll. Black areas are areas of cloud cover where no data is available. A red circle has been drawn on each image to show the location of the sample sites. A.) Image taken on January 11, 2006. B.) Image taken on January 13, 2006.

From http://oceancolor.gsfc.nasa.gov

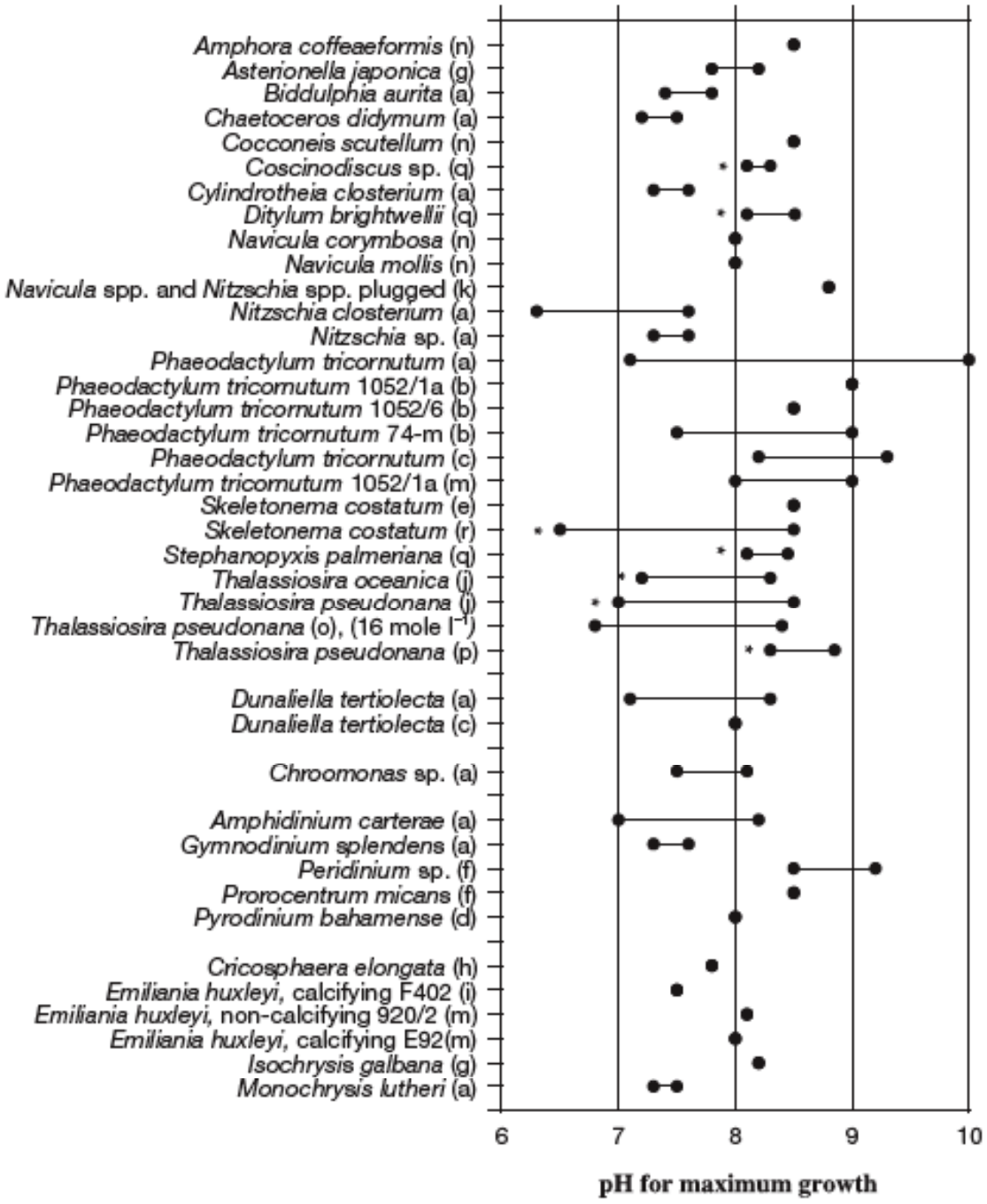

Figure 1.

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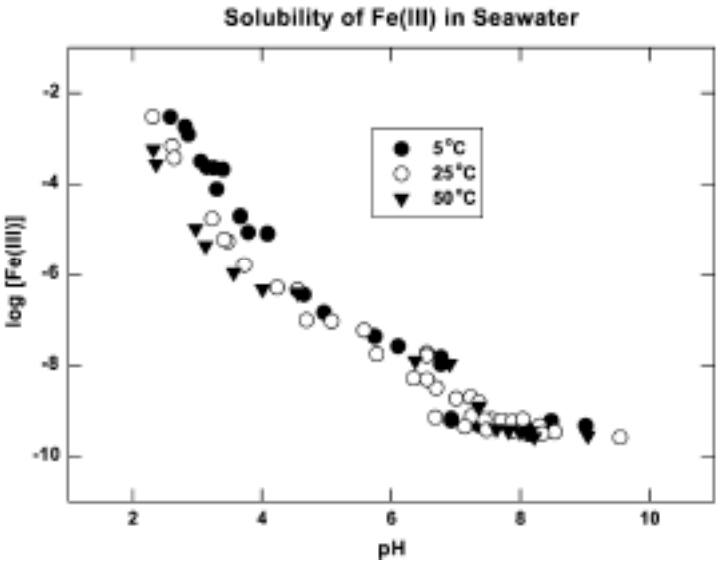

Figure 2.

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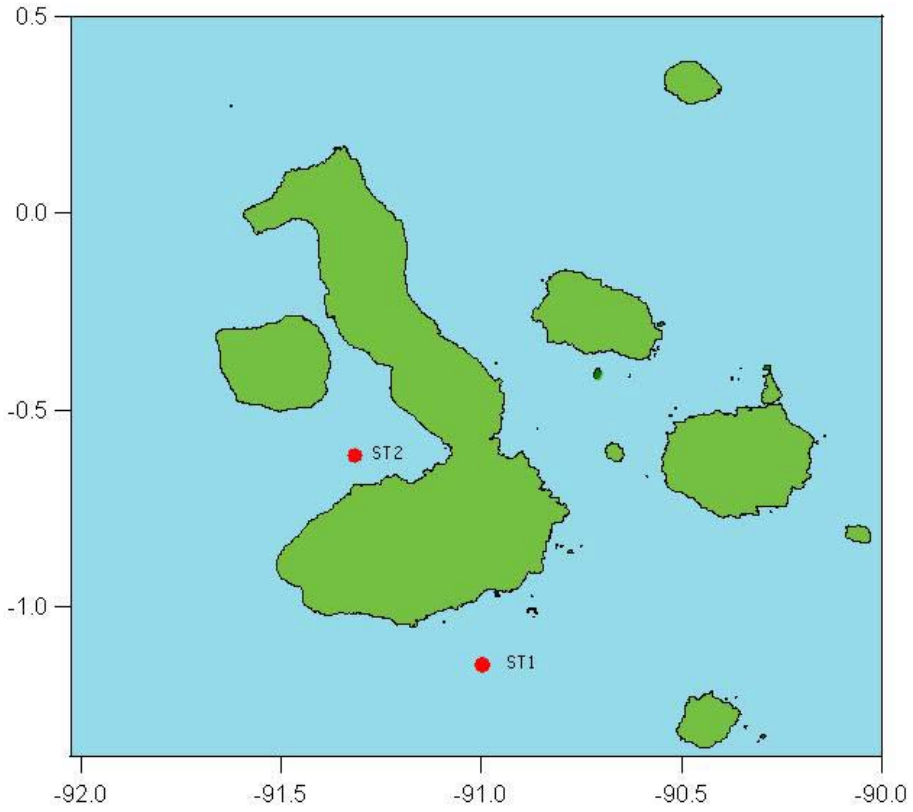

Figure 3.

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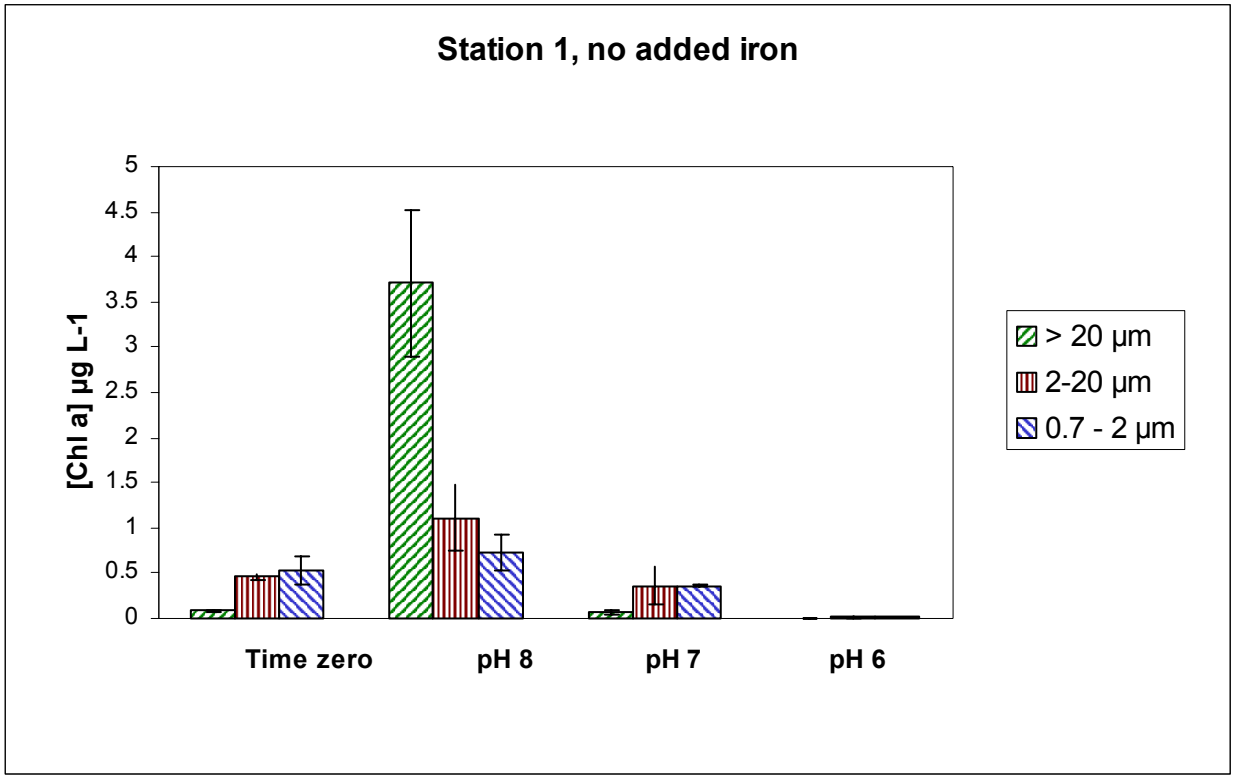

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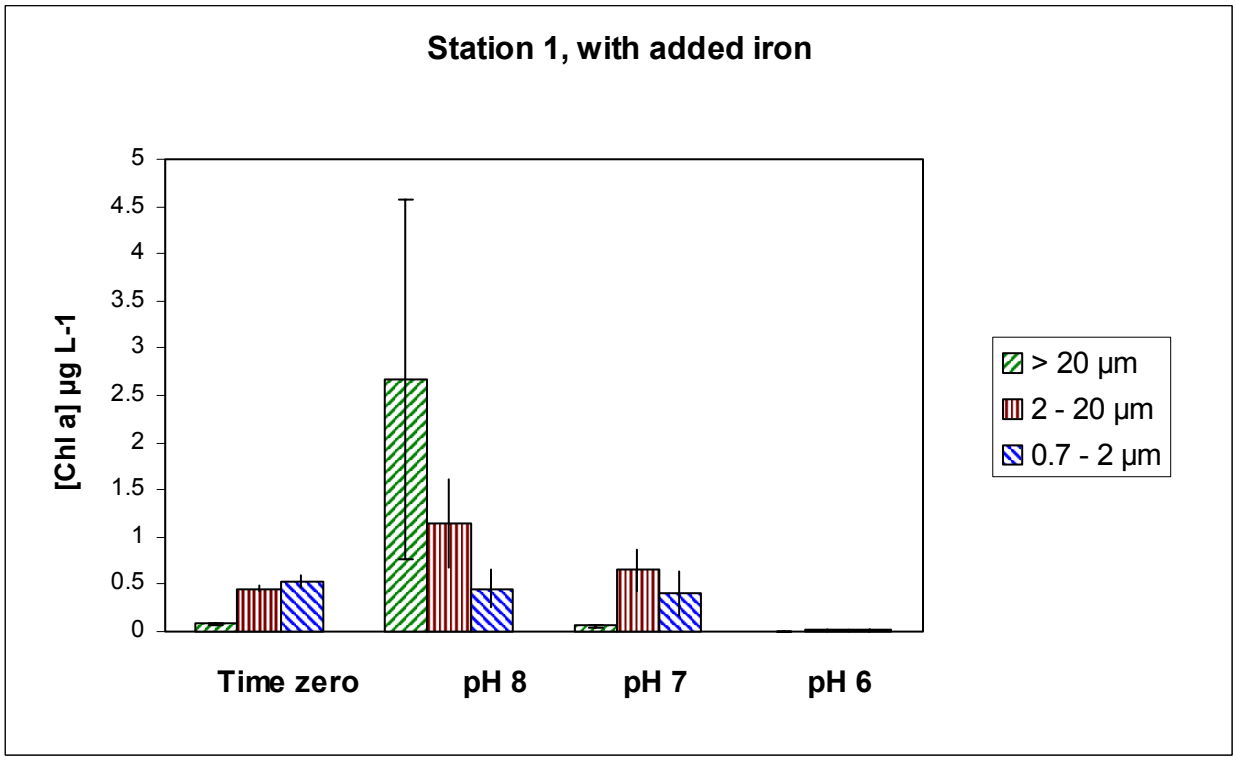

Figure 4.
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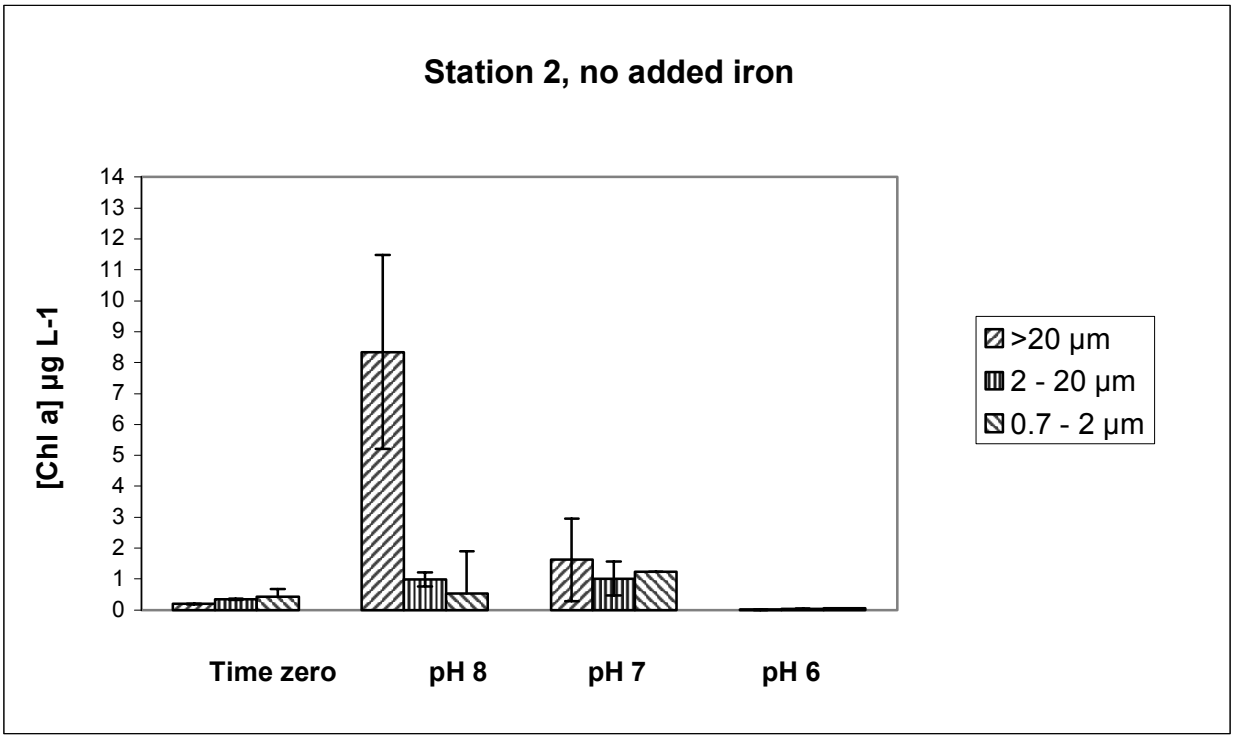
A.)



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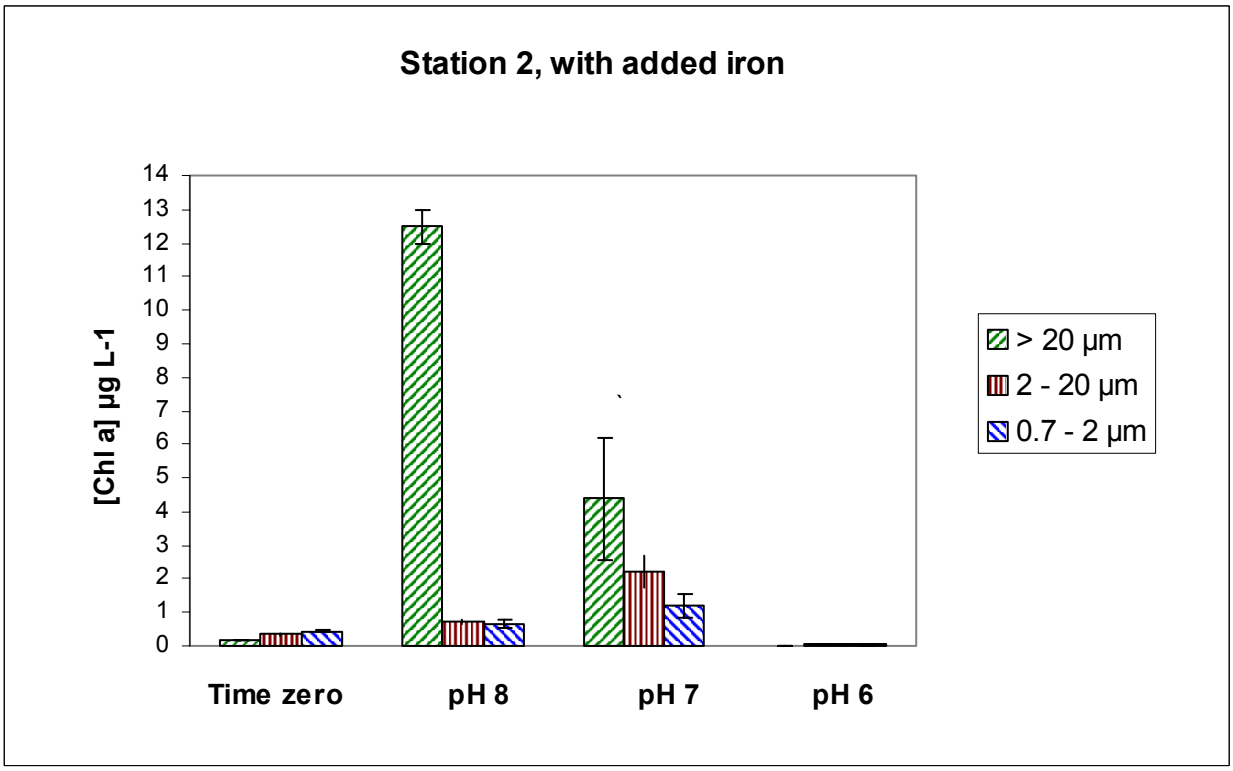

Figure 5.
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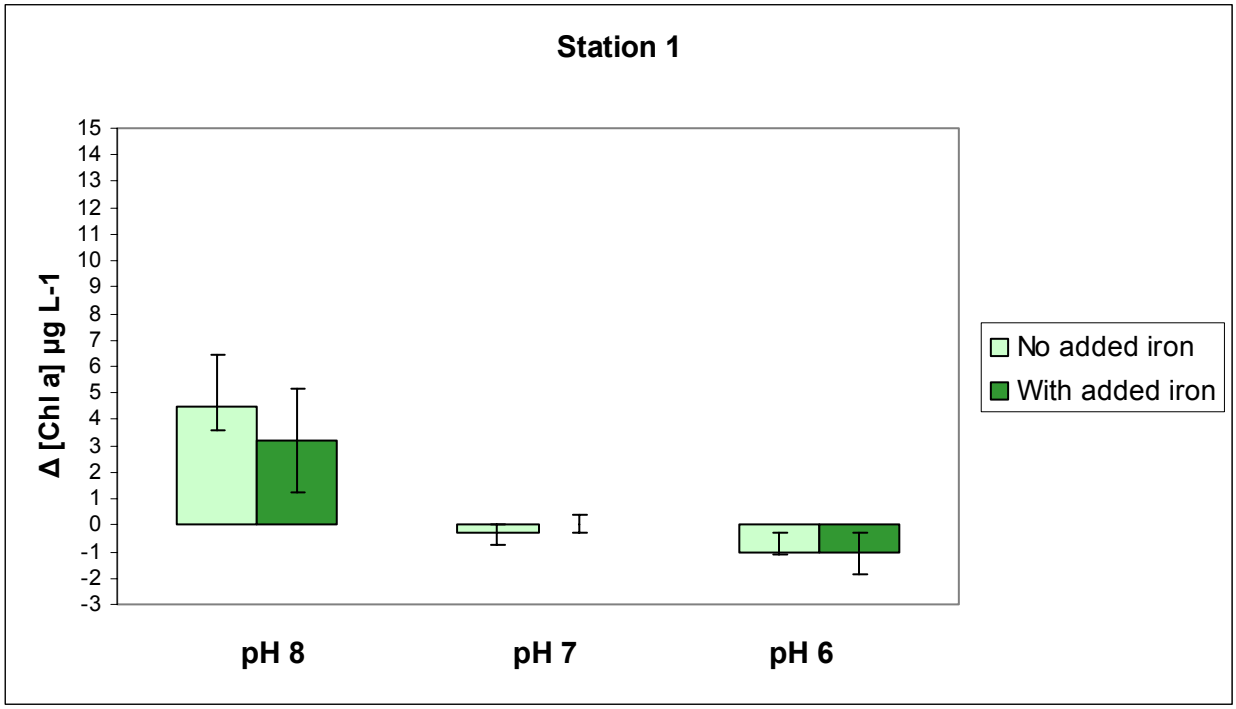

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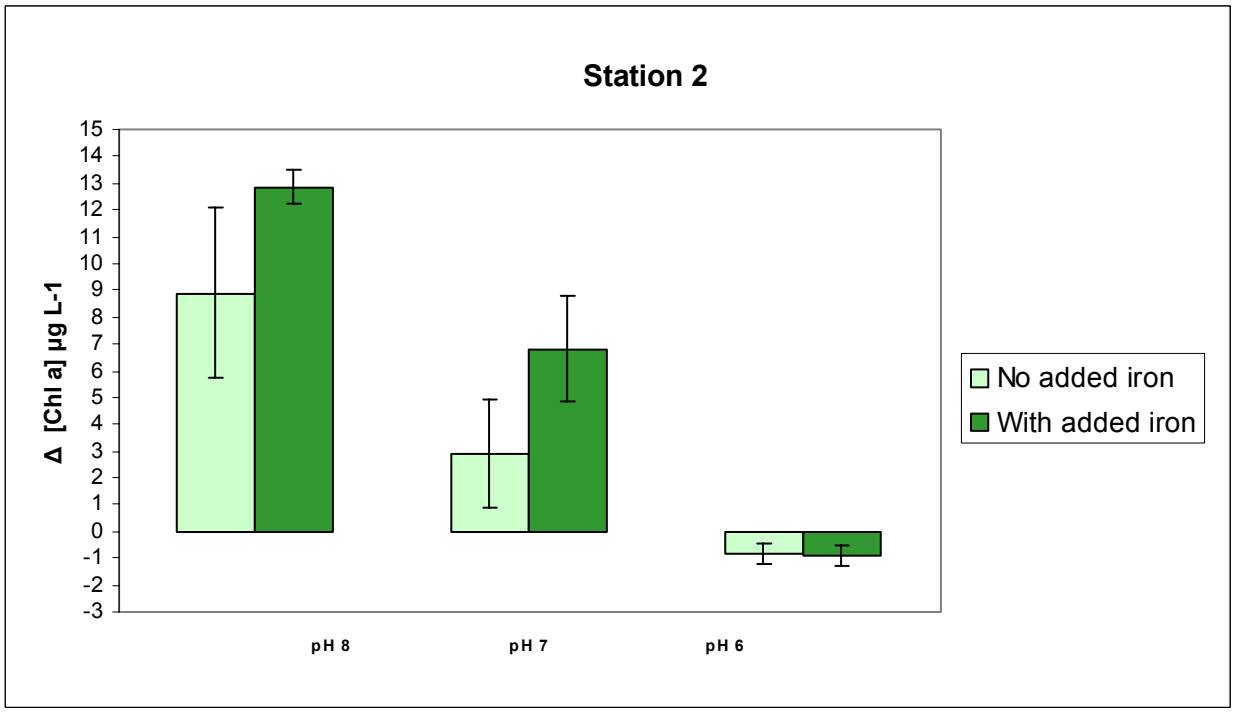

Figure 6.
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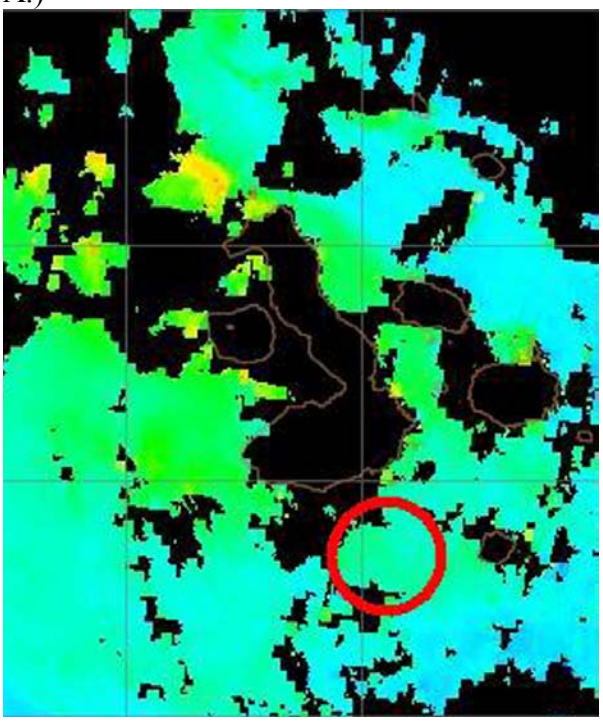
A.)



B.)

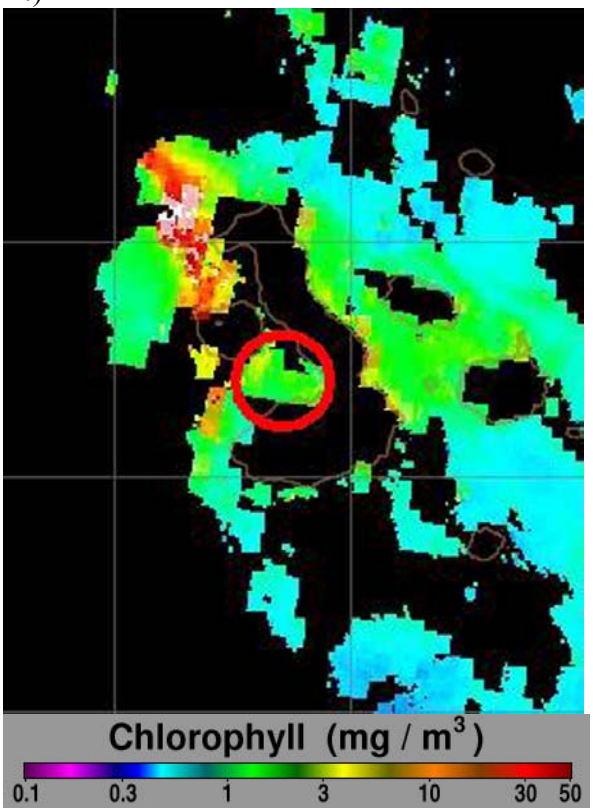


Figure 7.
Trina Litchendorf