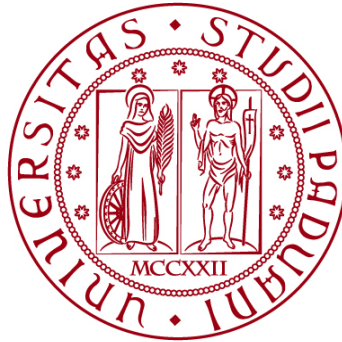


UNIVERSITÀ DEGLI STUDI DI PADOVA

DIPARTIMENTO DI BIOLOGIA

Corso di Laurea magistrale in Marine Biology



TESI DI LAUREA

**Effects of eutrophication and heatwave events on the
oxygen dynamics of algal turf**

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ANNO ACCADEMICO 2022/2023

ABSTRACT

Algal turfs are sparse to thick mats of filamentous macroalgae that colonize intertidal and subtidal hard substrata. Turfs are replacing native macroalgal forests in many coastal ecosystems globally, particularly in urbanized marine systems, with significant impacts on ecosystem functions and services. The recruitment of algal turfs has been related to both eutrophication and warming, but no studies have explored the combined effects of these two stressors on established turfs, and the potential role of the associated microbiome in mediating the effects of these stressors remains elusive. This study investigates: first, the oxygen productivity of algal turfs growing in oligotrophic or eutrophic conditions at different temperatures (20°, 22°, 24°, 28° and 32° C) and, second, how an heatwave event can further impact the system. Turfs were sampled from urban artificial structures in Venice Lagoon and grown in lab conditions exposed to two treatments: “fertilized”, which mimicked eutrophic conditions, and “control”, which mimicked baseline oligotrophic conditions. The oxygen dynamics of both treatments were recorded via an *in-situ* respirometry in dark and light conditions. In the second experiment the turf was grown at 28° C and in the same nutrient conditions and then exposed to a simulated marine heatwave event. The results of the first experiment showed that under baseline temperature conditions the turf is autotrophic regardless of nutrient load until 28° C, where the fertilized turf switches to a heterotrophic regime. In the second experiment, after the heatwave exposure the turf showed net oxygen consumption regardless of nutrient treatment, which can lead to negative impacts on the productivity of the system. To contextualize the relevance of the work, sea temperature data were analyzed to discover the number and intensity of heatwaves affecting the Venice Lagoon. The analysis confirmed the global trend of the increase in frequency and severity of Marine Heatwave Events in the Venice lagoon.

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1. INTRODUCTION

Macroalgae provide many ecosystem functions, both when dead and alive. When alive they supply the water column with oxygen, act as carbon sinks and offer shelter and food to a plethora of organisms (Christie et al., 2009, Duarte, 1996, Krause-Jensen & Duarte, 2016 and Norderhaug et al., 2005). When dead their decaying matter is a source of food for places where primary production is absent, like deep sea beds or intertidal shores (Filbee-Dexter & Scheibling, 2014, Hobday, 2000 and Ulaski et al., 2023).

Unfortunately, marine habitats worldwide are heavily exploited due to the rise of global population and related stressors (Gibson et al., 2007), which is causing a loss of habitat forming species and associated trophic webs and a rise of more ephemeral life forms (Krumhansl et al., 2016, Ling et al., 2009, Moy & Christie, 2012). Specifically, macroalgal canopy forests are decaying in favor of turf forming algae, with repercussion on marine seascapes worldwide (Dijkstra et al., 2019, Moy & Christie, 2012 and Strain et al., 2014). Filbee-Dexter and Wernberg, 2018, have related this switch to a handful of stressors, of which the two most prominent are eutrophication and higher temperatures. Eutrophication is a phenomenon related to high concentrations of nutrients in the waters, mostly caused by agricultural runoff or not properly treated sewage water (Dumont et al., 2005, and Harrison et al., 2005). The dissolved nutrients (mostly nitrogen and phosphorous) are then absorbed by less complex life forms, like phytoplankton, that then develop in algal blooms, often harmful (Glibert, 2020). The algal turf in particular benefits from eutrophication: its filamentous form allows it to uptake a high quantity of nutrients, opposed to more complex benthic communities like coral reefs or canopy forming forests (Andersen et al., 2010, den Haan et al., 2016, and Littler & Littler, 1980).

Furthermore, macroalgal forests are being impacted and suppressed by climate change. Incremental increases of temperature can slowly kill a macroalgal forest, or extreme event can severely lower its short-term survival (Tanaka et al., 2012, and Wernberg et al., 2016). To survive macroalgal forests need to shift their range towards cooler waters (either by shifting it towards deeper waters or poleward latitudes) (Wernberg et al., 2011). Heightened temperatures further prevent the recovery of the lost range by suppressing gamete recruitment and increasing the metabolic needs of the grazers (and consequentially their grazing rates) (Veenhof et al., 2022, and Yamaguchi et al., 2010). Once the algal forest disappears, the new space is readily colonized by turf algae, whose filamentous form creates a matrix that accumulates sediment and suppresses the recruitment of gametes and other larvae, and whose low nutrient content inhibits predation (Airoidi et al., 1998, Connel & Russel, 2010, Rowher and Youle, 2010, Verspagen et al., 2014). Overall, the algal turf seems favored by high temperatures and high nutrient loads, but no studies have explored if these two

stressors can act synergistically on turf algae and have a negative effect on its productivity.

1.1 ALGAL TURF: MORPHOLOGICAL DESCRIPTION AND ECOLOGICAL OVERVIEW

Algal turfs, also known as Epilithic Algal Community (EAC) (Connel et al., 2014, and Hatcher & Larkum, 1983), can grow on many different types of hard substrata, both natural and artificial (Airoldi, 1998 and Borowitzka et al., 1978), in both intertidal and subtidal zones of all waters in the world except for polar (Díaz et al., 2011, Filbee-Dexter et al., 2016, Hatcher & Larkum, 1983, Stewart, 1982 and Underwood et al., 1991). This algal assemblage does not yet have a standardized description (Connel et al., 2014), but many authors agree on the length of the blades being short (Gislén, 1930, and Steneck, 1988, defines it as comprised between 1 and 10 cm). The specie composition and the functional traits distribution of an algal turf community changes from site to site, but it is always composed by some *anchor species* and some *epiphytic species* (Airoldi, 2001 and Stewart, 1982). The anchor species in contact with the substrate are generally dominated by few taxa, while the epiphytic species are more diverse and more susceptible to predation and external stressors, so their composition is more variable during the year.

Generally, the morphological taxa composing the algal turf are mainly filamentous macroalgae, followed by calcareous (articulated and non articulated) and foliose algae, belonging mostly to Rhodophyta and Chlorophyta (Connel et al., 2014). These thalli easily entangle with each other creating a tight matrix, which has many advantages: when exposed to air it retains humidity, minimizing desiccation, and when grazed it favors branching of the thalli, making the pre existing structure more tightly woven and harder to breach by herbivorous fish (Taylor and Hay, 1984). However, on the long run a thicker turf is detrimental to its own productivity: the matrix offers resistance to the water flow forming a *diffusive boundary layer*, halting the exchange of nutrients with the external environment (Carpenter et al., 1991, Carpenter & Williams, 1993 and Schlichting & Gersten, 2016).

1.2 ALGAL TURFS IN THE CONTEXT OF BIOFOULING

As previously stated, algal turfs grow prevailingly on hard substrates, and are often associated with man-made structures (Coleman, 2003) as part of the “biofouling”, namely the unwanted colonization of more and more complex organisms of a surface (Dayton, 1971). This phenomenon happens as shortly as an hour after immersion in seawater and it is inevitable, unless extremely toxic chemical agents are used (Evans & Leksono, 2010, Mucko et al., 2014, and Yebra et al., 2004).

Biofouling is closely linked to ocean sprawl, the proliferation of man-made structures underwater (Bugnot et al., 2021, and Duarte et al., 2013). Introducing a new structure into an environment can change its overall ecology, especially when that specific environment lacks a natural counterpart (Bishop et al., 2017, Connel, 2000 and Heery et al., 2017). The changes in the hydrodynamics, turbidity, sediment size and shading can all alter the immediate surrounding benthic assemblages (Coates et al., 2014, Gill, 2005 and Glasby, 1999). The chemical composition of a structure can define its impact on its epibiotic cover, however the physical properties of the structure itself also have a significant impact (Becker et al., 2020, Chapman, 2003, Köhler, 1999, Grasselli & Airoldi 2021, Grasselli et al., 2024, and La Marca, 2022). For example, seawalls tend to harbor fewer species compared to other artificial habitats, while rip raps and breakwaters tend to display higher diversity and abundances, sometimes even higher than the surrounding hard bottoms (Gittman et al., 2016). The presence of crevices, shaded indentations, tiles with grooves and artificial rock pools offer settling substrate, protection from stressors, and an increase of the local biodiversity (Bradford et al., 2020, Chapman 2003, Chapman & Blockey, 2009, Moreira et al., 2007 and Strain et al., 2018).

The steepness of the structure also affects the density of organisms as well as the amount of space available for colonization of biofouling (Figure 1). In an intertidal flat with a small slope there is more colonizable space than a vertical wall and this can lead to new, unforeseen ecological interactions (Chapman, 2011). For example, Jackson et al., 2008, found out that an oyster population on a seawall led to a higher density of whelks, two species that rarely interact in the wild (Fairweather, 1988).

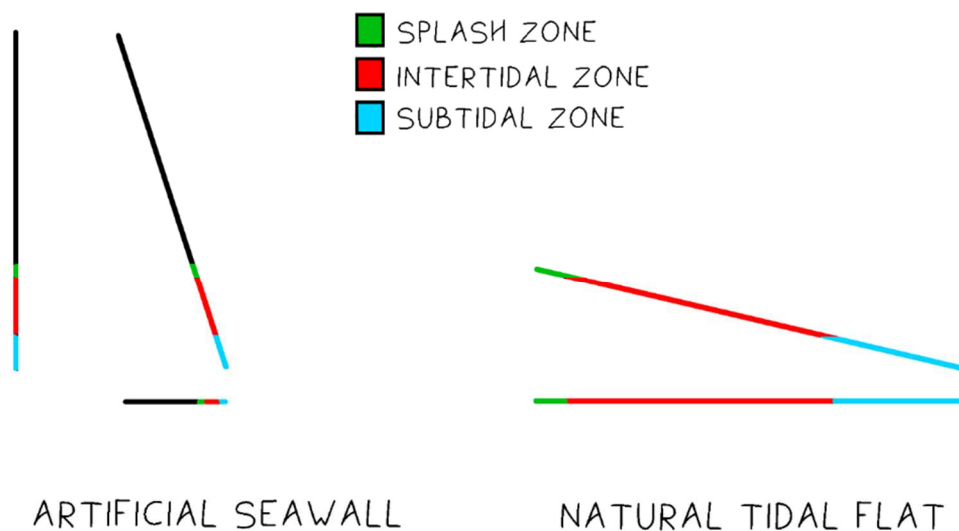


Figure 1 Difference in colonizable space based on inclination. Note the difference on the projection underneath the slope

1.3 EFFECTS OF EUTROPHICATION AND WARMING IN MARINE ECOSYSTEMS

Nutrient enrichment is one of the most pervasive and damaging stressors worldwide and one of the major drivers of eutrophication, hypoxia and anoxia in the waters: the organic load dumped in the waters is oxidized directly by the dissolved oxygen and taken up by alga, thus leading to exponential increases of algal biomass, which is then degraded by microbial populations, further increasing the oxygen demand (Jessen et al., 2015). Increase in nutrients, especially nitrogen, is also favoring fast growing species (Teichberg et al., 2010). Specifically, macroalgal forests are disappearing in favor of turf forming algae, with repercussions in all levels of the trophic web (Benedetti-Cecchi et al., 2001, Russel et al., 2005, and Mangialajo et al., 2008). This shift is exacerbated by ocean warming: both incremental increases of temperature and extreme heat events (heatwaves) influence the physiology of macroalgae (Lidiane-Pires et al., 2017, and Mancuso et al., 2023). Increments in temperature, supported by nutrient enrichment, favor photosynthesis and secondary metabolism up until a thermal threshold is reached, afterwards the algae suffer (Lidiane-Pires et al., 2017). Turf algae, having higher thermal tolerance (Provera et al., 2021), should continue to have a positive response to higher temperatures. However, the effects of eutrophication, ocean warming and their interactions on algal turfs are still unexplored.

1.4 MARINE HEATWAVES: CAUSES AND EFFECTS

A Marine HeatWave (MHW) has been defined by Hobday et al., 2016, as a span of time lasting over five days where the water temperature exceeds the 90th percentile of a historical temperature baseline measured in the previous thirty years (Figure 2).

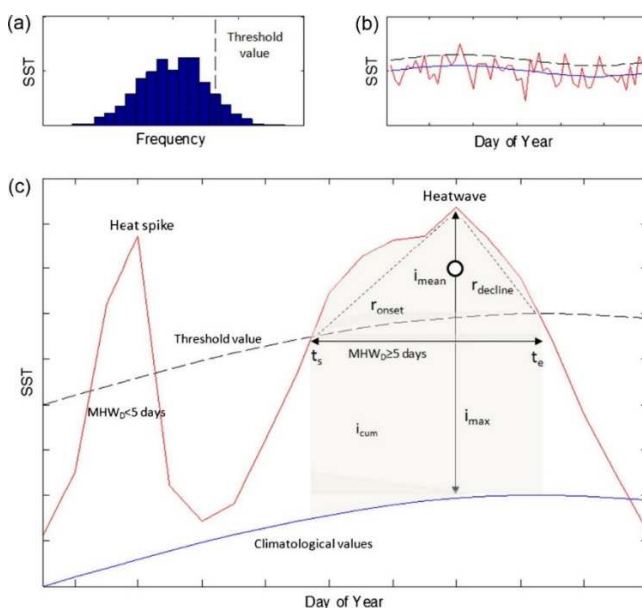


Figure 2 Example of a heatwave. SST stands for Sea Surface Temperature, MHW stands for Marine HeatWave, i stands for intensity, t stands for time. Extracted from Hobday et al., 2016

In recent years the frequency and the severity of these events has increased dramatically all around the world (Christidis et al., 2015, Frölicher et al., 2018, and Sanderson et al., 2018). The Arctic Ocean is losing its ice cap (ASIC; Arctic Ocean Ice Concentration) and the Eurasian continent is losing its snow cover (EASC; EurAsian Snow Cover), therefore less sun rays (both in the visible spectrum and the infrared spectrum) are reflected. Moreover, if the snow cover is absent, ground humidity is more likely to evaporate, adding to the latent heat of the atmosphere (Zhang et al., 2020). Europe skies are crossed by double jet streams, air channels of relative short height and wide girth found under the troposphere that stream from east to west and deeply influence the weather (Archer & Caldeira, 2008). These streams trap high pressure cells, thus not letting the heat escape (Rousi et al., 2022). These factors make Europe highly susceptible to heatwaves, with severe impacts in all facets of society. In 2003 a strong heatwave event killed 70 000 people in Europe, with a 92% mortality rate in people over 75 (Conti et al., 2005 and Robine et al., 2008), and triggered a documented mass mortality of rocky benthic communities in the Mediterranean Sea, from which many populations are still struggling to recover (Garrabou et al., 2008 and Gomez-Gràs et al., 2021). A MHW event can permanently alter the distribution of species in an area (Lonhart et al., 2019) and the remaining benthic assemblage will be severely weakened at a metabolic level, and therefore become more susceptible to mass mortality events (Hemraj et al., 2020). In contrast, MHWs have been shown to favor the proliferation of the algal turf (Gao et al., 2021), but the effects of such events on the physiology of an already established turf are yet to be discerned.

1.5 INTERACTIONS BETWEEN TURFS AND THEIR MICROBIOME

An understudied component of algal turfs is the microbiome. Turf algae, in contrast to canopy forming algae, exudate highly reduced Dissolved Organic Matter (DOC), which gets uptaken and degraded by the microbiome, making it grow exponentially and increasing its oxygen demand (Elsherbini et al., 2023 and Gregg et al., 2013). Roach et al., 2020, named the increase of microbial load due to high algal exudates in the water the “algae feeding hypothesis”, and further discovered that the microbiome associated to turfs is potentially very pathogenic. These characteristics of the microbiome could help the turf take over ecosystems by outcompeting and suffocating other organisms (Rowher and Youle, 2010). When exposed to high nutrient load the microbiome of canopy forming algae changes its composition (Mancuso et al., 2023). However, the microbiome associated with turf algae does not show the same response, proving to be particularly resistant to this kind of stressor (Messyasz et al., 2021). Other studies have shown that both incremental increases of temperature and isolated extreme warming events can shift the composition of the microbiome associated with both algae and seagrasses (Mancuso et al., 2023, Minch et al., 2017). The effect of high temperatures is overall deleterious for the microbial

assemblage since MHWs temperatures exceed the optimal operational temperature of the microbiome (Joint & Smale, 2017, Morissey et al., 2021, and Szitenberg et al., 2022). Overall, the effects of combined increases of temperatures and nutrient loads on the turf microbiome, and how its shifts will affect the turf community oxygen metabolism, are still unclear.

1.6 THE UNIQUE CHARACTERISTICS OF THE VENICE LAGOON

The lagoon of Venice (Italy) is one of the most famous and largest lagoons of the Mediterranean and it is situated in the north-eastern Adriatic Sea (Figure 3). Its peculiar morphology and history make it a prime example for studying the effects stressors related to urbanization (like eutrophication) and climate change (including increase in average temperatures as well as extreme heatwave events) on the marine environment. The lagoon has been inhabited by humans since the Roman times and has undergone drastic changes: the hydrodynamics have been altered, with entire rivers diverted from and to the lagoon, and artificial structures have been built, including urban seawalls and the characteristic *bricole*, wood posts used for navigation (D’Alpaos et al., 2010, Madricardo et al., 2019, and Modrzewska-Pianetti, 2013). The major sources of nutrients are untreated sewage waters coming from cities, the agricultural runoff coming from the rivers and industrial waste waters, which have increased the lagoon eutrophication (Cossu et al., 1987, Rova et al., 2019, and Sfriso et al., 2014). The baseline climatology of the lagoon was characterized by peaks of 32° C and 30° C of air and water temperature, respectively (ARPAV and hydrobiological station “Umberto d’Ancona”). However, the past few years have seen a warming trend (Amos et al., 2017, report 1,59° C per decade since 2008), and both the frequency and duration (in days) of MHWs have increased since the 1990s (Bartolini et al., 2013).

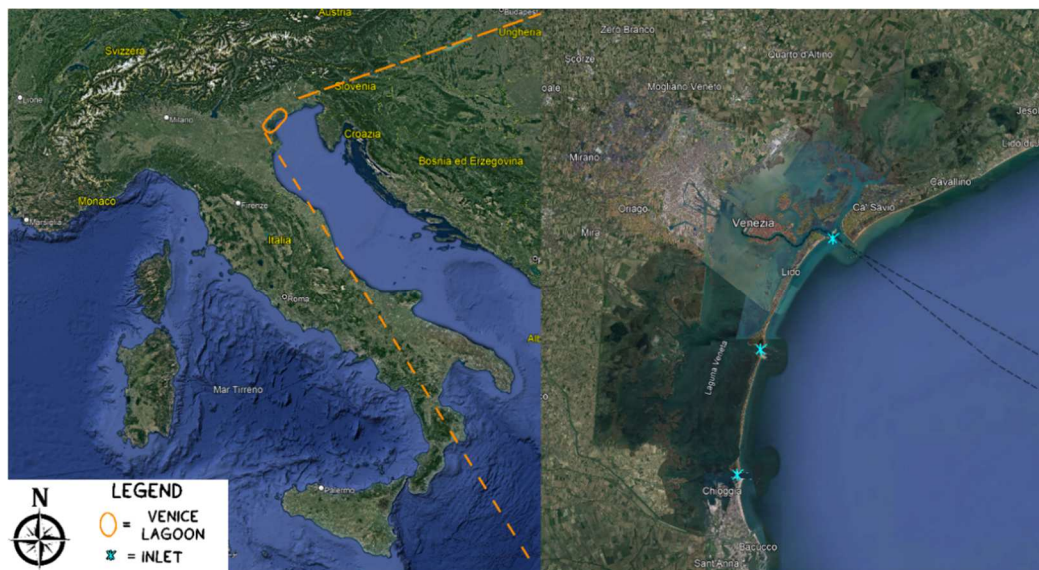


Figure 3 Map of Italy and the Lagoon of Venice. Images taken with Google Earth and modified with GIMP

1.7 AIMS OF THE STUDY

The recruitment and proliferation of the algal turf in urbanized marine systems has been related to both eutrophication and warming, but no studies have explored the combined effects of these two stressors on established turf, and the potential role of the associated microbiome remains elusive. This study investigates the net oxygen production (via in situ respirometry) of algal turfs that are part of the biofouling associated to urban artificial structures in the Venice Lagoon, how the whole turf community (algae and microbiome) oxygen dynamics respond to eutrophication and warming, and how highly stressful heatwave conditions can further impact the system. It is hypothesized that the production of the turf would increase in response to both increasing temperatures and nutrients, while the oxygen demand of the microbial community associated to turfs would increase in response to enhanced nutrient conditions. Furthermore, it is hypothesized that the production of the turf exposed to a heatwave event would be severely decreased, and the oxygen demand of the associated microbiome would increase, thus changing the whole community regime from autotrophic to heterotrophic.

2. MATERIALS AND METHODS

2.1 OXYGEN DYNAMICS AT INCREASING TEMPERATURES IN RESPONSE TO ENHANCED NUTRIENTS

2.1.1 SAMPLING AND ACCLIMATION SETUP

In the first experiment, the oxygen dynamics of the turf exposed to high or low nutrient loads were measured at different temperatures. The hypothesis were that the enhanced nutrients and temperatures would increase the oxygen production, but it would be counterbalanced by the oxygen demand of the microbiome in eutrophic conditions.

The algal turf samples were harvested in April 2023 from a floating jetty for an unused ferry stop located on the northern side of the Isola dell'Unione, connecting the cities of Chioggia and Sottomarina (Figure 1).

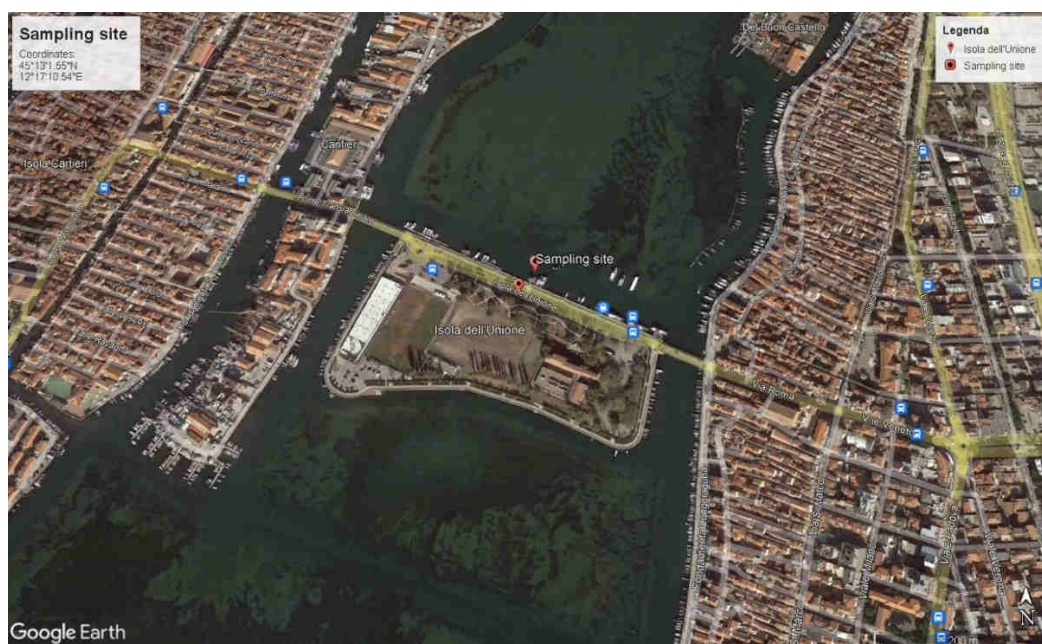


Figure 1 Map of Isola dell'Unione showcasing the sampling site. City on the left is Chioggia, city on the right is Sottomarina

Samples were stored in a bucket with salt water and brought to the laboratory at the hydrobiological station Umberto d'Ancona. The algal turf was then cleaned from epibionts; afterwards the algae were divided among ten 2L tanks, having care to represent all algal species found on the floating jetty (a combination of red and green algae). Five randomly interspersed tanks were treated with fertilizer to mimic eutrophic conditions, while the other five were kept as baseline nutrient conditions. The fertilized treatment consisted in one falcon tube filled with universal fertilizer (N/P/K ratio 22-07-14, brand OSMOCOTE) in

each tank. All tanks had an oxygenator and were illuminated with a lamp to simulate the light cycle (Figure 2).



Figure 2 The acclimatation setup in the lab

Before starting the respiration trials the algae had an acclimation period of one month, during which the positions of the tanks were switched to randomize the irradiation and the water was renewed every three days.

2.1.2 LIGHT CYCLE AND GROWTH CONDITIONS DURING THE ACCLIMATION: NUMBERS AND FORMULAS

The tanks were illuminated for twelve hours a day (ten hours of 100% intensity, with one hour rump-up and rump-down at the start and end of the day respectively, to allow for the light intensity to gradually increase and decrease). The LED white light (brand: Twinstar light, model: 60B) provided $57 \mu\text{mol photon/sec}^{-1} * \text{m}^{-2}$, a number calculated based on the global solar radiation (the amount of direct and reflected light received by a surface) that is found in the area (data from the Sant'Anna weather station, seven kilometers south of Chioggia; ARPAV). The solar radiation was converted in photon flux using the following formulas (Photovoltaic Education Website):

$$\sum \text{hours of daylight in April} = 391 \text{ h } 870 \text{ minutes} = 24330 \text{ minutes} \\ = 1459800 \text{ seconds}$$

$$\text{Average daily irradiance} = \frac{\text{mean solar radiation}}{\text{seconds of daylight}} = \frac{12,12 \text{ W/m}^2}{30} = 12,12 \text{ W/m}^2$$

$$\Phi = \frac{H * \lambda}{h * c} = \frac{12,12 \frac{\text{W}}{\text{m}^2} * 565 * 10^{-9} \text{m}^2}{300 * 10^8 \frac{\text{m}}{\text{s}} * 6,63 * 10^{-34} \frac{\text{J}}{\text{s}}} = 3,44 * 10^{19} \frac{\text{photons}}{\text{m}^2 * \text{s}}$$

White light emitted by the sun is the amount of all the wavelength of the visible spectrum (ranging from 380 nm to 750 nm), therefore the average of the two extremes was used as a wavelength proxy for this formula (Hecht, 2002).

$$N. \text{ micromoles photons} = \Phi * \frac{10^6}{\# \text{ Avogadro}} \\ = 3,44 * 10^{19} \frac{\text{photons}}{\text{m}^2 * \text{s}} * \frac{10^6}{6,022 * 10^{23}} = 57,2 \mu \frac{\text{mol}}{\text{m}^2 * \text{s}}$$

This number was rounded down to 57, since the lamp had a sensibility of 1 μmol .

2.1.3 OXYGEN DYNAMIC MEASUREMENTS

Two small (less than two grams of dry weight) algal turf subsamples (including representatives of both red and green algae), one from a tank with the fertilizer and one without the fertilizer, were put in watertight glass chambers filled with filtered lagoon seawater (mesh pore size: 1.0 μm , brand: Merck Millipore), with care to have both representative of red and green algae in the experimental sample. A third chamber was filled with seawater only, to provide a blank baseline. Every chamber was outfitted with a little spinning magnet to ensure throughout mixing of the water and had an optic receptor installed to monitor the dissolved oxygen dynamics. To ensure homogeneous and stable temperature the three chambers were immersed in an insulated tank filled with freshwater. The temperature was regulated with an external heater (brand: TECO tank chiller line, model: TK5000) and monitored with a thermometer (brand: HANNA instruments, model HI98509, Checktemp1™). The oxygen dynamics were monitored using three fiber optic cables connected to Pyroscience sensor technology hardware (model FireSting®-O2 (4 Channels)), which recorded the oxygen concentration with one-second intervals (Figure 3).

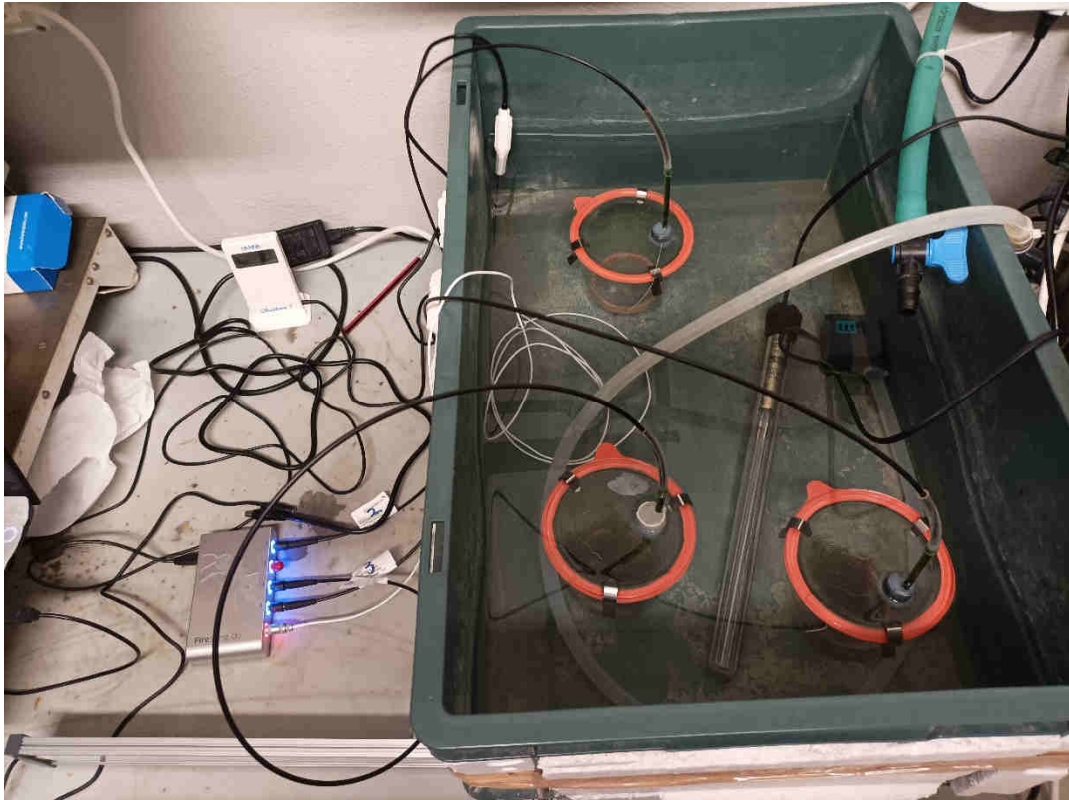


Figure 3 The experimental setup. On the left side, the white object on the top is the external thermal probe, the small rectangular device is the Pyroscience sensor with the four optical fibers, and the white object on the bottom is the LED lamp. On the right side, the freshwater tub has the three test chambers and the heating tubes inside of it

After the three chambers were set up, the algae were left in the dark and their oxygen fluctuations were recorded for twenty five minutes, with the first five minutes used as an acclimatation period.

Afterwards, the samples were illuminated by white LED lamp (brand: Twinstar light, model: 60B) and their oxygen fluctuations were recorded for an additional twenty minutes. This process was repeated at 20, 22, 24, 28 and 32 degrees Celsius. In every new trial a new sub sample of algal turf from the tanks was used. The process was repeated five times using subsamples from each of the five replicated fertilized and control tanks, for a total of twenty five trials. At the end of every trial the algal sub samples were gathered, divided by algal type (i.e. green or red) and stored in labelled aluminium dishes, while the chambers were drained and accurately rinsed in preparation for the next trial. The gathered algal turf samples were first desiccated at 40°C for 12 hours, then at 70°C for another 12 hours. Afterwards the dry weight was measured using an analytical balance (brand: Kern, model: ABJ 220-4NM).

Subsamples from each tank were stored in 96% ethanol for further microbial analyses, which are out of the scopes of the present thesis.

2.2 OXYGEN DYNAMICS UNDER THE COMBINED EUTROPHICATION AND HEATWAVE CONDITIONS

In a second experiment the oxygen dynamics of the turf were measured in response to both eutrophication and MHW. The hypothesis were that the turf productivity would not be heavily affected by heatwave conditions, since it is favored by them (Lidiane-Pires et al., 2017), and that the microbiome would not increase its oxygen demand in eutrophic conditions, since it is resistant to the combined kind of stressor (Messyas et al., 2021).

For this experiment a new batch of turf algae was sampled and brought back to the station following the same methodology of the first experiment. The algae were cleaned and separated in five replicated tanks, with and without fertilization treatment (see Experiment 1), then were put in a controlled room at 28° C (mean local water temperature in August) illuminated with the same lamp model and photon intensity of Experiment 1. The samples were grown in these conditions for one month. Afterwards, to simulate a heatwave event, the tanks were put in a bathing system and heated to 32° C for five days. Unfortunately, during the acclimation period all the algae in the tanks without fertilization died, so new algal turf was collected a week before the start of the heating treatment as control for baseline nutrient levels. The oxygen dynamics were tested initially at 32° C (mean temperature reached during a local heatwave) and then at 28° C (mean temperature reached during summer months).

The oxygen dynamics were measured following the same methodology and experimental setup of the first experiment. After every trial the subsamples were gathered and desiccated to measure the dry weight, like in the first experiment.

2.3 OXYGEN DYNAMICS

Oxygen dynamics inside the test chambers were recorded with the software Pyroscience Workbench (version 1.4.7.2305). The oxygen saturation was measured in percentage of Dissolved Oxygen (D.O.) and converted in mg/L with the Garcia and Gordon equation and the following formulas (Meyers, 2011):

$$DO_{mg/L} = DO_{\%} * [DO]$$

$$[DO] = DO_o * F_p * F_s$$

With [DO] as the baseline concentration of DO in mg/L, DO_o as the concentration in freshwater, F_p as the correction factor of atmospheric pressure and F_s as the correction factor for salinity.

$$DO_o = 1,42905 * e^{2,00907+3,22014*T_s+4,05010T_s^2+4,94457T_s^3-0,256847T_s^4+3,88767T_s^5}$$

With T_s being a scaled temperature with the formula:

$$T_s = \ln \frac{298,15 - t}{273,15 + t}$$

With t as the temperature in Celsius.

$$F_s = e^{[-0,00624523 - 0,00737614 * T_s - 0,0103410 * T_s^2 - 0,00817083 * T_s^3] * S - 4,88682 * 10^{-7} S^2}$$

With T_s as the scaled temperature and S as the salinity measured in parts per thousand, or PSU.

$$F_p = \frac{(P - u) * (1 - \theta_o * P)}{(1 - u) * (1 - \theta_o)}$$

With P as the atmospheric pressure measured in atmospheres, u as the vapor pressure of water in atmosphere and θ_o as the second virial coefficient of oxygen, with the following formulas:

$$\theta_o = 0.000975 - 1,42 * 10^{-5} * t + 6,43 * 10^{-8} * t^2$$

With t as the temperature measured in Celsius

$$u = e^{11,8571 - \frac{3840,70}{T} - \frac{216961}{T^2}}$$

With T as the temperature measured in Kelvin.

For each respirometry trial, the oxygen dynamics measured in the blank chamber was subtracted from the oxygen dynamics measured in the chambers with either fertilized or control algae to standardize the data. The resulting numbers were the actual oxygen dynamic caused by the sample (algae + microbial community).

The first five minutes of recordings were eliminated to remove the acclimation period. The remaining measures were split between the "light" period (in which the algae was illuminated) and the "dark" period (in which the algae was kept in the dark). In each replicate the light and dark period were both fitted to a regression line, with time as the independent variable and the oxygen (mg/L) as the response variable. Each resulting slope of this regressing model was then divided by the dry weight of its corresponding trial, estimating the amount of oxygen produced or consumed in one second per gram of dry weight of turf algae.

These formulas were applied to both the trials of the first experiment (testing the turf exposed to baseline temperature conditions) and the second experiment (testing the turf exposed to heatwave conditions).

The total Gross Primary Production of every trial of the two experiments was calculated by adding the absolute value of the oxygen consumed with respiration in dark conditions (obtained multiplying the linear slope of the oxygen dynamic

in dark conditions by 1200 seconds, a.k.a. 20 minutes, the time of the exposure to darkness) to the value of oxygen produced by photosynthesis in light conditions (obtained multiplying the linear slope of the oxygen dynamic in light conditions by 1200 seconds, a.k.a. 20 minutes, the time of the exposure to light).

2.4 NATURAL MHW DATA

To analyze the frequency and the intensity of MHWs in the Venice lagoon, data harvested from the hydrobiological station “Umberto d’Ancona” were used. The station is located on the San Domenico Island, at the northeastern point of Chioggia, and has been recording data about the lagoon’s physical properties, among which water temperature, since 1945. The data is public since 2007 in the context of the CLODIA Project: for the sustainable development of coastal environments (*Progetto CLODIA: per lo sviluppo sostenibile degli ambienti costieri*).

The functions used were MHW_detect and MHW_cat from the package heatwavesR (version 0.4.6). MHW_detect needs at least thirty years of daily temperature recordings to extrapolate the climatology baseline and detect marine heatwaves in a date locality, therefore the station data from 1990 to 2023 was used. MHW_cat classifies heatwave events based on percentiles and maximum temperature reached (Hobday et al., 2018) with the following formula:

$$MHW \text{ category (number)} = \frac{\Delta (T. \text{ registered} / \text{ historical mean})}{\Delta (90\text{th percentile} / \text{ historical mean})}$$

The categories range from I to IV:

- Category I: moderate heatwave (the number is between 1 and 2)
- Category II: strong heatwave (the number is between 2 and 3)
- Category III: severe heatwave (the number is between 3 and 4)
- Category IV: extreme heatwave (the number is above 4)

To visualize the data the function event_line from the package RmarineHeatWaves (version 0.17.0) was used. As its companion it needs at least thirty years of daily temperature recordings to compile the climatology, so the same data for heatwavesR was used.

2.5 STATYSTICAL ANALYSES OF THE OXYGEN DYNAMICS

The analyses were done using the statistical program R (version 4.1.2). To analyze the data from the first experiment a two-way ANOVA test was used to unravel the fertilization effect on oxygen dynamics at different temperatures. Specifically, the slope of oxygen consumption/production (either under light or dark conditions) was the response variables, while Temperature (five levels: 20, 22, 24, 28, 32) and Treatment (two levels: fertilized, control) were the independent fixed factors. The model also included the interaction between Temperature and Fertilization. The model residuals failed to follow a normal

distribution even after transformation, and therefore a PERMANOVA test was used. PERMANOVA is a non-parametric test that does not require the normality assumption (Anderson, 2017). However, this model showed heteroskedasticity, so then a Generalized Least Square test (Zuur et al., 2009) was employed with the function `gls` from the package `nlme` (version 3.1.162). When significant effects were detected (at the $\alpha=0.05$ level), further post-hoc testing were conducted using the Tukey-HSD test, through the function `emmeans` from the `emmeans` package (version 1.8.8).

To analyze the data of the second experiment a two-way ANOVA test was used, using the same variables of the ANOVA test used in first experiment, but as the first experiment the model residuals did not follow normal distribution, therefore a PERMANOVA test was employed. Like in the first experiment it showed heteroskedasticity, so a GLS was used, through the `gls` function from the `nlme` package (version 3.1.162).

3. RESULTS

3.1 OXYGEN DYNAMICS AT INCREASING TEMPERATURES IN RESPONSE TO ENHANCED NUTRIENTS

On dark conditions the control turf salways consumed oxygen at higher rates than the fertilized turfs at all temperatures (Figure 1). The nutrient load influenced the consumption (F-value = 7.37652, degrees of freedom = 1, p-value = 0.0097) but the temperature did not (F-value = 2.1315, degrees of freedom = 4, p-value = 0.0947 respectively), with no significant interaction (p-value = 0.8760). In light conditions there was a decrease in oxygen production with the increase of temperature until 28° C, when the fertilized group began to consume oxygen and the control group began to increase oxygen production (Figure 2). In fact, there was significant interaction between increased temperature and nutrient load (F-value = 3.506336, degrees of freedom = 4, p-value = 0.0152). Further post hoc testing revealed that the nutrient load significantly influenced the production at 28° C (p-value = 0.0005) and at 32° C (p-value = 0.0290).



Figure 1 Mean oxygen production in dark conditions

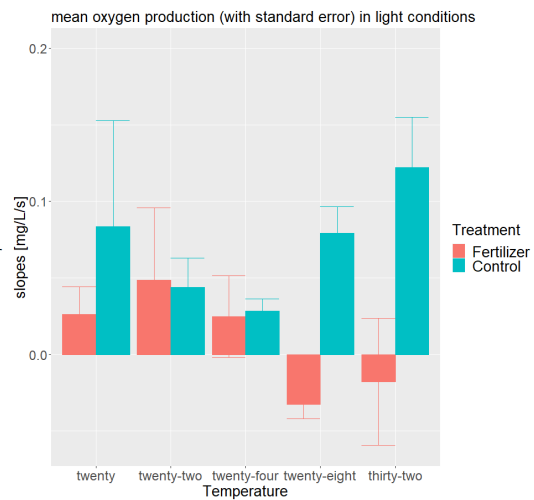


Figure 2 Mean oxygen production in light conditions

On average, the Gross Primary Production (GPP) of the controls was higher than that of the fertilized treatments at every temperature except 20° C (Table 1).

temperature	treatment	O2 balance [mg/L]	O2 standard error
20	fertilizer	241.5641	83.65985
	control	87.05822	15.97564
22	fertilizer	169.3561	36.33306
	control	200.2066	31.90381
24	fertilizer	108.3835	12.69584
	control	191.3802	71.56546
28	fertilizer	109.879	32.05205
	control	192.0165	22.31294
32	fertilizer	170.8997	15.69581
	control	272.7201	44.11234

Table 1 showcasing GPP rates at different temperatures and nutrient loads

3.2 OXYGEN DYNAMICS UNDER THE COMBINED EFFECTS OF EUTROPHICATION AND COMMUNITY RESPONSES TO HEATWAVE CONDITIONS

In heatwave conditions the oxygen change in light conditions was negative independently of nutrient treatment and temperature, as well as in dark conditions. The non fertilized turf always consumed less oxygen than the fertilized group, apart from the control group in dark conditions at 28° C (Figure 3 and 4). In dark conditions neither the temperature nor the nutrient load influenced the oxygen consumption (p-value = 0.8022 and p-value = 0.7613, respectively). In light conditions the nutrient load highly affected the oxygen consumption (p-value < 0.0001), while the temperature did not affect the oxygen consumption (p-value = 0.06838) with the factors influencing each other (p-value = 0.4557). However, when confronted the fertilization treatments were different at 28° C (p-value = 0.0008) and 32° (p-value = 0.0456), like in normal conditions.

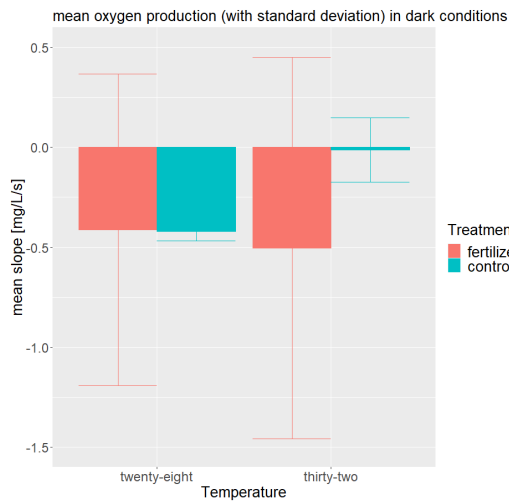


Figure 3 Mean oxygen production after heatwave event in dark conditions



Figure 4 Mean oxygen production after heatwave event in light conditions

The Gross Primary Production (GPP) was positive only for the non-fertilized group at 28° C (Table 2).

temperature	treatment	O2 balance [mg/L]	O2 standard error
28	fertilizer	-278.309	296.2462
	control	60.16437	246.5699
32	fertilizer	-430.172	740.2694
	control	-241.825	324.3483

Table 2 showcasing GPP rates at different temperatures and nutrient loads after a marine heatwave event

At the end of the experiment the algae presented extensive damage. Many had a brownish tint and some were even bleached. Some tanks of the control group were almost empty except for small clumps of algae covered in slimy goo, while other presented a debris covered algae mass.

3.3 FREQUENCY AND SEVERITY OF MHWS IN THE VENICE LAGOON

The data analysis with heatwaveR revealed 57 MHW events in the southern Venice lagoon since January, 1990. 17 of the events happened in the summer months, 17 in the spring, 12 in the autumn and 11 in the winter (Figure 5).

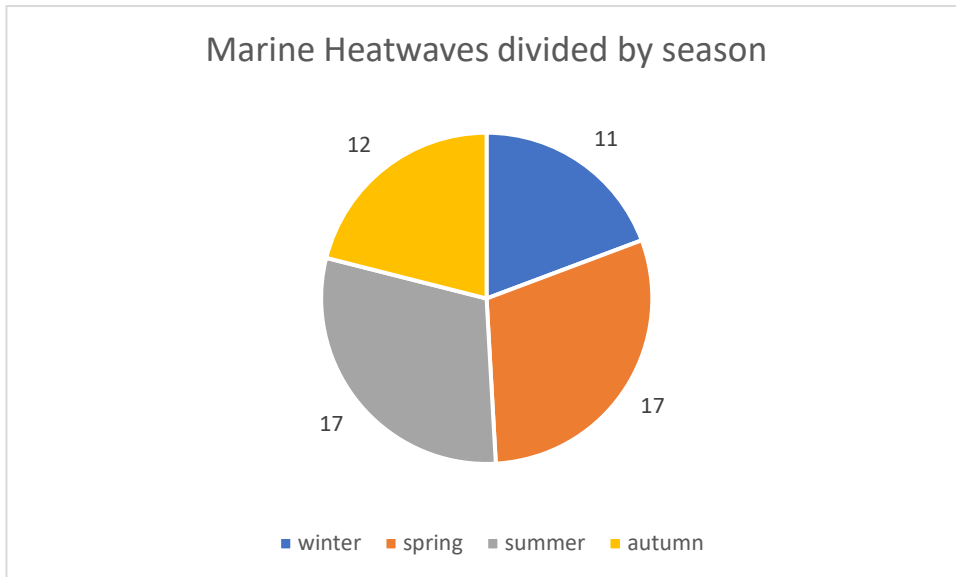


Figure 3 Marine heatwaves in the southern Venice lagoon from 1990 to 2022 divided by season. Made with Excel

In their totality, 43 of the events were moderate and 14 of which were strong (32,5% of the total). Fortunately, no severe and extreme events happened in the Venice Lagoon. The longest event was 26 days long and started the 3rd of February 2020 and ended the 28th of the same month, with the peak on the 11th. The year with the highest number of events was 2007 with 8 of them (Figure 6).

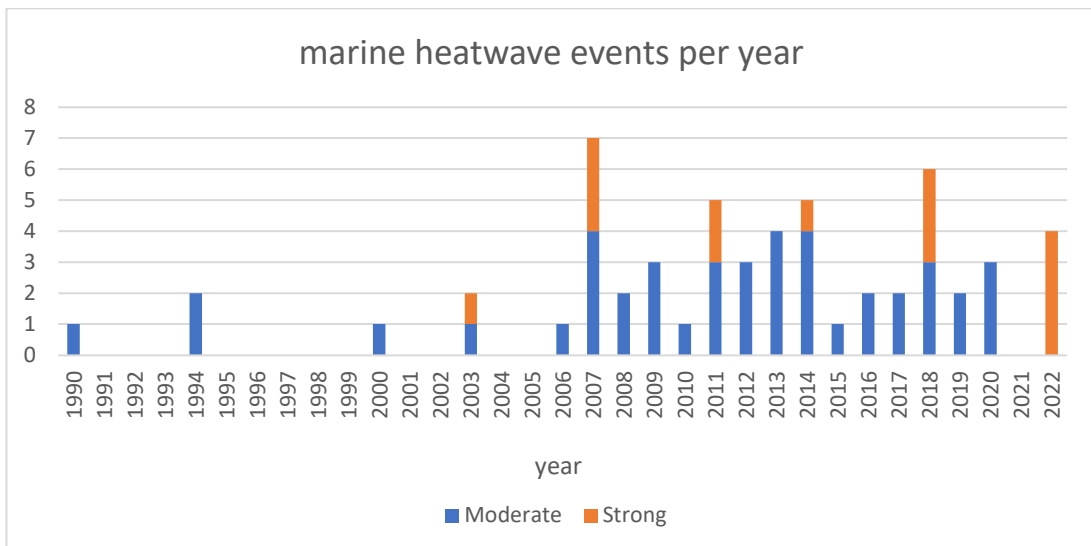


Figure 4 Marine Heatwave events in the southern Venice lagoon per year from 1990 to 2022. Made with Excel

During 2022 four heatwaves were detected, one in May, one in July, one in October and one in November. All of them were categorized as "strong" (Figure 7).

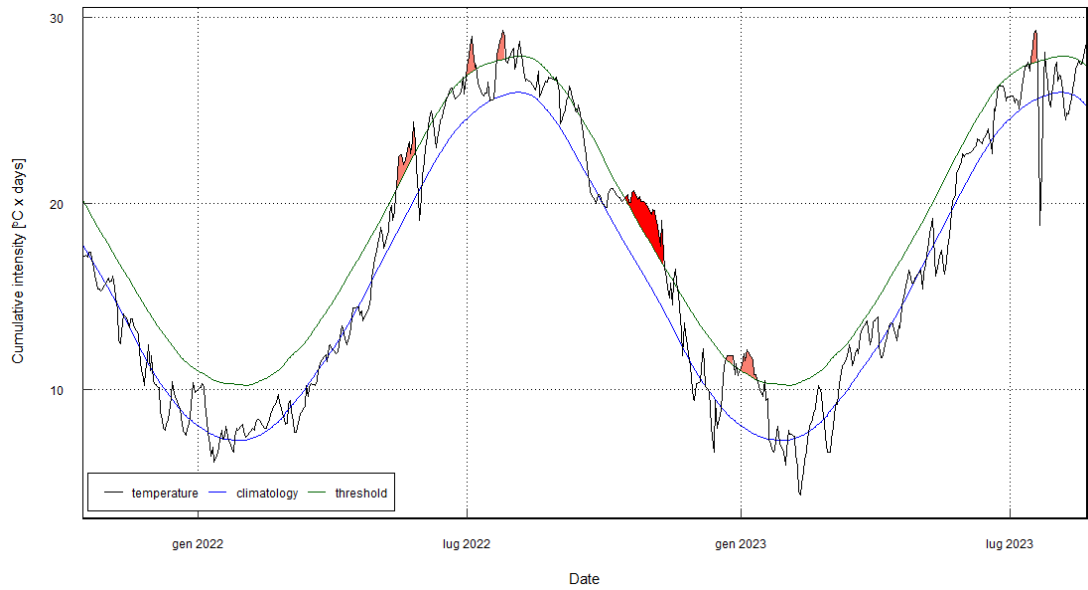


Figure 5 Marine heatwaves in the southern Venice lagoon in 2022. The blue line represents the baseline climatology, the green one represents the 90th percentile threshold. Made with RMarineHeatwaves package

2003 had two heatwave events, the longer one listed as “strong” and the shorter one listed as “moderate” (Figure 8).

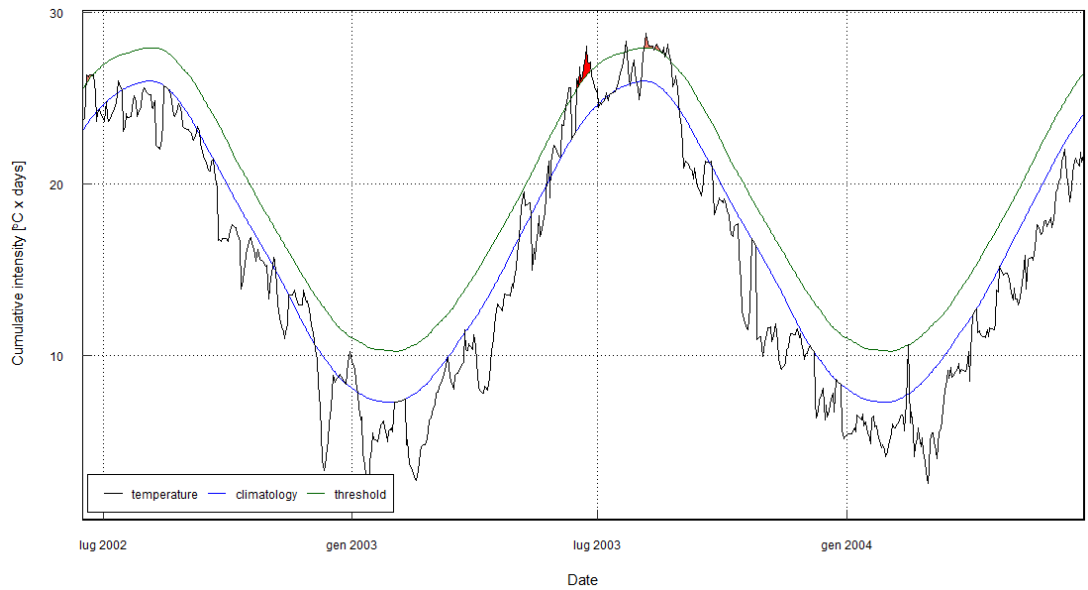


Figure 6 Marine heatwaves in the southern Venice lagoon in 2003. The blue line represents the baseline climatology, the green one represents the 90th percentile threshold. Made with RMarineHeatwaves package

4. DISCUSSION

Turf algae is a novel ecosystem that is proliferating along urbanized coastlines, often replacing the native canopy forming algae. Its presence is favored by high temperatures, heatwaves and eutrophication. However, the actual responses of turf algae to these stressors is still understudied.

4.1 TURF RESPONSES AT INCREASING TEMPERATURES AND NUTRIENTS LOADS

The first experiment shows that the algal turf is a net producer of oxygen (and potential carbon sequestrator) until 24° C, even under eutrophic conditions. After that, the turf will continue to be net autotrophic only under oligotrophic conditions. In contrast, under eutrophic conditions it will become a net consumer of oxygen, thus possibly impairing its beneficial effect on ecosystem services such as carbon sequestration and oxygen supply.

The results show a clear influence of the nutrient load on oxygen consumption at 28° C and 32° C. A possible explanation for this shift from net production to net consumption of oxygen could be the shift in the microbiome associated to turf algae happening under both eutrophic and high temperatures. It is known that pathogenic bacteria are especially abundant in the algal turf's microbiome in eutrophic conditions (Elsherbini et al., 2023, and Sharifa & Eguchi, 2011). Furthermore, the *Roseobacter* genus, a big component of the algal microbiome (which plays a major role in the reduction of nitrate to nitrite making it bioavailable to the algae), can synthesize oxygen under light conditions and can inhibit the growth of pathogenic bacteria (Ramanan et al., 2016, Szitenberg et al., 2022, and Shiba, 1991). Interestingly Szitenberg et al. (2022), found a strain of *Rosobacter* bacteria in temperate waters whose maximum operational temperature is 27° C. Therefore, it is possible that under eutrophic conditions there is a proliferation of photosynthetic bacteria with anti-pathogenic properties, and that the higher temperatures of the experiments (28 and 32 degrees Celsius) hinder their ability to provide such benefits to the turf, thus switching the regime of the turf algae-bacteria community from autotrophic to heterotrophic. Future analyses that will follow on the microbial community will allow to clarify this hypothesis.

4.2 OXYGEN DYNAMICS UNDER THE COMBINED EFFECTS OF EUTROPHICATION AND EFFECTS OF EUTROPHICATION AND WARMING UNDER HEATWAVE CONDITIONS

The turf algae, after the simulated heatwave event (experiment 2), presented net oxygen consumption in both the control and the fertilizer group. This result aligns with those obtained by other experiments on canopy forming macroalgae,

where heatwaves reduced their productivity, both during and after the event (Nepper Davidsen et al., 2018). However, this result contrasted with a recent study performed on turf algae, which showed high production at high temperatures and heatwave conditions (Provera et al., 2021). Therefore, this study suggests that the algal turf, like canopy forming macroalgae, does not have resistance against prolonged periods of thermal stress. Unfortunately, there seems to be no studies on the effects of heatwaves on turf physiology, which makes it difficult to formulate generalized hypothesis. As discussed in the previous paragraph, it is possible that the higher oxygen consumption in the fertilized group can be explained by the higher bacterial load. Furthermore, Fabbri et al., 2023, discovered that canopy forming algae can adapt to marine heatwaves at a population level. It is unclear if the algal turf shares the same capacity.

After the heatwave event the algae in the control tanks were highly degraded, with bleached tissues and a shroud of mucus, with little turf left in the tanks. The high mortality can be explained by a combination of stressors. The algal turf has higher demands of nitrogen at higher temperatures, so the absence of nutrients could have led the algae to starvation (Karcher et al., 2020). Furthermore, recent studies have shown that heatwaves change the microbiome composition, favoring pathogenic bacteria, like those belonging to the *Vibrio* genus (Doni et al., 2023). These two factors may have severely impacted the algae in the control tanks, leading to high mortality. The absence of remains can be explained by the fast degradation rates of the marine microbiome (Kristensen et al., 1995).

4.3 FREQUENCY AND SEVERITY OF MHWS IN THE VENICE LAGOON

To better place in context the possible detrimental effect of marine heatwaves events (MHWE) on turf algae, the trend of heatwave thorough the years was also evaluated. It was found that MHWs are increasing in severity and frequency in the past thirty years, confirming the local and global trend (Bartolini et al., 2013 and Christidis et al., 2015). Furthermore, it has been found that MHWEs do not happen only in the summer, but also in the winter and autumn. Interestingly the year 2003 was the first year on the record to have a MHW categorized as “strong” and has become notorious as a catastrophe on the Mediterranean ecosystems (Garrabou et al., 2008). And yet, the year 2022 showed a higher number of MHWs, whose effects lasted well into 2023 (Marullo et al., 2023), but no mass mortality events as extended as the ones reported in 2003 have been reported. A possible explanation could be found in that year colder climatology: it is known that an area subjected to colder temperatures suffers more mortality events than an area subjected to higher temperatures (Crisci et al., 2011). The year 2003 was overall colder and therefore the strong heatwave could have caused large die-offs. In contrast, 2022 hotter baseline climatology allowed

organisms to acclimatate to higher temperatures and thus resist better to marine heatwaves. More research in the field is needed to better understand when and how MHWs can have detrimental effects on the biota.

4.4 EXPERIMENTAL LIMITATIONS AND CONCLUSIONS

The algal turf is substituting canopy forests in marine urban areas and with climate change its range is expected to increase even further (Wernberg et al., 2016). This thesis suggests that the algal turf productivity depends on both temperature and nutrients loads. Specifically, the results of this thesis show that turf algae can produce more oxygen at higher temperatures but only in an oligotrophic environment. Moreover, in heatwave conditions turfs will switch to an heterotrophic regime.

It is important to stress that the experiments performed in this thesis were conducted in a close system in a laboratory. The water in the tanks was renewed every three days and the volume of water in each tank was very small compared to the quantity of fertilizer in each tank. Therefore the nutrient load in this experiment was likely reflecting extreme eutrophic conditions, while turf population in natural areas will likely be exposed to lower nutrient levels. Thus, future research should include multiple eutrophication levels to better understand the response of the algal turf with increasing temperatures. Furthermore, the samples of the microbial community have not been analyzed yet: once this will be done, they will allow to better comprehend how the turf-algae oxygen dynamic is affected by a changing climate.

This work showed that MHWs may have a detrimental effects on algal turf production, both under normal and eutrophic conditions. The limitations previously mentioned (the laboratory set up and the very high nutrients load) also apply in this case. Thus, more research is needed to fully understand the impacts of MHWs on turf algae productivity. Also, it should be stressed that turf algae is a morphological classification that comprises many different species. Different species may respond differently to both nutrients and temperatures. Therefore, future experiments should include a wide range of turf species to properly understand how eutrophication and heatwaves impairs turf algae and the related ecosystems functions.

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