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Changes In Net Ecosystem Production Over The Past 40 Years In Arctic Tundra Ponds Near Barrow, Alaska: Application Of Historic And Modern Techniques

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CHANGES IN NET ECOSYSTEM PRODUCTION OVER THE PAST 40
YEARS IN ARCTIC TUNDRA PONDS NEAR BARROW, ALASKA:
APPLICATION OF HISTORIC AND MODERN TECHNIQUES

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2013

DEDICATION

I dedicate this to all of those who supported me throughout this humbling experience. To God my creator, to my very understanding family and friends and I especially dedicate this to my husband Leo for his encouragement and unwavering belief in me.

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YEARS IN ARCTIC TUNDRA PONDS NEAR BARROW, ALASKA:
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by

NICKOLE ANN MILLER, B.S.

THESIS

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ABSTRACT

Arctic environments have gained interest recently due to their sensitivity to climate change. As warming has created longer growing seasons, extended ice-free periods as well as permafrost thaw, the production in freshwater ecosystems has the potential to be greatly impacted. It is hypothesized that as climate change and warming occurs, increases in primary production will occur and ponds will become carbon sinks. Net ecosystem production (NEP) was determined using phytoplankton and periphyton samples collected weekly during the growing season (June – August) from arctic tundra ponds near Barrow, Alaska. Enrichment with ^{14}C was used to determine both weekly photosynthetic rates and maximum rates of photosynthesis measured at multiple temperatures (8, 14 and 20°C) and light levels. All data collected from these experiments was compared to data collected in the 1970s. Free water metabolism was determined using a YSI logger installed in the pond throughout the growing seasons (2010-2). While there was no significant difference among phytoplankton NEP throughout the growing season in 1970-2 as compared to 2011-12, NEP was slightly higher during the latter half of the season in 2011-2. Photosynthesis – Irradiance (P-I) curves in 2012 did not reach maximum levels of photosynthesis at all temperature for phytoplankton or benthic algae; however, increases in maximum rates of photosynthesis appeared to have occurred. Free water metabolism showed positive net ecosystem production throughout the growing season in 2010-12 indicating the system to be net autotrophic. NEP, measured using both ^{14}C and free water metabolism, increased substantially at a threshold level of chlorophyll that was regularly exceeded in 2008-12, but rarely observed in the 1970s (1.19-1.30 $\mu\text{g/L}$). As the growing season continues to increase in length due to climate change, these results suggest that algal primary production in arctic tundra ponds will increase and tundra ponds may become vital carbon sinks in northern latitudes.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	v
ABSTRACT	vi
TABLE OF CONTENTS	vii
LIST OF FIGURES	viii
INTRODUCTION	1
METHODS	8
Study site	8
Quantification of net ecosystem production	9
Chlorophyll-a biomass.....	13
Photosynthesis – Irradiance curves.....	14
Free water metabolism (FWM)	14
Statistical analysis.....	17
RESULTS	18
Changes in NEP over time.....	18
Photosynthesis – Irradiance curves.....	22
Environmental drivers of primary production over the past 40 years	25
NEP measured using free water metabolism	28
Comparison between current years.....	32
Environmental drivers of free water metabolism	34
Environmental drivers of planktonic chlorophyll levels	35
Comparison of methods.....	38
Implication of Arctic freshwater production	40
DISCUSSION.....	42
Future research areas	48
CONCLUSION.....	50
REFERENCES	51
APPENDIX A.....	55
VITA.....	58

LIST OF FIGURES

Figure 1: Diagram of a representative relationship between net photosynthetic rate and irradiance (Falkowski and Raven, 2007).	3
Figure 2: IBP pond location near Barrow, Alaska. (Lougheed et.al, 2011)	8
Figure 3: Satellite image of IBP Ponds B, C, E used in study (Vargas, 2011).	9
Figure 4: 2 μCi of ^{14}C - NaHCO_3 being added to light and dark BOD bottles	11
Figure 5: Beckman Liquid Scintillation Counter (Beckman LS-5801) located in the Bioscience building at the University of Texas at El Paso.	11
Figure 6: Quench correction (2012 and 2011) relating to counts per minute (CPM): disintegrations per minute (DPM) ratio to the H# of the sample measured by Beckman LS-5801. A larger H# indicates a higher quench of the sample.	12
Figure 7: Oxygen saturation in water at a given temperature. $R^2 = 0.9999$	16
Figure 8: Weekly mean of phytoplankton production from IBP Pond C from historic (1970-3) and current (2011-12) analyses.	19
Figure 9: Yearly comparisons of weekly means phytoplankton production from IBP Pond C.	20
Figure 10: Benthic production ($\text{mgC}/\text{m}^2/\text{h}$) from IBP Pond C and E 2011 and 2012 (top). Benthic production ($\text{mgC}/\text{m}^2/\text{h}$) 1972 (bottom).	21
Figure 11: Photosynthesis-irradiance curves at three temperatures for: phytoplankton in IBP Pond A on July 3, 1973(top left), phytoplankton in IBP Pond C on July 9, 2012 (top right), benthic algae in IBP Pond B on July 3, 2012 (bottom left) and benthic algae in IBP Pond E on July 9, 2012 (bottom right).	23
Figure 12: Photosynthesis-irradiance curves for benthic algae in IBP Pond E averaged for 4 dates over the growing season of 2012 at 8, 14, and 20°C and four increasing light intensities.	24
Figure 13: Photosynthesis-irradiance curves for phytoplankton in IBP Pond C averaged for 4 dates over the growing season of 2012 at 8, 14, and 20°C and four increasing light intensities.	24
Figure 14: Regression tree of weekly phytoplankton NEP measured using ^{14}C radioisotopes from years 1970-73 and 2011-12.	26
Figure 15: Regression tree of weekly benthic NEP measured using ^{14}C radioisotopes in 2011 and 2012.	27
Figure 16: Regression tree of benthic NEP measured using ^{14}C radioisotopes in the 1970s.	27
Figure 17: Daytime NEP ($\pm 1\text{SE}$) averaged for summers of 2010-12.	28

Figure 18: Mean gross primary production (GPP), respiration (R) and net ecosystem production (NEP) averaged for August 2010-12, when sunsets occurred in Barrow, AK.	29
Figure 19: Mean Respiration (+/- 1 SE) for August 2010-12, when sunsets occurred in Barrow, AK.....	30
Figure 20: Mean gross primary production (+/- 1 SE) for August 2010-12, when sunsets occurred in Barrow, AK.....	30
Figure 21: Mean gross primary production (+/- 1 SE) for August 2010-12, when sunsets occurred in Barrow, AK.....	31
Figure 22: Mean diurnal flux of dissolved oxygen on similar dates in mid-June, mid-July and mid-August for 2010-12.....	31
Figure 23: Net ecosystem production comparisons among years 2010, 2011 and 2012 during August when sunsets occurred in Barrow, Alaska.....	32
Figure 24: Comparison of mean weekly chlorophyll measured using the YSI in 2010-2012.	33
Figure 25: Regression tree of daily NEP from IBP Pond C 2010-2 during August when sunsets occurred. $R^2 = 0.438$	34
Figure 26: Regression tree of FWM measured NEP at the end of the season when sunset occurred. $R^2=0.213$	35
Figure 27: Regression tree of weekly mean YSI measured chlorophyll concentrations in IBP Pond C for years 2010-2. $R^2= 0.51$	36
Figure 28: Regression tree of acetone-extracted Chlorophyll ($\mu\text{g/L}$) for IBP ponds B, C, and E from 1970-2 and 2010-2. $R^2= 0.27$	37
Figure 29: Regression tree of acetone extracted Chlorophyll ($\mu\text{g/L}$) from ponds along a gradient of nutrient enrichment in 2010-2. $R^2=0.214$	37
Figure 30: Comparison of methods used to measure production in IBP Pond C 2011-12: planktonic NEP determined via radioisotopes versus free water metabolism	38
Figure 31: Comparison of methods used to measure production in IBP ponds 2011-12: benthic NEP determined using radioisotopes versus free water metabolism	39
Figure 32: Comparison of methods of measuring CHL-a, using the optical sensor on the YSI and extraction in acetone, with concentrations calculated using Strickland and Parsons (YEAR) formula. $R^2=0.6236$	40
Figure 33: Comparison of weekly average CHL-a concentrations in 1970-3 and 2008-12 to threshold CHL-a values found by regression trees of NEP measured by ^{14}C radioisotope ($1.19 \mu\text{g/L}$) and FWM techniques ($1.3 \mu\text{g/L}$).	41

Figure34: Mean (\pm 1 standard error (SE)) phytoplankton chlorophyll-a biomass in IBP ponds B, C, and E for 1970-1973 vs 2008-2012 (from Hernandez et al. In prep).....	42
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INTRODUCTION

Interest in the Arctic environment has increased in recent history because of its sensitivity to climate change and the accelerated rate of warming in the region (Callaghan et al. 2004). Warming and associated lengthened snow- and ice-free periods (Stone et al., 2002) have the capacity to impact growing season length for primary producers (e.g. Smol et al. 2005). In particular, continuous daylight in summer allows for terrestrial primary producers to act as carbon sinks during the summer growing season; however, thawing of permafrost due to climate warming may reverse this trend (Schuur et al., 2009).

Increases in Arctic temperatures are causing warming and thawing of permafrost (Osterkamp, 2005; Zhang et al. 2005). Several authors have suggested that this thaw has led to increased inputs of nutrients such as nitrogen, phosphorus and dissolved organic carbons into Arctic freshwater ecosystems (Hobbie et al., 1999; Frey and Smith 2005; Schindler and Smol 2006; Anderson and Stedmon 2007; Frey and McLelland, 2009; Loughheed et al. 2011). Other recently observed changes in Arctic freshwater ecosystems include disappearance of ponds and lakes (Smith et al., 2005; Smol & Douglas, 2007), alterations to food web structure (Hobbie et al., 1999) and changes in biodiversity and the geographic range of species (Wrona et. al., 2006). Despite these recent studies, the impact of both warming and nutrient inputs into Arctic freshwaters, especially on rates of primary production and potential for carbon uptake, remains poorly understood.

The arctic contains many diverse freshwater ecosystems (Wrona et al., 2007), which are extremely important to many plants, animals and microorganisms (e.g. Smol et al., 2005, Cazzanelli et al., 2012). Freshwater environments in arctic regions are

characterized by low water temperatures and nutrient concentrations, thus preventing high levels of photosynthetic production from occurring (Markager et al., 1999). However, as temperatures are increasing in the Arctic, photosynthetic production could also increase. In fact, Stanley & Daley (1976) predicted that algae in the IBP ponds would reach maximum rates of production at 14°C for phytoplankton and 20°C for periphyton; these temperatures were rarely achieved in the 1970s yet warmer temperatures have been observed in recent studies (e.g. Loughheed et al. 2011).

Photosynthesis – Irradiance (P – I) curves are useful in determining the light-saturated or maximum rate of photosynthesis (P_{\max}) values of primary producers (Macedo, 2002; Hill & Boston, 1991; Kalff, 2002). A P – I curve is represented in (Figure 1), where photosynthesis increases along a gradient of light intensity and ultimately plateaus at P_{\max} . P – I curves can not only be used to show how photosynthetic production is influenced by light intensities, but also other factors such as nutrient concentrations or temperature. This allows for a better representation of optimal conditions for algal growth since algal growth can be limited by multiple factors (Nickish et al., 2008). For example, Litchman et al. (2003) used a P – I curve to compare algal photosynthetic rates at various levels of phosphorus and with varying light intensity to identify the ideal nutrient level and light condition for maximum algal growth in a freshwater river.

Although P – I curves can be created along nutrient gradients, temperature and light are the most common variables used. Coles & Jones (2000) used P – I curves to show that different algal species have different P_{\max} , and some species also may experience photoinhibition with increased light intensity and temperatures.

Photoinhibition occurs when irradiance exceeds the light saturation needed for maximum photosynthesis, resulting in a decline in photosynthetic production (β ; Figure 1; Falkowski and Raven, 2007). With temperatures and light regimes continuing to be altered in aquatic systems due to climate change, especially affecting length of the growing season (Nickish et al., 2008), the use of temperature and irradiance P – I curves could allow for predictions of future trends in primary production.

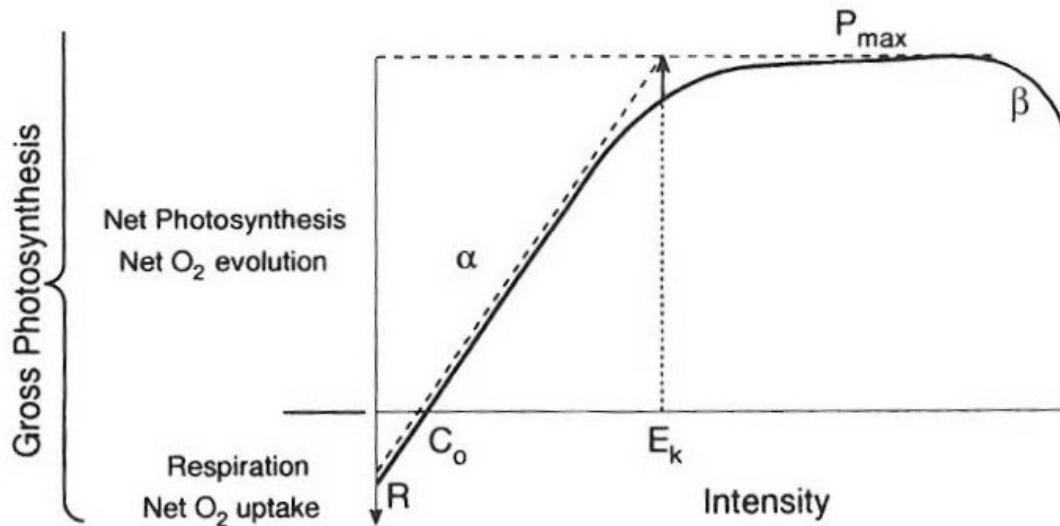


Figure 1: Diagram of a representative relationship between net photosynthetic rate and irradiance (Falkowski and Raven, 2007).

Recent studies have found that shifts in algal communities (Vargas, 2011) and algal nutrient limitation (Hernandez, 2012) have occurred in the IBP ponds over the past 40 years. In particular, nitrogen (N) or nitrogen-phosphorus (NP) co-limitation has replaced a previously observed P-limitation in the 1970s (Alexander et al, 1980; Hernandez 2012). Meta-analyses have also shown an increase in NP co-limitation in freshwater ecosystems worldwide (Elser et al., 2007). With continuing thawing of permafrost, the thickening active layer is likely releasing stored nutrients that were

previously unavailable (Hobbie et al. 1999; Frey and Smith, 2005; Frey and McClelland 2009). With increased nutrient inputs into Arctic freshwater systems, primary production may increase (Mesquita et al., 2010; Loughheed et al. 2011). Conversely increases of DOC have been found to have negative effects of primary production and biomass (Carpenter et al., 1998; Jones, 1992). Comparisons of current rates of primary production with additions of N, P and NP can aid in determining if further additions of nutrients into arctic tundra ponds could change the rate of carbon flux in these ecosystems.

In arctic ponds, primary producers can include aquatic plants, phytoplankton and benthic algae (periphyton) (Rautio et al., 2011). Phytoplankton are free floating algae and cyanobacteria that inhabit the water column or pelagic zone. It is one of the most studied primary producers in aquatic systems. Benthic algae or periphyton adheres to rocks and plants in the benthic region. Although fewer studies have been completed on benthic algae, it is believed to account for a large amount of total production in an aquatic ecosystem (Vadeboncoeur et al., 2006). Productivity is largely influenced by environmental factors and biological interactions such as light, temperature, nutrients and species composition (Kalf, 2002; Brawley et al., 2003). Understanding primary production can help us understand carbon fluxes in these ecosystems.

In the 1970's as part of the International Biological Project (IBP) Tundra Biome project, Stanley & Daley (1976) studied primary production in small tundra ponds near Barrow, Alaska. Through the use of P – I curves they found that periphyton and phytoplankton production increased until a certain light intensity at which production remained constant. It was also found that the highest rate of production for periphyton occurred at a temperature of 20°C compared to phytoplankton production which was

greatest at 14°C. This could be of great importance since as the climate is warming, water temperatures are shifting to optimal conditions for maximum algal production. In the 1970s, weekly measurements of production were also measured for both periphyton and phytoplankton in the IBP ponds. Results showed that production of periphyton peaked in mid-July and production of phytoplankton peaked at the beginning and end of the growing season.

Net primary production (NEP) is the difference between gross primary production and respiration. In aquatic ecosystems NEP can be used as an indicator of metabolic balance. When NEP is negative, the system is considered to be net heterotrophic where more respiration is occurring releasing carbon as opposed to when NEP is positive, gross primary production is greater than respiration possibly storing carbon (Cole et al., 2000). Measuring NEP of an aquatic ecosystem will help determine if the system is acting as a carbon sink or source.

There are multiple mechanisms that can be used to measure aquatic NEP. Historically, tracer methods using isotopes of carbon (^{14}C) have been used. In particular, the few existing studies of algal production in arctic aquatic environments have used tracer element methods (^{14}C) in incubations (Stanley and Daley, 1976; Kalff, 1971; Levine and Whalen, 2001; Whalen et al., 2008). Radiocarbon methods are good for low productivity systems like the high arctic due to the technique's sensitivity but require numerous assumptions and correction factors (Wetzel and Likens, 1991). ^{14}C methods are also known to be labor intensive and allow for human error. Changes in oxygen concentrations during incubations can also be used as an indicator of production. Carrigan et al. (2000) studied production and respiration in oligotrophic lakes located on

the Canadian Shield and found that ^{14}C measurements produced lower photosynthetic production rates than O_2 methods. One reason suggested as to why measurements differ include that ^{14}C incubation lengths can produce results that represent either gross production or net production (Hari et al., 2008; Harrison, 1995; Carignan et al., 2000). This is likely due reassimilation of carbon by algae during incubations, particularly in dark bottle measurements (Peterson, 1980).

More recently, free water metabolism, based on the continuous measurement of dissolved oxygen or carbon dioxide, has been used to estimate net primary production in aquatic ecosystems. Measurements are made by unmanned instruments such as weather stations and sensors placed in the aquatic system, and thus allow for continuous data to be collected over longer periods of time. These techniques have been successfully used in different aquatic environments including lakes and ponds (Cole et al., 2000; Gelda and Effler, 2002; Lauseter et al., 2006; Carignan et al., 2000). For example Christensen et al. (2013) was able to use O_2 measurements to determine a shallow pond in south-east Sweden was net heterotrophic as well as create photosynthesis-irradiance curves. Klotz (2013) used continuous O_2 measurements in two beaver ponds in New York to determine that pond NEP was positively correlated with irradiance and nutrient enrichments created autotrophic conditions.

Although free water metabolism techniques have largely been explored in temperate and subtropical regions, they may also prove pertinent in higher latitude regions like the Arctic (Staehr et al., 2012). Since FWM methods use various sensors deployed in the aquatic system to continuously record variables, these measurements combine temporal and spatial scales better than measurements that are done periodically

in small bottles (Harri et al., 2008) such as ^{14}C and O_2 methods. With continuous measurements by sensors, human error is minimized and variables can be easily computed to find net primary production. Free water methods also have an advantage that measurements are not taken in enclosures such as bottles and thus encompass both planktonic and benthic respiration (Pace and Prairie, 2005).

METHODS

Study site

In the late 1960s, research sites were established as part of the International Biological Program (IBP) near Barrow, Alaska, the northern most human settlement in the United States (Figure 2). The aquatic study sites of the IBP program consisted of multiple shallow ponds, located in low-centered ice wedge polygons that lay within a large drained thaw lake basin (Hobbie, 1980). These tundra ponds are completely frozen throughout the year except during the summer months of June – September. During the growing season, the permafrost that lies underneath this region also thaws.



Figure 2: IBP pond location near Barrow, Alaska. (Lougheed et.al, 2011)

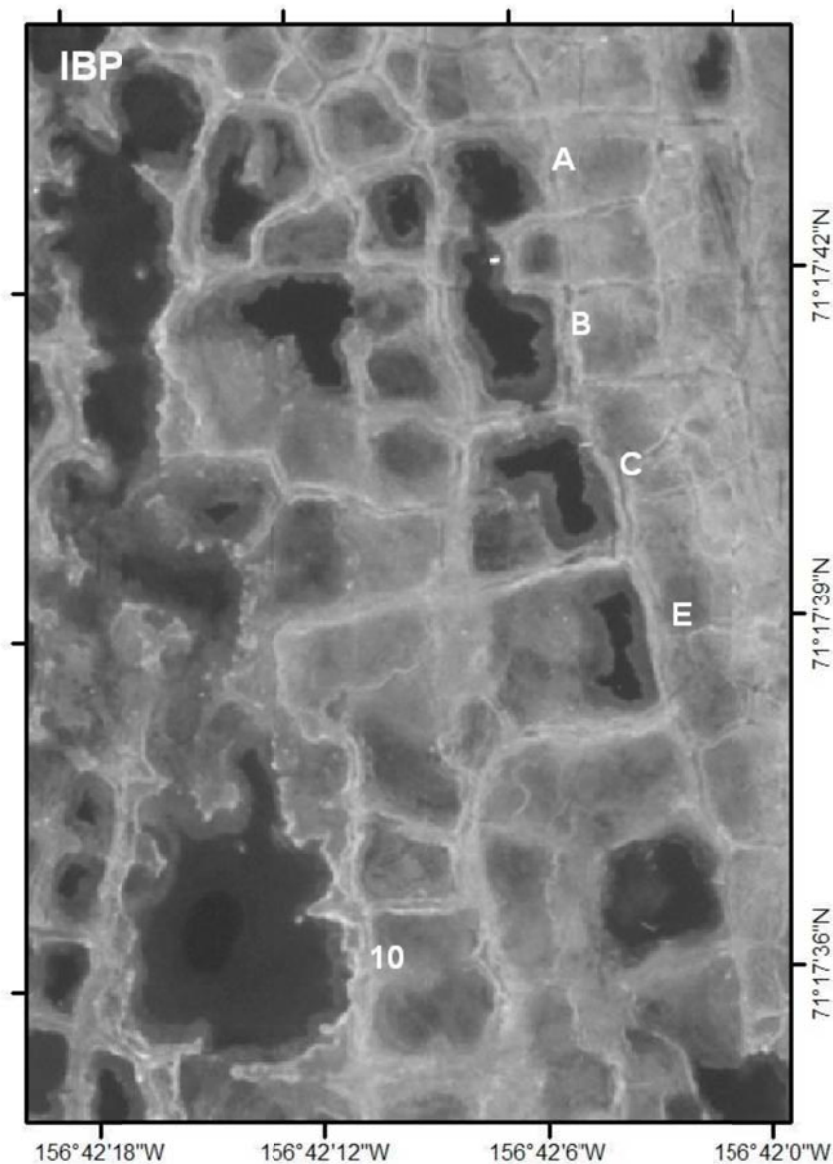


Figure 3: Satellite image of IBP Ponds B, C, E used in study (Vargas, 2011)

Quantification of net ecosystem production

To determine NEP of benthic and pelagic algae during the growing season (June-August) in 2012, periphyton and phytoplankton samples were collected on a weekly basis. Ponds were selected based on previous work in the 1970s (Stanley and Daley,

1976); however, periphyton samples were taken from a separate pond (IBP E) than phytoplankton (IBP C) in order to not disrupt or alter ongoing experiments occurring in Pond C. IBP ponds C and E are in very close proximity to each other (20 m) and periphyton biomass in these 2 ponds was not significantly different over summer 2012 ($p = 0.1286$, paired t-test). Phytoplankton was collected from the water column and filtered through an 80 μ m mesh to remove large invertebrates. Periphyton samples were collected from pond sediment surfaces at three different locations in each pond using a spatula and an inverted petri dish. All three periphyton sediment samples were combined into one composite sample.

Filtered water samples from IBP Pond C were placed in triplicate light and a single dark 60-mL BOD bottles. A control was also collected on each day to account for any background radiation. For periphyton incubations, 0.22g \pm 0.05 of sediment was added to each bottle. 2 μ Ci of ^{14}C - NaHCO_3 was added to each light and dark bottle (Figure 3). Bottles were then incubated for 4 hours in a water bath under light and temperature conditions that mimicked conditions outside on the day of sampling. Constant light was maintained using a 1000 MH LumensAire A/C Grow Light System. After incubations, 40-60 mL of the sample was filtered through Whatman GF/C filters. Filters were placed in scintillation vials and exposed to HCl fumes in a dark fume hood for 20 minutes to remove residual inorganic ^{14}C (Wetzel, 1965). Samples were then dried for 24-48 hours in a dark fume hood and frozen until further analysis.

After thawing, Ultima Gold F scintillation fluid was added to cover the filters then samples were analyzed weekly on a Beckman Liquid Scintillation Counter (Beckman LS-5801) (Figure 4) until stabilization of counts per minute (CPM) occurred at which point 5

additional readings were taken, averaged and used for analysis. CPM was converted to disintegration per minute (DPM) using a quench correction made using external standards (Figure 5).

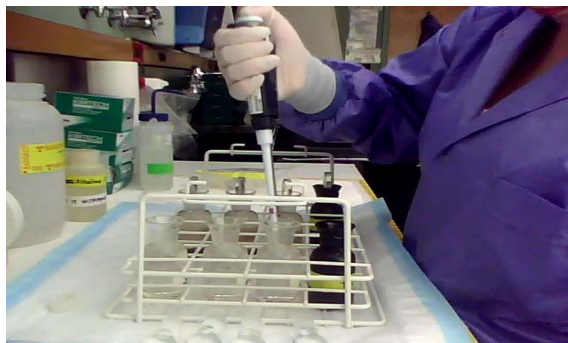


Figure 4: 2 μCi of ^{14}C - NaHCO_3 being added to light and dark BOD bottles



Figure 5: Beckman Liquid Scintillation Counter (Beckman LS-5801) located in the Bioscience building at the University of Texas at El Paso.

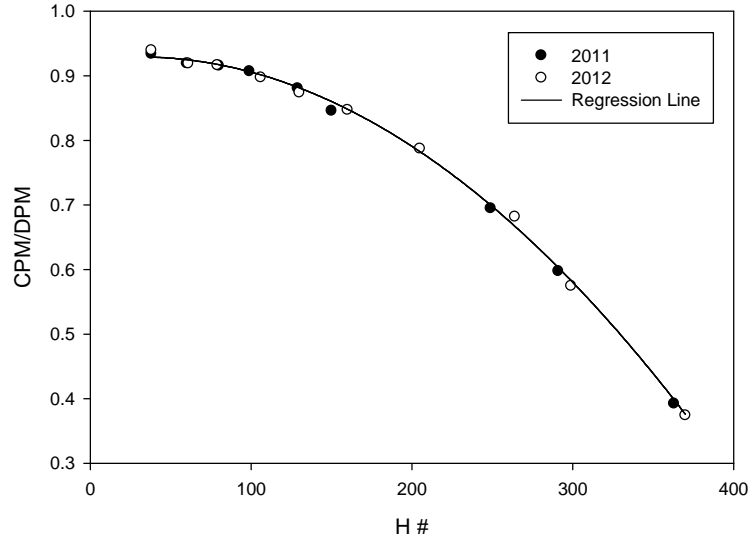


Figure 6: Quench correction (2012 and 2011) relating to counts per minute (CPM): disintegrations per minute (DPM) ratio to the H# of the sample measured by Beckman LS-5801. A larger H# indicates a higher quench of the sample.

Net ecosystem production was calculated using Equation 1, where NEP is net primary production, GPP is gross primary production obtained from the light bottle and respiration was obtained from the dark bottle (Cole et al., 2000).

$$NEP = GPP - \text{respiration} \quad (1)$$

NEP was expressed per liter for phytoplankton ($\mu\text{g C L}^{-1} \text{ h}^{-1}$) and per gram of sediment for periphyton ($\text{mg C g}^{-1} \text{ h}^{-1}$). Uptake of carbon was quantified as follows (Equations 2- 6, Likens and Wetzel, 1991).

$$^{12}\text{C assimilated } (\mu\text{g} / \text{L} / \text{h}) = \frac{(^{12}\text{C available}) \times (^{14}\text{C assimilated}) \times (\text{unit conversion, 1000})}{(^{14}\text{C available})} \quad (2)$$

Where the variables above are defined as:

$$^{12}\text{C available} = \text{total alkalinity} \times \text{pH factor} \quad (3)$$

$$^{14}\text{C assimilated} = [(total\ filter\ counts\ per\ second \times k_1) - (background \times k_1)] \times (isotropic\ effect, 1.06) \quad (4)$$

$$k_1 = \frac{(initial\ volume - ^{12}\text{C added})}{filtered\ volume} \quad (5)$$

$$^{14}\text{C available} = \frac{(\mu\text{Ci } ^{14}\text{C added}) \times (disintegrations\ of\ ^{14}\text{C}/sec^{\dagger})}{efficiency\ factor\ of\ scintillation\ counter^{\dagger\dagger}} \quad (6)$$

[†] rate of disintegration per μCi is a constant 3.7×10^4 disintegrations per second (dps)

^{††} efficiency factor was calculated based on the quench correction.

Alkalinity was determined using standard methods for low alkalinity samples (APHA, 1998), which is a potentiometric titration using 0.02N H_2SO_4 . Titrations were performed within 6 hours of collection using a Mettler Toledo G20 autotitrator.

Chlorophyll-a biomass

Phytoplankton and periphyton samples from each date were also analyzed for chlorophyll-a biomass. Collection of phytoplankton samples occurred by filtering one liter of pond water through Whatman GF/C filters. The filters were placed in test tubes, covered in aluminum foil then frozen until analysis. Periphyton samples were collected using the methods stated above. Algae were separated from the sediment by rinsing with distilled water and pouring off surface water; rinsing was repeated until surface water was clear. Subsamples were placed in test tubes, covered in aluminum foil and frozen until analysis.

Chlorophyll-a (CHL-a) was extracted in a 90% acetone solution over a 24 hour period. Filter lawns were disrupted by gently rubbing the filters with a glass stir rod. Samples were sonicated for 15 min, covered with aluminum foil and extracted in a

freezer for 24 hours. Absorbance of the extractant was measured with a Genesis 10UV spectrophotometer. Samples were corrected for turbidity and phaeopigments by acidification (Likens and Wetzel 1991). To allow for comparison to data from the 1970s, the concentration of phytoplankton chlorophyll-a was also calculated using Strickland and Parson's (1968) formula.

Photosynthesis – Irradiance curves

Maximum rate of photosynthesis (P_{\max}) under different temperature regimes was determined four times throughout the 2012 growing season for both phytoplankton and periphyton. Samples were collected and enriched with ^{14}C as described above. Bottles were incubated at four different light intensities, obtained by using 0, 1, 2 or 3 layers of fiberglass sheets (standard grey fiberglass window screens), and three different temperatures (8, 14, and 20°C), to allow comparison with Stanley and Daley (1976). Temperature was regulated using an aquarium chiller. After 4 hours of incubation, samples were processed as described above. Photosynthesis – irradiance (P – I) curves were created by plotting photosynthetic rate against light intensity for each temperature treatment.

Free water metabolism (FWM)

A YSI 6920 V2 Multiparameter Water Quality Sonde was deployed into IBP pond C throughout the summers (June-August) of 2010-2012, to record temperature, dissolved oxygen (DO) and chlorophyll every 15 minutes. Both chlorophyll and DO were recorded using YSI optical probes. A weather station was located approximately 30m away from the sonde and recorded wind speed at 2m (m/s) and air temperature. irradiance

was less than 2 PAR: from. Diffusion, NEP, etc were calculated using the formulas below (Equations 7-8; Cole et al., 2000)(Equation 9; regression line equation [Figure 6]) (Equation 10, 13-19; Staehr et al., 2010)(Equation 11; Wanninkhof, 1992)(Equation 12; Holtgrieve et al., 2010). Gross primary production (GPP) and respiration(R) (Equation 17-19) were calculated only for the latter half of the season (August 3rd to August 19th (Julian day 215 to 231) when PAR fell to near zero as the sun began to set.

$$NEP_{hr} = \Delta O_2 - \text{Diffusion} \quad (7)$$

$$\text{Diffusion} = k(O_2 - O_{2 \text{ sat}}) \quad (8)$$

$$O_{2 \text{ sat}} = 0.0057 * \text{Temperature } (^{\circ}C)^2 - 0.3863 \text{ Temperature } (^{\circ}C) + 14.583 \quad (9)$$

$$k_{600} = (2.07 + 0.215 U_{10}^{1.7}) / 100 \quad (10)$$

$$k = k_{600} (Sc/600)^{-0.5} \quad (11)$$

$$Sc = 1800.6 - 120.1T + 3.7818T^2 - 0.047608T^3 \quad (12)$$

$$U_{10} = U_z (1.4125z^{-0.15}) \quad (13)$$

$$NEP = GPP - R \quad (14)$$

$$\text{Day fraction} = (\# \text{ light measurements} - \# \text{ measurements}) / (\# \text{ of light measurements}) \quad (15)$$

$$NEP_{daytime} = (\text{mean NEP}) * (\text{day fraction}) * 24 \quad (16)$$

$$R_{daytime} = (R_{hr}) * (\text{day fraction}) * 24 \quad (17)$$

$$R_{day} = (R_{hr}) * 24 \quad (18)$$

$$GPP = NEP_{daytime} + R_{daytime} \quad (19)$$

O_2 : measured concentration of oxygen in water

$O_{2 \text{ sat}}$ is the concentration of O_2 in water if it was in equilibrium with the atmosphere

k is the gas exchange coefficient at a given temperature

$0.3I$: constant used when only short-term wind data is used

z : height of wind meter

Sc : Schmidt number in freshwater

R_{hr} : mean NEP during darkness

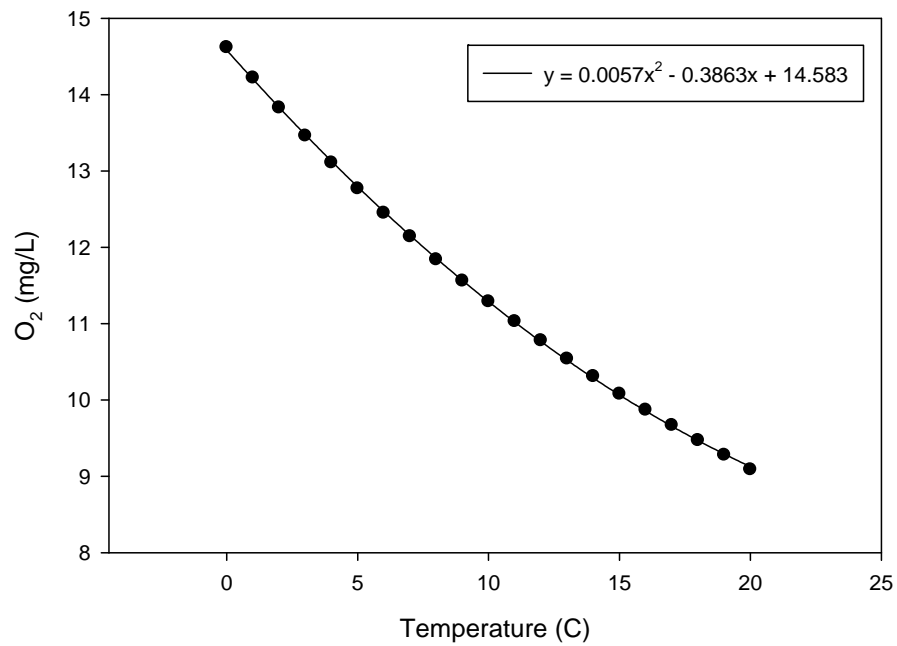


Figure 7: Oxygen saturation in water at a given temperature. $R^2 = 0.9999$

Statistical analysis

To allow comparisons among 1970s and current data, samples were first grouped by year and averaged according to the week of year. The averages were then compared using a paired t-test in R version 3.0.0. Data were log-transformed to meet the assumptions of normality. When data could not be normalized, non-parametric methods were used (e.g. Wilcoxon signed rank). Paired t-tests comparing multiple years were corrected using a Bonferroni correction.

All Regression trees were created using JMP 10 software and included the following environmental variables: soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), total phosphorus (TP), nitrate (NO_3), ammonia (NH_3), DOC, year, weekly mean of daily maximum water temperature, weekly mean of irradiance (PAR), silicon (Si) and mean specific conductance. Free water metabolism regression trees also included CHL-a ($\mu\text{g/L}$) for planktonic. Regression trees for CHL also included total nitrogen (TN). TN and TDP were not available from the 1970s and therefore could not be included with the 1970s regression trees.

RESULTS

Both temperature and algal biomass have increased significantly in IBP ponds over the past 40 years (Lougheed et al. 2011). More recent studies have indicated that, significantly higher maximum weekly temperatures were observed in 2010-11 as compared to 1970 and 1972 (paired t-test, $p=0.005$; Hernandez, 2012). 1970 through 1973 had significantly higher ($p=0.0015$, Wilcoxon signed rank test) mean maximum irradiance levels compared to mean maximum irradiance levels of 2010 through 2012. In addition,

Changes in NEP over time

Radioisotope uptake techniques indicated that there was no difference in phytoplankton NEP throughout the growing season in 1970-3 as compared to 2011-2 (Figure 8). However, phytoplankton NEP was significantly higher in 1970-3 during the beginning of the season (weeks 25-28) compared to 2011-12 ($p=0.05659$, paired t-test). During the latter half of the season (weeks 29-34) NEP was significantly greater in 2011-2 than in 1970-3 ($p=0.04215$, paired t-test). Production measured by ^{14}C was highly variable between years (Figure 9). NEP reached the highest levels in 2011, and was lowest in 1970 tending to have the lowest levels of production. Interestingly similar peaks in production were observed during week 27 in 1971 and 2012 and seen during week 28 of 2011. Substantially different methods were used to determine benthic NEP in 1972, as compared to 2011-2 thus the magnitude of the effects are not directly comparable;

however, the peak in benthic production peaks may have occurred earlier in the season in 2011-12 than it did in 1972 (Figure 10).

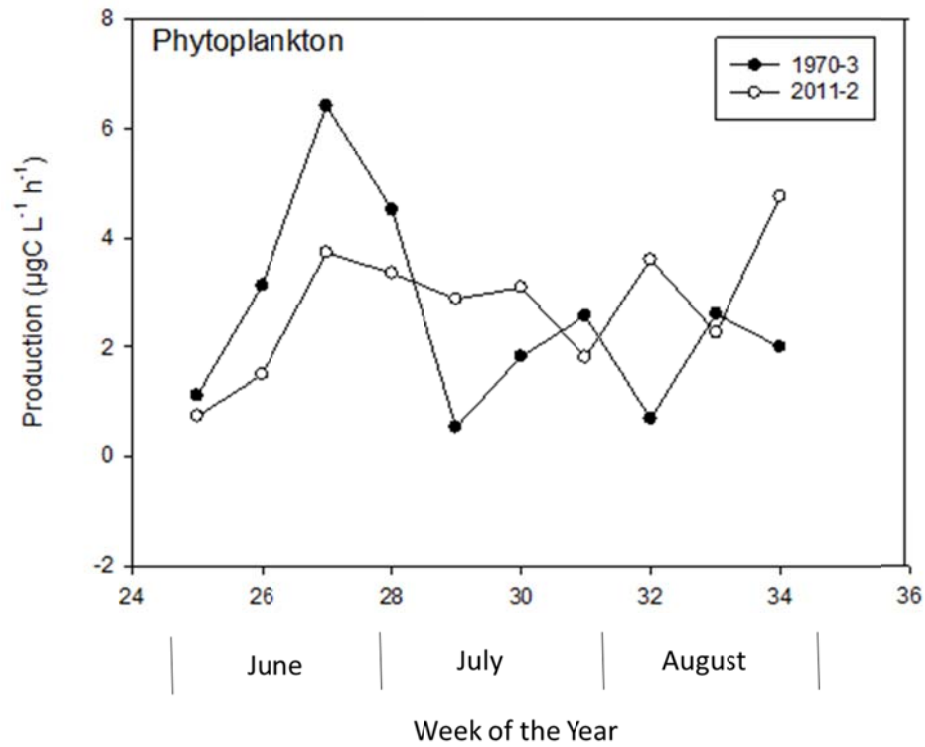


Figure 8: Weekly mean of phytoplankton production from IBP Pond C from historic (1970-3) and current (2011-12) analyses.

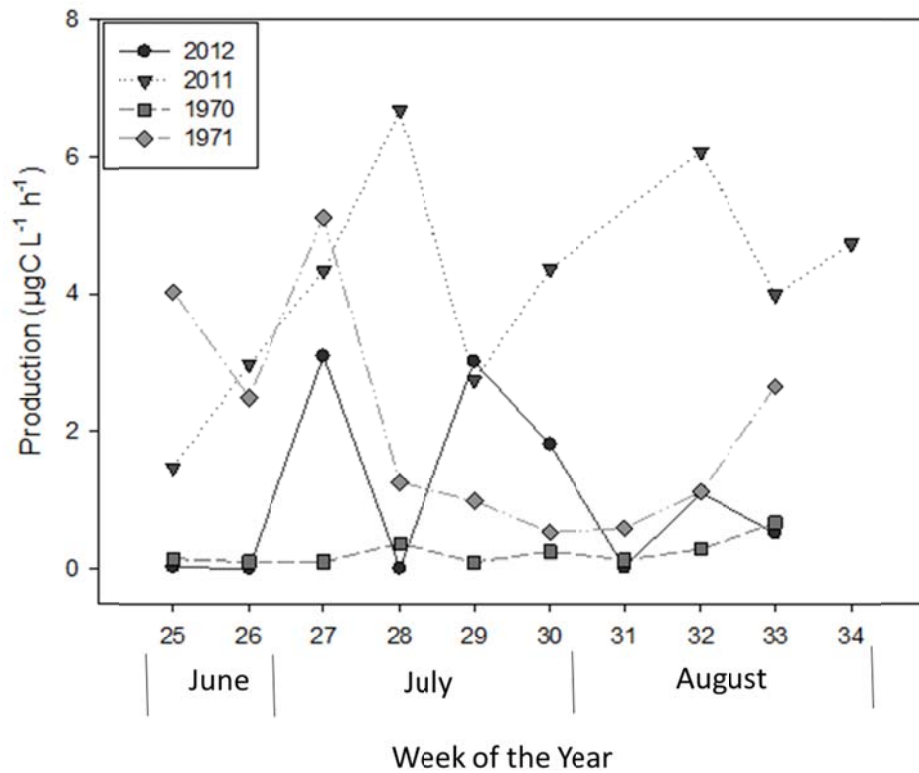
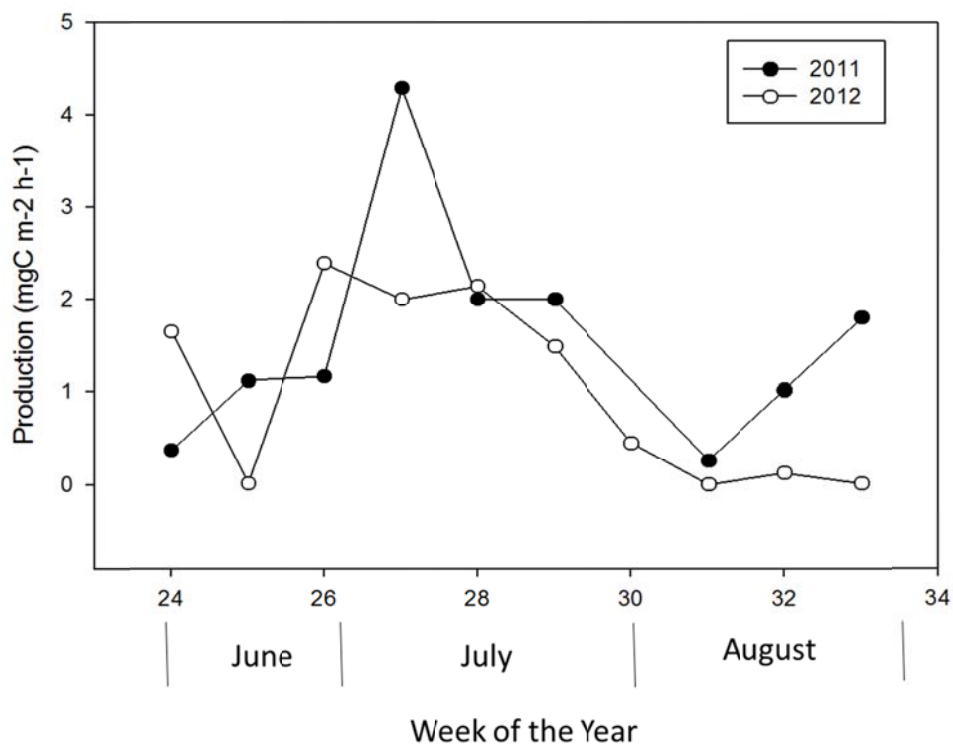


Figure 9: Yearly comparisons of weekly means phytoplankton production from IBP Pond C.



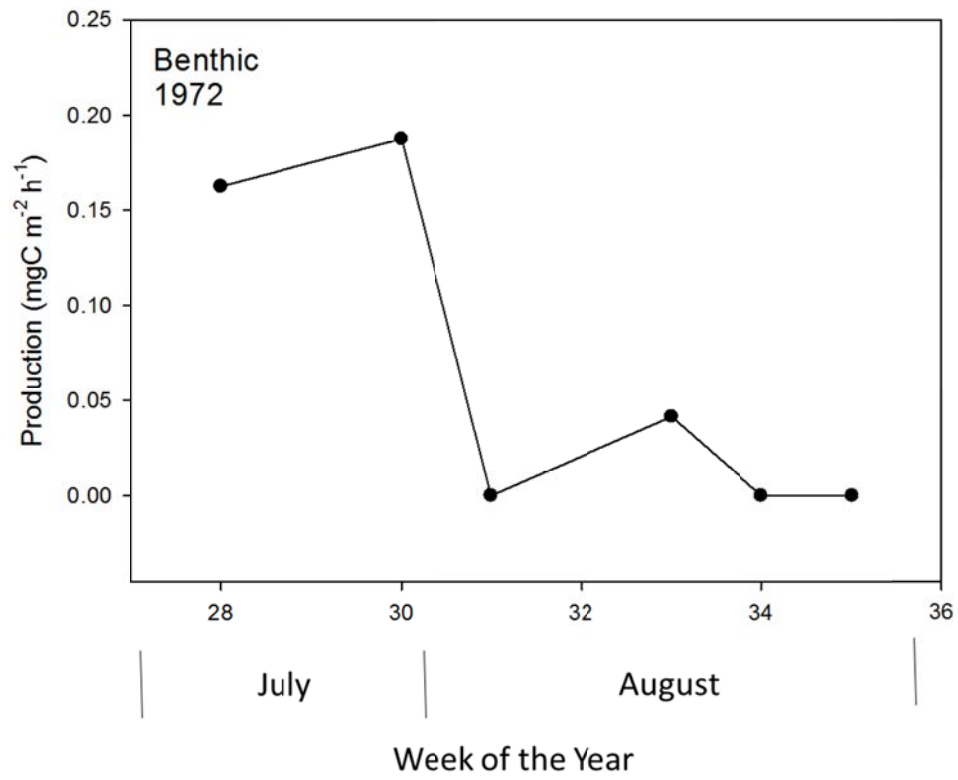


Figure 10: Benthic production ($\text{mgC}/\text{m}^2/\text{h}$) from IBP Pond C and E 2011 and 2012 (top). Benthic production ($\text{mgC}/\text{m}^2/\text{h}$) 1972 (bottom).

Photosynthesis – Irradiance curves

Photosynthesis – Irradiance (P - I) curves completed in 1973 by Stanley and Daley (1976) were recreated for comparison purposes in Figure 11 and indicate their findings of maximum rates of photosynthesis, which occurred for benthic algae at 20°C and for phytoplankton at 14°C. Conversely, P - I curves completed in 2012 (Figure 11) nearest to the date of P - I curves created in 1973 found maximum photosynthesis rates for benthic algae to occur at 8°C and phytoplankton occurred at 20°C. However, it appears that P_{\max} was not reliably achieved for most temperatures and irradiance levels for these data (Figure 11). Similarly, average P - I curves for the entire 2012 growing season (Figure 12) indicate that P_{\max} was never achieved for benthic algae. Benthic production continued to increase with irradiance and never leveled off. At lower irradiances, colder temperatures (8°C) produced the greatest benthic production, but at the highest irradiance level the greatest production may have been occurring at 20°C. Average phytoplankton P - I curves for 2012 (Figure 13) indicated that P_{\max} was achieved and photoinhibition occurred at the lower temperatures (8 and 14°C). On average, the maximum rate of photosynthesis for phytoplankton occurred at 20°C. Individual P - I curves created throughout the 2012 growing season are located in Appendix A.

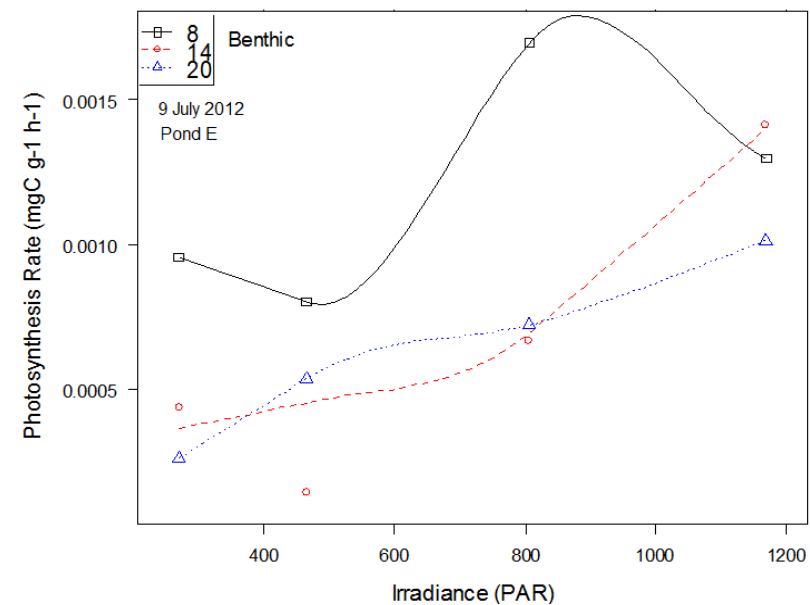
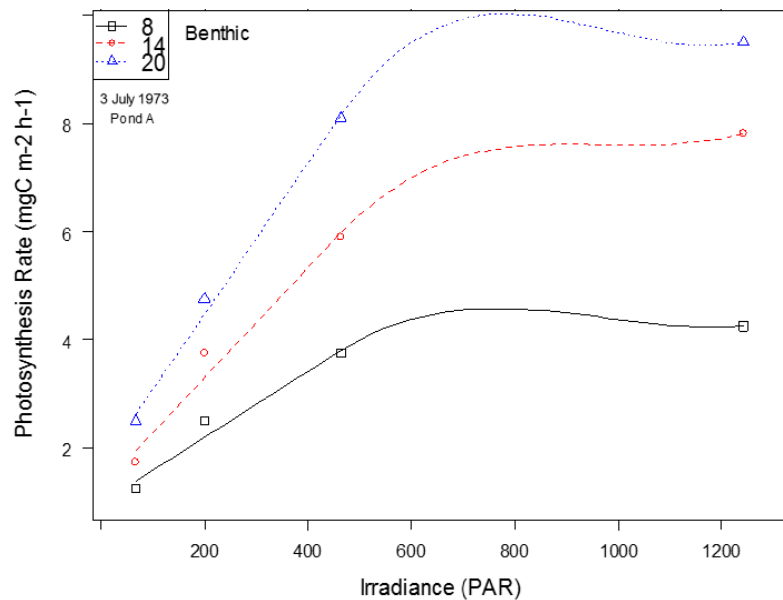
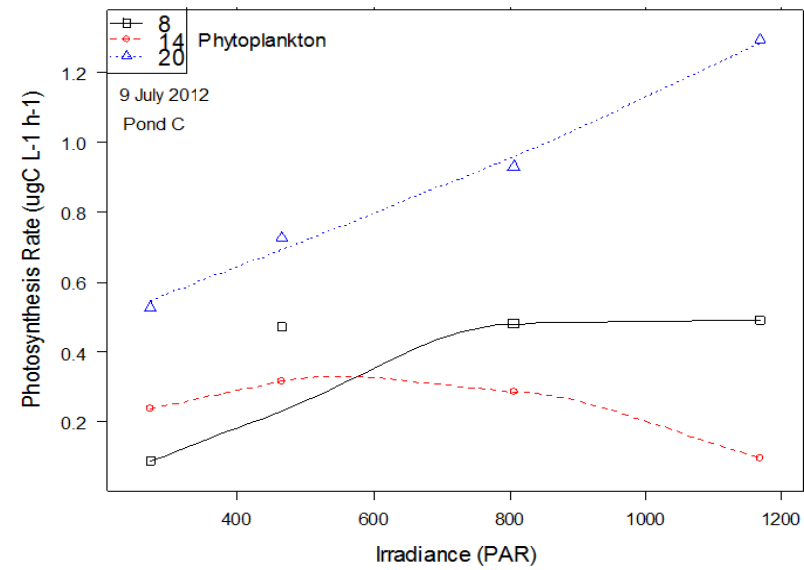
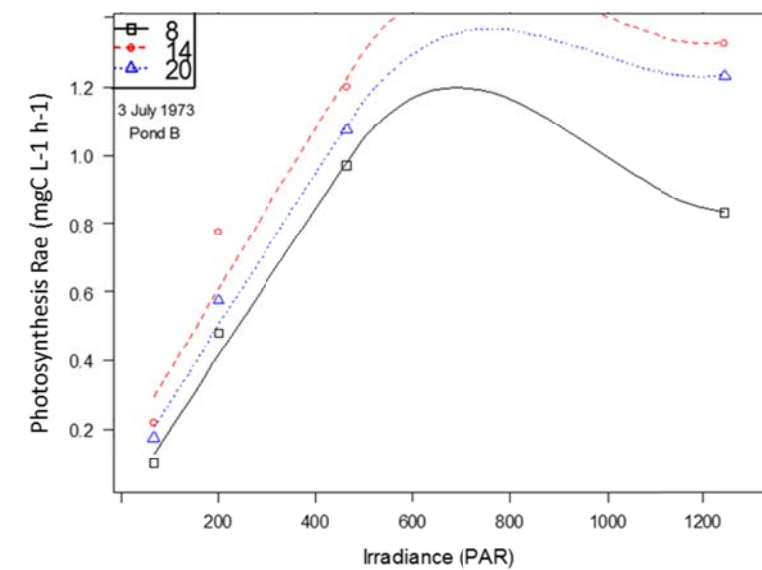


Figure 11: Photosynthesis-irradiance curves at three temperatures for: phytoplankton in IBP Pond A on July 3, 1973 (top left), phytoplankton in IBP Pond C on July 9, 2012 (top right), benthic algae in IBP Pond B on July 3, 2012 (bottom left) and benthic algae in IBP Pond E on July 9, 2012 (bottom right).

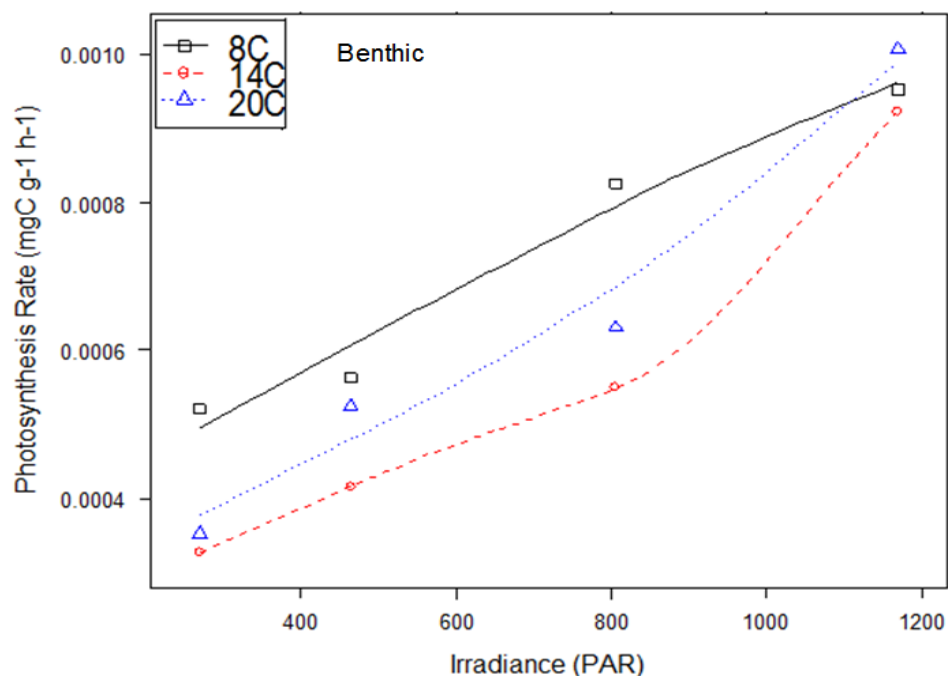


Figure 12: Photosynthesis-irradiance curves for benthic algae in IBP Pond E averaged for 4 dates over the growing season of 2012 at 8, 14, and 20°C and four increasing light intensities.

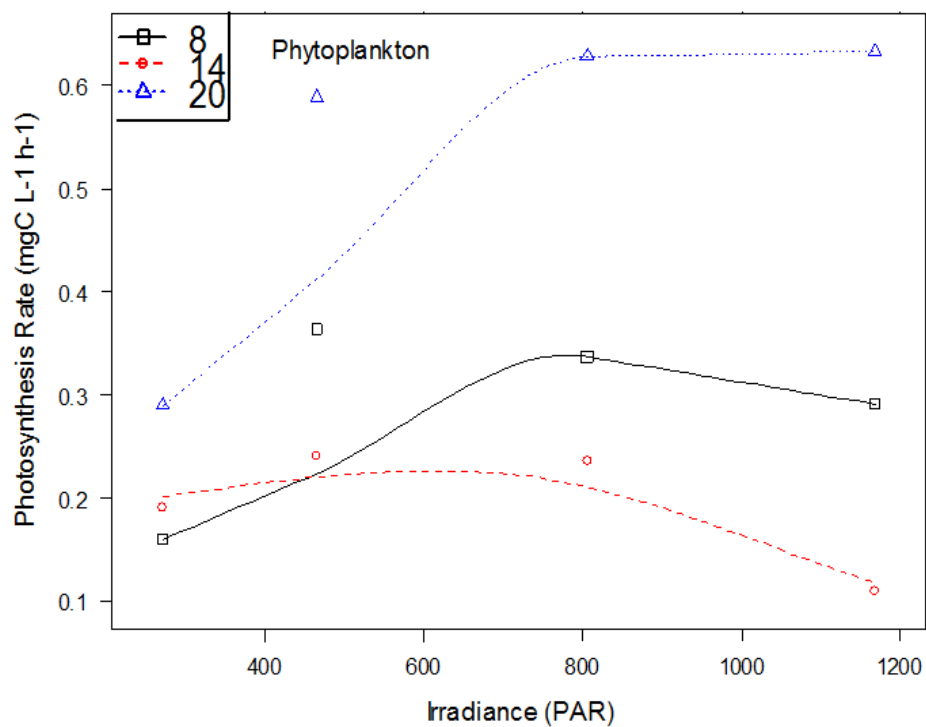


Figure 13: Photosynthesis-irradiance curves for phytoplankton in IBP Pond C averaged for 4 dates over the growing season of 2012 at 8, 14, and 20°C and four increasing light intensities.

Environmental drivers of primary production over the past 40 years

A regression tree of weekly planktonic NEP measured by radioisotope techniques for 1970-1 and 2010-2 explained 65% of the variation in the data ($R^2=0.645$, Figure 14) and indicated that 1970 had the lowest measured production of all years ($0.21 \mu\text{gC/L/h}$). In all other years, chlorophyll-a concentration had the greatest impact on NEP; when CHL-a concentrations were less than $1.19 \mu\text{g/L}$, NEP was low ($1.39 \mu\text{gC/L/h}$) compared to when CHL-a concentrations were greater than 1.19 and NEP averaged $3.07 \mu\text{gC/L/h}$. Of the lower NEP and CHL-a values ($n=27$) 89% were from the 1970s. When CHL-a concentrations were greater than $1.19 \mu\text{g/L}$, NEP was lowest in 2012 as compared to previous years, primarily 2011. Water temperature, irradiance and the level of nutrients in the water column had no apparent effect on phytoplankton NEP as measured by ^{14}C .

Because we were not able to recreate condition used for benthic NEP determinations in the 1970s, the current data are not directly comparable. Thus, we completed 2 separate regression trees for current and historic data. Regression trees of benthic NEP measured by ^{14}C in 2011 and 2012 explained 68% of variation in the data ($R^2 = 0.682$, Figure 15) and indicated that when water temperature was greater than 13.8°C , benthic NEP tended to be highest (1.49 mgC/g/h). When water temperature was less than 13.8°C NEP averaged 0.11 mgC/g/h .

Regression trees of benthic production measured by radioisotope techniques in the 1970s explained 32% of variation in the data ($R^2 = 0.324$, Figure 16) and indicated that NEP was lowest ($9.27 \text{ mgC/m}^2/\text{h}$) when TP was less than $19.8 \mu\text{g/L}$. With TP greater than or equal to $19.8 \mu\text{g/L}$ and SRP above $2.4 \mu\text{g/L}$ the most production occurred ($24.63 \text{ mgC/m}^2/\text{h}$).

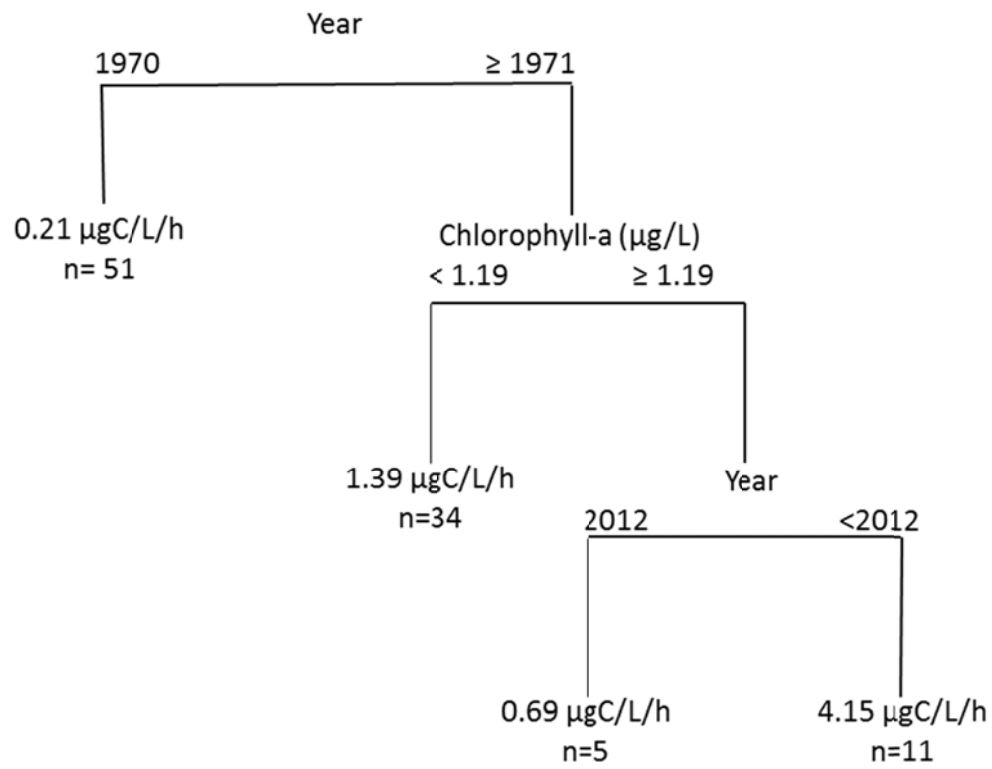


Figure 14: Regression tree of weekly phytoplankton NEP measured using ^{14}C radioisotopes from years 1970-73 and 2011-12.

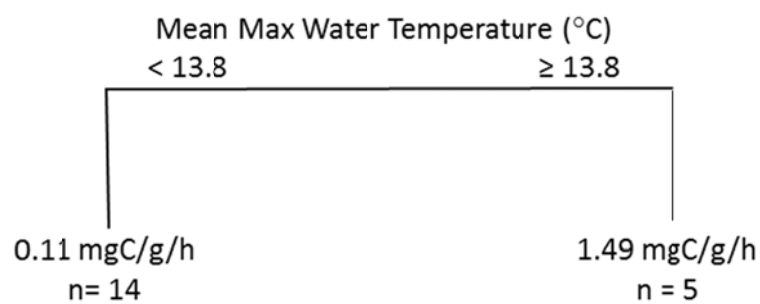


Figure 15: Regression tree of weekly benthic NEP measured using ^{14}C radioisotopes in 2011 and 2012.

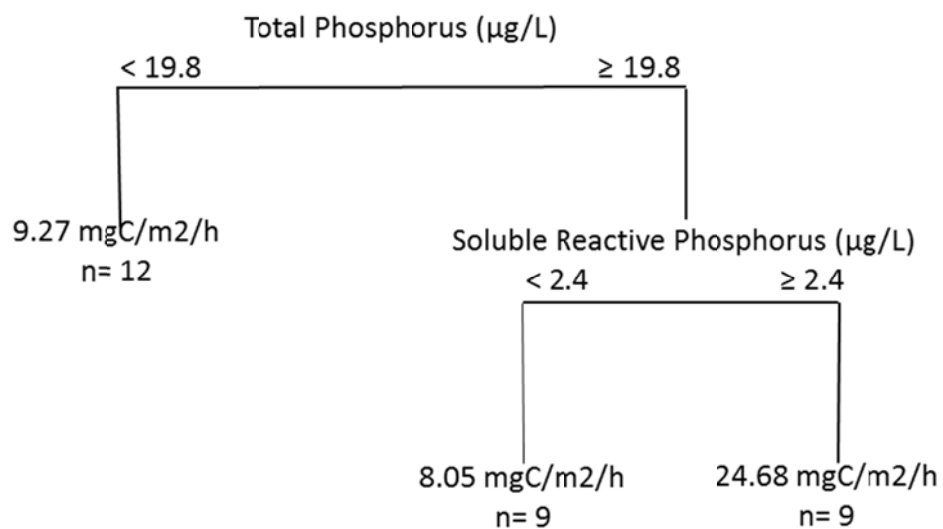


Figure 16: Regression tree of benthic NEP measured using ^{14}C radioisotopes in the 1970s.

NEP measured using free water metabolism

Mean daytime NEP was positive during the entire growing season (Figure 17). When NEP is negative, it indicates net heterotrophy where more O_2 is being consumed during respiration than what is being produced during gross primary production (Cole et al., 2000). The opposite is seen when NEP is positive, more O_2 is being produced during gross primary production than what is being consumed during respiration (net autotrophy). Only daytime NEP was measured during the entire growing season due to continuous sunlight not allowing for dark measurements.

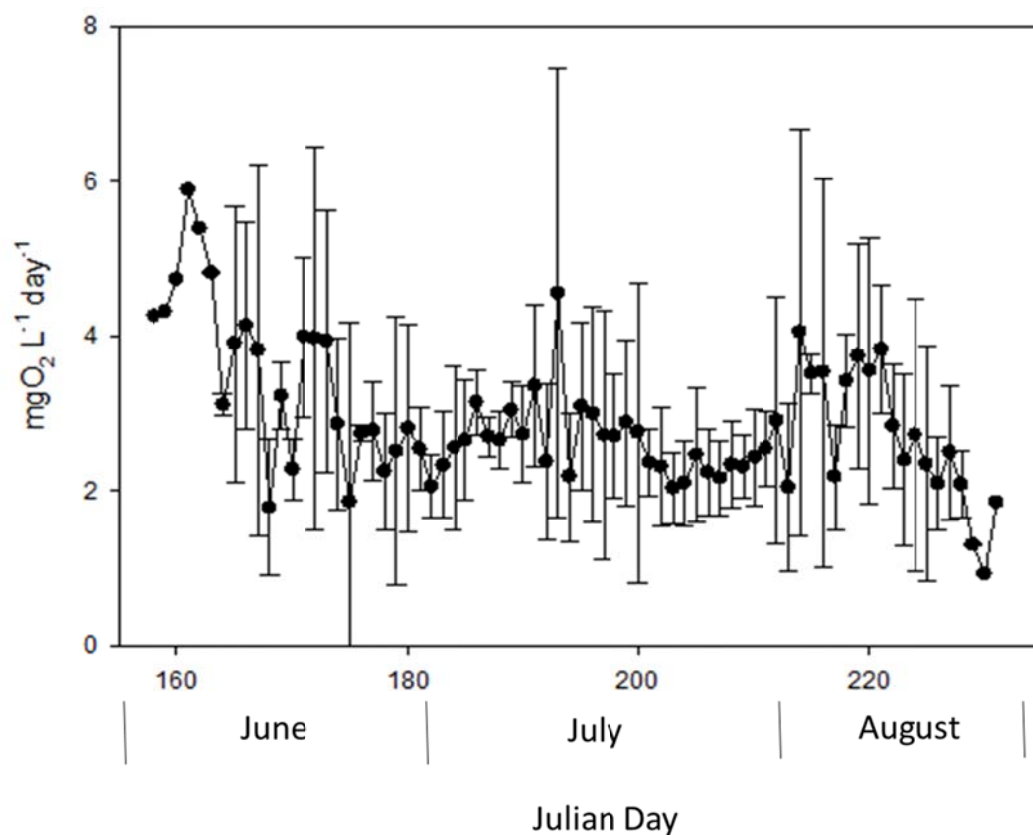


Figure 17: Daytime NEP (+/- 1SE) averaged for summers of 2010-12.

At the end of the season, when sunsets did occur, we were able to calculate NEP, GPP and R using the free water metabolism data. Gross primary production and respiration decreased towards the end of the summer, yet respiration never exceeded GPP causing mean NEP to be continuously positive and net autotrophic (Figure 18). Respiration averaged over 2010-12 ranged from 0.35 – 5.86 $\text{mgO}_2/\text{L}/\text{day}$ with a mean of 2.82 $\text{mgO}_2/\text{L}/\text{day}$ (Figure 19), gross primary production ranged from 1.37 – 10.11 $\text{mgO}_2/\text{L}/\text{day}$ with a mean of 4.94 $\text{mgO}_2/\text{L}/\text{day}$ (Figure 20) and net ecosystem production ranged from -0.96 – 4.45 $\text{mgO}_2/\text{L}/\text{day}$ with a mean of 2.12 $\text{mgO}_2/\text{L}/\text{day}$ (Figure 21).

To further illustrate the impact that sunsets had on diurnal oxygen measurements, we present representative dissolved oxygen (DO) fluxes for the beginning, middle and end of the season (Figure 22). Towards the end of the season (mid-August), oxygen levels dip after the sunset, reflecting the presence of respiration in the absence of photosynthesis. Conversely, a similar dip in DO levels is not apparent during June and July, which experience constant daylight, and where DO levels peak at mid-day.

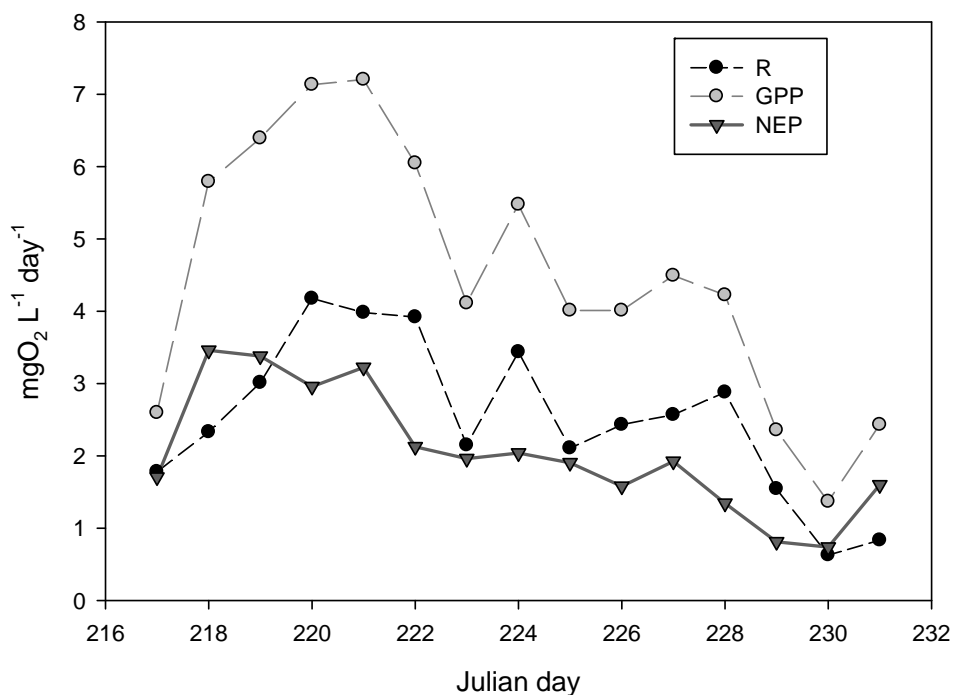


Figure 18: Mean gross primary production (GPP), respiration (R) and net ecosystem production (NEP) averaged for August 2010-12, when sunsets occurred in Barrow, AK.

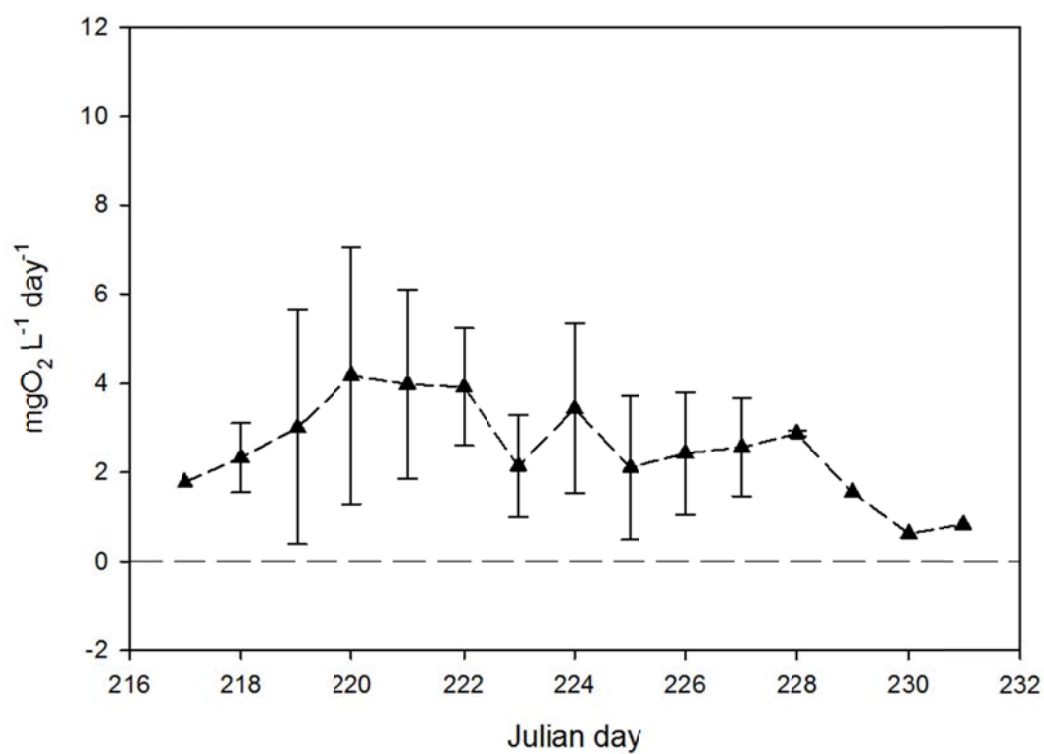


Figure 19: Mean Respiration (+/- 1 SE) for August 2010-12, when sunsets occurred in Barrow, AK

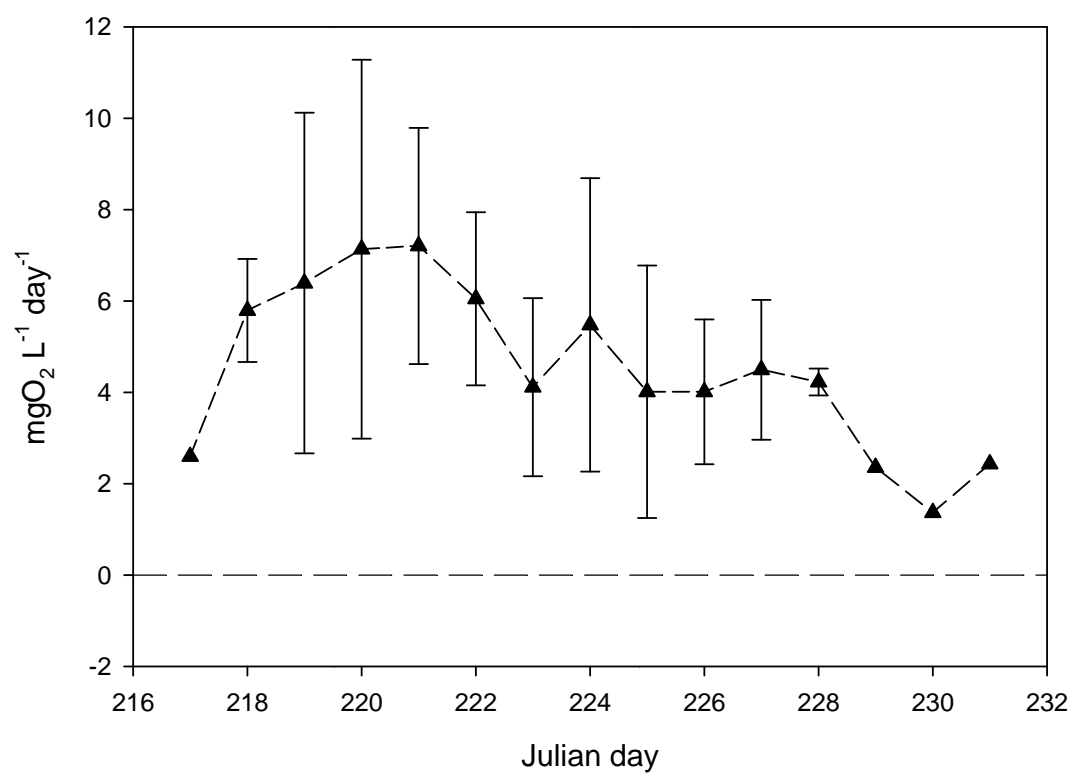


Figure 20: Mean gross primary production (+/- 1 SE) for August 2010-12, when sunsets occurred in Barrow, AK

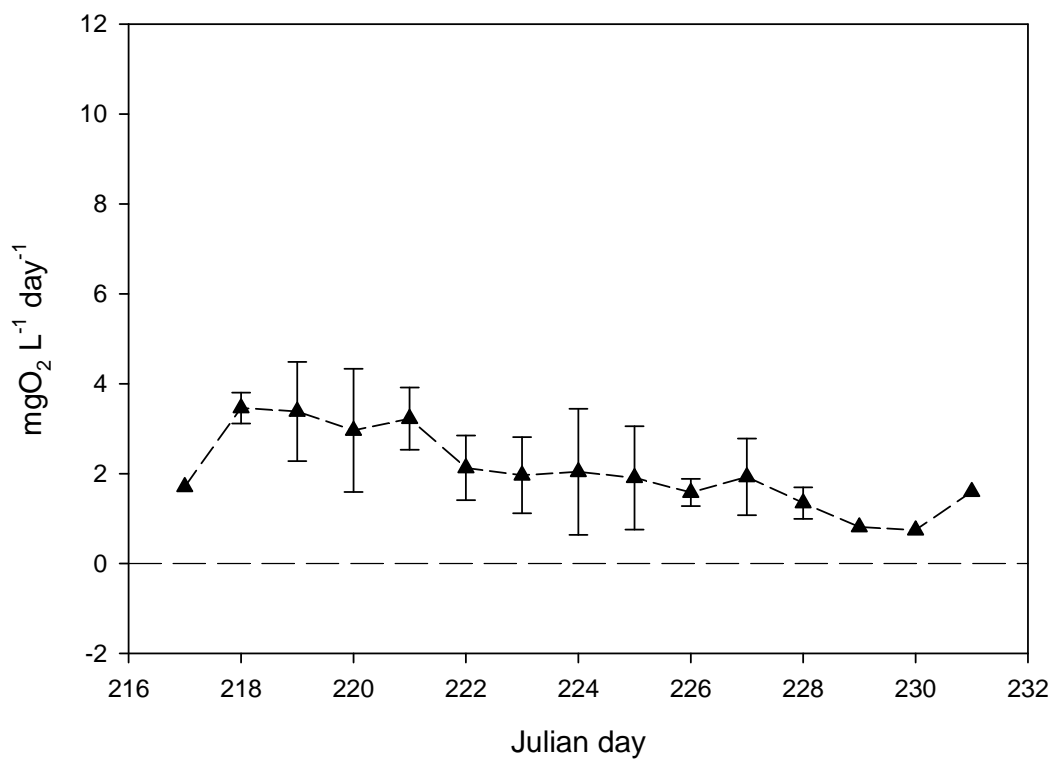


Figure 21: Mean gross primary production (± 1 SE) for August 2010-12, when sunsets occurred in Barrow, AK

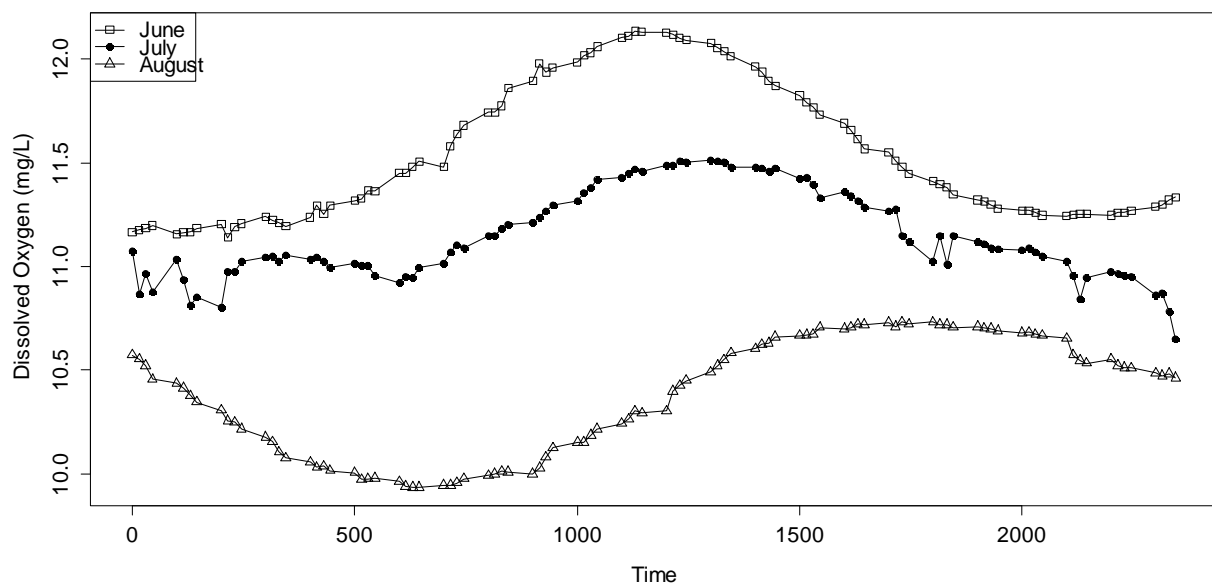


Figure 22: Mean diurnal flux of dissolved oxygen on similar dates in mid-June, mid-July and mid-August for 2010-12.

Comparison between current years

Net ecosystem production measured at the end of the season indicated that NEP was significantly greater in 2010 compared to 2012 but no significant difference was found among other years (Bonferonni corrected $p=0.0059$, Figure 23). Similarly, chlorophyll measured by the YSI in 2012 was significantly less than chlorophyll measured in 2011 and 2010 (respectively: Bonferonni corrected $p=0.0002$, $p=0.0053$, paired t-tests, Figure 24).

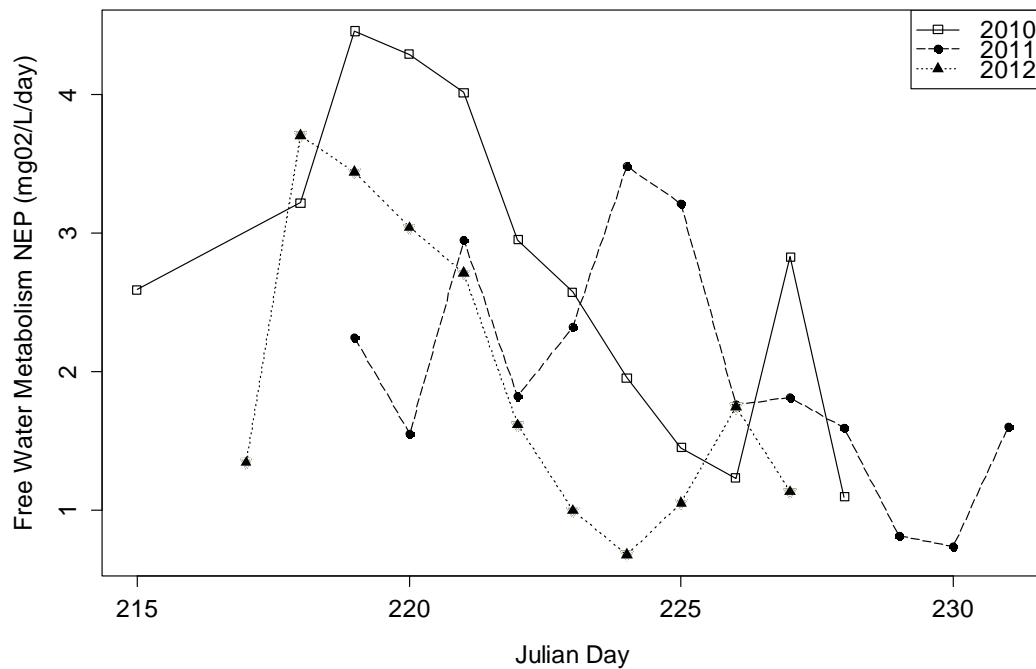


Figure 23: Net ecosystem production comparisons among years 2010, 2011 and 2012 during August when sunsets occurred in Barrow, Alaska

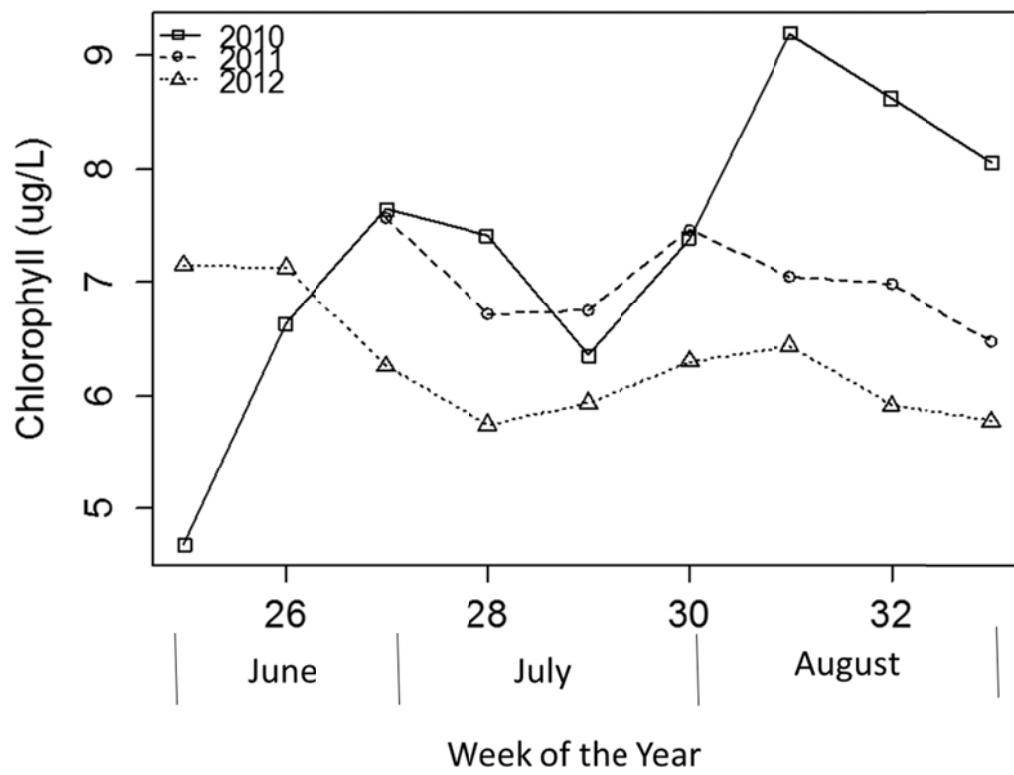


Figure 24: Comparison of mean weekly chlorophyll measured using the YSI in 2010-2012.

Environmental drivers of free water metabolism

Regression tree of mean daily NEP at the end of the season measured by free water metabolism in 2010-2 (Figure 25) explained 44% of the variation in the data. The first split indicated that NEP tended to be higher when soluble reactive phosphorus (SRP) was greater than or equal to 5.02 $\mu\text{g/L}$ (891.47 $\text{mgO}_2/\text{L/day}$). When less SRP was present, NEP was driven by nitrate (NO_3), with the greatest mean NEP observed above or equal to 15.72 $\mu\text{g/L}$ (1.41 $\text{mgO}_2/\text{L/day}$). At lower levels of NO_3 , highest NEP is observed at irradiance levels greater than or equal to 243.10 (PAR) (1.76 $\text{mgO}_2/\text{L/day}$). When a regression tree was created using only chlorophyll as a predictor variable, it indicated that when YSI chlorophyll concentration where greater than 6.56 ($\mu\text{g/L}$) more production occurred (2.45 $\text{mgO}_2/\text{L/h}$) (Figure 26, $r^2 = 0.231$).

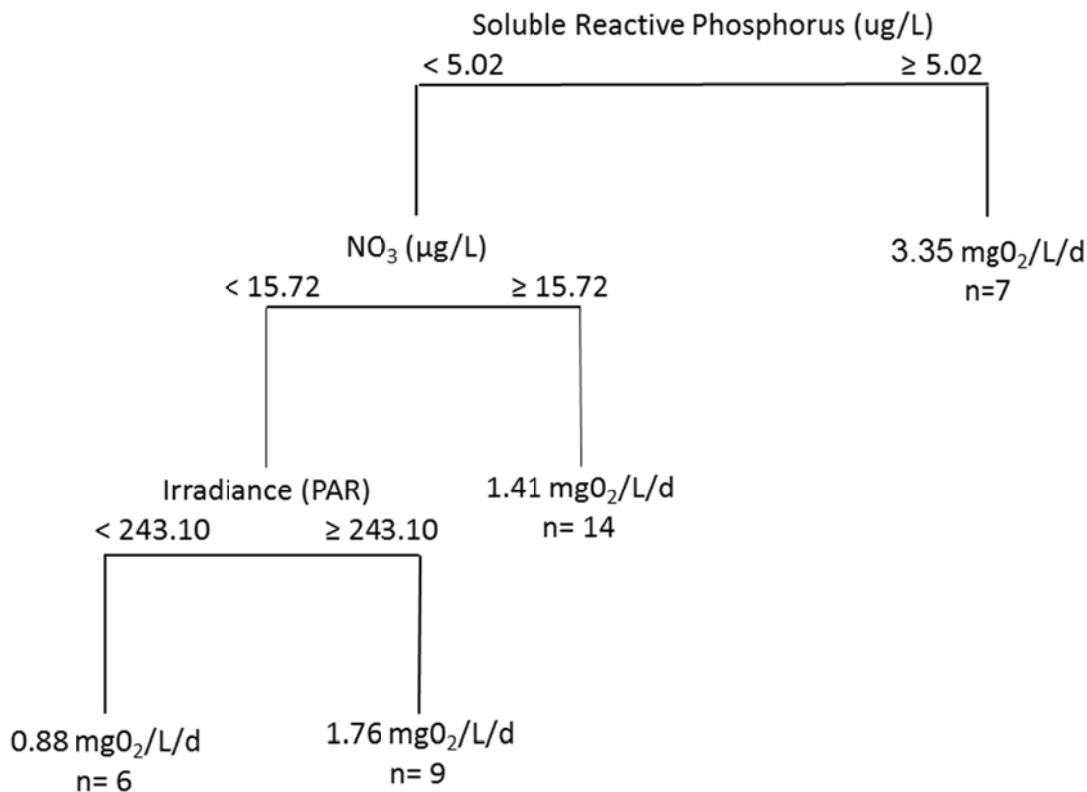


Figure 25: Regression tree of daily NEP from IBP Pond C 2010-2 during August when sunsets occurred. $R^2 = 0.438$.

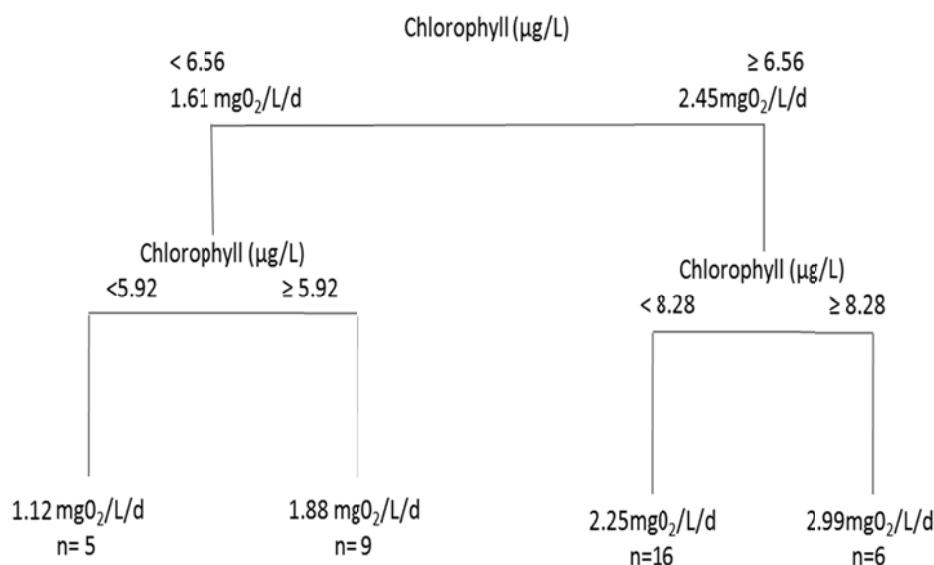


Figure 26: Regression tree of FWM measured NEP at the end of the season when sunset occurred. $R^2=0.213$

Environmental drivers of planktonic chlorophyll levels

A regression tree of weekly mean planktonic chlorophyll concentrations measured in IBP Pond C by the YSI sonde indicated year of measurement to have the greatest influence on chlorophyll followed by amount of DOC present in the pond (Figure 27). The amount of chlorophyll recorded in 2012 (5.75 $\mu\text{g/L}$) was less than the amount in 2010 and 2011 (7.31 $\mu\text{g/L}$). In 2010 and 2011, less chlorophyll was recorded when DOC was less than 22.48 mg/L than when DOC is equal or greater than 22.48 mg/L ($R^2=0.51$).

Regression trees of chlorophyll ($\mu\text{g/L}$) measured using acetone extraction of chlorophyll-a explained only 27% of variation in the data; however, this analysis confirmed the results from the previous tree where the highest levels of CHL were observed at greater concentrations of DOC (Figure 28). When DOC was greater or equal to 16.01 mg/L and average light extinction was greater than or equal to 0.02, the greatest amount of chlorophyll biomass occurred (3.2 $\mu\text{g/L}$). When DOC was less than

16.01 mg/L and temperature was less than 6.57°C, the least amount of chlorophyll biomass occurred (0.7 µg/L).

Finally, a regression tree including data from the IBP ponds, ponds located in a remote area far from the village of Barrow, and sites near the village of Barrow indicated when ammonia was greater than or equal to 135.8 µg/L, chlorophyll biomass was greatest (4.85 µg/L) (Figure 29). When ammonia was less than 135.8 µg/L, silica appeared to limit algal growth. When Si was greater than or equal to 432.81 µg/L, CHL concentrations were greater (3.91 µg/L). When Si was less than 432.81 µg/L and total nitrogen was less than 1.15, the lowest levels of chlorophyll were observed (1.36 µg/L) ($R^2=0.214$).

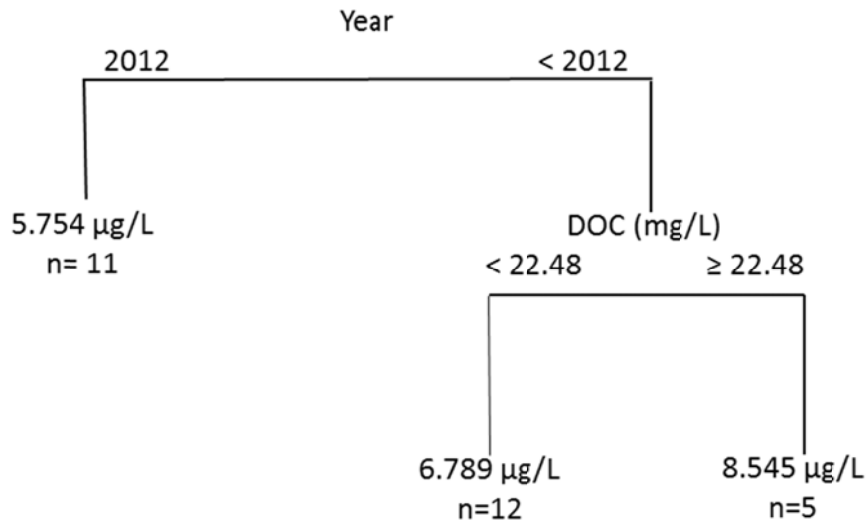


Figure 27: Regression tree of weekly mean YSI measured chlorophyll concentrations in IBP Pond C for years 2010-2. $R^2=0.51$.

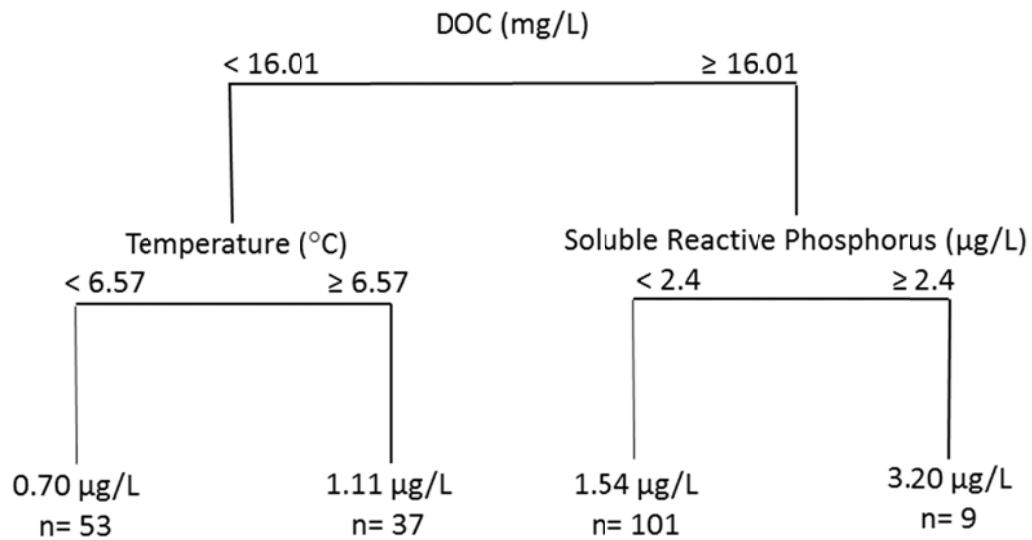


Figure 28: Regression tree of acetone-extracted Chlorophyll (µg/L) for IBP ponds B, C, and E from 1970-2 and 2010-2. $R^2=0.27$.

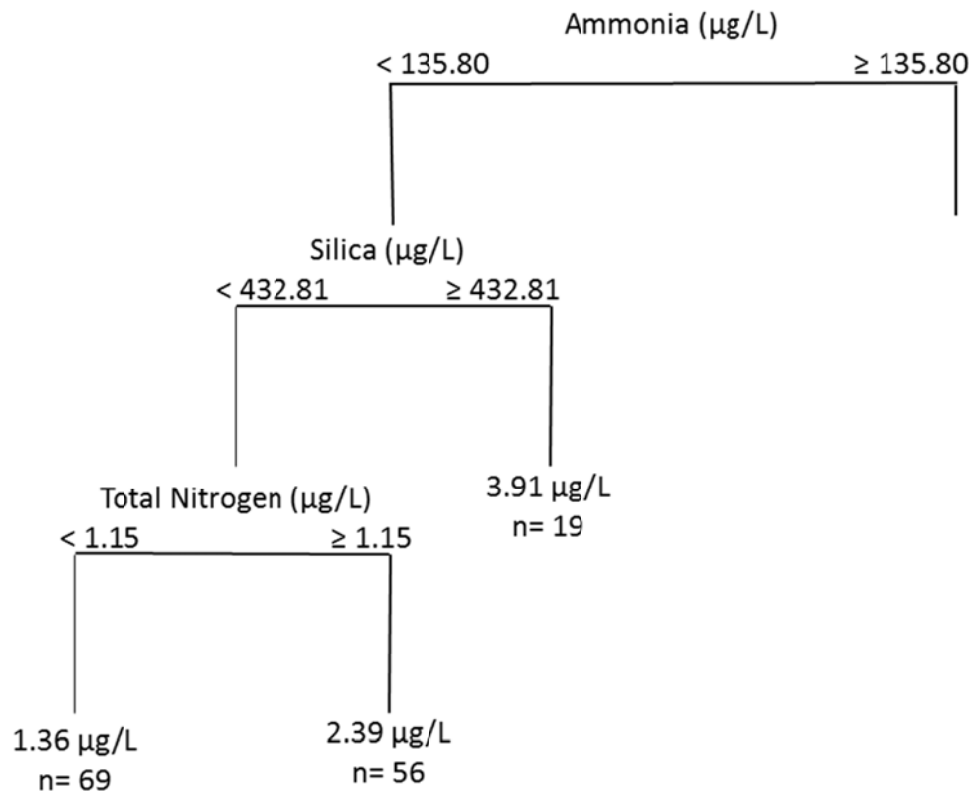


Figure 29: Regression tree of acetone extracted Chlorophyll (µg/L) from ponds along a gradient of nutrient enrichment in 2010-2. $R^2=0.214$.

Comparison of methods

Phytoplankton and benthic production measured by the radioisotope technique and free water metabolism in 2011-2 (respectively: Figure 30, Figure 31) were found to have no significant relationship. However, FWM NEP did appear to be significantly related to NEP measured using O_2 incubations in light-dark bottles in 2010 (not shown; $r^2=0.55$, $p<0.05$).

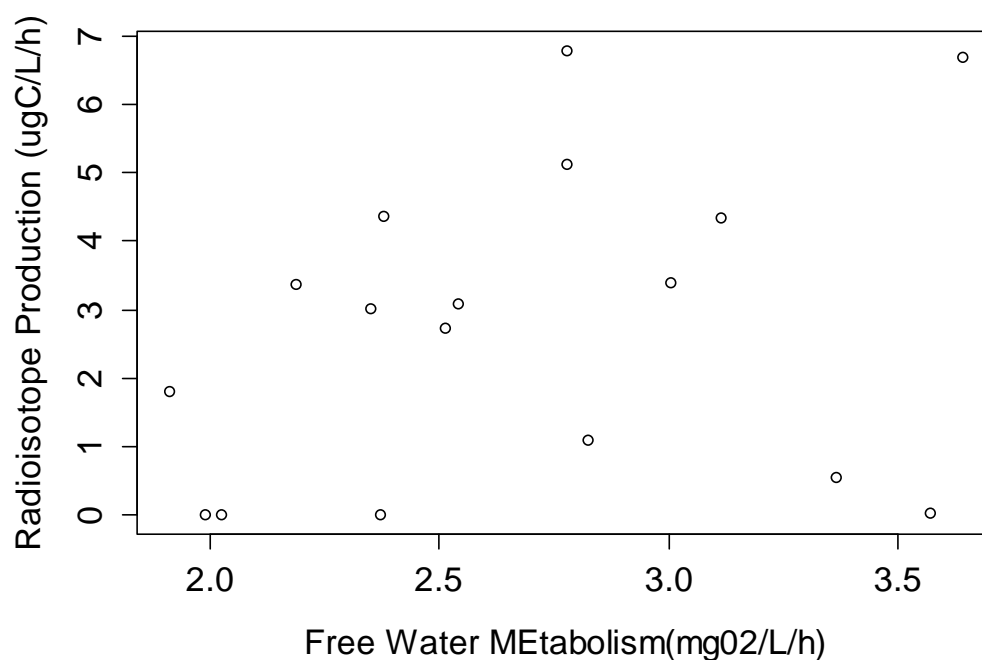


Figure 30: Comparison of methods used to measure production in IBP Pond C 2011-12: planktonic NEP determined via radioisotopes versus free water metabolism

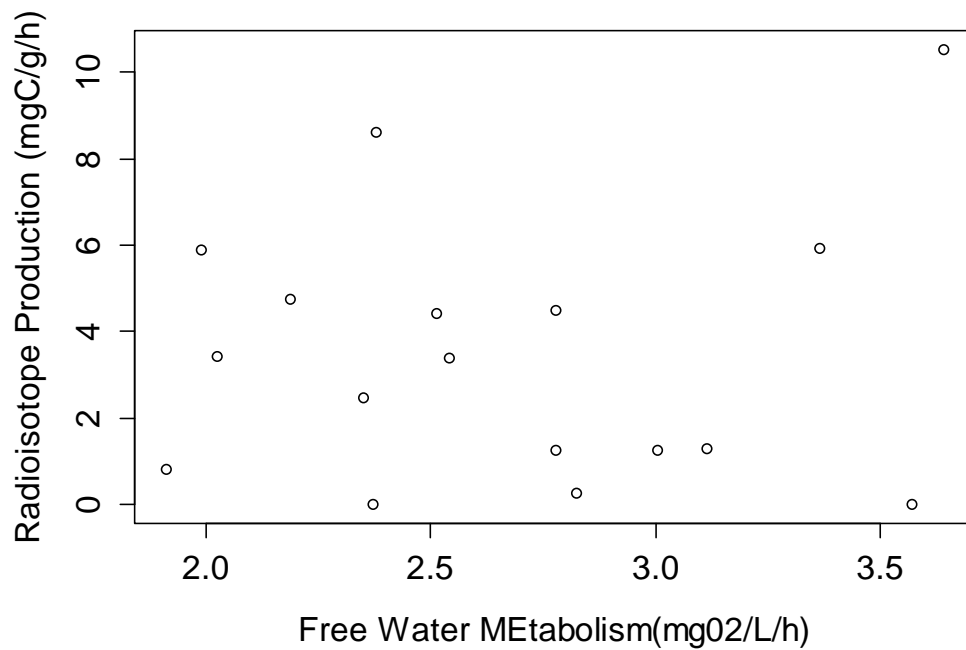


Figure 31: Comparison of methods used to measure production in IBP ponds 2011-12: benthic NEP determined using radioisotopes versus free water metabolism

CHL-a concentrations measured by the optical sensor in YSI and by extraction in 90% acetone were significantly related ($R^2=0.6236$, $p<0.0001$, Figure 32). It is well known that in situ optical sensors are not as accurate in estimating CHL-a as extractive analyses (YSI Environmental), and in this study, the YSI optical sensor tended to overestimate CHL-a by a factor of 4. For subsequent analyses, we converted CHL-a measured optically by the YSI a value equivalent to the extractive method using the formula of the regression line ($y= 0.2592x - 0.4044$).

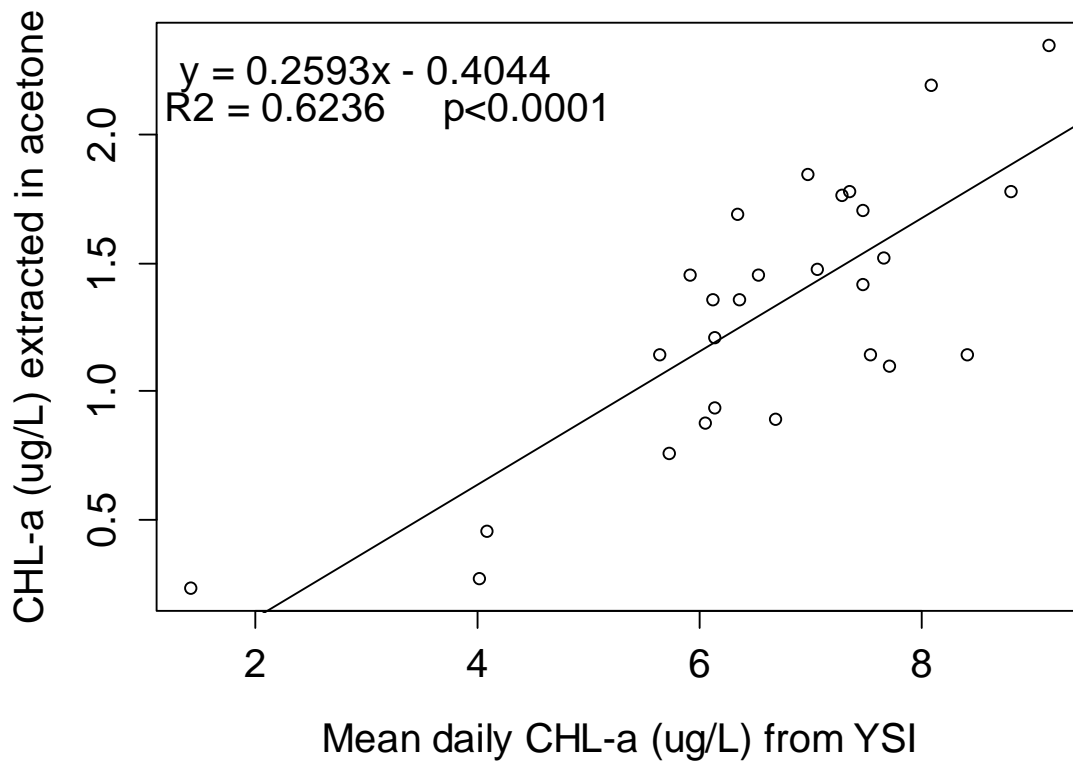


Figure 32: Comparison of methods of measuring CHL-a, using the optical sensor on the YSI and extraction in acetone, with concentrations calculated using Strickland and Parsons (YEAR) formula. $R^2=0.6236$.

Implication of Arctic freshwater production

NEP regression trees of radioisotope techniques indicated increases of production when CHL was equal to or greater than $1.19 \mu\text{g/L}$ and FWM NEP thresholds of $1.3 \mu\text{g/L}$ when converted from YSI CHL value (Figure 33). Chlorophyll values from 2008-12 exceed or met at the thresholds values 83% of the time and always exceed threshold values during the latter half of the season. Conversely, chlorophyll values only exceed the threshold during 25% of the season in 1970-3.

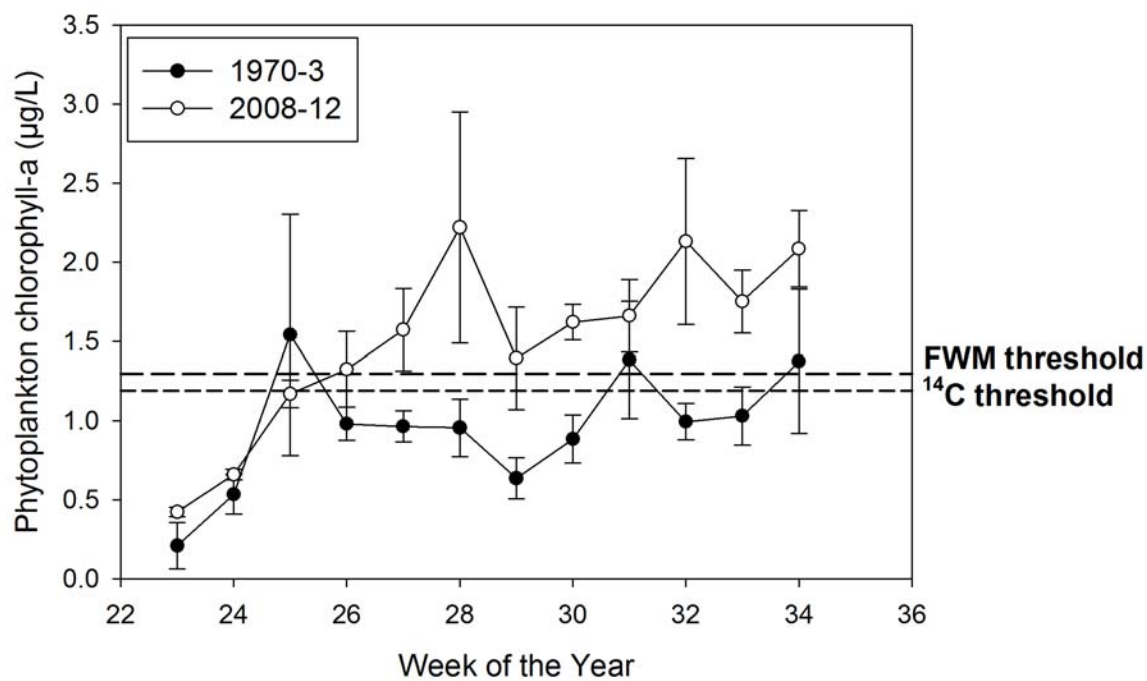


Figure 33: Comparison of weekly average CHL-a concentrations in 1970-3 and 2008-12 to threshold CHL-a values found by regression trees of NEP measured by ¹⁴C radioisotope (1.19 µg/L) and FWM techniques (1.3 µg/L).

DISCUSSION

Weekly average phytoplankton chlorophyll-a biomass from IBP Pond B, C and E was significantly greater in 2008-12 than chlorophyll-a biomass recordings from 1970-73 ($p=0.0022$) (Figure 34; Hernandez et al. In prep). The goal of the current study is to determine whether there were also changes in carbon uptake in these ponds, and what the primary drivers of these changes were.

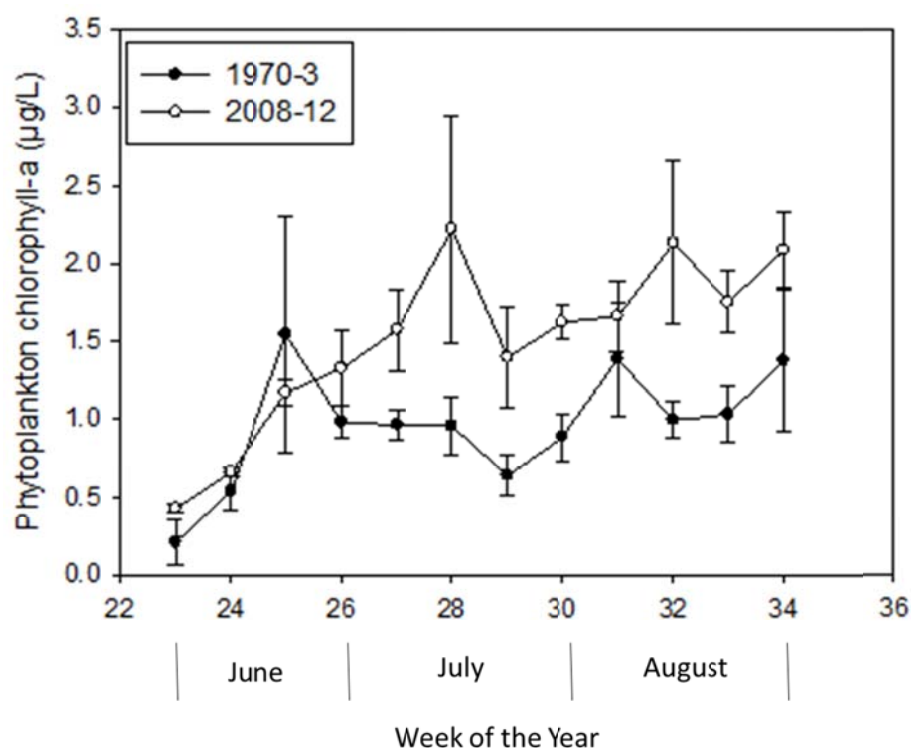


Figure34: Mean (\pm 1 standard error (SE)) phytoplankton chlorophyll-a biomass in IBP ponds B, C, and E for 1970-1973 vs 2008-2012 (from Hernandez et al. In prep).

Only some of our initial predictions regarding changes in algal biomass and production were supported by our analyses. Comparisons of phytoplankton net ecosystem production measured by radioisotope ^{14}C did not record consistent difference between the 1970s and 2011-2; however, regression trees indicated that year, in addition to other variables, was an important factor determining NEP.

Since phytoplankton are a primary food source for zooplankton greater zooplankton abundance should result in lower algal production (Williamson et al., 2010). In both 2011 and 2012, *Daphnia*

abundances peaked in week 28 (Vargas, unpubl. data). Declines in NEP around this time may have been due in part to zooplankton grazing. Incubations were done in small BOD bottles that represented only a small portion of the algae in ponds, thus peaks in NEP could also indicate that samples taken that week contained more algae by chance than what would be representative of pond conditions. Slight differences among methods used in current years compared to methods used in 1970-1973, most notably the need to complete ^{14}C incubations in a lab environment utilizing artificial irradiance instead of the field where natural sunlight can be used, limits our ability to make direct comparisons. This is especially relevant for benthic algae production measurement, which was completed using very different methods of sediment extraction from ponds in 2011-12.

Due to the challenges of recreating ^{14}C methods, we examined the feasibility of using an alternative and updated method of measuring NEP. Free water metabolism methods have the advantage of measuring both phytoplankton and benthic algae simultaneously (Pace and Prairie, 2005), which could help eliminate complications of method compatibility in the future studies. The continuous data will allow a better understanding of daily changes in NEP instead of weekly assessments made with ^{14}C incubations. Although there was no significant relationship between ^{14}C and FWM measured NEP, this is likely due to the lack of respiration measurements from FWM, the inability to combine phytoplankton and benthic measurements from ^{14}C and the renowned inaccuracies of ^{14}C particularly due to small bottle samples.

Daytime NEP from FWM in 2010-2 averaged $2.85 \text{ mgO}_2/\text{L}/\text{day}$ and NEP measured at the end of the season in August when sunsets occurred averaged $2.12 \text{ mgO}_2/\text{L}/\text{day}$. In both daytime NEP and NEP measured by the difference of GPP and R, the ponds were net autotrophic having positive sum of O_2 indicating greater gross primary production as compared to respiration. Cole et al. (2000) suggested that when O_2 values are positive the ponds have the potential to be taking up more carbon than they are releasing, making them carbon sinks. NEP values found were greater than findings by Staehr et al.

(2010) in which FWM NEP was approximately 1 mg O₂/L/day in three lakes in northern Wisconsin. Findings by Cole et al. (2000) found even lower seasonal mean NEP in Lake Paul (0.349 mgO₂/L/day). While NEP at the very end of the season when more darkness occurred in Barrow, was more similar to Staehr's and Cole's findings, our findings are not directly comparable to those of Staehr et al. (2010) and Cole et al. (2000) due to vast biological differences of the ecosystems studied. For instance, IBP ponds are located above permafrost and completely freeze approximately nine months of the year preventing fish from inhabiting these ponds. Barrow ponds also experience continuous sunlight preventing respiration values being obtained where Staehr et al. (2010) and Cole et al. (2000) were able to obtain respiration for dark measurements. Conversely to the previous comparisons, Christensen et al. (2013) found that in a small pond located in a lime stone quarry in southeast Sweden, mean NEP of 12 mg O₂/m²/day. These values are similar to findings in IBP ponds where mean daytime NEP was found to be 12.23 mg O₂/m²/day. Although the pond environment studied by Christensen et al. (2013) is more similar to that of IBP ponds, there still exist important biological differences such the presence of permafrost as well as continuous sunlight. The lack of comparative data further emphasizes the need to expand the use of free water metabolism techniques to arctic environments.

Not surprisingly, phytoplankton chlorophyll concentrations were found to be a primary driver of both free water metabolism and phytoplankton NEP as measured by radioisotopes. In both FWM and radioisotope NEP regression trees, more algal production occurred when CHL was greater or equal to a threshold concentration 1.19 to 1.41 µg/L. For the majority of the growing season in 2008-12, phytoplankton CHL concentrations exceeded these thresholds, while these threshold concentrations were only exceeded 25% of the time during the growing season of 1970-3. While direct comparisons of NEP among years of NEP based on radioisotopes revealed no obvious increase in carbon uptake over the past 40 years, it is likely that differences in protocols, including sediment extraction techniques and radioisotope incubation environments, may have masked any changes. Extrapolation based on

chlorophyll-a concentrations, which are more comparable among years, suggest that total carbon uptake may have changed through time.

Historically, freshwater ecosystems in the Arctic have been identified as phosphorus limited. For example, Peterson et al. (1983) found phosphorus limitation of benthic algal growth in arctic tundra streams, while Alexander et al. (1980) found phosphorus limitation of phytoplankton in arctic tundra ponds. Both historic analysis by Stanley (1976a), as well as regressions trees reported here of data collected from IBP ponds B, C and E over 1970-73 in the 1970s showed that benthic production in the 1970s was primarily driven by phosphorus concentrations, with greater benthic NEP under conditions of phosphorus enrichment. In the 1970s, Stanley's (1976a) whole pond phosphorus fertilization experiments showed benthic algae photosynthesis rates increased in ponds that had phosphorus addition compared to those that did not. In mid-June benthic photosynthesis rates doubled in fertilized ponds and continued to increase through August. These findings support the findings that benthic NEP was primarily driven by phosphorus concentrations. Conversely, benthic production from current years (2011-2) was not influenced by nutrient concentrations but rather greater benthic production was observed at higher temperatures. With current pond temperatures 2°C warmer than in the 1970s (Lougheed et al. 2011), warming could be one potential reason for autotrophic FWM measurements in present-day study.

Chlorophyll concentrations in the IBP ponds measured from both the YSI sonde and acetone extraction were largely influenced by dissolved organic carbon (DOC) concentrations. Interestingly, regression trees showed high concentrations of DOC (≥ 22.48 mg/L and ≥ 16.01 mg/L in YSI measured CHL and acetone extracted CHL-a regression trees, respectively) to be related to greater amounts of CHL (1.81 μ g/L and 1.63 μ g/L, both expressed as acetone extracted CHL). Conversely, Carpenter et al. (1998) found that DOC lead to decreased chlorophyll biomass likely due to shading effects in four manipulated small deep lakes in Wisconsin. An important difference between lakes studied by Carpenter

et al. (1989) and IBP ponds is presence of permafrost. We suggest that DOC could be a conservative tracer of permafrost thaw in these arctic aquatic ecosystems (Reyes and Loughheed, In Prep). When permafrost thaws, it releases a variety of macro- and micronutrients into an ecosystem; some such as ammonia and soluble reactive phosphorus would be quickly used by algae in the system and others, such as DOC, would not. Reyes and Loughheed (In Prep) conducted incubation of thawing permafrost and measured nutrients being released. Findings indicated that as permafrost thawed more nutrients were released, including DOC. This is further supported by the fact that, at higher levels of DOC, high light extinction was shown to be related to higher levels of CHL-a biomass. High light extinction indicates lower water clarity, which would tend to lead to lower chlorophyll levels; however, if this is a tracer of nutrient release from permafrost it may help explain higher chlorophyll levels.

Recent studies have found nitrogen and phosphorus co-limitation of algae in freshwater ecosystems (Elser et al., 2007; Symons et al., 2012; Ogbebo et al., 2009). Similarly, regression trees of chlorophyll concentrations in ponds along a gradient of disturbance supported findings by Hernandez (2012) in which phytoplankton growth in the IBP ponds is currently nitrogen or nitrogen-phosphorus co-limited. The regression tree indicated that higher levels of ammonia and total nitrogen lead to greater levels of CHL concentrations in these ponds. Interestingly, higher silica concentrations were also found to result in increased CHL concentrations. Silica is known to be a limiting factor for diatom growth and can therefore be a factor regulating primary production (Marin-Jezequel et al., 2000). Wyatt et al. (2010) found that algal biomass in boreal wetlands in Alaska was co-limited by a combination of nitrogen, phosphorus and silica. Current related work in IBP ponds has found that the relative abundance of diatoms has increased since the 1970s (Vargas, 2011); the abundant diatoms may depend highly on silica, which appears to be limiting in these systems. Although results seem to indicate increases of silica are related to increases of CHL-a, further investigation of effects of Si on CHL in arctic ponds is much needed.

Our photosynthesis-irradiance curves were not as informative as we would have hoped, largely because of the limitations of working in a remote location that prevented us from monitoring our data as they were collected. Additional challenges included regulation of the use of ^{14}C to only be permitted in a laboratory setting, which prevented the use of natural light that was used during incubations in the 1970s. Nonetheless, we acquired some interesting results. Averaged over the entire 2012 season, both phytoplankton and benthic algae photosynthesis rates were greatest at warmer temperatures (20°C), while Photosynthesis – Irradiance curves completed by Stanley and Daley (1976) showed maximum rates of photosynthesis of phytoplankton to occur at 14°C and maximum rates of photosynthesis of benthic algae to occur at 20°C . Vargas (2011) found that algal community composition varied throughout the growing season and has changed in the IBP ponds over the past 40 years. Alexander et al. (1980) reported IBP pond communities to be dominated by Cyanophyta and Chlorophyta in 1972 during mid-July whereas Vargas (2011) indicated that Bacillariophyceae accounted for an average of 80% of benthic biomass in IBP ponds. Additionally Vargas (2011) found species of Cryptophyta and Euglenophyta that were not recorded by Alexander et al. (1980). This change in community composition of algae in IBP ponds could be a major factor in the changes seen in P – I curves. Photoinhibition was observed only in phytoplankton at lower temperatures. Conversely, Markager et al. (1999) consistently observed photoinhibition at irradiance levels above $1000\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ in 4 arctic lakes, and Stanley and Daley (1976) also observed photoinhibition of phytoplankton in IBP ponds at 8°C . These results suggest that, even though tests indicated otherwise, we may not have been using sufficiently high illumination levels, or appropriate light wavelengths to achieve comparable results as mentioned before with the use of natural sunlight to artificial grow lights.

Future research areas

- While free water metabolism techniques suggested that IBP ponds are net autotrophic, other measurements are needed to better determine if ponds are acting as carbon sinks or sources. Continuous measurements sensors for CO₂ are available and have been shown to be well suited for CO₂ monitoring (Hari et al., 2008). Continual CO₂ monitoring could be used to confirm fluxes seen in FWM experiments and aid in determining if arctic tundra ponds are acting as carbon sinks.
- The design of the algal incubations for Photosynthesis – Irradiance needs much improvement in order to determine maximum rates of benthic and planktonic algae. The design of the incubations did not have high enough irradiance levels to allow P_{max} to occur for both types of algae; the primary challenge was that due to current regulations of the use of ¹⁴C we were not permitted to complete these analyses in the field as they were done in the 1970s. A method allowing incubations to be conducted under natural sunlight would greatly improve our ability to compare among years. More replicates of each light condition could also improve photosynthesis measurements and provide more reliable P-I curves.
- Very little research has been done in arctic aquatic ecosystems looking at factors controlling phytoplankton and benthic algal biomass. As findings suggest that silica could be a limiting factor in phytoplankton CHL-a biomass, mesocosm experiments could be conducted incorporating silica, nitrogen and phosphorus addition similar to those done in boreal wetlands by Wyatt et al. (2010). Similarly, nutrient diffusing substrate experiments similar to those conducted by Hernandez (2012) could be modified to include silica limitation.
- DOC was found to be related to increases CHL concentrations in this study, but in other studies often related to decreased CHL and production. Although it is believed that increase of DOC indicate permafrost thaw which would release other limiting nutrients such as nitrogen and

phosphorus future studies could create incubations using water from permafrost cores comparing algal growth.

CONCLUSION

Several changes in IBP ponds have occurred over the past 40 years. As temperatures continue to increase and nutrients are being released into the ecosystem, algal production and chlorophyll biomass will be impacted and effect carbon fluxes in the system. Higher levels of nutrients such as DOC and nitrogen in the ponds was found to be related to increases in chlorophyll-a biomass. These findings are consistent with other Arctic freshwater studies. Interestingly silica was also found to increase CHL levels, since this relationship is less well studied we suggest nutrient limitation experiments be done to better understand silica's impacts on CHL and NEP. Not surprisingly, increased levels of CHL where shown to be related to higher levels of NEP. A more modern method of measuring NEP, free water metabolism of O_2 , proved to be very useful in determining that the ponds were net autotrophic. In order to better determine if ponds are acting as carbon sinks or sources, we suggest using FWM techniques measuring CO_2 . As the growing season continues to increase in length due to climate change and permafrost thaw continues to increase, these results suggest that primary production in arctic tundra ponds will increase and tundra ponds may become vital carbon sinks in northern latitudes.

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APPENDIX A

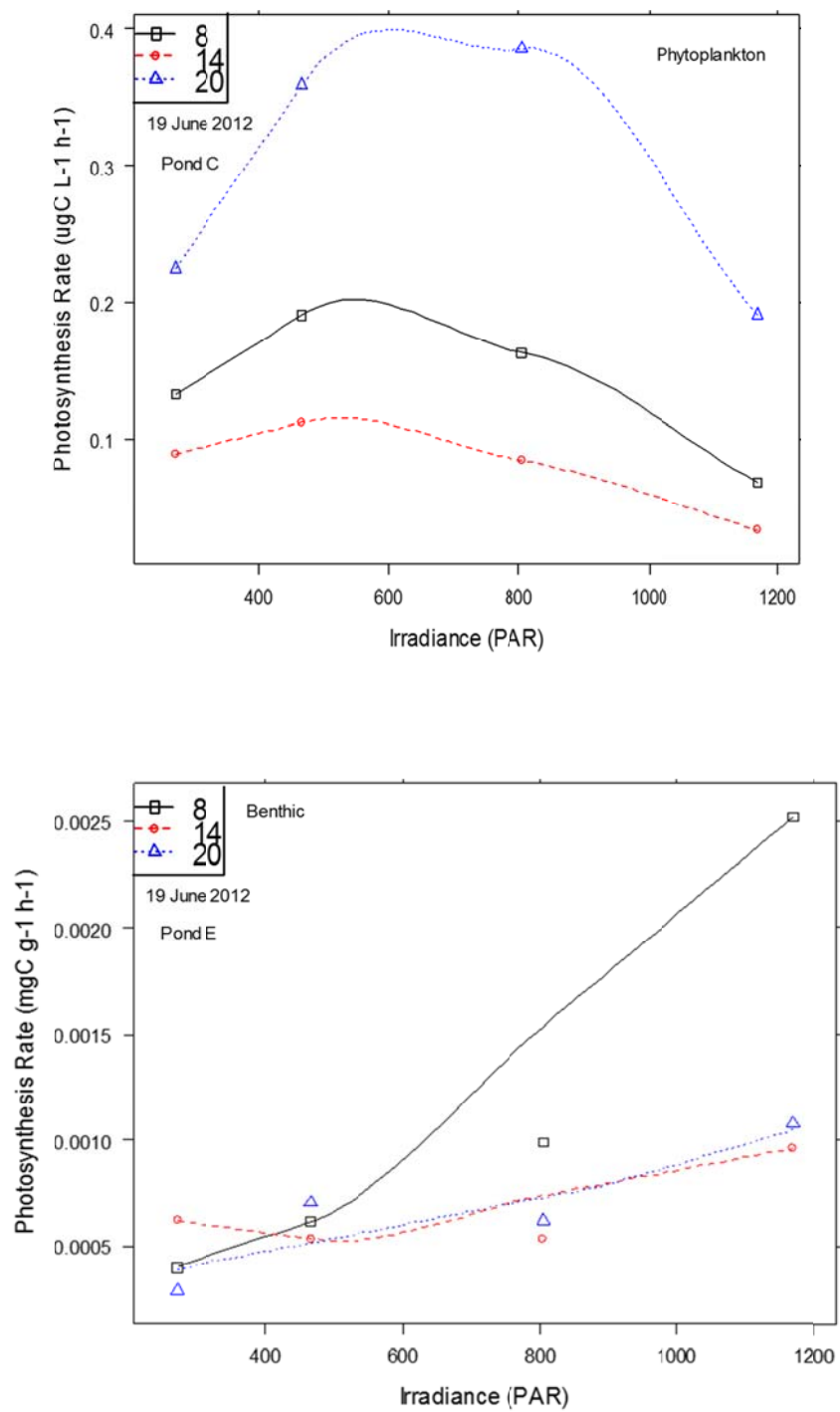


Figure A.1: Phytoplankton P-I curve 19 June 2012 (top). Benthic P-I curve 19 June 2012 (bottom)

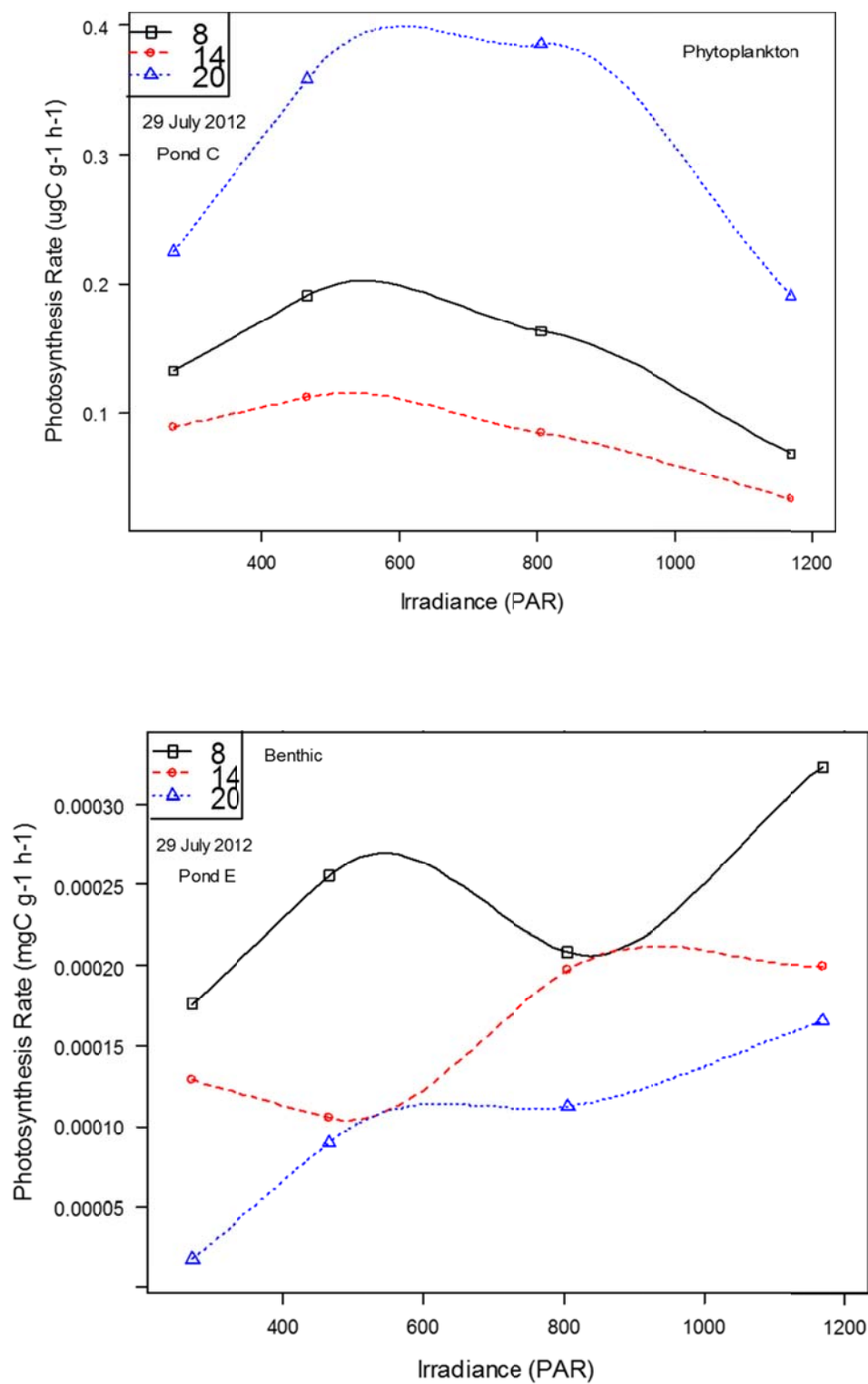


Figure A.2: Phytoplankton P-I curve 29 July 2012 (top). Benthic P-I curve 29 July 2012 (bottom)

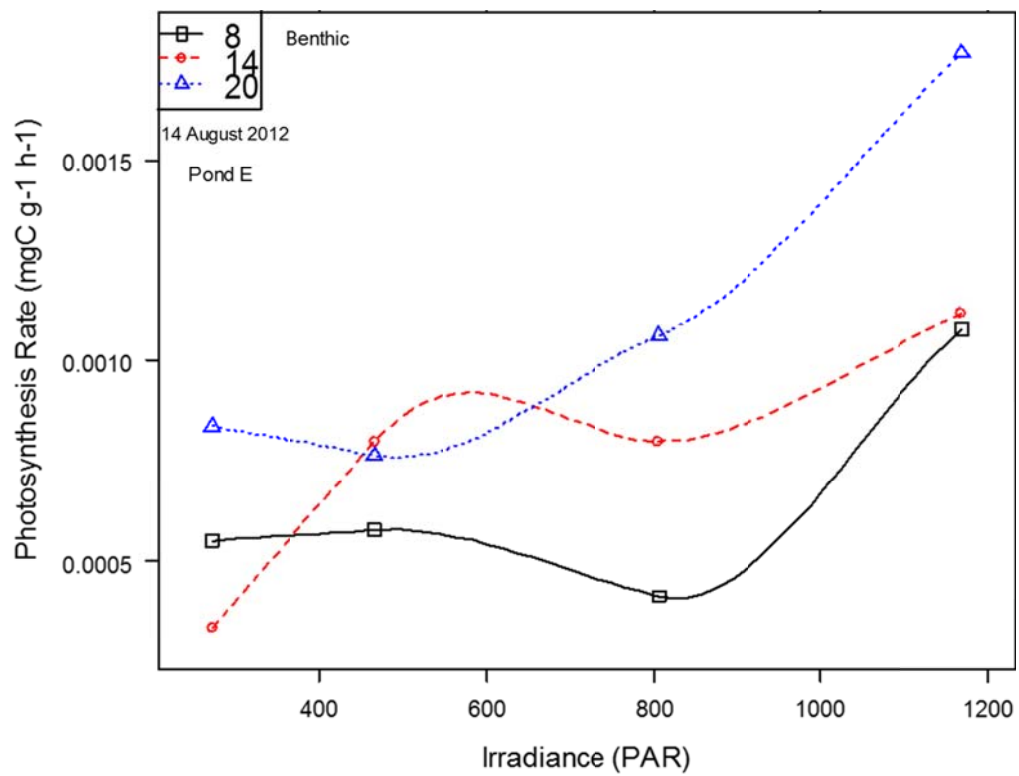
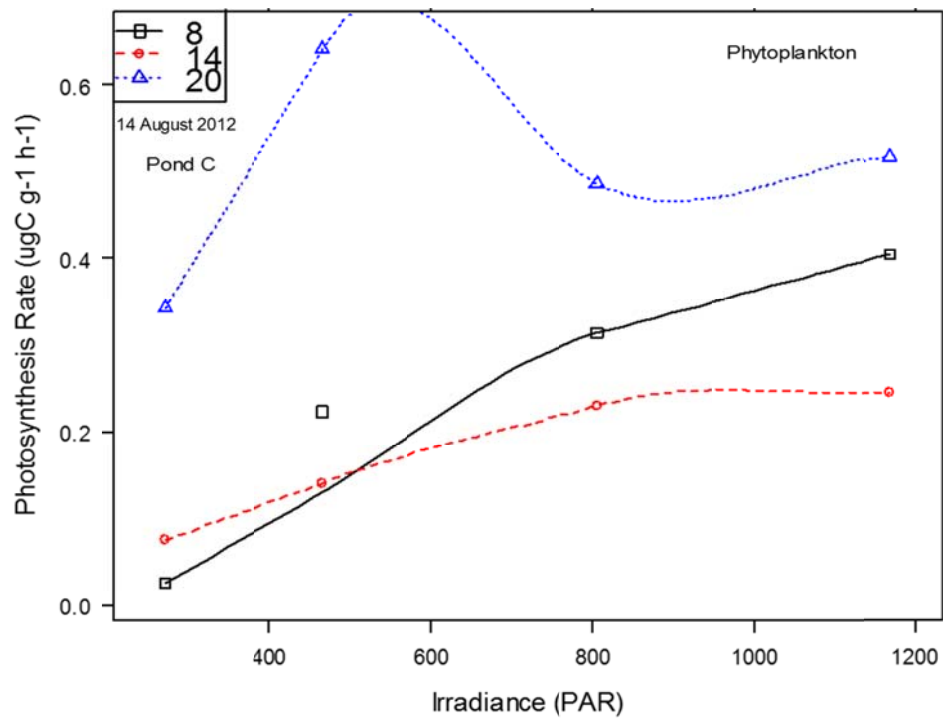


Figure A.3: Phytoplankton P-I curve 14 2012 (top). Benthic P-I curve 29 July 2012 (bottom)

VITA

Nickole Miller completed her undergraduate degree in Biological Sciences focusing on Ecology and Evolutionary Theory from the University of Texas at El Paso in 2011. While working on her undergraduate degree she tutored remedial higher school students in mathematics and science. After completing her Bachelor's Degree she began working with Dr. Loughheed to obtain her Masters in Biological Sciences. Her master's research focused on Arctic tundra ponds leading her to spend a summer in Barrow, Alaska. Miller is currently residing in Colorado where she hopes to obtain a job working on maintaining the water of quality of lakes and creating out reach programs.

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