COLUMBUS STATE UNIVERSITY

AN ANALYSIS OF THE EFFECTS OF TEMPERATURE AND OTHER ENVIRONMENTAL FACTORS ON MICROORGANISMAL PRODUCTIVITY WITHIN AQUATIC ECOSYSTEMS USING LONG-TERM DATA FROM VARIOUS LTER AND ILTER SITES

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AN ANALYSIS OF THE EFFECTS OF TEMPERATURE AND OTHER ENVIRONMENTAL FACTORS ON MICROORGANISMAL PRODUCTIVITY WITHIN AQUATIC ECOSYSTEMS USING LONG-TERM DATA FROM VARIOUS LTER AND ILTER SITES

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ABSTRACT

Global climate change is a phenomenon resulting in more extreme weather patterns and species diversity loss. In this study, I explore the impacts of climate change on regional patterns of microbial productivity. Variation in microbial productivity was explained using temperature, salinity, and dissolved oxygen as predictors in regression models with data from the LTER and iLTER network of sites that ranged from the poles to the equator. I found a positive relationship between temperature and productivity. Antarctica and Arctic sites exhibited the strongest positive relationships supporting prior research demonstrating temperature as one of the driving forces of productivity change in polar ecosystem composition and productivity. In addition to the temperature-productivity relationship, I found a positive relationship between chlorophyll concentration and productivity, a negative relationship between salinity and productivity, and a negative relationship between light irradiance and productivity indicating how other environmental factors affect productivity at the microscopic level. To compare microbial productivity among regions, I merged the data from the different sites into a single analysis of productivity. Productivity change in Antarctica was significantly different from the other sites based on the interaction between time, temperature, and location that indicated temperature effects on productivity were increasing faster in Antarctica than at other latitudes, confirming the single site analysis results. This study adds to a growing body of literature demonstrating that the impacts of climate change are stronger near the poles.

INDEX WORDS: Microorganismal productivity, temperature, climate change

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Introduction

Global climate change affects complex processes including rates of decomposition in microbial loops, nutrient cycling, and ocean acidification (Rochera et al., 2019, Hansel et al. 2020). Studying the processes that govern global climate change momentum is just as important as studying the consequences of that momentum (Wachnicka et al. 2013, Rochera et al., 2019, Ha¨nsel et al. 2020). Understanding the effects of global climate change and the principles that govern it will enable better forecasting of consequences, information for policy makers, and provide for more meaningful proposals to mitigate current and future impacts of global climate change.

Climate change affects large scale spatial and temporal processes. The complex decadal weather cycles of the Southern Pacific Ocean known as ENSO or El Nino and La Nina are two examples. These complex weather patterns are a result of the interactions of atmospheric and oceanic processes that influence the weather around the entire planet. Climate change increases the severity and variability of weather phenomena like hurricanes and drought that make predicting when they may occur less predictable (Wachnicka et al. 2013, Yang et al. 2018). Some of the regions impacted by the fluctuations created by these weather systems include the western pacific and the gulf coast of the United States, where these changes have led to alterations in the aquatic food web, such as with changes to diatom assemblages, which further alter ecosystem functionality (Wachnicka et al. 2013, Hissano et al., 2018, Lindegren et al. 2018, Yang et al. 2018). Other large-scale consequences garnered by global climate change include the loss of ice during the summer months and the establishment of woody plant life and shrubbery near the poles (Sistla et al., 2013, Umbanhowar et al., 2017, Rochera et al., 2019). In addition, other large-scale effects of climate change include alterations to ecosystem productivity in aquatic ecosystems such as Lake Kasumigaura in Japan and other such large water bodies (Hader et al. 2014, Matsuzaki et al. 2018). Though climate change radiates through ecosystems at large spatial scales the changes begin at the smallest spatial scales where microorganismal community composition is altered (Hisano et al., 2018). Examples of these changes in functionality include toxic cyanobacterial blooms that reduce oxygen levels and increases in tree mortality that decrease carbon sequestration by a forest (Rapp et al., 2012, Caron et al., 2013, Hissano et al., 2018).

Understanding how global climate change has influenced aquatic and marine ecosystems is critical because they are collectively the largest and most important climate regulators on the earth (Sarmento et al. 2010). For instance, oceans serve as one of the largest carbon sinks on earth (Sarmento et al. 2010, Crichton et al. 2021). Microorganisms serve as a carbon pump that helps to bury carbon through synthesis, transformation, and breakdown of carbon compounds, while other organisms like bacteria use these compounds to facilitate growth and other biological processes (Crichton et al. 2021). Afterwards, the carbon is gradually moved to the deep ocean and is buried (Crichton et al. 2021). These intricate processes such as nutrient recycling rates at the ocean surface are impacted by temperature leading to a reduction in the efficiency of the carbon pump as demonstrated by temperature dependent models (Crichton et al. 2021). Furthermore, microorganismal productivity represents an important portion of the planet’s productivity. For example, upwards of 50% of the ocean’s primary productivity is represented by phytoplankton while in the Baltic Sea bacterial productivity represents almost 15% of the ecosystem’s productivity (Kuosa et al., 1989, Caron et al., 2012). Microbial productivity has also been shown to control food-chain length and other trophic factors, especially in ecosystems where bottom-up linkages are important (Kaunzinger et al., 1998, Lindegren et al. 2018, Matsuzaki et al. 2018). These microorganisms have also been shown to help determine the quality of certain ecosystems, such as with the diatom assemblages in Florida Bay (Wachinicka et al. 2011). And with the continued progress of climate change with its consequences impacting so many things, it is thus very important to understand how its continued progress will impact some of the smallest denizens of this planet, especially when long term studies such as those conducted in Antarctica have already shown changes in microorganismal activity (Schofield et al., 2018).

Temperature is likely the most important aspect of the abiotic environment affecting microorganismal productivity (Sander et al., 1993, Mills et al., 2008, Matsuzaki et al. 2018). Temperature effects on microbial productivity can be attributed to enzymatic activity that enables microbes to exploit available nutrients and be resilient to UV LIGHT (Stanley 2010, Hader et al. 2014). Such increases in metabolic activity can cascade to affect food chain length, community structure, bacterial respiration, heterotrophic grazing, and body size (Shiah et al. 1994, Stanly 2010, Woodward et al. 2010, Wachnicka et al. 2013). Another linkage can be observed in places like the Arabian gulf, where productivity and diversity are coupled with factors such as the availability of iron and light (Al-Najjar et al. 2019).

Droughts are expected to increase in severity and frequency with increasing temperatures which are expected to impact community structure (Woodward et al. 2010). Experiments reveal that diatoms become the dominant algal form in some aquatic ecosystem experiencing droughts (Woodward et al. 2010). Evidence of this can already be seen in places like Florida, where microorganismal assemblages have been affected by periods of severe drought that have coincided with ENSO events (Wachnicka et al. 2013). Other linkages include the promotion of more rain in the Arctic, leading to the decreased prominence of smaller water bodies, temperature affecting primary productivity in places such as lake Kasumigaura, the geological record showing that changing climate has an impact on microbial productivity (Stanly 2010, Umbanhowar et al. 2017, Matsuzaki et al. 2018).

In this study, I use existing datasets in the LTER and iLTER network to explore the relationship between temperature and microorganismal productivity with time series analysis using temperature to predict changes in productivity, add additional environmental variables to the initial temperature-only model to account for additional variation in microbial productivity, and then compare the relationship between microorganismal productivity and temperature among locations to determine if there are any differences in productivity based on site or climate type. Given these objectives, I hypothesize that microorganismal productivity will increase with increasing temperatures, adding environmental variables will explain additional information in microbial productivity and there will be differences in productivity across both site and climate type. I predict these outcomes because metabolic processes increase with increasing temperatures up to an optimum after which they decline (Garzke et al. 2020). Second, adding more predictor variables to models should explain additional variation in microbial productivity given the complexity of biological systems (Woodward et al. 2010, Hader et al. 2014, Matsuzaki et al. 2018). Third, the combination of biological complexity, climatological differences, and geological differences among the sites (from the poles to the tropics) included in this study will produce differences among sites that will highlight the differential effects of climate change around the globe.

Methods

I tested the relationship between temperature and microorganismal productivity within aquatic ecosystems, using long term data gathered from LTER (long term ecological research) and iLTER (international long term ecological research) sites. I defined productivity as the change in growth or abundance of microorganisms over time. I selected sites that had at least ten years of continuous data with the last data collected within the last five years. Regions that were included in the study were Antarctica, the Arctic, California, the Czech-republic, Florida, and Japan (Table 1 and 2).

Though, temperature is an important factor affecting microbial productivity, there are other factors both biotic and abiotic, such as chlorophyll concentration, dissolved oxygen, and salinity influence productivity. Therefore, I included these factors as covariates with temperature when these data were collected alongside temperature and productivity. Multiple types of productivity measurements were included in this study because different sites used different methods.

Site Descriptions

Antarctica: The Antarctica LTER site is located west of the Antarctic peninsula at the Palmer research station (Table 1). Data collected at this site typically focuses on the polar marine biome with interests in subjects such as changes in the ecosystem, phytoplankton

(Scofield et al. 2018). These data were gathered during annual cruises of the western Antarctic peninsula (Palmer station LTER et al., 2020). Productivity was measured using leucine incorporation during protein synthesis by heterotrophic bacteria (Smith and Azam 1989). This method does not measure the photosynthetic rates for microbes (Kirchman et al. 1985). Temperature and salinity were other environmental factors that were collected during cruises Table 4).

Artic: The Artic LTER site is located at the Toolik Lake Field Station in Alaska. The site and its surrounding streams and lakes are the site from which the data regarding microbial productivity and the other abiotic and biotic factors, which include chlorophyll, dissolved oxygen, and primary productivity, were collected (Table 4). Productivity measurements were measured with leucine and is used to study the effects of climate change on the Artic tundra, nutrient cycling (Hobbie et al. 2017, Kendrick et al. 2018, Table 1).

California: The California LTER focuses on the California current ecosystem that is a coastal upwelling biome (California current ecosystem LTER et al., 2020). Research typically focuses on the effects of factors such as La Nina, ecosystem structure, and other subject matters (Cordero-Quirós et al. 2019, Rykaczewski 2019). Data for this study was gathered from semi-regular cruises held along the coastal region (California current ecosystem LTER et al., 2020, Table 1). The productivity measurements for this site were made using leucine incorporation, salinity was measured at this site (Table 4).

Czech-republic: The Czech-republic iLTEr is a site spread over numerous ecosystems. Data for this study was gathered from the Rimov reservoir and pertained primarily to bacterial abundance, temperature, and Chlorophyll a taken at regular intervals (Czech-republic iLTER et al., 2021, Table 4, Table 1).

Florida: The Florida LTER site is located in the coastal and freshwater marshes of the Everglades in southern Florida. Data for this study was gathered on a regular basis from the freshwater sections of Shark River Slough and Taylor Slough in Everglades National Park (Birceno et al. 2021, Table 4, Table 1). Productivity measurements at this site were taken through the use of thymidine incorporation (Table 1).

Japan: The Japanese iLTER is located in. Japan and covers a wide variety of ecosystems including Lake Kasumigaura and Ikawa Forest Station. Due to the varied ecosystems, data and research from this site includes trophic interactions, productivity, and more (Matsuzaki et al. 2018). Data for this study was gathered from different stations across Lake Kasumigaura (Japan iLTER et al., 2021). Productivity was measured using the incorporation of 13C in primary producers like phytoplankton (Matsuzaki et al. 2018). Chlorophyll *a*, dissolved inorganic carbon, and light irradiance were also measured this site (Table 4, Table 1).

Data Analysis and Model Generation

I aggregated all the variables into the highest possible temporal resolution that was common to all of the datasets to facilitate comparisons among sites using a single analysis. The mean of the variables was taken at either monthly, seasonally, or yearly intervals depending on the site. Temporal autocorrelation was removed via differencing ((n+1)-n) (Abdulhafedh 2017). The first model created for each site was the single variable model that only included temperature. The second modeling approach included additional explanatory variables known to affect productivity and species composition. Third, a hierarchical multivariable model was created using AIC to determine the model that explained the most variation among a set of different multivariable models for both the Arctic and Japanese sites because both sites had abiotic, biotic, and temporal variables within their datasets. Temperature was included in every model. Additional abiotic variables we considered included dissolved oxygen and light irradiance, while biotic variables consisted of chlorophyll *a* concentration. I also included the temporal variables year and month. These additional variables were then used to categorize the combined model with the lowest AIC value created with the abiotic model, the biotic model, the combined, containing both abiotic and biotic variables, and the temporal, containing only temporal variables. All multivariable models contained temperature as an explanatory variable.

Site And Climate Comparison

A three-way ANOVA was performed and tested for the interaction between the sites, years, and temperature variation. Tukey's post-hoc test was performed to determine which sites were different from each other and determine interactions. A second three-way ANOVA with interaction was performed in a similar manner to the first three-way ANOVA, but instead of site as one of the interactive factors it was replaced with the site's region (polar, sub-tropical, temperate, Table 1). All data manipulations and analyses were performed using R and the Tidyverse package. Data analysis and model generation were performed using R and the following packages, Car, Leaps, MASS, Multcomp, and Tidyverse.

Results

Model fit for the temperature only regression models were relatively low (Table 1). A slight trend towards a positive slope is apparent, based on the coefficients, at the Artic, Czech-republic, and Japan sites indicating that rising temperatures led to increasing productivity (Figs. 3, 7, 11, Table 2). This relationship is especially prominent at the Arctic site where the coefficient was 0.30. The temperature coefficients at the Czech-republic and Japan were weak (0.04 and 0.02, respectively) even though the slope was positive. Despite these low fits, the model fits were significant for both the Arctic and the Czech-republic ($P<0.05$, Table 2).

In contrast to the positive fits observed in the Arctic, Czech-republic, and Japan, weak negative fits were observed for the temperature only model in Antarctica (Fig. 1), California (Fig. 5), and Florida (Fig. 9, Table 2). The weak negative fits indicate that the temperature only model did not account for the change in productivity very well and more explanatory variables should be included to improve model fit.

Model Hierarchy & Multivariable Model

The combined model was the best at explaining productivity at both the Arctic and Japan sites. The Arctic model (AIC = 145.46, $R^2= 0.33$, $P < 0.05$) included chlorophyll *a* ($\beta = 1.45$), dissolved oxygen ($\beta = -1.19$), primary productivity ($\beta = 0.11$), and temperature ($\beta = 0.164$, Table 4, Fig. 4). Dissolved oxygen was the only variable with a negative coefficient indicating that as dissolved oxygen increases productivity declines. The other variables were positively related to productivity indicating that they increased together.

The Japan model (AIC = 1255.15, $R^2 = 0.14$, P-value <0.05) included chlorophyll *a* (β = 0.01), dissolved inorganic carbon (β = -0.03), light irradiance (β <0.00), and temperature (β = 0.03, Table 4, Fig. 12). The model also showed a negative relationship between productivity and dissolved inorganic carbon and between productivity and light irradiance, indicating that as either explanatory variable increased, productivity decreased (Table 4). The temporal did not increase the amount of variation explained by the model (Table 3).

The biotic model for the Czech-republic was an improvement on the temperature only model. The biotic model had a weak fit ($R^2 = 0.02$), but it also proved to be significant with a p-value less than 0.05, and was composed of temperature (β = 0.03) and chlorophyll (β = 0.02, Table 4). This model had a relatively low fit, but the variables were still significant given the p-value, showing that they still had an effect on productivity (Fig. 8).

In contrast to the temperature only model for Antarctica, the biotic model for Antarctica improved model fit ($R^2 = -0.34$ to $R^2 = 0.07$). Temperature (β = 268.07) and chlorophyll *a* (β = 5.85) were included in the final model and were among the largest standardized partial regression coefficients among all of the models at all of the sites (Table 4, Fig. 2).

The abiotic model for California had a fit of (-0.33) and was composed of temperature (β = -1.46) and salinity (β = -20.99, Table 4). In contrast to every other site though, the abiotic model for California had a negative coefficient associated with both temperature and salinity suggesting that as both temperature and salinity increased productivity decreased (Fig. 6).

Though improved as compared to the temperature only model, the abiotic model for Florida still had a negative fit ($R^2 = -0.03$). Temperature (β = 0.14) and salinity (β = 0.01, Table 4,

Fig. 10) both accounted for little of the variation in the data based on the model R^2 value. The weak positive relationship indicated that productivity increased with temperature and salinity.

Site And Climate Comparison

The site comparison revealed differences in productivity among sites. Differences among sites depended on variation among years and temperatures recorded at sites (Site-by-Temperature-by-Year, Table 5). Antarctica was different from all other sites except California (Tukey < 0.05, Table 6, Fig. 13). Productivity at the Antarctic site was far greater than every other site, where Antarctica's range for change in productivity extended from -50 to 50 with an outlier closer to 100, while every other site's range tended to hover between -20 and 20 (Fig. 13). However, when the sites were grouped by region, I found no differences in microbial productivity (Fig. 14 and Table 7).

Discussion

Climate change affects the planet at multiple spatial and temporal scales. For example, El Nino and ENOS weather patterns operate across decades and around the planet by impacting species composition in local communities (Woodward et al. 2010, Yang et al. 2018). I explored the effects of climate change in a variety of aquatic ecosystems in different regions of the world and compared those effects among regions using changes in microbial productivity in response to changes in temperature. I hypothesized that increases in temperature would lead to increases in productivity because metabolic processes are largely governed by temperature

(Woodward et al. 2010, Hader et al. 2014, Garzke et al. 2020). I did observe the hypothesized relationship between temperature and productivity at individual sites and among regions. These results support a growing body of literature demonstrating the positive relationship between productivity and temperature (Hader et al. 2014, Matsuzaki et al. 2018). Similar to other studies near the poles, I found that the effects of climate change were greater near the poles (Hader et al. 2014).

Temperature variation accounted differences in productivity, but other factors also contributed to explaining productivity. Model fit between temperature and productivity was generally low compared to other models. There are many factors that contributed to this result, both in the nature of the analysis and in the myriad abiotic and biotic factors that vary over space and time. To compare sites, I aggregated data taken at different spatial and temporal scales that may have obscured patterns between temperature and productivity. Collection methods at the different sites could have affected relationships. For example, productivity in Antarctica was measured using leucine incorporation, while in the Czech-republic abundance was used as a measure of productivity. Other variables likely covaried with temperature and productivity and accounted for variations in productivity. For example, nutrient availability and ecosystem composition influence productivity (Hader et al. 2014, Matsuzaki et al. 2018). Other studies have found inverse relationships between productivity (phytoplankton biomass) and increasing temperatures. Despite these factors, I still did observe the hypothesized positive relationship between temperature and productivity, further highlighting the fact that despite varying collection methods a positive relationship between temperature and productivity was observed. This pattern was strongest at the poles where experiments conducted in Antarctica and the Artic found that the addition of iron increased phytoplankton productivity that suggest that temperature alone does not limit primary productivity (Hader et al. 2014, Al-Najjar et al. 2019).

Given the many factors that impact productivity, I built different multivariable models that accounted for these factors in addition to temperature in order to better understand the factors impacting productivity. I observed an improved model fit as hypothesized, showing the various relationships between the factors and productivity. This included the positive relationship between chlorophyll and microbial productivity in Antarctica, the Artic, the Czech-republic, and Japan (Table 4). This result is similar to those found in Matsuzaki et al. 2018. Furthermore, these results support the type of microorganisms from which the productivity measurements were taken at each site. Bacteria and other heterotrophs for both Antarctica and the Arctic, microorganisms which graze and prey upon primary producers, such as the phytoplankton in Japan, for which chlorophyll is used in photosynthesis (Hader et al. 2014). The measurement of productivity in the Czech-republic was abundance, similar relationships between daphnia and phytoplankton, where increases in phytoplankton populations have been followed by increases in daphnia populations (Hader et al. 2014). Based on this, it can be concluded that, increases in chlorophyll correspond with increases in heterotrophic productivity.

Other noteworthy results observed from the multivariable models, were the negative relationships between salinity and light irradiance to productivity. The relationship I observed between salinity and productivity was negative. Prior research has found declines in the abundance of certain diatoms with increasing salinity levels indicating an alteration to the ecosystem composition and thus indicating an alteration to the ecosystem's productivity (Wachnicka et al. 2013). In addition, increases in salinity increase the penetration of light, especially short-wave light, which can damage cellular processes, leading to alterations in productivity (Hader et al. 2014). Thus, the observed negative relationship between salinity and productivity are in-line with previously stated observations and experiments.

The light irradiance and productivity relationship that was observed in Japan was not expected. Productivity at this site was for phytoplankton and would be expected to have higher activity with increasing light. For example, site in Alaska, Antarctica, and the Artic, algal blooms have increased with increasing light in addition to other environmental factors such as temperature (Hader et al. 2014). Alternatively, increases in short wavelengths of light can damage cellular processes leading to a decline in productivity (Hader et al. 2014). Therefore, increases in light irradiance could damage phytoplankton cells leading to declines in productivity.

The various sites I chose enabled me to compare productivity among sites and regions as they relate to temperature and time. Antarctica was different from every other site except California. Previous studies have found that higher latitudes experience greater impacts of climate change (Woodward et al. 2010). The northern portion of the western Antarctic peninsula has transitioned due to climate change from a short efficient food web, where larger phytoplankton and zooplankton dominate and energy is evenly distributed amongst trophic levels to a more open food web structure, where smaller phytoplankton and grazers dominate, further altering the productivity of the region (Schofield et al. 2018). In conjunction with this, the loss of sea ice in the region, there have been changes to the mixed layer depth, such as with the southern portion of the western Antarctic peninsula, where the upper ocean mixed depth has decreased by a factor of two, which has altered the regions productivity even more (Schofield et al. 2018). Furthermore, temperate and tropical regions are expected to be more productive when compared to polar regions due to warmer temperatures promoting more metabolic activity (Sarmento et al. 2010, Woodward et al. 2010). Finally, another reason for the differences observed between Antarctica and the other sites could be a matter of nutrient distribution, which has been shown to impact both productivity and composition (Rochera et al. 2019). For example, nutrient gradients observed in Antarctica have shown the shallower more eutrophic waterbodies to be more productive, when compared to deeper more oligotrophic waterbodies of the region (Rochera et al. 2019). And, though there was no direct comparison between the various depths associated with the collection of productivity within this study, given that the productivity data at the Antarctic site was taken just off the coast of the peninsula at a shallow depth may explain why the change was so large suggesting that climate change effects might be strongest in shallow ecosystems near the poles.

I expected there to be more similarities between Antarctica and the Arctic because of their polar locations and similar collection procedures. However, differences likely stemmed from variation in the habitats sampled, the Arctic sites included Arctic and sub-Arctic lakes, while Antarctic sites included shallow marine systems. Other reasons for the differences between both these regions could also stem from variation in heterotrophic grazing that offsets growth after population booms because of the increased grazing by predators such as daphnia (Hader et al. 2014). Second, the interactive effect between temperature and year could be driving this difference, especially given that fluctuations in nutrients have been observed in-line with fluctuations in temperature observed at varying times of the year (Rochera et al. 2019).

Though differences were observed when comparing productivity between the various sites, when sites were grouped into regions there was no differences in productivity. I expected differences among regions that ranged from polar, to sub-tropical because warmer temperatures tend to promote higher metabolic processes there should be a difference between the productivity of the various climates (Garzke et al. 2010). Though this result was unexpected there could be various reasons for its occurrence. For example, higher latitudes are warming rapidly that is leading to a myriad number of alterations within these ecosystems, some of which include changes to ecosystem composition which leads to changes in ecosystem productivity in one direction or another (Woodward et al. 2010, Wachnicka et al. 2013,Scofield et al. 2018).

In conclusion, this meta-analysis points to the far-reaching impacts of climate change and the need to better mitigate its impacts. First, it points to the positive relationship between temperature and microorganismal productivity, especially within polar regions as has been found in other studies comparing polar and temperate locations (Hader et al. 2014 and Matsuzaki et al. 2018). This trend will likely accelerate given the predicted increases in ocean temperatures of about 2°C over the next 100 years (Sarmento et al. 2010). These results demonstrate that climate change effects will cascade up the food web and disrupt community and ecosystem structure with unknown consequences but consequences that will surely affect ecosystem services to humans. Thus, this study along with many others contribute to the mounting evidence that steps must be taken to curb the effects of climate change. Expansion of this work should include additional sites and larger datasets that will provide better resolution to the effects of rising temperatures on microbial productivity and consequently, ecosystem function.

Tables and Figures

Table 1: Description, spatial location, collection frequency, and microorganismal productivity measurement for each chosen LTER and iLTER site.

Site Name	**Site Location**	**Site Climate**	**Site Type**	**Temporal Scale**	**Productivity Collection Frequency**	**Productivity Measurement**	**Productivity Units**
Antarctica	-63.8513°N -64.1815°W	Polar	coastal	2003-2017	seasonal	Leucine	Pmol/L/hr – production per liter per hour
Arctic	68.63°N 68.63°S - 149.613°E -149.613°W	Polar	lake and lake inlets	2000-2018	seasonal	Leucine	ug/C/day – production per liter per day
California	32.85317°N -117.733°W	Temperate	coastal	2007-2017	seasonal at irregular yearly intervals	Leucine	Âµg/L/day – production per day
Czech-republic	48.8332°N 14.4832°E	Temperate	in-land lake	1991-2019	monthly	Bacterial abundance	10^9/L – bacterial abundance per liter
Florida	25.761°N 25.761°S - 80.727°E -80.727°W	sub-tropical	coastal and rivers	2001-2018	monthly	Thymidine	Bacterial Production daily rate
Japan	36.0491°N 140.3792°E	Temperate	in-land lake	1981-2018	monthly	C13	gC m-2 d-1- Gross production per unit area per day

Table 2: R^2 values, p-values, coefficients, and other results from the temperature only model (site productivity = x*site temperature+b).

Site	**R2 Value**	**P-Value**	**Coefficients**	**Intercept**
Antarctica	-0.35	0.47	130.08	0.83
Arctic	0.1	0.03	0.3	-0.03
California	-0.49	0.91	0.11	0.47
Czech-republic	0.01	0.04	0.04	<0.05
Florida	<-0.01	0.38	0.14	0.33
Japan	<0.05	0.25	0.02	-0.03

Table 3: The model hierarchy and the AIC values associated with each model as determined by AIC analysis of the Artic and Japanese dataset.

Site	Model Type	Model Rank	Model Independent Variables	AIC Values
Artic	Combined	1	Temperature, Chlorophyll, Dissolved Oxygen, Primary Productivity	145.46
Artic	Biotic	2	Temperature, Primary productivity, Chlorophyll	149.38
Artic	Abiotic	3	Temperature, Dissolved Oxygen, pH	174.38
Artic	Temporal	4	Temperature, Month, Year	175.04
Japan	Combined	1	Temperature, Chlorophyll, Dissolved inorganic Carbon, Light irradiance,	1255.15
Japan	Biotic	3	Temperature, Chlorophyll	1321.02
Japan	Abiotic	2	Temperature, Dissolved inorganic carbon, Light irradience	1286.77
Japan	Temporal	4	Temperature, Year	1368.31

Table 4: The R^2 values, p-values, model type, and variables associated with each multivariable model along with their associated coefficients. Temp. = Temperature, °C; DO = Dissolved oxygen, mL/L; PP = Primary productivity; DIC = Dissolved Inorganic Carbon

Site	**Model Type**	**R^2**	**P**	**Temp.**	**Chl *a***	**DO**	**PP**	**Salinity**	**DIC**	**Light irradiance**
Antarctica	Biotic	0.07	0.28	268.07	5.85	NA	NA	NA	NA	NA
Artic	Combined	0.33	<0.05	0.16	1.45	-1.19	0.11	NA	NA	NA
California	Abiotic	-0.33	0.67	-1.46	NA	NA	NA	-20.99	NA	NA
Czech-republic	Biotic	0.02	<0.05	0.03	0.02	NA	NA	NA	NA	NA
Florida	Abiotic	-0.03	0.69	0.14	NA	NA	NA	0.01	NA	NA
Japan	Combined	0.14	<0.05	0.03	0.01	NA	NA	NA	-0.13	<0.00

Table 5: The results of the factorial ANOVA among sites.

Factors	**Sum of squares**	**Degrees of Freedom**	**F-value**	**P-value**
Site	587.30	5.00	4.19	<0.05
Temperature	566.20	1.00	20.20	<0.05
Year	30.70	1.00	1.10	0.30
Site and Temperature	611.40	5.00	4.36	<0.05
Site and Year	587.20	5.00	4.19	<0.05
Temperature and Year	569.40	1.00	20.32	<0.05
Site, Temperature, and Year	614.80	5.00	4.39	<0.05
Residuals	25894.40	924.00	na	Na

Table 6: The results of the Tukey's post-hoc test of the three-way ANOVA.

Factor 1	**Factor 2**	**Estimate**	**Standard Error**	**T-value**	**P-value**
Arctic	Antarctica	-3810.25	890.20	-4.28	<0.05
California	Antarctica	-2048.27	5276.52	-0.39	1.00
Czech-republic	Antarctica	-3759.24	829.08	-4.53	<0.05
Florida	Antarctica	-3634.38	879.36	-4.13	<0.05
Japan	Antarctica	-3766.59	828.98	-4.54	<0.05
California	Arctic	1761.98	5221.68	0.34	1.00
Czech-republic	Arctic	51.01	334.18	0.15	1.00
Florida	Arctic	175.87	444.49	0.40	1.00
Japan	Arctic	43.66	333.91	0.13	1.00
Czech-republic	California	-1710.97	5211.61	-0.33	1.00
Florida	California	-1586.11	5219.84	-0.30	1.00
Japan	California	-1718.32	5211.59	-0.33	1.00
Florida	Czech-republic	124.86	304.13	0.41	1.00
Japan	Czech-republic	-7.35	80.15	-0.09	1.00
Japan	Florida	-132.21	303.83	-0.44	1.00

Table 7: The results of the three-way ANOVA among regions.

Factors	**Sum of squares**	**Degrees of Freedom**	**F-value**	**P-value**
Climate	2.3	1	0.08	0.78
Temperature	5.6	1	0.19	0.67
Year	6.7	2	0.11	0.89
Climate and Temperature	2.4	1	0.08	0.78
Climate and Year	4.6	2	0.08	0.92
Temperature and Year	6.6	2	0.11	0.89
Climate, Temperature, and Year	4.7	2	0.08	0.92
Residuals	27854	936		

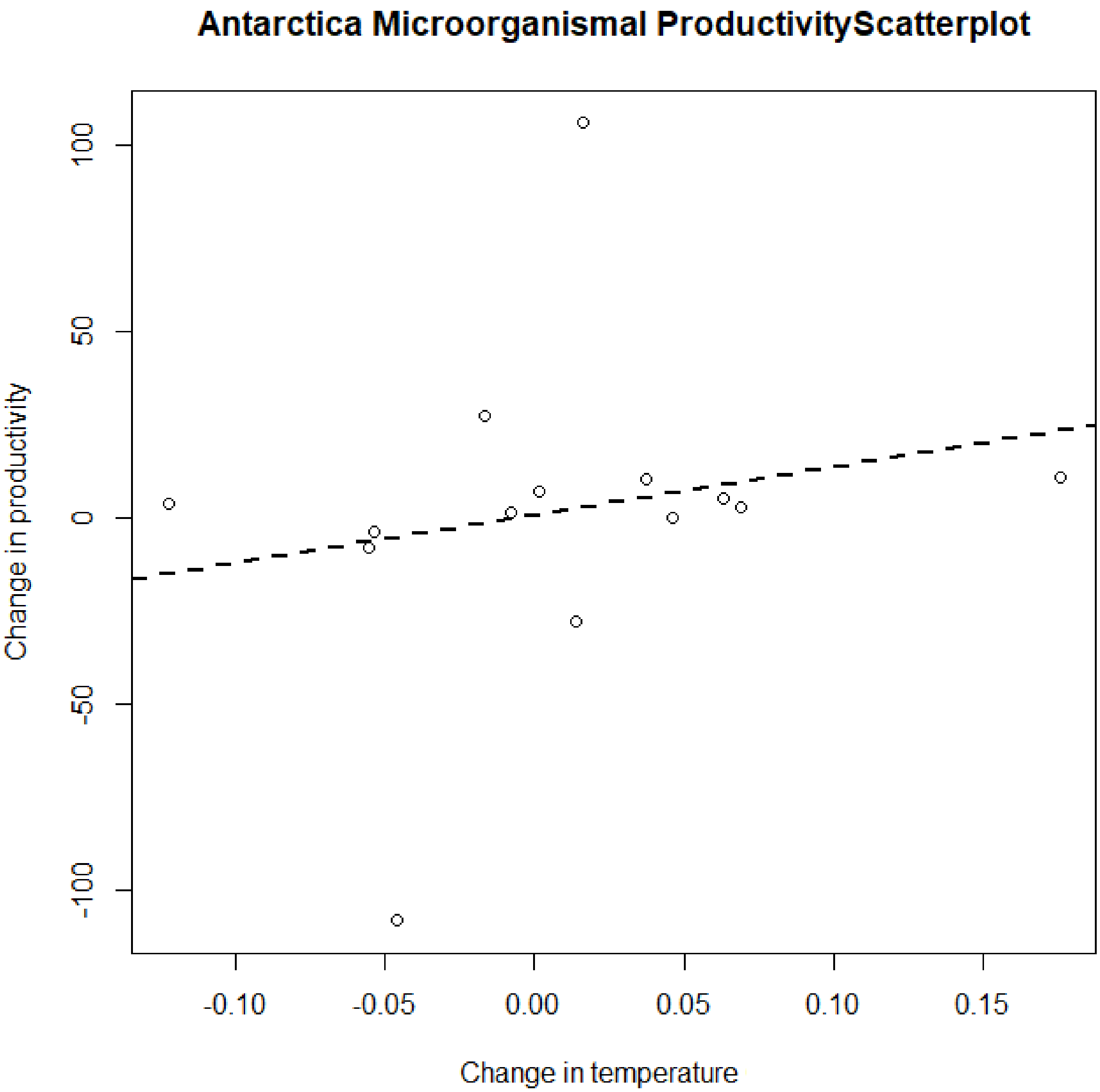

Fig. 1: Partial regression plot of the relationship between change in temperature and change in productivity with the temperature only model in Antarctica. R^2 = -0.35 P = 0.47. Productivity was measured at this site via leucine incorporation.

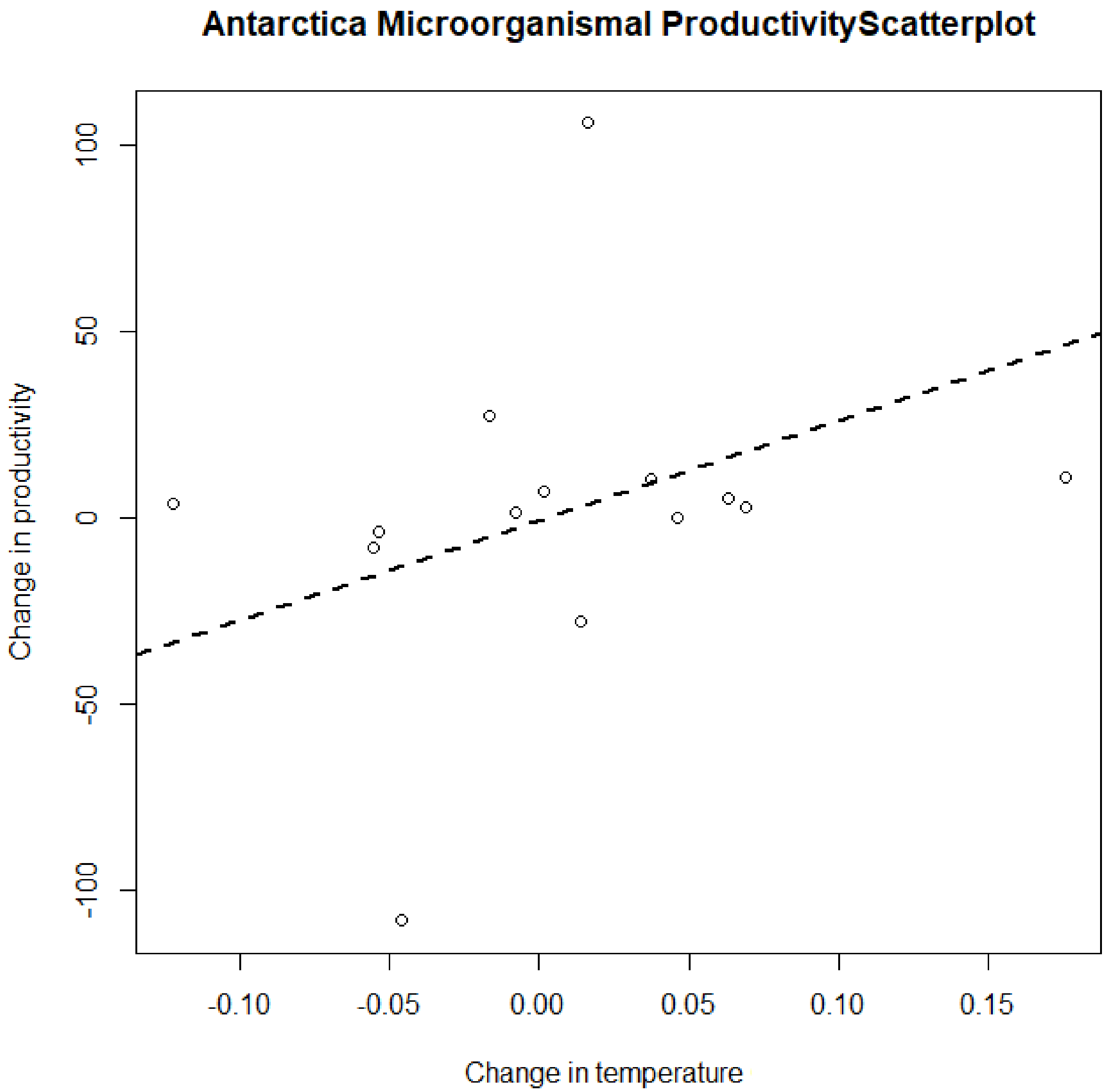

Fig. 2: Partial regression plot of the relationship between change in temperature and productivity with the biotic model in Antarctica, which contained both temperature and chlorophyll as independent variables. $R^2 = 0.07$ $P = 0.28$. Productivity was measured at this site via leucine incorporation.

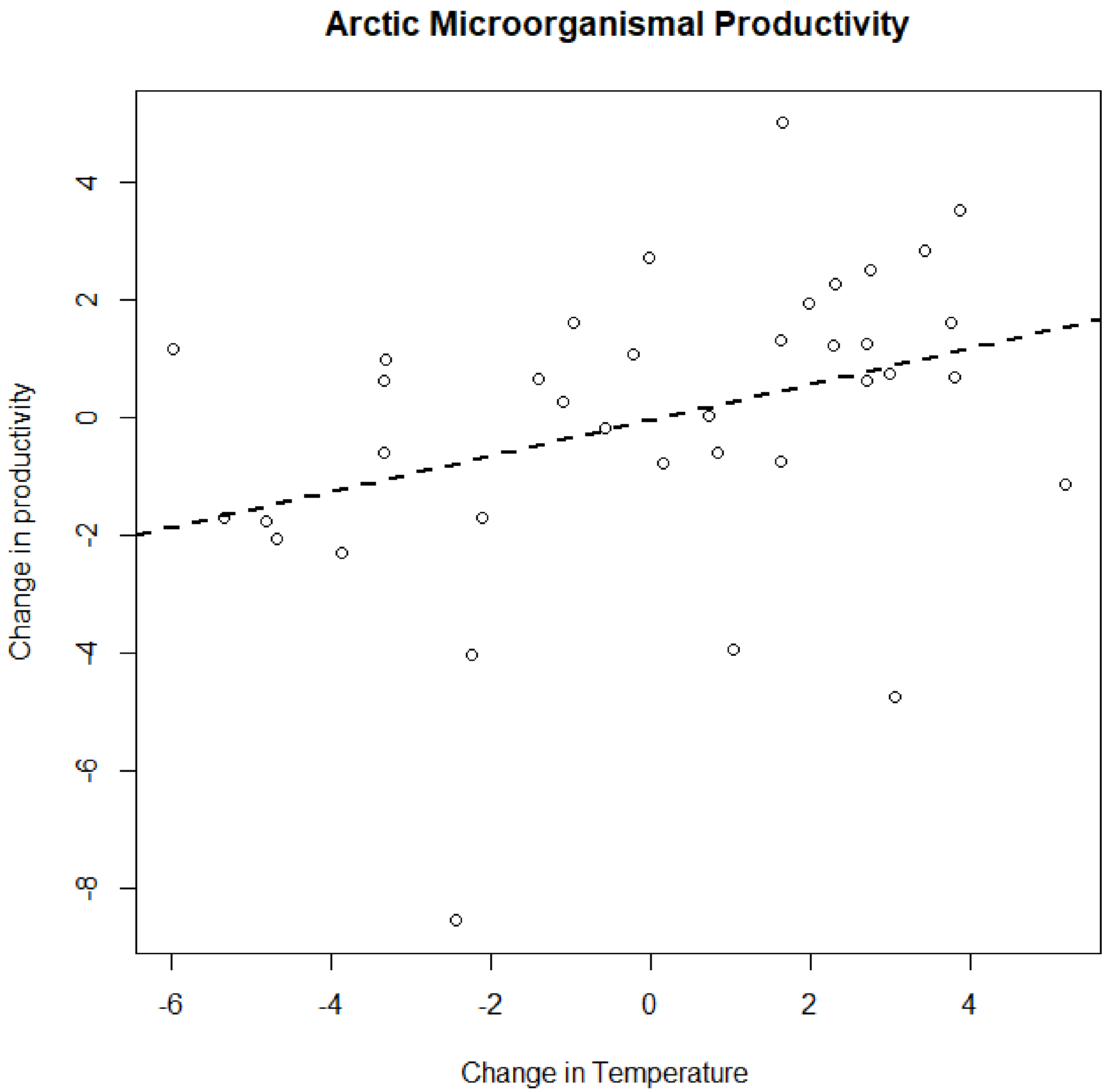

Fig. 3: Partial regression plot of the relationship between change in temperature and change in productivity with the temperature only model in the Arctic. $R^2 = 0.1$ $P = 0.03$. Productivity was measured at this site via leucine incorporation.

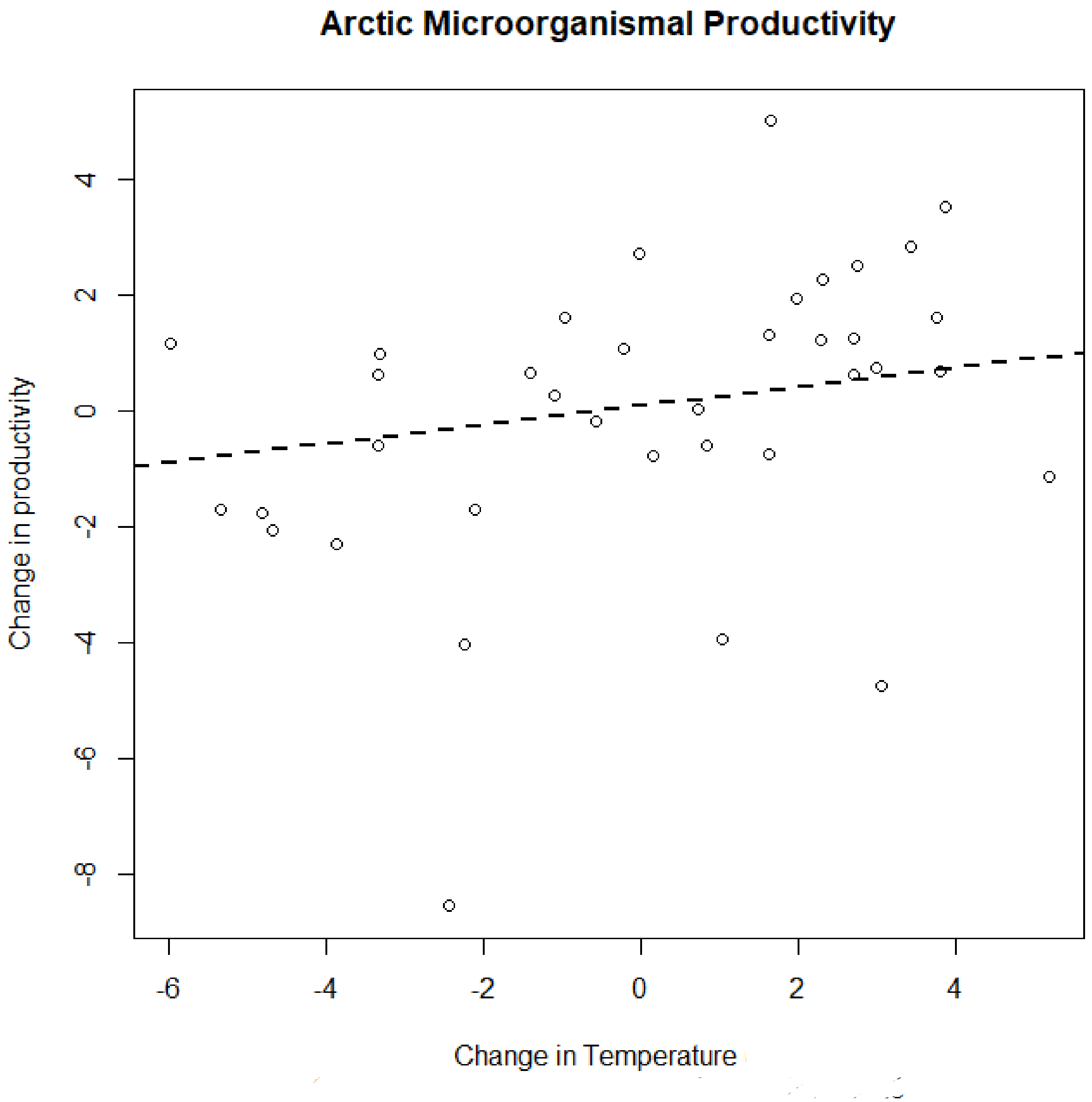

Fig. 4: Partial regression plot of the relationship between change in temperature and productivity with the combined model in the Arctic. The explanatory variables are temperature, primary productivity, dissolved oxygen, and chlorophyll. $R^2 = 0.33$ P-value <0.05. Productivity was measured at this site via leucine incorporation.

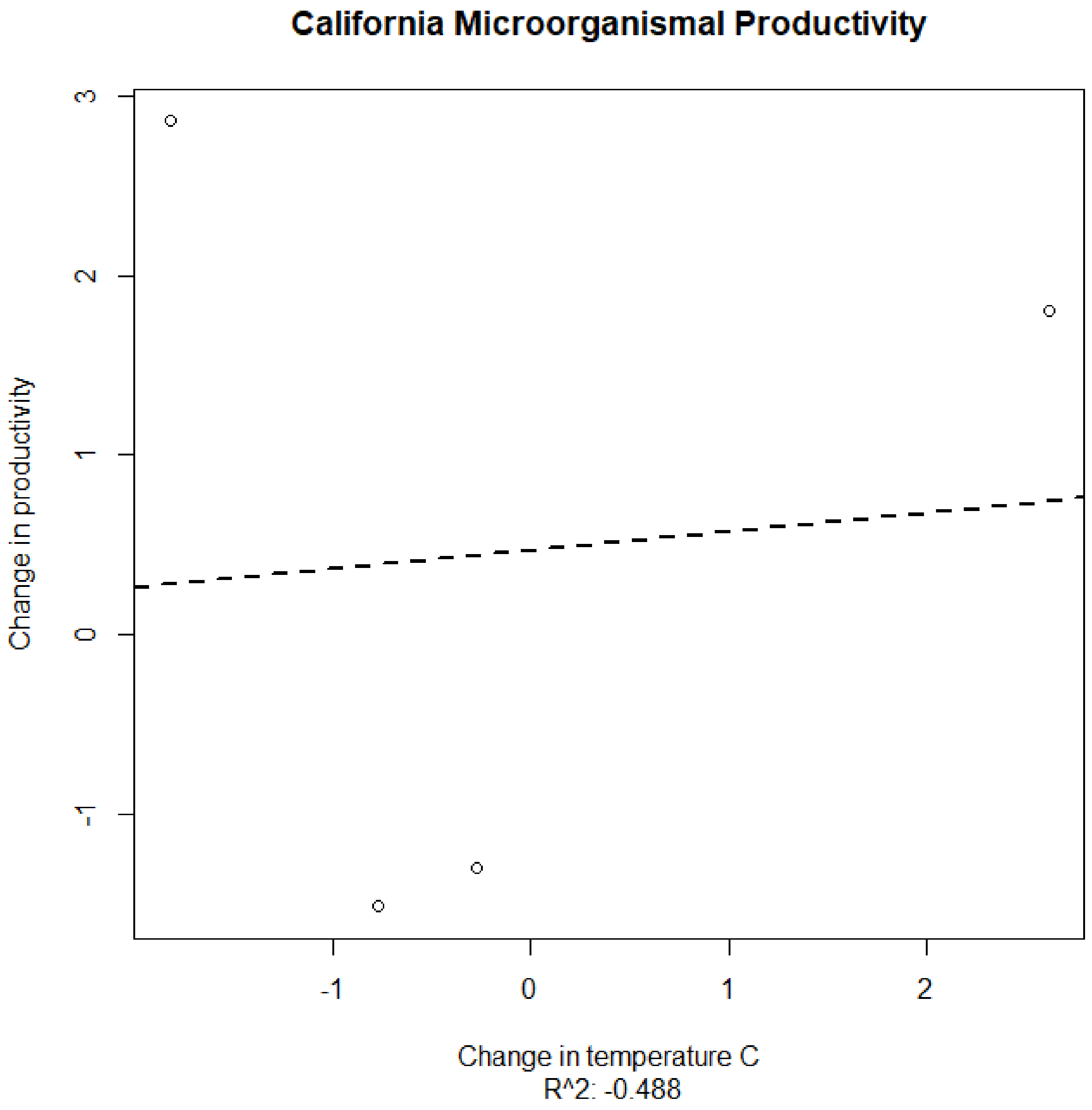

Fig. 5: Partial regression plot of the relationship between change in temperature and change in productivity with the temperature only model in California. R^2 = -0.49 P-value = 0.91. Productivity was measured at this site via leucine incorporation.

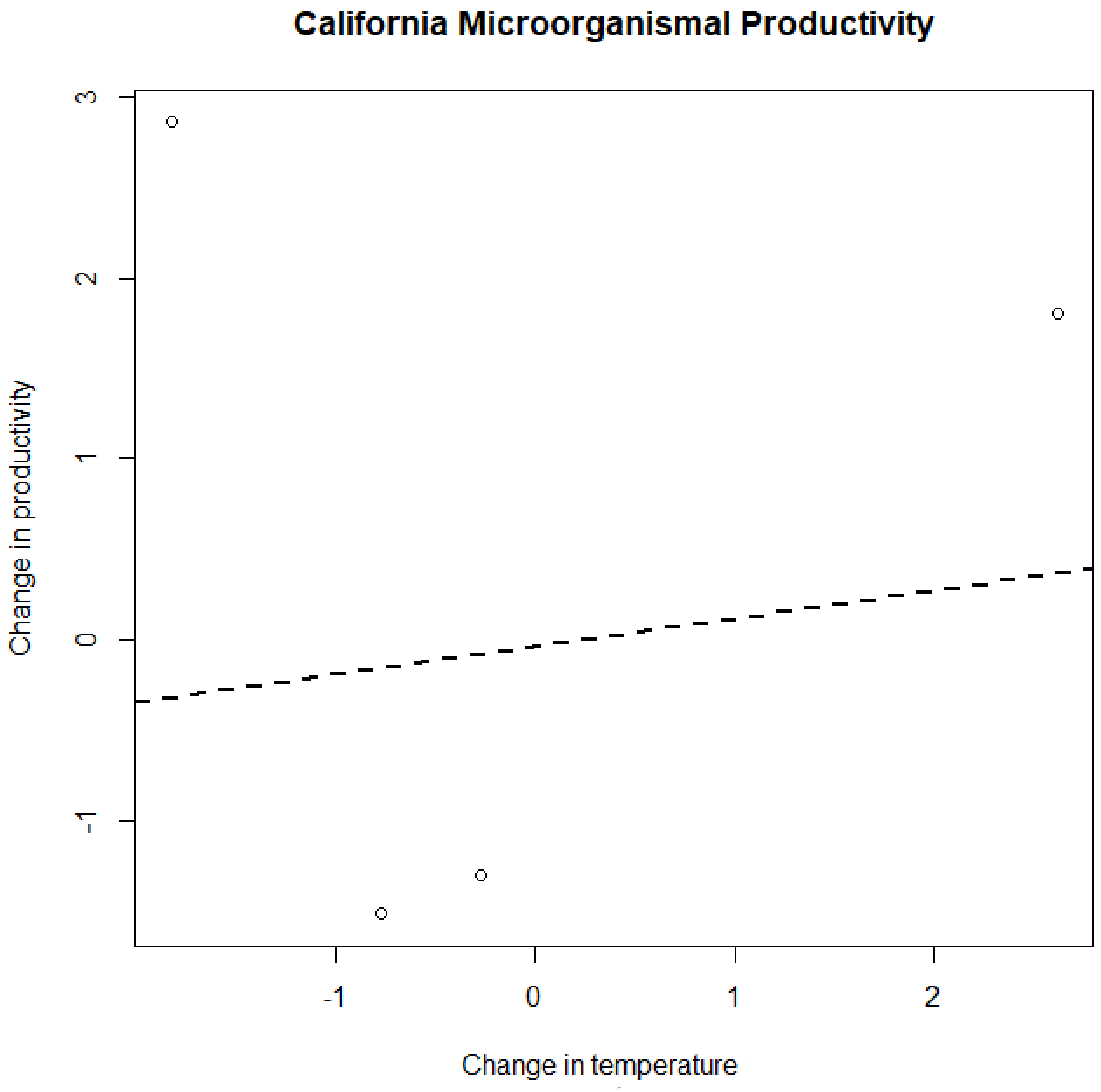

Fig. 6: Partial regression plot between change in temperature and productivity with the abiotic model in California with temperature and salinity as the independent variables. $R^2 = -0.33$ $P = 0.67$. Productivity was measured at this site via leucine incorporation.

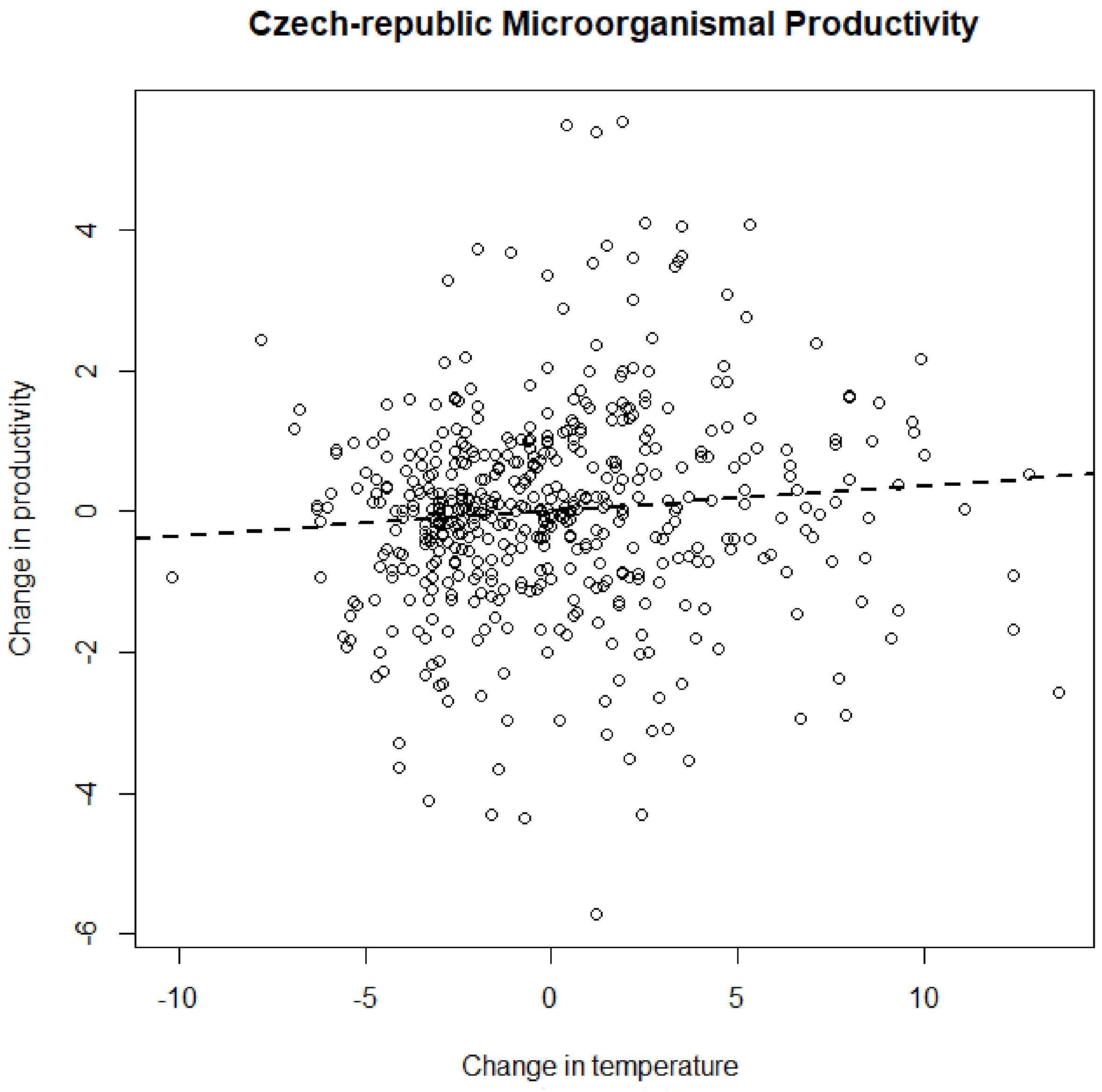

Fig. 7: Partial regression plot of the change in temperature and change in productivity with the temperature only model in the Czech-republic. $R^2 = 0.01$ $P = 0.04$. Productivity at this site was measured via abundance.

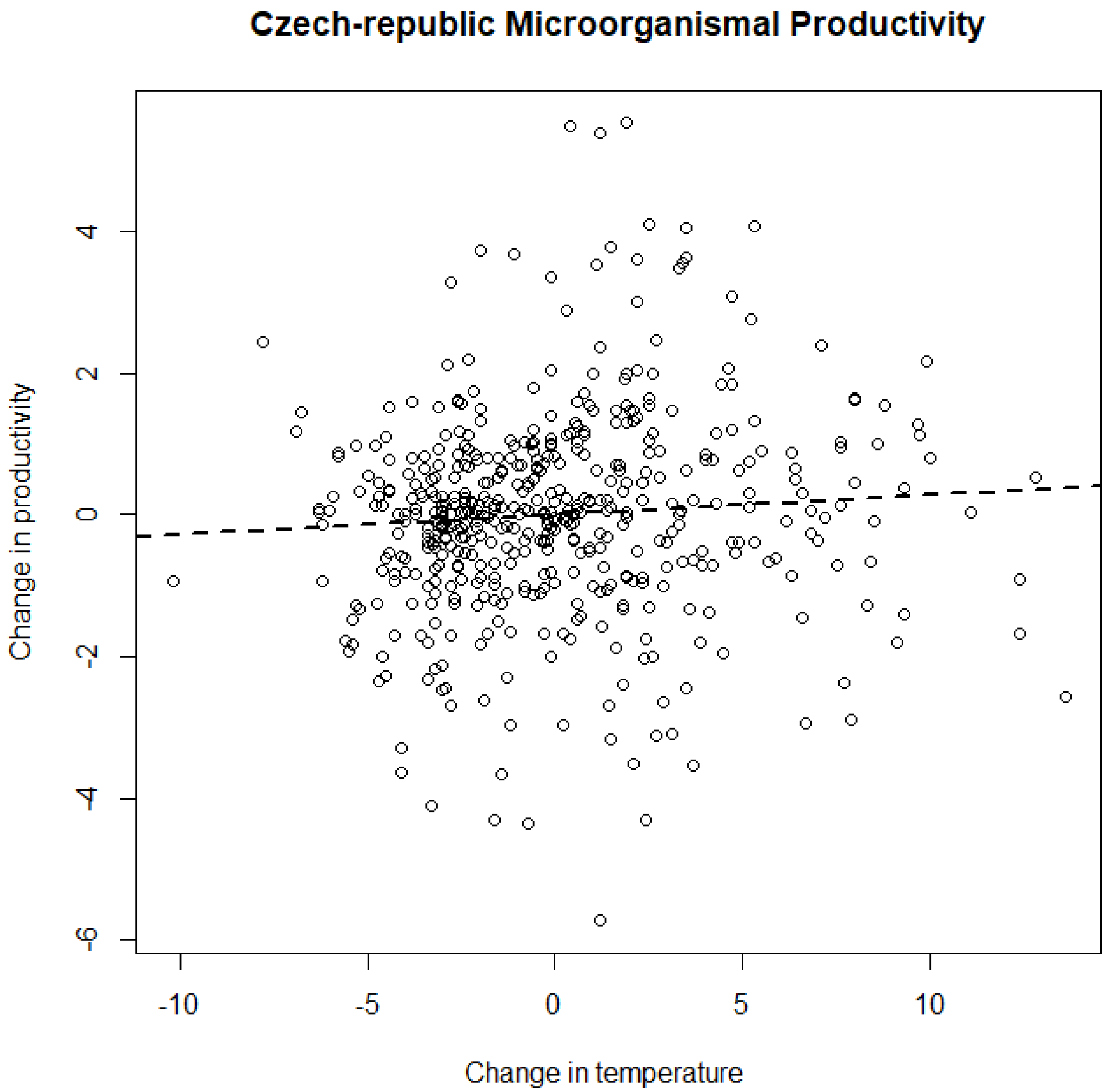

Fig. 8: Partial regression plot of the change in temperature and productivity with the biotic model in the Czech-republic, with temperature and chlorophyll as the independent variables. R^2 = 0.02 P < 0.05. Productivity at this site was taken via abundance.

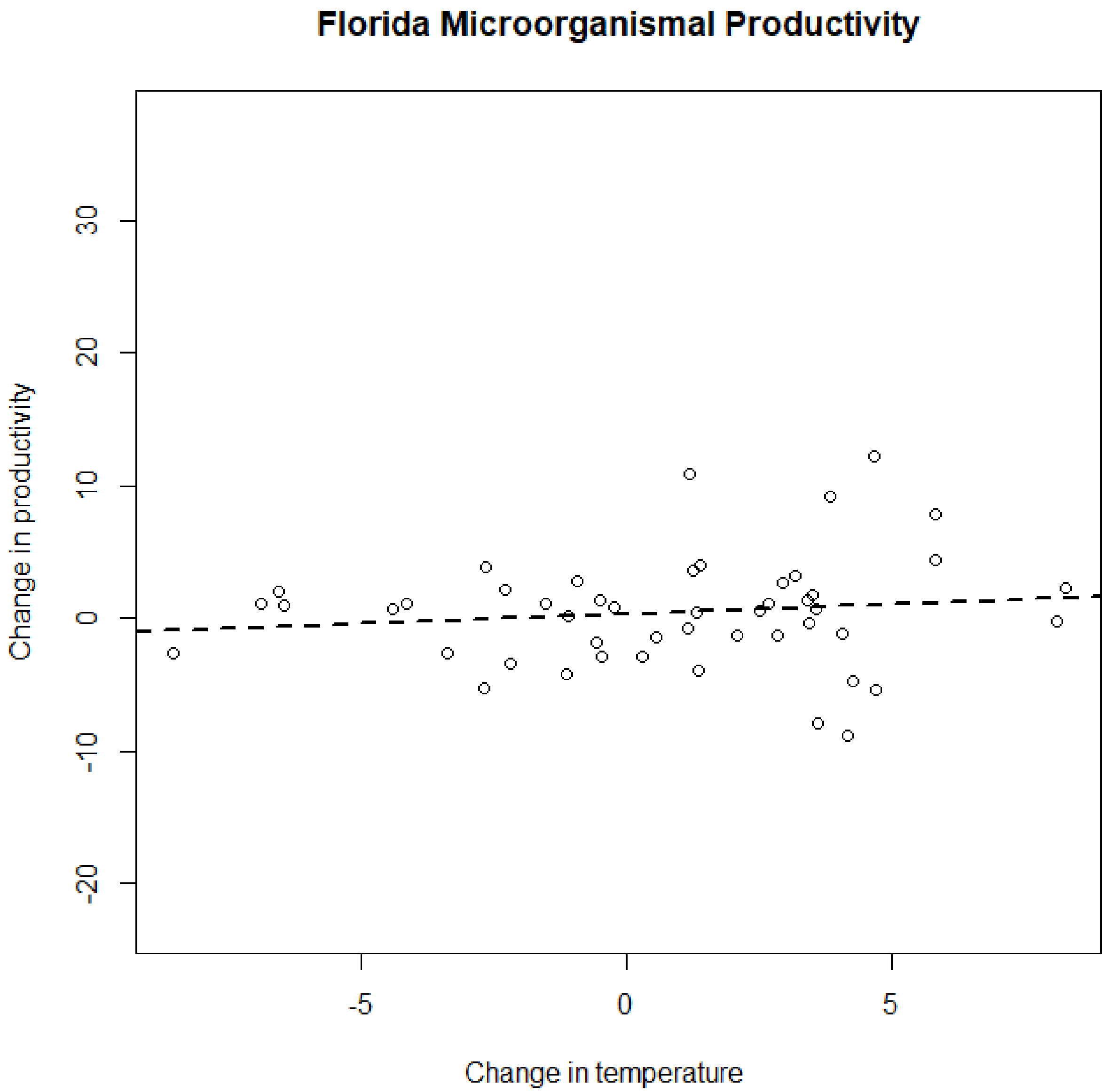

Fig. 9: Partial regression plot of the change in temperature and change in productivity with the temperature only model in Florida. $R^2 < -0.01$, $P = 0.38$. Productivity at this site was collected via thymidine incorporation.

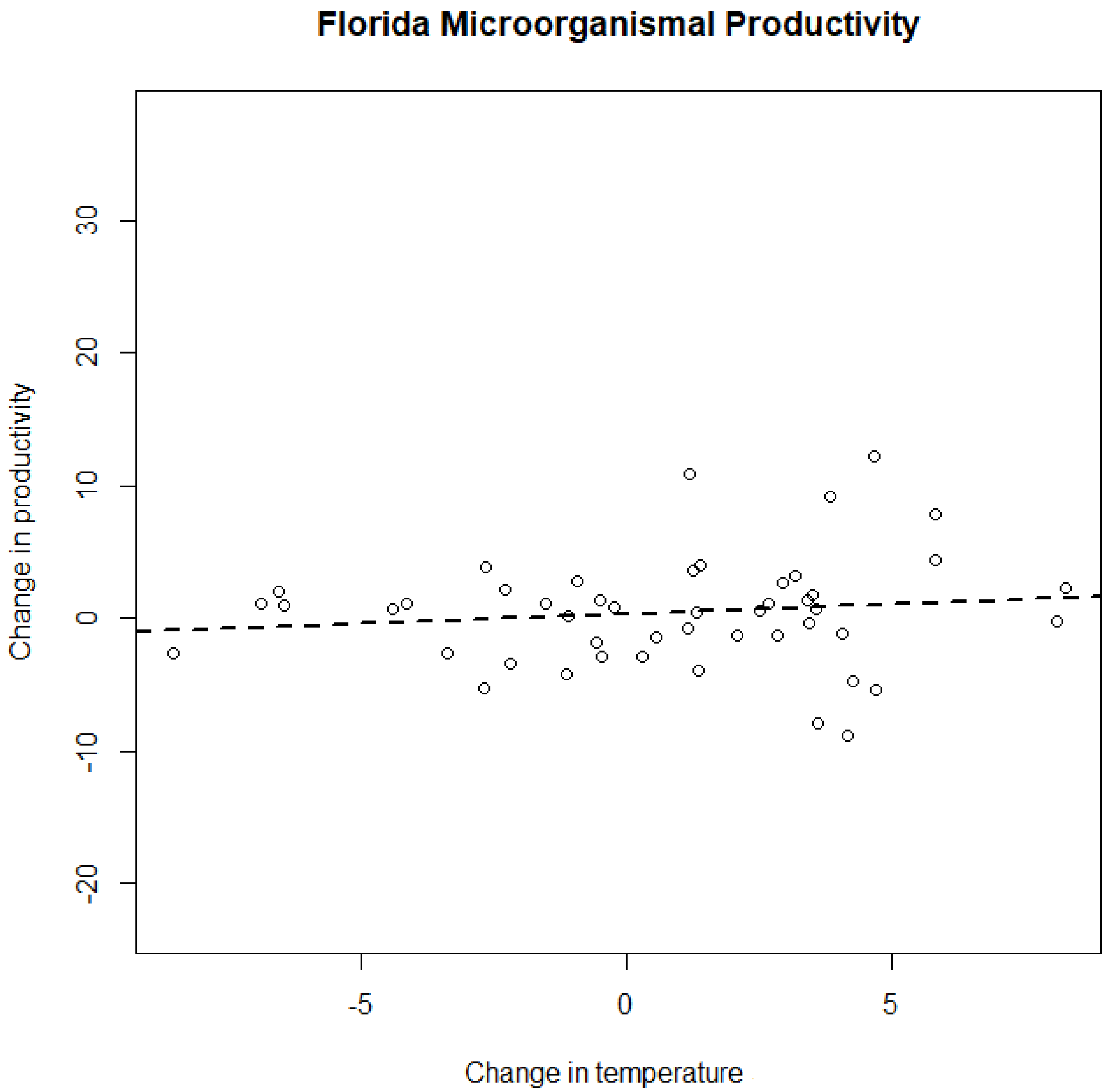

Fig. 10: Partial regression plot of the change in temperature and productivity with the abiotic model in Florida. Temperature and salinity were independent variables. R^2 =-0.03 P-value = 0.69. Productivity at this site was collected via thymidine incorporation.

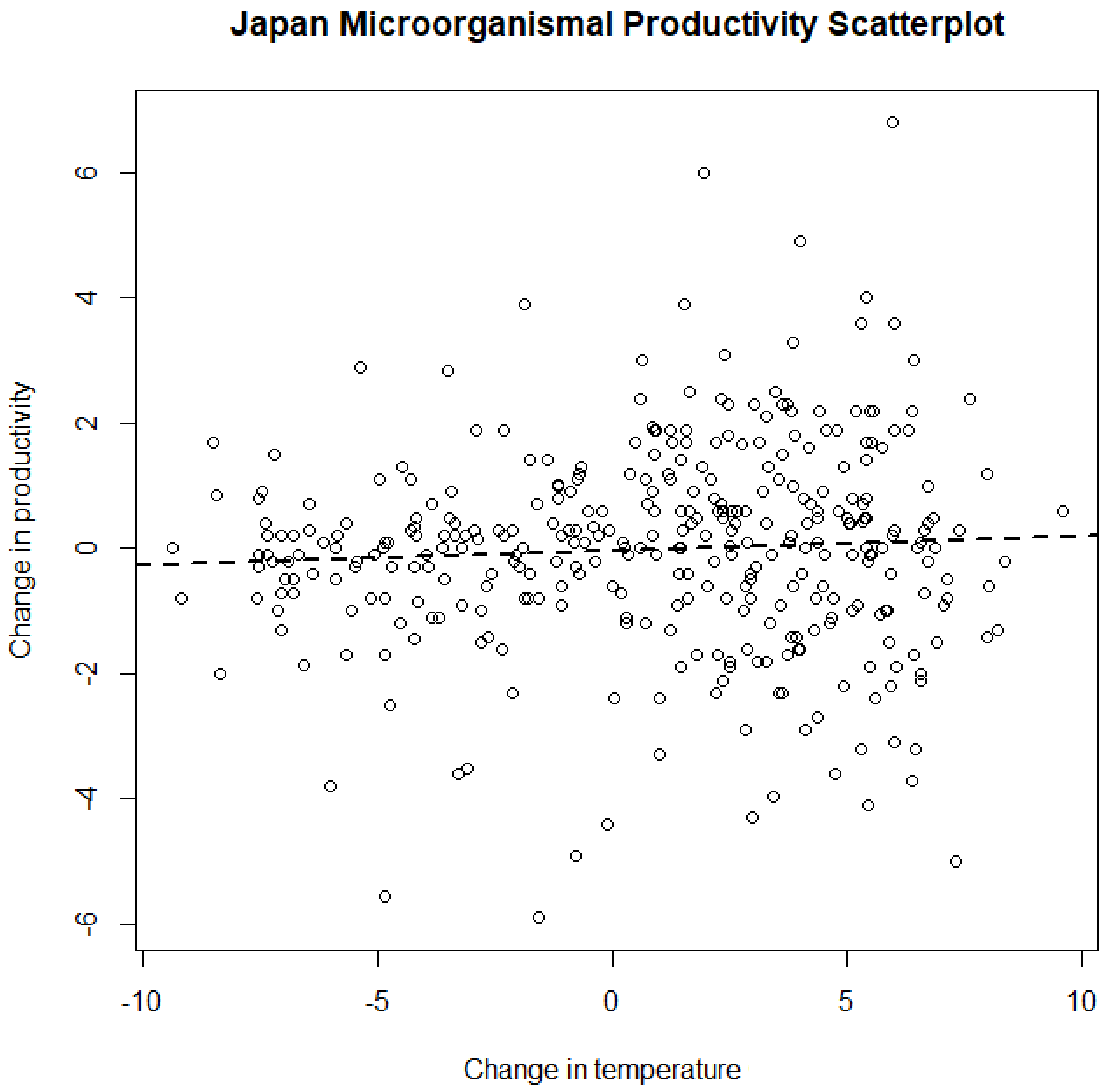

Fig. 11: Partial regression plot of the change in temperature and change in productivity with the temperature only model in Japan. $R^2 < 0.05$ P = 0.25. Productivity was collected via carbon-13 incorporation.

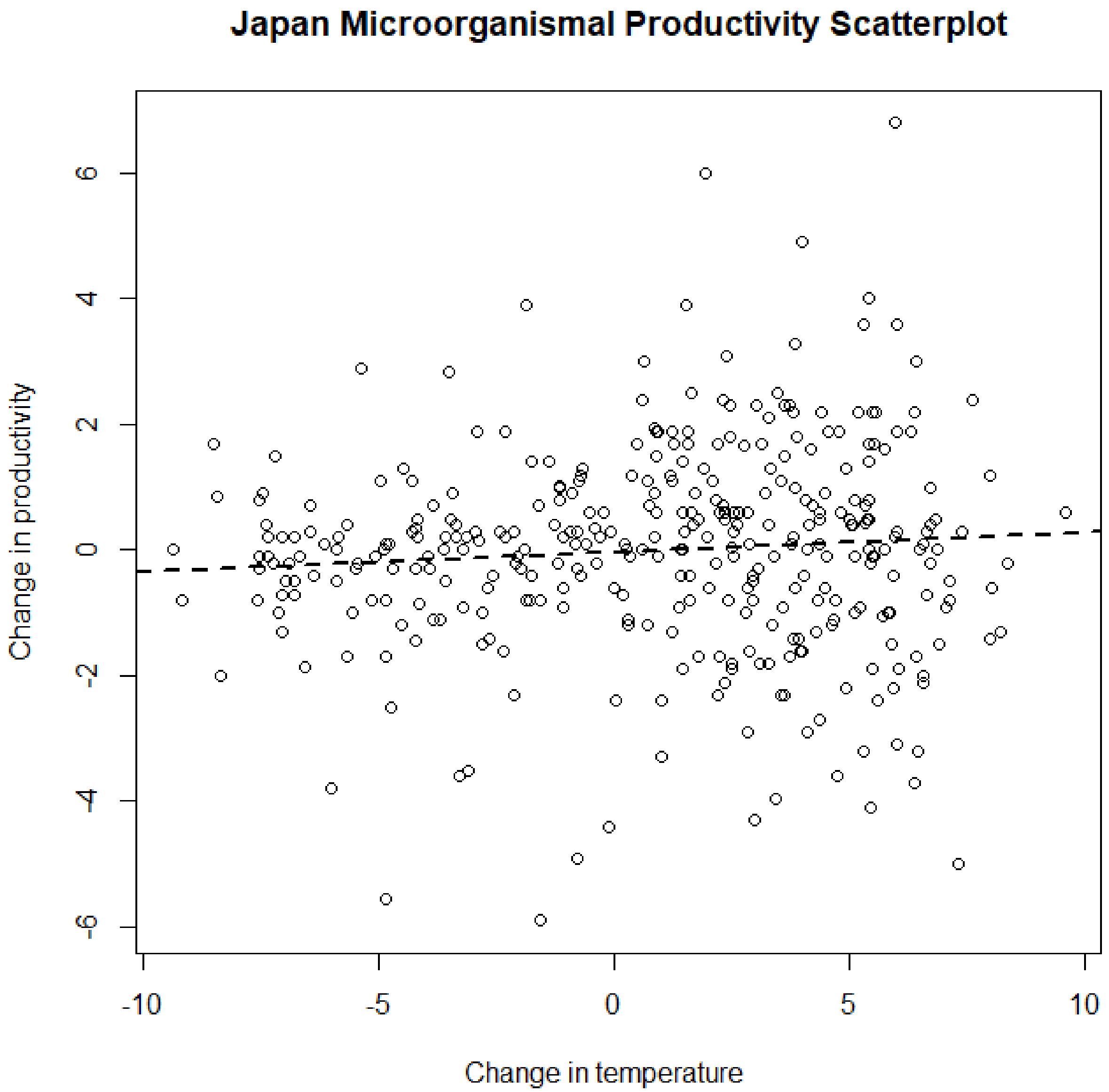

Fig. 12: Partial regression plot between the change in temperature and productivity with the combined model in Japan. The explanatory variables were temperature, light irradiance, dissolved inorganic carbon, and chlorophyll. $R^2 = 0.14$ P-value <0.05. Productivity was collected via carbon-13 incorporation.

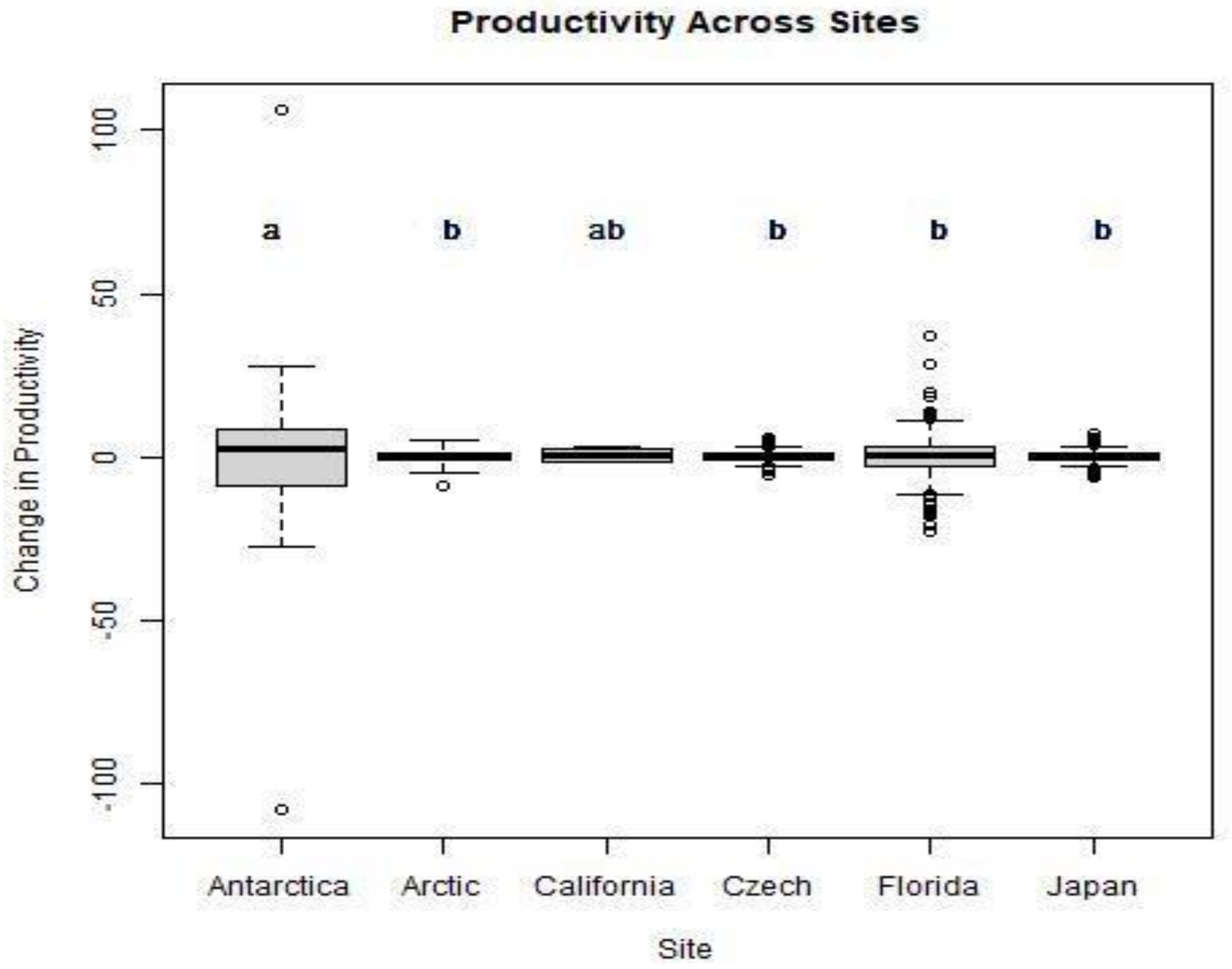

Fig. 13: A boxplot depicting the productivity among sites. Sites with different letters represent significant differences. Medians (bold), upper and lower quartiles (shaded boxes), extreme data points (bars), and outliers (circles) that were 1.5 times past the upper and lower quartiles.

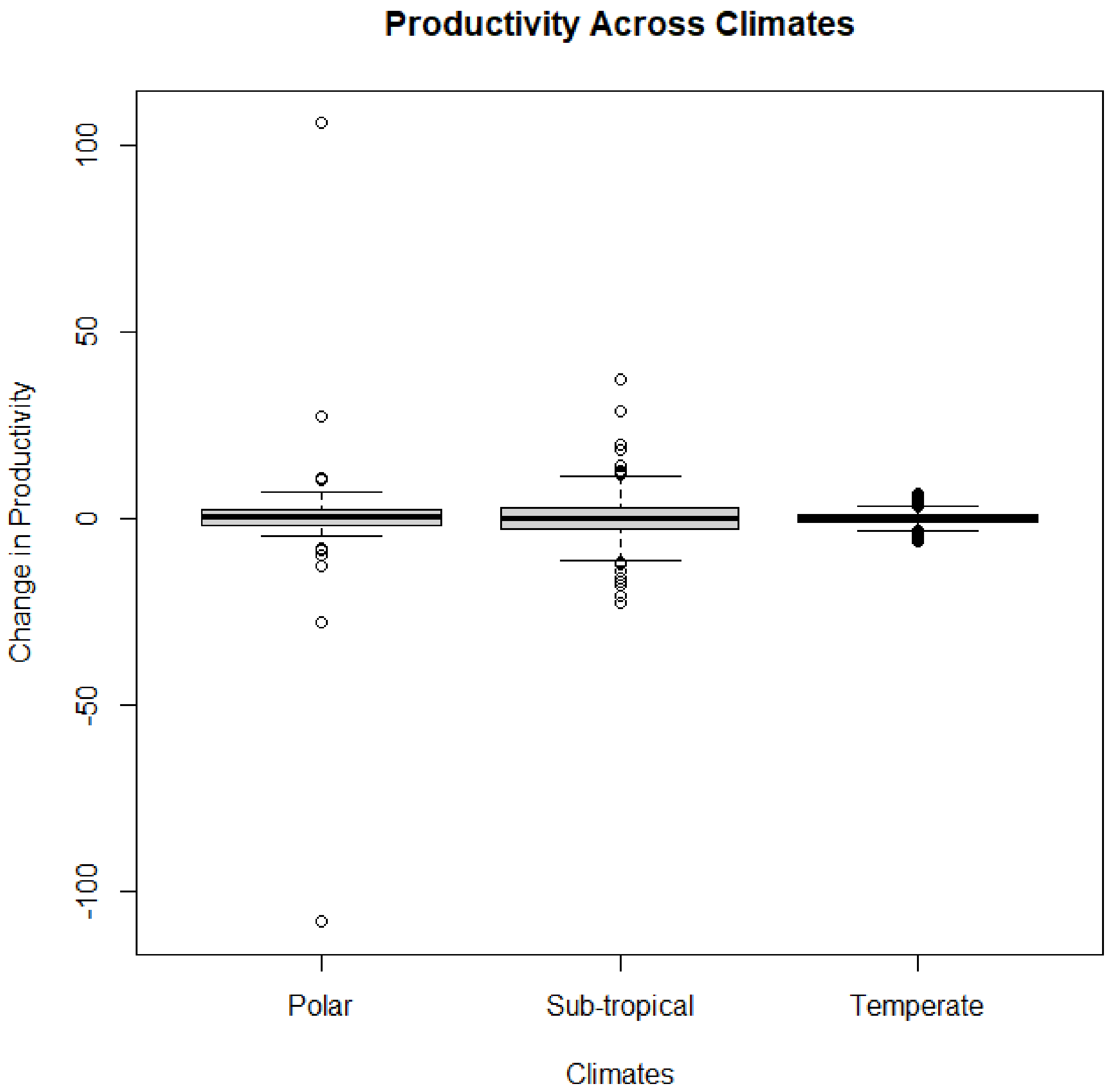

Fig. 14: A boxplot showing the change in productivity among regions. There were no differences among regions. Antarctica and the Arctic are classified as polar, Florida is classified as sub-tropical, and California, the Czech-republic, and Japan are classified as temperate. Medians (bold), upper and lower quartiles (shaded boxes), extreme data points (bars), and outliers (circles) that were 1.5 times past the upper and lower quartiles.

Bibliography

Abdulhafedh, A. (2017). How to detect and remove temporal autocorrelation in vehicular crash data. *Journal of Transportation Technologies*, *07*, 133–147. https://doi.org/10.4236/jtts.2017.72010

Al-Najjar, M. A., Munday, C., Fink, A., Abdel-Moati, M. A. R., Hamza, W., Korte, L., Stuut, J.-B., Al-Ansari, I. S., Al-Maslamani, I., & de Beer, D. (2020). Nutritive effect of dust on microbial biodiversity and productivity of the Arabian Gulf. *Aquatic Ecosystem Health & Management*, *23*, 122–135. https://doi.org/10.1080/14634988.2019.1676541

Briceno H. 2020. *Microbial Sampling from Shark River Slough and Taylor Slough, Everglades National Park, South Florida (FCE LTER) from January 2001 to Present.* Environmental Data Initiative. https://doi.org/10.6073/pasta/73e3a958c9d7b1eeaf55fa41b4815b6d. Dataset accessed 7/28/2020.

Bottle samples from CCE process cruises in the California Current System, 2007 - 2017 (ongoing). Environmental data Initiative. https://doi.org/10.6073/pasta/a9e128532f5d03e23a83c3c2005abae2. Dataset accessed 7/28/2020.

Caron, D. A., & Hutchins, D. A. (2012). The effects of changing climate on microzooplankton grazing and community structure: Drivers, predictions and knowledge gaps. *Journal of Plankton Research*, *35*, 235–252. https://doi.org/10.1093/plankt/fbs091

Cordero-Quirós, N., Miller, A. J., Subramanian, A. C., Luo, J. Y., & Capotondi, A. (2019). Composite physical–biological El Niño and La Niña conditions in the California current system in

CESM1-POP2-Bec. *Ocean Modelling*, *142*, 101439. https://doi.org/10.1016/j.ocemod.2019.101439

Crichton, K. A., Wilson, J. D., Ridgwell, A., & Pearson, P. N. (2021). Calibration of temperature-dependent ocean microbial processes in the cgenie.muffin (v0.9.13) earth system model. *Geoscientific Model Development*, *14*, 125–149. https://doi.org/10.5194/gmd-14-125-2021

Duque, A., & Rakic, P. (2011). Different effects of bromodeoxyuridine and [3h]thymidine incorporation into DNA on cell proliferation, position, and fate. *Journal of Neuroscience*, *31*, 15205–15217. https://doi.org/10.1523/jneurosci.3092-11.2011

Fukushima, T. (2021). Water quality in-situ observations. https://db.cger.nies.go.jp/gem/moni-e/inter/GEMS/database/kasumi/contents/datalist.html

Garzke, J., Connor, S. J., Sommer, U., & O'Connor, M. I. (2019). Trophic interactions modify the temperature dependence of community biomass and ecosystem function. *PLOS Biology*, *17*. https://doi.org/10.1371/journal.pbio.2006806

Hisano, M., Searle, E. B., & Chen, H. Y. (2017). Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. *Biological Reviews*, *93*, 439–456. https://doi.org/10.1111/brv.12351

Hobbie, J. E., & Bettez, N. (2003). Climate forcing at the Arctic Lter Site. *Climate Variability and Ecosystem Response in Long-Term Ecological Research Sites*. https://doi.org/10.1093/oso/9780195150599.003.0011

Häder, D.-P., Villafañe, V. E., & Helbling, E. W. (2014). Productivity of aquatic primary producers under Global Climate Change. *Photochem. Photobiol. Sci.*, *13*, 1370–1392. https://doi.org/10.1039/c3pp50418b

Hänsel, M. C., Schmidt, J. O., Stiasny, M. H., Stöven, M. T., Voss, R., & Quaas, M. F. (2020). Ocean warming and acidification may drag down the commercial Arctic cod fishery by 2100. *PLOS ONE*, *15*. https://doi.org/10.1371/journal.pone.0231589

Kaunzinger, C. M., & Morin, P. J. (1998). Productivity controls food-chain properties in Microbial Communities. *Nature*, *395*, 495–497. https://doi.org/10.1038/26741

Kendrick, M. R., Hershey, A. E., & Huryn, A. D. (2018). Disturbance, nutrients, and antecedent flow conditions affect macroinvertebrate community structure and productivity in an Arctic River. *Limnology and Oceanography*, *64*. https://doi.org/10.1002/lno.10942

Kirchman, D., K'nees, E., & Hodson, R. (1985). Leucine incorporation and its potential as a measure of protein synthesis by bacteria in natural aquatic systems. *Applied and Environmental Microbiology*, *49*, 599–607. https://doi.org/10.1128/aem.49.3.599-607.1985

Kling G. 2019. *Bacterial Production Data for lake and stream samples collected in summer 2012 through 2018, Arctic LTER, Toolik Lake Field Station, Alaska.* Environmental Data Initiative. https://doi.org/10.6073/pasta/308b10a7626734082e9d3e43195b8853. Dataset accessed 7/28/2020.

Kuosa, H., & Kivi, K. (1989). Bacteria and heterotrophic flagellates in the pelagic carbon cycle in the northern Baltic Sea. *Marine Ecology Progress Series*, *53*, 93–100. https://doi.org/10.3354/meps053093

Lindegren, M., Checkley, D. M., Koslow, J. A., Goericke, R., & Ohman, M. D. (2017). Climate-mediated changes in marine ecosystem regulation during El Niño. *Global Change Biology*, *24*, 796–809. https://doi.org/10.1111/gcb.13993

Matsuzaki, S.-ichiro S., Suzuki, K., Kadoya, T., Nakagawa, M., & Takamura, N. (2018). Bottom-up linkages between primary production, zooplankton, and fish in a shallow, hypereutrophic lake. *Ecology*, *99*, 2025–2036. https://doi.org/10.1002/ecy.2414

Matsuzaki, S. (2018). Photosynthesis and primary production in Lake Kasumigaura . http://db.cger.nies.go.jp/JaLTER/ER_DataPapers/archives/2016/ERDP-2016-01/metadata

Mills, M. M., Moore, C. M., Langlois, R., Milne, A., Achterberg, E., Nachtigall, K., Lochte, K., Geider, R. J., & J. La, R. (2008). Nitrogen and phosphorus co-limitation of bacterial productivity and growth in the oligotrophic subtropical North Atlantic. *Limnology and Oceanography*, *53*, 824–834. https://doi.org/10.4319/lo.2008.53.2.0824

Palmer Station Antarctica LTER and H. Ducklow. 2020. Bacterial properties in discrete water column samples at selected depths, collected aboard Palmer LTER annual cruises off the coast of the Western Antarctica Peninsula, 2003 - 2019. ver 7. Environmental Data Initiative. https://doi.org/10.6073/pasta/32683b1152c89e8eb8879639146b34fe (Accessed 2022-01-09).

Rains, M.. 2016. Subsurface Water Temperatures taken in Shark River Slough and Taylor Slough, Everglades National Park, South Florida (FCE) from May 2010 to Present. Environmental Data Initiative. https://doi.org/10.6073/pasta/56a7c2c88e4e20dc8c2b0100c3de9a1d. Dataset accessed 2021-10-10.

Rapp, J. M., Silman, M. R., Clark, J. S., Girardin, C. A., Galiano, D., & Tito, R. (2012). Intra- and interspecific tree growth across a long altitudinal gradient in the Peruvian Andes. *Ecology*, *93*, 2061–2072. https://doi.org/10.1890/11-1725.1

Rochera, C., & Camacho, A. (2019). Limnology and Aquatic Microbial Ecology of byers peninsula: A main freshwater biodiversity hotspot in Maritime Antarctica. *Diversity*, *11*, 201. https://doi.org/10.3390/d11100201

Rovai, A. S., Twilley, R. R., Castañeda-Moya, E., Midway, S. R., Friess, D. A., Trettin, C. C., Bukoski, J. J., Stovall, A. E. L., Pagliosa, P. R., Fonseca, A. L., Mackenzie, R. A., Aslan, A., Sasmito, S. D., Sillanpää, M., Cole, T. G., Purbopuspito, J., Warren, M. W., Murdiyarso, D., Mofu, W., … Riul, P. (2021). Macroecological patterns of forest structure and allometric scaling in mangrove forests. *Global Ecology and Biogeography*, *30*, 1000–1013. https://doi.org/10.1111/geb.13268

Rykaczewski, R. R. (2019). Changes in mesozooplankton size structure along a trophic gradient in the California current ecosystem and implications for small pelagic fish. *Marine Ecology Progress Series*, *617-618*, 165–182. https://doi.org/10.3354/meps12554

Sander, B. C., & Kalff, J. (1993). Factors controlling bacterial production in marine and freshwater sediments. *Microbial Ecology*, *26*. https://doi.org/10.1007/bf00177045

Sarmento, H., Montoya, J. M., Vázquez-Domínguez, E., Vaqué, D., & Gasol, J. M. (2010). Warming effects on marine microbial food web processes: How far can we go when it comes to predictions? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 2137–2149. https://doi.org/10.1098/rstb.2010.0045

Schofield, O., Brown, M., Kohut, J., Nardelli, S., Saba, G., Waite, N., & Ducklow, H. (2018). Changes in the upper ocean mixed layer and phytoplankton productivity along the West Antarctic Peninsula. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *376*, 20170173. https://doi.org/10.1098/rsta.2017.0173

Shiah, F. K., & Ducklow, H. W. (1994). Temperature and substrate regulation of bacterial abundance, production and specific growth rate in Chesapeake Bay, USA. *Marine Ecology Progress Series*, *103*, 297–308. https://doi.org/10.3354/meps103297

Sistla, S. A., Moore, J. C., Simpson, R. T., Gough, L., Shaver, G. R., & Schimel, J. P. (2013). Long-term warming restructures arctic tundra without changing net soil carbon storage. *Nature*, *497*, 615–618. https://doi.org/10.1038/nature12129

Stanley, S. M. (2010). Relation of phanerozoic stable isotope excursions to climate, bacterial metabolism, and major extinctions. *Proceedings of the National Academy of Sciences*, *107*, 19185–19189. https://doi.org/10.1073/pnas.1012833107

Umbanhowar, C., Camill, P., Edlund, M., Geiss, C., Durham, W., Kreger, D., Molano, W., Raskob, C., Stocker, M., Tvera, A., & Williams, J. (2013). Contrasting changes in surface waters and barrens over the past 60 years for a subarctic forest–Tundra site in northern Manitoba based on remote sensing imagery. *Canadian Journal of Earth Sciences*, *50*, 967–977. https://doi.org/10.1139/cjes-2012-0162

Wachnicka, A., Gaiser, E., Wingard, L., Briceo, H., & Harlem, P. (2013). Impact of late holocene climate variability and anthropogenic activities on Biscayne Bay (Florida, U.S.A.): Evidence from diatoms. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *371*, 80–92. https://doi.org/10.1016/j.palaeo.2012.12.020

Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: Impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 2093–2106. https://doi.org/10.1098/rstb.2010.0055

Wrona, F. J., Prowse, T. D., Reist, J. D., Hobbie, J. E., Lévesque, L. M., & Vincent, W. F. (2006). Climate change effects on aquatic biota, ecosystem structure and function. *AMBIO: A Journal of the Human Environment*, *35*, 359–369. https://doi.org/10.1579/0044-7447(2006)35[359:cceoab]2.0.co;2

Yang, S., Li, Z., Yu, J.-Y., Hu, X., Dong, W., & He, S. (2018). El Niño–Southern Oscillation and its impact in the changing climate. *National Science Review*, *5*, 840–857. https://doi.org/10.1093/nsr/nwy046

Znachor, P. (2021). Rimov reservoir. https://deims.org/ef2ae321-6e94-4170-9616-9a54f529643c